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Intra-annual variation in planktonic ciliate species composition (Protista: Ciliophora) in different strata in a shallow floodplain lake

Variação intra-anual na composição de espécies de ciliados planctônicos (Protista: Ciliophora) em diferentes estratos de uma lagoa rasa de planície de inundação

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Abstract: Aim: We aimed to evaluate the variation in planktonic ciliate species composition in different strata of the Guaraná Lake, encompassing high and low water periods, at the Upper Paraná River floodplain. **Methods:** Samplings were collected monthly between March 2007 and February 2008, from the epilimnion, metalimnion and hypolimnion. Ciliates samples were filtered using a plankton net of 10µm mesh size and identified *in vivo* under an optical microscope. **Results:** Among 112 species identified, 13 were found exclusively during the high water periods and 39 during the low water period. Results of nonparametric extrapolation indices evidenced that the observed richness represented between 70% and 90% of the estimated richness. Regarding the variation in species composition, Beta1 index showed that the alteration in composition between strata during the low water period was slightly greater than that registered during high waters. Cluster analysis evidenced a higher dissimilarity in ciliate species composition between periods than among the different strata. The greatest variation in species composition was verified during the distinct hydrological periods, whereas no significant differences were observed for the different strata analysed. **Conclusions:** We found that in the pelagic compartment, ciliate species composition changed significantly between hydrological periods, and a higher similarity in species composition among strata was observed during the high water period. Therefore, alterations in the vertical distribution seem to be related to the homogenizing effect of the floods in the water column stability.

Keywords: protist; plankton; species richness; diversity; freshwater.

Resumo: Objetivo: Avaliou-se a variação na composição de espécies de ciliados, em diferentes estratos na lagoa do Guaraná, englobando períodos de águas altas e baixas, na planície de inundação do alto Rio Paraná. **Métodos:** As amostragens foram realizadas mensalmente entre março de 2007 e fevereiro de 2008, em três diferentes profundidades: epilimínio, metalimínio e hipolimínio. Depois de concentradas as amostras em rede de plâncton (10µm), os organismos foram identificados *in vivo* com auxílio de microscópio óptico. **Resultados:** Dentre as 112 espécies de ciliados identificadas, 13 foram encontradas exclusivamente no período de águas altas e 39 espécies no período de águas baixas. Os resultados do índice de extrapolação não paramétrica evidenciaram que a riqueza observada representou entre 70% e 90% da riqueza estimada para o ambiente. A variação da composição de espécies, quantificada pelo índice Beta1, indicou que a alteração da composição entre as profundidades nas águas baixas foi ligeiramente maior do que a registrada nas águas altas. A análise de Cluster evidenciou uma maior dissimilaridade na composição de espécies de ciliados entre os períodos do que entre as amostras das diferentes profundidades. As maiores diferenças na composição de espécies foram verificadas para os distintos períodos hidrológicos, enquanto que não foram observadas diferenças significativas em relação aos diferentes estratos da coluna de água. **Conclusões:** Verificou-se que, no compartimento pelágico a composição de espécies da comunidade de ciliados planctônicos mudou significativamente entre os períodos hidrológicos, e que uma maior similaridade na composição de espécies entre os estratos foi observada durante o período de águas altas. Dessa forma, alterações na distribuição vertical da composição podem estar relacionadas ao efeito homogeneizador das inundações na estabilidade da coluna de água.

Palavras-chave: protista; plâncton; riqueza de espécies; diversidade; água doce.

1. Introduction

River-floodplain systems are characterized by a great diversity of water bodies, including lotic, semi-lotic and lentic environments (Junk et al., 1989). This great environmental diversity, together with the connectivity among those habitats, and the exchange of organisms between the river and the adjacent floodplain, provide a high biodiversity, due to periods of low and high waters that result in a unique environmental condition, determined by the flood pulses (Neiff, 1990). The hydrological connectivity resulting from the flood pulse act as a homogenizing factor in the habitats of the Upper Paraná River floodplain (Thomaz et al., 2007). In fact, several studies show the importance of the flood pulse in structuring aquatic communities in floodplains (Algarte et al., 2009; Arrieira et al., 2017; Lansac-Tôha et al., 2009; Train & Rodrigues, 2004).

Ciliates are important components of food webs in floodplain environments, acting as a link between bacteria and flagellates and higher trophic levels (Azam et al., 1983; Segovia et al., 2015), besides feeding on phytoplankton organisms (Sherr & Sherr, 2002). However, as opposed to temperate regions, where temperature is the main factor structuring ciliate communities (Graham et al., 2004; Müller et al., 1991), in floodplain habitats of tropical regions the hydrological regime constitutes the major force influencing those protists (Pauleto et al., 2009). This temporal alteration of the hydrological regime provides the occurrence of species that are adapted to this condition, which is facilitated by mechanisms to persist in the environment during unfavorable periods (Lytle & Poff, 2004). For example, ciliate encystment allows some species to tolerate physical and chemical stresses and reduce their metabolic losses and risk of predation (Taylor, 1981).

Distinct ciliate communities are found in specific compartments within the same environment (Finlay & Esteban, 1998b; Zingel & Ott, 2000) showing clear patterns of vertical distribution (Mieczan, 2008). Oligotrichs usually dominate in the epilimnion in lakes of temperate regions, although individuals belonging to Prostomatida, Peritrichia and Haptorida are also frequently found in this water layer. Scuticuciliates, prostomatids and haptorids are usually more numerous in the intermediate layer (metalimnion) and scuticuciliates, heterotrichs and prostomatids are more representative in the hypolimnion (Mieczan, 2008; Zingel & Ott, 2000). On the other hand, in tropical lakes, which are usually shallower than temperate lakes, studies approaching ciliate vertical distribution are still scarce. Thus, we evaluated the variation in ciliate species composition in different strata and two hydrological periods in the Guaraná Lake, at the Upper Paraná River floodplain.

