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The effect of seasonality on the structure of rotifers in a black-water shallow lake in Central Amazonia

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ABSTRACT

Rotifers have often been used as indicators of sudden changes in physical and chemical features of the aquatic environment. Such features vary greatly during flood pulse events in small lakes connected to major floodplains. However, few are the studies that investigate the consequences of the flood pulse in rotifer species composition, abundance, richness and diversity, especially in Amazonian lakes. We analyzed samples from a small blackwater lake of an “igarapé” connected permanently to the Negro river, in Central Amazonia. Samples were taken twice a year for two years, comprising flooding and receding periods of the flood pulse. Rotifer abundance increased significantly after draught events, and electrical conductivity and turbidity were intrinsically related to such variation. Species composition also changed from flooding to receding periods. Some taxa, such as *Brachionus zahniseri reductus* and *Lecane remanei* were restricted to receding periods, while *Brachionus zahniseri*, *Brachionus gillardi* and *Lecane proiecta* were only present during flooding. A shift in the composition of rotifer families was observed from one period to another, showing the effect of renewing waters of the flood pulse. These results suggest that the flood pulse acts as a driving force and stressing condition, considerably altering rotifer community dynamics, either changing species composition or decreasing abundance.

Key words: floodplain, flood pulse, “igarapé”, Rotifera, zooplankton.

INTRODUCTION

The value of zooplankton as an indicator of ecological conditions stems from its position in the food web, between the top-down regulators (fish)

and bottom-up factors (phytoplankton) (Jeppesen et al. 2011). Rotifers are a well-represented and important component of zooplankton in freshwaters (Nogrady et al. 1993), and due to their unique physiology, short life cycle and their multiple niches, they are considered refined sensors

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to monitor shifts in physical and chemical features of the water column.

Several studies have highlighted the potential of rotifers as indicators of environmental conditions such as trophic state, pH or salinity in both temperate and tropical aquatic ecosystems (*e.g.* Kuczynski 1987, Branco et al. 2000, 2002). Besides responding to shifts in physical and chemical conditions (*e.g.* Branco et al. 2005, Souza et al. 2011), the spatial and seasonal distribution of rotifers also indicate the intensity of biotic interactions such as competition and predation by vertebrates and invertebrates (Nogrady et al. 1993, Walsh et al. 2006).

Few studies have addressed ecological aspects of zooplankton communities and rotifer assemblages in small streams (called “igarapés”) and their associated lakes in Central Amazonia. These ‘igarapés’, altogether, are remarkable in many ways: high content of dissolved humic substances, acid pH, low electrical conductivity (8.4-15 S.cm²) and low primary production (Sioli 1975, Brandorff and Andrade 1978, Walker 1981). Some studies on zooplankton of clearwater, blackwater and whitewater floodplain lakes should, however, be mentioned (*e.g.* Brandorff and Andrade 1978, Hardy 1980, Hardy et al. 1984, Brandorff and Hardy 2009).

Since these “igarapés” are part of a floodplain river system, they are subjected to variations in the water level – a phenomenon called flooding pulse, which can affect the dynamics of aquatic communities, causing shifts in species composition and diversity (Paidere 2009). Junk et al. 1989, identified the flood-pulse as being responsible for productivity and the existence of the entire Amazon river-floodplain system. Generally, the flood pulse, due to changes in the physical and chemical environment, affects the biota, which responds through morphological, anatomical, physiological adaptations, hence producing characteristic community structures (Junk et al. 1989).

The flood pulse itself is a seasonal driving force (Junk et al. 1989) and within its distinct phases (flooding, flood, receding and draught) seasonal flooding allows aquatic organisms to redistribute themselves within the spatial mosaic of the river-floodplain (Rodríguez and Lewis Jr 1994, 1997). Gradually changing water level forces aquatic organisms of the shallow littoral zone to continually colonize new habitats (Arrington and Winemiller 2006).

Reviewing the art status of rotifer studies in natural environments of floodplains in South America, Aoyagui and Bonecker (2004) concluded that there were few studies addressing this group in spite of the vast and heterogeneous territorial extent, and the various floodplain environments not even explored. In Brazil, considering the variety and complexity of the several river basins and the presence of floodplain systems including numerous lakes (Carvalho et al. 2001), the knowledge on rotifer ecology in these aquatic ecosystems is relatively scarce.

This study evaluated the influence of flood pulses in the rotifers community of a small “igarapé” lake in the Rio Negro floodplain. Thus, the aim of this study was to associate rotifers species richness, density and diversity with changes caused by the flood-pulse and its influence in the physical and chemical variables. Furthermore, we also tried to observe spatial changes in the assemblage. We hypothesized that distinct phases of the flood pulse – in this case, flooding and receding periods – will strongly influence the rotifer assemblage structure, either increasing species richness, varying species composition or increasing diversity.

MATERIALS AND METHODS

STUDY SITE AND ITS CHARACTERISTICS

The studied “igarapé” lake belongs to the Negro river floodplain (Amazonia, Brazil) and it is located nearby the city of Manaus (3°02'17.47"S 60°15'07.85"W). This shallow waterbody is regionally named

Lake Arrombado (LARR) and it is part of Tupé's Sustainable Development Reserve (Reserva de Desenvolvimento Sustentável – RDS Tupé). LARR (Figure 1) is a black-water shallow lake

surrounded by native forest and is characterized by a high content of humic dissolved substances, as in most freshwater environments connected to the Rio Negro basin (Brandorff and Hardy 2009).

