Spatial and temporal patterns of ciliate species composition (Protozoa: Ciliophora) in the plankton of the Upper Paraná River floodplain

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(With 6 figures)

Abstract

Spatial and temporal patterns of plankton ciliates species composition in the Paraná River floodplain were investigated. Samplings were carried out in twelve environments in two distinct hydrological periods (limnophase and potamophase). A total of 61 species of ciliates were recorded, and among them 21 are classified as pelagic while 40 are considered preferentially as littoral species. The registered species belong to eleven orders, and among them, Prostomatida was the most specious followed by Hymenostomatida and Peritrichida. The ciliate species composition was significantly distinct between periods, but not among environments. In this way, typically pelagic species characterized the ciliate community during the limnophase period, while the littoral species were predominant during the potamophase period. Our results strongly support the idea of the flood pulse as the main factor driving the composition pattern of the planktonic ciliates community in the Paraná River floodplain.

Keywords: planktonic ciliates, species composition, floodplain, Paraná River.

Padrões espaciais e temporais da composição de espécies de ciliados (Protozoa: Ciliophora) no plâncton da planície de inundação do Alto Rio Paraná

Resumo

No presente estudo foram investigados os padrões espaciais e temporais da composição de espécies de ciliados planctônicos na planície de inundação do Alto Rio Paraná. As amostras foram obtidas em 12 ambientes, em dois períodos hidrológicos distintos (limnofase e potamofase). Foram registradas 61 espécies de ciliados entre as quais 21 foram classificadas como pelágicas enquanto 40 foram consideradas preferencialmente litorâneas. As espécies registradas pertencem a 11 ordens, sendo Prostomatida foi a mais especiosa, seguida por Hymenostomatida e Peritrichida. A composição de espécies de ciliados foi significativamente distinta entre os períodos hidrológicos, enquanto que entre os ambientes, diferenças na composição não foram evidenciadas. Dessa forma, espécies tipicamente pelágicas caracterizaram a comunidade de ciliados na limnofase, enquanto que espécies litorâneas foram preponderantes para a composição de ciliados na potamofase. Os resultados suportam a idéia do pulso de inundação como principal fator controlador dos padrões de composição da comunidade de ciliados planctônicos na planície de inundação do Alto Rio Paraná.

Palavras-chave: ciliados planctônicos, composição de espécies, planície de inundação, Rio Paraná.

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1. Introduction

Due to their fluvial dynamics, floodplains are characterized by the presence of several water bodies, with a high diversity of lotic, lentic and semi-lotic environments, that should be integrally analyzed, as an unit denominated the "river-floodplain system" (Junk et al., 1989). The seasonal alternation between the dry and the flood periods establishes a particular environmental situation characterized by "hydrological pulses" (Neiff, 1990). Because of this high level of spatial and temporal heterogeneity, floodplains have one of the highest levels of biodiversity among the known aquatic environments. The connectivity among the environment must be considered as an essential factor that strongly contributes to the spatial and temporal dynamic of these ecosystems (Ward et al., 1999).

In the Upper Paraná River floodplain, studies of the biodiversity and different ecological aspects of many aquatic communities, including planktonic communities, have been performed over several years (Lansac-Tôha et al., 2009). These studies demonstrated the relevance of the flood pulse and the hydrological connectivity on the communities' structures. However, surveys of the biodiversity and ecology of protozoa ciliates are still scarce in the Neotropical region, especially in the floodplain systems.

Protozoans play a relevant role in the metabolism of aquatic ecosystems. According to Finlay and Esteban (1998), the predation of protozoans on the other microorganisms stimulates the microbial community, and increases the nutrients cycling that would otherwise remain in the bacterial biomass. Considering the seasonal succession of the plankton community, the ciliates are efficient predators of the phytoplankton (Schweizer, 1997), acting as competitors to the rotifers and microcrustaceans, though these protozoans are also consumed by these predators of larger body size (Müller et al., 1991).

The trophic state is essential for the determination of the pattern of variation in the spatial and temporal distribution of planktonic ciliates (Velho et al., 2005). In the lotic environments, the flushing rate is a central factor affecting the organization of aquatic communities. Seasonal changes in this discharge regime play an important function, structuring the ciliates assemblages and determining their role in the trophic food web (Primc-Habdija et al., 1998; Bereczky, 1998).

This study analyzed the variation in the species composition during distinct hydrological periods (limnophase or lower water period, and potamophase or high water period) and environments (lakes, rivers and channels) in the Upper Paraná River floodplain. Additionally, this study emphasized the relative importance of flood pulse, connectivity and hydrodynamics as driving the patterns of ciliates species composition.

2. Material and Methods

2.1 Study area

The study was performed in twelve environments in the Upper Paraná River floodplain (22° 40'-22° 50' S and 53° 10'-53° 40' W), belonging to Paraná, Baía and Ivinheima systems. Within each system, four environments were selected, including the main river, a closed lake, an open lake and a channel (see Figure 1).