We hypothesized that planktonic ciliate species composition would be different among strata of the water column, considering that the lower strata would be more dissimilar due to the contribution of species associated with the sediment (not typically planktonic). Moreover, we predict that species composition among strata during high waters would be more similar than during low waters, based on seasonal alterations determined by the hydrological regime and considering that the flood pulse is the main factor structuring ciliate communities.

2. Material and Methods

2.1. Study area

Guaraná lake (22°43'S-53°18'W) is located in the Upper Paraná River floodplain, Brazil (Figure 1). This lake has 4.2 ha area and 3.2 m mean depth, it is usually covered by floating aquatic macrophytes

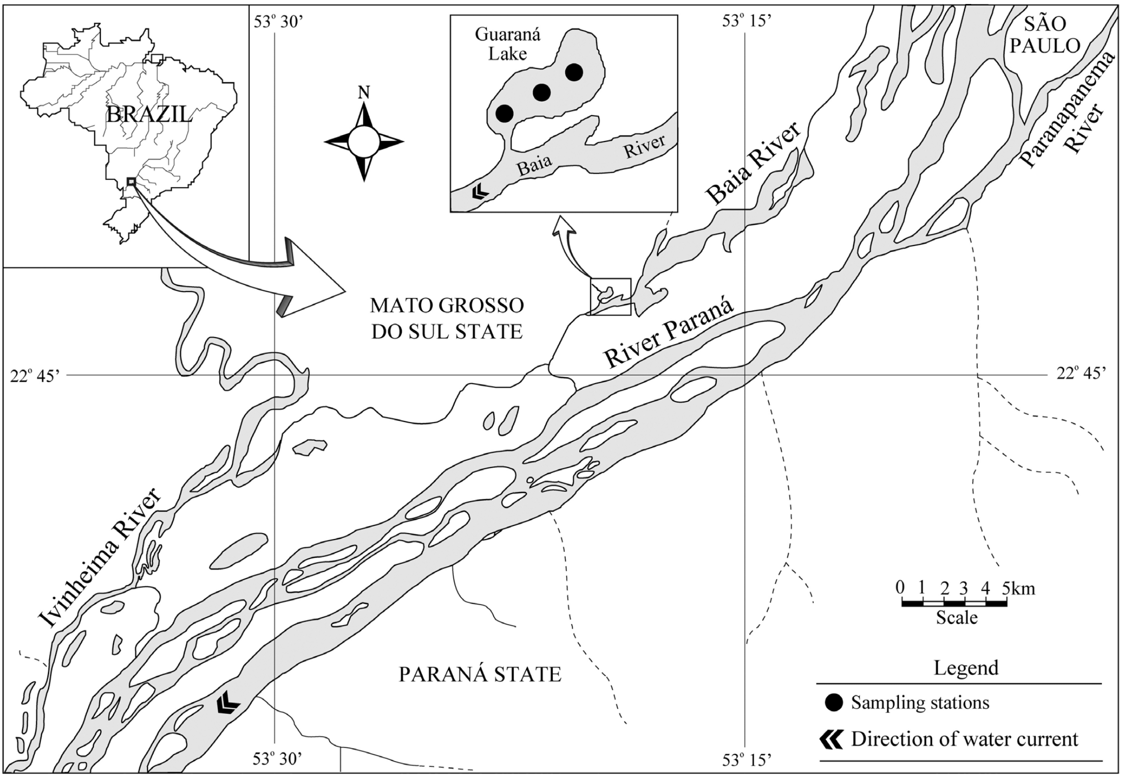

Figure 1. Study area showing the sampling sites at the Guaraná Lake.

(mainly *Eichhornia crassipes* (Mart.) Solms., *E. azurea* (Swartz) Kunth., *Pistia stratiotes* Linnaeus). It is connected to the Baía River by a 70m length channel (UEM, 2002). Mean values of some abiotic variables registered in our study were as follows: water temperature 25 °C, dissolved oxygen 5mg/L, pH 6.32, chlorophyll-*a* 10.85 µg/L, total phosphorus 32.3 µg/L, total nitrogen 1mg/L (see egovia et al., 2014 for a detailed table with all abiotic variables during high and low water periods).

2.2. Sampling and laboratory analysis

Sampling was performed in the Guaraná Lake from March 2007 to February 2008. Two-liter water samples were taken at three sampling sites in three different depths: epilimnion (approximately 20cm below the water/air interface), metalimnion (determined as the half of the total depth of the water column at the time of sampling) and hypolimnion (approximately 20 cm above the substrate), since thermal stratification was not observed in any occasion.

Samples were stored in 5 L bottles, kept cool and transported to the laboratory. Afterwards, samples were concentrated from 5 L to 100 ml using a plankton net of 10 µm mesh size. We counted the ciliates according to the live counting technique proposed by Madoni (1984), in which 10 replicates of 100 µl drops are counted per sample, under an optical microscope (Olympus CX-41), within a maximum period of 6 hours after sampling. Species were identified according to specialized bibliography: Corliss (1979), Dragesco & Dragesco-Kernéis (1986), Edmondson (1959), Foissner et al. (1991, 1992, 1994, 1995, 1999), Foissner & Berger (1996) and Patterson (1992).

2.3. Data analyses

Samples were categorized in two hydrological periods according to the average depth registered throughout the study period (Figure 2). We considered the months which exceeded the average depth (March, April and December 2007; January and February 2008) as high water period, whereas the other months were considered as low water period (May to November 2007).