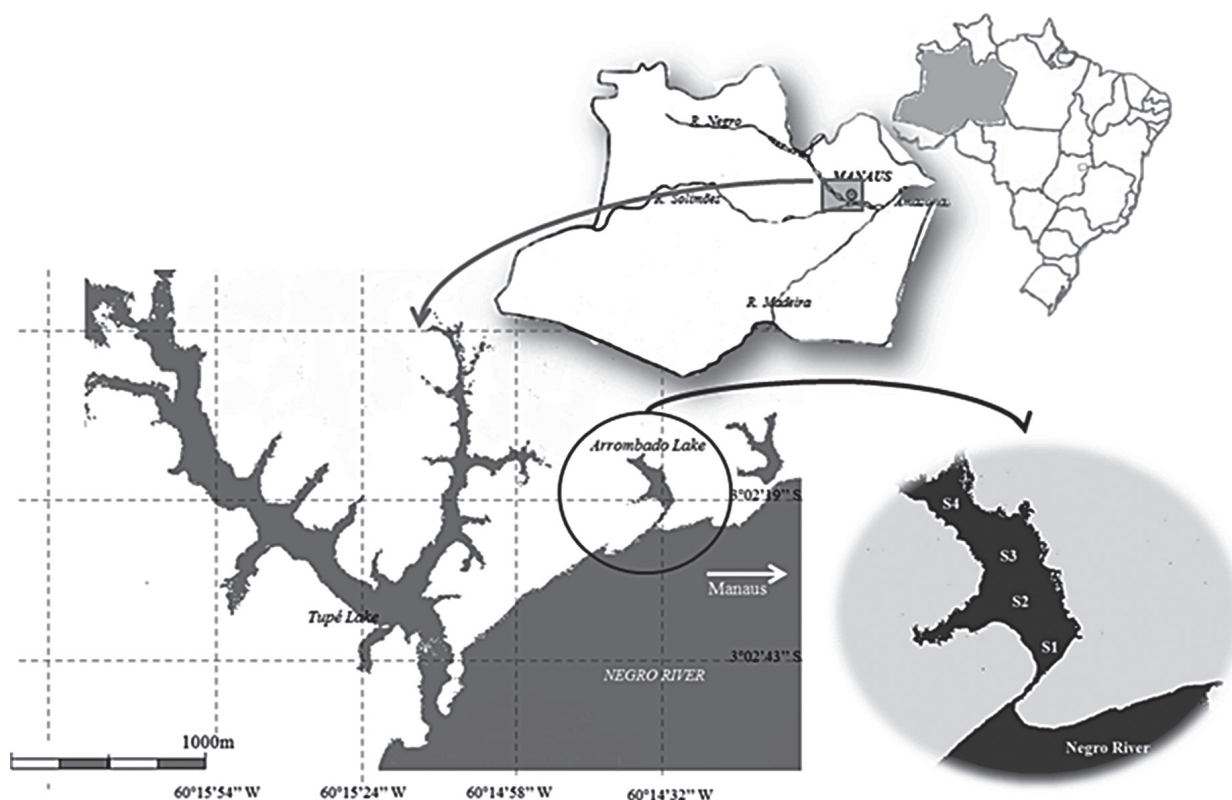


Figure 1 - Location of Arrombado Lake (LARR), Central Amazonia, Negro River Floodplain, Brazil. In detail, LARR and the sampling stations.

Nonetheless, during the study LARR had a permanent connection to the main river (Rio Negro) through the mouth within a sandbar, which is intermittent and, at low water level, only a narrow channel remains open to the river. Four sampling stations were determined comprising a gradient from the mouth of the lake to the inner part near the forest.

Station 1 - Located exactly at the connection channel of the lake and the main river.

Station 2 - First sampling station inside the lake.

Station 3 - Located in the middle of the lake, in an open area.

Station 4 - Located near the forest, a littoral sampling site. It is the station located farthest away from the sandbar.

SAMPLING

Sampling periods were chosen to match two distinct hydrological cycles of two consecutive flood pulses of the Negro River (AM). Samples were taken in two periods of falling waters (August of 2006 and 2007) and two periods of rising waters (March of 2007 and 2008). Sampling also matched periods of higher and lower rain precipitation of the two consecutive cycles.

Bucket filtration of 100L of under-surface water using a 68 μ m-mesh size net for zooplankton

was performed in the field, and samples were immediately fixed with buffered formaldehyde in a 4% concentration. This sampling was done with two replicates for the quantitative zooplankton analysis. Horizontal hauls using a net of 68 μm -mesh size were done at each sampling point for qualitative analysis. Water temperature ($^{\circ}\text{C}$), dissolved oxygen (mg.L^{-1}) and electric conductivity ($\mu\text{S.cm}^{-1}$) were measured in all of the sampling stations using a multi-probe device (YSI-85 model). pH was determined with a pH-meter (Thermo Scientific Orion 5[®]). Depth was measured using a depth-measurer and water transparency was measured using a Secchi disc depth.

DATA ANALYSES

Qualitative analyses of zooplankton were performed under an optical microscope integrated to microphotograph equipment used to optimize species recognition. Taxa identification was made using taxonomic studies performed by Koste (1978), Nogrady et al. (1993), Fernando (2002), Segers (2007). Quantitative samples were counted in a Sedgewick-Rafter counting cell. Species diversity (H') and evenness (J') were calculated using the Shannon-Wiener index – natural log.

Statistical analyses were also used to integrate biotic characteristics using Statistica 7.0 software package for Windows Vista and Windows 7. A factorial analysis of variance (f -ANOVA) was performed to elucidate possible interactions between the two categorical factors (different seasons and sampling stations) and check for significant statistical differences between biotic dependent variables. The significance level used was $P < 0.05$. All data were pre-tested for a normality fitting (Shapiro-Wilks test) and homocedasticity (Levenne's test). Variables which did not match such assumptions were either log-transformed or removed from f -ANOVA.

