

Comparison among zooplankton communities in hydrologically different lentic ecosystems

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Received: 14/09/15

Accepted: 03/03/17

ABSTRACT

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Marginal lagoons in wetlands, which differ from artificial reservoirs, are subject to water level significant variations and can provide a high diversity of zooplankton. This study sought to determine whether communities of cladocerans and copepods differ in terms of richness, density and food preferences in small artificial reservoirs and marginal lagoons, which have different hydrological regimes and connections with other aquatic environments. During the dry and rainy seasons, samples were taken from a set of 12 small artificial reservoirs in the northwestern region of the São Paulo state (Brazil) and in six marginal lagoons of the Paranapanema River wetland in the southeastern region of the São Paulo state (Brazil). We found a greater richness of zooplankton species (observed and estimated) in lagoons than in reservoirs. The species composition was significantly different in both ecosystems, and only cladocerans were more abundant in the lagoons. Although lagoons presented higher gamma diversity than reservoirs, the lagoons had lower beta diversity, reflecting the environment connections in wetlands to organisms' dispersion. Filter feeders were the most abundant group in both type of environment, but significant differences were observed in omnivores capturing prey, which were denser in reservoirs than in lagoons. The comparison between both kinds of ecosystem showed that zooplanktonic community differs in relation to the richness, density and trophic guild. We suggest that the influence of the hydrodynamics in lagoons, provided by lateral river connections, represents an important force in the aquatic community structuration, resulting in higher species diversity. This study evidences that ecosystems that are subject to connections with other aquatic environments and to water level variations can provide a higher diversity of aquatic communities, and that this kind of ecosystem are important to preserve the aquatic biodiversity.

Key words: Cladocera, Copepoda, function groups, floodplain.

RESUMO

Comparações entre comunidades zooplanctônicas de ecossistemas lênticos hidrológicamente diferentes

Lagoas marginais em áreas alagadas, diferentemente de represas artificiais, estão sujeitas a variações significativas de nível de água e podem abrigar alta diversidade de espécies zooplanctônicas. Este estudo tem como objetivo verificar se em pequenos açudes artificiais e em lagoas marginais, que diferem em seu regime hidrológico e na conexão com outros ambientes aquáticos, as comunidades de cladóceros e de copépodos diferem no que se refere à riqueza, densidade e preferências alimentares. Durante as estações seca e chuvosa, foram obtidas amostras em 12 pequenos açudes artificiais, na região noroeste do Estado de São Paulo (Brasil), e em seis lagoas marginais ao Rio Paranapanema, na região sudeste do Estado de São Paulo (Brasil). Encontramos maior riqueza (tanto observada quanto estimada) de espécies zooplanctônicas nas lagoas do que nos açudes. A composição em espécies foi estatisticamente diferente em ambos ecossistemas e apenas os cladóceros foram mais abundantes nas lagoas. Embora tenham apresentado maior diversidade gama, as lagoas apresentaram menor diversidade beta, refletindo o efeito das conexões entre os ambientes nas áreas alagáveis para a dispersão dos organismos. A guilda mais abundante em ambos os ambientes foi filtradores, entretanto, diferença estatística foi observada em onívoros que capturam presas, que foram mais abundantes nos açudes do que nas lagoas. A comparação dos dois tipos de ecossistema mostrou que a comunidade zooplanctônica se deferencia no que se refere à riqueza, densidade e guildas tróficas. Sugerimos que a influência na hidrodinâmica das lagoas, proporcionada principalmente pela conexão com o rio lateral, constitui uma

força importante na estruturação das comunidades aquáticas como a zooplânctônica, promovendo maior diversidade de espécies. Este trabalho evidencia que os ecossistemas sujeitos à conexões com outros ecossistemas aquáticos e a variações de nível de água apresentam maior diversidade de espécies aquáticas, sendo importantes para a manutenção da biodiversidade aquática.

Palavras chave: Cladocera, Copepoda, grupos funcionais, áreas alagadas.

INTRODUCTION

In countries with important aquatic resources, such as Brazil, it has been common practice to dam rivers to provide electrical energy. However, the effect of damming the lotic ecosystem has been noted, especially in floodplains downstream the dams, where the characteristics of flood pulses changed after the implantation of reservoirs (Agostinho *et al.*, 2004; Pelicice & Agostinho, 2007).

Some studies have shown the effect of the flood pulse on the homogenization of aquatic ecosystems in floodplains (Carvalho *et al.*, 2001; Thomaz *et al.*, 2007; Scholl *et al.*, 2012), where the flood provides a mixture of nutrients, gases and organisms among the lagoons, making more similar the abiotic characteristics and biota. In contrast, during low water periods, the reduced connectivity among aquatic environments makes the autochthonous processes more important, resulting in greater limnological differences among lagoons (Carvalho *et al.*, 2001). For the zooplankton community, Lansac-Toha *et al.* (2009) had also highlighted the importance of potamophase in the exchange of fauna among environments to increase the species richness.

These observations emphasize the importance of connectivity and water retention time as determinants of the community structure in the lagoons of floodplains, as also noted by other authors (Ward *et al.*, 1999; Zimmermann-Timm *et al.*, 2007; José de Paggi & Paggi, 2008). The connectivity provides the inputs from and outputs to the river environment, resulting in physical and chemical variations in the water as well as differences in biotic factors, such as phytoplankton density, competition and predation rates, which influence the composition of communities. Other kinds of environment as Mediterranean wetlands

are example where the variations of water level in a hydrological year can result in increases in zooplankton diversity (Galindo *et al.*, 1994; Boix *et al.*, 2001)

However, lentic environments, such as small reservoirs, are not subject to the great water level variations occurring in the lagoons of floodplains. Although they have similar depths to lagoons and an elevated richness of zooplankton species, especially in the littoral zones (Castilho-Noll *et al.*, 2010; Castilho-Noll *et al.*, 2012), these reservoirs are isolated and more stable environments, from a hydrological point of view, and provide different conditions for the establishment of zooplankton communities.

