Acta Limnologica Brasiliensia

Publication of the
Brazilian Association of
Limnology

Thematic Section: Upper Paraná River Floodplain

Acta Limnologica Brasiliensia, 2017, vol. 29, e102
http://dx.doi.org/10.1590/S2179-975X0117
ISSN 2179-975X on-line version

Copepod assemblage structure (Crustacea: Copepoda) along a longitudinal environmental gradient in a tropical river-floodplain system, Brazil

Estrutura da assembleia de copépodes (Crustacea: Copepoda) em um gradiente longitudinal ambiental em um sistema rio-planície de inundação tropical, Brasil

---

Welinton Sousa Palhiarini[1]*, Leilane Talita Fatoreto Schwind[2], Rodrigo Leite Arrieira[2],
Luiz Felipe Machado Velho[2,3] and Fábio Amodêo Lansac-Tôha[2]

[1]Programa de Pós-graduação em Biologia Comparada – PGB, Universidade Estadual de Maringá – UEM, Av. Colombo, 5790, Campus Universitário, CEP 87020-900, Maringá, PR, Brazil

[2]Núcleo de Pesquisas em Limnologia Ictiologia e Aquicultura – Nupélia, Departamento de Biologia, Universidade Estadual de Maringá – UEM, Av. Colombo, 5790, Campus Universitário, CEP 87020-900, Maringá, PR, Brazil

[3]Programa de Pós-Graduação em Tecnologias Limpas, Instituto Cesumar de Ciência, Tecnologia e Inovação – ICETI, Centro Universitário Cesumar – UNICESUMAR, Av. Guedner, 1610, CEP 87050-900, Maringá, PR, Brazil
*e-mail: w.s.palhiarini@gmail.com

Cite as: Palhiarini, W.S. et al. Copepod assemblage structure (Crustacea: Copepoda) along a longitudinal environmental gradient in a tropical river-floodplain system, Brazil. *Acta Limnologica Brasiliensia*, 2017, vol. 29, e102.

Abstract: Aim: In this study, we analyzed the structure of the copepod community along a longitudinal axis of the last undammed stretch of the Upper Paraná River floodplain, downstream of Porto Primavera reservoir. We hypothesized that (i) copepod assemblage would show an increase in the abundance of organisms, species richness and specific diversity with the distance from the Porto Primavera reservoir, due to the arrival of species from adjacent lakes and tributaries; (ii) copepod abundance and species richness would be higher in tributaries and adjacent lakes located at the floodplain, which show higher environmental heterogeneity and function as a species source; and (iii) spatial patterns of copepod assemblage structure are related to the environmental gradient, since copepods show a rapid response to the variation of environmental conditions. **Method:** Sampling was performed quarterly from August 2013 to July 2014, at the subsurface of the pelagic region. Sampling sites were located along the Paraná River, in seven of its tributaries, and in eight lakes located in its floodplain. **Results:** We identified 29 species belonging to two families: Cyclopidae (21 species) and Diaptomidae (eight species). On contrary of our first hypothesis, ANOVA results showed a significant decrease in copepod abundance in the downstream direction. Similarly, the tributaries showed higher values of ecological attributes in the upstream stretch. RDA results showed that in axis 1, the Paraná River and the lakes were positively correlated with conductivity, pH, temperature and suspended organic matter, characterized by the most abundant copepod species. The tributaries, on the other hand, were negatively correlated with turbidity, total nitrogen, total phosphorus and depth. Axis 2 showed a positive correlation of the Paraná River with conductivity and suspended organic matter, and a higher abundance of *Argyrodiaptomus azevedoi*, *Notodiaptomus iheringi*, *N. henseni*, *N. cearensis* and *N.* cf. *spinuliferus*. On the other hand, the lakes were positively correlated with temperature and pH and also with a higher abundance of *Thermocyclops minutus* and *T. decipiens*. **Conclusion:** We highlight the importance of the maintenance of the ecological integrity of the Upper Paraná River floodplain, especially of its tributaries, in order to support the high biodiversity registered in the last undammed stretch. Furthermore, we highlight the importance of manipulation of water levels in reservoirs located upstream of this stretch, a necessary condition to maintain the hydrological connectivity between floodplain habitats and the main river.

Keywords: zooplankton; dam; cascading reservoir continuum concept; flood pulse; hydrological connectivity.

Resumo: Objetivo: Este estudo analisou a estruturação da comunidade de copépodes ao longo de um eixo longitudinal do último trecho livre de barramento do sistema rio-planície de inundação do alto rio Paraná a jusante da barragem de Porto Primavera. Nossas hipóteses foram que (i) a comunidade de copépodes apresentará aumento na abundância de organismos, riqueza e diversidade específica de espécies à medida que se distância da barragem de Porto Primavera devido ao incremento de espécies de lagoas marginais e tributários; (ii) os atributos da comunidade serão maiores em tributários e lagoas marginais localizadas na planície de inundação pois a mesma apresenta maior heterogeneidade ambiental e atual como uma fonte de espécies; (iii) o padrão de composição de espécies será correlacionado ao gradiente ambiental tendo em vista que os copépodes apresentam rápida resposta a variação das condições ambientais. **Método:** As amostragens foram realizadas trimestralmente, em 2013 e 2014, à subsuperfície da região pelágica, ao longo do rio Paraná, em sete de seus tributários e em oito lagoas localizadas em sua planície de inundação. **Resultados:** Foram identificadas 29 espécies, pertencentes ás famílias Cyclopidae (21 espécies) e Diaptomidae (8 espécies). Ao contrário da primeira hipótese, os resultados da ANOVA evidenciaram um decréscimo significativo na abundância de copépodes desde montante até jusante, na calha principal do rio Paraná. Os resultados da RDA mostraram que no eixo 1, o rio e as lagoas foram correlacionados positivamente condutividade, pH, temperatura e material orgânico em suspensão, caracterizada pelas principais espécies de copépodes. Os tributários, por outro lado, foram correlacionados negativamente com turbidez, nitrogênio total, fóforo total e profundidade. O eixo 2 houve correlação positiva do rio Paraná com condutividade elétrica e material orgânico em suspensão, e maior abundância de *Argyrodiaptomus azevedoi*, *Notodiaptomus iheringi*, N. *henseni*, *N. cearensis* e *N.* cf. *spinuliferus*. Por outro lado, as lagoas foram correlacionadas positivamente com pH e temperatura e também maior abundância de *Thermocyclops minutus* e *T. decipiens*. **Conclusão:** Dessa forma, destaca-se a importância da manutenção da integridade ecológica da planície de inundação do alto rio Paraná na manutenção da elevada biodiversidade registrada nesse último trecho livre de represamentos desse importante rio tropical. Ressalta-se ainda a importância da manipulação da vazão dos reservatórios a montante desse trecho, condição necessária à existência de uma conectividade hídrica entre planície e rio principal.

Palavras-chave: zooplâncton; barragem; conceito de reservatórios contínuos em cascata; pulso de inundação; conectividade hídrica.

1. Introduction

Suitable environmental conditions are essential for the proper functioning and maintenance of watercourses, as described by the River Continuum Concept (Vannote et al., 1980). According to this theory the riparian vegetation, adjacent lakes and tributaries influence the patterns of environmental conditions in river systems. Therefore, aquatic communities are structured according to longitudinal changes in environmental gradients along the river.