Canonical Correspondence Analysis (CCA) was used to assess the relationship between

physical and chemical variables and abundance of frequent taxa. CCA was executed using R software. The CCA was performed using abundance data of species which had a 50% occurrence or higher, thus classified as frequent species (Gomes 1989). Such limiting 50% tenet enables an overall look upon the effects of seasonality in the community. Data were log transformed ($\log x + 1$) to satisfy a normality fitting. In R, the library used was Vegan (v. 2.0-1, compiled in R version 2.13.2) and Monte-Carlo hypothesis test was adjusted to 999 permutations.

RESULTS

PHYSICAL AND CHEMICAL FACTORS

Hydrological data from the Negro River were obtained from the Brazilian National Water Agency for the studied period (Figure 2), and confirmed that the samplings were performed during the flooding waters of 2006 and 2007 and receding waters of 2007 and 2008. The annual variation in water level of the Negro River was between 9 and 12 m.

Total depth and electrical conductivity were higher in all of the sampling stations during falling waters. Additionally, water transparency was slightly lower in most sampling stations during this hydrological period, (Table I). The lowest concentration of dissolved oxygen occurred during the receding period of 2007, whereas the highest occurred during the same period of 2006. The highest water temperature was measured in falling waters of 2006 in all sampling stations while the lowest was recorded in the same period of the consecutive year (Aug 2007). On the other hand, pH was higher during the rising period of 2008 and lower during flooding of the previous year.

ROTIFER SPECIES COMPOSITION AND ABUNDANCE

Fifty-five rotifer species were identified, belonging to 15 taxonomical families (Table II). Monogononta rotifers accounted for most species ranked. Bdelloidea was treated as a gross taxonomic group due to difficulties involving specific identification.

Brachionidae, Lecanidae and Trichocercidae were the most species-rich families – with 16, 10 and 5 species each, respectively. Higher values

of species richness occurred during rising water period of 2008 in all sampling stations (Figure 3). During rising waters species richness peaked at

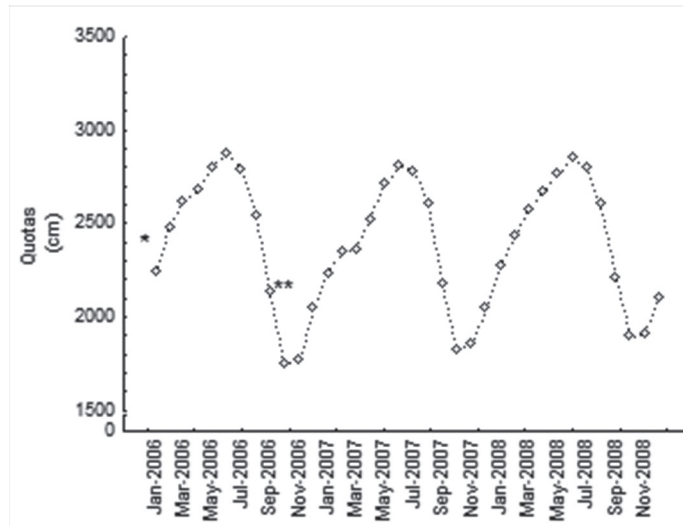


Figure 2 - Hydrological quotas (cm) of the Negro River floodplain during two consecutive years. (*) Indicates flooding period and (**) indicates receding water period. Source: Brazil's National Water Agency (ANA).

TABLE I
Physical and chemical variables from the Arroimado lake during receding (August 2006 and 2007) and flooding (March 2007 and 2008) periods. (n.o.) = Values not obtained. SD= standard deviation. Means were calculated using the values of the four sampling stations.

Variables	August 2006			March 2007			August 2007			March 2008		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Conductivity (μS/cm)	9.08	0.05	9.1 - 9.0	5.00	0.2	5.3 - 4.9	9.78	0.22	10.0 - 9.5	7.33	0.15	7.5 - 7.2
Transparency (m)	0.78	0.10	0.9 - 0.7	1.05	0.1	1.1 - 1.4	0.88	0.37	1.4 - 0.6	0.91	0.12	1.0 - 0.8
Dissolved Oxygen (mg/L)	5.14	0.48	5.6 - 4.7	3.92	0.11	4.1 - 3.8	2.81	0.52	3.4 - 2.1	4.23	0.43	4.6 - 3.6
Temperature (°C)	30.05	0.37	30.3 - 29.5	28.80	0.27	29 - 28.4	28.75	0.06	28.8 - 28.7	29.20	0.20	29.9 - 28.9
Total depth	3.60	0.55	4.0 - 3.0	1.88	0.75	2.5 - 1.2	3.91	0.64	4.8 - 3.0	2.63	0.66	3.8 - 0.8
pH	4.99	n.o.	n.o.	4.58	n.o.	n.o.	4.68	n.o.	n.o.	5.42	n.o.	n.o.

station 4. The most frequent families encountered were Brachionidae, Synchaetidae and Lecanidae. Thus, the most common species were *Keratella americana*, *Polyarthra vulgaris* and *Lecane melini*, which were present in all samples.

Rotifer density reached the highest values during flooding of 2008 in all sampling points (Figure 4). However, rotifer abundance peaked (64849 ind.m⁻³) at sampling station 2, during the receding water of the first hydrological cycle analyzed.

Rotifers were primarily dominated by Brachionidae with high densities of *Brachionus zahniseri* during the entire studied period. *B. zahniseri* and *B. zahniseri* var. *reductus* showed population shifts: the former dominated only during flooding whereas the latter dominated only during receding periods.

Lecanidae was mainly represented by *Lecane melini* in all stations. *Lecane remanei* was also important during the receding water period in all sampling stations.