Differently from small reservoirs, lakes located in floodplains can present significant changes in their morphometric characteristics and in water quality during the year. The flood and flow pulses are the driving factors determining the changes in the state of the lakes lateral to a river. Clearly, two phases can be recognized during a hydrological year: the potamophase, when the marginal lake is connected with the river and in the limnophase the lake is isolated from the lotic ecosystem (Neiff, 1999). During the association phase of the lake with the river, connectivity is an important characteristic, determined by an exchange of sediment, particulate and dissolved material, and biota among the two ecosystems. Usually, the flood pulse can be predictable, with monomodal frequency and a high amplitude, as recorded in the Amazonian floodplain or, to present a predictable or unpredictable nature, with a polymodal frequency and varying amplitude in the low-order streams (Junk *et al.*, 2014).

Some authors have described the flood pulse in floodplains as a disturbance that contributes to an increase in biodiversity (Ward *et al.*, 1999). However, Henry (2005) has proposed that in wet-

Table 1. Names, range of coordinates and characteristics of the lagoons and reservoirs sampled. *Nomes, intervalos de coordenadas e características das lagoas e açudes amostrados.*

	Lagoons	Reservoirs
Names	Mian, Barbosa, Poço das Pedras, Coqueiral ¹ , Cavalos ¹ , Camargo ¹ .	G1, G2, G3, G4, G5, G6, G7, G9R1, G9R2, G9R3, P1, P2.
Coordinates	48°37'W and 23°29'S	48°33'W to 50°20'W and 20°29'S to 21°36'S
Depth (m):		
• rainy season	2.5–3.13	1.9–5.1
• dry season	2.7–3.3	1.3–4.9
Macrophytes in littoral zone	Abundant ²	Scarce
Wetland	Yes ³	No
River influence	Parapanema River is close to the lagoons and connected directly or indirectly with them	Small streams as tributaries of the reservoirs

¹ Sampled in Panarelli *et al.*, 2010 and Casanova & Henry, 2004;

² Henry *et al.*, 2014;

³ Henry, 2014.

lands close to a large reservoir, such as the Jurumirim Reservoir in the Parapanema River, the flood pulse cannot be considered to be a disturbance, as in the floodplains, because there is a buffer effect of the floods promoted by the ecotone river-reservoir. Even in this artificial wetland, the connectivity of marginal lagoons with the river has a great importance and can create conditions for the development of a community that differs from isolated aquatic ecosystems.

In this way, this study aimed at determining whether zooplankton communities differ in

terms of species richness, diversity, density and food preferences in two different types of tropical aquatic ecosystems: lagoons in an artificial wetland and small reservoirs.

Our hypothesis was that zooplankton communities from lagoons in an artificial wetland would present higher richness, diversity and density than the zooplankton communities from small reservoirs. This hypothesis is supported by the fact that lagoons present stronger water level variations, which can function as a disturbance, favoring biodiversity. Many studies have

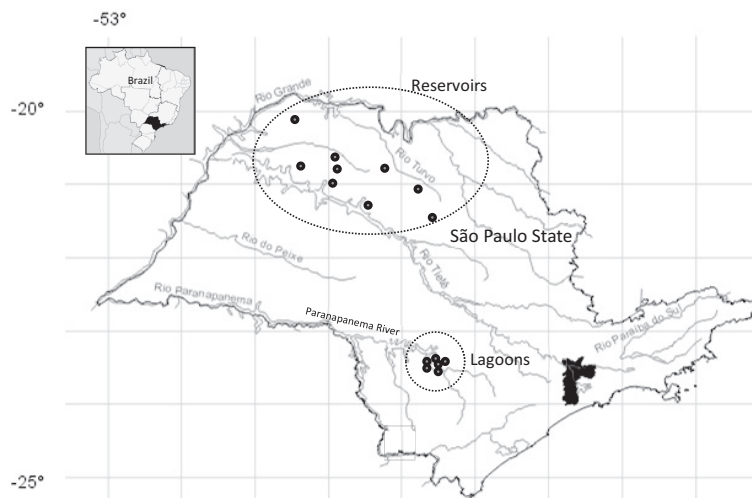


Figure 1. Map from São Paulo State, Brazil, highlighting both type of ecosystems studied-Reservoirs in Northwestern region of the State and Lagoons in Southeastern region of the State. *Mapa do Estado de São Paulo, Brasil, com destaque para os dois tipos de ecossistemas estudados-Açudes na região Noroeste do Estado e Lagoas na região Sudeste do Estado.*

shown the importance of the flood plain to the zooplankton biodiversity but no comparison with reservoirs was found in the literature.

MATERIAL AND METHODS

Study area

During the dry and rainy seasons, samples were taken from a set of twelve small artificial reservoirs and from three lagoons, which are marginal and connected to the Paranapanema River at the mouth zone into Jurumirim Reservoir, both the two types of aquatic ecosystems located in the São Paulo State, Brazil (Fig. 1, Table 1). The humid region shaped by lagoons and river at the confluence zone with a reservoir was classified by Junk *et al.* (2014), as an “artificial” wetland. The small reservoirs were located in rural areas and originated from the dams of small streams. In Table 1 some characteristics have been presented of each kind of environment.

