

Intra and inter-annual structure of zooplankton communities in floodplain lakes: a long-term ecological research study

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Abstract: Water flow management has significantly changed the natural dynamic of floods, which are responsible for the structure and dynamic of aquatic communities in river-floodplain systems. With the aim to elaborate a conceptual framework that describes the main ecological factors associated with zooplankton community structure in the Upper Paraná River, we investigated the mechanisms that regulate the communities structure and their response to inter-annual and hydro-sedimentological variations in the floodplain and the biological factors associated with species abundance in those communities. For this we conducted samplings every six months (potamophase in March and limnophase in September) to characterize intra and inter-annual variations in community structure between 2000 and 2008. The intra-annual differences on the species richness, abundance, Shannon diversity index, and evenness, were conducted using Bayesian procedures to show probabilistic predictions of the data fit to main variation sources. Non-metric multi-dimensional scaling (NMDS), multi-response permutation procedure (MRPP), and indicator species analysis (IndVal) were run to assess and characterize the seasonality of the community structure. During high water (potamophase), hydrologic connectivity favoured exchange and dispersal of species in some lakes, increasing local diversity; during low water (limnophase), higher local productivity favoured opportunistic taxa, increasing species dominance and decreasing local diversity. Food resources and density of small-size fish were biological factors associated with the seasonal dynamic of the zooplankton community; these factors were dependent on hydrosedimentological phase (potamophase or limnophase). Water levels and limnological modifications related to water flow management have promoted replacement and impoverishment of aquatic biota in affected lakes and have indicated the ecological importance of a natural dynamic flood, which displays regular flood pulses. The conceptual model presented encompassed interactions between diverse environmental variables to more understandable mechanisms of the main sources of community variation. *Rev. Biol. Trop.* 60 (4): 1819-1836. Epub 2012 December 01.

Key words: diversity, community structure, environmental monitoring, bayesian procedures, conceptual framework, wetlands.

Diversity of zooplankton in river-floodplains system is frequently ascribed to interactions between habitat diversity and flood pulse (Robertson & Hardy 1984, Vásquez & Rey 1989, Rodrigo *et al.* 2003, De Paggi & Paggi 2007, Lansac-Tôha *et al.* 2009). Such interactions are caused by the dynamics of flooding, which is the driving force for variation in communities and their responses to spatial and temporal variations in river-floodplain systems (Junk *et al.* 1989, Neiff 1990). These

community variations depend on the frequency, intensity (water volume), amplitude, and seasonality (period of occurrence) of the phases of the hydro-sedimentological pulse, which fluctuates between limnophase (low water) and potamophase (high water) (Neiff 1990). During limnophase, water bodies are disconnected because floodplain waters are restricted to rivers, channels, backwaters, and lakes; in potamophase, on the other hand, the increase in water volume promotes connections amongst

water bodies. These hydro-sedimentological phases are characterised by distinct faunal assemblages, which show different functional properties related to the predominance of different ecological mechanisms in each phase.

Modifications of flow, due to human activities (e.g. reservoir management), and consequent changes in the flood dynamic, have placed floodplains amongst the most threatened habitats on Earth, significantly endangering biodiversity in these ecosystems (Tockner & Stanford 2002, Dudgeon *et al.* 2006). This occurs because reservoirs reduce the natural amplitude of water levels variation, consequently changing the dynamics of aquatic communities (Ward & Stanford 1995). The resulting ecological damage may have economic and social impacts in human communities, since recent studies indicated that biodiversity ensures the maintenance of ecosystem processes, buffering the effects of detrimental changes (Galat & Lipkin 2000, Joy & Death 2002, Naeem 2002, Srivastava & Vellend 2005).

An extensive literature exists showing the associations between local environmental variations and the structure of zooplankton communities (Dodson 1992, Schell *et al.* 2001, Hoback *et al.* 2002) and the influence of human activities on these communities (e.g. Beaver *et al.* 1998, Dodson & Lillie 2001, Dodson *et al.* 2005, Angeler & Moreno 2007, Dodson *et al.* 2007). However, there is a paucity of information about zooplanktonic indicator species (such as those developed for phytoplankton by Reynolds *et al.* 2002) due to the wide niche ranges of most zooplanktonic species, despite several reports of species-specific responses to environmental variation (Cottenie *et al.* 2001, Cardoso & Marques 2004, Aoyagui & Bonecker 2004, Trevisan & Forsberg 2007).

The development of experimental approaches, and the capacity to control variables, have provided more accurate models for making inferences about the environmental effects of human activities on organisms. However, it is still difficult to reproduce environmental conditions that simulate the complexity and high degree of environmental variability in

nature (Franklin 1987). Nevertheless, medium- and long-term data from long-term ecological research (LTER) studies have provided a bridge between empirical studies and the development of ecological models, informing social, economic, and political strategies for improved management of floodplain ecosystems (Baker *et al.* 2000, Barbosa *et al.* 2004).

The present study evaluates the temporal variability in the structure of zooplankton communities in lakes influenced by both natural flood pulse and anthropogenic operation of reservoirs. We tested the following hypotheses: (i) attributes of the zooplanktonic community are influenced by hydro-sedimentological phases; (ii) these attributes show patterns of covariation within communities; (iii) hydro-sedimentological phases are characterized by different zooplanktonic assemblages (composition and dominance); and (iv) these phases distinctly influence the biotic factors (e.g. resource availability and predation patterns) associated with zooplankton abundance. Over a nine-year period, changes in the structure of the zooplankton community were evaluated to investigate associations between environmental factors and species response to environmental seasonality, as well as the influence of specific biotic factors (resource availability and predation) related to the hydro-sedimentological phases on zooplankton abundance. Finally, we formulated a conceptual framework and theoretical models to describe the structure of community patterns observed in floodplain zooplankton communities.

MATERIALS AND METHODS

Study area: The Upper Paraná River floodplain (Fig. 1) comprises a variety of habits such as secondary channels, backwaters, tributaries, and temporary and permanent lakes (Agostinho *et al.* 2004). Currently, three conservation units are present in this area, indicating the relevance of the region for biodiversity conservation; however, their ecological integrity is threatened by a chain of upstream reservoirs.

