

Relationship between the structure of zooplankton community and the water level in a floodplain lake from the Pantanal, Mato Grosso State, Brazil

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ABSTRACT. The hydrological condition of floodplain systems alters the structure and dynamic of aquatic communities. We suggest that the structure of zooplankton community changes according to the flood phases and connectivity. This study was carried out in a floodplain lake located in the Northern Pantanal (Brazil). Zooplankton density varied considerably over time, although the sampling stations presented similar densities. The densities ranged from 2,000 ind. m⁻³ in the high water phase to more than 2,300,000 ind. m⁻³ during the low water phase when the lake remains isolated. The densities of the groups also presented a temporal variation. Rotifers described the community mainly in the low water phase and microcrustaceans during the high water phase. Variations in the total zooplankton and groups densities were significantly correlated to the PCA 1 axis (negatively composed by water depth and positively by turbidity) and to the food availability (phytoplankton).

Keywords: plankton, community structure, connectivity, floodplain lake.

RESUMO. Relação entre a estrutura da comunidade zooplanctônica e o nível da água em uma lagoa de inundação do Pantanal de Mato Grosso, Brasil. A condição hidrológica de sistemas inundáveis altera a estrutura e a dinâmica das comunidades aquáticas. Com isso, sugerimos que a estrutura da comunidade zooplanctônica se altera de acordo com as fases da inundação e conectividade. Este estudo foi realizado em uma lagoa de inundação da parte norte do Pantanal (Brasil). A densidade zooplanctônica variou consideravelmente ao longo do tempo, embora as estações amostrais apresentarem densidades similares. As densidades variaram de 2.000 ind. m⁻³ na fase de águas altas para mais de 2.300.000 ind. m⁻³ durante a fase de águas baixas quando a lagoa esteve isolada. As densidades dos grupos também apresentaram variação temporal. Os rotíferos foram relativamente mais importantes durante as águas baixas e os microcrustáceos durante a fase de águas altas. Variações na densidade do zooplâncton e grupos foram significativamente correlacionados com o eixo 1 da PCA (composta negativamente pela profundidade da água e positivamente com a turbidez) e a disponibilidade alimentar (fitoplâncton).

Palavras-chave: plâncton, estrutura da comunidade, conectividade, lagoa de inundação.

Introduction

The hydrological conditions of river-floodplain systems alters the dynamic of the biota, leading the inhabiting organisms to develop several modifications, such as population size and the ability to colonize new habitats, thus changing the structure of the aquatic communities in these environments (JUNK et al., 1989; NEIFF, 1990).

The zooplankton community, in freshwater environments, is mainly represented by Rotifera, Cladocera and Copepoda; these organisms play an important role in the energy flow and nutrient cycling

in these environments (PAYNE, 1986). Therefore, changes in the structure and dynamic of this community are strikingly relevant both for the community and for the metabolism of the entire ecosystem (LANSAC-TÔHA et al., 2004).

Many authors have argued the influence of the water level on the structure and dynamic of the zooplankton in the floodplains from the Amazon basin (ROBERTSON; HARDY, 1984; BOZELLI, 1994) and from the upper Paraná river (SENDACZ, 1997; LANSAC-TÔHA et al., 2004; BONECKER et al., 2005). These studies have shown that the flood regime changes directly (e.g., dilution effect)

and/or indirectly (e.g., food availability) the composition, dominance and abundance of the community. On the other hand, during the dry period the community recovers and the influence of local factors (e.g., competition) seems to be more important.

The connectivity among the different floodplain environments also affects the aquatic community structure (AMOROS; ROUX, 1988; WARD; STANFORD, 1995), mainly by favoring the interchange of fauna. In a river and in a connected lake from the upper Paraná river floodplain, Aoyagui and Bonecker (2004) verified that the connectivity explained more the rotifer species richness than the abundance. However, this local factor varied according to the water level and the degree of connectivity among the environments (ALVES et al., 2005). Some lakes present a wide channel to connect them to rivers or other lakes, while others are directly connected to the rivers through a narrower channel. Moreover, some environments are connected only during the flood period and this factor promotes more changes on the biota in these environments than in the other.