Human activities such as reservoir construction have caused environmental disturbances and altered aquatic ecosystems, promoting changes in the hydrodynamics and chemical and physical characteristics of river systems, thus influencing the structure of aquatic communities (Simões et al., 2015; Agostinho et al., 2016). In this context, the Serial Discontinuity Concept (Ward & Stanford, 1995), which complements the River Continuum Concept, highlights that river impoundments promote discontinuity in the longitudinal dynamics and alterations in biotic and abiotic components. However, aquatic communities and nutrients could show a gradient downstream of the dam, becoming gradually closer to the original conditions of the river. In some aquatic ecosystems, one can observe large reservoirs constructed in cascades, as is the case of the Paraná River (Agostinho et al., 2007). Despite having a 230 km undammed stretch, this river suffers the effects of 34 cascading reservoirs located upstream of Porto Primavera reservoir (Agostinho et al., 2008).

The construction of Porto Primavera reservoir has drastically affected the Upper Paraná River floodplain, since discharge control altered the flood regime, nutrient concentration along the river and, consequently, influenced the establishment of aquatic communities (Agostinho et al., 2004b).

The Cascading Reservoir Continuum Concepts, in turn, attempts to predict the dynamics of these systems. This concept hypothesizes the existence of an interconnection between ecological processes in each type of reservoir, in the upstream-downstream direction, and the influence of lateral systems connected to the rivers, such as adjacent lakes and tributaries (Barbosa et al., 1999; Stanford & Ward, 2001), considering the differences in their communities (Barbosa et al., 1999). Thus, this concept has been used to evaluate the possibility of reestablishment of the original environmental conditions and the organization of aquatic communities in environments under the influence of reservoir construction.

In this sense, the study of the zooplankton community is relevant due to its high species diversity (Lansac-Tôha et al., 2009) and sensitivity to environmental alterations, making it a potential bioindicator of changes in these ecosystems (Maia-Barbosa et al., 2006). This community has been considered a key factor for the comprehension of alterations in aquatic environments (Eskinazi-Sant'anna et al., 2013), providing knowledge on ecological processes in hydrographic basins (Maia-Barbosa et al., 2006; Shah et al., 2013).

Among the organisms belonging to the zooplankton community, the copepods are generally filter-feeding organisms with a diet basically composed of phytoplankton (Perbiche-Neves et al., 2007), bacteria and detritus (Smith et al., 1979). Thus, copepods have a relevant ecological role in freshwater ecosystems, as they feed on primary producers and transfer the energy to higher levels of the food web (Sugumaran, 2016).

Alterations in physical and chemical factors caused by reservoir construction promote changes in food composition, altering the community structure of copepods (Perbiche-Neves et al., 2014). These changes can determine the type of feeding of copepods and favor the development of certain species, influencing on the community structure (Matsumura-Tundisi & Tundisi, 2003; Napiórkowski et al., 2006). In this context, alteration in the structure and dynamics of the copepod community can be an indicator and a reflex of changes in aquatic ecosystem functioning, as observed by Pedrozo & Rocha (2005).

Considering the sensitivity that some species show to environmental changes, in environments affected by reservoir construction, we aimed to verify the structure of the copepod assemblage along a longitudinal axis of the last undammed stretch of the Upper Paraná River floodplain, downstream of Porto Primavera reservoir.

We evaluated the hypotheses that (i) copepod assemblage would show an increase in the abundance of organisms, species richness and diversity with the distance from the Porto Primavera reservoir, due to the arrival of species from adjacent lakes and tributaries; (ii) copepod abundance and species richness would be higher in tributaries and adjacent lakes located at the floodplain, which show higher environmental heterogeneity and function as a species source; and (iii) spatial patterns of copepod assemblage structure are related to the environmental gradient, since copepods show a rapid response to the variation of environmental conditions.

2. Material and Methods

2.1. Study Area

Our study was performed in the last undammed stretch of the Upper Paraná River floodplain, between UHE Engenheiro Sérgio Motta (Porto Primavera reservoir) and Itaipu Reservoir (Figure 1). The Paraná River, which belong to the Prata basin, has an extension of 4,695 km, and has more than 145 great reservoirs along its course, all of them more than 10 meters tall, and of which 20% show an area greater than 100 km^2 (Agostinho et al., 2004b, 2007).

The mean declivity of the Upper Paraná River is 0.18m/km. In the studied stretch, its declivity is reduced (0.09m/km), and the river exhibits a broad anastomosing channel and an extensive alluvial plain, with accumulation of sediment in the riverbed, creating inlets and small islands (over 300), or large islands and a restricted floodplain (Agostinho, 1993).

The studied stretch of the Upper Paraná River showed an extensive floodable area of 480 km before the construction of Porto Primavera reservoir. However, after the dam construction, the floodplain was reduced to an extension of 230 km (Agostinho et al., 2004b). The river-floodplain system has several tributaries. On its left bank, Paranapanema, Ivaí and Piquiri are the main tributaries, and at the right bank Baía, Iguatemi, Ivinhema and Amambaí are the most important. This flood plain system can reach 20 km of width in its right bank, and show a series of adjacent lakes (Agostinho et al., 2004b).