Table II
Taxonomic inventory of rotifers in LARR and species occurrence during
two phases of the flood pulse (receding and flooding). Bold symbols
summarizes occurrence in: B= both phases; R= receding; F= flooding

<p>ASPLANCNIDAE</p> <p><i>Asplanchna sieboldi</i> Gosse, 1850 ^B</p> <p>BDELOIDEA</p> <p><i>Bdeloidea</i> sp1. ^B</p> <p><i>Bdeloidea</i> sp2. ^B</p> <p>BRACHIONIDAE</p> <p><i>Anuraeopsis fissa</i> Gosse, 1851 ^B</p> <p><i>Brachionus calyciflorus</i> Pallas, 1766 ^B</p> <p><i>Brachionus caudatus</i> Barrois & Daday 1894 ^F</p> <p><i>Brachionus dolabratus</i> Harring, 1915 ^F</p> <p><i>Brachionus gillardi</i> Hauer, 1966 ^F</p> <p><i>Brachionus havanaensis</i> Rousselet, 1911 ^F</p> <p><i>Brachionus mirus</i> Daday, 1905 ^F</p> <p><i>Brachionus zahniseri</i> Ahlstrom, 1934 ^F</p> <p><i>Brachionus zahniseri</i> var. <i>reductus</i> Hauer, 1956 ^R</p> <p><i>Keratella americana</i> Carlin, 1943 ^B</p> <p><i>Keratella cochlearis</i> Gosse, 1851 ^B</p> <p><i>Macrochaetus sericus</i> Gosse, 1867 ^F</p> <p><i>Notholca lamellifera</i> Vassilijewa & Kutikova, 1969 ^F</p> <p><i>Platys quadricornis</i> Ehrenberg, 1832 ^B</p> <p><i>Platyonus patulus</i> Müller, 1786 ^R</p> <p><i>Trichotria tetractis</i> Ehrenberg, 1830 ^F</p> <p>CONOCHILIDAE</p> <p><i>Conochilus coenobasis</i> Skorikov, 1914 ^B</p> <p>EUCHLANIDAE</p> <p><i>Dipleuchlanis propatula</i> Gosse, 1886 ^B</p> <p><i>Euchlanis dilatata</i> Ehrenberg, 1832 ^F</p> <p>GASTROPODIDAE</p> <p><i>Gastropus</i> sp. Imhof, 1898 ^B</p> <p><i>Ascomorpha saltans</i> Bartsh, 1870 ^R</p> <p>HEXARTHRIIDAE</p> <p><i>Hexarthra</i> sp. Schmarda, 1854 ^F</p>	<p>LECANIDAE</p> <p><i>Lecane bulla</i> Gosse, 1886 ^B</p> <p><i>Lecane curvicornis</i> Murray, 1913 ^B</p> <p><i>Lecane kuiticowa</i> Koste, 1972 ^F</p> <p><i>Lecane luna</i> Müller, 1776 ^R</p> <p><i>Lecane lunaris</i> Ehrenberg, 1832 ^B</p> <p><i>Lecane melini</i> Thomasson, 1953 ^B</p> <p><i>Lecane papuana</i> Murray, 1913 ^F</p> <p><i>Lecane proiecta</i> Hauer, 1956 ^F</p> <p><i>Lecane quadridentata</i> Ehrenberg, 1830 ^R</p> <p><i>Lecane remanei</i> Hauer, 1964 ^R</p> <p>LEPADELLIDAE</p> <p><i>Lepadella patella</i> Müller, 1786 ^F</p> <p><i>Xenolepadella monodactyla</i> Bérzins, 1960 ^F</p> <p>MYTILLINIDAE</p> <p><i>Mytilina macrocera</i> Jennings, 1894 ^R</p> <p>NOTOMMATIDAE</p> <p><i>Cephalodella</i> sp. Bory de St. Vincent, 1826 ^F</p> <p><i>Monommata</i> sp. Bartsch, 1870 ^F</p> <p>SYNCHAETIDAE</p> <p><i>Ploesoma truncatum</i> Levander, 1894 ^B</p> <p><i>Polyarthra vulgaris</i> Carlin, 1943 ^B</p> <p><i>Synchaeta oblonga</i> Ehrenberg, 1832 ^B</p> <p>TESTUDINELLIDAE</p> <p><i>Testudinella patina</i> Hermann, 1783 ^B</p> <p>THRIOCERCIDAE</p> <p><i>Trichocerca bicristata</i> Gosse, 1887 ^B</p> <p><i>Trichocerca capucina</i> Wierzejski & Zacharias, 1893 ^B</p> <p><i>Trichocerca similis</i> Wierzejski, 1893 ^B</p> <p><i>Trichocerca similis chatoni</i> Wierzejski, 1893 ^B</p> <p><i>Trichocerca</i> sp. Lamarck, 1801 ^B</p> <p>TRICHOSPHAERIDAE</p> <p><i>Filinia longiseta</i> Ehrenberg, 1834 ^B</p>
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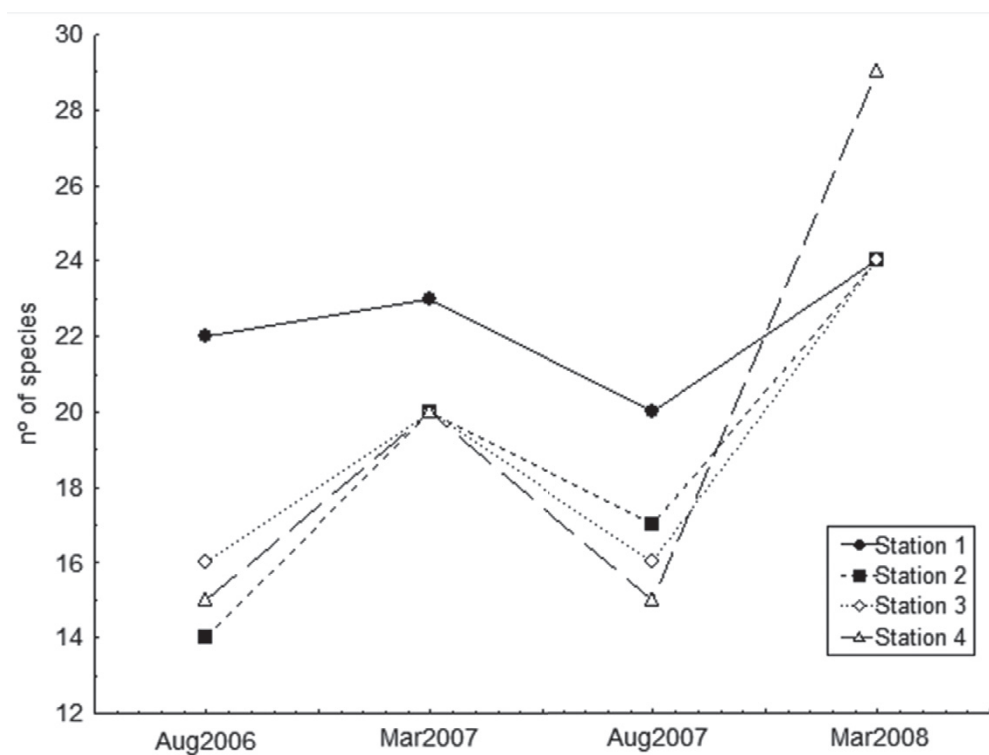