The Paraná system consists of the Paraná River and associated floodplain lakes in the islands and "várzea". The stretch of this river that was studied presents a braided channel, with mean current flow relatively high, varied width and extensive islands and lateral bars. In this stretch, the river is 4.0 m in mean depth, and it can reach a maximum depth of 15.0 m (Thomaz et al., 1992). In this system, we collected samples in the Paraná River, Cortado channel, Garças (open lake) and Osmar (closed lake), see Figure 1.

The Baía system encompasses the Baía River and several associated lakes along its course, and it is connected to Paraná River through a channel in its lower portion. This sinuous river presents varied width, a mean depth of 3.2 m, low declivity and low current flow, and is directly influenced by the hydrological regime of Paraná River (Thomaz et al., 1991) In this system, we collected samples in the Baía River, Curutuba Channel, Guaraná (open lake) and Fechada (closed lake), see Figure 1.

The Ivinheima system is formed by the Ivinheima River and floodplain lakes associated with this river, which is one of the main tributaries located at the right bank of the Paraná River. It has a mean depth of 3.9 m. It presents turbulent waters and runs parallel to the Paraná River in its lower stretch. It is connected to the Baía River through the Curutuba River, and to the Paraná River through the Ipoitã Channel and two other channels (Thomaz et al., 1992). In this system, we collected samples in the Ivinheima, Ipoitã channel, Patos (open lake) and Ventura (closed lake), see Figure 1.

2.2 Sampling and laboratory analysis

Samplings were carried out in February 2007 (potamophase period) and August 2007 (limnophase period). Samples (2 L) were taken in triplicate in the pelagic zone from each environment using the Van Dorn bottle. The material was stored in plastic flasks and transported to the laboratory where it was concentrated via a plankton net (10 μm). The ciliates were analyzed in vivo, within a maximum period of 6 hours after the sampling, using an optical microscope (Olympus CX-41), based mainly on the work Foissner and Berger (1996) and Foissner et al. (1999).

2.3 Data analyses

In order to estimate the ciliate species richness and analyze which portion of the expected total species richness was recorded in the present survey, different nonparametric extrapolating indices based on incidence
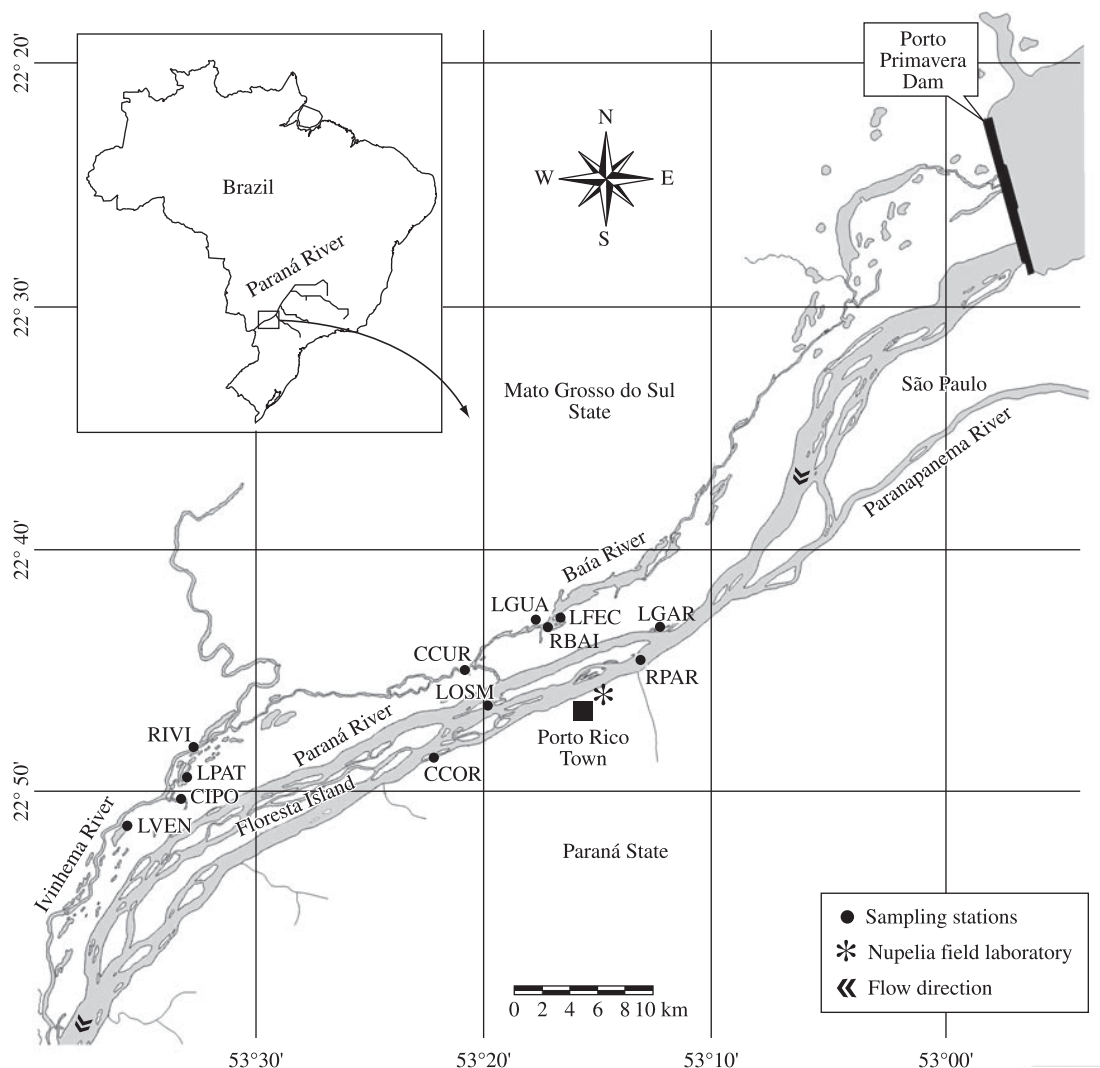
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Figure 1. Study area with the location of the sampling stations. Paraná River (RPAR); Baía River (RBAI); Ivinheima River (RIVI); Ipoitã Channel (CIPO); Curutuba Channel (CCUR); Cortado Channel (CCOR); Garças Lake (LGAR); Patos Lake (LPAT); Fechada Lake (LFEC); Guaraná Lake (LGUA); Ventura Lake (LVEN) and Osmar Lake (LOSM).