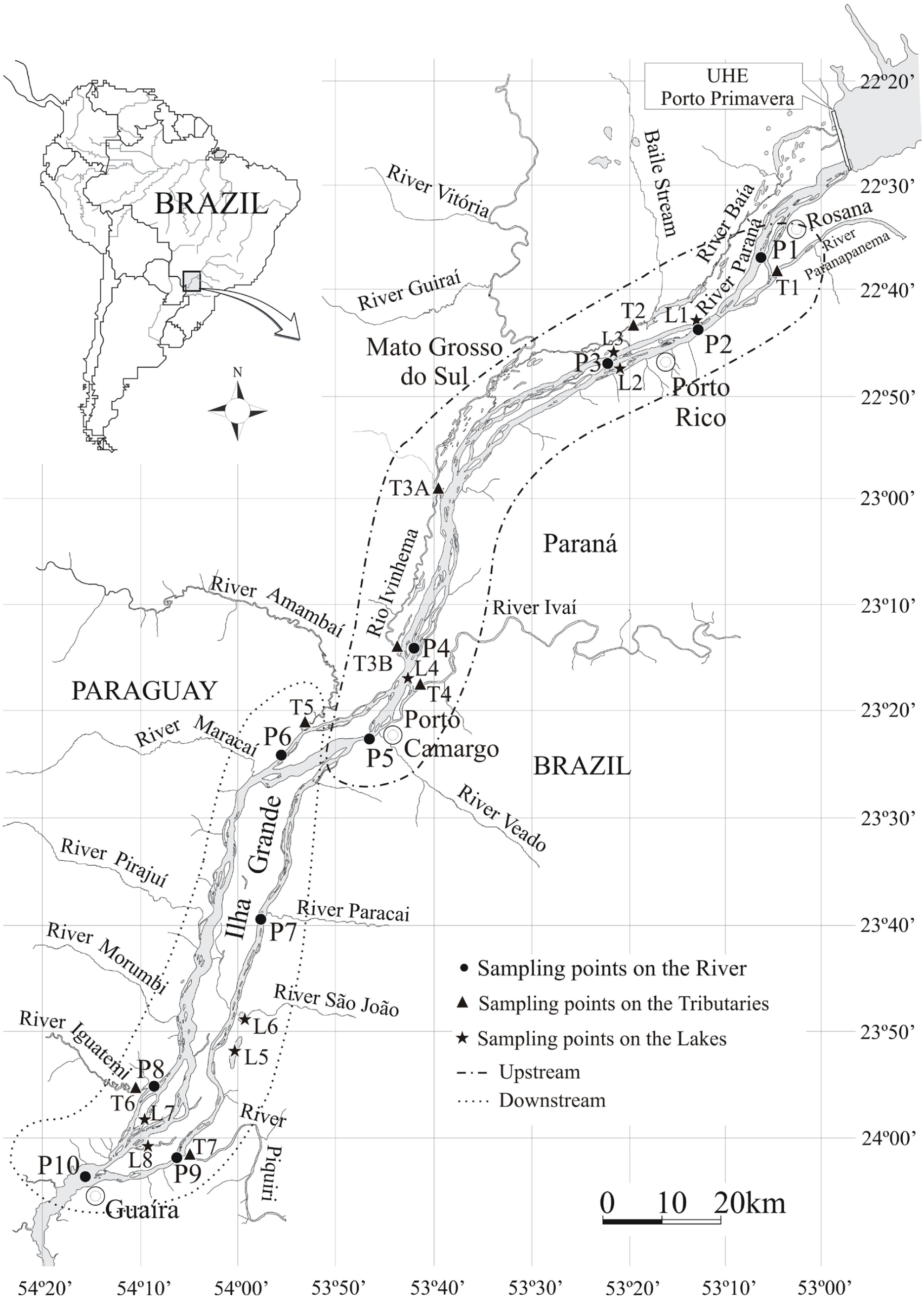

Figure 1. Sampling sites in the Upper Paraná River floodplain, between Porto Primavera reservoir and Itaipu Reservoir. Upstream: stretch directly influenced by Porto Primavera reservoir and the large tributaries of the left river bank; Downstream: stretch influenced by the small tributaries of the right river bank and Itaipu reservoir.

2.2. Field surveys

Copepod sampling was performed in August (low water period) and November (high water period) 2013, and February (high water period) and May (low water period) 2014. Sampling was performed at the subsurface 30 cm of the central region, distributed in transects along a longitudinal axis of the Paraná River, from downstream Porto Primavera reservoir to the beginning of Itaipu Reservoir. We sampled in 10 sampling sites in the river channel with three replicates (left bank, center, and right bank), which were distributed upstream and downstream of the mouths of the seven largest tributaries, which were also sampled. Besides the lotic systems, we also sampled eight adjacent lakes, located in the floodplain itself. Thus, we obtained a total of 180 samples, 120 in the Paraná River, 28 in tributaries, and 32 in lakes.

Plankton samplings were performed in the morning, with a suction pump, by filtering 600 liters of water per sample through a plankton net of 68 µm mesh size. Samples were further fixed in a 4% formaldehyde buffered with calcium carbonate.

2.3. Environmental parameters sampling

The following environmental parameters were measured in each sampling site in the field: water transparency (m) (Secchi disk), pH (digital portable pH meter), conductivity ($\mu S.cm^{-1}$) (digital portable conductivity meter), and turbidity (NTU) (digital turbidimeter), temperature (°C), and dissolved oxygen (saturation % and $mg.L^{-1}$) (YSI digital oximeter).

In the laboratory, total nitrogen (Mackereth et al., 1978) and phosphorus were determined (Golterman et al., 1978). Organic and inorganic suspended matter ($\mu g.L^{-1}$) were determined by gravimetry (Wetzel & Likens, 1991).

Data on these physical and chemical variables were provided by the Laboratory of Basic Limnology of the Research Nucleus in Limnology, Ichthyology and Aquaculture (Nupelia) of the State University of Maringá.

Data on the water levels of the Paraná River were provided by the Itaipu Reservoir, of the monitoring station of São José (22° 43' 04"S, 53° 10' 36"O) (altitude above mean sea level – amsl).

2.4. Laboratory analysis

In the laboratory, we identified copepods using specialized literature (Santos-Silva, 2000; Lansac-Tôha et al., 2002; Silva, 2003; Perbiche-Neves et al., 2015). Individuals were counted under a binocular optic microscope, using Sedgewick-Rafter chambers. A minimum of 50 individuals were counted in three subsequent subsamples, obtained with a Hensen-Stempel pipette (2.5 mL) (method modified from Bottrell et al., 1976). Samples with a reduced number of individuals were counted entirely. Final density was expressed in individuals per cubic meter ($ind.m^{-3}$). The subsample method, despite providing a reliable estimate of abundance, underestimates species richness, since rare species may not be registered. Considering that, in order to determine species richness, we analyzed subsequent subsamples of each sample until no new species were registered.

2.5. Statistical analyses

In order to verify the species diversity (H') of copepods in each sampling site, as described in hypotheses (i) and (ii), we calculated the Shannon-Wiener index (Pielou, 1975), which is described by – $H' = - \sum (ni/N) \times \log^2 (ni/N)$, in which ni is the number of individuals of the ith species and N is the total number of individuals.

In order to test hypotheses (i) and (ii), we used Analysis of Variance (ANOVA) (Sokal & Rohlf, 1991) to verify if there are significant differences ($p<0.05$) in the abundance, richness and diversity of copepod species between sampling sites along the longitudinal axis of the river, lakes and tributaries. Moreover, we performed Fisher's LSD post-hoc test to identify significant differences between upstream and downstream of the sampled environments. The longitudinal axis was arbitrarily categorized in two stretches: upstream, represented by sampling sites P1 to P5 for the Paraná River, T1 to T4 for tributaries, and L1 to L4 for lakes; and downstream, represented by sites P6 to P10 for the Paraná River, T5 to T7 for tributaries and L5 to L8 for lakes.

Previously to all analyses, we logarithmized abundance data and checked the normality and homocedasticity assumptions. When assumptions were not met, we performed a Kruskal-Wallis test, using software Statistic 7.0 (Statsoft Inc., 2005).

In order to test hypothesis (iii) and evaluate the influence of the environmental heterogeneity on the structure of the planktonic copepods, we used a Redundancy Analysis (RDA) (Legendre & Legendre, 1998). Results were based on the values of total inertia and percentage of explanation of each retained axis ($p<0.05$). The abundance of organisms was logarithmized to reduce the influence of rare species and then transformed according to the Hellinger procedure (Legendre & Gallagher, 2001). Furthermore, the effect of multicolinearity between environmental variables was tested through the Variance Inflation Factor (VIF). These analyses were performed in software R. version 3.1.3 (R Development Core Team, 2015), using the package 'vegan' (Oksanen et al., 2012).

3. Results

3.1. Environmental characterization

In general, environmental variables showed low spatial variability during the study period in the different sampling sites. However, turbidity showed an increase in the upstream-downstream direction (P1 to P10). We also observed an increase in total phosphorus concentrations in the sampling sites located at the upstream stretch (P6 to P10), which are influenced by tributaries at the right bank of the Paraná River (Table 1).

Table 1. Mean values and standard deviation of environmental variables in sampling sites of the Upper Paraná River floodplain. River: upstream-downstream (P1 to P10).