We used a nonparametric procedure for the extrapolation of the species accumulation curve, based on incidence data: Jackknife 1, Jackknife 2 and Bootstrap, to estimate ciliate species richness and analyse which portion of the expected total species richness was registered in our study. Estimators were calculated using software EstimateS (Colwell, 2006).

Ciliate species were arranged according to their preferential habits (following Berger & Foissner, 2003) as planktonic (adapted to the pelagic compartment) or non-planktonic (associated to a substrate, from the littoral or benthic zones). The frequency of occurrence of ciliate species was calculated through the percentage of samples in which those species occurred (Fr=n*100/N, where **n** = species occurrence in the analysed samples and **N** = total number of analysed samples). According to their frequency of occurrence, species were then grouped in: constant (76% to 100% of samples), frequent (51% to 75% of samples), accessory (26% to 50% of samples) and accidental (less than 25% of samples) species.

Nonmetric multidimensional scaling (MDS) was performed to summarize patterns in species composition, based on Jaccard distance. Significant differences were tested through a Permutational Multivariate Analysis of Variance (PERMANOVA) determined by 999 permutations. MDS and PERMANOVA were performed in software R (R Core Team, 2013) using "vegan" package (Oksanen et al., 2016).

We used Beta 1 diversity index (Harrison et al., 1992) to quantify the turnover in ciliate species composition regarding the vertical distribution and hydrological periods, which was estimated through the expression: $\beta\text{-}1 = \{[(S/\alpha)-1]/(N-1)\}\times 100$, where **S** is the total number of ciliate species registered in each sampling site, α is the mean number of species found in the samples and **N** is the number of sampling units.

Cluster analysis (Hammer et al., 2001), based on Jaccard similarity coefficients, were performed to verify similarities in vertical and temporal distributions of ciliate species. Cophenetic Correlation Coefficient was calculated to estimate the representativeness of the dendrograms relative to the original data.

3. Results

In our study, 112 ciliate species were identified (Table 1). Nonparametric extrapolation indices results showed that the observed richness represented between 70% and 90% of the estimated richness. Bootstrap (124 species) was the index that better reflected the observed species richness (Figure 3).

Among the identified species, 13 were registered only during the high water period, whereas 39 species where registered only during the low water period. Nine species occurred exclusively at the epilimnion, four species only at the metalimnion and 21 species were registered only at the hypolimnion.

A total of 32 species were registered in all strata and both hydrological periods. *Halteria grandinella* Mueller, 1773, *Urotricha farcta* Claparède & Lachmann, 1859 and *Tintinnidium* cf. *pusillum* Entz, 1909, were registered in over 50% of the samples in each stratum, both during high and low water periods (Table 1).

Ciliate species belonging to 14 orders were identified. Heterotrichida, Hymenostomatida and Prostomatida showed the highest number of species (14 species each), followed by Haptorida, Hypotrichida and Scuticociliatida (13 species each), and Peritrichida (11 species). However, considering only frequent or constant species, Oligotrichida, Prostomatida (eight species each) and Peritrichida (six species) showed the highest number of species (Table 1).

Considering the number of ciliate species in each of the analysed months, Prostomatida, Oligotrichida

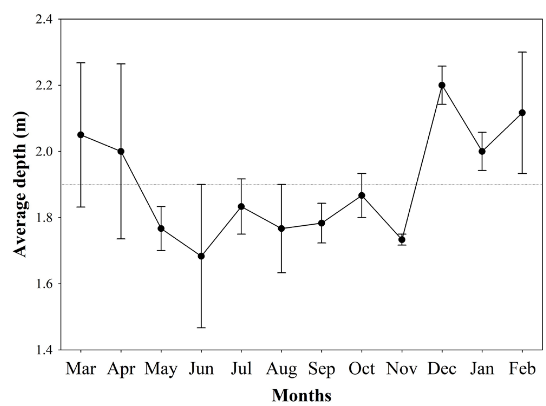

Figure 2. Average water depth registered at the Guaraná Lake during the study period (black dots = mean, bar = standard error).

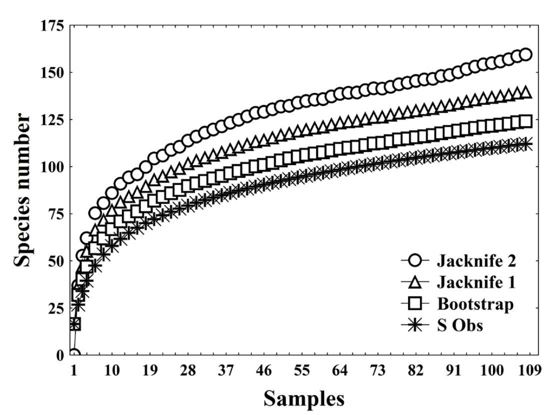

Figure 3. Nonparametric estimators for ciliate species richness in the Guaraná Lake.

Table 1. List of ciliate species registered in distinct strata (Ep = Epilimnion; Me = Metalimnion; Hy = Hypolimnion) in two hydrological periods (High water and Low water) at Guaraná Lake (H = Preferential Habitat; *P* = planktonic species and *N* = non-planktonic species).

