Acta Limnologica Brasiliensia

Publication of the Brazilian Association of Limnology

Thematic Section: Upper Paraná River Floodplain

Acta Limnologica Brasiliensia, 2017, vol. 29, e101
http://dx.doi.org/10.1590/S2179-975X10816
ISSN 2179-975X on-line version

Structure and dynamic of planktonic ciliate community in a large Neotropical river: the relevance of the pluviosity and tributaries in the biodiversity maintenance

Estrutura e dinâmica da comunidade de ciliados planctônicos em um grande rio Neotropical: a relevância da pluviosidade e tributários na manutenção da biodiversidade

Orlando Pelissari Negreiros[1], Bianca Trevizan Segovia[1], Fernando Miranda Lansac-Tôha[1], Bianca Ramos de Meira[1], Paulo Roberto Bressan Buosi[1], Adalgisa Fernanda Cabral[1,2], Heloisa Santos Silva[1], Fábio Amodêo Lansac-Tôha[1] and Luiz Felipe Machado Velho[1,3]*

[1]Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais – PEA, Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura – Nupelia, Departamento de Biologia, Universidade Estadual de Maringá – UEM, Av. Colombo, 5790, CEP 87020-900, Maringá, PR, Brazil

[2]Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Goiás – UFG, Campus 2, Rodovia Goiânia-Nerópolis, Km 5, Itatiaia, CEP 7400-1970, Goiânia, GO, Brazil

[3]Programa de Pós-graduação em Tecnologias Limpas, Instituto Cesumar de Ciência, Tecnologia e Inovação – ICETI, Centro Universitário Cesumar – Unicesumar, Av. Guedner, 1610, CEP 87050-900, Maringá, PR, Brazil

*e-mail: felipe.velho@gmail.com

Cite as: Negreiros, O.P. et al. Structure and dynamic of planktonic ciliate community in a large Neotropical river: the relevance of the pluviosity and tributaries in the biodiversity maintenance. *Acta Limnologica Brasiliensia*, 2017, vol. 29, e101.

Abstract: Aim: We investigated the spatial and temporal patterns of abundance and diversity of planktonic ciliate community, in the last undammed stretch of the Upper Paraná River, Brazil. **Methods:** In order to reach this result, seven field campaigns were performed over two years. Plankton samples were collected from 10 transects through this stretch of the river (230 Km), near the banks and on the center, as well on seven of its tributaries. **Results:** 118 ciliate species were identified, among which the peritrichs were the most abundant while the order Hymenostomatida was the most specious group. We recorded a remarkable increase in abundance and species richness along the river, especially in the rainy period. Moreover, in this period we found an increase in the beta-diversity along the river, which consists in a remarkable distinction among the low, middle and high stretch of the river. In this way, continuous changes in the community structure of planktonic ciliates were evidenced, highlighting the importance of the precipitation and tributaries in the maintenance of the highest regional diversity in the studied area. **Conclusion:** Our results strongly suggest the requirement for conservation actions with the purpose to maintain those tributaries undammed, in order to avoid biotic homogenization processes and the consequent reduction of aquatic biodiversity in this important neotropical ecosystem.

Keywords: Protist; Ciliophora; abundance; species richness; lotic environments.

Resumo: Objetivo: Investigaram-se no presente estudo os padrões espaciais e temporais da abundância e diversidade de espécies da comunidade de ciliados planctônicos, no último trecho livre de barramentos da planície de inundação do alto rio Paraná, Brasil. **Métodos:** Sete amostragens foram realizadas no período de dois anos. Amostras de ciliados foram coletadas ao longo de 10 transectos deste rio (230 Km), nas margens e no centro, bem como em sete de seus tributários. **Resultados:** Cento e dezoito espécies foram identificadas, dentre as quais, a ordem Peritrichia foi a mais abundante e Hymenostomatida a mais especiosa. Foi evidenciado um aumento na abundância e riqueza de espécies ao longo do rio, especialmente no período chuvoso. Além disso, neste período foi registrado um incremento da diversidade beta ao longo do rio, consistindo em uma grande diferença entre os trechos a montante, intermediário e jusante da área de estudo. Assim, a gradativa alteração na estrutura da comunidade de ciliados evidenciou uma grande influência das chuvas e dos tributários na manutenção da alta diversidade regional no trecho estudado. **Conclusão:** Os resultados evidenciam a necessidade de ações de conservação com o intuito de preservar os tributários livres de barramentos, a fim de evitar processos de homogeneização biótica e a consequente redução da biodiversidade aquática neste importante ecossistema neotropical.

Palavras-chave: Protista; Ciliophora; abundância; riqueza de espécies; ambientes lóticos.

1. Introduction

In continental aquatic ecosystems, biodiversity is affected by the geographical variation in fluvial processes and modifications due to disturbance regimes, such as hydrological retention, connectivity, geomorphological complexity and nutrient input, both from the riparian zone and from the river basin (Poff et al., 2007; Thorp et al., 2008). In river-floodplain systems, changes in the hydrological regime (floods) are considered the main driving forces affecting biodiversity (Thomaz et al., 2007). During floods, floodplain habitats are highly connected, causing intensive changes between the main river course and adjacent environments, reflecting in the abiotic and biotic factors of the system (Junk et al., 1989; Agostinho et al., 2004; Thomaz et al., 2007; Bozelli et al., 2015). Even considering environments other than floodplains, rainfall and drought regimes promote expressive changes in the habitats, evidencing differences in the structure of communities present in those systems (McCabe & Wolock, 2002; Velho et al., 2003)

However, despite the substantial effects that alterations in hydrological regime exert in those ecosystems (sensu Neiff, 1990; Ward et al., 1999), anthropogenic impacts, such as processes associated with dam construction, have been responsible for the major modifications observed in continental aquatic ecosystems (Agostinho et al., 2008; Souza Filho, 2009). In this way, the interruption of the natural river course results in alterations in the physical and chemical characteristics of the water, and stablishes a barrier for species dispersal promoting biotic homogenization, since this barrier favours the establishment and dominance of cosmopolitan invasive species over native ones (Power et al., 1996; Richter et al., 1998). It is noteworthy that the impact caused by dams may extend over distances of hundreds of kilometers (Poff et al., 2007).

Accordingly, Porto Primavera damming (PR, Brazil) resulted in modifications in the natural river processes, both downstream and upstream of the reservoir. Among these alterations, a great reduction in the amplitude of flood pulses in the Upper Paraná River floodplain was verified (Agostinho et al., 2002), as well as variation in water characteristics, such as a gradual reduction of total phosphorus load and continuous increase in water transparency in the main river course and adjacent environments downstream (Souza-Filho & Stevaux, 2004; Roberto et al., 2009). In this context, besides the river-floodplain interactions, the contribution of tributaries for the longitudinal gradient of the river regarding the structure of aquatic communities is also relevant, considering that those tributaries contribute to the input of organic and inorganic particulate matter (Stanford & Ward, 2001). This contribution causes a greater variation and heterogeneity in these confluence zones, thus minimizing the effects of dam control on river flow rates, besides supporting the maintenance of diversity in rivers impacted by those constructions (Agostinho et al., 1997; Benda et al., 2004; Braghin et al., 2015). Therefore, the prominent role of distinct lotic environments in the ecosystems is evident, considering that they act as a link among the different compartments of the system, promoting the distribution and propagation of aquatic organisms, affecting local diversity and, consequently, regional diversity of those communities (Rice et al., 2001; Poff et al., 2007).

Among the aquatic communities, ciliates play an important role in aquatic ecosystem dynamics, due to their small size, rapid life cycle and high metabolic rates (Fenchel, 1982). Ciliates feed on bacteria, cyanobacteria, phytoplankton and other protists (Weisse, 2002; Sherr & Sherr, 2002), and constitute important prey for microcrustaceans (Stoecker & Capuzzo, 1990) and rotifers (Arndt, 1993). Thus, ciliates are recognized as key components in planktonic communities, representing a relevant trophic link between microbial and classical food chains (Mironova et al., 2012) and constituting significant nutrient remineralizers (Beaver & Crisman, 1989) However, despite the recognized importance of these protists in the microbial food webs (Pomeroy, 1974; Azam et al., 1983), few studies were performed in lotic ecosystems, specially aiming to evaluate factors influencing community structuring in those environments (Sola et al., 1996; Scherwass et al., 2010; Kiss et al., 2009).

We investigated the contribution of tributaries associated with the Paraná River in the maintenance of ciliate diversity in this system, in two distinct periods (rainy and drought) in the last non-dammed stretch of the river in Brazilian territory, between the Porto Primavera (SP) and Itaipu (PR) dams. We hypothesized that the physical and biological processes occurring in the tributaries, together with the contribution of rainfalls as a dispersal factor, would be sufficient to maintain the species pool and to increase biotic heterogeneity in the Paraná River, resulting in longitudinal alterations of the ciliate community structure and consequently in a high regional diversity in this region. In this context, we expected i) differences in ciliate community composition between the river stretches; ii) a higher richness and abundance of ciliates in the downstream stretch; iii) an increase in ciliate diversity from downstream Porto Primavera to upstream Itaipu, due to the contribution of tributaries, which constitute a source of species to the Paraná River, supporting the maintenance of diversity and biotic heterogeneity in this important aquatic ecosystem; iv) rainfalls are of great importance for dispersal processes of ciliate species, determining an increase in the regional diversity of the main river during the rainy season.