Points	Temp (°C)	Depth (m)	Secchi (m)	Turb (NTU)	T H_2O (°C)	DO (mg/L)	pH	Cond (uS/cm)	TSM (ug/L^{-1})	IMS (mg/L^{-1})	SOM (mg/L^{-1})	Alc (mEq/L^{-1})	TN (ug/L^{-1})	TP (ug/L^{-1})
P1	29.16 ± 3.33	2.40 ± 0.55	2.31 ± 0.59	2.15 ± 0.74	24.88 ± 3.13	7.75 ± 0.82	7.51 ± 0.22	61.22 ± 3.97	2.30 ± 0.75	1.26 ± 0.63	1.03 ± 0.54	712.96 ± 106.08	660.00 ± 91.50	18.63 ± 15.48
P2	22.29 ± 3.56	5.56 ± 1.05	2.60 ± 0.67	3.63 ± 1.58	23.99 ± 3.13	7.81 ± 0.68	7.51 ± 0.14	62.48 ± 2.53	3.50 ± 2.19	2.17 ± 1.48	1.32 ± 0.79	709.02 ± 113.00	618.03 ± 74.85	11.20 ± 2.09
P3	25.62 ± 5.98	3.50 ± 1.34	2.00 ± 0.83	3.87 ± 1.61	24.46 ± 3.52	7.83 ± 0.74	7.48 ± 0.17	61.27 ± 1.49	4.97 ± 2.51	3.68 ± 2.11	1.29 ± 0.45	601.77 ± 155.83	561.77 ± 50.73	13.25 ± 2.94
P4	24.87 ± 2.54	4.46 ± 0.66	1.94 ± 0.47	6.46 ± 1.45	24.87 ± 2.94	7.88 ± 0.53	7.25 ± 0.22	59.50 ± 4.12	6.67 ± 1.99	5.02 ± 1.53	1.65 ± 0.70	594.20 ± 145.84	577.18 ± 66.61	19.06 ± 4.48
P5	28.62 ± 3.62	5.45 ± 0.55	1.95 ± 0.60	7.43 ± 1.55	25.10 ± 3.02	7.65 ± 0.77	7.10 ± 0.10	56.49 ± 2.49	5.38 ± 1.43	4.05 ± 1.07	1.33 ± 0.50	596.56 ± 172.15	459.37 ± 127.32	20.89 ± 4.08
P6	29.58 ± 4.20	2.57 ± 0.24	1.41 ± 0.25	7.61 ± 2.07	25.34 ± 3.04	7.84 ± 0.39	6.96 ± 0.33	60.60 ± 1.33	4.82 ± 1.75	3.87 ± 1.62	0.95 ± 0.34	596.74 ± 168.25	663.14 ± 78.14	18.23 ± 7.05
P7	25.50 ± 2.33	3.06 ± 0.46	1.47 ± 0.55	11.71 ± 2.58	25.2 ± 3.40	7.58 ± 0.73	6.99 ± 0.15	50.05 ± 2.9	6.84 ± 2.95	5.48 ± 2.36	1.35 ± 0.58	531.75 ± 127.99	442.22 ± 146.49	25.34 ± 8.95
P8	29.00 ± 2.12	3.30 ± 0.22	1.23 ± 0.37	9.86 ± 3.29	25.98 ± 3.30	7.66 ± 0.60	6.89 ± 0.14	50.01 ± 3.05	4.39 ± 2.18	3.65 ± 1.88	0.73 ± 0.32	525.6 ± 126.35	528.46 ± 78.78	25.18 ± 5.98
P9	31.91 ± 3.04	2.22 ± 0.04	1.45 ± 0.25	7.55 ± 2.00	25.87 ± 3.24	7.91 ± 0.73	6.80 ± 0.39	60.38 ± 0.92	3.64 ± 0.94	2.89 ± 0.94	0.75 ± 0.19	657.12 ± 147.84	627.93 ± 109.79	21.84 ± 4.44
P10	24.75 ± 2.62	2.78 ± 0.11	1.48 ± 0.43	11.26 ± 4.23	24.80 ± 3.49	7.72 ± 0.76	6.66 ± 0.28	51.58 ± 2.25	3.38 ± 1.43	2.77 ± 1.28	0.60 ± 0.17	559.71 ± 142.95	701.74 ± 88.92	26.68 ± 7.92
T1	25.75 ± 2.30	4.92 ± 0.80	2.45 ± 1.30	5.67 ± 2.90	24.1 ± 3.00	7.77 ± 0.60	7.43 ± 0.20	64.92 ± 2.30	2.82 ± 2.40	1.49 ± 1.40	1.32 ± 1.20	794.62 ± 155.8	981.75 ± 220.60	18.06 ± 4.40
T2	27.75 ± 5.90	2.35 ± 0.40	1.43 ± 0.80	4.89 ± 1.30	24.07 ± 4.50	6.93 ± 1.30	6.59 ± 0.40	30.63 ± 12.4	1.32 ± 0.60	0.85 ± 0.50	0.47 ± 0.20	247.10 ± 64.40	759.04 ± 79.80	32.73 ± 13.80
T3A	23.25 ± 7.80	4.82 ± 0.40	0.63 ± 0.20	16.07 ± 2.40	24.42 ± 4.10	7.07 ± 0.90	6.81 ± 0.30	42.75 ± 2.30	3.50 ± 1.70	2.65 ± 1.30	0.85 ± 0.40	507.97 ± 136.80	711.01 ± 95.10	39.23 ± 9.90
T3B	22.5 ± 4.30	5.60 ± 0.30	0.8 ± 0.20	16.47 ± 3.0	25.35 ± 3.70	6.85 ± 0.60	6.60 ± 0.40	40.55 ± 3.50	3.60 ± 1.30	2.91 ± 1.10	0.69 ± 0.20	449.32 ± 105.60	694.51 ± 80.50	43.20 ± 7.10
T4	25.87 ± 4.10	6.20 ± 0.50	0.62 ± 0.20	18.20 ± 5.00	25.37 ± 4.30	8.15 ± 0.50	6.96 ± 0.60	60.67 ± 2.90	3.73 ± 1.40	2.99 ± 1.20	0.73 ± 0.30	620.62 ± 170.40	1118.74 ± 127.50	39.99 ± 9.20
T5	27.00 ± 3.30	4.03 ± 0.50	0.48 ± 0.20	25.10 ± 9.00	23.93 ± 3.60	7.17 ± 0.50	6.27 ± 0.30	31.83 ± 1.20	5.35 ± 2.00	4.53 ± 1.80	0.82 ± 0.20	318.53 ± 76.20	916.28 ± 162.80	36.52 ± 13.80
T6	32.25 ± 3.40	2.92 ± 1.00	0.47 ± 0.10	23.14 ± 6.80	24.65 ± 3.20	7.75 ± 0.70	6.14 ± 0.50	18.77 ± 1.20	4.82 ± 3.10	4.02 ± 2.60	0.79 ± 0.50	181.70 ± 76.60	669.55 ± 53.40	16.87 ± 11.00
T7	31.75 ± 3.80	8.45 ± 1.10	0.83 ± 0.20	15.595 ± 4.90	24.25 ± 4.10	8.11 ± 0.90	6.49 ± 0.40	47.45 ± 3.40	2.56 ± 2.20	1.93 ± 1.70	0.63 ± 0.50	548.77 ± 165.80	947.81 ± 211.40	25.78 ± 4.10
L1	21.50 ± 2.80	2.02 ± 0.60	0.73 ± 0.20	14.14 ± 4.10	23.72 ± 4.00	7.36 ± 1.30	6.97 ± 0.20	58.92 ± 4.10	3.45 ± 1.30	2.61 ± 0.90	0.84 ± 0.30	734.62 ± 160.60	683.32 ± 193.40	30.95 ± 3.10
L2	25.00 ± 6.00	1.53 ± 1.00	1.36 ± 0.80	4.91 ± 2.20	25.6 ± 5.20	10.41 ± 2.00	8.50 ± 0.90	62.33 ± 1.10	1.62 ± 0.60	1.12 ± 0.60	0.49 ± 0.00	571.30 ± 129.70	728.04 ± 44.10	13.91 ± 2.40
L3	25.75 ± 7.40	1.32 ± 0.50	0.81 ± 0.30	8.45 ± 2.10	24.42 ± 4.50	7.45 ± 0.90	6.86 ± 0.20	53.15 ± 2.30	1.37 ± 0.40	0.91 ± 0.30	0.45 ± 0.10	489.15 ± 89.40	761.96 ± 129.10	32.92 ± 8.90
L4	27.50 ± 1.00	1.76 ± 0.20	0.45 ± 0.20	17.93 ± 4.90	23.73 ± 1.60	7.45 ± 0.60	6.25 ± 0.60	56.60 ± 2.80	0.85 ± 0.60	0.53 ± 0.40	0.32 ± 0.30	710.10 ± 85.30	1041.16 ± 135.60	64.55 ± 21.40
L5	27.33 ± 3.60	3.46 ± 0.60	0.45 ± 0.10	33.69 ± 4.60	27.43 ± 2.80	7.10 ± 0.60	15.17 ± 10.80	24.64 ± 11.80	1.44 ± 1.50	0.98 ± 1.10	0.45 ± 0.30	254.10 ± 35.10	1139.70 ± 357.70	41.83 ± 7.40
L6	26.66 ± 4.90	1.53 ± 0.00	0.63 ± 0.10	13.38 ± 1.00	26.66 ± 2.80	5.97 ± 0.80	6.65 ± 0.40	32.66 ± 3.00	2.08 ± 2.20	1.52 ± 1.60	0.56 ± 0.60	335.73 ± 47.40	926.45 ± 438.20	30.07 ± 13.70
L7	29.25 ± 1.80	3.00 ± 0.20	1.45 ± 0.10	4.35 ± 1.00	24.90 ± 3.00	18.79 ± 20.00	6.06 ± 0.50	63.00 ± 6.30	0.29 ± 0.20	0.13 ± 0.20	0.15 ± 0.10	650.57 ± 203.60	870.62 ± 495.30	24.97 ± 6.20
L8	24.00 ± 2.50	2.41 ± 0.40	1.18 ± 0.20	3.46 ± 0.90	24.85 ± 3.80	6.07 ± 0.80	5.99 ± 0.50	46.10 ± 4.60	0.87 ± 0.60	0.42 ± 0.40	0.44 ± 0.20	452.87 ± 109.50	839.19 ± 173.60	27.86 ± 4.70