Constancy index: Constant | Frequent | Accessory | Accidental | Absent

Species	H	High water Ep	High water Me	High water Hy	Low water Ep	Low water Me	Low water Hy
COLPODIDA							
Colpoda steinii Maupas, 1883	*N*	Accidental	Accidental		Accidental	Accidental	Accidental
Cyrtolophosis mucicola Stokes, 1885	*N*	Frequent	Accessory	Frequent	Accessory	Accessory	Accessory
Platyophrya vorax Kahl, 1926	*N*						Accidental
CYRTOPHORIDA							
Chlamydonella alpestris Foissner, 1979	*N*				Accidental	Accidental	Accidental
Odontochlamis alpestris Foissner, 1981	*N*					Accidental	
HAPTORIDA							
Actinobolina sp.	*P*		Accidental	Accidental		Accidental	
Askenasia volvox Eichwald, 1852	*P*				Accidental	Accidental	Accessory
Chaenea stricta Dujardin, 1841	*N*				Accidental		
Didinium nasutum Mueller, 1773	*N*			Accidental		Accidental	Accidental
Dileptus anastatica	*N*						Accidental
Enchelys gasterosteus Kahl, 1926	*N*			Accidental	Accidental	Accidental	Accidental
Enchelys sp.	*N*	Accessory	Accidental	Accidental	Accidental	Accessory	Accessory
Lacrymaria olor Mueller, 1786	*N*				Accidental		
Lagynophrya acuminata Kahl, 1935	*P*	Accessory	Accidental	Accidental	Accidental	Accidental	Accessory
Mesodinium pulex Claparède & Lachmann, 1859	*P*	Accessory	Accessory	Accessory	Frequent	Frequent	Frequent
Monilicaryon monilatus Stokes, 1886	*N*				Accidental		Accidental
Paradileptus ellephantinus Svec, 1897	*P*	Frequent	Accessory	Accessory	Frequent	Frequent	Frequent
Spathidium sp.	*N*	Accidental					
HETEROTRICHIDA							
Bursaridium pseudobursaria Fauré-Fremiet, 1924	*P*	Accidental			Accessory	Accidental	Accidental
Caenomorpha medusula Perty, 1852	*N*			Accidental			
Caenomorpha uniserialis Levander, 1894	*N*			Accidental			
Climacostomum virens Ehrenberg, 1838	*P*	Accidental	Accessory	Accidental	Accidental		Accidental
Condylostoma sp.	*N*				Accidental		
Linostomella vorticella Ehrenberg, 1833	*P*				Accidental	Accidental	
Phyalina sp.	*N*					Accidental	Accidental
Spirostomum minus Roux, 1901	*N*		Accidental	Accidental	Accidental	Accidental	Frequent
Spirostomum teres Claparède & Lachmann, 1858	*N*						Accessory
Stentor coeruleus Pallas, 1766	*N*						Accidental
Stentor muelleri Ehrenberg, 1831	*N*	Accidental	Accidental	Accidental			
Stentor multiformis Mueller, 1786	*N*			Accidental	Accidental		Accidental
Stentor niger Mueller, 1773	*N*				Accidental		
Stentor roeselii Ehrenberg, 1835	*N*	Accidental			Accidental		Accidental
HYMENOSTOMATIDA							
Dexyostoma campylum Stokes, 1886	*N*	Accidental	Accidental				
Disematostoma buetschilii Lauterborn, 1894	*P*	Accessory	Accessory	Accessory	Accessory	Accidental	Accidental
Epenardia myriophilii Penard, 1922	*N*						Accidental
Frontonia acuminata Ehrenberg, 1833	*N*						Accidental
Frontonia leucas Ehrenberg, 1833	*N*	Accidental	Accidental	Accidental			Accidental
Lembadion lucens Maskell, 1887	*N*	Accessory	Accidental	Accidental	Accidental	Accidental	Accidental
Ophryoglena sp.A	*N*				Accidental		Accidental
Ophryoglena sp.B	*N*						Accidental
Paramecium bursaria Ehrenberg, 1831	*P*						Accidental
Paramecium caudatum Ehrengerb, 1833	*N*				Accidental		
Paramecium putrinum Claparède & Lachmann, 1859	*N*						Accidental
Stokesia vernalis Wenrich, 1929	*P*	Accessory	Accessory	Frequent	Frequent	Constant	Frequent
Tetrahymena pyriformis Ehrenberg, 1830	*N*	Accessory	Accidental	Accidental	Accidental	Accidental	Accidental
Urocentrum turbo Mueller, 1786	*N*	Accessory	Accessory	Accidental	Accessory	Accidental	Accidental

Table 1. Continued...

Constancy index: Constant (black) | Frequent (dark grey) | Accessory (grey) | Accidental (light grey) | Absent (white)