Samples

Zooplankton sampling was conducted in both the littoral and limnetic zones, using a suction

pump and a plankton mesh net of 45 μm . The organisms were anesthetized with carbonated water and fixed with 4% formalin. The identification was performed with light microscopy using specific identification keys (Reid, 1985; Elmoor-Loureiro, 1997; Elmoor-Loureiro *et al.*, 2004; Silva & Matsumura-Tundisi, 2005; Silva, 2008). The counting of microcrustaceans was performed using in 1-ml sub-samples in Petri dishes and a stereoscopic microscope. A minimum of 60 individuals of the most abundant class was counted in the sub-samples. The number of the counted sub-samples was determined when the coefficient of variation was less than 0.20 (McCauley, 1984). For samples with a low density of organisms, the whole sample was counted.

Species composition in the lagoons was also supported by the data from Panarelli *et al.* (2010) and Casanova & Henry (2004).

In all the aquatic ecosystems, the following physical and chemical factors of the water were measured: depth and transparency by sounding and a Secchi disk, respectively; temperature with a Toho Dentam ET-3 thermistor; electrical conductivity with a Hatch conductivity meter; pH with a Micronal B380 pH meter; and dissolved oxygen through the Winkler method (Golterman *et al.*, 1978).

Table 2. Average and standard deviation of the physical-chemical factors in the dry and rainy season in reservoirs and lagoons sampled, and statistical results for comparison between environments for each season. *Média e desvio padrão dos fatores físicos e químicos na estação seca e chuvosa nos açudes e lagoas amostradas, e resultados estatísticos para comparações entre ambientes para cada estação.*

		Reservoir		Lagoon		Reservoir \times Lagoon			
		Dry season	Rainy season	Dry season	Rainy season	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Depth (m)	Average	1.67	2.01	2.64	2.29	-1.72	0.09	-0.47	0.64
	SD	1.34	1.34	0.51	0.83				
Secchi disk (m)	Average	1.02	1.17	1.53	0.80	-1.68	0.1	1.14	0.26
	SD	0.72	0.78	0.32	0.11				
Temperature ($^{\circ}\text{C}$)	Average	22.73	26.01	19.05	25.38	3.58	0.001	1.07	0.29
	SD	2.39	1.16	1.49	1.69				
pH	Average	6.48	6.61	5.95	5.91	2.02	0.05	1.91	0.07
	SD	0.63	0.87	0.29	0.25				
Conductivity ($\mu\text{S}/\text{cm}$)	Average	27.18	38.57	58.22	41.60	-2.5	0.02	-0.18	0.86
	SD	29.80	41.09	8.99	7.81				
DO (mg/L)	Average	5.77	4.22	4.03	3.43	2.15	0.04	1.04	0.31
	SD	1.92	1.62	0.84	1.80				

Data analysis

We investigated the effects of lagoons and reservoirs physical and chemical factors on microcrustaceans using redundancy analysis (RDA), available in Vegan package in R program. The analysis was made through an incidence matrix of the microcrustaceans species.

For some analysis, as the beta diversity and ANOSIM, we added data of species presence and absence from other three lagoons located at the same artificial wetland and close to the lagoons from this study (Fig.1, Table 1). These additional data came from previous studies made by one of the co-author (Panarelli *et al.*, 2010; Casanova & Henry, 2004).

Analyses of similarity (ANOSIM) and Non-Metric Multidimensional Scaling (NMDS) were performed to detect the differences between the compositions of both types of ecosystem. Then, the SIMPER analysis was used to determine which species contributed the most to the differences between the sites. This analysis was performed in Primer Program 6.0.

The diversity of the planktonic microcrustaceans in lagoons and reservoirs was analyzed using the following indices: species richness (S), Shannon diversity (H'), Inverse of Simpson (as proposed by Jost, 2006), Shannon entropy- $\exp(H')$ (as proposed by Jost, 2006), Pielou's Equability (J ; Gotelli & Graves, 1996, Legendre & Legendre, 1998). Species richness as gamma diversity, was compared between both environment using species accumulation curves through the rarefaction method (Gotelli & Graves, 1996, Legendre & Legendre, 1998). Moreover, richness was estimated by the richness estimators Jackknife 1 and Chao 1. Based on Baselga & Orme (2012) we calculated beta diversity using Sorensen and Jaccard index. All statistical analyses

were performed using R software version 2.15.1 (R Development Core Team 2012), and the packages vegan version 2.0-4 (Oksanen *et al.* 2012).

Significant differences between environments were examined using a *t*-test or Mann-Whitney (*U*), depending on the data distribution.

According to Williamson & Reid (2001) for copepods and Elmoor-Loureiro (2007) for cladocera, the following functional groups of the microcrustaceans have been identified: filter feeders, phytoplankton scrapers, omnivores capturing prey and omnivorous consumers of suspended particles. To evaluate the differences of functional guilds between the two types of habitats, lagoons and reservoirs, a MANOVA test for multivariate abundances was performed with the average densities of organisms based on functional trait. This analysis has been recommended in comparisons with dependent variables which is different in size (Warton & Hudson, 2004)

RESULTS

Environment factors were more distinct between both types of ecosystem in the dry than in the rainy season (Table 2). Temperature, pH and dissolved oxygen were higher in reservoirs than in lagoons, but conductivity was higher in lagoons. In RDA analyses lagoons were grouped but no variable could be associated with them (Fig. 2). On the other hand, reservoirs have not formed a group, reflecting more variation among them, and some of them were correlated with Secchi disk (G3R) and conductivity (G93R, G91D). Secchi disk, pH, DO and conductivity are important factors determining the species incidence, with a level of significance of $p = 0.028$. RDA1 and RDA2 explained 0.57 of data (Table 3).