Tributaries: T1 = Paranapanema; T2 = Baía; T3A = Ivinhema; T3B = Ivinheminha.; T4 = Ivaí; T5 = Amambaí; T6 = Iguatemi; T7 = Piquiri; Lakes: L1 = Garças; L2 = Pombas; L3 = Xirica; L4 = Ivaí; L5 = Xambrê; L6 = São João; L7 = Pavão; L8 = Saraiva; Temp = Temperature; Turb = Turbidity; TH_2O = Water temperature; DO = Dissolved Oxygen; Cond = Conductivity; TSM = Total Suspended Matter; SIM = Suspended Inorganic Matter; SOM = Suspended Organic Matter; Alc = Alkalinity; TN = Total Nitrogen; TP = Total Phosphorous.

Water level showed little variation between sampling periods. The lowest value was observed in May 2014 (233.94 amsl), and the highest in February 2014 (235.83 amsl). Water levels varied only 1.89 m between those periods of low and high water levels (Figure 2).

3.2. Structure of the copepod assemblage

We identified 29 species, belonging to two families: Cyclopidae (21 taxa) and Diaptomidae (8 taxa) (Table 2). Among Cyclopidae, only *Eucyclops elegans*, *E. ensifer*, *Mesocyclops meridianus*, *Microcyclops anceps*, *Paracyclops chiltoni*, *Thermocyclops decipiens* and *T. minutus* were registered in all types of environments. Among Diaptomidae, all species except *Notodiaptomus* sp. were observed in all types of environments (Table 2).

Thermocyclops minutus and *T. decipiens* (Cyclopoida) showed the highest mean abundance in the lakes, whereas *Notodiaptomus henseni* and *N. cearensis* (Calanoida) were the most abundant in the river (Figure 3).

Significant differences in the copepod abundance (F = 4.33; $p = 0.04$) were found between stretches considering the sampling sites located in the Paraná River, with higher means in the upstream sites

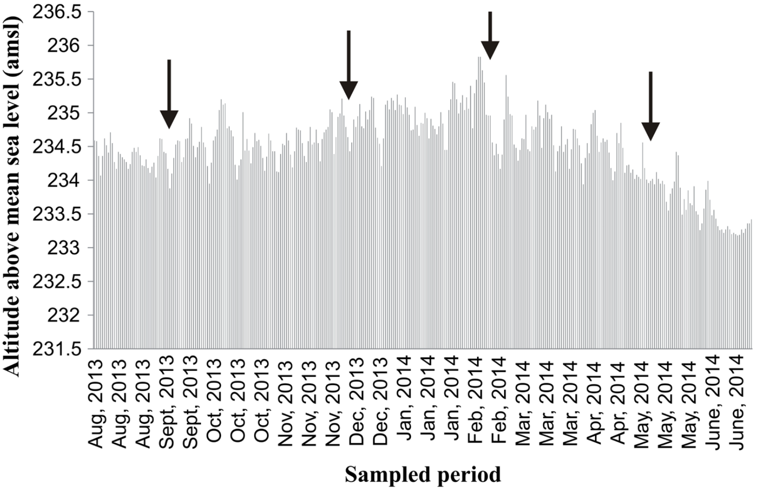

Figure 2. Variation in water level in relation to sea level (amsl) from August 2013 to July 2014. Areas signed with arrows represent sampled months. The value zero in the y-axis is represented by 231.5 (level zero corrected by altitude above mean sea level).

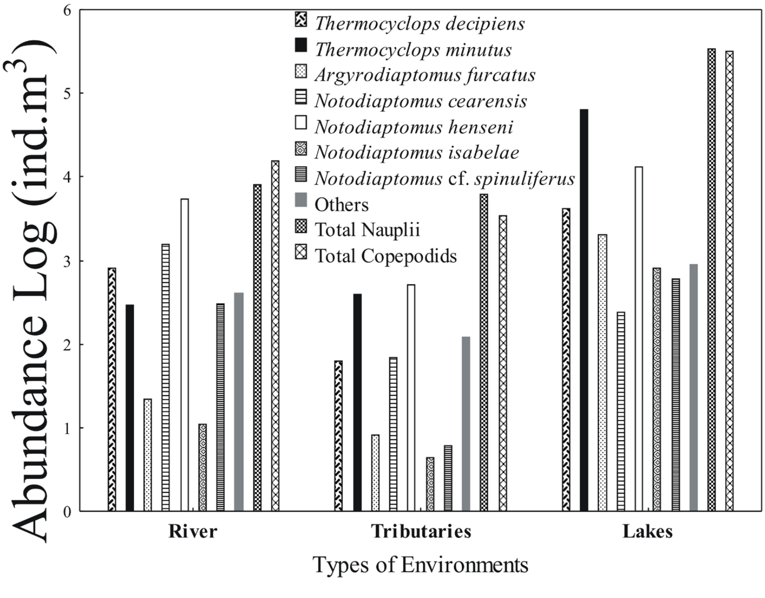

Figure 3. Copepod abundance in the three types of environment sampled. Only the most abundant species were considered.

Table 2. Species list and spatial occurrence of copepods collected in this study in the Upper Paraná River floodplain.