Although the Pantanal is one of the world's largest wetlands, little is known about the flood effect on its zooplankton community. Among the existing researches, we highlight those performed by Espíndola et al. (1996), in a lake permanently connected to the river channel, and by Neves et al. (2003), in permanently isolated lakes, which show the effect of water level fluctuation on the zooplankton composition and abundance. Different from these systems, the Coqueiro lake (local of the present study) besides being submitted to water level fluctuation, it also presents a temporary connectivity to the river channel and adjacent floodplain, which result in changes in spatial and temporal patterns of present communities (LOVERDE-OLIVEIRA et al., 2009; FANTIN-CRUZ et al., 2010). Therefore, this study analyzed the influence of the water level and connectivity on the structure and dynamic of the zooplankton community in Coqueiro lake. We assume that the density of the community and groups were closely associated to the changes in the habitat during the flood phases.

Material and methods

Study area

Coqueiro lake is located in the Pantanal of Poconé, in the Nossa Senhora do Livramento County (Mato Grosso State, Brazil), and is connected to a tributary of the Cuiabá river (Figure 1), one of the

main rivers in the Northern Pantanal. In this area, the river flows through a low lying relief, forming a fluvio-lacustrine plain subject to floods. The maximum amplitude and flood duration in the area are 2.5 m and 166 days, respectively.

The regional climate is warm and humid, with summer rainfalls and dry winter. The precipitation ranges from 800 to 1,400 mm/year, with 80% of rainfall occurring from November to March. The mean annual temperature varies between maxima of 29 to 32°C and minimum of 17 to 20°C.

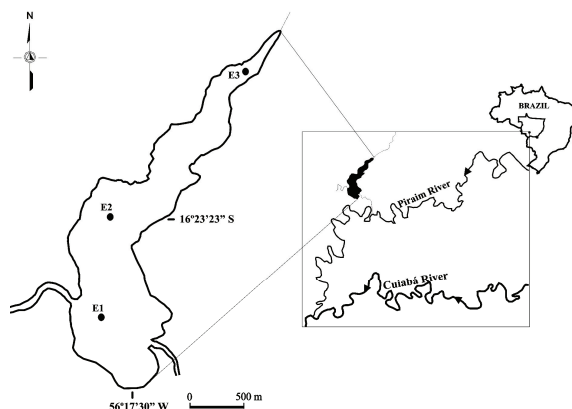


Figure 1. Location of Coqueiro lake, Pantanal of Poconé, Mato Grosso State, and sampling stations (E1, E2, E3).

The lake is elongated, covering an area of 2.2 to 2.5 km², with an average depth varying from 0.7 to 1.5 m and a volume of 1.51 to 3.64 x 10⁶ m³, during the low and high water periods, respectively. In the last period, a connection is observed between Coqueiro lake and the Cuiabá river floodplain (LOVERDE-OLIVEIRA et al., 2007; FANTIN-CRUZ et al., 2008a). The environment presents *Eichhornia azurea* and *E. crassipes* stands throughout its banks, and during the high water phase, there is temporary colonization of the *Egeria najas* (rooted submerged macrophyte) that may cover 40% of the lake (LOVERDE-OLIVEIRA, et al., 2009).

Samplings were carried out monthly from April 2002 to May 2003 at three sampling stations: E1 – the limnetic region under the influence of a channel that connects the Coqueiro lake to Piraim river; E2 – the limnetic region; and E3 – the littoral region close to aquatic macrophytes stands (Figure 1).