Table 3. Importance of the components for the RDA analysis (Figure 2). *Importância dos componentes para a análise de RDA (Figura 2).*

Importance of components	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Eigenvalue	0.5786	0.311	0.2018	0.1903	0.15246	0.10606
Proportion Explained	0.3757	0.2019	0.131	0.1235	0.09899	0.06886
Cumulative Proportion	0.3757	0.5776	0.7086	0.8321	0.93114	1

Table 4. List of species found in the studied reservoirs (R) and lagoons (L). *Lista de espécies que ocorreram nos açudes (R) e nas lagoas estudadas (L).*

Species	R	L	Abbrev.	Species	R	L	Abbrev.
Cladocera				(continuation)			
Sididae				Chydoridae			
<i>Diaphanosoma brevireme</i> Sars 1901	x	x	Diabre	<i>Alona glabra</i> Guerne & Richard, 1893	x		Alogla
<i>Diaphanosoma birgei</i> Korineck, 1981	x	x	Diabir	<i>Alona guttata</i> Sars, 1862	x	x	Alogut
<i>Diaphanosoma spinulosum</i> Herbst, 1967	x	x	Diaspi	<i>Alona manacantha</i> Sars, 1901	x	x	Aloman
<i>Pseudosida bidentada</i> Herrick, 1884	x		Psebid	<i>Alona poppei</i> Richard, 1897	x		Alopop
<i>Pseudosida ramosa</i> (Daday, 1904)		x	Pseram	<i>Alona ossiani</i> Sinev, 1998	x	x	Alooss
<i>Latonopsis australis</i> Sars 1888	x		Lataus	<i>Alona intermedia</i> (Sars, 1862)	x	x	Aloint
Bosminidae				<i>Alona verrucosa</i> (Sars, 1901)	x	x	Alover
<i>Bosmina hagdmani</i> Stingelin, 1904	x	x	Boshag	<i>Karualona mulleri</i> (Richard, 1897)	x		Karmul
<i>Bosmina longirostris</i> (O.F. Muller, 1785)	x		Bosong	<i>Alona iheringula</i> Sars 1901	x		Aloihe
<i>Bosmina tubicen</i> Brehm, 1953	x	x	Bostub	<i>Leberis davidi</i> (Richard, 1895)		x	Lebdav
<i>Bosmina freyi</i> De Melo & Hebert, 1994		x	Bosfre	<i>Camptocercus dadayi</i> Stingelin, 1913	x	x	Camdad
<i>Bosminopsis deitersi</i> Richard, 1895		x	Bosdei	<i>Camptocercus australis</i> Sars, 1896		x	Camaus
Moinidae				<i>Euryalona orientalis</i> (Daday, 1898)	x	x	Eurori
<i>Moina minuta</i> Hansen, 1899	x	x	Moimin	<i>Graptoleberis occidentalis</i> Sars, 1901	x	x	Graocc
Daphniidae				<i>Kurzia polypsina</i> Hudec, 2000	x		Kurpol
<i>Ceriodaphnia cornuta cornuta</i> Sars, 1886	x	x	Cercor	<i>Kurzia longirostris</i> (Daday, 1898)		x	Kurlon
<i>Ceriodaphnia silvestrii</i> Daday, 1902	x	x	Cersil	<i>Leydigia ipojucae</i> Brehm, 1938	x		Leyipo
<i>Ceriodaphnia pulchella</i> Sars, 1862	x		Cerpul	<i>Leydigiopsis brevirostris</i> Brehm, 1938	x		Leybre
<i>Ceriodaphnia richardi</i> Sars, 1901	x		Cerric	<i>Leydigiopsis megalops</i> Sars, 1901	x		Leymeg
<i>Daphnia gessneri</i> Herbst, 1967	x	x	Dapges	<i>Leberis davidi</i> (Richard, 1895)		x	Lebdav
<i>Daphnia ambigua</i> Scourfield, 1947	x	x	Dapamb	<i>Leydigiopsis ornata</i> Daday, 1905		x	Leyorn
<i>Scapholeberis armata</i> Herrick, 1882	x	x	Scaarm	<i>Notoalona sculpta</i> (Sars, 1901)	x	x	Notscu
<i>Simocephalus iheringi</i> Richard, 1897	x		Simihe				
<i>Simocephalus latirostris</i> Stingelin, 1906	x	x	Simlat	Copepoda			
<i>Simocephalus serrulatus</i> (Koch, 1841)	x	x	Simser	<i>Mesocyclops cf. brasilianus</i> Kiefer, 1933	x		Mesbra
<i>Simocephalus daphnoides</i> Herrick 1883		x	Simdap	<i>Mesocyclops ogunnus</i> Onabamiro, 1957		x	Mesogu
Ilyocryptidae				<i>Microcyclops alius</i> Kiefer, 1935	x		Micali
<i>Ilyocryptus spinifer</i> Herrick, 1882	x	x	Ilyspi	<i>Microcyclops anceps</i> (Richard, 1897)	x	x	Micanc
Macrothricidae				<i>Macrocyclops albidus</i> Herbst, 1962	x	x	Macalb
<i>Macrothrix elegans</i> Sars, 1901	x	x	Macele	<i>Paracyclops fimbriatus</i> (Fischer, 1853)	x	x	Parfim
<i>Macrothrix laticornis</i> (Jurine, 1820)	x	x	Maclat	<i>Thropocyclops prasinus</i> (Kiefer, 1931)	x	x	Thrpri
<i>Macrothrix paulensis</i> (Sars, 1901)	x	x	Macpau	<i>Mesocyclops meridianus</i> (Kiefer, 1926)	x		Mesmer
<i>Macrothrix spinosa</i> King, 1853	x	x	Macspi	<i>Thermocyclops decipiens</i> (Kiefer, 1929)	x	x	Thedec
Chydoridae				<i>Thermocyclops minutus</i> (Lowndes, 1934)	x	x	Themim
<i>Alonella lineolata</i> Sars, 1901	x	x	Alolin	<i>Notodiaptomus conifer</i> (Sars, 1901)	x	x	Notcon
<i>Alonella brasiliensis</i> Bergamin, 1935	x		Alobra	<i>Scolodiaptomus corderoi</i> (Wright, 1936)	x		Scocor
<i>Alonella dentifera</i> (Sars, 1901)	x		Aloden	<i>Notodiaptomus iheringi</i> (Wright, 1935)	x	x	Notihe
<i>Alonella dadayi</i> Birge, 1910		x	Alodad	<i>Argyrodiaptomus furcatus</i> Sars, 1901	x		Argfur
<i>Disparalona hamata</i> (Birge, 1879)		x	Disham	Diaptominae sp.	x		Diapto
<i>Chydorus pubescens</i> Sars, 1901	x	x	Chypub				
<i>Chydorus nitidulus</i> Schödler, 1862	x		Chynit				
<i>Chydorus dentifer</i> Daday, 1905	x		Chyden				
<i>Chydorus eurynotus</i> Sars, 1901	x	x	Chyeur				
<i>Dadaya macrops</i> (Daday, 1898)	x		Dadmac				
<i>Disparalona leptorhyncha</i> Smirnov, 1996	x		Dislep				
<i>Ephemeroporus barroisi</i> (Richard, 1894)	x		Ephbar				
<i>Ephemeroporus hybridus</i> (Daday, 1905)	x	x	Ephhyb				
<i>Ephemeroporus tridentatus</i> (Bergamin, 1931)	x	x	Ephtri				
<i>Pseudochydorus globosus</i> (Baird, 1850)	x		Pseglo				
<i>Pleuroxus similis</i> Baird, 1843	x		Plesim				
<i>Acroperus harpae</i> Baird, 1843	x	x	Acrhar				