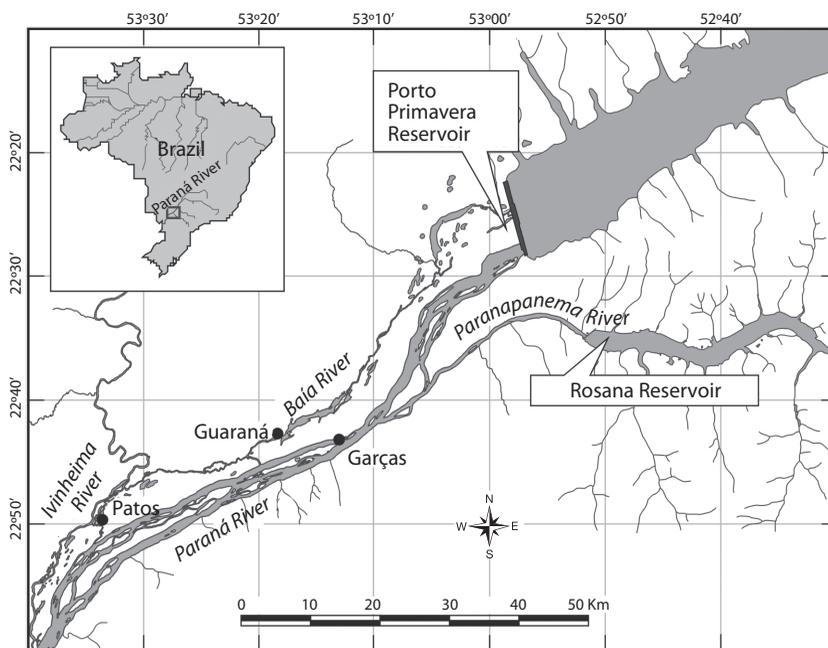


Fig. 1. Location of the Upper Paraná River floodplain and the sampling sites: GAR-Garças Lake; GUA-Guaraná Lake; PAT-Patos Lake. The floodplain is located downstream from two reservoirs, the Rosana Reservoir and the Porto Primavera Reservoir.

Sampling was conducted in three lakes (Table 1), each perennially connected to a different floodplain river, and influenced by variations in the water levels of the Paraná or Ivinheima rivers (Fig. 2). The level variation in the Garças Lake is directly associated with levels of the Paraná River, which are strongly related to operation of a reservoir located 30km upstream. Lake Guaraná is connected to the Baía River which follows a course parallel to the Paraná River. The hydrodynamics of the Baía River is influenced by floods on the Paraná River. Patos Lake is located in a

dam-free region in the Ivinheima River State Park; consequently, this lake exhibits a hydro-sedimentological dynamic distinct from the two other studied lakes (Rocha 2002).

These two rivers showed different flood dynamics; strong floods occurred in 2005 and 2007 in the Paraná River, and in 2001 and 2005 in the Ivinheima River (Fig. 2). Extreme droughts occurred in 2001 and 2003, respectively, in the Paraná and Ivinheima rivers. Floods in the Paraná River were more often than in the Ivinheima River (Table 2), but most Paraná floods were shorter (amplitude)

TABLE 1
Coordinate geographic and morphometric characteristics of the lakes (Garças, Guaraná and Patos) in the Upper Paraná River floodplain

	Garças Lake	Guaraná Lake	Patos Lake
Latitude	22°43'27.18 S	22°43'16.68 S	22°49'33.66 S
Longitude	53°13'4.56 W	53°18'9.24 W	53°33'9.9 W
Mean depth	2.0m	2.1m	3.5m
Area	14.1ha	4.2ha	113.8ha

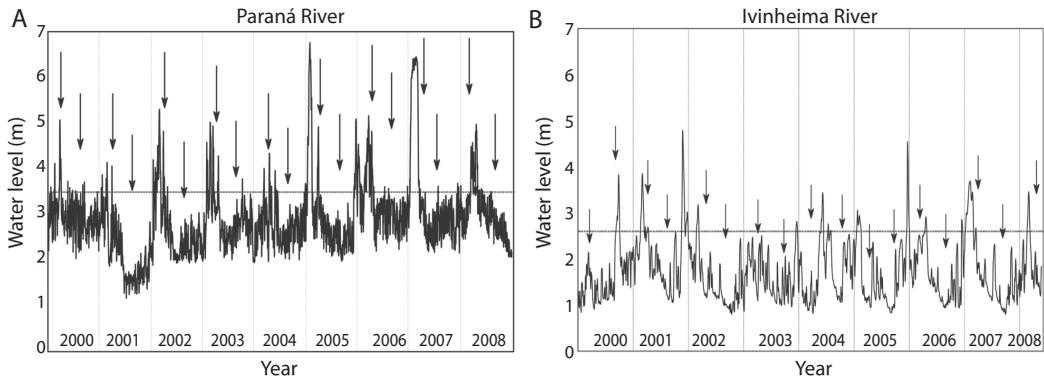


Fig. 2. Variation of water level in the Paraná and Ivinheima rivers, 2000-2008, in the Upper Paraná River floodplain. Arrows indicate the sampling periods.

TABLE 2
Water level properties of the Paraná and Ivinheima rivers during the study period 2000-2008

	Paraná River	Ivinheima River
Maximum level (m)	6.7	4.8
Minimum level (m)	1.1	0.8
Number of flood pulses	73	21
Amplitude mean	5.9	14.3
Number of flood pulses ≤ 5 days of amplitude	54	7
Number of flood pulses > 5 days of amplitude	19	14

than in the Ivinheima River. The indicative reference levels for floods, which distinguish the limnophase and potamophase, were 3.5m (Paraná River) and 2.6m (Ivinheima River), measured in gauges in these two rivers (Rocha 2002, Thomaz *et al.* 2004). When river levels reach approximately these intensities, flood waters overflow marginal levels and inundate surrounding floodplains and associated aquatic systems (Rocha 2002). Generally, limnophase occurs during winter (ca. May-October) and potamophase occurs during summer (ca. November-March). The daily water levels of the Paraná and Ivinheima rivers were furnished by Itaipu Binacional.