Species	H	High water Ep	High water Me	High water Hy	Low water Ep	Low water Me	Low water Hy
HYPOTRICHIDA							
Aspidisca cicada Mueller, 1786	*N*				Accidental		Accidental
Aspidisca lynceus Mueller, 1773	*N*		Accidental				Accidental
Aspidisca turrita Ehrenberg, 1831	*N*						Accidental
Euplotes moebiusi Kahl, 1932	*N*				Accidental		
Euplotes sp.	*N*	Accidental	Accidental	Accidental			
Holosticha monilata Kahl, 1928	*N*						Accidental
Hypotrichidium conicum Ilowaisky, 1921	*P*	Accidental			Accidental		
Oxytricha sp.	*N*			Accidental	Accidental		Accidental
Spiretella plancticola Gelei, 1933	*N*				Accidental	Accidental	Accidental
Steinia platystoma Ehrenberg, 1831	*N*	Accessory	Accidental		Accidental	Accidental	Accidental
Stichotricha aculeata Wrzesniowski, 1886	*N*	Accidental	Accidental	Accidental	Accidental		Accidental
Uroleptus cf. *piscis* Mueller, 1773	*N*				Accidental	Accidental	Accessory
Hypotrichida sp.	*N*						Accidental
KARYORELICTIDA							
Loxodes magnus Stokes, 1887	*N*	Accessory	Accessory	Accessory	Accidental	Accidental	Accessory
NASSULIDA							
Microthorax pusillus Engelmann, 1862	*N*		Accidental			Accidental	
OLIGOTRICHIDA							
Codonella cratera Leidy, 1877	*P*			Accidental	Constant	Frequent	Constant
Halteria grandinella Mueller, 1773	*P*	Constant	Constant	Constant	Frequent	Frequent	Frequent
Limnostrombidium sp.	*P*	Frequent	Frequent	Accessory	Accidental	Accidental	Accidental
Pelagostrombidium mirabile Penard, 1916	*P*	Constant	Frequent	Accessory	Frequent	Accessory	Accidental
Rimostrombidium humile Penard, 1922	*P*	Frequent	Frequent	Constant	Accessory	Accessory	Accessory
Rimostrombidium lacustris Foissner & Pratt, 1988	*P*	Accessory	Accessory	Accessory	Accessory	Frequent	Frequent
Strobilidium caudatum Fromentel, 1876	*N*	Accidental		Accidental	Accidental		
Tintinnidium cf. *pusillum* Entz, 1909	*P*	Constant	Constant	Frequent	Constant	Constant	Constant
Tintinnidium fluviatile Stein, 1863	*P*				Accessory	Accessory	Frequent
PERITRICHIDA							
Campanella umbellaria Linnaeus, 1758	*N*	Accidental	Accidental	Accidental	Accidental	Accessory	Accidental
Epicarchesium pectinatum Zacharias, 1897	*P*	Accidental	Accidental	Accessory	Accessory	Accessory	Accessory
Epistylis anastatica Linnaeus, 1767	*P*						Accidental
Epistylis pygmaeum Ehrenberg, 1838	*P*	Frequent	Accessory	Frequent	Accidental	Accessory	Accessory
Opercularia nutans Ehrenberg, 1831	*N*			Accidental			
Pelagovorticella natans Fauré-Fremiet, 1924	*P*		Accidental		Accidental	Accessory	Accidental
Vorticella aquadulcis Stokes, 1885	*N*	Accidental	Accidental	Accidental	Frequent	Frequent	Frequent
Vorticella campanula Ehrenberg, 1831	*N*	Accidental	Accidental	Accidental		Accidental	Accidental
Vorticella convallaria Linnaeus, 1758	*N*	Accidental	Accidental	Accidental			
Vorticella picta Ehrenberg, 1831	*N*	Accessory	Accidental	Accessory			
Zoothamnium procerus Kahl, 1935	*N*						Accidental
PLEUROSTOMATIDA							
Litonotus alpestris Foissner, 1978	*N*						Accidental
Litonotus crystallinus Vuxanovici, 1960	*N*			Accidental			
Loxophyllum utricularie Penard, 1922	*N*						Accidental
PROSTOMATIDA							
Balanion planctonicum Foissner, Oleksiv & Mueller, 1990	*P*	Frequent	Constant	Frequent	Accessory	Accessory	Accessory
Bursellopsis spumosa Schmidt, 1920	*P*				Accidental	Accidental	Accidental
Coleps elongatus Ehrenberg, 1831	*N*	Accidental	Accidental	Accessory	Accessory	Accessory	Accessory
Coleps hirtus Mueller, 1786	*N*	Accidental	Accidental	Accessory	Accessory	Accessory	Accessory
Coleps sp.	*N*	Accessory	Accidental	Accidental	Accidental	Accidental	Accidental
Holophrya discolor Ehrenberg, 1833	*N*	Accidental	Accidental	Accidental	Accidental	Accidental	Accidental
Holophrya ovum Ehrenberg, 1831	*N*	Accidental		Accessory	Accidental	Accessory	Accessory

Table 1. Continued...

Constancy index: ■ Constant ■ Frequent ■ Accessory ■ Accidental □ Absent

Species	H	High water Ep	High water Me	High water Hy	Low water Ep	Low water Me	Low water Hy
Holophrya teres Ehrenberg, 1833	*N*		Accidental	Accidental			Accidental
Placus luciae Kahl, 1926	*N*					Accidental	Accidental
Plagiocampa rouxi Kahl, 1926	*N*	Accidental	Accidental	Accessory	Accidental	Accidental	Frequent
Urotricha farcta Claparède & Lachmann, 1859	*N*	Constant	Constant	Frequent	Frequent	Frequent	Constant
Urotricha furcata Schewiakoff, 1892	*P*		Accidental				
Urotricha platystoma Stokes, 1886	*P*	Accidental		Accidental			
Urotricha sp.	*P*	Accessory	Accidental	Accessory	Constant	Frequent	Frequent
SCUTICOCILIATIDA							
Calyptotricha lanuginosa Penard, 1922	*N*	Accessory	Accidental	Accessory	Accessory	Accessory	Accessory
Cinetochilum margaritaceum Ehrenberg, 1831	*N*	Accessory	Accidental	Accessory	Accidental	Accidental	Accidental
Cristigera cf. *phoenix* Penard, 1922	*N*	Accidental	Accidental	Accidental		Accidental	Accessory
Ctedoctema acanthocryptum Stokes, 1884	*N*		Accidental		Accidental		Accidental
Cyclidium glaucoma Mueller, 1773	*N*	Frequent	Frequent	Frequent	Accessory	Accessory	Accessory
Cyclidium heptatricum Schewiakoff, 1893	*N*	Accidental	Accidental	Accidental	Accidental	Accidental	Accidental
Dexiotricha granulosa Kent, 1881	*N*	Accidental	Accessory	Accessory	Accidental	Accidental	Frequent
Dexiotricha sp.	*N*			Accidental	Accidental	Accidental	Accidental
Histiobalantium sp.	*P*	Accidental			Accidental		Accidental
Loxocephalus luridus Eberhard, 1862	*N*						Accidental
Philasterides armatus Kahl, 1926	*N*					Accidental	
Platynematum sociale Penard, 1922	*N*				Accidental		Accidental
Pleuronema cf. *smalli* Borror, 1972	*N*	Accidental					
SYNHYMENIIDA							
Chilodontopsis depressa Perty, 1852	*N*					Accidental	Accidental

and Scuticociliatida showed the greater number of species. Haptorida and Peritrichida also showed a high number of species (Figure 4).