2. Methods

2.1. Study area

The study was performed at the Upper Paraná River floodplain system (Figure 1), in the border of Mato Grosso do Sul and Paraná states. It covers 230 km extension of a non-dammed stretch of the Paraná River, between downstream of Porto Primavera hydroelectric power station and upstream of Itaipu hydroelectric power plant, comprising several secondary channels, lakes and rivers (Souza-Filho & Stevaux, 2004). This area encompasses several conservation units, such as the Ilha Grande National Park, which comprises several islands and constitutes an area of limited anthropogenic activity.

Besides the Paraná River, seven tributaries located along this stretch were analysed (Paranapanema, Baía, Ivinhema, Ivaí, Amambai, Iguatemi and Piquiri rivers). Both Paraná and Paranapanema rivers are impacted by damming.

2.2. Sampling and laboratory analysis

Samples were taken during two distinct hydrological periods – four campaigns in the rainy period (October 2013, February and November 2014, and February 2015) and three in the dry period (August 2013, May and August 2014), along 10 line transects at the Paraná River, with three sampling sites per transect (right margin, centre and left margin), and at seven tributaries. Important limnologic variables affecting the ciliate community were measured: water temperature (°C), dissolved oxygen (mg/L; YSI 550A digital portable oximeter), pH, conductivity (μS/cm; portable potentiometer), total nitrogen (μg/L; Mackereth et al., 1978) and total phosphorus (μg/L; Golterman et al., 1978), water transparency (m; Secchi disk) and depth (m).

Samples for ciliate analysis were taken at the subsurface (10-20 cm below the air-water interface). In the field, 50 L of water were concentrated in to 5 L flasks using 10 μm plankton net, and kept cool in a thermal box. At the laboratory, the 5 L sample was again concentrated to 100 mL using the same 10 μm plankton net and the ciliates were analysed *in vivo* by counting 10 aliquotes of 100μl (Madoni, 1984). Identification was performed using an optical microscope (Olympus CX-41) at a magnification of 100-400×, based mainly on the work of Foissner & Berger (1996) and Foissner et al. (1999).

2.3. Data analyses

A Permutational Multivariate Analysis of Variance (PERMANOVA, McArdle & Anderson, 2001) was performed using presence/absence matrices to test for differences in ciliate composition among stretches (upstream, middle and downstream) in the Paraná River and tributaries.

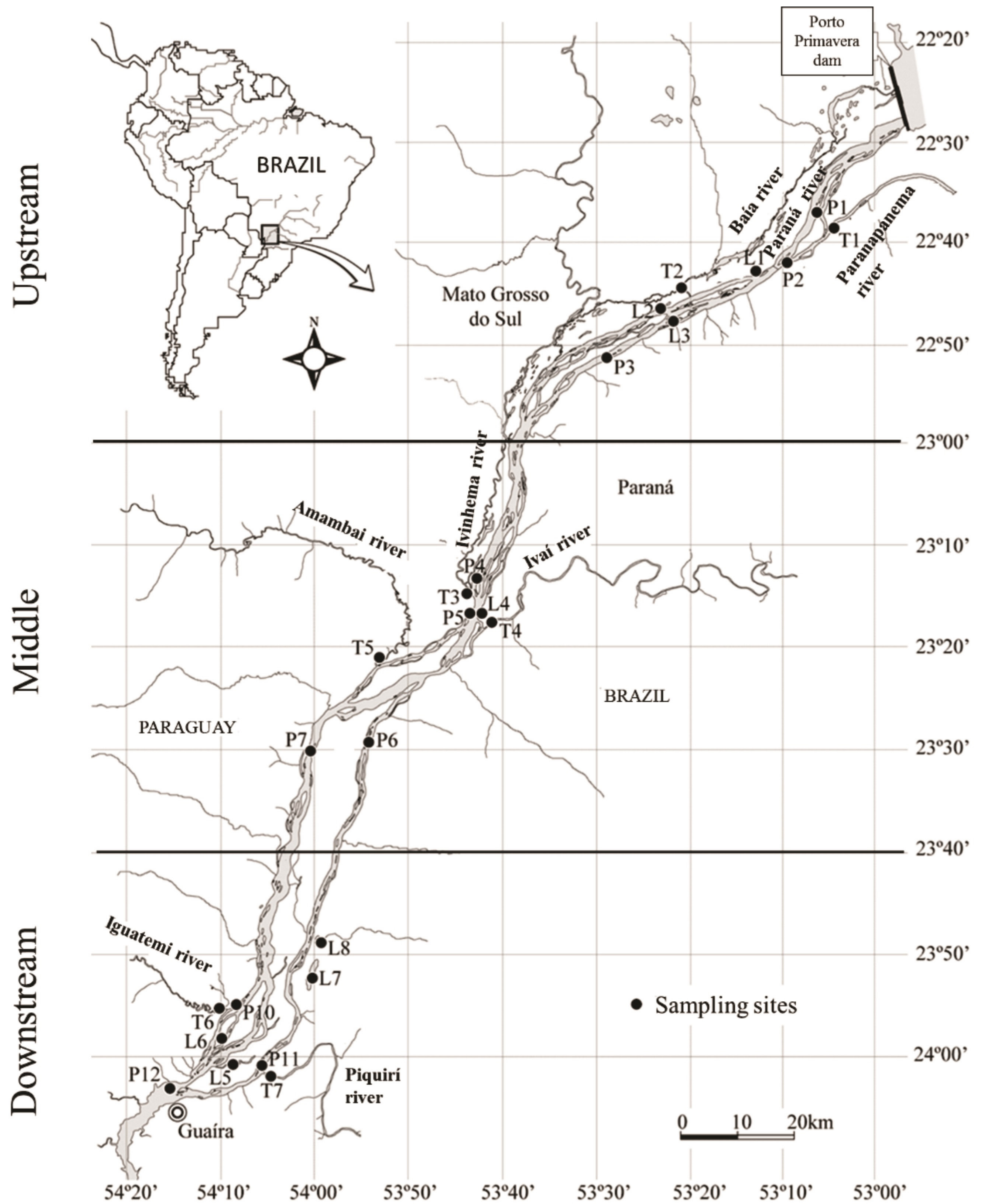

Figure 1. Map of the study area showing the sampling sites in the Paraná River and tributaries.

To evaluate the local contribution of each tributary to the regional composition we performed tests for the homogeneity of multivariate dispersions (PERMDISP, Anderson, 2006), which stablishes unique centroids for each level in each factor along the river. From the centroid positions, this analysis uses the variation in the multidimensional space within each group and among groups.

A Redundancy Analysis (RDA) was performed to examine the relationship between ciliate community structure and the set of explanatory variables, using multiple linear regressions of the ordination scores against environmental variables. Significance of the analysis was tested through permutation tests and significance of RDA axis was tested using ANOVA.

Analyses were performed using software R version 3.0 (R Development Core Team, 2012) and package *vegan* (Oksanen et al., 2011).

3. Results

3.1. Composition of planktonic ciliate species

A total of 117 taxa of planktonic ciliate species were registered in the Upper Paraná River Floodplain and its tributaries between August 2013 and May 2015 (Table 1).

The ciliate species belong to 13 orders, and Hymenostomatida was the most representative

Table 1. Ciliate species list recorded in distinct environments – main river and tributaries – of the Upper Paraná River Floodplain, between 2013 and 2015.

		RIVER			TRIBUTARIES		
		U	M	D	U	M	D
COLPODIDA	*Colpoda inflata*			X			
	C. steinii			X			
	Cyrtolophosis mucicola	X	X	X			
CYRTOPHORIDA	*Chilodonella uncinata*	X		X	X	X	
	Odontochlamys alpestris		X				
	Pseudochilodonopsis sp.	X		X			
HAPTORIDA	*Actinobolina* sp.	X					
	Actinobolina vorax				X		
	Askenasia volvox		X				
	Cyclotrichium viride	X	X			X	
	Enchelys gasterosteus		X	X			X
	Lagynophrya acuminata		X	X	X		
	Mesodinium pulex	X		X		X	X
	Monodinium sp.				X		
	Paradileptus elephantinus	X	X				
	Phialina spp.	X	X	X		X	
	Spathidium sensu lato						
	Trachelius ovum			X			
HETEROTRICHIDA	*Spirostomum* sp.					X	
	Spirostomum minus		X				
	Stentor amethystinus				X		
	S. muelleri		X				
	S. niger					X	
	S. roeselii	X	X			X	X
HYMENOSTOMATIDA	*Calyptotricha lanuginosa*	X	X	X	X	X	X
	Cinetochilum margaritaceum	X	X	X	X	X	X
	Colpidium colpoda	X		X			
	Ctedoctema acanthocryptum	X	X				
	Cyclidium sp.		X			X	
	Cyclidium glaucoma	X	X	X	X	X	X
	C. heptatrichum	X	X	X		X	
	Dexiostoma campylum		X				
	Dexiotricha granulosa					X	
	Dexiotrichides centralis		X				
	Disematostoma buetschlii	X					
	Frontonia acuminata	X	X				
	F. angusta						X
	F. atra		X	X		X	X
	F. leucas	X	X	X			
	Glaucoma scintillans		X			X	
	Kahlilembus attenuatus			X			
	Lembadion sp.		X				
	Lembadion bullinum					X	
	L. lucens					X	
	Marituja pelagica	X					
	Ophyoglena spp.				X	X	
	Paracolpidium truncatum		X				
	Paramecium aurelia-complex		X	X			X
	Philasterides armatus	X	X	X			X
	Stokesia vernalis	X			X	X	X
	Tetrahymena piryformes	X	X	X	X		
	Urocentrum turbo	X	X	X		X	X
	Uronema nigricans	X	X	X	X	X	X

U = upstream; M = middle; D = downstream.