Sampling of zooplankton and environmental variables: Samplings were conducted every six months (potamophase in March and limnophase in September) between 2000 and 2008 to characterize intra and inter-annual

variations in community structure. Environmental data were water temperature ($^{\circ}\text{C}$), concentration of dissolved oxygen (mg/L) (YSI oximeter), pH, electrical conductivity ($\mu\text{S}/\text{cm}$) (DIGIMED potentiometer), total alkalinity ($\mu\text{eq}/\text{L}$) (Gran titration; Carmouze 1994), water transparency (cm) (Secchi depth), chlorophyll *a* concentration ($\mu\text{g}/\text{L}$) (Golterman *et al.* 1978), organic and inorganic suspended solids (mg/L), nutrients ($\mu\text{g}/\text{L}$) (nitrate Bergamin *et al.* 1978, ammonia Mackereth *et al.* 1978, total phosphorus Golterman *et al.* 1978), and density of fish (catch per unit effort, CPUE) with standard lengths $< 7\text{cm}$. The fish sample represents small species and young individuals from medium and large species; although this size group includes non-planktivorous species, the young individuals of larger species are potential consumers of zooplankton. These fishes were captured using gillnets of different mesh sizes ranging from 2.4 to 4cm opposite

knots. Further information about CPUE can be found in Fernandes *et al.* (2009); further information on methods of water analysis and their spatio-temporal dynamics can be found in Roberto *et al.* (2009).

Zooplankton was sampled in the pelagic region during the morning (between 7 and 11h), using a motorised pump with the boat moving at a constant velocity (to take a composite sampling from each lake), and plankton net (68 μ m) to filter 600L of water per sample (Lansac Tôha *et al.* 2009). The samples were preserved in formaldehyde (4%) buffered with calcium carbonate. Individuals were identified to the lowest taxonomic level possible using taxon-specific literature (Vucetich 1973, Koste 1978, Reid 1985, Matsumura-Tundisi 1986, Segers 1995, Velho & Lansac-Tôha 1996, Elmoor-Loureiro 1997). Zooplankton abundance was determined using a Sedgewick-Rafter counting chamber under an optical microscope and results were given in ind/m³. At least 80 individuals were counted (Bottrell *et al.* 1976) in each of three sequential samples, obtained with a Hensen-Stempel pipette (2.5mL).

The zooplankton community was analysed in terms of species richness, abundance, Shannon diversity index, evenness (Krebs 1999), non-metric multi-dimensional scaling (NMDS), multi-response permutation procedure (MRPP), and indicator species analysis (IndVal) (Dufrene & Legendre 1997).

Uni-dimensional dependent variables (species richness, abundance, Shannon diversity index, and evenness) were analysed with Bayesian procedures; these are more flexible than conventional statistics because traditional assumptions are not required, and they permit probabilistic predictions; conventional statistics, on the other hand, are restricted to statements about long-run averages obtained from hypothetical replicates of sampled data (McCarthy 2007). Furthermore, in general, Bayesian procedures provide more precise estimates of model parameters, because it is possible to incorporate knowledge acquired in previous studies into the structure of the model (Choy *et al.* 2009).

Local and hydro-sedimentological effects on community attributes (species richness, abundance, Shannon diversity index, and evenness) were evaluated with a Bayesian model analogous to factorial ANOVA, aiming to verify how hydro-sedimentological variations influence the attributes of the zooplankton community in the studied lakes. Hydro-sedimentological effects consisted of two levels (potamophase and limnophase), while local effect with three levels (corresponding to the three lakes). We assumed that the dependent variable, Y_{ab} (community attributes of phase a and locality b), were normally distributed (μ_{ab} , σ^2) with $\varepsilon \sim N(0, \sigma^2)$, where $E(Y_{ab}) = \mu_0 + \alpha_a + \beta_b + \alpha\beta_{ab} + \varepsilon$. In this model, μ_0 is the mean of the data, α is the effect of the hydro-sedimentological phase, β is the locality effect, $\alpha\beta$ is the interaction effect, and the subscripts a and b are phases and locality levels, respectively. We assumed *a priori* non-informative, approximately normal distribution (0, 10³; mean and standard deviation, respectively) for the parameters of this equation. The Bayesian credibility interval for the hydro-sedimentological and local effects was simulated using Markov chain Monte Carlo methods with 20 000 iterations and a burn-in of 1 000 iterations. All the chains analysed reached convergence. Both abundance and richness data were log transformed to decrease the range of data variation.

We used the Pearson correlation to determine how attributes covariate within communities; and if they were associated with water levels (mean of the 30 days before samplings; because it represent a temporal dynamic of the water level that can contribute to temporal variations of the assemblages due to time lag of the zooplankton responses).

Variations in the structure of the zooplankton community were summarised using NMDS, searching the best solution for representation in two dimensions. NMDS does not require assumptions about the distribution patterns of species abundance and is suitable for ecological data structures inflated by zeros (McCune & Grace 2002). Differences between limnophase and potamophase community structures

were analysed using MRPP (Zimmerman *et al.* 1985) with 10 000 randomizations. This is a non-parametric permutation procedure applied to a previously defined similarity or dissimilarity matrix. We used the Bray-Curtis dissimilarity method, conducting the analysis with transformed data to reduce discrepancies amongst the abundances of different species [$\log_2(x+1)$, where x represents the abundance of individuals (m^3)]. Rare species, defined as having a frequency of occurrence lower than 10%, were removed from the analyses to facilitate the observation of environmental patterns.

Associations of environmental variables with community structure were determined by Envfit. Envfit is a function of the Vegan package (R programming language) that determines the environmental vectors that best represent the distribution of community structures using a permutation procedure (Oksanen *et al.* 2008). To avoid collinearity, we removed some environmental variables that were highly correlated ($r > 0.70$). Following this criterion, water temperature and pH were eliminated owing to their high correlations with dissolved oxygen.