The lake depth (m) was measured with a limnimetric ruler. Water temperature (°C) and electric conductivity (µS cm⁻¹) were analyzed at the water subsurface of each sampling station using digital portable equipments (MC126 Mettler-Toledo), as well as pH (MP120 Mettler-Toledo), dissolved oxygen (mg L⁻¹) (MO128 Mettler-Toledo), and turbidity (NTU) (HACH 2100

turbidimeter). Using sterilized polyethylene flasks (1000 mL), water samples were also taken under the water surface of each sampling station for the analyses of total phosphorus and chlorophyll-*a*. These samples were maintained on ice, afterwards in the laboratory they were filtered (Whatman GF/C membranes). Total phosphorus ($\mu\text{g L}^{-1}$) was analyzed through the spectrophotometric method (GOLTERMAN et al., 1978; MACKERETH et al., 1978). Chlorophyll-*a* ($\mu\text{g L}^{-1}$) was extracted with ethanol and analyzed according to Nusch and Palme (1975).

Zooplankton samples were taken at the water subsurface of each sampling station using a manual suction pump (100 liters per sample) and the material was filtered through a plankton net (68 μm), and preserved in formaldehyde (4%) buffered with calcium carbonate. In the laboratory, Rotifera, Cladocera and Copepoda species were quantified from subsamples (1 mL). A minimum of 250 individuals were quantified per sample, and the number of subsamples was determined according to the variation coefficient of $< 20\%$ between them. Whenever were found, the entire sample was quantified. Samples with low number of individuals were integrally counted.

ANOVA (two-way) was applied to evaluate whether the total zooplankton and groups densities differed significantly among the sampling stations and the flood phases. The assumptions (homoscedasticity and normality) were previously tested and the density data were transformed into $\log_{10}(x+1)$. The significance level considered in the analyses was 0.05.

The abiotic variables and chlorophyll-*a* concentration were employed in a Principal Component Analysis (PCA) to characterize the spatial and temporal variation of the data. The data were transformed into $\log_{10}(x+1)$, except the pH. The axes were retained for interpretation when their eigenvalues were > 1.0 , according to the Kaiser-Guttman criterion (JACKSON, 1993). The limnological variables that presented a correlation coefficient of > 0.70 were considered as important variables explaining the spatial and temporal variation.

Pearson Correlation Analysis was employed to evaluate the influence of the limnological variables (PCA axes scores) and food availability (chlorophyll-*a* concentration) on the total zooplankton and group densities. The significance level considered in the analyses was $p < 0.05$.

Results

Fluviometric level and limnological variables

From the prediction that the flood and the connectivity are the main responsible for the

changes in the habitat and, consequently, in the communities, three flood phases were determined according to the water level variations of Cuiabá river and Coqueiro lake, and the connection between the lake and the river channel: phase I (falling, April to June 2002); phase II (low water, July to December 2002); and phase III (rising and high water, January to May 2003; Figure 2).

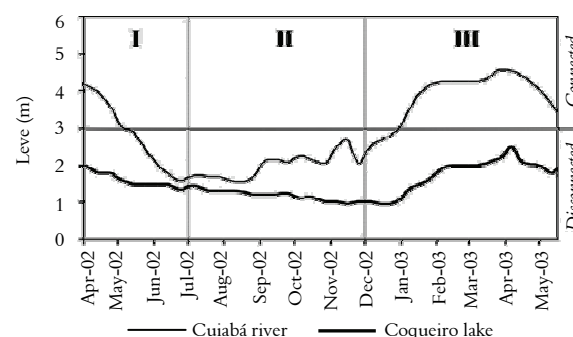


Figure 2. Water level variation of Cuiabá river and Coqueiro lake (m), and duration of the river-lake connection during the sampling periods (I-falling; II-low water; III-rising and high water; Source: modified from Loverde-Oliveira et al. (2007)).

The limnological variables and chlorophyll-*a* concentration presented a temporal variation: phase I – low values of dissolved oxygen; phase II – higher concentrations of phosphorus, chlorophyll-*a* and turbidity (about 80% of inorganic matter and 20% of organic matter, in agreement with Loverde-Oliveira et al. (2009)), and shallower depths; phase III – reduced turbidity, deeper depths and higher values of electric conductivity (Table 1).

Table 1. Mean values of limnological variables, chlorophyll-*a* concentration and zooplankton abundance for each sampling station (E1, E2, E3) and flood phases (I – falling, II – low, III – rising and high water).