Table 1. Continued...

		RIVER			TRIBUTARIES		
		U	M	D	U	M	D
HYPOTRICHIDA	*Aspidisca cicada*	X	X	X	X	X	X
	Euplotes aediculatus		X			X	X
	E. moebiusi	X	X	X		X	
	Histriculus vorax			X		X	
	Holosticha pullaster			X			
	Hypotrichida	X					
	Hypotrichidium conicum			X			
	Oxytricha setigera	X					
	Stichotricha aculeata		X				X
LOXODES	*Loxodes* sp.						X
NASSULIDA	*Leptopharynx costatus*		X			X	
	Microthorax pusillus			X			
	Nassula picta	X	X		X		
	Nassulopsis elegans				X		
OLIGOTRICHIDA	*Codonella cratera*	X	X	X	X	X	X
	Halteria grandinella	X	X	X	X	X	X
	Limnostrombidium sp.	X	X	X	X	X	
	Pelagostrombidium sp.					X	
	Rimostrombidium humile	X	X	X		X	X
	R. lacustres	X	X		X	X	X
	Tintinnidium sp.	X	X	X	X	X	X
	Tintinnopsis sp.	X	X	X		X	
PERITRICHIA	*Campanella umbellaria*	X	X	X		X	X
	Carchesium pectinatum		X				
	C. polypinum	X	X			X	X
	Cothurnia annulata		X				
	Epicharchesium pectinatum			X			
	Epistylis sp.	X	X				
	Epistylis chrysemydis		X	X			
	E. coronata	X	X	X	X		X
	E. galea		X				
	E. hentscheli			X		X	
	E. procumbens			X		X	
	E. pygmaeum	X	X				
	Opercularia articulata		X				
	Ophrydium sp.			X			
	Pseudovorticella chlamydophora					X	
	Scyphidia rugosa		X				
	Vorticella sp.		X	X			
	Vorticella aquadulcis-complex	X	X	X	X	X	X
	V. campanula	X	X	X	X	X	X
	V. convallaria-complex	X	X	X	X	X	X
	V. infusonium-complex			X			
	V. natans		X			X	
	V. octava-complex		X			X	
PLEUROSTOMATIDA	*Acineria incurvata*			X			
	A. uncinata		X				X
	Amphileptus sp.		X				
	Amphileptus punctatus	X					
	Litonotus alpestris		X				
	L. lamella		X				
	L. varsaviensis		X				

U = upstream; M = middle; D = downstream.

Table 1. Continued...

		RIVER			TRIBUTARIES		
		U	M	D	U	M	D
PROSTOMATIDA	*Balanion planctonicum*	X	X	X	X	X	X
	Coleps sp.		X		X		X
	Coleps hirtus	X	X	X	X	X	X
	C. spetai		X		X	X	
	Holophrya sp.		X				
	Holophrya discolor	X	X	X		X	X
	H. ovum		X				
	H. teres		X				
	Plagiocampa rouxi			X		X	
	Uroticha sp.	X	X	X	X	X	X
	Urotricha farcta	X	X	X	X	X	X
SUCTORIA	*Metacineta mystacina*		X	X		X	
	Sphaerophrya magna	X				X	

U = upstream; M = middle; D = downstream.

order with 29 species, followed by Peritrichida (23 species). Most of the Oligotrichida species were observed in all sampled environments; this group is known by the frequent occurrence of its species in freshwater environments. The genus *Vorticella* was also representative in all sampled environments and transects.

Regarding the dry period, PERMANOVA results show that amongst the three stretches analyzed, the ciliate species composition was distinct between the upstream and middle stretches (Pseudo-*F*: 1.6527; p = 0.0012) and between upstream and downstream stretches (Pseudo-*F*: 1.946; p<0.001), whereas the species compositions of the middle and the downstream stretches did not differ (Pseudo-*F*: 0.90728; p = 0.618).

In the rainy period, the PERMANOVA showed remarkable differences in the ciliate species composition between the three stretches: upstream and middle (Pseudo-*F*: 2.3168; p = 0.0072), upstream and downstream (Pseudo-*F*: 2.7779; p = 0.0022), and middle and downstream (Pseudo-*F*: 1.7804; p = 0.029). These results evidence changes occurring in the biota along the last undammed section of the Paraná River. These differences may be attributed to the Porto Primavera Dam, which can retain an enormous amount of nutrients. However, the tributary rivers contribute to a nutrient replacement in the river, especially in the rainy period, supporting the differences of the species composition in the three stretches.

3.2. Abundance and species richness of planktonic ciliates

Higher values of ciliate abundance were recorded in the middle stretch, while the upstream stretch showed the lowest values (Figure 2).

A similar pattern was found for the species richness (Figure 3). The tributary rivers located in the middle stretch presented high values of species richness, especially in the rainy period, being considered as a potential source of species which increased the number of ciliate species in the Paraná River.

The results of species abundance distribution recorded in the Paraná River main channel evidenced a remarkable greater ciliate abundance and the predominance of planktonic species such as *Urotricha farcta, Rimostrombidium humile, Balanion planctonicum,* and *Tintinnidium* sp. during the dry period, along the whole course of the river. On the other hand, during the rainy period a greater dominance was observed, with the predominance of non-planktonic species of the genus *Vorticella* (Figure 4).

The same pattern was, in general, observed for the tributaries, regarding the ciliate dominance and abundance. However, it is important to highlight the lower densities of ciliates in these environments and that the predominance of *Vorticella* species during the rainy period was evidenced only at the upstream stretch (Figure 5).

The increase in species richness (Figure 6) occurred along the river, reaching the highest values at the sampling sites located in the middle stretch of the studied area. In the rainy period we recorded a major point-by-point species increase, as well as a superior number of species in relation to the dry period (64 and 49 species, respectively). The middle stretch was the greater contributor for the species

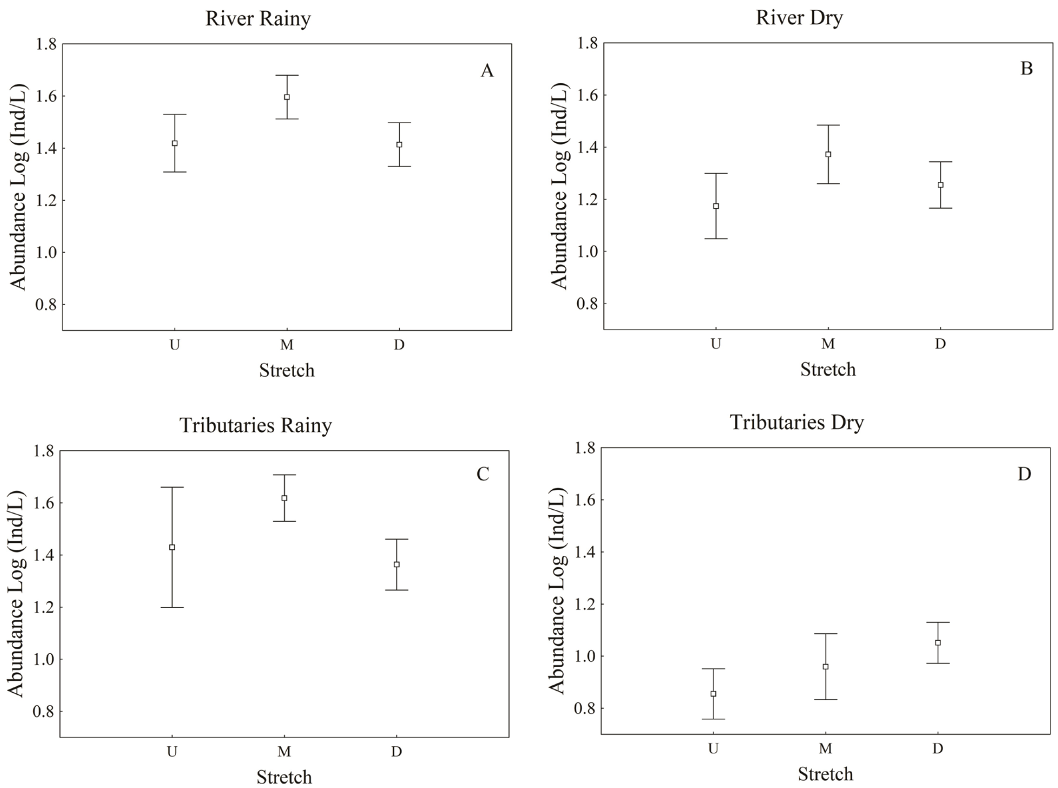

Figure 2. Ciliate abundances registered in the Paraná River during the rainy (A) and dry (B) periods and its tributaries during the rainy (C) and dry (D) periods in each stretch – upstream (U), middle (M), and downstream (D).