Figure 3 - Species richness (number of species) recorded in the Arrombado Lake during the study period in all sampling stations. aug=August; mar= March.

Lecane proiecta was found only during flooding periods at low numbers. Synchaetidae was equally important to characterize the rotifers assemblage, especially in receding water periods in stations 2 and 3. *Synchaeta oblonga*, *Polyarthra vulgaris* and *Ploesoma truncatum* were very important species due to their high density values. Nonetheless, *P. truncatum* unlike the two other species mentioned, occurred only during one phase of the hydrological cycle in both years: the receding water period.

Some population shifts were remarkable. The most striking example of such shifts is the appearance of *Brachionus zahniseri* var. *reductus* only during receding periods and *B. zahniseri* restricted to flooding periods. Other species such as *Lecane remanei*, *L. proiecta*, *Macrochaetus sericus*, *Monommata* sp. and *B. gillardi*, also had their abundances directly linked to seasonality (Table II).

Species diversity (Shannon-Wiener) ranged from 1.1 (Station 2, flooding 2008) to 2.15 (Station 1, receding period of 2007). In general, slightly higher values occurred during receding waters of both years. On the other hand, evenness showed noticeable seasonal oscillation with highest values during receding waters and values during flooding, except in station 1 during receding waters of 2006 (Figure 5).

BIOTIC AND ENVIRONMENTAL INTEGRATION

Results of the hypothesis test showed that seasonal differences were found in the rotifer community of LARR. Rotifer richness ($P < 0.001$, $F_{(1,14)} = 17.67$), evenness ($P < 0.001$, $F_{(1,14)} = 18.43$), abundance ($P = 0.05$, $F_{(1,14)} = 4.03$) and diversity ($P = 0.01$, $F_{(1,14)} = 7.75$) were higher either during receding or flooding periods, as shown in the last section.

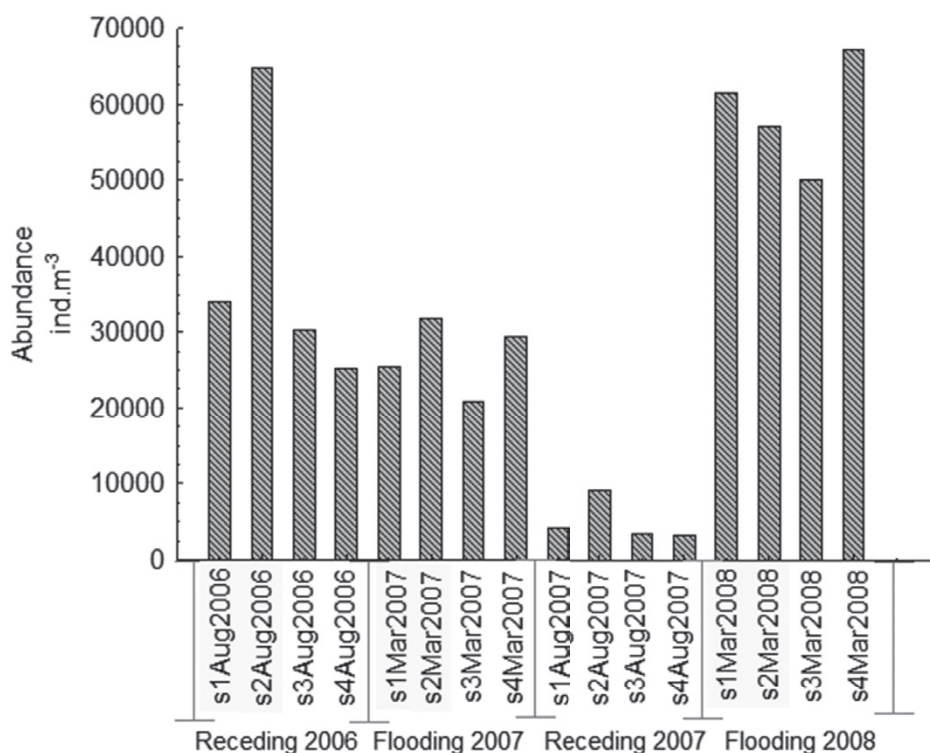


Figure 4 - Total abundance (ind.m⁻³) of rotifers during flooding (August) and receding (March) phases of two consecutive years in all the sampling stations (s1, s2, s3 and s4).

However, these response variables did not differ spatially ($P > 0.05$, $F_{(1,14)} = 0.26$) nor were affected by the interaction of seasonality and spatial distribution ($P > 0.5$; $F_{(12,13.8)} = 1.03$).