Variables	Station			Phases		
	E1	E2	E3	I	II	III
Water temperature ($^{\circ}\text{C}$)	27.9	27.7	27.7	26.4	28.5	28.1
Maximum depth - z_{max} (m)	1.5	1.6	1.2	1.5	1.0	1.9
Turbidity (NTU)	28	30	17	26	37	8
Electrical conductivity ($\mu\text{S cm}^{-1}$)	30	26	22	26	23	30
pH	5.9	6.3	5.4	5.8	6.2	5.4
Dissolved oxygen (%)	41	41	13	21	37	37
Total phosphorus ($\mu\text{g L}^{-1}$)	222	309	190	204	283	223
Chlorophyll- <i>a</i> ($\mu\text{g L}^{-1}$)	26	24	16	16	39	6
Total zooplankton (ind. $\text{m}^{-3} \times 10^3$)	394	311	305	112	637	111
Rotifera (ind. $\text{m}^{-3} \times 10^3$)	238	198	211	19	469	31
Cladocera (ind. $\text{m}^{-3} \times 10^3$)	75	57	18	53	52	46
Copepoda (ind. $\text{m}^{-3} \times 10^3$)	81	54	75	39	116	33
Nauplii (ind. $\text{m}^{-3} \times 10^3$)	50	31	66	27	86	19
Cyclopoida						
Copepodids (ind. $\text{m}^{-3} \times 10^3$)	17	12	3	3	16	9
Adult (ind. m^{-3})	3665	2539	617	637	3037	2340
Calanoida						
Copepodids (ind. $\text{m}^{-3} \times 10^3$)	6	5	3	3	8	2
Adult (ind. m^{-3})	3824	3500	1047	5726	3421	272

Principal component analysis

The PCA results pointed out that the first three axes (eigenvalues > 1.0) explained 73.75% of total data variability. PCA1 (33.62%) was negatively correlated to depth and positively to turbidity, while PCA2 (24.73%) was positively correlated to dissolved oxygen, and PCA3 (15.28%) was negatively correlated to water temperature. Only these variables presented a correlation coefficient > 0.70 associated to the respective axes (Table 2). These results indicate that PCA1 reflected the seasonal variation of the data, since water level was one of the most important variables compounding this axis. We also found that the turbidity varied inversely with water depth, a variation that represents the two extremes of the flood phases.

Table 2. PCA results from the limnological variables studied in Coqueiro lake between April 2002 and May 2003. Bold values represent the variables that contributed to the axes formation ($cv > 0.70$).

Variables	PCA 1	PCA 2	PCA 3
Depth	-0.790	0.370	0.172
Water temperature	0.027	0.348	-0.842
Dissolved oxygen	0.330	0.796	0.140
pH	0.582	0.444	0.378
Electrical conductivity	-0.408	0.674	0.181
Turbidity	0.881	-0.209	0.198
Total phosphorus	0.582	0.381	-0.358
Explained (%)	33.62	24.73	15.29

Relative abundance

The relative abundance evidenced a great change in the community structure during the flood phases. The highest contribution came from microcrustaceans especially in phases I and III (48–42% cladocerans and 35–30% copepods, respectively), whereas rotifers contributed to the relative abundance mainly during the phase II (74%) (Figure 3).

Density

The lowest densities of zooplankton were recorded in phases I and III when Coqueiro lake was connected to the river channel (12,000 ind. m^{-3} at station E1 in April 2002; 2,000 ind. m^{-3} at station E2 in March 2003; and 5,000 ind. m^{-3} at station E3 in April 2002 and 2003). Otherwise, higher densities were registered when the lake became shallower and isolated during the phase II, with peaks in November at stations E2 and E3 (1,316,000 ind. m^{-3} and 2,385,000 ind. m^{-3} , respectively) and in December at station E1 (1,200,000 ind. m^{-3}) (Table 1 and Figure 3).

