Continuity effects on rotifers and microcrustaceans caused by the construction of a downstream reservoir in a cascade series (Iguaçu River, Brazil)

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Abstract

This study evaluated changes in the community of rotifers and microcrustaceans associated with the construction of a large and dendritic reservoir in Iguaçu River (Brazil), as the last reservoir of a sequence of five cascading systems. Differences were clear between pre-filling and post-filling phases for organisms and some of environmental variables. In the pre-filling phase, the community was more homogeneous along the downstream river gradient, and spatial compartmentalization in the new reservoir was common during the post-filling phase. From 140 identified taxa, 10 species occurred exclusively in the pre-filling phase and 32 in the post-filling phase. After completion of the fifth reservoir filling-up, opportunistic, pioneer and fast-developing species quickly dominated, and downstream of the fourth reservoir the pre-filling decreasing gradient of richness, diversity and evenness disappeared. Richness of rotifers and cladocerans, cladocerans diversity, and evenness of rotifers, cladocerans and copepods were generally higher in the post-filling phase. A non-metric multidimensional analysis based on a presence/absence matrix depicted a homogeneous and dense group of species associated to the pre-filling phase and a second, dispersed group related to the post-filling phase. Spearman correlations pointed out significant positive effects of transparency on rotifer species richness in the post-filling phase, and negative effects on the microcrustacean richness in the pre-filling phase. Dam construction caused disruption of the downstream lotic gradient along the series of dams, leading to the development of distinct species in lentic spatial compartments.

Keywords: Rotifera, Cladocera, Copepoda, Iguaçu River.

Efeitos contínuos sobre rotíferos e microcrustáceos causados pela construção de um reservatório a jusante de uma série em cascata, Rio Iguaçú, Brasil

Resumo

Esse estudo analisou os efeitos da construção de um reservatório largo e dendrítico no Brasil sobre a comunidade de rotíferos e microcrustáceos, sendo o último reservatório de uma cascata de cinco. Houve claras diferenças entre as fases pré e pós-enchimento para os organismos e para algumas variáveis ambientais. Na fase pré-enchimento, a comunidade foi mais homogênea no gradiente longitudinal no rio a jusante, e na fase pós-enchimento houve compartimentalização espacial no novo reservatório. Dos 140 táxons identificados, dez espécies ocorreram exclusivamente na fase pré-enchimento e 32 na fase pós-enchimento. Após o enchimento, espécies oportunistas, pioneiras e de rápido desenvolvimento foram dominantes, e desapareceu o gradiente de decréscimo a jusante do quarto reservatório para a riqueza, diversidade e equitabilidade durante a fase pré-enchimento. A riqueza de rotíferos e cladóceros, a diversidade de cladóceros, e a equitabilidade de rotíferos, cladóceros e copépodes foram elevadas na fase pós-enchimento. A análise de escalonamento multidimensional não-métrico sobre a matriz de presença e ausência mostrou um grupo homogêneo e denso de espécies e meses de amostragem na fase pré-enchimento, e outro grupo disperso na fase pós-enchimento. Correlações de Spearman apontaram efeitos significativos da transparência sobre a riqueza de rotíferos na fase pós-enchimento, e efeitos negativos sobre a riqueza de microcrustáceos na outra fase. Os efeitos da construção do reservatório causaram rompimento no gradiente lótico contínuo a jusante do quarto reservatório observado na fase pré-enchimento, permitindo o desenvolvimento de espécies em compartimentos espaciais lênticos.

Palavras-chave: Rotifera, Cladocera, Copepoda, Rio Iguaçu.

1. Introduction

The damming of rivers leads to significant changes in the abiotic environment and in the biological communities both upstream and downstream (Marzolf, 1990; Straskraba and Tundisi, 1999; Garrido and Bozelli, 2000; Ribeiro Filho et al., 2011). Changes in abiotic conditions are induced by reduction of water velocity, increase of water transparency, and the possibility of formation of thermal and chemical stratification. For plankton communities, changes occur in several ecological attributes such as species richness, diversity and abundance of phytoplankton and zooplankton, when lotic species are replaced by lentic species after stabilisation of the system (Pedrozo et al., 2012). The interactions occurring between the river basin and the impounded water lead to the establishment of spatial gradients (longitudinal and lateral gradients) of biotic and abiotic variables in the reservoir main channel (Perbiche-Neves and Nogueira, 2010; Perbiche-Neves et al., 2011). The formation of many side-arms generally associated with tributary rivers is common in dendritic reservoirs, which can also contribute to the formation of lateral gradients (Ward, 1989; Van Den Brink et al., 1994; Bonecker et al., 2001).

In reservoirs, zooplankton communities exhibit structural changes along longitudinal and lateral gradients, because of the interaction with environmental factors such as water flow, physical and chemical stratification, and tributary entrances (Nogueira, 2001; Sampaio et al., 2002; Sartori et al., 2009). Higher densities are expected to occur in transition zones, both between the main river and the reservoir and between tributaries and the reservoir (backwater areas) (Marzolf, 1990; Van Den Brink et al., 1994). In cascade series of reservoirs, the upstream reservoirs - especially those of the storage type with a high retention time - affect the zooplankton downstream (Sampaio et al., 2002; Nogueira et al., 2008; Perbiche-Neves and Nogueira, 2010, 2013), exporting fauna by drifting process (Mitsuka and Henry, 2002; Perbiche-Neves et al., 2012). The organisms tend to disperse downstream, but construction of a new dam can stop this process due to the development of lentic conditions. Although there are many reservoir cascades in the world, the effects of a new impoundment at the end of a series of reservoirs have rarely been studied.

After the filling of a new reservoir, aquatic communities tend to follow a continuous process of changes and succession (Garrido and Bozelli, 2000; Pedrozo et al., 2012). In the initial years after impoundment, irregular reproduction cycles for many species of zooplankton occur (Perbiche-Neves et al., 2007; Serafim-Júnior et al., 2010). Colonisation processes range from r- to k-strategist species, initially with the dominance of small species (including rotifers, protozoans, small cladocerans and cyclopoid copepods), which tend to be replaced by large species, such as large cladocerans and calanoid copepods (Matsumura-Tundisi et al., 1991; Santos, 1995; Bonecker et al., 2001; Pedrozo et al., 2012). However, in the Neotropical region, comparative studies on zooplankton community in the pre- and post-impoundment phases remain scarce (Lansac-Tôha et al., 1999; Bonecker et al., 2001; Velho et al., 2001; Pedrozo et al., 2012), and additional investigations are needed to understand the succession mechanisms along the different filling stages.