Taxonomic position	River	Tributaries	Lakes
ORDER CICLOPOIDA			
FAMILY CYCLOPIDAE			
Acanthocyclops robusts (Sars, 1863)	x		
Eucyclops elegans (Herrick, 1884)	x	x	x
Eucyclops ensifer Kiefer, 1936	x	x	x
Eucyclops prinophorus (Kiefer, 1936)			x
Ectocyclops rubescens Brady, 1904		x	
Macrocyclops albidus (Jurine, 1820)			x
Mesocyclops sp.	x		x
Mesocyclops aspericornis (Daday, 1906)	x		x
Mesocyclops ellipticus Kiefer, 1936	x		x
Mesocyclops longisetus (Thiébaud, 1912)	x		
Mesocyclops meridianus (Kiefer, 1926)	x	x	x
Mesocyclops ogunnus Onabamiro, 1957	x		
Metacyclops laticornis (Lowndes, 1934)		x	x
Metacyclops mendocinus (Wierzejski, 1892)		x	
Microcyclops sp.		x	x
Microcyclops alius Kiefer, 1935			x
Microcyclops anceps (Richard, 1897)	x	x	x
Microcyclops finitmus Dussart, 1984			x
Paracyclops chiltoni (Thomson, 1882)	x	x	x
Thermocyclops decipiens (Kiefer, 1929)	x	x	x
Thermocyclops minutus (Lowndes, 1934)	x	x	x
ORDER CALANOIDA			
FAMILY DIAPTOMIDAE			
Argyrodiaptomus azevedoi (Wright, 1935)	x	x	x
Argyrodiaptomus furcatus (Sars, 1901)	x	x	x
Notodiaptomus sp.			x
Notodiaptomus cearensis (Wright, 1936)	x	x	x
Notodiaptomus henseni (Dahl, 1894)	x	x	x
Notodiaptomus iheringi Wright, 1935	x	x	x
Notodiaptomus isabelae (Wright, 1936)	x	x	x
Notodiaptomus spiniger (Brian, 1925)	x	x	x
Notodiaptomus cf. *spinuliferus* (Dussart, 1985)	x	x	x

(Figure 4a). Differences were not significant for species richness (F = 0.8; p = 0.37) and diversity (F = 1.04; p = 0.31) (Figure 4b and c).

Copepod abundance (F = 5.19; p = 0.02), species richness (F = 9.14; $p < 0.01$), and diversity (F = 11.91; $p < 0.01$) were significantly different between stretches considering the sampling sites located in the tributaries (Figure 5a, b and c). Higher values of all the attributes were found in sites located upstream.

Considering the lakes, ANOVA showed significant differences for copepod abundance (F = 7.51; p = 0.01) between stretches, with higher mean values found in sites located downstream (Figure 6a). Species richness (F = 0.12; p = 0.73) and diversity (F = 2.19; p = 0.15) did not show significant differences between stretches located upstream and downstream (Figure 6b and c).

Copepod abundance differed significantly between types of environments according to Kruskal-Wallis (H = 47.33; $p < 0.001$). Tributaries showed lower mean values of this attribute, while higher mean values were registered in lakes (Figure 7a). ANOVA also indicated significant differences between types of environments for species richness (F = 44.46; $p < 0.01$) and diversity (F = 8.56; $p < 0.01$). Regarding species richness, a significant difference was found between the three types of environments, while for diversity, sites located in the main channel and in the lakes differed significantly from sites located in the tributaries. Highest mean values of species richness and diversity were found in sampling sites located in the Paraná River, while lowest mean values of these attributes were found in tributaries (Figure 7b and c).

RDA revealed an association between the copepod assemblage structure and environmental

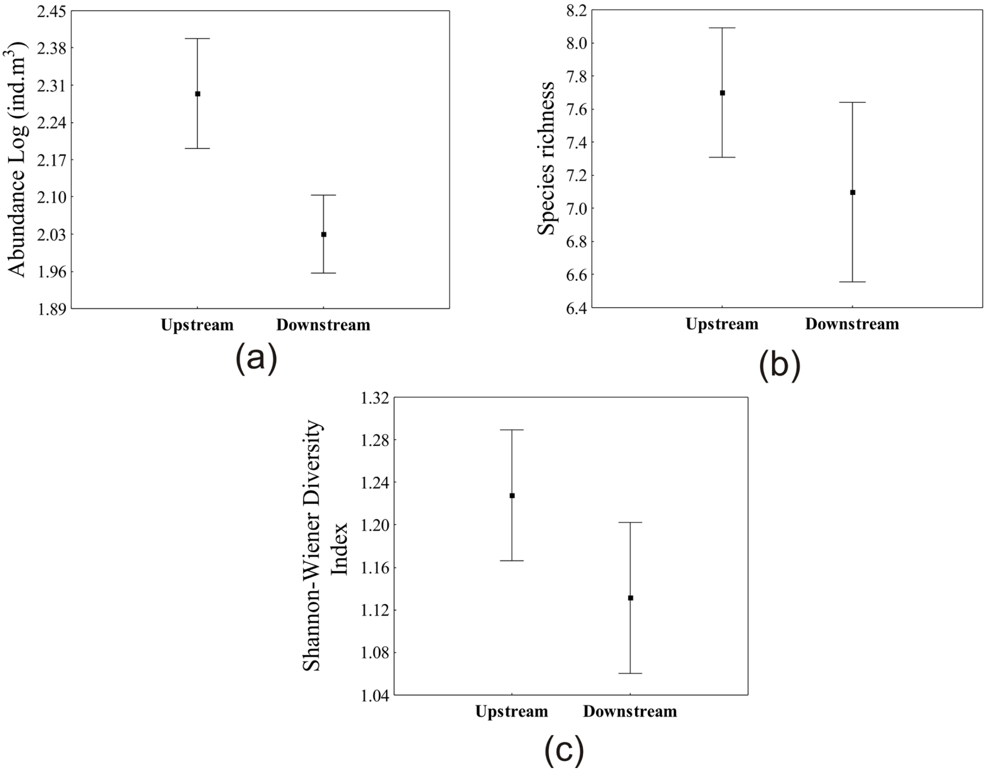

Figure 4. Copepod abundance (a), species richness (b) and diversity (c) in the sampled stretches (upstream and downstream) of the main channel of the Paraná River. Symbols represent mean values and vertical bars represent standard error.

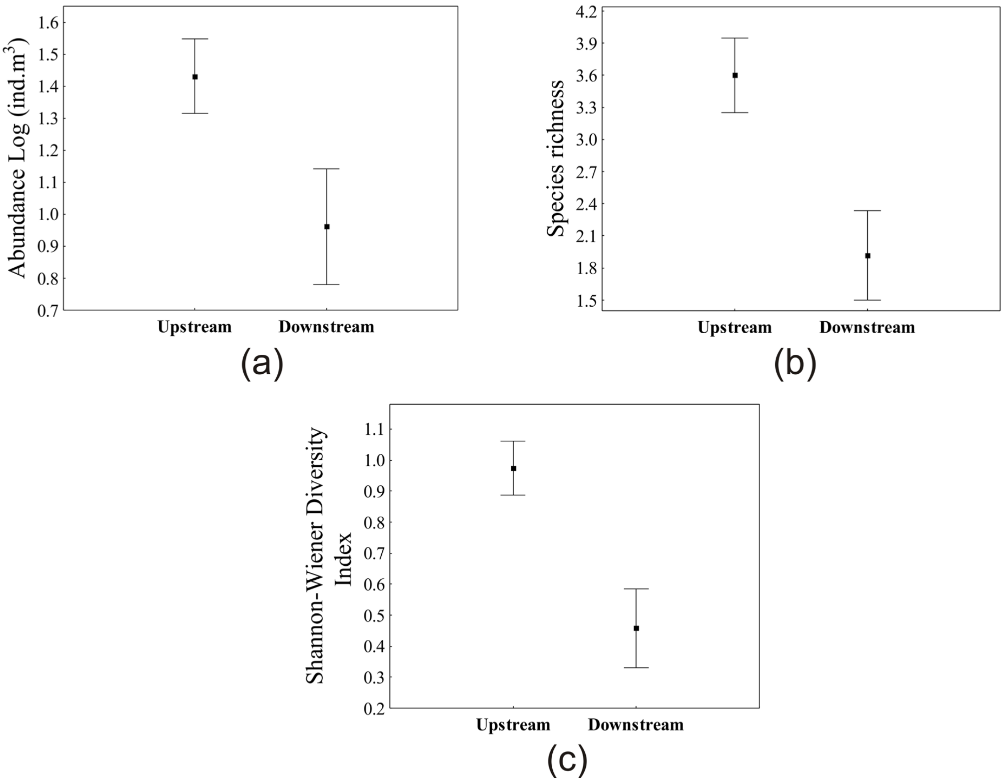

Figure 5. Copepod abundance of organisms (a), species richness (b) and diversity (c) recorded in the tributaries sampled in the different stretches (upstream and downstream) of the Paraná River. Symbols represent mean values and vertical bars represent standard error.