The density of total zooplankton, rotifer and copepod differed significantly among the flood phases, but no significant differences were found among the sampling stations (Table 3). Considering the mean densities of zooplankton (months and stations) in the different flood phases, the water volume of the lake increased 130% in the phase III and zooplankton density decreased 83%.

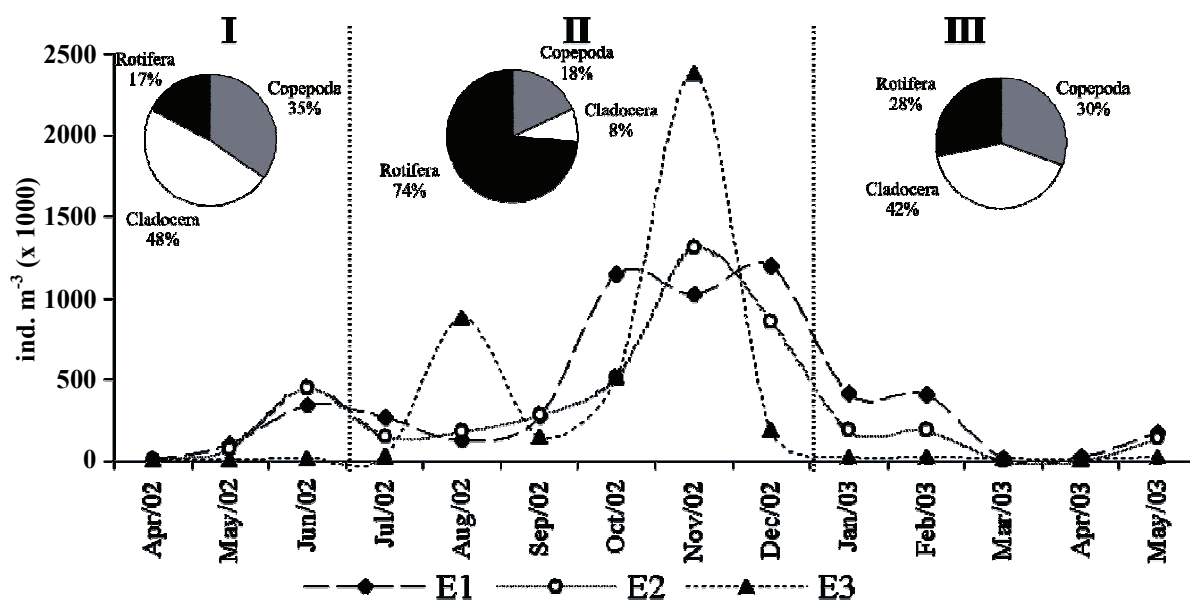


Figure 3. Relative abundance (%) of Rotifera, Cladocera and Copepoda and total zooplankton density (ind. m^{-3}) during the flood phases (I- falling, II- low water and III -rising and high water) at the sampling stations located in Coqueiro lake (E1, E2 and E3).

Table 3. ANOVA results for the density of zooplankton and different groups for sampling phases and sampling stations. Bold values indicate significant variations ($p < 0.05$).

Effect/Groups	GL	F	P
Zooplankton			
Station	2	1.268	0.293
Phase	2	13.274	<0.001
Rotifera			
Station	2	0.848	0.436
Phase	2	18.093	<0.001
Cladocera			
Station	2	1.992	0.150
Phase	2	2.044	0.141
Copepoda			
Station	2	1.914	0.161
Phase	2	9.848	<0.001

Rotifer densities were also higher during the lake isolation (phase II), showing a maximum value at station E3 (1,935,000 ind. m^{-3}) in November and lower densities during phase III, mainly at station E2 (507 ind. m^{-3}) in April 2003 (Table 1 and Figure 4a).