Once we verified intra-annual patterns in the structure of the zooplankton community, we used a Bayesian multiple regression analysis to assess whether the same biotic factors influenced zooplankton abundance during the phases (limnophase and potamophase). In the multiple regression model, the following explanatory variables were selected to distinguish biological factors that regulate zooplankton abundance: chlorophyll *a* concentration, as an indicator of food resource availability, and fish density (standard length < 7 cm), as an indicator of predation pressure. We considered that the dependent variable (Y , community abundance) was normally distributed (μ , σ^2) with $\varepsilon \sim N(0, \sigma^2)$, where $E(Y_i) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \varepsilon$. We also considered that the parameter β_1 (fish density) presented *a priori* a non-informative normal distribution, $\beta_1 \sim N(0, 10^3)$. Moreover, the parameters β_0 (intercept) and β_2 (chlorophyll *a* concentration) were normally distributed with positive values $N(\mu > 0, 10^3)$; because, the food availability β_2 always has a positive effect on

zooplankton abundance. The Bayesian credibility interval for the regression coefficients was simulated using a Markov chain Monte Carlo method with 100 000 iterations, a burn-in of 1 000 iterations, and a thinning interval of 15 to minimise autocorrelation. All the analysed chains reached convergence.

The analyses were developed with R software version 2.8.1 (Development Core Team), using the VEGAN package (Oksanen *et al.* 2008) for the multivariate analyses and BRugs for the Bayesian analyses.

RESULTS

Zooplankton composition and diversity:

The zooplankton community was represented by 342 species, including 196 rotifers, 76 testate protozoans, 50 cladocerans, and 20 copepods. Guaraná Lake contained 267 species; Garças Lake, 242 species; and Patos Lake, 189 species. Seventy species were restricted to Garças Lake, 42 species to Guaraná Lake, and 13 species to Patos Lake. A total of 143 species were common to all three lakes.

The mean species richness was highest in Patos Lake (mean=40, SD=12), followed by Guaraná Lake (35; 14) and Garças Lake (29; 12). The *a posteriori* credibility interval pointed to differences in the effects of locality on species number (Fig. 3a), mainly between Garças Lake, which had the lowest value, and Patos Lake, which had the highest value for species richness. Community abundance did not differ amongst localities, but was higher during limnophase and lower during potamophase (Fig. 3b). The *a posteriori* credibility interval of the hydro-sedimentological phase effects indicated a positive effect of the limnophase on community abundance. Rotifers were the most abundant group, and Testate amoebae was the least abundant one (Fig. 4). In general, the limnophase also showed higher variation of abundance than potamophase.

Species diversity and evenness presented patterns of variation similar to species richness, with a strong effect for the interaction between locality and seasonality (Fig. 5a and

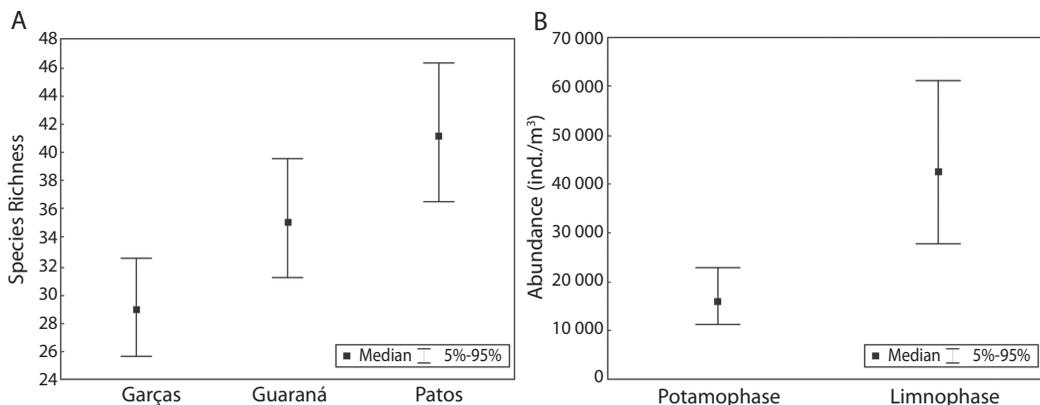


Fig. 3. Bayesian median and credibility interval of the *a posteriori* distribution of (A) species richness in each lake, and (B) abundance of zooplankton communities in the limnophase and potamophase.

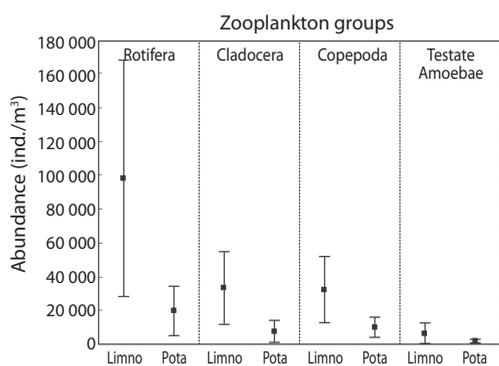


Fig. 4. Abundance of zooplankton groups (mean and standard error) for each hydrosedimentological phase (Limno - limnophase; Pota - potamophase) in connected lakes from Upper Paraná River floodplain.

b); this interaction was characterized by lower values of evenness (mean=0.48) and Shannon diversity (mean=2.7bits/ind) during limnophase in Garças Lake, suggesting a negative effect of the limnophase in this locality. On the other hand, the same period showed a positive effect on species diversity (3.2bits/ind) and evenness (0.69) in Patos Lake. No hydrosedimentological phase effects were detected in Guaraná Lake.

Relationship between community attributes and water level: Community attributes

presented significant correlations with each other (Table 3). Increased species abundance was associated with decreased Shannon diversity index and evenness. Thus, at lower abundances, the species were distributed more uniformly, and, consequently, diversity was higher. Therefore, the most frequent association observed was between evenness and Shannon diversity index; i.e. homogeneous distributions amongst organisms favoured an increase in the Shannon diversity index. Elevation of water levels was associated with decreased zooplankton abundance, thereby increasing the Shannon diversity index and evenness in these communities.

Structure of the zooplankton community: The hydro-sedimentological phases (potamophase and limnophase) were characterized by different structures of the zooplankton communities in the three lakes (Fig. 6; MRPP<0.01). IndVal results (Table 4) showed that 48 of 342 species significantly distinguish the hydro-sedimentological phases, with 20 species characteristic of the limnophase and 28 species characteristic of the potamophase.