Regarding the distinct strata, Prostomatida showed the highest number of species in each vertical compartment, especially at the metalimnion. Scuticociliatida, Haptorida and Oligotrichida were also important in all strata, whereas Nassulida occurred only at the metalimnion, Pleurostomatida occurred only at the hypolimnion, and Synhymeniida was absent at the epilimnion (Figure 5).

Over 70% of the ciliate species (82 species) could be considered non-planktonic and associated with some type of substrate, whereas only 26.8% (30 species) are truly planktonic. Thus, there was a dominance of non-planktonic species, mainly in March and May, when those organisms represented over 66% of the total species number. (Figure 6).

Considering the two hydrological periods, non-planktonic species remained dominant, mainly during the low water period when 71 non-planktonic species (71.7%) and 28 planktonic species (28.3%) were registered. In the same way, during the high water period 49 non-planktonic (67.1%) and 24 planktonic (32.9%) species were found (Figure 7A).

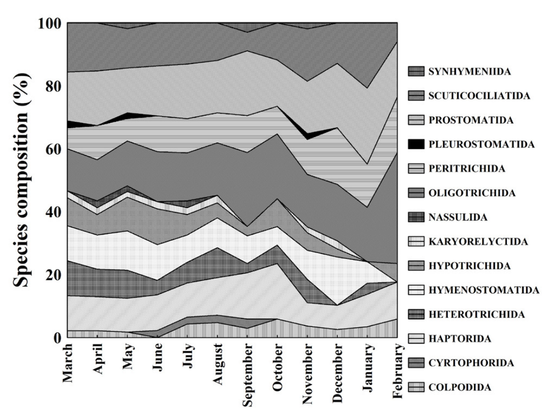

Figure 4. Composition by order (%), registered in the analysed months at Guaraná Lake.

Regarding the vertical distribution of the preferential habitat, a greater number of non-planktonic species was registered in all strata. The highest relative contribution of non-planktonic species percentage was found in the hypolimnion (70 species, corresponding to 72.2% of total species), followed by the epilimnion (54 species, or 67.5% of total species) and metalimnion (47 species, equivalent to 65.3% of total species) (Figure 7B).

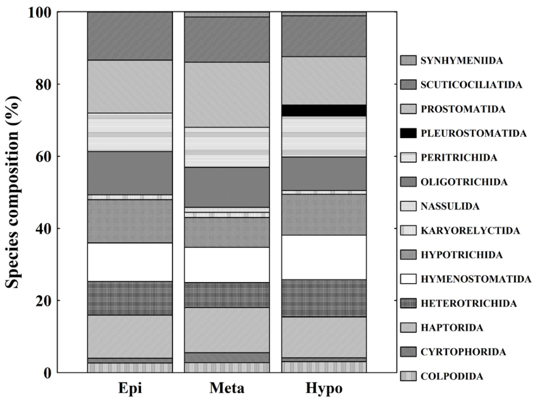

Figure 5. Composition by order (%) registered in the distinct strata in the Guaraná Lake. Epi=Epilimnion, Meta=Metalimnion, Hypo=Hypolimnion.

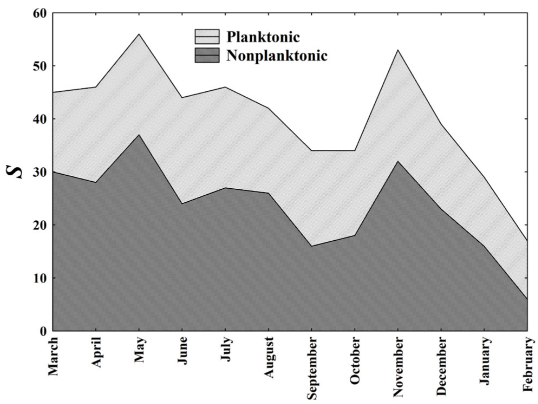

Figure 6. Species richness of planktonic and non-planktonic ciliates, analysed monthly at Guaraná Lake.