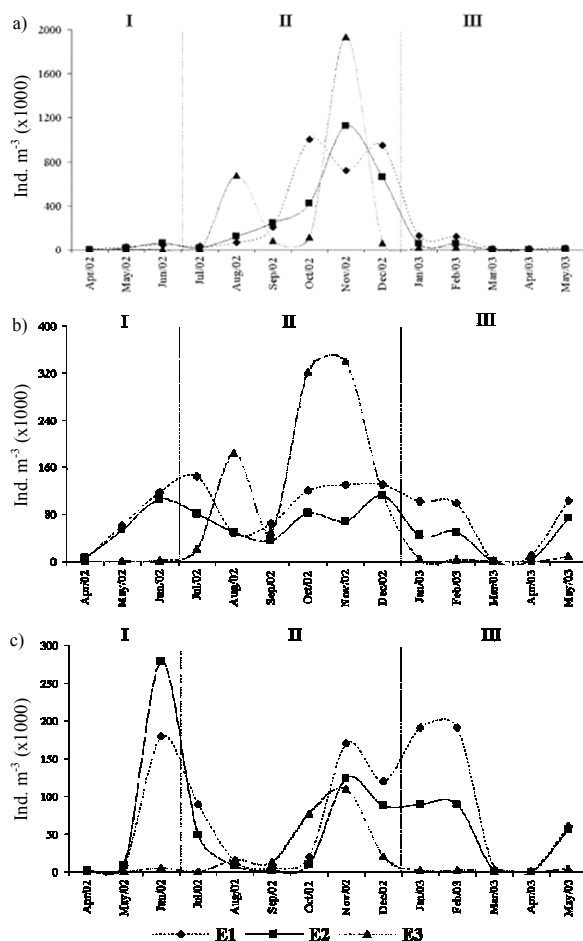


Figure 4. Density of Rotifera (a), Copepoda (b), and Cladocera (c) during the flood phases (I- falling, II- low water and III -rising and high water) at the sampling stations in Coqueiro lake (E1, E2 and E3).

Copepods represent the second most important group regarding the number of individuals and, like

the rotifers, they presented higher densities in the phase II, with maximum density at station 3 (340,000 ind. m^{-3}) in November. Low number of organisms was observed in this same sampling station (160 ind. m^{-3}) in April 2003, during the phase III (Table 1 and Figure 4b).

The relative abundance of the development stages from Copepoda showed a different contribution during the flood phases. In both groups (Cyclopoida and Calanoida), nauplii were the most representative stage, especially in the phase II. Cyclopoida copepodids and adults were relatively important in the phase III and these stages of Calanoida presented a greater contribution during the phase I, mainly adults (Table 1 and Figure 5).

Cladocerans were the least abundant group, presenting highest densities during the intermediate periods between the flood phases (Figure 4c). This fact was corroborated by the absence of significant differences in density values among the phases (Table 3). Both the highest and lowest densities were recorded in the phase I at station E2 (278,250 ind. m^{-3} , June 2002) and at station E3 (47 ind. m^{-3} , April 2002), respectively (Figure 4c).

Pearson Correlation

Pearson Correlation Analysis revealed significant positive correlations between total zooplankton, rotifer, cladoceran and copepod densities with PCA1 (represented negatively by depth and positively by turbidity) and chlorophyll-*a* (Table 4). Independently of the group, higher densities were found at shallow depth and high turbidity, and high food availability. Among these groups, rotifers presented the highest correlation coefficient, indicating that this group is the most sensitive in relation to the hydrological regime and limnological conditions of the lake.

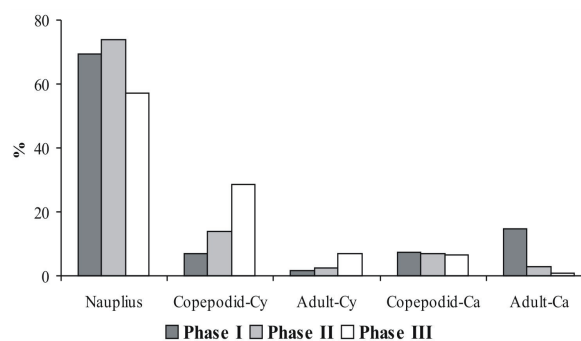


Figure 5. Relative abundance of development stages from Copepoda (Cy - Cyclopoida; Ca - Calanoida) during the flood phases (I- falling, II- low water and III -rising and high water) at the sampling stations in Coqueiro lake (E1, E2 and E3).