In Patos and Guaraná Lakes, the limnological features most associated with community structure were dissolved oxygen and inorganic suspended solids in the limnophase, and electrical conductivity in the potamophase. Lower

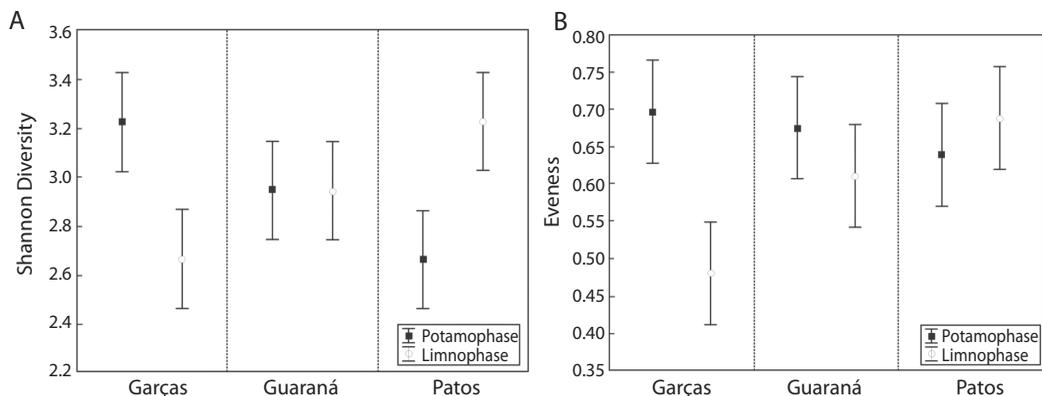


Fig. 5. Bayesian median and credible interval of the distribution *a posteriori* of the index of Shannon diversity (A) and evenness of the zooplankton community (B) in each lake on different hydrosedimentological phases.

TABLE 3
Pearson correlation between zooplankton community attributes in the Garças, Guaraná, and Patos lakes during the study period 2000-2008

Garças	N	S	H	E
N	1.00			
S	0.06	1.00		
H	-0.54*	0.39	1.00	
E	-0.56*	0.05	0.93*	1.00
L	-0.54*	0.23	0.60*	0.52*

Guaraná	N	S	H	E
N	1.00			
S	-0.03	1.00		
H	-0.53*	0.21	1.00	
E	-0.50*	-0.38	0.82*	1.00
L	-0.67*	0.07	0.43	0.38

Patos	N	S	H	E
N	1.00			
S	0.06	1.00		
H	-0.54*	0.39	1.00	
E	-0.56*	0.05	0.93*	1.00
L	-0.17	0.12	0.47*	0.47*

N-total abundance; S-species richness; H-Shannon diversity index; E-evenness; L-water level. *-significant correlations ($p < 0.05$).

values of dissolved oxygen (range=0.5-7mg/L) and inorganic suspended solids (0.1-3.8mg/L) were observed during potamophase. Higher

values of dissolved oxygen (6.8-9.5mg/L) and inorganic suspended solids (0.2-8.8mg/L) were observed in the limnophase. Lower values of electrical conductivity were observed in the limnophase, while higher values occurred in the potamophase.

A large number of variables were associated with the structure of the zooplankton community in Garças Lake (dissolved oxygen, inorganic suspended solids, ammonium, chlorophyll *a*, and Secchi depth) showing a variation in the local productivity. During potamophase, an increase in water transparency (Secchi depth reaching 2.4m) was recorded and lower levels of dissolved oxygen (range=2.5-7.8mg/L), inorganic suspended solids (0.2-1.5mg/L), and chlorophyll *a* (1.2-9.1mg/L).

Intra-annual variability of trophic relationships in the zooplankton community:

Biological factors likely responsible for variation in abundance were analysed with a Bayesian multiple regression model that suggested positive associations between zooplankton abundance and chlorophyll *a* concentration during limnophase (Fig. 7a). It is likely that an increase in resource availability during this phase favours an increase in total abundance. During potamophase, in Guaraná and Patos Lakes, community abundance was negatively associated with fish abundance (Fig. 7b), suggesting an effect of predation.

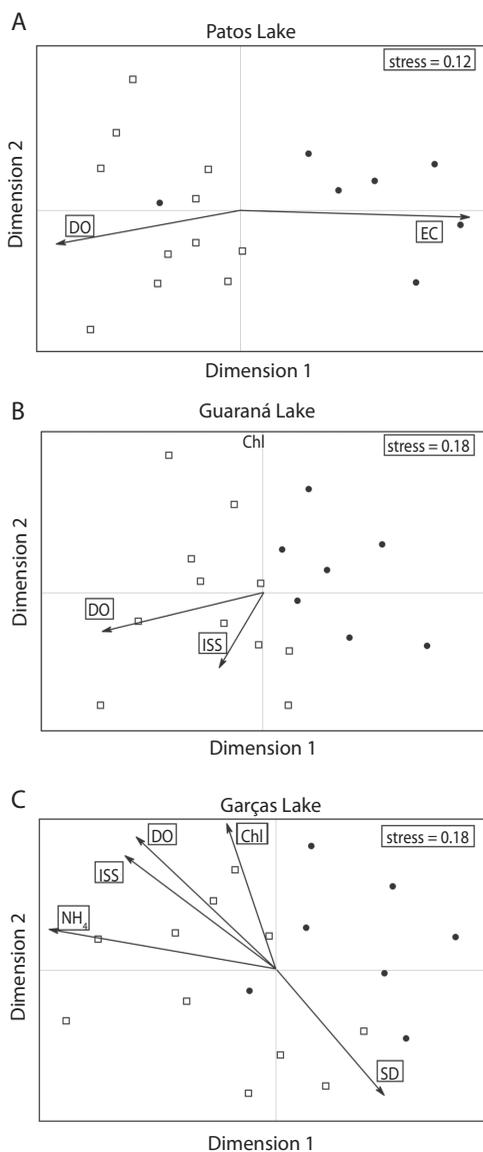


Fig. 6. Bidimensional scatter plot of the non-metric multidimensional scaling of the lakes in the Upper Paraná River floodplain: (A) Patos Lake; (B) Guaraná Lake; (C) Garças Lake. Sampling units during the period from 2000 to 2008: □-limnophase ●-potamophase. DO-dissolved oxygen; EC-electrical conductivity; WT-water temperature; SD-Secchi depth; TA-total alkalinity; ISS-inorganic suspended solids; NH₄-ammonium; Chl-chlorophyll *a*.