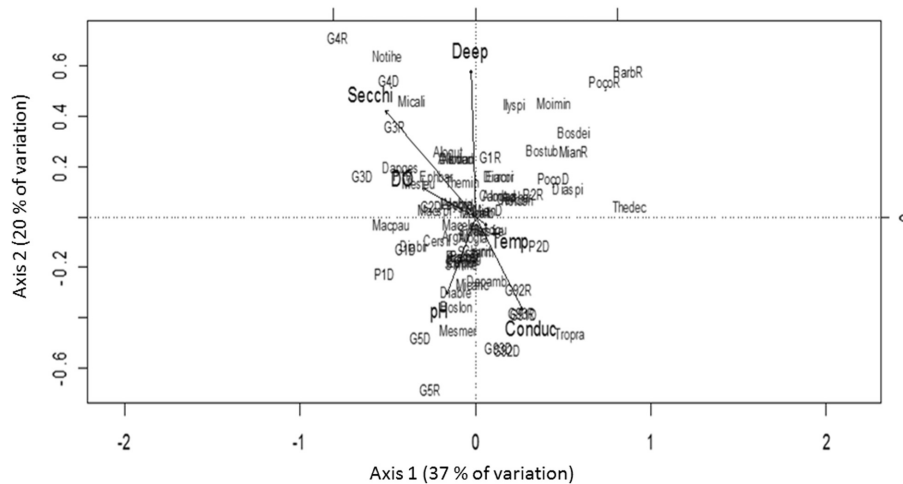


Figure 2. Redundancy Analysis (RDA) of the physico-chemical factors to incidence microcrustaceans in the studied environments. Arrows indicate physical and chemical factors: Depth, Secchi disk, DO, Temperature, Conductivity and pH. Places sampled are G1, G2, G3, G4, G5, G6, G7, G9R1, G9R2, G9R3, P1, P2 (reservoirs), and Mian, Barb = Barbosa, Poço = Poço das Pedras (lagoons). R = rainy season; D = dry season. For species abbreviations see table 4. *Análise de Redundância (RDA) dos fatores físicos e químicos para a incidência de microcrustáceos nos ecossistemas estudados. Setas indicam os fatores físicos e químicos: Profundidade, disco de Secchi, DO, Temperatura, Condutividade e pH. Locais amostrados: G1, G2, G3, G4, G5, G6, G7, G9R1, G9R2, G9R3, P1, P2 (açudes), e Mian, Barb = Barbosa, Poço = Poço das Pedras (lagoas). R = estação chuvosa; D = estação seca. Para as abreviações das espécies, ver tabela 4.*

We found 82 species of planktonic and phytoplanktonic microcrustaceans, some of which were common to both types of environments and others that were recorded only in one of the ecosystems (Table 4), e.g. *Bosminopsis deitersi* Richard, 1895, which was identified exclusively in lagoons. Twelve species were found only in lagoons and twenty-four only in reservoirs. Cladocerans seem to be more associated with lagoons and copepods with reservoirs (Fig. 2). Many species from the Chydoridae family were observed in the ecosystems (Table 4), but at low densities.

The comparison of the species compositions showed that lagoons and reservoirs were significantly different (ANOSIM global $R = 0.583$, $p = 0.002$) (Fig. 3). The following species contributed most to the differentiation of the ecosystems: *Diaphanosoma spinulosum* Herbst, 1975 ($p = 0.01$) and *Moina minuta* Hansen, 1899 ($p = 0.004$), which were more abundant in lagoons; *Bosminopsis deitersi* ($p = 0.0002$), which was found only in lagoons; and *Thermocyclops decipiens* (Kiefer, 1929) ($p = 0.009$), which was more abundant in reservoirs.