In this study, we examined the composition, richness, alpha diversity and evenness of rotifers and microcrustaceans in relation to environmental variables, comparing a year before and a year after the construction of a large and dendritic reservoir in the Iguaçu River, south of Brazil. We tested two hypotheses: 1) that the decreasing gradient downstream from the last reservoir will disappear after damming of the new reservoir, due to the establishment of lentic conditions favourable to some rotifers and microcrustaceans, such as increase in water transparency and chlorophyll; 2) that richness, diversity and evenness will increase in the post-filling phase, for the same reasons.

2. Material and Methods

The study was carried out in the low stretch of the Iguaçu River, in the Paraná State, south of Brazil. The climate in this region is Cfa sub-tropical (Koppen), usually with two distinct seasons: cool-dry (winter) and warm-wet (summer). The mean annual rainfall ranges from 1,500 to 1,700 mm.

The studied reservoir (Figure 1), named Salto Caxias Reservoir (25°32’35”S; 53°29’43”W), is the last in a series of five large reservoirs in this river, all used for hydropower generation. The series of reservoirs along Iguaçu River is: Foz do Areia, Segredo, Salto Santiago, Salto Osório and Salto Caxias. A sixth new reservoir (Capanema) is being built in Iguaçu River few kilometres downstream Salto Caxias dam. The Salto Caxias Reservoir construction was completed in September of 1998 and is located in the final stretch of the Iguaçu River. The lake has a surface area of 141 km^2 with an annual dam discharge of 3.6×10^6 m^3. The mean water retention time of the lake is 38 days, the mean depth is 40 m and the maximum is 60 m close to the dam.

For this study, a total of nine sampling sites were selected along the Iguaçu River stretch and its tributaries (Figure 1). The organisms were sampled monthly, from March of 1997 to February of 1998 (pre-impoundment phase) and from April of 1999 to March of 2000 (post-impoundment phase), totalling 216 samples. Samples were collected by filtering 300 L of water of sub-surface through 64-µm plankton net, with the aid of a motorised pump Stihl P835 and flow of 40 L/h. Organisms were immediately preserved in 4% buffered formalin. For microscopic analysis, sample aliquots of 1mL were obtained using Hensen-Stempel pipettes. Bdelloidea rotifers and Harpacticoida copepods, as well as nauplii and copepodites of Cyclopoida and Calanoida, were not identified to lower taxonomic level. Rotifers and copepod nauplii were analysed in Sedgwick-Rafter chambers and adult cladocerans and adult and copepodites of copepods in gridded acrylic chambers, under an optical microscope and stereomicroscope, respectively.

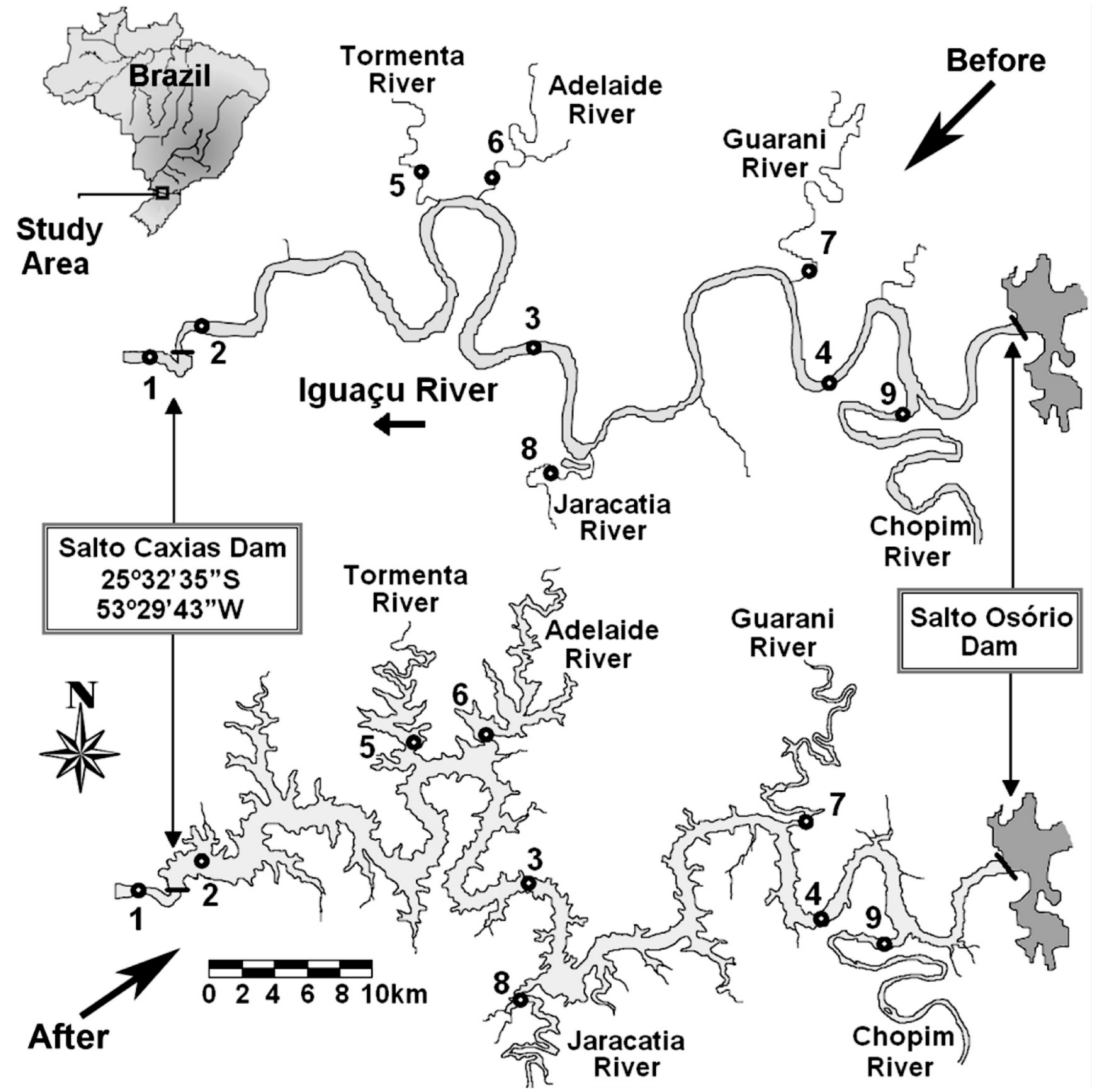

Figure 1. Map of study area and sampling sites in the pre-filling phase and post-filling phase of the Iguaçu River, at the Salto Caxias Reservoir.