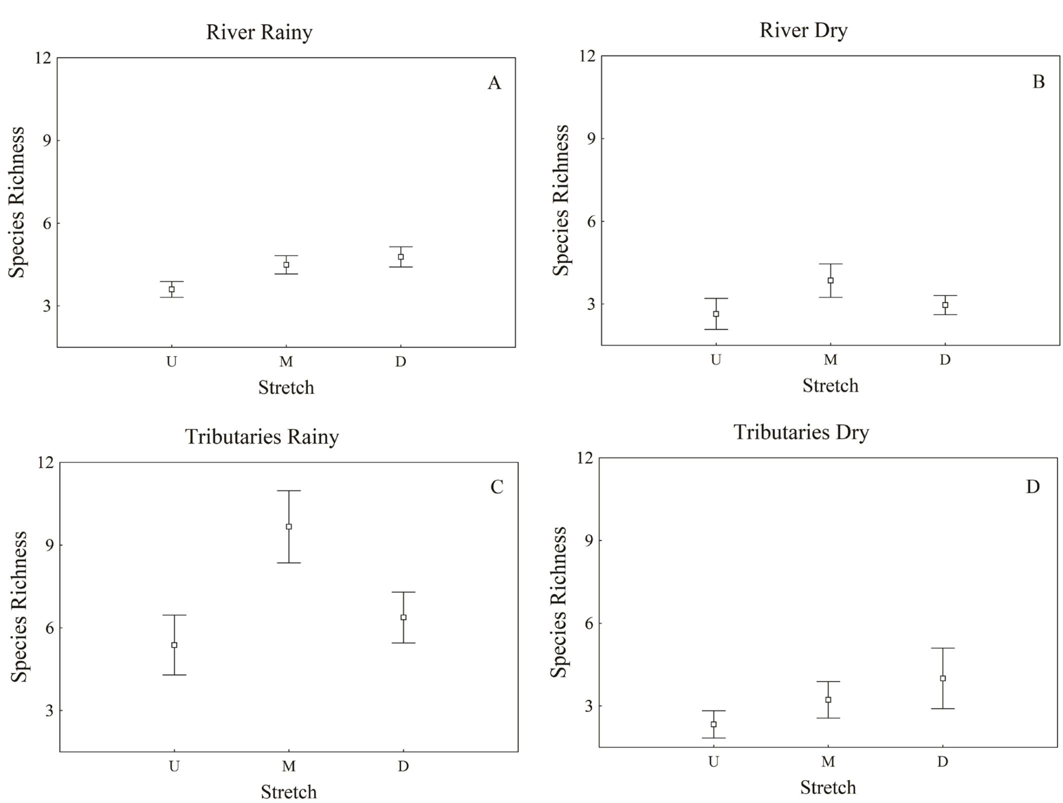

Figure 3. Ciliate species richness registered in the Paraná River during the rainy (A) and dry (B) periods and its tributaries during the rainy (C) and dry (D) periods in each stretch – upstream (U), middle (M), and downstream (D).

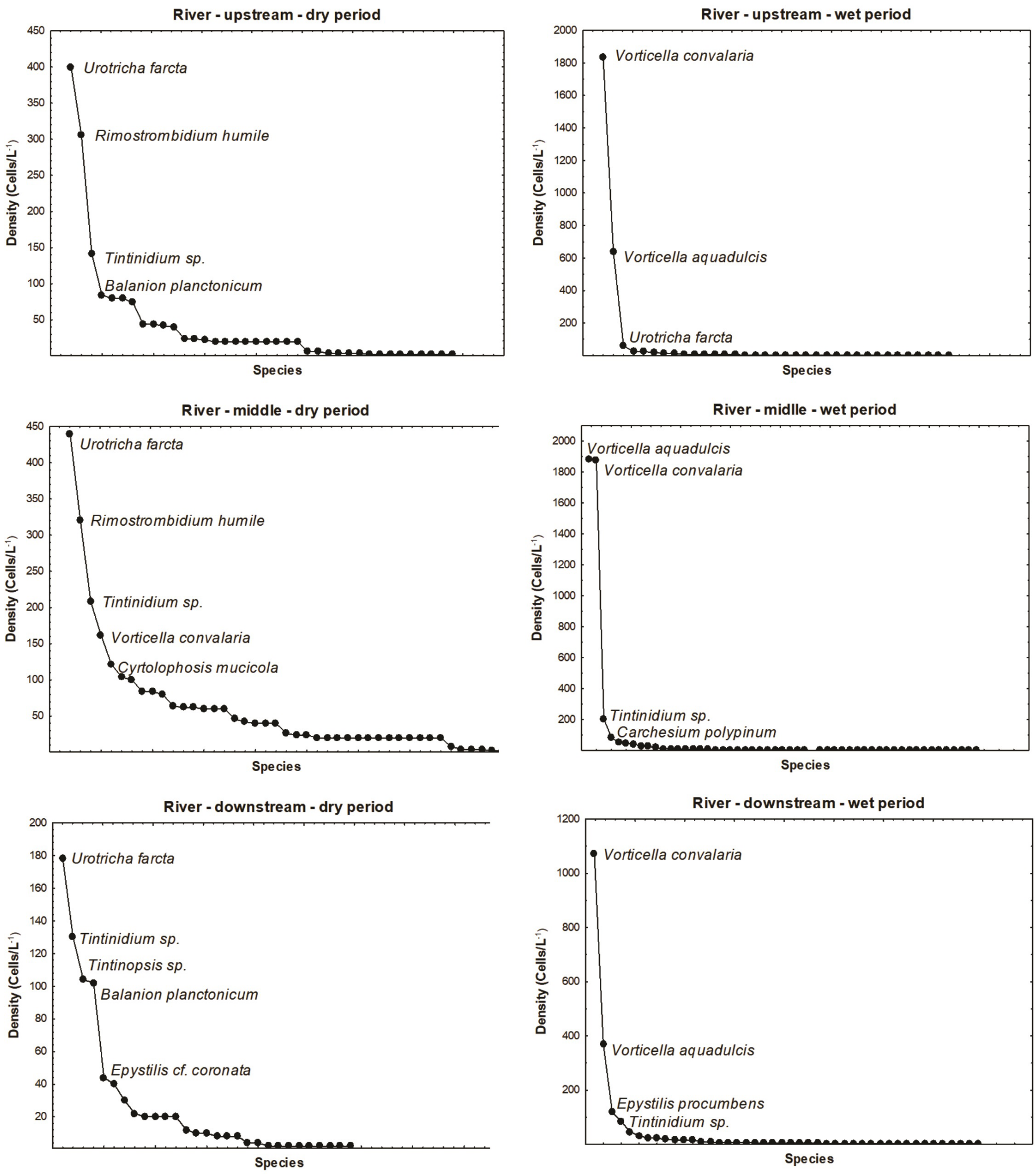

Figure 4. Plots of ciliates species abundance distribution in Paraná River main channel during the dry and wet periods.

richness, specifically, the sites P6 and P7, downstream the Amambai river and upstream the Iguatemi River.

3.3. Dissimilarity between the sampling sites

The results of the homogeneity of multivariate dispersions (PERMDISP) indicated low similarity between the three stretches, suggesting major changes in the ciliate community along the river. During the rainy period (Figure 7), there was a high variation in the first sampling site, which is quite close to the Porto Primavera Dam and after the first tributary. Nonetheless, the variation observed in the further sampling sites was lower than that recorded in the first one, increasing again in the midst and final sampling sites of the river.

In the dry period (Figure 8) we found a contrary pattern to the rainy period. High values of variation were registered in the initial sampling points – next to the dam – with the highest values observed in the sites between P2 and P3. In the sampling sites of the middle and downstream, the variation tended to decrease.