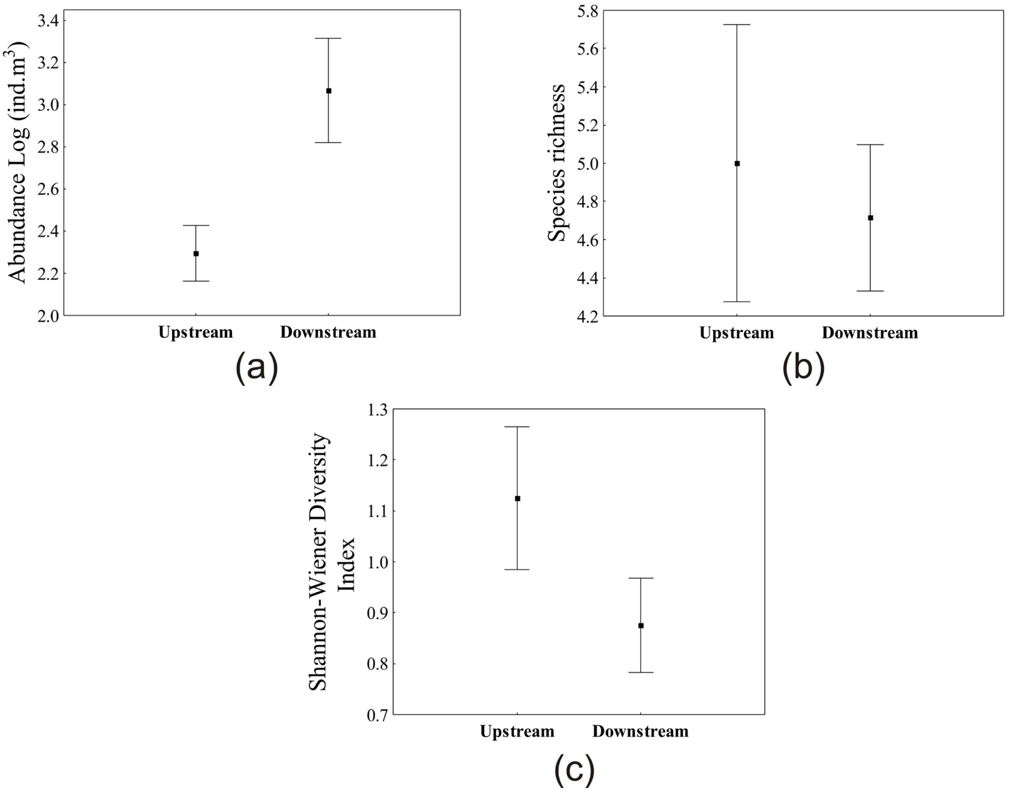

Figure 6. Copepod abundance (a), species richness (b) and diversity (c) recorded in the lakes sampled in the different stretches (upstream and downstream) of the Paraná River. Symbols represent mean values and vertical bars represent standard error.

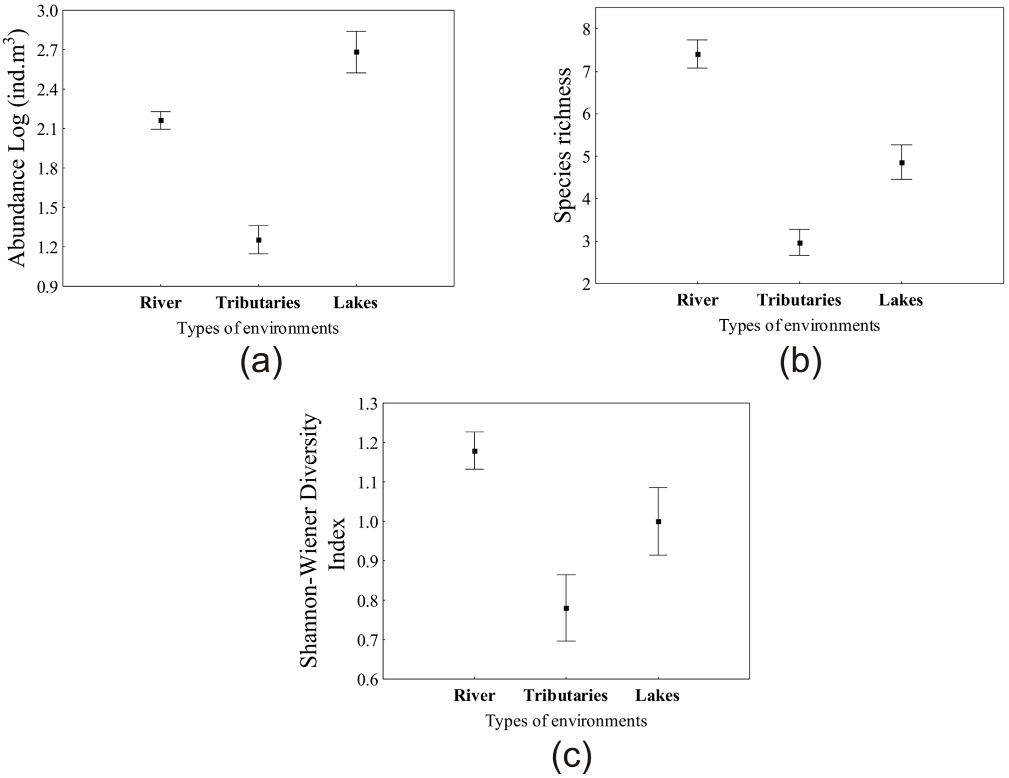

Figure 7. Copepod abundance (a), species richness (b), and diversity (c) in each type of environment sampled. Symbols represent mean values and vertical bars represent standard errors.

variables ($p < 0.05$), and the ordination model explained 57% of the variance in the data. Axis 1 explained 42% of the variance in the data and discriminated the sampling sites located in Paraná River and adjacent lakes, positively related to this axis and characterized by higher values of conductivity, pH, temperature and suspended organic matter, and also by the occurrence and abundance of the main copepod species, from the sampling sites located in the tributaries, negatively related to this axis, and which showed higher values of turbidity, total nitrogen, total phosphorus and depth.

Axis 2 explained 25% of the variance in the data and discriminated the sampling sites located in the Paraná River, with higher values of conductivity and suspended organic matter and characterized by the occurrence and higher abundances of diaptomids *Notodiaptomus iheringi*, *N. cearenses*, *N.* cf. *spinuliferus* and *N. henseni*, from the sampling sites located in the lakes, with higher pH and temperature, where cyclopids *Thermocyclops minutus* and *T. decipiens* predominated (Figure 8). Moreover, this analysis evidenced that higher nutrient concentrations (TN and TP) were positively related to axis 2, associated with sampling sites from the lakes and tributaries, which indicates a higher trophic state in these environments.