Species of rotifers, copepods and cladocerans were classified as their habits in planktonic or non-planktonic, according to Koste (1978), Segers (1995), Lima et al. (1998), and Serafim-Júnior et al. (2003).

The frequency of occurrence of each taxon was calculated by considering the numbers of samples in which the species were found in relation to the total number of samples. Species richness was determined according to the number of species recorded in each sample. Individual abundance and the Shannon-Wiener diversity index ($H'=\Sigma pi.\log_2.p_i$), where pi is the proportion of $taxon_i$ in the sample, and evenness ($E=H'/H'max$) (Pielou, 1984) were also determined.

Data of richness, diversity and evenness were examined by a factorial analysis of variance (ANOVA), using as factors the filling phases (pre- and post-filling), sampling sites, and the interaction between both. ANOVA detected the effects of phases on sampling sites, using the significant differences in the interaction to represent the changes in ecological attributes. The assumptions of normality and homoscedasticity were previously checked with Shapiro-Wilk test and Levene test, respectively. The analysis was run in Statistica 6.0 (STATSOFT INC, 2002).

The VEGAN and MASS packages in the software R Cran Project (R CORE DEVELOPMENT TEAM, 2012) were used for non-metric multidimensional analysis (NMDS, using isoMDS) to separate species and sampling months between pre- and post-filling phases, based on a presence/absence matrix. First, all data of sampling sites and months were analysed, but due to the excessive number of lines we opted to estimate a mean among sampling sites for each sampling date, for the final analyses. Bray-Curtis distance was used. The convergent solutions were found by several trials. For scaling, centring, PC rotation and half change scaling were used.

Eleven environmental variables were measured in each sampling site, including: temperature, electrical conductivity, dissolved oxygen and pH (Horiba U10 probe), transparency (Secchi disk), chlorophyll (Talling and Driver, 1963), alkalinity total phosphorus (Strickland and Parsons, 1960), total nitrogen (Mackreth et al., 1978), total solids (TS) and total suspended solids (TSS). In the pre-filling phase limnological variables were measured in the water surface, and in the post-filling phase water samples were taken with a Van Dorn bottle in several depths, selected according to transparency, values. Sonde measurements were made on board immediately after sampling, and sample jars were frozen subsequently for later chemical analysis. Mean values of each limnological variable were calculated for the entire water column for statistical analysis. One-way ANOVA was performed to test for significant differences in limnological variables between pre- and post-filling phases. Spearman correlations were estimated between environmental variables and rotifer and species richness in pre- and post-filling phases, in order to distinguish environmental influences on rotifers and microcrustaceans richness. Statistical analyses were performed on Statistica 6.0 (STATSOFT INC, 2002).

3. Results

A total of 140 taxa were identified in both phases, 10 of which were only recorded in the pre-impoundment phase, and 32 only in the post-impoundment phase. Most species are shown in Table 1 (except very rare species which were not used in all statistical analysis). We found 99 species of rotifers distributed in 20 families. Eight species of rotifers were only found in the pre-impoundment phase and 21 in the post-impoundment phase. The most common rotifers in the pre-impoundment phase were *Keratella cochlearis* (61%), *Polyarthra vulgaris* (61%), *K. americana* (51%), *Conochilus coenobasis* (44%) and *Ploesoma truncatum* (43%). In the post-impoundment phase, *Polyarthra vulgaris* (89%), *K. cochlearis* (84%), *C. coenobasis* (83%), *C. unicornis* (82%), *Collotheca* sp. (81%), *K. americana* (80%) and *Hexarthra intermedia brasiliensis* (74%) were common.

Among the microcrustaceans, 26 species of cladocerans and 15 species of copepods were identified, the latter comprised by seven species of Cyclopidae and eight species of Diaptomidae.

Moina reticulata was only observed in the Iguaçu River (site 3) during the pre-impoundment phase. In contrast, seven species of Cladocera were exclusive to the post-impoundment phase. The most common cladocerans in the pre-impoundment phase were *Ceriodaphnia cornuta* (32%), *Daphnia gessneri* (27%) and *Bosmina hagmanni* (25%). In the post-impoundment phase, *Moina minuta* (80%) was the most common, followed by *B. hagmanni* (78%), *C. cornuta* (66%) and *Bosminopsis deitersi* (63%).

Thermocyclops decipiens (41%) and *Argyrodiaptomus furcatus* (27%) were dominant in the pre-impoundment phase. In the post-impoundment phase, the dominant species were *T. decipiens* (58%), followed by *Microcyclops anceps* (36%), *Notodiaptomus henseni* (25%), *N. anisitsi* (22%) and *N. deitersi* (22%). Five species of copepods were only found in the post-impoundment phase. Significant differences for important ecological attributes were detected between the pre- and post-filling phases, for rotifers, cladocerans and copepods (Table 2). The interaction between phases and sites was significant for richness and evenness of rotifers, for evenness of copepods, and for all attributes of cladocerans (Table 1). Among the sampling sites, only the evenness of rotifers was not different. Rotifer richness was usually high in the post-filling phase (Figure 2a) when differences among sampling sites were minor; the opposite was observed in the pre-filling phase, when low rotifer richness occurred at the tributaries. Rotifer evenness was higher in the pre-filling phase and in tributaries; during the post-filling phase evenness increased in the main channel (Figure 3b).