3.4. Influence of environmental variables

The results of the redundancy analysis (RDA) were significant in both hydrological periods ($p<0.05$). The first and second axes of the RDA were significant ($p<0.05$) and retained for the interpretation of the river in the rainy period (adjusted $R^2 = 0.1$; $p = 0.001$; Figure 9). Axis 1 separated the upstream

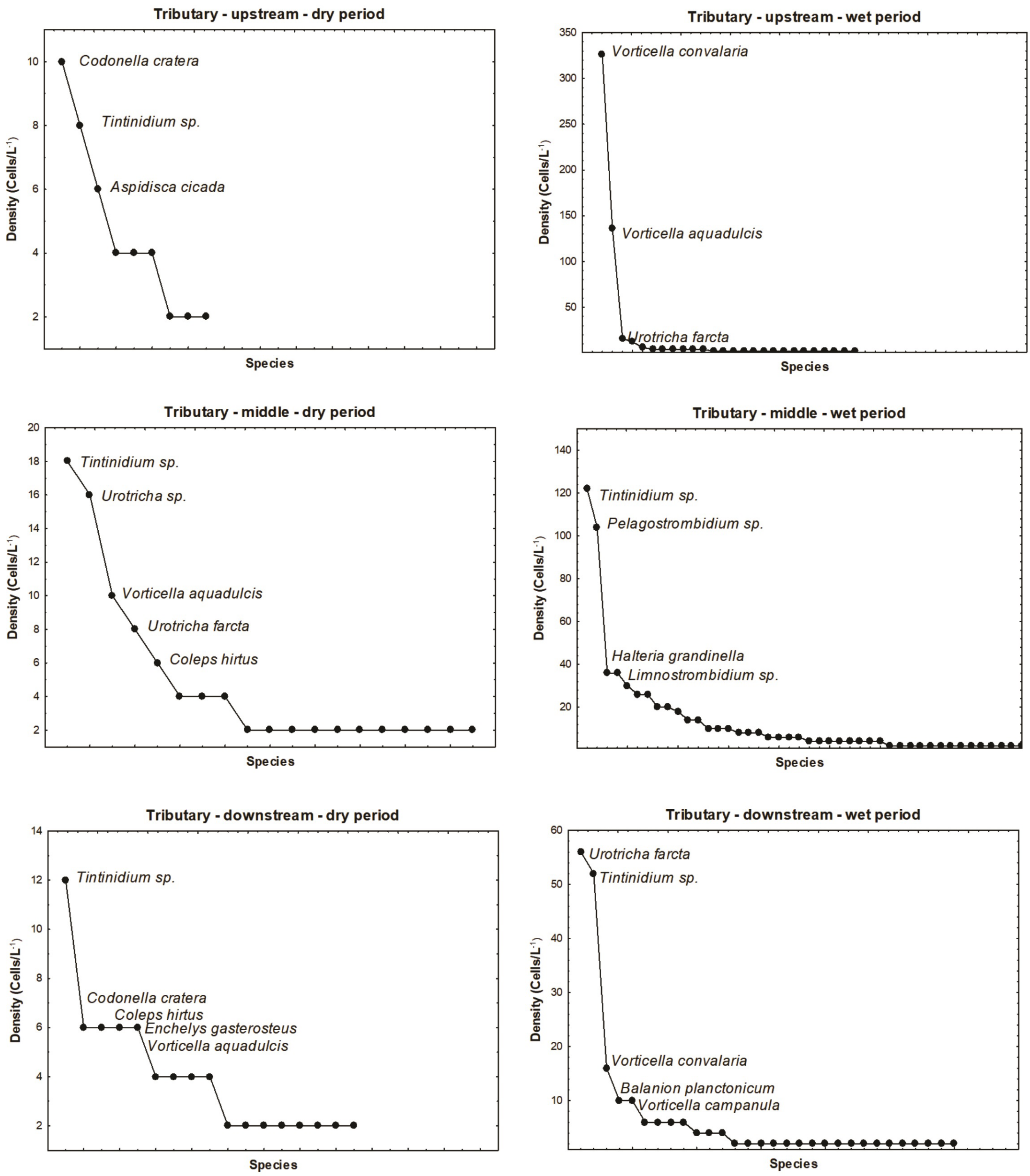

Figure 5. Plots of ciliates species abundance distribution in the tributaries of Paraná River during dry and wet periods.

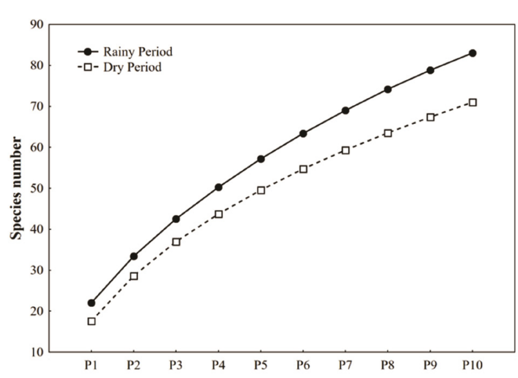

Figure 6. Graphic representation of the species increment in the Paraná River towards downstream.

stretch from the middle and downstream stretches. The first was related to total nitrogen, temperature, depth, conductivity, and dissolved oxygen, while the other two were related to turbidity, total phosphorus, and orthophosphate.

In the dry period, both axes were also significant (p<0.05) and interpreted (adjusted R^2 = 0.1; p = 0.001), and the same pattern found for the rainy period was observed as well (Figure 10), although the upstream stretch was characterized by a major importance of conductivity, pH, depth and total nitrogen, and separated from the others by the axis 2. The middle and downstream stretches

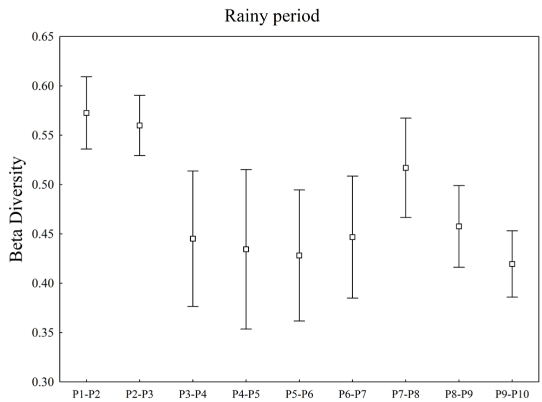

Figure 7. Species variation along the Paraná River during the rainy period. The dots represent the mean values and the bars represent the standard deviations.

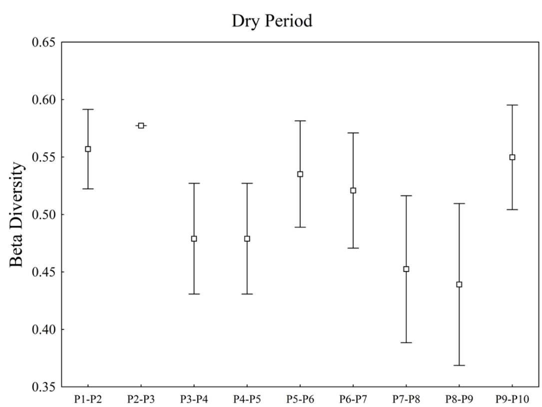

Figure 8. Species variation along the Paraná River during the dry period. The dots represent the mean values and the bars represent the standard deviations.

were related to turbidity, orthophostphate, total phosphorus, amonium, nitrate, and dissolved oxygen.

In both periods, the middle and downstream stretches were related to an increase of nutrients and turbidity, strengthening the importance of the tributaries confluence to the main river. Along the main river, it was possible to verify the increment in the nutrient concentration and in the water turbidity as the distance from the dam increases. Regarding ciliate species, *Tintinnidium* sp. was related to the middle and donwnstream stretches in both periods, whereas *Rimostrombidium humile* and *Urotricha farcta* were associated to the stretches more distant from the dam.

3.5. Tributaries contribution

As expected, the upstream dam negatively impacted the diversity of cilitated protozoa in the

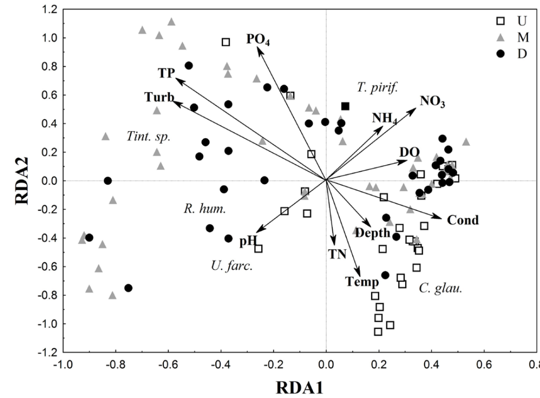

Figure 9. Ordination diagram for the two first axes of the Redundancy Analysis, according to the environmental variables and ciliate abundance along the three stretches of the Paraná River in the rainy period. Cond = conductivity; D = downstream; DO = dissolved oxygen; Depth = habitats' depth; M = middle; NO3 = nitrate; NH4 = ammonium; PO4 = orthophosphate; Temp = temperature; TN = total nitrogen; TP = total phosphorus; Turb = turbidity; Up = upstream.