Bayesian *a posteriori* probabilities (0.99, 0.98, and 1.00; Patos, Guaraná, and Garças lakes, respectively) support the hypothesis

that resource availability controls zooplankton abundance during limnophase. Regarding predation effects, Patos and Guaraná lakes presented high probabilities (0.94 and 0.82, respectively) of negative effect of predation on zooplankton abundance. Otherwise, the low probability in Garças Lake (0.06) suggested little evidence of a predatory effect in this locality.

DISCUSSION

Zooplankton composition and diversity:

Lansac-Tôha *et al.* (2009) recorded about 540 species of cladocerans, copepods, rotifers, and testate protozoans in the pelagic region from several localities in the Upper Paraná River floodplain. In the present study, we recorded 63% of these species in the three lakes studied; these lakes are permanently connected to rivers, thus enhancing diversity through constant exchange of fauna with other environments (Ward *et al.* 1999, Aoyagui & Bonecker 2004, Alves *et al.* 2005). In general, high species diversity in floodplains is a result of interactions between structural heterogeneity and functional diversity. Structural heterogeneity refers to the complexity of interconnected environments, formed by a mosaic of hydrologic landscapes including rivers, secondary channels, backwaters, and tributaries, each with distinct hydrodynamic features (lotic, semi-lentic, and temporary and permanent lakes) (Junk 2002, Agostinho *et al.* 2004). Ward & Tockner (2001) suggested that functional diversity in riverine environments is a consequence of the interaction promoted by natural disturbances (e.g. floods) on functional processes (e.g. nutrient cycling, energy flow, and biotic interactions) in the different water bodies. These disturbances (floods) contribute to an increase of biodiversity because it favours spatial and temporal turnover amongst species. Thus, however we sampled only connected lakes, this interaction functional contributed to the high local diversity.

The high accumulated species richness values in Guaraná Lake (267 species) and

TABLE 4

List of indicator species of the hydro-sedimentological phases (Potamophase and Limnophase) determined by IndVal analysis for the study period 2000-2008, in the Patos, Garças and Guaraná lakes. Only significant species are listed

Limnophase	Potamophase
Testate protozoan	
<i>Centropyxis aculeata</i> Ehrenberg, 1932	<i>Arcella vulgaris undulata</i> Deflandre, 1928
<i>Centropyxis ecornis</i> Ehrenberg, 1841	<i>Arcella conica</i> Playfair, 1917
<i>Cucurbitella dentata quinquilobata</i> Gauthier- Lièvre and Thomas, 1960	<i>Arcella gibbosa</i> Pénard, 1890
<i>Diffugia gramen</i> Pénard, 1902	<i>Arcella mitrata spectabilis</i> Deflandre, 1928
	<i>Centropyxis aerophila</i> Deflandre, 1929
Rotifera	
<i>Brachionus calyciflorus</i> Pallas, 1766	<i>Brachionus dolabratus</i> Haring, 1914
<i>Brachionus mirus</i> , Daday 1905	<i>Brachionus falcatus</i> Zacharias, 1898
<i>Conochilus unicoloris</i> Rousselet, 1892	<i>Dipleuchlanis protatula propatula</i> Gosse, 1886
<i>Hexarthra mira</i> Hudson, 1871	<i>Epiphanes clavatula</i> Ehrenberg, 1832
<i>Keratella cochlearis</i> Gosse, 1851	<i>Epiphanes macrourus</i> Barrois and Daday, 1894
<i>Kellicotia bostoniensis</i> Rousselet, 1908	<i>Filinia terminalis</i> Plates, 1886
<i>Keratella Americana</i> Carlin, 1943	<i>Lecane bulla</i> Gosse, 1851
<i>Ploesoma truncatum</i> Levander, 1894	<i>Lecane cornuta</i> Müller, 1786
<i>Synchaeta pectinata</i> Ehrenberg, 1832	<i>Lecane curvicornis</i> Murray, 1913
<i>Trichocerca inermis</i> Linder, 1904	<i>Lecane lunaris</i> Ehrenberg, 1832
<i>Trichocerca stylata</i> Gosse, 1851	<i>Lecane leontina</i> Turner, 1892
	<i>Lecane ludwigi</i> Eckstein, 1883
	<i>Lecane luna</i> Müller, 1776
	<i>Lecane papuana</i> Murray, 1913
	<i>Plationus patulus macracanthus</i> Daday, 1905
	<i>Plationus quadricornis quadricornis</i> Ehrenberg, 1832
	<i>Testudinella patina patina</i> Hermann, 1783
Cladocera	
<i>Bosmina hagmanni</i> Stingelin, 1904	<i>Chydorus eurynotus</i> Sars, 1901
<i>Bosminopsis deitersi</i> Richard, 1895	<i>Disparalona dadayi</i> Birge, 1878
<i>Ceriodaphnia cornuta</i> Sars, 1886	<i>Ilyocryptus spinifer</i> Herrick, 1884
<i>Daphnia gessneri</i> Herbst, 1967	<i>Moina minuta</i> Hansen, 1899
	<i>Macrothrix elegans</i> Sars, 1901
Copepoda	
<i>Notodiaptomus amazonicus</i> Wright, 1935	

Garças Lake (242 species) are likely due to temporal replacements of local fauna in these lakes; species frequently observed at the beginning of the study gradually disappeared, and other species started to appear during the time frame of the study. An increase in the frequency of hydrodynamic disturbances in the Paraná River (many short flood pulses) might have

negatively influenced the occurrence of common species, and favoured species resistant to disturbance. Furthermore, the operation of a reservoir, that began one year before this study, could contribute to these patterns, since during the aging of reservoirs there is a change in its fauna (Agostinho *et al.* 1999), which also affects the downstream lakes.