A comparison between microcrustacean species richness accumulation curves from both kind of environment (Fig. 4) showed that reservoirs presented a higher gamma diversity than lagoon, estimated by rarefaction, that presented the stabilization of the curve. However, the estimator Jackknife 1 and Chao 1 indicated that each lagoon was significantly richer than each reservoir (Table 5). This highly significant results could be also observed in the positive Pearson's correlation between the observed richness and that estimated by Chao 1 ($r = 0.997$) and between the observed richness and estimated by Jackknife 1 ($r = 1.0$). The richness by rarefaction was higher in lagoons than reservoirs with p marginally significant (Table 5). There weren't significant differences between lagoons and reservoirs for others diversity index as Shannon, Inverse of Simpson, Exp (H') and equability of Pielou (Table 5).

Reflecting a higher fauna homogenization, beta diversity was lower in lagoons ($\beta = 0.69$) than in reservoirs ($\beta = 0.89$); the same was observed in turnover (lagoons = 0.57, reservoirs = 0.84); but for nestedness, lagoons presented higher value (0.11), than reservoirs (0.04).

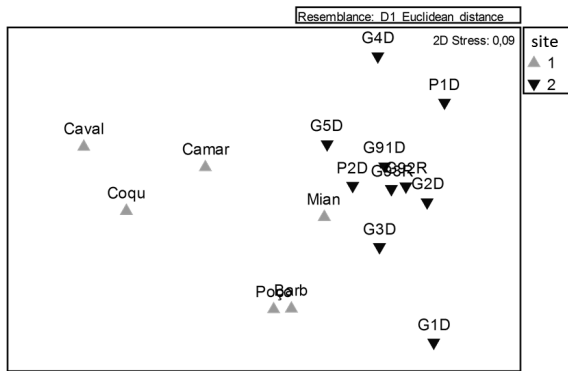


Figure 3. Non-Metric Multidimensional Scaling (NMDS) analysis of cladoceran and copepod species compositions. (Triangle 1 = lagoons-Mian, Barb = Barbosa, Poço = Poço das Pedras, Camar = Camargo, Caval = Cavalos, Coqu = Coqueiral; Triangle 2 = reservoirs-G1, G2, G3, G4, G5, G6, G7, G9R1, G9R2, G9R3, P1, P2). *Análise de Escalonamento Multidimensional Não-Métrico (NMDS) da composição de espécies de cladóceros e copépodos (Triângulo 1 = lagoas-Mian, Barb = Barbosa, Poço = Poço das Pedras, Camar = Camargo, Caval = Cavalos, Coqu = Coqueiral; Triângulo 2 = açudes-G1, G2, G3, G4, G5, G6, G7, G9R1, G9R2, G9R3, P1, P2).*

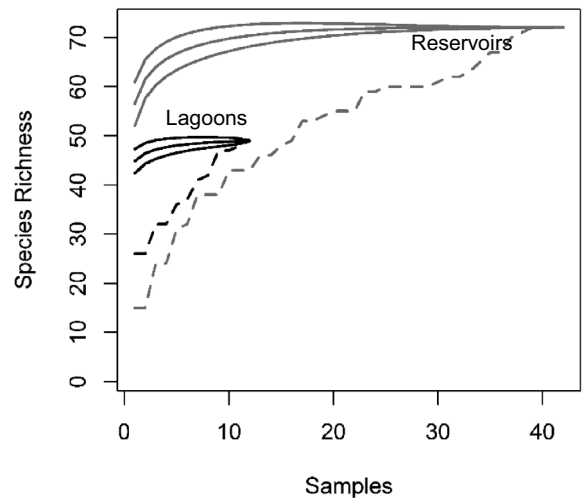


Figure 4. Microcrustacean species accumulation curves (Lagoons, Reservoirs) and collector curves (Lagoons, Reservoirs). *Curva de acumulação de espécies de microcrustáceos (Lagoas, Açudes) e curvas do coletor (Lagoas, Açudes).*

Table 5. Species richness, diversity values and statistical results for both type of studied ecosystems. *Valores de riqueza e diversidade de espécies e resultados de comparações estatísticas para os dois tipos de ambientes estudados.*

			Reservoir × Lagoons	
	Reservoirs	Lagoons	<i>t</i>	<i>p</i>
<i>S</i> _{obs}	6.2	14.2	4.4	<0.001
<i>S</i> _{raref}	5.8 ± 3.25	7.2 ± 1.78	-1.8	0.07
<i>H'</i>	0.12 ± 0.067	0.12 ± 0.04	-0.33	0.74
<i>D</i> ₂	3.3 ± 2.074	2.3 ± 0.172	0.78	0.43
Exp (<i>H'</i>)	1.13 ± 0.076	1.13 ± 0.05	-0.26	0.79
<i>J</i>	0.57 ± 0.28	0.50 ± 0.16	0.91	0.36
<i>S</i> _{Chao 1}	8.14 ± 4.08	14.9 ± 6.92	-3.24	0.006
<i>S</i> _{Jackknife 1}	8.14 ± 4.08	14.7 ± 6.33	-3.37	0.005

*S*_{obs} = observed species richness; *S*_{raref} = species richness estimated by rarefaction; *H'* = Shannon-Wiener index; *D*₂ = inverse Simpson index; Exp (*H'*) = exponential of Shannon entropy; *J* = Pielous's equability; *S*_{Chao 1} = species richness estimated by first-order Chao; *S*_{Jackknife 1} = species richness estimated by first-order Jackknife.

The richness average observed for cladocerans ($U = -4.2, p < 0.001$) and copepods ($t = 2.0, p < 0.05$) were statistically higher in lagoons than in reservoirs (Fig. 5). Cladocera was the richest group and contributed most to the differences between the ecosystems.

The total densities of microcrustaceans did not differ between the two types of ecosystems.

However, a significant difference in the Cladocera densities ($U = -2.8, p = 0.004$) was observed, with lagoons showing higher values than those of reservoirs. However, copepods were more abundant in reservoirs than in lagoons.