data were used. Jacknife1 and 2, and Bootstrap estimators were used, and the calculation was done using the EstimateS software (Colwell, 2006).

The classification of pelagic and littoral species was done according to Berger and Foissner (2003). The occurrence frequency of a particular species was calculated as the percentage of samples in which the species occurs ($Fr = n * 100 / N$, where n = occurrences of the species in the analyzed samples and N = total number of analyzed samples). According to this occurrence, the species were classified into the four proposed groups as follows: constant species (i.e. occurring in 76-100% of the samples), frequent species (i.e. occurring in 51-75%), accessory species (i.e. occurring in 26-50% of the samples), and accidental species (i.e. occurring in below 25% of the samples).

Detrended Correspondence Analysis (DCA) (Hill and Gauch, 2004) was performed to summarize changes in the ciliates composition among the environments and between the hydrological periods. This analysis was carried out using the PC-ORD software (version 4.1; McCune and Mefford, 1999).

Aiming to quantify the alterations in the ciliate species composition between the hydrological periods and in the several environment types, the Beta (β-1) index was estimated (Harrison et al., 1992) through the following expression:

$$\beta - 1 = \{[(S / \alpha) - 1] / (N - 1)\} \times 100 \qquad (1)$$

where S is the total number of ciliate species recorded at each environment type; α is the mean number of species

Table 1. Faunistic survey of ciliate species recorded in the different types of environments and periods in the Upper Paraná River floodplain. (H = Habitat; P = pelagic species and L = littoral species) (Ri = Rivers, Ch = Channels; OL = Open lakes; CL = Closed lakes) (Code = codes used in DCA analysis). Constancy index:

Species	H	Potamophase				Limnophase				Code
		Ri	Ch	OL	CL	Ri	Ch	OL	CL	
COLPODIDA										
Colpoda steinii Maupas, 1883	P				░	░	░	░		Cst
Cyrtolophosis mucicola Stokes, 1885	L	▒	░	░	░	░	░	░		Cmu
HAPTORIDA										
Actinobolina sp.	P			░		░	░		░	Act
Askenasia volvox (Eichwald, 1852) Kahl, 1930	P		░			░	░	▓		Avo
Lacrymaria olor (Mueller, 1786) Bory Saint-Vincent, 1824	L		░				░	░	░	Lol
Lagynophrya acuminata Kahl, 1935	P	░	░	░				▓	▒	Lac
Mesodinium pulex (Clap. and Lach., 1859) Stein, 1867	P	░	▒	░	▒		░	▓	▓	Mpu
Paradileptus ellephantinus (Svec, 1897) Kahl, 1931	P	░	░	░		░		▓		Pel
Spathidium sp.	L		░	░						Spa
HETEROTRICHIDA										
Spirostomum minus Roux, 1901	L							░		Smi
Stentor muelleri Ehrenb., 1831	L			░	░					Smu
Stentor niger (Mueller, 1773) Ehrenb., 1831	L	░	░							Sni
Stentor roeselii Ehrenb., 1835	L	░								Sro
HYMENOSTOMATIDA										
Dexiotricha granulosa (Kent, 1881) Foissner et al., 1994	L			░						Dgr
Disematostoma buetschilii Lauterborn, 1894	P			░						Dbu
Frontonia acuminate (Ehrenb., 1833) Buetschilii, 1889	L								░	Fac
Frontonia atra (Kahl, 1931) Buetschilii, 1889	L			░						Fat
Lembadion lucens (Maskell, 1887) Kahl, 1931	L				░					Llu
Paramecium bursaria (Ehrenb., 1831) Focke, 1836	L		░							Pbu
Stokesia vernalis Wenrich, 1929	P		░			▒		▓	░	Sve
Tetrahymena pyriformis Ehrenb., 1830	L		░	▒						Tpy
HYPOTRICHIDA										
Aspidisca cicada (Mueller, 1786) Clap. and Lach., 1858	L		░							Aci
Aspidisca lynceus (Mueller, 1773) Ehrenb., 1830	L							░		Aly
Holosticha monilata Kahl, 1928	L									Hmo
Oxytricha sp.	L	░	░					░		Oxy