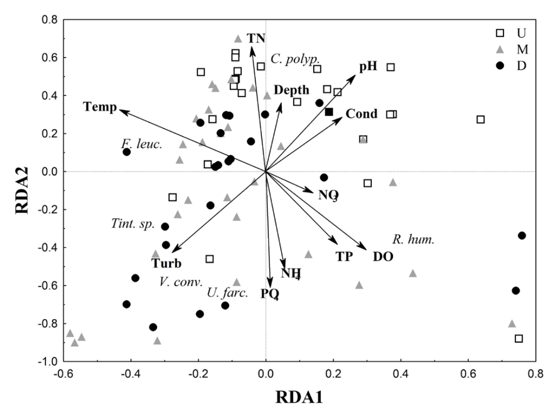

Figure 10. Ordination diagram for the two first axes of the Redundancy Analysis, according to the environmental variables and ciliate abundance along the three stretches of the Paraná River in the dry period. Cond = conductivity; D = depth; DO = dissolved oxygen; Down = downstream; M = middle; NO3 = nitrate; NH4 = ammonium; PO4 = orthophosphate; Temp = temperature; TN = total nitrogen; TP = total phosphorus; Turb = turbidity; Up = upstream.

main channel of the Paraná River. In this way, it was expected that the tributaries input along the Paraná River would attenuate the limiting effect of the upstream dam, such that both abundance and richness of ciliate species increase gradually toward downstream in the last undammed section of the Paraná River.

In the tributaries, the highest values of ciliate abundance and species richness were generally recorded in the rainy period (Figure 11), mainly due to the presence of both periphytic and benthonic species in the water column, such as some peritrichs and colpodids commomly found in these environments. Therefore, the tributaries contribution in increasing the values of these attributes in the main river channel was also higher in this period, significantly increasing the ciliate abundance and species richness in the stretches more distant from the dam.We recorded a minor contribution of the tributaries to the ciliate abundance and species richness to the Paraná River main channel in the dry period (Figure 11).

4. Discussion

The structure of the planktonic ciliate community was significantly distinct among the studied stretches, especially during the rainy period. Our results indicate that the ciliate diversity of the river is quite reduced right after the dam. Other studies shown that several changes may occur in the regions closer to the dam, which may result in biodiversity loss of some aquatic communities (Stanford & Ward, 2001; Poff et al., 2007) and a decrease in planktonic protists over the river course (Scherwass et al., 2010).

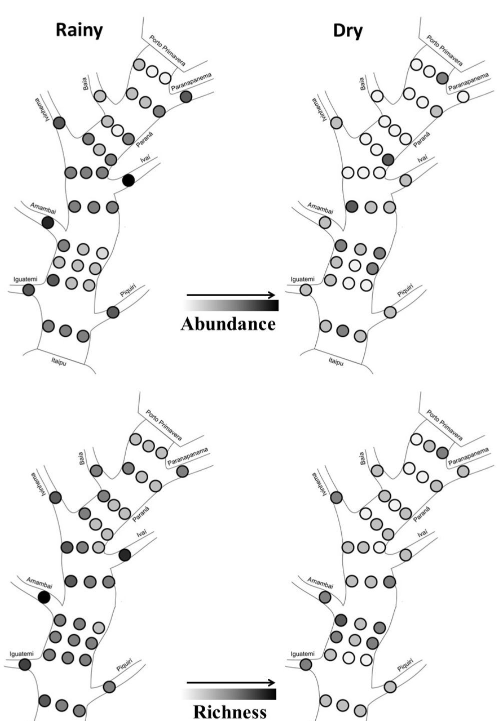

Figure 11. Schematic model showing the gradual change of the ciliate species abundance and richness as a resulting of the tributaries entrance along the main channel of the Paraná River on both periods.

A more considerable change was verified in the rainy period than in the dry period. We observed a paramount distinction of the sites closer to the dam in the rainy period, suggesting a great variation amongst the species in these localities in relation to the other sampling sites. Our results show that the closer the sites are to the dam, the less species occur. The nutrients and species from stretches upstream are retained in the reservoir created by the dam, which contributes to the low values of species richness in the sampling sites right after it. Besides, there is no connection of any tributary or lakes in the neighbouring areas, hence limiting the arrival of species from other environments.

Nearly after the confluence zone of the second tributary (Baía River), at the left bank of the Paraná River, it was observed a great variation in the species composition due to the species increment from the smaller river to the main one. The pattern of great variation in the sampling sites toward downstream was verified in the whole river. The other sites of the initial stretch have a directly confluence with two distinct tributaries, located on the right bank of the Paraná River.

We recorded relatively high values of ciliate abundance in the Baía River, which is characterized by the high levels of humic and other organic compounds (Train & Rodrigues, 1997) due to the agriculture and farming activities on its surroundings, which result in a suitable environment for the stablishment and development of several ciliate populations. The positive correlation between ciliate abundance and organic matter is a quite common subject in studies (Blatterer, 2002).

The second tributary (Ivinhema River) is the main river of a conservation unity, which is therefore well preserved, showing high values of ciliate species richness in the sampling site located at its mouth in Paraná River. Some ciliate species have positive relationships with well-preserved environments (Lair et al., 1999), which might explain the relatively high local diversity in this tributary.

At the main channel of the Paraná River, the highest values of ciliate local diversity and abundance were observed in the sampling sites closer to the confluences with tributaries. In this way, for the zooplankton community, the dam-free tributaries play a role as source of species for the larger rivers, which are normally impacted with damming (Braghin et al., 2015). Moreover, the amount of variation in species composition in the mouths of the tributaries at the main river suggests a greater biotic heterogeneity promoted by the smaller rivers, evidencing their importance in maintaining the arrival of species to larger rivers.

The sampling sites located at the middle stretch showed the higher values of variation in species composition, while the lowest values were found in the sites located at the upstream stretch. The tributaries converging into both middle and downstream stretches are undammed rivers, and punctually contributed to increase the diversity in the main river. Other factor that might have influenced the relatively high diversity found in the main river is that the studied area in located inside the Ilha Grande National Park, which limit the anthropogenic impacts in the locality.

Although we focused on the limnetic region of the environments, few of the most abundant species were exclusively planktonic. Several species with high frequency of occurrence and high abundances have generalist habits, and some are even commonly found in the benthos. Kiss et al. (2009) affirm that most of protist species observed in running waters come from the benthonic compartment. Amongst the recorded species, some were reported in studies on periphytic (Mieczan, 2010) and soil ciliate communities (Foissner & Berger, 1996; Foissner et al., 1999; Bamforth, 2001; Esteban et al., 2006).

The occurrence of both periphytic and benthic ciliate species in the pelagic compartment of the environments may be attributed to some factors related to the damming of the rivers. Since the water flow, intensity, and duration of the flood pulse of these rivers are regulated, factors such as precipitation in adjacent environments may support the maintenance of the ciliate diversity.

Precipitation occurred in approximately 50% of the days during the sampling campaigns in the rainy period, and in about 14% of the days during the dry period. Precipitations occurring in these environments act similarly to the effects caused by the flood pulse, which are the main regulators of the biotic changes. The flood pulse provides an increase in the similarity between the different environments through the connectivity among systems of the floodplain, as well as an increase in the river flow (McCabe & Wolock, 2002).

The dry period affected the hydrometric level of the Paraná River, hence decreasing the connectivity of the main river with the different floodplain environments. These unsuitable conditions do not contribute to the arrival of new species in the system and, combined with the lotic characteristics of the rivers, which limit the occurrence of planktonic ciliate species (Horvath & Lamberti, 1999), the Paraná River remained with low values of ciliate abundance and richness even in the sampling sites located downstream.

Besides the direct effects of the precipitation, periphytic species are constantly carried by the rapid waters because of the rainfall. Previous studies on the effect of the water flow in periphytic algae demonstrate that a minimum water current have influence in species detaching from their substrates, causing a reduction in community species richness (Ryder et al., 2006).

Typical soil species usually present in the banks and littoraneous regions of the rivers were more susceptible to be carried to the pelagic region in the rainy period, considering that during the rain, the sediment is revolved and the connectivity amongst environments is increased. Moreover, we suggest that the typical benthonic species found in the limnetic region may be, at least in part, coming from the turbulence caused by the rain in the sediment, which induces the mixture of the superficial and deep waters. As shown in earlier studies on zooplankton communities, the increase in connectivity in floodplain systems favors species exchange among the different compartments, such that species coming from the benthos and littoraneous region may be found in the planktonic compartment (Lansac-Tôha et al., 2009). Apparently, the rainy period determines the occurrence of several species and contribute to their dispersion as well, increasing the biotic heterogeneity of the system. In addition, the confluence between tributaries and the main river also was associated with high levels of ciliate diversity.

Thus, we observed remarkable changes in the species composition among the sampling sites. Regarding the ciliate taxa, *Tintinnidium* sp. was closely related to the middle and donwnstream stretches in both periods. This genus is very common in the pelagic compartment (Pauleto et al., 2009; Kiss et al., 2009), probably benefiting of its lorica to tolerate the hydrodinamics in lotic environments. Other essentially planktonic species, such as *Rimostrombidium humile* and *Urotricha farcta*, usually observed in different environments of this floodplain, were associated to the stretches more distant from the dam, indicating that they might be retained upstream. Once the main river receives water from tributaries and connected lakes, in the middle and downstream stretches, these species return to occur with high abundances in the main river channel.

A total of 117 planktonic ciliate taxa were registered, a regional diversity similar to others found in studies on lotic environments (Kiss et al., 2009; Tirjaková & Vďačný, 2013). On the other hand, when considering the local diversity, we recorded only four species per sample, in average. So, despite the high number of species, the local diversity was considered low.