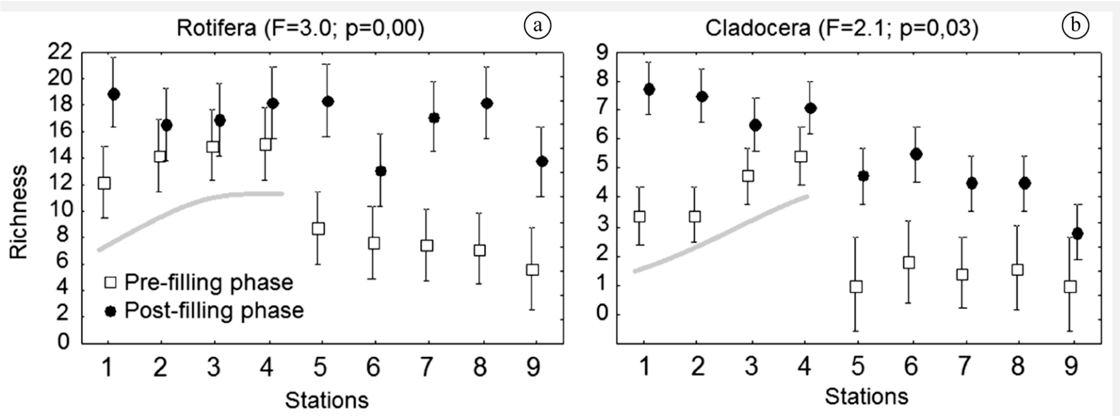

Figure 2. Mean values and standard error for richness of rotifers (a) and cladocerans (b), which showed significant interactions in the bifactorial ANOVA.

Table 1. List of almost all species found in our study, with abbreviations used in NMDS and habitat classification (C) in planktonic (pk) or non-planktonic (npk). Species not identified in species level were not classified.

Rotifera	Ab.	C	Rotifera	Ab.	C
Anuraeopsis naviculata Rousselet, 1910	Anav	pk	*Platyas quadricornis* (Ehrenberg, 1832)	Pqua	pk
Ascomorpha ecaudis (Perty, 1859)	Aeca	npk	*Platyias quadricornis brevispina* (Daday, 1905)	Pbrev	pk
Ascomorpha ovalis (Bergendal, 1892)	Aova	npk	*Platyonus patulus* (O. F. Müller, 1786)	Plpat	npk
Ascomorpha saltans Bartsch, 1870	Asal	pk	*Platyonus patulus* var. *macracanthus* (Daday, 1905)	Plmac	npk
Asplanchna sieboldi (Leydig, 1854)	Asieb	pk	*Ploesoma truncatum* (Levander, 1894)	Ptrun	pk
Brachionus angularis Gosse, 1851	Bang	pk	*Polyarthra dolichoptera* (Idelson, 1925)	Pdoli	pk
Brachionus budapestinensis Daday, 1885	Bbud	pk	*Polyarthra remata* (Skorikov, 1896)	Prem	npk
Brachionus calyciflorus Pallas, 1766	Bcal	pk	*Polyarthra vulgaris* (Carlin, 1943)	Pvul	pk
Brachionus caudatus insuetus Ahlstrom, 1940	Bins	npk	*Pompholyx complanata* Gosse, 1851	Pcom	npk
Brachionus caudatus personatus Ahlstrm, 1940	Bpers	pk	*Ptygura* sp.	Ptysp	
Brachionus falcatus falcatus Zacharias, 1898	Bfal	pk	*Scaridium longicaudatum* (O. F. Müller, 1786)	Scari	npk
Brachionus quadridentatus (Hermanns, 1783)	Bqua	pk	*Synchaeta* sp.1	Sysp1	
Brachionus mirus reductus (Koste, 1972)	Bred	pk	*Synchaeta* sp.2	Sysp2	
Cephalodella gibba (Ehrenberg, 1838)	Cgib	npk	*Testudinella ahlstromi* (Hauer, 1956)	Tahls	npk
Cephalodella stenrossi Wulfert, 1937	Cste	npk	*Testudinella patina patina* (Hermann, 1783)	Tpat	npk
Collotheca sp.	Cosp		*Trichocerca* (*D*) *similis grandis* (Hauer, 1965)	Tsim	pk
Collotheca sp.	Csp		*Trichocerca capucina* Wierzejski & Zacharias, 1893	Tcap	pk
Conochilus coenobasis Skorikov, 1914	Cocoe	npk	*Trichocerca cylindrica chattoni* De Beauchamp, 1907	Tchat	pk
Conochilus unicornis Rousselet, 1892	Couni	npk	*Trichocerca fusiformis* Levander, 1894	Tfusi	pk
Corulella obtusa (Gosse, 1886)	Cobt	npk	*Trichocerca haueroensis* (Gillard, 1967)	Tmucr	pk
Dicranophorus epicharis Harring & Myers, 1928	Depic	npk	*Trichocerca insignis* (Lauterborn, 1898)	Tins	pk
Dicranophorus caudatus brasiliensis Koste, 1972	Dcbra	pk	*Trichocerca parvula* Carlin, 1939	Tparv	npk
Dipleuchlanis propatula (Gosse, 1886)	Dipro	npk	*Trichocercapusilla* (Lauterborn, 1898)	Tpus	pk
Encentrum sp.	Encsp		*Trichocerca* sp.	Trisp	
Epiphanes clavatula (Ehrenberg, 1832)	Epcla	npk	*Trichocerca rousseleti* (Voigt, 1902)	Trous	pk

Table 1. Continued...