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Table 1. Continued...

Species		Potamophase				Limnophase				
	H	**Ri**	**Ch**	**OL**	**CL**	**Ri**	**Ch**	**OL**	**CL**	**Code**
Stichotricha aculeata Wrzesniowski, 1886	L	░			░				░	Sac
KARIORELICTIDA										
Loxodes magnus Stokes, 1887	L	░	░		░					Lma
OLIGOTRICHIDA										
Codonella cratera (Leidy, 1877) Imhof, 1885	P					▓	▒	█	█	Ccr
Halteria grandinella (Mueller, 1773) Dujardin, 1841	P	▒	░	▒	▓	▒		█	█	Hgr
Limnostrombidium sp.	P	▒	▒	▒	▒	░	▒	▒	█	Lim
Rimostrombidium humile (Penard, 1922) Petz and Foissner, 1992	P	░	▒	▒	░			█	▓	Rhu
Rimostrombidium lacustris (Foissner et al., 1988) Petz and Foissner, 1992	P	░	▒	▒	░	▒		▒	█	Rla
Tintinnidium fluviatile (Stein, 1863) Kent, 1881	P					█			░	Tfl
Tintinnidium sp.	P	▒	▒	▒	▒	█	▓	█		Tin
PERITRICHIDA										
Campanella umbellaria (Linn., 1758) Goldfuss, 1820	L	░	▒							Cum
Epicarchesium pectinatum Zacharias, 1897	P	░		░	▒	░	░	▓	▒	Epe
Epistylis coronata Nusch, 1970	L					░				Eco
Epistylis pygmauem Ehrenb., 1838	P	░		░				▒	░	Epy
Opercularia nutans (Ehrenb., 1831) Stein, 1854	L					░				Onu
Pseudovorticella chlamydophora (Penard, 1922) Jankowski, 1976	L								░	Pch
Vorticella aquadulcis Stokes, 1885	L	░		░		▒	░	█	█	Vaq
Vorticella campanula Ehrenb., 1831	L		░	▒				░		Vca
PLEUROSTOMATIDA										
Litonotus lamella (Mueller, 1773) Foissner et al., 1995	L									Lla
PROSTOMATIDA										
Balanion planctonicum Foissner et al., 1994	P	▓	▒	▒	▓	░	░	▓	▓	Bpl
Bursellopsis sp.	P			░				░		Bur
Bursellopsis spumosa (Schmidt, 1920) Corliss, 1960	P	░	░							Bsp
Coleps elongatus Ehrenb., 1831	L	▒		░						Cel
Coleps hirtus (Mueller, 1786) Nitzsch, 1827	L					░	▓	▓		Chi
Coleps sp.	L							░	░	Col
Enchelys sp.	L							▒	▓	Enc
Holophrya discolor Ehrenb., 1833	L					░		░	▒	Hdi
Holophrya ovum Ehrenb., 1831	L			░				░		Hov

Table 1. Continued...

Species	Potamophase					Limnophase				
	H	**Ri**	**Ch**	**OL**	**CL**	**Ri**	**Ch**	**OL**	**CL**	**Code**
Holophrya teres (Ehrenb., 1833) Foissner et al., 1994	L									Hte
Urotricha farcta Clap. and Lach., 1859	L									Ufa
Urotricha sp.	P									Uro
SCUTICOCILIATIDA										
Calyptotricha lanuginosa (Penard, 1922) Wilbert and Foissner, 1980	L									Cla
Cinetochilum margaritaceum (Ehrenb., 1831) Perty, 1849	L									Cma
Ctedoctema acanthocryptum Stokes, 1884	L									Cac
Cyclidium glaucoma Mueller, 1773	L									Cgl
Cyclidium heptatricum Schewiakoff, 1893	L									Che
Pleuronema cf. *smalli* Dragesco, 1968	L									Psm

■ Constant   ■ Frequent   ■ Acessory   ■ Accidental   ☐ Lacking

found in the samples; and N is the number of sampling units.