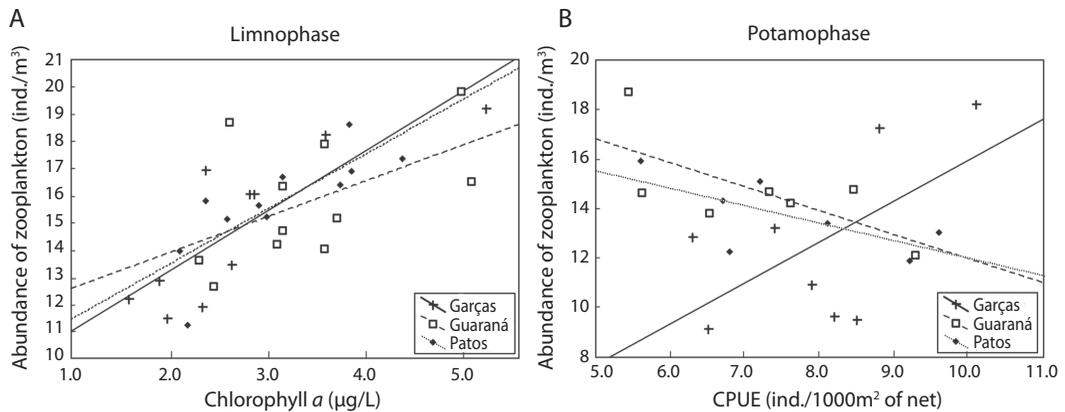


Fig. 7. Association between zooplankton abundance (\log_2) and (A) chlorophyll *a* concentration (\log_2) during limnophase; (B) fish abundance (\log_2) during potamophase. Lines represent linear best fit equations. CPUE-catch per unit effort.

Interestingly, high values of accumulated richness did not result in greater mean diversities. Mean diversity was higher in Patos Lake than in other lakes. In Patos Lake, the water level variability occurred naturally and human interventions, such as impoundments that control overland water flow, were not present. This suggests that sites with fewer human disturbances have a higher mean diversity and greater number of specialized niches (Ricklefs & Schluter 1993). Thus, the results indicate that water level and limnological modifications recorded after 2000 (Roberto *et al.* 2009) contributed to qualitative impoverishment and replacement of aquatic biota in Garças and Guaraná lakes (diminishing the local species richness, but increasing the accumulated species richness), highlighting the ecological importance of natural flood dynamics (with regular flood pulses), as observed in the Ivinheima River.

Some studies have suggested that floods lose substantial characteristics in localities where hydrological control is exerted by reservoirs (Kingsford 2000, Dudgeon *et al.* 2006, Steinberg *et al.* 2009); the controlled floods that occur in these managed localities do not produce the same effects as observed under natural conditions. Under regulated conditions, flood characteristics are modified by, for example, reductions in sediment load, large variations in

the frequency of the pulse, and reduced amplitudes of water level variations. Thus, regulated rivers are subject to fewer pronounced floods and droughts and to fewer stochastic events.

Relationship between community attributes and water level: The associations of community attributes identified in this study (species richness, Shannon diversity index, evenness, and abundance) were also reported by Paidere *et al.* (2007) and Lindholm *et al.* (2007). These relationships characterize the behaviour of the zooplankton community according to two main scenarios: (i) at low abundances, fauna uniformly distributed, evenness increases, an increase in the diversity index is favoured, and species coexistence is promoted by minimizing competitive exclusion (Paidere *et al.* 2007); (ii) at high abundances, few species predominate, which decreases the evenness and the diversity of species. Water level influences the community dynamic, decreasing the total abundance but increasing the diversity of species.

Structure of the zooplankton community: Hydro-sedimentological phases were distinguished by the structures of zooplankton communities in the studied lakes (MRPP). Studies performed in South American floodplain systems have found higher abundances

of some zooplanktonic species during dry periods or limnophase (Brandorff & Andrade 1978, Saunders & Lewis Jr. 1989, Paggi & De Paggi 1990, Lansac-Tôha *et al.* 1993, Lima *et al.* 1998, Rossa & Bonecker 2003, De Paggi & Paggi 2007; Henry *et al.* 2011), when the hydrodynamic conditions were more stable, thus promoting primary productivity which supports large populations of zooplanktonic organisms due to higher water residence time (Baranyi *et al.* 2002). In contrast, during potamophase, we observed a dilution effect in which organisms were more dispersed in the water column (Bozelli 2000, Lansac-Tôha *et al.* 2009). Furthermore, the environmental conditions were disadvantageous for the development of large zooplankton populations, due to higher hydrodynamic instability, decreases in autochthonous productivity (lower chlorophyll *a* concentration), and increases in predation pressure by fish.

Seasonal patterns in the structure of zooplankton communities were strongly correlated with environmental variables: dissolved oxygen, inorganic suspended solids, and electrical conductivity. These variables were indicative of processes that influence the zooplankton community during limnophase, such as higher concentration of dissolved oxygen during the limnophase is partially due to primary production which, in turn, may increase zooplankton densities.

Community structure in Garças Lake was characterised by inter-annual variations related to variations system productivity. The upstream reservoir reduced sediment transport and promoted increase in water transparency and a decrease in nitrogen and phosphorus (Roberto *et al.* 2009). In this lake, there was an increase in the number of environmental variables associated with the structure of the zooplankton community, indicating that this local community is more susceptible to sources of variation. This effect is attenuated in Guaraná Lake, because the particular biogeochemical composition of this site sustains nutrient levels higher than those present in the influx waters from the Paraná River.

Species that characterize limnophase occur at higher abundances and frequencies in this period. Amongst them, *Keratella cochlearis* has shown high abundances during dry periods in both natural and affected environments (Beaver *et al.* 1998, Rossa & Bonecker 2003, Cardoso & Marques 2004). The reproductive effort this species is highest in productive habitats in controlled experiments (Nagae unpublished data). The increased abundance of Bosminidae species (*Bosmina hagmanni* and *Bosminopsis deitersi*) and *Daphnia gessneri* in limnophase is also related to higher productivity (Matsumura-Tundisi 1984, Lopes *et al.* 1997, Lima *et al.* 1998, Branco *et al.* 2000, Rejas *et al.* 2005).