Rotifera	Ab.	C	Rotifera	Ab.	C
Euchlanis dilatata Ehrenberg, 1832	Edil	npk	*Trichotria tetractis* (Ehrenberg, 1830)	Trtetr	npk
Euchlanis incisa incisa Carlin, 1939	Einc	npk	*Trichocerca scipio* Pejler, 1962	Tsci	pk
Euchlanis incisa mucronata (Ahlstrom, 1934)	Emuc	npk	**Cladocera**		
Filinia longiseta (Ehrenberg, 1834)	Flon	pk	*Alona fasciculata* Daday, 1905	Afasc	npk
Gastropus hyptopus Ehrenberg, 1838	Ghyp	pk	*Alona guttata* Sars, 1862	Agut	npk
Hexarthra intermedia brasiliensis (Hauer 1953)	Hbra	pk	*Alona intermedia* Sars, 1862	Ainte	npk
Hexarthra mira (Hudson, 1871)	Hmira	pk	*Bosmina freyi* De Melo & Hebert, 1994	Blong	pk
Horaella thomasoni Koste, 1973	Htho	pk	*Bosmina hagmanni* Stingelin, 1904	Bhag	pk
Kellicottia bostoniensis (Rousselet, 1908)	Kbost	pk	*Bosmina haueronensis* Delachaux, 1918	Bhaue	pk
Keratella americana Carlin, 1943	Kame	pk	*Bosmina tubicen* Brehm, 1939	Btub	pk
Keratella cochlearis Gosse, 1851	Kcoc	pk	*Bosminopsis deitersi* Richard, 1834	Bdei	pk
Keratella lenzi (Hauer, 1953)	Klen	pk	*Ceriodaphnia cornuta* Sars, 1886	Ccor	pk
Keratella tropica (Apstein, 1907)	Ktro	pk	*Ceriodaphnia cornuta rigaudi*	Ccorr	pk
Lancinularia sp.	Lansp		*Ceriodaphnia* sp.	Cersp	
Lecane bulla (Gosse, 1851)	Lbul	npk	*Chydorus eurynotus* Sars, 1901	Ceur	npk
*Lecane closterocerca (*Schmarda, 1859)	Lclos	npk	*Chydorus pubescens* Sars, 1901	Cpub	npk
Lecane cornuta (Müller, 1786)	Lcor	npk	*Coronatella monacantha* Sars (1901)	Cmon	npk
Lecane curvicornis (Murray, 1913)	Lcur	npk	*Daphnia gessneri* Herbst, 1967	Dges	pk
Lecane flexvile (Gosse, 1886)	Lfle	npk	*Daphnia parvula* (Fordyce, 1905)	Dpar	pk
Lecane halyclista Harring & Myers, 1926	Lhaly	npk	*Diaphanosoma birgei* Korineck 1981	Dbirg	pk
Lecane hamata (Stokes, 1896)	Lham	npk	*Diaphanosoma brevireme* Sars 1901	Dbrev	npk
Lecane hornemanni (Ehrenberg, 1834)	Lhorn	npk	*Guernella rafaelis* Richard, 1892	Graf	npk
Lecane leontina (Turner, 1892)	Lleo	npk	*Ilyocryptus spinifer* Herrick, 1882	Ispinr	npk
Lecane ludwigii (Eckstein, 1883)	Lich	npk	*Leydigia* sp.	Leyd	
Lecane ludwigii f. *laticaudata* (Herrick, 1885)	Llud	npk	*Macrothrix spinosa* King, 1853	Maspi	npk
Lecane luna (O. F. Müller, 1776)	Lluna	npk	*Moina minuta* Hansen, 1899	Mmin	pk
Lecane lunaris (Ehrenberg, 1832)	Llun	npk	*Nicsmirnovius* cf. *fitzpztricki* (Chien, 1970)	Nfit	npk

Table 1. Continued...

Rotifera	Ab.	C	Rotifera	Ab.	C
Lecane monostyla (Daday, 1897)	Lmon	npk	*Phryxura dadayi* Birge, 1910	Pdad	npk
Lecane papuana (Murray, 1913)	Lpap	npk	**Copepoda**		
Lecane quadridentata (Ehrenberg, 1832)	Lqua	npk	*Argyrodiaptomus furcatus* (Sars, 1901)	Afurc	pk
Lecane scutata (Harring & Myers, 1926)	Lscut	npk	*Notodiaptomus anisitsi* (Daday, 1905)	Nanis	pk
Lecane signifera (Jennings, 1896)	Lsig	npk	*Notodiaptomus conifer* (Sars, 1901)	Nconi	pk
Lecane sp.	Lecsp		*Notodiaptomus deitersi* (Poppe, 1981)	Ndei	pk
Lecane stenroosi (Meissner, 1908)	Lsten	npk	*Notodiaptomus henseni* (Dahl, 1891)	Nhen	pk
Lecane stichea Harring, 1913	Lstic	npk	*Notodiaptomus iheringi* (Wright, 1935)	Niher	pk
Lepadella acuminata (Ehrenberg, 1834)	Leacu	npk	*Notodiaptomus spinuliferus* Dussart & Matsumura-Tundisi, 1985	Nspi	pk
Lepadella benjamini Harring, 1916	Lben	npk	*Notodiaptomus transitans* (Kiefer, 1929)	Ntran	pk
Lepadella ovalis (O. F. Müller, 1786)	Lova	npk	*Notodiaptomus* sp.	Nsp	
Lepadella patela (O. F. Müller, 1786)	Lpat	npk	*Mesocyclops longisetus curvatus* (Thiébaud, 1914)	Mlon	npk
Lophocaris salpina (Ehrenberg, 1834)	Lsal	npk	*Mesocyclops meridianus* (Kiefer, 1926)	Mmer	pk
Macrochaetus sericus (Thorpe, 1893)	Mser	npk	*Metacyclops* sp.	Metsp	
Manfredium eudactylota (Gallagher, 1957)	Meud	npk	*Microcyclops sp.*	Micsp	
Mytilina ventralis (Ehrenberg, 1832)	Mven	npk	*Paracyclops chiltoni* (Thomson, 1882)	Pchil	npk
Notholca sp.	Notsp		*Thermocyclops decipiens* (Kiefer, 1929)	Tdec	pk
Notomata copeus Ehrenberg, 1834	Ncop	npk	*Thermocyclops minutus* (Lowndes, 1934)	Tmin	pk
Notomata sp.	Nsp				

Cladoceran richness (Figure 2a) and diversity (Figure 3a) was high in the post-filling phase, with higher values in the main channel. In the pre-filling phase, a decreasing downstream trend of the richness and diversity was verified from site 4 towards site 1, and lower values also occurred in the tributaries. Rotifer evenness (Figure 3c) in the main channel of the Iguaçu River was similar in the pre- and post-filling phases. However, in the tributaries evenness was higher in the post-filling phase, with a minor variation among sites.