A Cluster Analysis (expressed by a dendrogram) based on the Jaccard index was carried out to verify the similarity of the ciliates species composition among the environment types and between periods. The Cophenetic Correlation Coefficient was calculated to estimate how much the dendrogram represented the original data.

Finally, in order to test the statistical significance of the differences in the distribution of scores from the different periods and environments derived from a DCA, we performed an ANOVA (Statsoft, 2000), considering $p < 0.05$ as significant.

3. Results

Considering both periods and environments, 61 ciliate species were identified (as shown in Table 1). The results from the non-parametric extrapolating index demonstrated that the observed richness represented between 71 and 91% of the estimated richness. Bootstrap (67 species) was the extrapolating index that best reflected the observed richness (see Figure 2).

Among the 61 identified species, 18 species were recorded only during the potamophase and 11 species were found only during the limnophase (as shown in Table 1). Fourteen species occurred exclusively in lentic environments, while six species were registered only in lotic ones.

The ciliates species found belong to 11 orders, and among them, Prostomatida presented a higher number of species (12 species), followed by Hymenostomatida and Peritrichida (8 species each), as well as Oligotrichida and Haptorida (7 species each), as shown in Table 1.

Considering the different environments and periods, Oligotrichida and Prostomatida show a higher species richness. Peritrichida presented a high species richness especially in the rivers; Scuticociliatida presented, in general, a high number of species in lotic environments (rivers and channels); Haptorida was important in channels in both periods and in the closed lakes during limnophase; and Hymenostomatida present high species richness only in the closed lakes during the potamophase (see Figure 3).
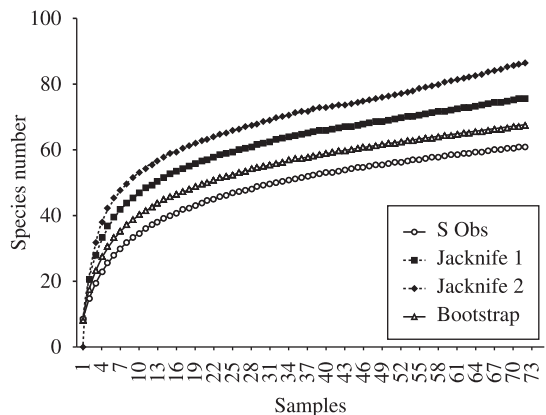

Figure 2. Results from the non-parametric extrapolating index of the species richness of planktonic ciliates in the Upper Paraná River floodplain.
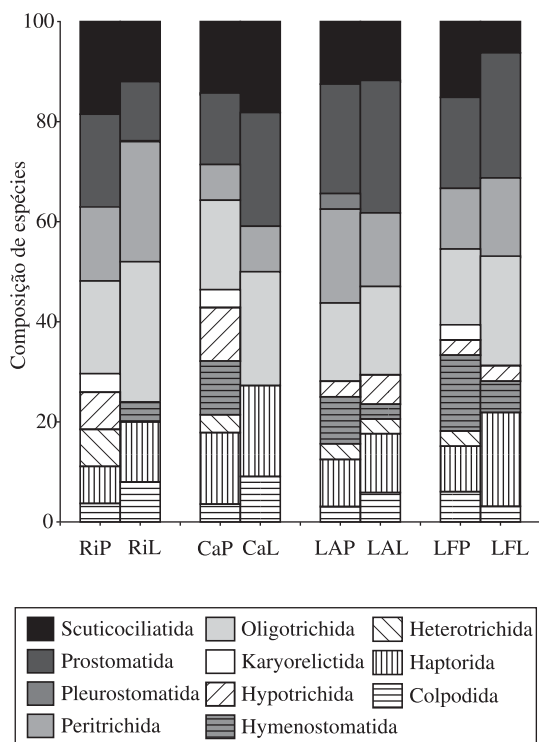
Figure 3. Percentage of the number of ciliates species per order verified in the different environment types and periods in the Upper Paraná River floodplain (Ri P = rivers potamophase; RiL = rivers limnophase; ChP = channels potamophase; ChL = channels limnophase; OLP = open lakes potamophase; OLL = open lakes limnophase; CLP = closed lakes potamophase; CLL = closed lakes limnophase).

In general, Oligotrichida, Prostomatida and Haptorida were more speciose during the limnophase, whereas Hymenostomatida and Scuticociliatida tended to present a great number of species during the potamophase (see Table 1).

Among the 61 identified species, 21 are classified as pelagic while 40 are considered preferentially as littoral species. During the potamophase, in most of the environments, a higher number of littoral species in relation to pelagic ones was observed. On the other hand, during the limnophase, in general, there was a greater contribution of pelagic species (as shown in Table 1).

According to the frequency of occurrence, most species were recorded in a few samples of each environment and period, and they were considered as accidental. Among them, 14 (13 littoral species) were registered only in one environment type and during only one period (as shown in Table 1). On the other hand, pelagic species were more frequent than littoral ones mainly in the lakes during the limnophase (as shown in Table 1).