Canonical Correspondence Analysis (CCA) indicated that the environmental variables explained 61.6% of rotifers assemblage variation among samples. The first and second axes accounted for 52.3% and 5.3% of species data variance, respectively. The canonical axis was also assessed as significant using the Monte Carlo permutation test ($P = 0.001$; $F_{(3,12)} = 5.782$).

On the CCA triplot (Figure 6), samples and frequent species were grouped as to differences or similarities along an environmental gradient, mostly represented by axis 1. Axis 1 of the CCA was highly influenced by electrical conductivity

and Secchi disc depth values, mirroring the gradient caused by seasonality. Axis two, on the other hand, represented mostly pH and dissolved oxygen variations.

A clear seasonality gradient represented mostly by axis 1 can be seen by a sharp differentiation of receding (even numbers) and flooding (odd numbers) samples. Species occurrence clearly reflected these distinct hydrological periods. Thus, species which occurred only during the receding phase (such as *B. zahniseri reductus* and *L. remanei*) can be seen in the right half of the chart while species which occurred during flooding (such as *B. zahniseri*, *L. proietta*, *B. gillardi* and *M. sericus* amongst others) can be observed in the left half of the chart. Additionally, frequent species throughout the entire study can also be observed, occurring in the middle of the graphic.

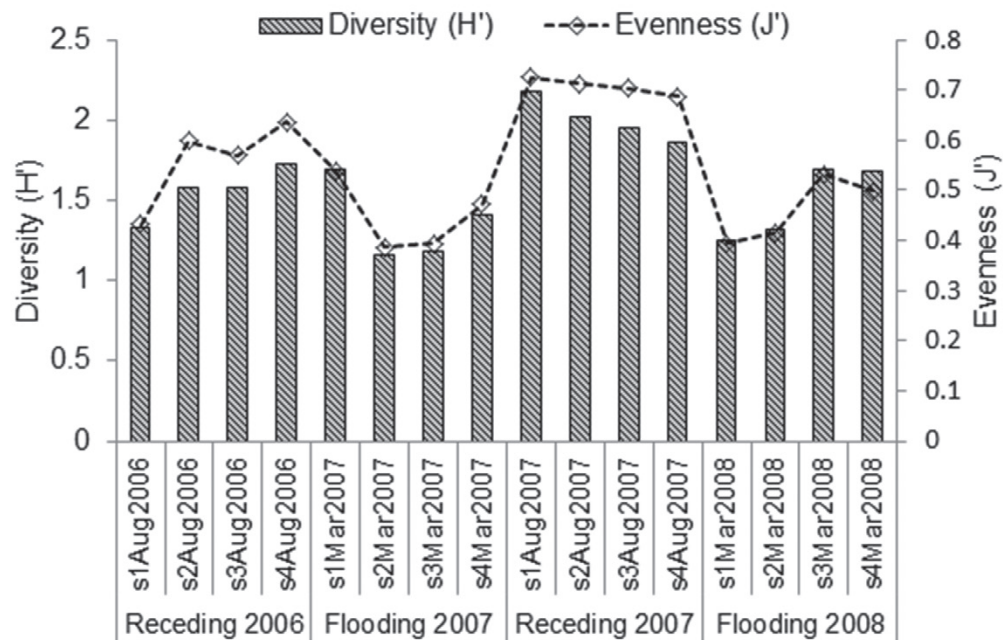


Figure 5 - Diversity (bars) and evenness (line) indexes of all sampling stations (s1, s2, s3 and s4) during the two consecutive hydrological cycles (August and March).

DISCUSSION

ROTIFER SPECIES COMPOSITION AND ABUNDANCE

Overall, our results suggest that flood events strongly influence rotifer abundance, richness and species composition through direct and indirect effects, either through the variation of physical and chemical variables, or by increasing the role of the Negro river as a source of species. Local processes, such as competition, predation, resource constraints and disturbance, mostly influence local community structure and diversity (Cottenie and Meester 2004). Thus, in our study, these local processes might be responsible for changes in species composition, together with regional processes such as dispersal - that provides movement among patches and theoretically, ongoing species turnover through extinction and recolonization (Allen et al. 2011).

Our study showed the predominance of some rotifers families, as Brachionidae, Lecanidae and

Trichocercidae, which have also been recorded throughout different studies, not only in the Amazon floodplain as in other Brazilian freshwater ecosystems (Bonecker et al. 2009, Aoyagui and Bonecker 2004, Bozelli 1992). High species richness of these three families are likely to be associated with a wide range of habitats found in the studied lake, leading to the predominance of species with different habits and niches - littoral species, pelagic and benthic.

The family Brachionidae was the most abundant and frequent taxa in our study. In this group, there was a predominance of the *Brachionus* genus, in which most of the littoral and pelagic species are commonly found in the warmer waters in the interior of the subtropical region (Kutikova and Fernando 1995). The species *Brachionus zahniseri* and *B. zahniseri* var. *reductus* were important since they had alternating patterns in their population dynamics in relation to the flood pulses. As to this marked