For copepods, only evenness had a significant difference between phases, being higher in the post-filling phase. There was a decrease gradient of evenness downstream Salto Osório Reservoir, corresponding to the upstream zone in the pre-filling phase (Figure 3d).

The NMDS clearly separated species groups of rotifers and microcrustaceans between pre- and post-filling phases (Figure 4). In both taxa, the pre-filling phase station grouping was less spread than in the post-filling phase indicating a more homogeneous condition in the former. For rotifers (Figure 4a), two convergent solutions were found after 14 tries and the stress was 6.56, showing a pre-filling group with many species of low abundance, in contrast to a post-filling group with few highly abundant species, typical of lentic conditions.

No convergent solutions were found for the microcrustacean data, and the best solution occurred after

20 tries, with a stress of 7.03 (Figure 4b). The results of richness and abundance analyses were similar for rotifers and microcrustaceans. Typical lotic and littoral cladocerans and copepods were present in the pre-filling phase and were absent in the post-filling phase, when organisms adapted to lentic environments were dominant.

For the environmental variables (Table 3), ANOVA showed significant differences ($p < 0.05$) between the pre- and post-filling phases for water transparency, chlorophyll, alkalinity, and total solids, with high values in the post-filling phase, except for total solids. There were few significant Spearman correlations among rotifer and microcrustacean richness with environmental variables in the pre- and post-filling phases (Table 2). Rotifer richness was positively correlated with water transparency in the post-filling phase, and negatively with microcrustaceans

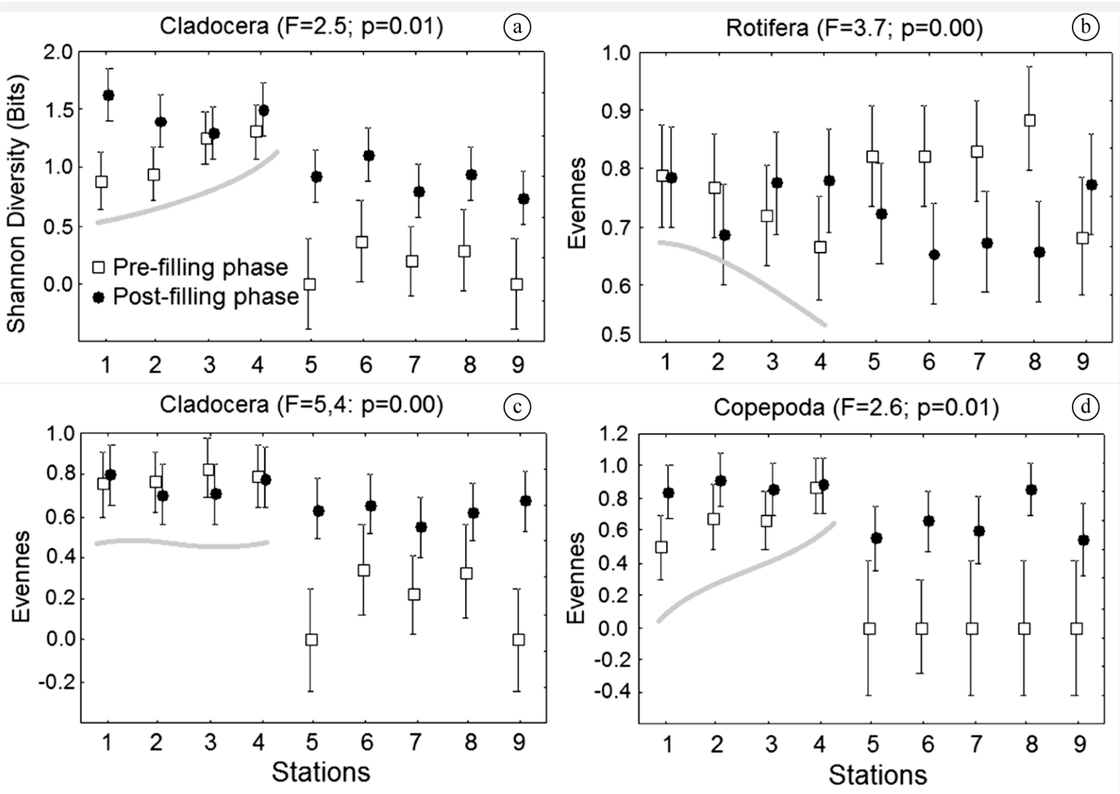

Figure 3. Mean values and standard error for Shannon-Wiener diversity of cladocerans (a), and evenness of rotifers (b), cladocerans (c) and copepods (d), which showed significant interactions in the bifactorial ANOVA.

Table 2. Results of the factorial ANOVA (F and p) for richness (S), diversity (H') and evenness (E) of rotifers and microcrustaceans.

Groups	DF	Rotifers		Cladocerans		Copepods
Attributes/Effects		**F**	**p**	**F**	**P**	**F**
Richness (S)						
Phase	1	98.2	**0.00**	129.7	**0.00**	20.5
Sites	8	6.3	**0.00**	16.3	**0.00**	3.8
Phase* Sites	8	3.0	**0.00**	2.1	**0.03**	0.2
Diversity						
Phase	1	25.1	**0.00**	76.1	**0.00**	37.4
Sites	8	4.2	**0.00**	18.4	**0.00**	6.4
Phase* Sites	8	1.1	0.30	2.5	**0.01**	0.7
Evenness						
Phase	1	6.4	**0.01**	31.8	**0.00**	51.4
Sites	8	0.5	0.83	11.0	**0.00**	8.6
Phase* Sites	8	3.7	**0.00**	5.4	**0.00**	2.6

* Bold values are significant ($p < 0.05$). DF = degrees of freedom.