Eight species were registered in all environments and periods: *Limnostrombidium* sp., *Rimostrombidium humile*, *R. lacustris* and

Tintinnidium sp. (Oligotrichida), *Balanium planctonicum*, *Urotricha farcta* and *Urotricha* sp. (Prostomatida), and *Cyclidium epitatricum* (Scuticociliatida) (as shown in Table 1).

During the potamophase, only the prostamatids (*U. farcta*, in channels and open lakes, and *Urotricha* sp., in the channels) were considered as constant species (as shown in Table 1). On the other hand, during the limnophase, several species were classified as constant in the lakes, such as *Codonella cratera, Limnostrombidium* sp., *Rimostrombidium humile, R. lacustris, Halteria grandinella* and *Tintinnidium* sp. (Oligotrichida), *Vorticella aquadulcis* (Peritrichida), *Urotricha farcta* and *Urotricha* sp. (Prostomatida) and *Cyclidium epitatricum* (Scuticociliatida) (as shown in Table 1). The occurrence of *Codonella cratera, Coleps hirtus* and *Enchelys* sp. were only in the limnophase, and these species were classified as constant or frequent species (as shown in Table 1).

The turnover rate of the ciliates species composition between sampling periods, quantified by the Beta 1 index, in each environment type showed that greater changes in species composition were observed in the lotic environments, rivers (75.6%), and channels (66.7%), while lower changes were recorded in the open lakes (53.1%).

A Cluster Analysis evidenced a higher dissimilarity of the ciliates species composition between periods (potamophase and limnophase) than among environment types (see Figure 4). In this way, the analysis discriminated two groups: the first one compounded by sampling units from the potamophase and the other from the limnophase (see Figure 4).

A Detrended Correspondence Analysis (DCA) corroborated the Cluster analysis evidencing a discrimination of the sampling sites under limnophase, negatively correlated with the axis 1, from those sampling sites under potamophase, positively correlated to the same axis (see Figure 5a).

Through the scores distribution derived from the DCA, it was possible to observe that *Holophrya discolor, Ctedoctema acanthocryptum, Coleps hirtus, Lagynophrya acuminata, Enchelys* sp., *Askenasia volvox, Codonella cratera, Actinobolina* sp., *Stokesia vernalis, Tintinnidium* sp. and *Urotricha* sp., most of them typically pelagic, were negatively correlated with the axis 1 and determined the discrimination of the limnophase samples. On the other hand, *Coleps elongatus, Tetrahymena pyriformis, Cyclidium glaucoma, Epistylis pygmaeum, Campanella umbellaria, Cyrtolophosis mucicola, Bursellopsis* sp., *Stichotricha aculeata, Calyptotricha lanuginosa* and *Vorticella campanula*, most of them littoral species, were positively correlated with the same axis, characterizing the ciliates community composition during the potamophase (see Figure 5b).

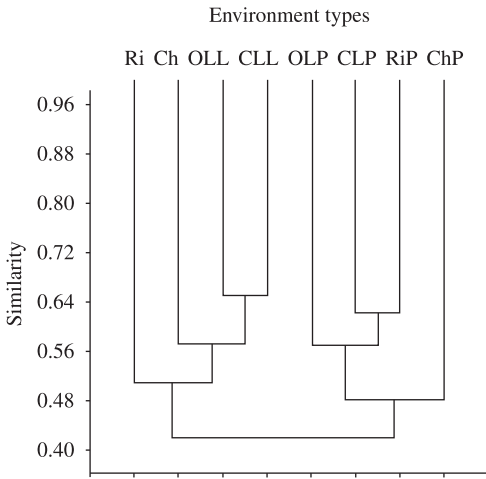The ANOVA results indicated significant differences between the scores from the sampling periods

Figure 4. Cluster analysis based on the occurrence of plankton ciliate species in the different environment types from the Upper Paraná River floodplain (Cophenetic Correlation Coefficient = 0.82; measurement = discordance percentage; linkage method = UPGA) (RiL = rivers limnophase; ChL = channels limnophase; OLL = open lakes limnophase; CLL = closed lakes limnophase; RiP = rivers potamophase; ChP = channels potamophase; OLP = open lakes potamophase; CLP = closed lakes potamophase).

(F = 23.87; p = 0.00007), whereas the differences among environmental types were not statistically significant (F = 0.683; p = 0.567) (see Figure 6).

4. Discussion

The knowledge regarding the total diversity in an environment or ecosystem is strongly influenced by the sampling effort. However, the total number of species recorded in the present study (61 species) was higher than observed in other studies (Bossolan and Godinho, 2000; Wiackowski et al., 2001; Gomes and Godinho, 2003; Carrick, 2005; Cardoso, 2007), which registered between 17 and 36 ciliate species in plankton samples.