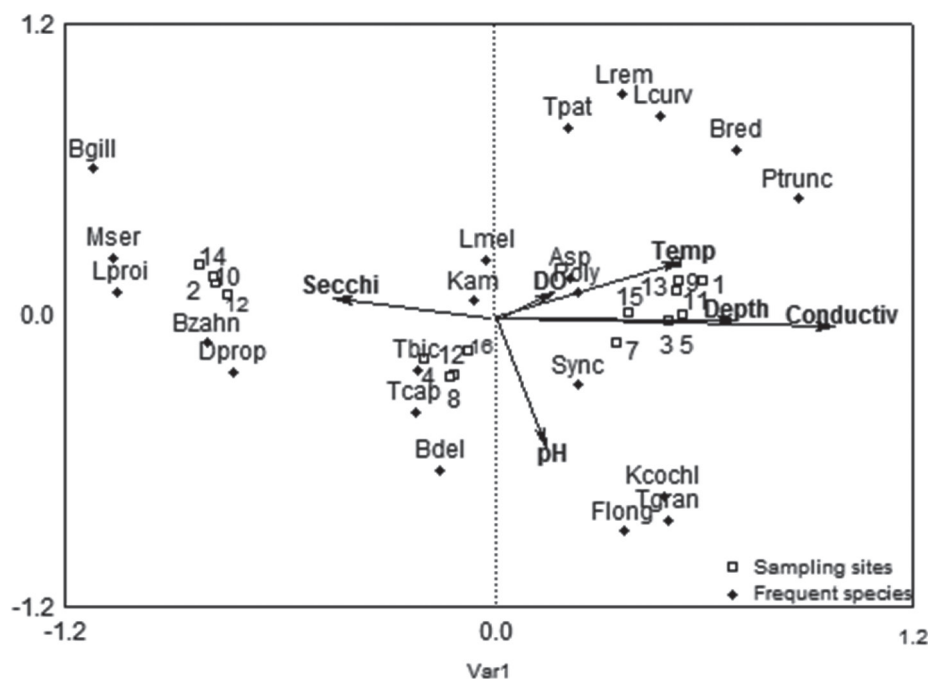


Figure 6 - CCA Ordination Diagram displaying physical and chemical variables (arrows), sampling sites (\square) and frequent species occurrence (\diamond). Numbers (1 to 16) read: **Even numbers**= Flooding of 2007 and 2008; **Odd numbers**= Receding period of 2006 and 2007; **1 to 4**= Station 1; **5 to 8**=Station 2; **9 to 12**= Station3; **13 to 16**= Station 4. Biotic variables read: **Mser**= *Macrochaetus sericus*; **Lproi**= *Lecane proicta*; **Bgill**= *Brachionus gillardi*; **Dprop**= *Dipleuchlanis propatula*; **Bzahn**= *Brachionus zahniseri*; **Bdel**= *Bdloidea*; **Tcap**= *Trichocerca capucina*; **Tbic**= *Trichocerca bicristata*; **Kam**= *Keratella americana*; **Lmel**= *Lecane melini*; **Sync**= *Synchaeta oblonga*; **Poly**= *Polyarthra* sp; **Asp**= *Asplanchna sieboldi*; **Tpat**= *Testudinella patina*; **Lrem**= *Lecane remanei*; **Lcurv**= *Lecane curvicornis*; **Flong**= *Filinia longiseta*; **Tgran**= *Trichocerca similis grandis*; **Kcochl**= *Keratella cochlearis*; **Bred**= *Brachionus zahniseri* var. *reductus*; **Ptrunc**= *Plesoma truncatum*. Physical and chemical variables: **Secchi**= transparency; **DO**= dissolved oxygen; **pH**= pH; **Depth**= total depth; **Conductiv**= electrical conductivity; **Temp**= water temperature.

population shift, it's important to emphasize that in spite of being a variation of the same species, *B. zahniseri* var. *reductus* has a larger body size and longer antero-dorsal and ventral margin spines (Koste 1978). Possible explanations for such shift in species dominance are multiple: as an example, drastic changes in environmental conditions could have caused hatching of resting eggs.

Nevertheless, unfavorable conditions can on the other hand, induce the production of resting eggs by some rotifer species (Nogrady et al. 1993), such as *B. zahniseri* and *B. zahniseri reductus*. Shiel et al. (1998) also stated the importance of resting eggs for

rotifer community structure, implying that, regardless of the dispersal mechanism, such strategy was clearly the source for colonization of ephemeral ponds, for example. In a study on Cristalino and Tarumã-Mirim lakes, Hardy (1980) also indicated a shift in *Brachionus* genera composition from one season to another. In this study, *B. zahniseri reductus* had higher contribution to the abundance of rotifers during July, while *B. gessneri* (synonym of *B. zahniseri*) was mainly important in February (Hardy 1980).

In addition, intraspecific and interspecific competition amongst rotifers, for example, might help shape rotifers community structure, and might

also be the cause for species differentiation (Snell 1978). The two different forms of the same species of *B. zahniseri*, could be looked upon as belonging to a partitioned population, therefore competition between clones might be plausible.

In the Lecanidae family, on the other hand, we can also point out two important species: *Lecane melini* - which has a small range of occurrence, being found mainly in Amazonian waters and endemic of the neotropical region (Segers 2007) - and *Lecane remanei* - first described in the waters of the Amazon (Hauer 1965, Koste 1978). *L. remanei* also showed patterns of change in its population, according to the flood pulses.

Lecane remanei and *Brachionus gillardi* were important indicators of changes in the water column. *L. remanei* was mostly present during receding water periods, while *B. gillardi* was restricted to flooding periods. Both species were dominant, together with *B. gessneri* and *L. melini*. In this case, changes in rotifers species dominance could also be explained by food quality and vulnerability to predation pressure by other organisms, such as, the rotifer *Asplanchna* sp. (Ooms-Wilms et al. 1999). Thus, interspecific competition should not be discarded specially due to differences in trade-offs between gleaner-opportunistic species in varying resources environments (Kirk 2002).