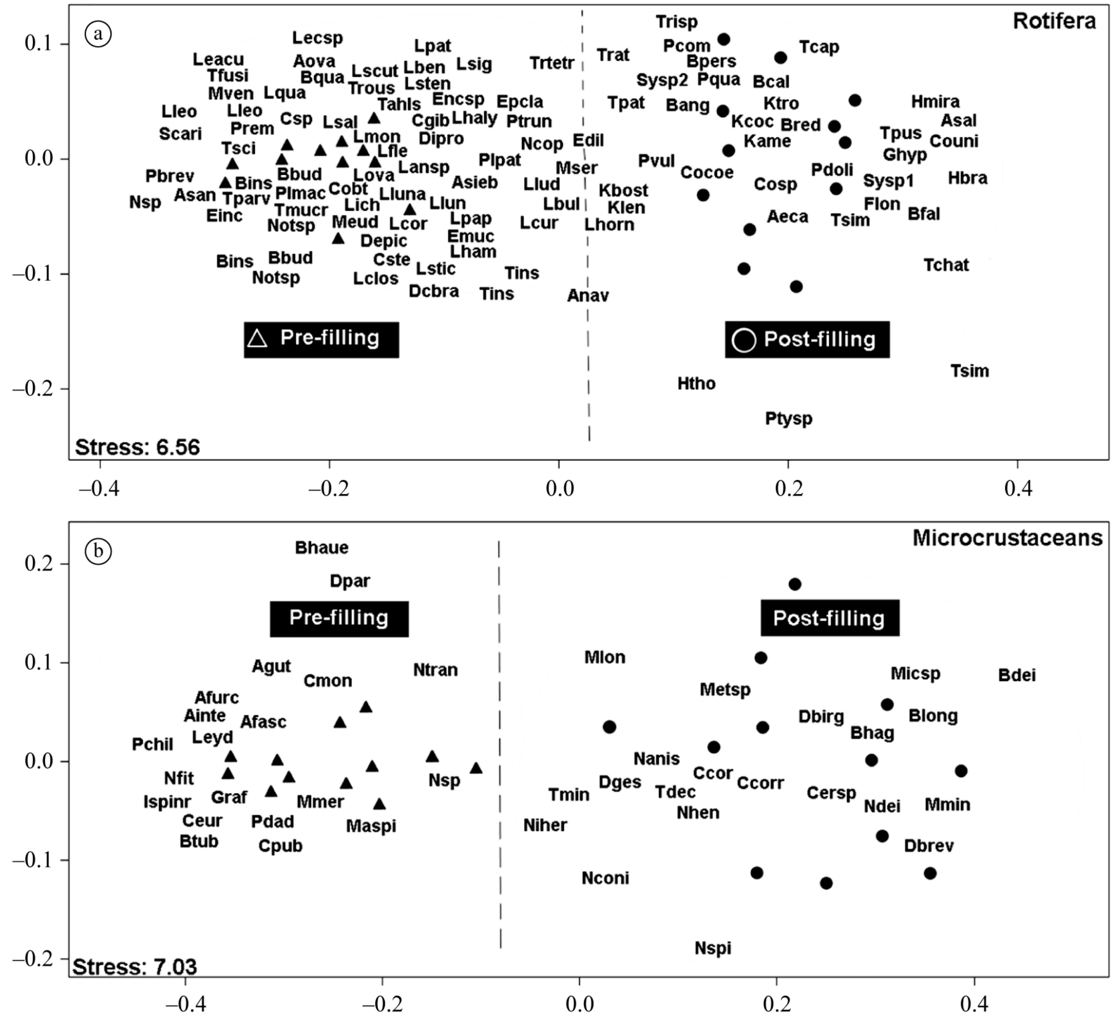

Figure 4. NMDS analyses for the zooplanktonic community between pre- and post-filling phases. (a) Rotifera. (b) Microcrustaceans (Cladocera and Copepoda). For codes see Table 1.

Table 3. Mean values ± standard deviation of environmental variables, with ANOVA results (in bold are significant differences at $p < 0.05$ level; NS = not significant); and results of Spearman correlation among Rotifera and microcrustacean species richness and environmental variables.

Variables	Mean±SD		Rotifera (S)		Microcrustaceans (S)	
	Pre	Post	Pre	Post	Pre	Post
Transparency (cm)	**87.5 ± 57.78**	**229.58 ± 79.41**	–0.45	**0.66**	**–0.56**	0.08
Water temperature (°C) ^{NS}	21.29 ± 2.74	22.62 ± 1.66	0.20	–0.08	0.15	**–0.60**
Chlorophyll (µg.L^{-1})	**1.99 ± 0.08**	**2.84 ± 0.26**	0.30	–0.07	0.13	0.15
Conductivity (µS.cm^{-1}) ^{NS}	35 ± 1.35	38.17 ± 1.90	**–0.69**	–0.28	–0.47	–0.40
Alkalinity (mg.L CaCO3)	**7.67 ± 2.05**	**18.06 ± 2.23**	–0.37	–0.22	–0.37	0.41
Dissolved oxygen (mg.L^{-1}) ^{NS}	7.73 ± 0.09	7.04 ± 0.08	–0.07	**–0.67**	0.10	0.37
pH ^{NS}	7.01 ± 0.60	7.16 ± 1.42	–0.17	–0.43	–0.14	–0.13
TS (mg.L^{-1})	**58.42 ± 0.29**	**40.08 ± 0.57**	0.05	–0.21	0.33	–0.04
TSS (mg.L^{-1}) ^{NS}	12.23 ± 23.63	10.46 ± 9.63	0.34	0.31	**0.57**	0.05
Total phosphorus (mg.L^{-1}) ^{NS}	0.04 ± 1.08	0.03 ± 2.39	0.33	–0.31	**0.58**	–0.44
Total nitrogen (mg.L^{-1}) ^{NS}	0.65 ± 0.45	0.66 ± 0.56	0.02	0.02	0.15	–0.53

In bold are significant correlations at the $p < 0.05$ level. NS = not significant.

in the pre-filling phase. Rotifer richness was negatively correlated with conductivity in the pre-filling phase. Rotifers and microcrustaceans were negatively correlated with dissolved oxygen and water temperature, respectively, in the post-filling phase. Microcrustaceans were positively correlated with total suspended solids and total phosphorus in the pre-filling phase.