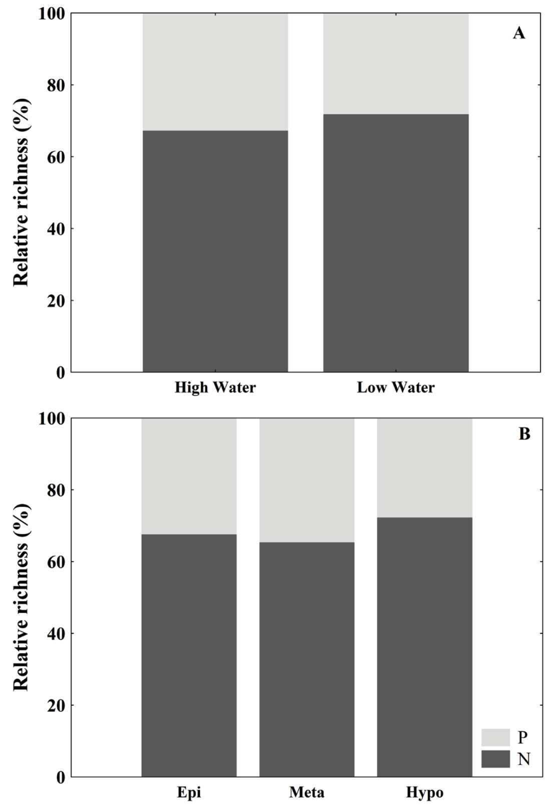

Figure 7. Relative species richness (%) of planktonic (P) and non-planktonic (N) ciliates in two hydrological periods (A) and three different strata (B) in the Guaraná Lake. Epi=Epilimnion, Meta=Metalimnion, Hypo=Hypolimnion.

Ciliate species turnover indicated that the alteration in composition among strata was slightly higher during the low water period (26%) than in the high water period (20.2%) (Figure 8A). Considering the turnover in composition in each stratum between hydrological periods, changes were more pronounced. Higher turnover rate was registered in the hypolimnion (33.8%), followed by the metalimnion (26.3%) and the epilimnion (21%) (Figure 8B).

Cluster analysis (Cophenetic Correlation Coefficient = 0.87) showed a higher dissimilarity in ciliate species composition between hydrological periods than among strata. Therefore, the analysis distinguished two groups coinciding with the hydrological periods. Moreover, there was a higher similarity between the epilimnion and the metalimnion (0.64) during the low water period, and a higher similarity between the metalimnion and the hypolimnion (0.71) during the high water period (Figure 9).

MDS results showed that sampling units were separated only regarding the two hydrological periods, but not regarding the different strata (Figure 10). PERMANOVA statistically confirmed significant differences in ciliate composition between the hydrological periods (Pseudo-F=4.0236; $p<0.001$), whereas no significant differences were found in the pairwise comparison between epilimnion and metalimnion (Pseudo-F=0.31467; $p=0.996$), between epilimnion and hypolimnion (Pseudo-F=0.80554; $p=0.713$) nor between metalimnion and hypolimnion (Pseudo-F=0.6299; $p=0.903$).

4. Discussion

The high number of ciliate species registered in the Guaraná Lake not only exceeds the gamma diversity found in freshwater environments both in Brazil (Bossolan & Godinho, 2000; Cardoso, 2007; Dias et al., 2008; Gomes & Godinho, 2003)

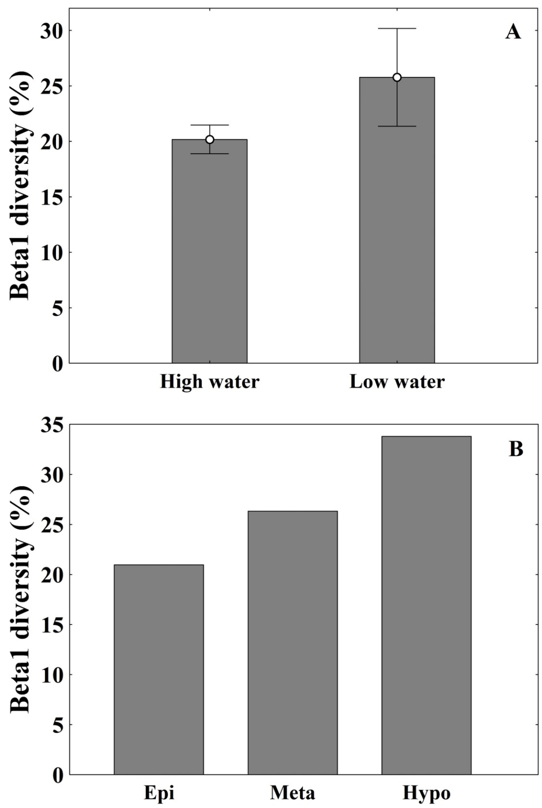

Figure 8. Beta1 diversity index showing species turnover (%) among strata during two hydrological periods (A) and between hydrological periods in the distinct strata (B). Epi=Epilimnion, Meta=Metalimnion, Hypo=Hypolimnion.

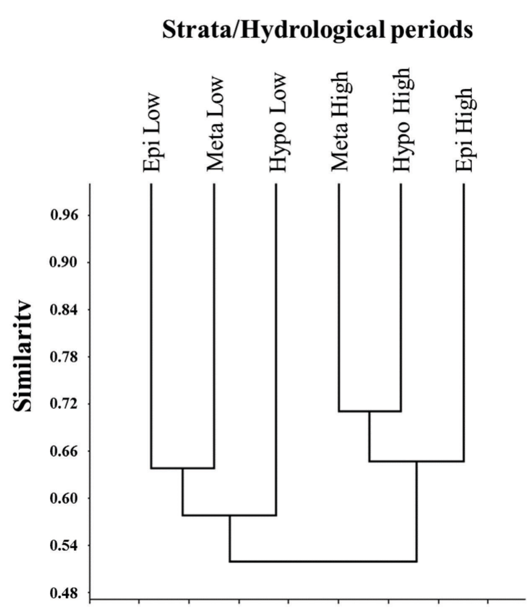

Figure 9. Cluster analysis based on ciliate species occurrence in distinct strata (Epi=epilimnion, Meta=metalimnion, Hypo=hypolimnion) in two hydrological periods (High water and Low water periods) at Guaraná Lake.