This great diversity recorded in the Upper Paraná River floodplain is due to the high connectivity among the compartments (littoral, benthic and pelagic) of the different environments, which determines the occurrence of non-planktonic species in the pelagic zone. This contribution of littoral species to the pelagic zone in this floodplain has been evidenced for other zooplanktonic groups, with significant occurrence of testate amoebae, rotifers and microcrustacean species coming from other compartments (Lansac-Tôha et al., 2009). Pfister et al. (2002) also demonstrated the importance of a high environmental heterogeneity to the pelagic ciliates diversity in 58 German lakes (140 species).

The structure of ciliate communities is strongly affected by physical, chemical and geomorphological characteristics (Madonni and Baghiroli, 2007). According to
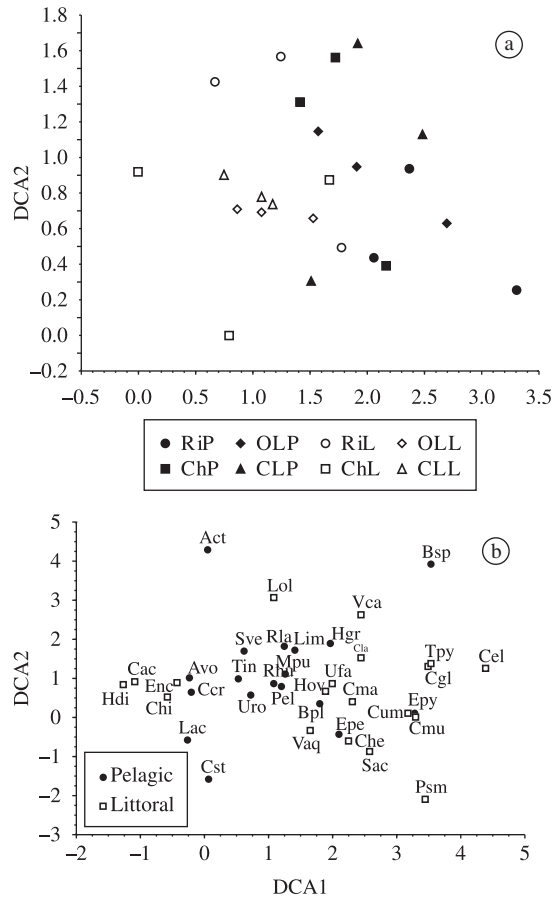

Figure 5. a) Scores distribution of samples and b) species along the DCA axes defined by ciliates composition in the Upper Paraná River floodplain. (RiL = rivers limnophase; ChL = channels limnophase; OLL = open lakes limnophase; CLL = closed lakes limnophase; RiP = rivers potamophase; ChP = channels potamophase; OLP = open lakes potamophase; CLP = closed lakes potamophase). Species codes are presented in the Table 1.

Andrushchshyn et al. (2003), in dynamic environments, abiotic factors are constantly changing and they are reflected in biotic changes such as species composition. In this way, a long-term monitoring study seems to be the most accurate method to register the real composition of ciliate procta, especially in an ecosystem with temporal dynamics as complex as the Upper Paraná River floodplain.

The difference between the observed species number (61 species) in relation to those estimated by the different non-parametric extrapolating indices (between 67 and 86 species) can be explained by the great number of non-pelagic species. In general, these species have a low frequency of occurrence, and these indices are based on the occurrence of rare species.

The higher number of exclusive species in the lakes, in relation to those registered only in the rivers and channels, seems to be related to the high stability of water
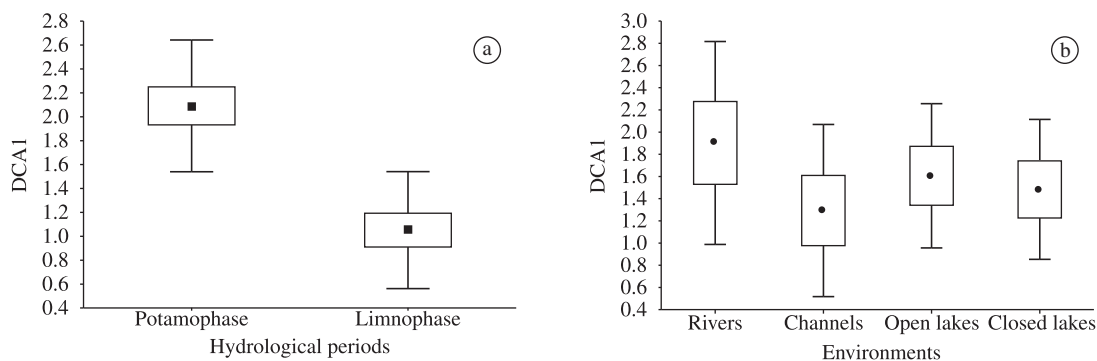
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Figure 6. DCA scores from the ciliates composition in the a) sampling periods and b) environments from the Upper Paraná River floodplain (■ = mean; □ = standard error; I = standard deviation).

flow in lentic environments. Also, the higher influence of ciliates species associated with the littoral zone in the plankton compartment of lentic environments explains the higher number given the higher abundance of aquatic macrophytes in the lakes when compared to the rivers.