Another interesting remark, as to the rotifer composition in LARR, is the presence of *Lecane proiecta* in distinct phases of the flood pulse. *L. proiecta* is also endemic to South and Central America (Segers 2007) and has been recently found to be associated to Brazilian floodplain lakes (Bonecker et al. 2009, Joko et al. 2008). The restricted presence of *L. proiecta*, for example, in one season or another was also discussed by Ulloa (2004) who similarly found higher densities in high water seasons. On the other hand, Vásquez and Rey (1989) reported highest abundances of *L. proiecta* during the low water phase. The reason for *L. proiecta* population shift in our study is possibly due to the flooding of

the adjacent forest, small ponds and puddles which could help with the recolonization by this species. *L. proiecta* is often associated with floating-grass meadows (Koste 1978). In addition, Saunders III and Lewis Jr (1988) also indicated that the abundance of *L. proiecta* alone could suggest that off-channel habitats were important sources for the planktonic community as a whole.

Shifts in total rotifer abundance were seen in different phases and the lowest densities were observed in the receding period of 2007. Duration and strength of the flood pulse might be good explanations as to why such shifts occurred. Some authors, however, explain highest and lowest values of zooplankton abundance based on different premises (1) either being based on the dilution effect caused by the increase in water volume in high water periods (Bozelli et al. 2000) (2) or by assuming that the progressive increase in zooplankton density – from the middle-receding all the way through early-flooding periods – could be associated to the input of nutritious substances from the flooded forest (Brandorff and Andrade 1978, Carvalho 1983).

BIOTIC AND ENVIRONMENTAL INTEGRATION

Seasonality is a main factor shaping rotifers assemblage in LARR. Such marked seasonality reflected in the studied community, is associated to the flood pulse itself. As most *varzea* and shallow lakes of the river-floodplain systems, LARR has an extensive variation of the water volume during hydrological cycles. These variations are caused by the flood pulse, which is the major driving force determining productivity and community structure of aquatic organisms (Junk et al. 1989). Flooding also causes cyclical changes in abiotic variables, intimately connected to rotifer assemblage variations. For instance, input of leaves and organic matter directly into the lake during flooding, associated to decomposition processes, is probably the cause for the higher values of electrical conductivity and depth

(Thomaz et al. 1992) observed in our study in the beginning of the receding water periods, after the high water season.

Flood events also cause shifts in habitat composition and in floodplain-river systems. Thus, high diversity of habitats and species richness derived from gradients from the main channel to lateral areas, related with water current, produce a large spectrum of habitats (Roach et al. 2009). Nonetheless, Burdis and Hoxmeier (2011) specify the increase of diversity due to the presence of vegetation associated rotifers. A small spatial distinction observed in species richness – a higher number of taxa in Station 4 – could be explained by the presence of an array of habitats. Station 4 is a shallow pelagic zone influenced by the presence of a littoral zone comprised by submerged macrophytes and flooded vegetation.

Another very important feature of the studied ecosystem is the presence of humic substances, which are products of incomplete decomposition of allochthonous organic carbon. Humic substances have ecological functions mostly related to iron and phosphorus bioavailability, light penetration and most of all, pH control (Steinberg et al. 2006). Rotifers, through exhibiting a wide range of pH tolerance as a group (Berzins and Pejler 1987, 1989), might be indicators of pH variations on the water column. Some species are often associated to highly acidic environments (see review in Deneke 2000) and since this variable explained most of axis 2 of the CCA it is important to highlight its importance in shaping aquatic communities.

The influence of the hydrological regime on the composition and structure of rotifers assemblages, as well as other zooplankton groups, has also been observed in other floodplains environments (e.g. Lansac-Tôha et al. 1992, Bonecker et al. 2009, Paggi and José de Paggi 1990, José de Paggi et al. 2012, Koste and Robertson 1983, Bozelli 1992, Saunders III and Lewis Jr 1989). Lansac-Tôha et al. (2009) argued that the increase of habitat connectivity

shaped rotifers communities as an indirect effect of seasonality, and Keppeler and Hardy (2004) found correlations between electrical conductivity and rotifers abundance, as did we. Those studies restate the importance of seasonality and the flood pulse and invite us to search for patterns in these alluvial environments to further understand ecosystem functioning and structure, especially concerning their trophic relations and nutrient cycling.

In a nutshell, the flood pulse was also the main factor structuring the rotifers assemblage mainly through alterations in the electrical conductivity and water transparency between receding and flooding phases. Shifts in species dominance, diversity increase and abundance increment in the rotifer assemblage depicted the changes caused by water level fluctuation, either directly or indirectly.

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RESUMO

Os rotíferos têm sido utilizados com indicadores de mudanças súbitas de características físicas e químicas do ambiente aquático. Tais características sofrem grandes variações durante o pulso de inundação em pequenos lagos associados a planícies de inundação. No entanto, poucos estudos investigam quais são as consequências deste pulso de inundação sobre a composição, abundância, riqueza e diversidade de rotíferos, especialmente em lagos amazônicos. Neste estudo, foram analisadas amostras de um pequeno lago de águas escuras de um igarapé conectado permanentemente com o rio Negro, na Amazônia Central. As amostras foram coletadas duas vezes por ano durante dois anos, compreendendo os períodos de enchente e vazante do pulso. A abundância de rotíferos aumentou

significativamente após eventos de seca e a condutividade elétrica e a turbidez foram intrinsecamente relacionadas a esta variação. A composição de espécies também variou entre os períodos de enchente e vazante. Alguns táxons, como *Brachionus zahniseri reductus* e *Lecane remanei* foram restritos a períodos de vazante, enquanto *B. zahniseri*, *B. gillardi* e *L. proiecta* foram presentes apenas durante fases de enchente. Uma mudança na composição de famílias de rotíferos foi observada entre um período e outro, ilustrando o efeito de renovação de águas do pulso de inundação. Estes resultados sugerem que o pulso de inundação age como força direcionada e condição estressante que altera consideravelmente a dinâmica da comunidade de rotíferos, seja modificando a composição de espécies ou diminuindo sua abundância.

Palavras-chave: planície de inundação, pulso de inundação, igarapé, Rotifera, zooplâncton.

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