Table 4. Pearson correlation between total and zooplankton group densities and PCA axes and chlorophyll-*a* concentration. Bold values indicate significant correlations ($p < 0.01$).

Variables	PCA1	PCA2	PCA3	Chlorophyll- <i>a</i>
Total zooplankton	0.78	0.16	0.07	0.67
Rotifera	0.84	0.08	-0.11	0.70
Cladocera	0.49	0.20	0.20	0.38
Copepoda	0.64	0.23	0.19	0.61

Discussion

The floodplain hydrological regime is responsible for the temporal patterns of aquatic communities in the environments due to the variation in the limnological features and spatial heterogeneity (degree of connectivity between the habitats). These effects also influence the biotic relationships among the communities (AMOROS; ROUX, 1988; JUNK et al., 1989; NEIFF, 1990; WARD; STANFORD, 1995).

The low densities of zooplankton observed during the phases I and III were related to the dilution effect (BOZELLI, 1994; ESPÍNDOLA et al., 1996) and the consequent loss of individuals from the lake to the river. In addition, an increase in the lake volume was verified during these phases due to the marginal overflow, which also promoted an increase in habitat availability for the individuals' colonization. Furthermore, deeper depths of the lake during the phases I and III reduced the wind effect on the water column circulation and the sediment was trapped at the bottom of the lake. In the absence of re-suspended sediment, the nutrients were also trapped, the water transparency increases and chlorophyll-*a* concentrations decreases, suggesting a reduction in the food availability for zooplankton. The ANOVA results evidenced the significant variation in zooplankton density among the flood phases, while the correlation results indicated that zooplankton densities varied inversely to the lake depth.

The absence of significant differences in the total zooplankton and group densities among the sampling stations may be associated to the homogenization of the water column, consequence of wind effects during phase II; and to flooding during phase I and III. Loverde-Oliveira et al. (2009) found a similar pattern: she did not found significant differences in phytoplankton biomass and density and in limnological variables among sampling stations and in the vertical water column in the studied lake, corroborating our results. Thomaz et al. (2007) showed that the homogenization effect in the flood phase is a strong discriminating factor on the structure and dynamics of aquatic community and limnological characteristics.

On the other hand, higher densities were observed in the phase II. During this phase, the lake was shallower and presented higher turbidity values (suspended inorganic matter predominated in the water column) and chlorophyll-*a* concentration when compared to the phases I and III. This increase in suspended inorganic matter may act as substrate for bacteria colonization (LIND et al., 1997), which may supply further food resource for some zooplanktonic organisms. Meantime, at high concentrations, it may create negative effects on the community, as recorded by Bozelli (1994) in an Amazon lake impacted by bauxite tailings. In general, studies performed in Brazilian floodplains relate the turbidity to the availability of food resource for the zooplankton, due to the association with bacteria (CARVALHO, 1983; ESPÍNDOLA et al., 1996; ULLOA, 2004).

The body size structure of the organisms from the zooplankton community had also changed among the flood phases. During phase II, there was a predominance of small-sized individuals (rotifers), while large-sized individuals (copepods and cladocerans) were relatively important in the phases I and III. Studies carried out by Espíndola et al. (1996) and Neves et al. (2003) in Pantanal lakes also registered an increase in the proportion of microcrustaceans during the high water phase when compared to the low water phase.

These results could be related to the intensity of biotic interactions resulting from flooding and connectivity between the lake and the river. In general, fish predation is more efficient on cladocerans and copepods (ZARET, 1980). However, predation pressure varies according to the habitat size, which leads to the assumption that, during the phase II when the lake is isolated, predation on microcrustaceans is much higher than in the phase I and III when the lake does not present defined limits. This hypothesis corroborates the results verified by Ximenes et al. (2011) in marginal lakes from Cuiabá river (Pantanal/Mato Grosso State) that observed a reduction from 67 to 42% in the contribution of microcrustacean (cladoceran and copepods) in the feeding of zooplanktivorous fish, between the low and high water periods. In this same region, Fantin-Cruz et al. (2008b) also registered the negative effect of the fish abundance on the microcrustacean density, relating this result to the habitat size.