We suggest that this result may be related to several factors commonly observed in lotic environments, in which the ciliates are not able to establish and develop great populations. Among these factors, the running waters may be the primordial one in determining the low abundances and species richness of ciliates. Because of the running waters, other important factors in structuring the ciliate community, such as food availability and habitat structure have their role minimized by the water flow (Hart & Finelli, 1999; Blatterer, 2002).

This hydrodynamics also affects the ciliates search for food and escape from predators, supporting the theory that the lotic environments do not favor local diversity of the ciliates, as verified other studies on protist organisms (Hart & Finelli, 1999; Naudin et al., 2001; Pauleto et al., 2009).

Although lotic environments do not favor the local establishment of the communities of planktonic protists, the present study shows a great regional diversity, resulting from the contribution of the tributaries. However, we highlight the relevance of the water flow for the regional diversity, since such diversity is determined by the individual abilities to overcome distance and barriers between environments, which affect the dispersion and colonization of new areas (Hubbell, 2001). In this way, despite not contributing for the local diversity, the water flow has great contribution in regional scales, once the dispersion of the ciliates occurs naturally by the water flow (Blatterer, 2002). Therefore, the river plays a positive role in accelerating ciliate dispersion, thus decreasing the time for the species to reach and colonize other localities, in which they find favorable conditions for the establishment, development, and persistence of the populations, such as lakes.

In the same manner that the rain and the tributaries may widely contribute for the biotic heterogeneity and for the enrichment of the regional species pool, when anthropogenic impacts, especially those related to damming, occur without a conservation management plan or environmental impact studies, the consequences for the environment may be disastrous for the biotic communities and for the ecosystem functioning and services.

The importance of the rivers as sources of dispersion and propagation along the whole system, the contribution of tributaries and precipitation for increasing the regional diversity of the main river, and the enhancing of the biotic heterogeneity of the whole system were clearly demonstrated in the present study. Furthermore, the results suggest a major relevance of the conservation unities (Ivinhema State Park and Ilha Grande National Park) in the maintenance of the hydrodynamics integrity within the studied area, since they were of paramount importance for the elevated diversity of the planktonic organisms found throughout the system, as well as for their dispersion, which assure the maintenance of the biodiversity of microorganisms. We emphasize that the dispersal potential of lotic environments and the importance of the tributaries as sources of species for the main river, may act as homogenizing factors if the tributaries are dammed. Hence, we strongly suggest that tributaries remain undammed, to avoid the severe impacts that have a potential to cause biotic homogeneity and the consequential reduction in biodiversity of the whole ecosystem.

Acknowledgements

We would like to thank CNPq and Grupo Usaçucar for the financial support and Nupélia/PEA/UEM as well as the ICMBio - Parque Nacional de Ilha Grande for all facilities and logistical support. We would also like to thank Capes, CNPq and Unicesumar/ICETI for fellowships.

References

AGOSTINHO, A.A., GOMES, L.C., FERNANDEZ, D.R. and SUZUKI, H.I. Efficiency of fish ladders for neotropical ichthyofauna. *River Research and Applications*, 2002, 18(3), 299-306. http://dx.doi.org/10.1002/rra.674.

AGOSTINHO, A.A., JÚLIO, J.H.F., GOMES, L.C., BINI, L.M. and AGOSTINHO, C.S. Composição, abundância e distribuição espaço-temporal da ictiofauna. In: A.E.A.M. VAZZOLER, A.A. AGOSTINHO and N.S. HAHN, eds. *A planície de inundação do Alto Rio Paraná: aspectos físicos, biológicos e socioeconômicos*. Maringá: EDUEM, Nupélia, 1997, pp. 179-208.

AGOSTINHO, A.A., PELICICE, F.M. and GOMES, L.C. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2008, 68(4, Suppl), 1119-1132. PMid:19197482. http://dx.doi.org/10.1590/S1519-69842008000500019.

AGOSTINHO, A.A., THOMAZ, S.M. and GOMES, L.C. Threats for biodiversity in the floodplain of the Upper Paraná River: effects of hydrological regulation by dams. *Ecohydrology and Hydrobiology*, 2004, 4(3), 255-268.

ANDERSON, M.J. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 2006, 62(1), 245-253. PMid:16542252. http://dx.doi.org/10.1111/j.1541-0420.2005.00440.x.

ARNDT, H. Rotifers as predators on components of the microbial web. *Hydrobiologia*, 1993, 255-256, 231-246. http://dx.doi.org/10.1007/BF00025844.

AZAM, F., FENCHEL, T., FIELD, J.G., GRAY, J.S., MEYER-REIL, L.A. and THINGSTAD, F. The ecological role of water column microbes in the sea. *Marine Ecology Progress Series*, 1983, 10, 257-263. http://dx.doi.org/10.3354/meps010257.

BAMFORTH, S.S. Proportions of active ciliate taxa in soils. *Biology and Fertility of Soils*, 2001, 33(3), 197-203. http://dx.doi.org/10.1007/s003740000308.

BEAVER, J.R. and CRISMAN, T.L. The role of ciliated protozoa in pelagic freshwater ecosystems. *Microbial Ecology*, 1989, 17(2), 111-136. PMid:24197241. http://dx.doi.org/10.1007/BF02011847.

BENDA, L., ANDRAS, K., MILLER, D. and BIGELOW, P. Confluence effects in rivers: interactions of basin scale, network geometry, and disturbance regimes. *Water Resources Research*, 2004, 40(5) http://dx.doi.org/10.1029/2003WR002583.

BLATTERER, H. Some conditions for the distribution and abundance of ciliates (Protozoa) in running waters: Do we really find every species everywhere? *Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen*, 2002, 28(2), 1046-1049.

BOZELLI, R.L., THOMAZ, S.M., PADIAL, A.A., LOPES, P.M. and BINI, L.M. Floods decrease zooplankton beta diversity and environmental heterogeneity in an Amazonian floodplain system. *Hydrobiologia*, 2015, 753(1), 233-241. http://dx.doi.org/10.1007/s10750-015-2209-1.

BRAGHIN, L.S., FIGUEIREDO, B.R., MEURER, T., MICHELAN, T.S., SIMÕES, N.R. and BONECKER, C.C. Zooplankton diversity in a dammed river basin is maintained by preserved tributaries in a tropical floodplain. *Aquatic Ecology*, 2015, 49(2), 175-187. http://dx.doi.org/10.1007/s10452-015-9514-7.

ESTEBAN, G.F., CLARKE, K.J., OLMO, J.L. and FINLAY, B.J. Soil protozoa: an intensive study of population dynamics and community structure in an upland grassland. *Applied Soil Ecology*, 2006, 33(2), 137-151. http://dx.doi.org/10.1016/j.apsoil.2005.07.011.

FENCHEL, T. *Protozoa ecology: biology of free-living phagotrophic protists*. Madison: Science Tech Publishers, 1982.

FOISSNER, W. and BERGER, H. A user-friendly guide to the ciliates (Protozoa, Ciliophora) commonly used by hydrobiologists as bioindicators in rivers, lakes, and waste waters, with notes on their ecology. *Freshwater Biology*, 1996, 35(2), 375-482.

FOISSNER, W., BERGER, H. and SCHAUMBURG, J. *Identification and ecology of limnetic plankton ciliates*. Munich: Bavarian State Office for Water Management, 1999.

GOLTERMAN, H.L., CLYMOS, R.S. and OHMSTAD, M.A.M. *Methods for physical and chemical analysis of fresh water*. Oxford: Blackwel Scientific Publication, 1978.

HART, D.D. and FINELLI, C.M. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics*, 1999, 30(1), 363-395. http://dx.doi.org/10.1146/annurev.ecolsys.30.1.363.

HORVATH, T.G. and LAMBERTI, G.A. Mortality of zebra mussel, *Dreissena polymorpha*, veligers during downstream transport. *Freshwater Biology*, 1999, 42(1), 69-76. http://dx.doi.org/10.1046/j.1365-2427.1999.00462.x.

HUBBELL, S.P. *The unified neutral theory of biodiversity and biogeography*. Princeton: University Press, 2001.

JUNK, W.J., BAYLEY, P.B. and SPARKS, R.E. The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 1989, 106(1), 110-127.

KISS, A.K., ACS, E., KISS, K.T. and TÖRÖK, J.K. Structure and seasonal dynamics of the protozoan community (heterotrophic flagellates, ciliates, amoeboid protozoa) in the plankton of a large river (River Danube, Hungary). *European Journal of Protistology*, 2009, 45(2), 121-138. PMid:19285382. http://dx.doi.org/10.1016/j.ejop.2008.08.002.

LAIR, N., JACQUET, V. and REYES-MARCHANT, P. Factors related to autotrophic potamoplankton, heterotrophic protists and micrometazoan abundance, at two sites in a lowland temperate river during low water flow. *Hydrobiologia*, 1999, 394(1), 13-28. http://dx.doi.org/10.1023/A:1003552021726.