Regarding the contribution of functional groups to each type of ecosystem, filter feeders were the most abundant group, and their contribution was more evident in lagoons than in reservoirs (Fig. 6). We found statistically difference between the guilds from lagoons and reservoirs

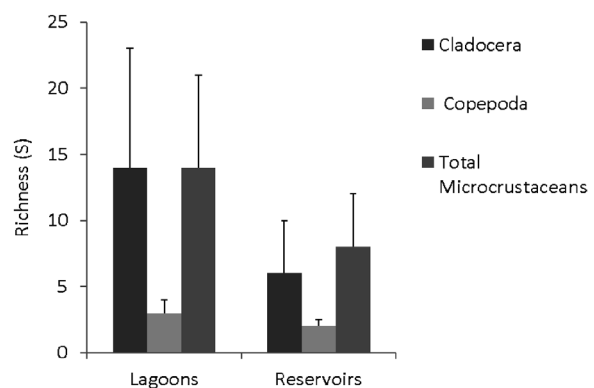


Figure 5. Average and standard deviation of the species richness (*S*) of the Cladocera, Copepoda and total microcrustaceans in both ecosystem types. *Média e desvio-padrão da riqueza de espécies (S) de Cladocera, Copepoda e microcrustáceos totais em ambos os tipos de ecossistemas.*

($F = 30.25$, $p = 0.009$). Omnivorous capturing prey were the guild that differed between both type of environment ($F = 61.53$, $p = 0.0002$) (Fig. 6). Omnivorous capturing prey and omnivorous consumers of suspended particles were more representative in reservoirs than in lagoons.

DISCUSSION

Our results show that the zooplankton communities significantly differ between the types of environment studied (small reservoirs and marginal lagoons of an artificial wetland) in terms of species taxonomic composition and abundance of functional groups. Our initial hypothesis was corroborated but not completely, because we couldn't observe a high level water variation in lagoons. However, because the influence from the lateral river in the lagoons, which there isn't in the reservoirs, we consider lagoons more hydrologically unstable than the reservoirs.

Differences between lagoons and reservoirs weren't so evident based on physical and chemical factors. It probably happened because we sampled the environments only in two periods in an annual cycle, which it's not sufficient to show all the variation. Only in dry season some differences could be observed and probably they are related with the limnophase when the lagoons are more isolated (Neiff, 1999). Besides de fact that in this study we couldn't observe variations in the depth for the three lagoons sampled, Henry (2005) had pointed out that some other lagoons in the artificial wetland of Paranapanema River can have a variation of 2.3-3.0 m in the water level in an annual cycle, indicating that the lagoons in this area have the potential to present this hydrological instability in level water. Other differences can be observed in characteristics pointed in Table 1, which can be determinant for organisms, as macrophytes abundance and river influence, that will be discussed.

In floodplain ecosystems, the water input from the river to the lagoons promotes an introduction of nutrients, suspended material and species that can change the internal dynamics of the lagoons (Junk *et al.*, 1989, Ward *et al.*, 1999).

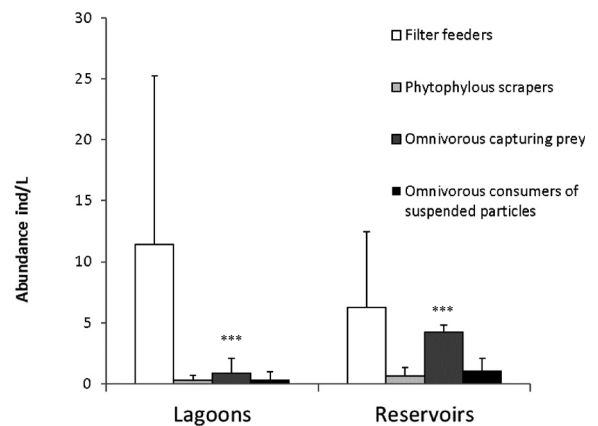


Figure 6. Average and standard deviation of the densities of the functional groups observed in both ecosystems (***) $p < 0.001$). Média e desvio padrão das densidades dos grupos funcionais observados em ambos os ecossistemas (***) $p < 0.001$.

For example, Thomaz *et al.* (2003) had asserted that the flood pulse confers some effects on decomposition processes that are not observed in aquatic environments where the level water is more constant and is not subject to flooding. The greater richness of microcrustaceans observed and estimated in lagoons compared with reservoirs and the differences in densities and functional groups also provides strong evidence for the effect of water level variations and the connectivity on aquatic communities because this seasonal process is the main difference between these types of aquatic environments. As mentioned before marginal lagoons in the artificial wetland of Paranapanema River present great variation on water level during the year (Henry, 2005). The small reservoirs studied are hydrologically less variable ecosystems and they are not influenced by the water level increases. This occurs because they originated from the damming of small streams and they don't have connections with a lateral large river. Flood pulse aging as a disturbance (Ward *et al.*, 1999) and a controlling factor of the zooplankton communities (Junk *et al.*, 1989) was also confirmed by our results. The connectivity and retention time of water are important processes related to the flood pulse that regulate and control the richness and densities of the zooplanktonic community in many other environments (Zimmermann-Timm

et al., 2007; José de Paggi & Paggi, 2008; Lansac-Tôha *et al.*, 2009; Güntzel *et al.*, 2010).

Henry (2005) has suggested that wetlands close to the mouth zone of a river in large reservoirs, such as the Jurumirim Reservoir, present different dynamics from the floodplains because of the buffer effect promoted by the ecotone river-reservoir. Thus, the hydrologic level variation in the confluence zone of the introduction of the tributary (Parapanema River) into the Jurumirim Reservoir cannot be considered to be a disturbance that promotes the increase in the number of species. Differently from the results of Henry (2005), even with a buffer effect, the water input in the marginal lagoons from the Parapanema River has the potential to promote the dispersion of many zooplankton species, such as cladocerans, and, consequently, provides important functions to the ecosystem, such as those related to the aquatic food web.