4. Discussion

Detailed rotifers and microcrustaceans species inventories for the Iguaçu River can be found in several studies (Lopes et al., 1997; Ghidini et al., 2009; Serafim-Júnior et al., 2010; Perbiche-Neves et al., 2007, 2012). Among the 140 identified planktonic and non-planktonic species, the littoral Lecanidae (rotifer) and Chydoridae (cladoceran) species contributed significantly to the total richness in the pre-filling phase. In contrast, planktonic forms dominated in the post-filling phase. Similar results were also found in the Corumbá Reservoir in Goiás State (Lansac-Tôha et al., 1999; Bonecker et al., 2001). The number of species identified in our study (140 species) is higher than that identified by Lopes et al. (1997) in Segredo Reservoir (90 species), and by Perbiche-Neves et al. (2012) in Salto Caxias Reservoir (92 species). This may be attributed to the longer period of study and higher sampling effort in nine sampling sites. The effect of filling on the organisms caused an increase of species richness (131 taxa) compared to the pre-impoundment phase (106 taxa), as previously observed in other reservoirs in Brazil for zooplankton (Pedrozo et al., 2012) and for phytoplankton (Bicudo et al., 2006).

Most rotifer species that occurred exclusively in the pre-impoundment phase are littoral and frequently associated with river potamoplankton (Paggi and Jose de Paggi, 1990). The species that occurred exclusively in the post-impoundment phase were mainly planktonic, and were favoured by recently established lentic conditions. Most of the littoral species were found in the backwater sampling sites, with the exception of *Platyias quadricornis,* which was found in the main channel of the reservoir, probably originating upstream.

The Chydoridae presented the highest number of species among the cladoceran. However, the most frequent cladocerans belonged to the Daphniidae and Bosminidae families, which are commonly found in tropical water bodies (Dumont, 1994). *Bosmina hagmanni*, *Ceriodaphnia cornuta*, *C. cornuta rigaudi*, *Daphnia gessneri* and *Moina minuta* were the most frequent species in the pre-and post-filling phases. These species are frequent in the Neotropical region (Dodson and Silva-Briano, 1996; Pinto-Coelho, 1998; Nogueira, 2001; Sendacz et al., 2006; Perbiche-Neves and Nogueira, 2010). *Moina reticulata,* which only occurred in the pre-filling phase, is endemic to the Neotropical region (Paggi, 1993). After inundation of the reservoir, the emergence of littoral species exclusive to this phase may be explained by upstream export, which was more frequent at the backwater sites. In addition, *Bosmina huaroensis* was found only in the post-filling phase.

Copepods were clearly favoured by inundation as several species only occurred in the post-impoundment phase, as observed in other studies (Lansac-Tôha et al., 1999). Regarding the most frequent species of Cyclopidae (Cyclopoida), *Thermocyclops decipiens* is widely distributed in the Neotropical region (Landa et al., 2007; Santos-Wisniewski and Rocha, 2007) and often co-exists with *T. minutus* (Reid, 1989). However, co-existence was not often observed during this study, nor in the Segredo Reservoir (Lopes et al., 1997), located upstream in the same river. *Mesocyclops longisetus* and *M. meridianus* occurred only in the post-filling phase, favoured by the lentic new conditions.

The changes found by other studies (e.g., Garrido and Bozelli, 2000; Pedrozo et al., 2012) were supported by the ANOVA results, which showed significant changes for most ecological attributes of rotifers and microcrustaceans and also for some environmental/limnological variables, considering the interaction between sites and phases. For the tributaries, there was no change in the spatial variation trend, which is different from that observed for the sites located at the main channel of the Iguaçu River, as previously discussed. The NMDS grouped sampling sites, rotifers and microcrustacean species in the pre-filling phase, while the post-filling phase formed a disperse group in the plot graph of this analysis. Non-planktonic species dominated in pre-filling phase, in contrast with reservoir phase, when distinct spatial compartments appeared and caused an aggregated group in the NMDS analyses.

Studies on the spatial distribution of zooplankton from impounded rivers show a reduction in both density and species richness below dam (Unni and Naik, 1997; Mitsuka and Henry, 2002), consistent with the serial discontinuity concept proposed by Ward and Stanford (1983).

The Salto Caxias Reservoir is the fifth largest dam along the Iguaçu River, and the continuous succession of reservoirs has affected the composition of the rotifers and microcrustaceans community in the pre- and post-filling phases of this new reservoir. First, the decreasing gradient of ecological attributes before filling is a result of the drift of organisms from the upstream reservoir (Salto Osorio Reservoir). Second, the rotifers and microcrustaceans species exported downstream from Salto Osorio Reservoir colonised the new reservoir, as shown by NMDS (Perbiche-Neves et al., 2012). Probably the same trend will occur in the sixth new reservoir. Similar results of fast colonisation were found by Garrido and Bozelli (2000) during the filling of another large reservoir in Brazil. The higher species richness in the Iguaçu River compared to tributaries in both phases is probably due to the drift of species downstream from upstream reservoirs and the large size of the river, as occurs in most rivers connected to permanent or temporary bodies of water, from where individuals are exported (Pourriot et al., 1997; Lopes et al., 1997; Viroux, 2002; Perbiche-Neves and Nogueira, 2010; Perbiche-Neves et al., 2012).

Although Rotifera richness was positively correlated with water transparency in the post-filling phase, positive effects must have occurred also for microcrustaceans, due to the higher richness after filling the reservoir, consistent with the negative correlation found in the pre-filling phase. Turbidity, total suspended solids (TSS) or transparency can directly affect the organisms, especially microcrustaceans, in rivers and reservoirs (Panarelli et al., 2001; Casanova and Henry, 2004; Perbiche-Neves and Nogueira, 2013), and can be positive if phytoplankton were related to suspended solids or another potential food for these organisms, as found in our data relative to the positive correlation between TSS and microcrustacean richness. Total phosphorus can enhance phytoplankton primary productivity, thus affecting food resources for microcrustaceans. Conductivity seems to affect negatively copepods (Matsumura-Tundisi and Tundisi, 2003), but our results also showed negative effects on rotifers.

The two postulated hypotheses were accepted. We conclude that the formation of a reservoir tends to favour opportunistic coloniser species able to tolerate the new environmental conditions (e.g., increased transparency and chlorophyll content), or those species that easily adapt to the new environmental conditions.

The colonisation process in the Salto Caxias Reservoir has occurred distinctly between the Iguaçu River and tributaries, as shown by the different values presented by the ANOVA, the NMDS results and by comparing with literature about downstream reservoir effects. The rupture in lotic continuity was evident also by the results of the NMDS, separating clearly the homogeneous pre-filling phase and post-filling disperses phases.

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