In potamophase, planktonic and littoral species are distributed in the pelagic region, because littoral species are displaced from the littoral region by hydrodynamic instability. *Lecanidae*, *Epiphanes clavatula*, and *Dipleuchlanis propatula propatula* (littoral rotifers), Chydoridae species (littoral cladocerans) and *Moina reticulata* (a pelagic cladoceran) were frequently observed during potamophase in other studies conducted in this same floodplain (Lima *et al.* 1998, Rossa & Bonecker 2003, Alves *et al.* 2005).

Intra-annual variability of trophic relationships in the zooplankton community:

Data on chlorophyll *a* concentrations support the hypothesis that food availability increases community abundance during limnophase periods, reflecting a positive effect of resource availability; this pattern was observed in all three lakes, and in other studies conducted in floodplain environments over shorter time periods (Bozelli 1996, Beaver *et al.* 1998, Azevedo & Bonecker 2003, Trevisan & Forsberg 2007). A negative association of zooplanktonic abundance with fish density was observed in Guaraná and Patos Lakes, suggesting an effect of zooplanktivorous fishes. Zooplankton organisms are important components of the diets of small fish in lakes of the Upper Paraná River floodplain, mainly during potamophase (Russo & Hahn 2006, Crippa *et al.* 2009, Hahn & Crippa 2006). The

potamophase, floods, which are regional-scale processes, result in dilution of the populations and homogenization of environments, whereas in limnophase, local processes, such as productivity, separately influence the succession of isolated communities.

Conceptual framework for variability in the structure of zooplankton communities in floodplains:

The main variation sources of zooplankton communities in connected lakes, that are influenced by the flood dynamic in the Upper Paraná River floodplain, were summarized as follows (Fig. 8):

a) Flood dynamic processes, which influence the zooplankton community structure physically and biologically:

Physically, flood dynamic processes are responsible for the expansion and contraction of environments because they define the size and conditions of the habitat, as well as the quantity and quality of resources. Biologically, the floods change the structure and dynamic of the zooplankton community by defining the relationships between community attributes; an increase in connectivity favours the exchange and dispersion of species, which increases zooplankton diversity. During limnophase, biotic interactions are stronger because high abundances of a few dominant species decrease the evenness and the species diversity.

b) Variations in limnological conditions, which characterize distinct 'assemblages':

During potamophase, an increase in water transparency and electrical conductivity and a decrease in dissolved oxygen and chlorophyll *a* were associated with increased abundance of some species. During limnophase, a reduction in the size of water bodies increases available food resources, because productivity in each locality is enhanced by increased concentrations of nutrients and chlorophyll *a*. These conditions support the growth of opportunistic taxa that were able to exploit habitat conditions, resulting in increased species dominance and decreased species richness.

c) Factors intrinsic to each phase, which are related to resource availability and predation, which, in turn, influence the total abundance of zooplanktonic organisms:

In limnophase, the greater availability of food resources supported high zooplankton abundances. In potamophase, however, despite the dilution effect due to the greater volume of water, the decrease in zooplankton abundance may be in part due to fish predation, where the community structure presents marked seasonality.

These findings emphasise the complexity of interactions between physical, chemical, and biological factors in floodplain environments, as noted by other authors, and highlight the important contribution of the hydro-sedimentological phases to the seasonal dynamic of the community. Moreover, the present study overcomes the temporal limitations of previous studies, by considering inter-annual variability in the data, based on a long-term ecological research programme. Although the number of replicates was small, generalisations are based on the results of the present research combined with an extensive literature on floodplain systems.

The conceptual model presented above encompasses the interactions between diverse environmental variables to more complete understanding of the main sources of community variation. Although the model is schematically simple, it does not devalue the environmental complexity (spatial and temporal) that supports and maintains floodplain biodiversity, but instead it facilitates an understanding of system dynamics that is critical for eventual development of management and conservation proposals.

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RESUMEN

El manejo del régimen de inundación ha cambiado de manera significativa la dinámica natural de las inundaciones, que son responsables de la estructura y dinámica de las comunidades acuáticas en sistemas río-planicie de inundación. En este sentido, investigamos cómo la estructura de las comunidades zooplanctónicas responde a variaciones estacionales e interanuales en los sistemas de llanura de inundación, y los factores biológicos asociados con la abundancia de especies de las comunidades zooplanctónicas. Elaboramos también, un marco conceptual que describe los principales factores ecológicos asociados con la estructura de las comunidades para los sistemas del Alto río Paraná. Para ello se realizaron muestreos cada seis meses (potamofase en marzo y en septiembre limnofase) para caracterizar las variaciones intra e interanuales en la estructura de la comunidad entre 2000 y 2008. Las diferencias estacionales de la riqueza de especies, abundancia, índice de diversidad de Shannon y equitatividad, se llevaron a cabo utilizando procedimientos Bayesianos para mostrar predicciones probabilísticas de los datos ajustados para las principales fuentes de variación. Análisis de ordenamiento no-métrico multi-dimensional (NDMS); procedimientos de permutación de respuestas múltiples (MRPP) y análisis de especies indicadoras (IndVal) fueron utilizados para evaluar y clasificar la estacionalidad de la estructura de la comunidad. Durante aguas altas (potamofase), la conectividad hidrológica favoreció el intercambio y dispersión de las especies en algunas lagunas, incrementando la diversidad local; durante aguas bajas (limnofase), la alta productividad local favoreció los táxones oportunistas, incrementando las especies dominante y disminuyendo la diversidad local. La disponibilidad de recursos alimenticios y la densidad de pequeños peces fueron los factores biológicos asociados con la dinámica estacional de la comunidad zooplanctónica; los cuales dependen de la fase hidrosedimentológica (potamofase o limnofase). Modificaciones del régimen hidrológico y limnológico relacionados con el manejo de inundación han promovido el reemplazo y empobrecimiento de la biota acuática, en las lagunas sin conexión afectadas, enfatizando así la importancia ecológica de la dinámica natural de inundaciones, que presenta pulsos regulares de inundación. El modelo conceptual que se presenta abarca desde interacciones entre diversas variables ambientales hasta mecanismos más comprensibles de las principales fuentes de variación de la comunidad.

Palabras clave: diversidad, estructura de la comunidad, manejo ambiental, procedimientos Bayesianos, modelo conceptual, humedales.

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