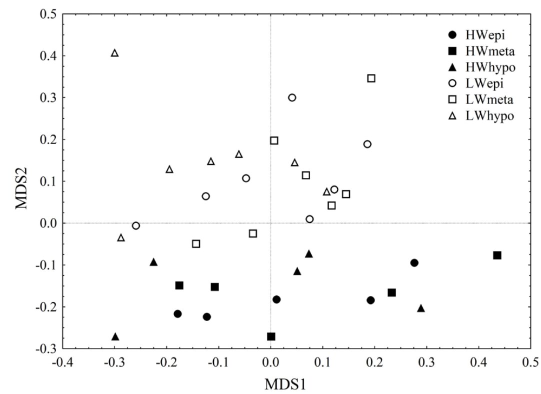

Figure 10. Multi-dimensional scaling (MDS) plot based on Jaccard distances in three different strata in two hydrological periods (HWepi = epilimnion during high waters; HWmeta = metalimnion during high waters; HWhypo = hypolimnion during high waters; LWepi = epilimnion during low waters; LWmeta = metalimnion during low waters; LWhypo = hypolimnion during low waters).

and other regions of the globe (Carrick, 2005; Mayer et al., 1997; Muki et al., 2005; Song, 2000a; Wiackowski et al., 2001), but is also similar to the number of species found by Madoni & Braghiroli (2007) in six sampling sites in an Italian river system, and by Pfister et al. (2002) in 58 north German lakes of distinct trophic status.

Previous samplings performed by Pauleto et al. (2009) in the Guaraná Lake found only 36 ciliate species, however, their sampling design was different: one sample was taken during the high water and one during the low water period. Meanwhile, in our study, in which samplings were performed monthly during a whole year at this same lake, 112 ciliate species were found. This supports the idea that long-term approaches with high sampling effort are necessary in order to determine the total diversity of dynamic environments, which encompasses both active and passive diversities (Finlay & Esteban, 1998a).

Our results evidenced the great biodiversity of floodplain lakes which is, in part, determined by the contribution of non-planktonic organisms from the littoral region and the sediment (Lansac-Tôha et al., 2009). Indeed, non-planktonic ciliates constituted most of the species richness registered in the pelagic compartment of Guaraná Lake. Ciliate species richness is, in general, favoured by the occurrence of macrophyte banks (Song, 2000b), especially the more diverse ones, which support higher species richness and abundance of non-planktonic organisms (Karus et al., 2014), contributing to the increment of species of the planktonic community.

The massive contribution of non-planktonic organisms in the pelagic compartment was also observed in studies approaching the zooplankton community in the Upper Paraná River floodplain (Alves et al., 2010; Bonecker et al., 1998; Lima et al., 1998), which evidenced that the faunal exchange between lake compartments occurred mainly during floods due to greater habitat connectivity, leading to the presence of both planktonic and non-planktonic species within the community.

Most of the truly planktonic species are, in general, cosmopolitan, and are thus commonly registered in lake habitats (Pfister et al., 2002). Although *Urotricha farcta* typically inhabits mainly the benthic compartment, it is also found in the pelagic region of lakes and rivers of reduced water flow rates (Berger & Foissner, 2003). Organisms belonging to this genus, despite their small size, are efficient predators and highly adaptable and tolerant, and are one of the few to be present even in extremely acidic lakes (pH = 3.0) (Packroff, 2000).

Halteria grandinella and *Tintinnidium* cf. *pusillum*, besides other species that were common in our study, such as *Rimostrombidium humile* and *Pelagostrombidium mirabile,* belong to the order Oligotrichida and are characteristic of the pelagic compartment of lentic environments (Mieczan, 2007; Müller, 1989). These organisms are filter-feeders and feed on bacteria and/or small sized algae, besides being totally adapted to the pelagic environment (Foissner & Berger, 1996). We found a high number of species belonging to Prostomatida and Scuticociliatida, which are important in the metalimnion and the hypolimnion of stratified lakes (Zingel, 2005), reinforcing the influence of littoral and benthic regions in ciliate species composition of the pelagic compartment of the lake. The constant presence of those ciliate orders, which are mostly omnivorous or bacterivorous, suggests a continuous input of organic matter from the marginal zone to the central region of the lake, facilitated in environments with reduced dimensions such as the Guaraná Lake.

We found a greater turnover in species composition of the distinct strata during low waters than during high waters. Similarly, the greater temporal turnover found at the hypolimnion suggests the development of a distinctive community at the bottom of the lake at certain stages of the year. These findings are corroborated by the Cluster results (see Figure 10), which indicates the lowest similarity between samples from the hypolimnion and the other strata during the low water period. During low waters, the wind action is more pronounced because lakes are shallower, inducing water circulation and destratification (Thomaz et al., 2004), which lead to a higher similarity in the ciliate species composition between the epilimnion and metalimnion strata. Meanwhile, in the hypolimnion we found the highest number of exclusive ciliate species, which indicates that a unique community was formed in this water layer. On the other hand, during high waters, there is a relatively stable thermal stratification (Thomaz et al., 2004), which likely resulted in the distinction of the epilimnion from the other two water layers.

Although we found differences in ciliate species composition among strata, a higher dissimilarity was found between hydrological periods in Guaraná Lake. In fact, the flood pulse is recognized as the main factor structuring aquatic communities (Junk et al., 1989; Neiff, 1990), and was also found to be the major factor influencing the ciliate community in the Upper Paraná River floodplain lakes (Pauleto et al., 2009).

In summary, our hypotheses were corroborated, since we found that, in the pelagic compartment, ciliate species composition changed significantly between hydrological periods, and a higher similarity in species composition among strata was observed during the high water period. Therefore, alterations in the vertical distribution seem to be related to the homogenizing effect of the floods in the water column stability.

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