LANSAC-TÔHA, F.A., BONECKER, C.C., VELHO, L.F.M., SIMÕES, N.R., DIAS, J.D., ALVES, G.M. and TAKAHASHI, E.M. Biodiversity of zooplankton communities in the Upper Paraná River floodplain: interannual variation from long-term studies. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2009, 69(2,Suppl. Suppl), 539-549. PMid:19738961. http://dx.doi.org/10.1590/S1519-69842009000300009.

MACKERETH, F.Y.H., HERON, J.G. and TALLING, J.J. *Water analysis: some revised methods for limnologists*. Cumbria: Freshwater Biological Association, 1978. Scientific Publication, vol. 36.

MADONI, P. Estimation of the size of freshwater ciliate populations by a subsampling technique. *Hydrobiologia*, 1984, 111(3), 201-206. http://dx.doi.org/10.1007/BF00007200.

MCARDLE, B.H. and ANDERSON, M.J. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, 2001, 82(1), 290-297. http://dx.doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2.

MCCABE, G.J. and WOLOCK, D.M. A step increase in stream flow in the conterminous United States. *Geophysical Research Letters*, 2002, 29(24), 38-1. http://dx.doi.org/10.1029/2002GL015999.

MIECZAN, T. Periphytic ciliates in three shallow lakes in eastern Poland: A comparative study between a phytoplankton-dominated lake, a phytoplankton macrophyte lake and a macrophyte-dominated lake. *Zoological Studies*, 2010, 49(5), 589-600.

MIRONOVA, E., TELESH, I. and SKARLATO, S. Diversity and seasonality in structure of ciliate communities in the Neva Estuary (Baltic Sea). *Journal of Plankton Research*, 2012, 34(3), 208-220. http://dx.doi.org/10.1093/plankt/fbr095.

NAUDIN, J.J., CAUWET, G., FAJON, C., ORIOL, L., TERZIĆ, S., DEVENON, J.L. and BROCHE, P. Effect of mixing on microbial communities in the Rhone River plume. *Journal of Marine Systems*, 2001, 28(3), 203-227. http://dx.doi.org/10.1016/S0924-7963(01)00004-5.

NEIFF, J.J. Ideas para la interpretacion ecologica del Paraná. *Interciencia*, 1990, 15(6), 424-441.

OKSANEN, J., BLANCHET, F.G., KINDT, R., LEGENDRE, P., MINCHIN, P.R., O'HARA, R.B., SIMPSON, G.L., SOLYMOS, P., STEVENS, M.H.H. and WAGNER, H. *Vegan: Community Ecology Package. R package version 2.0-8* [software]. 2011 [viewed 13 Dec. 2016]. Available from: http://CRAN.R-project.org/package=vegan

PAULETO, G.M., VELHO, L.F.M., BUOSI, P.R.B., BRÃO, A.F.S., LANSAC-TÔHA, F.A. and BONECKER, C.C. Spatial and temporal patterns of ciliate species composition (Protozoa: Ciliophora) in the plankton of the Upper Paraná River floodplain. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2009, 69(2, Suppl), 517-527. PMid:19738959. http://dx.doi.org/10.1590/S1519-69842009000300007.

POFF, N.L., OLDEN, J.D., MERRITT, D.M. and PEPIN, D.M. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America*, 2007, 104(14), 5732-5737. PMid:17360379. http://dx.doi.org/10.1073/pnas.0609812104.

POMEROY, L.R. The ocean's food web, a changing paradigm. *Bioscience*, 1974, 24(9), 499-504. http://dx.doi.org/10.2307/1296885.

POWER, M.E., DIETRICH, W.E. and FINLAY, J.C. Dams and downstream aquatic biodiversity: potential food web consequences of hydrologic and geomorphic change. *Environmental Management*, 1996, 20(6), 887-895. PMid:8895411. http://dx.doi.org/10.1007/BF01205969.

R DEVELOPMENT CORE TEAM. *R: language and environment for statistical computing* [software]. Vienna: R foundation for Statistical Computing, 2012 [viewed 13 Dec. 2016]. Available from: http://www.r-project.org

RICE, S.P., GREENWOOD, M.T. and JOYCE, C.B. Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. *Canadian Journal of Fisheries and Aquatic Sciences*, 2001, 58(4), 824-840. http://dx.doi.org/10.1139/f01-022.

RICHTER, B.D., BAUMGARTNER, J.V., BRAUN, D.P. and POWELL, J. A spatial assessment of hydrologic alteration within a river network. *Regulated Rivers: Research and Management*, 1998, 14(4), 329-340. http://dx.doi.org/10.1002/(SICI)1099-1646(199807/08)14:4<329::AID-RRR505>3.0.CO;2-E.

ROBERTO, M.C., SANTANA, N.F. and THOMAZ, S.M. Limnology in the Upper Parana River foodplain: large-scale spatial and temporal patterns, and the infuence of reservoirs. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2009, 69(2, Suppl), 717-725. PMid:19738977. http://dx.doi.org/10.1590/S1519-69842009000300025.

RYDER, D.S., WATTS, R.J., NYE, E. and BURNS, A. Can flow velocity regulate epixylic biofilm structure in a regulated floodplain river? *Marine & Freshwater Research*, 2006, 57(1), 29-36. http://dx.doi.org/10.1071/MF05099.

SCHERWASS, A., BERGFELD, T., SCHÖL, A., WEITERE, M. and ARNDT, H. Changes in the plankton community along the length of the River Rhine: Lagrangian sampling during a spring situation. *Journal of Plankton Research*, 2010, 32(4), 491-502. http://dx.doi.org/10.1093/plankt/fbp149.

SHERR, E.B. and SHERR, B.F. Significance of predation by protists in aquatic microbial food webs. *Antonie van Leeuwenhoek*, 2002, 81(1-4), 293-308. PMid:12448728. http://dx.doi.org/10.1023/A:1020591307260.

SOLA, A., SERRANO, S. and GUINEA, A. Influence of environmental characteristics on the distribution of ciliates in the River Henares (Central Spain). *Hydrobiologia*, 1996, 324(3), 237-252. http://dx.doi.org/10.1007/BF00016396.

SOUZA FILHO, E.E. and STEVAUX, J.C. Geology and geomorphology of the Baía-Curutuba Ivinheima river complex. In: S.M. THOMAZ, A.A. AGOSTINHO and N.S. HAHN, eds. *The Upper Paraná river and its floodplain: physical aspects, ecology and conservation*. Leiden: Backhuys Publishers, 2004, pp. 1-29.

SOUZA FILHO, E.E. Evaluation of the Upper Paraná River discharge controlled by reservoirs. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2009, 69(2, Suppl), 707-716. PMid:19738976. http://dx.doi.org/10.1590/S1519-69842009000300024.

STANFORD, J.A. and WARD, J.V. Revisiting the serial discontinuity concept. *Regulated Rivers: Research and Management*, 2001, 17(4-5), 303-310. http://dx.doi.org/10.1002/rrr.659.

STOECKER, D.K. and CAPUZZO, J.M. Predation on protozoa: its importance to zooplankton. *Journal of Plankton Research*, 1990, 12(5), 891-908. http://dx.doi.org/10.1093/plankt/12.5.891.

THOMAZ, S.M., BINI, L.M. and BOZELLI, R.L. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*, 2007, 579(1), 1-13. http://dx.doi.org/10.1007/s10750-006-0285-y.

THORP, J.H., THOMS, M.C. and DELONG, M.D. *The riverine ecosystem synthesis: toward conceptual cohesiveness in river science*. London: Elsevier, 2008.

TIRJAKOVÁ, E. and VĎAČNÝ, P. Analysis and evolution of water quality of the upper Váh River (northern Slovakia) by long-term changes in the community structure of ciliates (Protista: Ciliophora). *Biologia*, 2013, 68(4), 667-678. http://dx.doi.org/10.2478/s11756-013-0211-5.

TRAIN, S. and RODRIGUES, L.C. Temporal fluctuations of the phytoplankton community of the Baía River, in the upper Paraná River floodplain, Mato Grosso do Sul, Brazil. *Hydrobiologia*, 1997, 361(1-3), 125-134. http://dx.doi.org/10.1023/A:1003118200157.

VELHO, L.F.M., LANSAC-TÔHA, F.A. and BINI, L.M. Influence of environmental heterogeneity on the structure of testate amoebae (Protozoa, Rhizopoda) assemblages in the plankton of the upper Paraná river floodplain, Brazil. *International Review of Hydrobiology*, 2003, 88(2), 154-166. http://dx.doi.org/10.1002/iroh.200390011.

WARD, J.V., TOCKNER, K. and SCHIEMER, F. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Research and Management*, 1999, 15(1), 125-139. http://dx.doi.org/10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0.CO;2-E.

WEISSE, T. The significance of inter- and intraspecific variation in bacterivorous and herbivorous protists. *Antonie van Leeuwenhoek*, 2002, 81(1-4), 327-341. PMid:12448731. http://dx.doi.org/10.1023/A:1020547517255.

Received: 13 December 2016
Accepted: 29 May 2017