The differences observed were more evident in cladocerans than in copepods. With the capacity to produce resting eggs, the cladocerans can re-colonize the marginal lagoons, as shown in the study by Panarelli *et al.* (2008). Furthermore, the resting eggs provide a good way for cladocerans to disperse and can be transported by the wind and animals and through the hydrological connectivity. The fact of some cladoceran species were identified only in lagoons and in a higher density reveals that the dispersion process is determinant for these microorganisms. For example, *Bosminopsis deitersi*, which was not sampled in the studied reservoirs, was a constantly present cladoceran species observed in other lagoons from floodplains (e.g., Dabés, 1995; Campos *et al.*, 1996; Espíndola *et al.*, 1996; Lima *et al.*, 1996; Wisniewski *et al.*, 2000; Keppeler, 2003; Neves *et al.*, 2003; Brandorff & Hardy, 2009). The classification of *Bosminopsis deitersi* as a “typically riverine species” (Panarelli *et al.*, 2003) provides clues about the tolerance of this species to the hydrodynamics of the lagoons and its use of the river as a means of dispersal, to occupy new environments in the wetlands. Zooplanktonic species of small size, such as *B. deitersi* (approximately 230 μm , L.R. Stephan, unpublished data) have advantages for catching

food in these lagoons because these species can live, swim and feed on phytoplankton in the middle of macrophytes, which are very abundant. Another reason for the prevalence of the small-size zooplankton is the presence of fish in lagoons, which mainly prey on large zooplankton (Bonecker *et al.*, 2011).

In addition to promoting species diversity, marginal lagoons can also provide some important ecosystem functions that are performed by the species. As shown by our data, most of the filter feeding functions of plankton in lagoons are performed by cladoceran species, which have an important role in the grazing food chain because they are a food source for the upper trophic levels (e.g., fishes, especially for young fishes).

The comparison between the filter feeder densities from the littoral and limnetic zones in this study showed a marked difference in lagoons, and this difference was associated with the macrophyte communities. Qualitative observations made in the field during this study showed that lagoons presented a more diverse and abundant macrophyte community than did the reservoirs. Over the last few years, many studies have focused on the importance of macrophytes in the floodplains, where the high abundance of these aquatic plants and the input of organic matter makes the decomposition rates higher than the production in the littoral zones (see revision in Thomaz *et al.*, 2003). These data suggest that in the littoral zones of floodplains, the communities were more diverse and the processes were more dynamic than those in the littoral zones of the small reservoirs. In the studied reservoirs, the apparent hydrological stable conditions of the water, compared to those observed in lagoons, made the differences between the littoral and limnetic zones less marked. These results are reflected by the taxonomic attributes of the community, such as the abundance of feeding-type groups.

Another effect of floods on the floodplains involves the level of homogenization in the aquatic ecosystems, which could be the cause of the lower beta diversity in the lagoons than in the reservoirs observed in this study. High beta diversity can be found in lagoons, especially during the disconnection period with the river (Ward and

Stanford, 1995); in this situation, lagoons are influenced by autochthonous factors that structure the community and increase the differences between zooplankton communities (Carvalho *et al.*, 2001). According to Bini *et al.* (2001), environmental variability is the main factor promoting high beta diversity in floodplains. However, when there is hydrological connectivity (temporary or permanent) among the lagoons and rivers, which is increased during high water, an increase in the similarity among lagoons is observed (Carvalho *et al.*, 2001), making them more homogeneous (Thomaz *et al.*, 2007). Chlorophyll a, suspended matter, and richness and diversity of zooplankton species have been reported as factors with high variation among lagoons in the dry season and less variation in the rainy season (Scholl *et al.*, 2012). Isolation is a significant factor of the ecosystem that affects the species turnover and could explain the high beta diversity in the small reservoirs studied. Because the reservoirs are completely isolated, they present highly heterogeneous environmental characteristics that are reflected by the greater differences in the zooplankton communities. Unlike the lagoons, in reservoirs there was not a dispersion force represented by the connectivity.

The zooplankton communities in the floodplains have an important role in biodiversity because of two contrasting factors: the heterogeneity introduced by the flood dynamic, when the lagoons are disconnected, which increases the richness; and the capacity to provide high levels of dispersion of the organisms, by the flood water which connect the environments. The dispersion can also occur through the resistance forms, which can be taken by water, wind or animals (Lopes *et al.* 2016). In this way, zooplankton can be preserved in shallow lakes even in stressful conditions, such as in temporary lagoons. Therefore, the maintenance and preservation of floodplains are important to the local and regional biodiversity.

We believe that our results provide an important contribution to the conservation arguments regarding the floodplains because they reinforce that these types of wetlands are unique and that all of the dynamics must be preserved for conservation of the communities.

CONCLUSION

The comparison of the attributes of the zooplankton communities (richness and species composition, density and functional diversity) showed that both types of ecosystems –lagoons and small reservoirs– are different regarding the zooplankton communities, especially Cladocera. The results show the importance of the river flood pulse and connection between environments to the biodiversity and functioning of the lagoons.

These results confirm the importance of the maintenance and preservation of the floodplains for the zooplankton biodiversity and, consequently, for many functions related to the trophic interactions of the ecosystem.

ACKNOWLEDGEMENTS

We would like to thank H. A. Rodrigues and J. P. Maiorano for help in the sampling and E. F. Santos for help in statistics. This study was financed by resources granted by Fapesp (Process 2007/05134-4).

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