The predominance of Prostomatida and Oligotrichida orders in the Upper Paraná River floodplain was related to their pelagic habitat, and it also explain the improvement provided by their contribution in species number to the composition of ciliates during the limnophase period, when the compartment isolation and water column stability are more pronounced. Thus, this hydrological period would favor the occurrence of truly pelagic ciliates in the Upper Paraná River floodplain. Prostomatida and Oligotrichida also dominated the pelagic ciliate communities in 58 German lakes (Pfister et al., 2002). Zingel (2005) found these two orders in an Eastern European Lake, plus Haptorida, as the most important in the epilimnion.

Oligotrichida frequently compose the most diverse group of ciliates in the pelagic compartment (Müller et al., 1991; Song, 2000; Mieczan, 2007). The frequent presence of organisms from this order is due to their filtering feeding habit and their high adaptability to inhabiting the water column. Also, they do not need any substrate or other organisms for attachment, i.e., they are euplanktonic organisms (Fenchel, 1982).

On the other hand, the addition of the orders Hymenostomatida and Scuticociliatida, omnivores and even litter eater species, during the potamophase suggests the influence of the allochtonous organic matter to the protozoan communities. According to Scherwass et al. (2005), the particulate detritus is an important food resource for flagellates and ciliates.

In general, the high species richness from Prostomatida, Hymenostomatida and Peritrichida, especially represented by littoral species, as well as the typically pelagic order, Oligotrichida, in the Upper Paraná River floodplain, suggest a complex interaction between littoral organisms and those truly planktonic

organisms in the pelagic zone. Indeed, littoral species were more speciose than pelagic ones. However, the pelagic species have higher frequencies of occurrence and, in general, their frequency was constant. These species are adapted to move, develop and reproduce in the water column, using resources produced in the pelagic zone, whereas the littoral species grow on a substrate in other compartments, which are not always present in the pelagic zone.

In this way, euplanktonic species are distributed more homogeneously in the pelagic zone of several of environments studied, while the littoral species have a more restricted distribution because they are occasionally carried to the water column. This fact can also explain the high importance of plankton species during the limnophase and the littoral species during the potamophase.

Among the species recorded in all environments and periods, there is a great number of Oligotrichida, corroborating the studies of Bossolan and Godinho (2000) and Kalinowska (2004), which documented *Strombidium* spp. (in the present study *Limnostrombidium* sp., *Rimostrombidium humile* and *R. lacustris*) as the most common species in the lakes studied. Furthermore, Müller et al. (1991) attribute the small Prostomatida (*Urotricha* and *Balanion* genera) as among the most important species in the studied lakes. Song (2000) considers *Cyclidium* spp. as the species reaching very high values of frequency in two Chinese lakes.

According to Zingel (2005), the Prostomatida *Urotricha* spp. present the same distribution pattern observed for the Oligotrichida in the Verevi Lake (East European), which is also the same taxon observed in the Upper Paraná River floodplain. The *Urotricha* spp. feed on algae and bacteria (Berger and Foissner, 2003) and are free or attached to allochtonous material, which explains why these are the only species frequent both during the potamophase and limnophase. In other words, apparently they are more adapted to the temporal changes in the floodplain.

Beta diversity results showed great alterations in the species composition for all environment types determined by a great input of allochtonous species in the pelagic zone during the potamophase (see DCA results), when a great part of littoral region is flooded. However, this species turnover is slightly pronounced in lentic environments, suggesting that this input of allochtonous species, to a greater or lesser extent, is occurring throughout the hydrological period in the pelagic zone of the lakes.

One of the main discussions about the ecology of floodplains is related to the relative importance of the flood pulse (regional and temporal factor), and connectivity and hydrodynamics (spatial and local factors) on the structure of aquatic communities. In this way, some authors have attributed the flood pulse as the main factor structuring the distinct aquatic communities in the Upper Paraná River floodplain (Lima et al, 1998; Bonecker et al., 2005). On the other hand, some studies have suggested that the spatial heterogeneity in floodplain systems, including the differences in the hydrodynamic and connectivity, is an important factor on the communities' organization, more than the temporal changes determined by the flood pulse (Velho et al., 2004; Higuti et al., 2007).

In the present study, the results obtained regarding the planktonic ciliate community, in both Cluster and DCA analyses, revealed that ciliate species composition was significantly distinct between periods, while among environments with differing degrees of connectivity and hydrological characteristics differences in composition were not evident. In this way, the results demonstrated that the typically pelagic species characterized the ciliates community during the limnophase period while littoral species were preponderant in the composition of ciliates during the potamophase period. In conclusion, our results strongly support the idea of the flood pulse as the main factor driving the composition pattern of the planktonic ciliates community in the Paraná River floodplain.

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