In mesocosm experiments in a lake in the Pantanal, Paiva (2007) found an alteration in the proportion of representatives of the zooplankton community, with a decrease in the proportion of rotifers and an increase in the proportion of

cladocerans and copepods in treatments with fish exclusion when compared to the control (samples taken from the lake). Therefore, the structure of the zooplankton community during the low water period was controlled by this biotic interaction between the communities (predation).

The rotifer predominance in the phase II was also directly and significantly correlated to the chlorophyll-*a* concentration and to turbidity and inversely to the lake depth. Several authors have argued the importance of phytoplankton as source of food for rotifers in freshwater environments (AOYAGUI; BONECKER, 2004; AGASILD; NÓGES, 2005).

Besides that, during the phase II, the environment presented low variability compared to the river when considering the flow, due to the absence of connection between the lake and river and the dilution effect. In studies about rotifers in different environments from the upper Paraná river floodplain, Aoyagui and Bonecker (2004) also observed high density of this group in lakes that are isolated during low water, attributing this factor to the absence of connectivity and to the low current flow.

Regarding the copepods, the predominance of nauplii (young stages) over adults within the community is a common pattern in floodplains (PAGGI; JOSÉ DE PAGGI, 1990; NEVES et al., 2003; LANSAC-TÔHA et al., 2004). This fact may result from the continuous reproduction of these organisms, as well as the greater predatory pressure of invertebrates and vertebrates on adults rather than on nauplii (DUMONT et al., 1994).

The greater relative contribution of Cyclopoida adult (mainly *Mesocyclops longisetus curvatus*) observed at phase III may also be related to the presence of submerged macrophytes, since these organisms are commonly found associated with aquatic macrophytes in floodplain lakes (PAGGI; JOSÉ DE PAGGI, 1990). Otherwise, Calanoida adult (mainly *Notodiaptomus amazonicus*) predominated during the phase I, which may be attributed to the low concentration of food and to fish predation. This group is comprised by excellent filter-feeding organisms (ALLAN, 1976), and the lower concentration of chlorophyll-*a* in this phase may have favored these copepods.

Cladoceran densities did not show a clear pattern of temporal variation according to the flood phases, but the densities were directly and significantly related to turbidity and chlorophyll-*a* concentration and inversely to the lake depth, as observed in the other groups. Nevertheless, the food resource availability seems not to be the most important

controlling factor on the population densities because phytoplankton biomass and turbidity (representing the bacterial biomass, as discussed above) were high in the low water phase and cladoceran densities were higher between the flood phases (at the end of the falling water phase and the beginning of the rising phase).

The competition between rotifers and these microcrustaceans was not considered since the most abundant cladocerans were larger (*Ceriodaphnia cornuta*, *Diaphanosoma birgei* and *Moina minuta*) than the most abundant rotifer species (*Lecane proicta*, *Brachionus falcatus*, *B. mirus*, *B. dolabratus*, *B. caudatus*, *Filinia longiseta* and *Keratella americana*). This difference promotes the exploitation of different size of food particles.

Conclusion

As reported in this paper, the zooplankton community may suffer the influence of many abiotic (hydrological regime and turbidity) and biotic factors (algal biomass), as well as by the complex interactions among these factors. The zooplankton community from Coqueiro lake presented remarkable temporal variations in density and structure. These variations were associated with temporal fluctuations in the depth of the water column, which give rise to hydrological connectivity. This connectivity leads to the dilution and homogenization of the organisms' density, the creation of new habitats, and changes in predator-prey relationships, among other aspects. However, according to Shiel et al. (2006), it is difficult to distinguish the effects of seasonal variations from other abiotic and biotic factors that act concomitantly upon the community.

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