4. Discussion

We observed a longitudinal gradient of nutrients along the sampled stretch of the Paraná River. This tendency of lower values of total phosphorous concentrations and turbidity in sampling sites closer to Porto Primavera reservoir is certainly related to the effects of upstream reservoir cascades causing several alterations downstream, such as the reduction in the transport of suspended matter transport, decrease in nutrient concentrations causing oligotrophication, increase in water transparency, and discontinuity of physical and chemical characteristics (Barbosa et al., 1999). These effects have been widely reported as possible causes of changes in the aquatic biota (Istvánovics et al., 2010; Bortolini et al., 2016) and have been observed for the Upper Paraná River floodplain (Agostinho et al., 2008; Mantovano et al., 2015; Simões et al., 2015) and other reservoirs in the world (Ney, 1996).

Water levels showed little variation between sampling periods, which did not allow for a characterization of low water and high water periods. Inundations of important impact over habitats adjacent to the Paraná River occur when water levels reach at least 4.6 meters (Souza-Filho, 2009). In this way, we evaluated only the spatial scale, while the temporal scale was not taken into

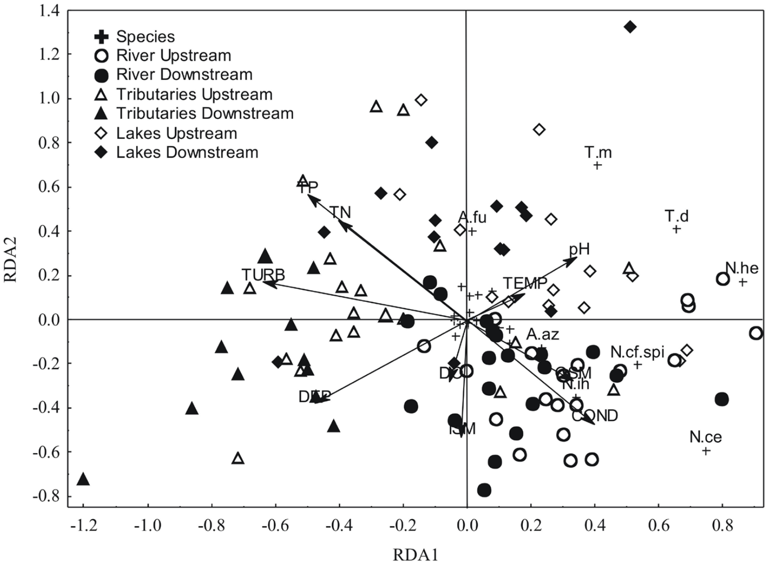

Figure 8. Bidimensional representation of Redundancy Analysis (RDA) between copepod abundances and environmental variables of the sampling sites. COND = conductivity; TN = total nitrogen; DEP = depth; TP = total phosphorous; TEMP = temperature; TURB = turbidity; DO = dissolved oxygen; SOM = suspended organic matter; SIM = suspended inorganic matter. Species: A.az = *A. azevedoi*; A.fu = *A. furcatus*; N.ih = *N. iheringi*; T.m = *T. minutus*; T.d = *T. decipiens*; N.he = *N. henseni*; N.cf.spi = *N.* cf. *spinuliferus*; N.ce = *N. cearensis*. For better visualization, only species mostly associated to each axis are showed.

account, considering that the effect of flood pulse on the copepod assemblage could not be tested.

Considering the structure of the copepod assemblage, the numeric predominance of *T. minutus*, *N. henseni*, *T. decipiens* and *N. cearensis* has been reported in studies approaching this assemblage in freshwater ecosystems (Nogueira et al., 2008; Lansac-Tôha et al., 2004, 2009; Ferrareze & Nogueira, 2011).

Copepod abundance decreased with the distance from Porto Primavera reservoir, in the upstream-downstream direction. This pattern of decreasing abundance could also be observed in other studies performed in environments located downstream of reservoirs (Mitsuka & Henry, 2002; Chang et al., 2008; Perbiche-Neves et al., 2012; Grabowska et al., 2013).

This decrease in abundance is probably caused by the influence of flow velocity in the stretch downstream of the reservoir (Mitsuka & Henry, 2002; Chang et al., 2008; Portinho et al., 2016). Thus, there is an expressive contribution of the reservoir fauna for the community structure immediately downstream of the reservoir, which frequently suffers a decrease along the dowstream stretch, which exhibits with lotic characteristics. The abundance of these organisms is influenced by hydrodynamic conditions, since the current velocity affects the availability of food resources through the removal of nutritive compounds of the biotic community (Mitsuka & Henry, 2002). Furthermore, the reproduction of planktonic organisms is also limited by the high current velocity (Ward, 1994), considering that these organisms are exported in a downstream direction in a rate that is frequently higher than their reproductive capacity. In addition, the large volume of water coming from downstream, promotes a dilution effect in the abundance of copepods (Nadai & Henry, 2009; Neto et al., 2014).

Moreover, lentic environments such as floodplain lakes favor the development of planktonic populations, including copepods (Viroux, 1997; Velho et al., 2001). Since the upstream stretch is more extensive and characterized by an elevated number of lakes and secondary channels, we suggest that the higher values of copepod abundance observed in sampling sites located upstream of the Paraná River could also be the result of the contribution of fauna from environments adjacent to the floodplain. However, the absence of flood during the studied period leads us to disregard this idea. In this sense, Casanova & Henry (2004) verified that low water levels determined a small contribution of lakes, both in terms of abundance and diversity, to the increment of copepod species in the Paranapanema River.

Thus, it is more plausible to assume that the higher abundance of copepods in the stretch closer to Porto Primavera reservoir was due to the arrival of copepods coming from the reservoir. The higher water retention time in the reservoir frequently favors an increase in the abundance of these microcrustaceans (Sartori et al., 2009).

The higher diversity of copepod species in the main river channel was probably determined by the influence of tributaries, mainly those located at the right bank (Baía, Ivinhema and Ivinheminha), in the floodplain. This result suggests an importance of these tributaries for species dispersal, which maintains a higher diversity of copepods in the main river channel despite the low abundance found in this environment. Velho et al. (2004) suggested that the Paraná River functions as a collector of the fauna from all the floodplain.

The redundancy analysis showed that environmental conditions influenced the structure of the copepods assemblage. In this way, the highest copepod abundances and occurrence in lakes corroborate the pattern frequently registered for zooplankton, owing to the lentic characteristic of these environments, which allow the successful reproduction and establishment of populations, especially of copepods (Paggi & Paggi, 1990). In our study, cyclopoid species, especially *T. minutus* and *T. decipiens*, predominated in these environments, characterized by the higher values of water temperature and pH. Due to the higher water residence time and reduced flow velocity of these lakes, compared to the river, one could expect that calanoids would be better adapted and predominate in these environments (Ferrareze & Nogueira, 2011), and that cyclopoids would predominate in sampling sites located at the Paraná River. However, we observed an inverse pattern, which could be explained by the fact that the studied lakes were mainly mesotrophic, which favours cyclopoid species (Landa et al., 2007), to the detriment of calanoid species, which prevail in oligotrophic environments.

In the Paraná River, as previously highlighted, calanoids dominated, in terms of abundance and occurrence. This suggests that this predominance is determined by the influence of the upstream reservoir (Porto Primavera), which retain both nutrients and sediments (Agostinho et al., 2004a), promoting oligotrophication, considering that this is the last of a long series of reservoirs located at the Paraná River basin. Other authors also registered a similar pattern of calanoid abundance in lotic environments impacted by upstream reservoirs (Lopes et al., 1997; Portinho et al., 2016).

In turn, tributaries were characterized by the low occurrence and abundance of copepods, likely due to the high current velocity of these environments. Therefore, although tributaries show considerably high values of nutrient concentration, which was also verified in the lakes, the water residence time, extremely reduced in these environments, limits the development of populations of copepods (Pourriot et al., 1997). Moreover, higher turbidity values found in these tributaries can limit the occurrence of these organisms, by obstructing the respiratory tract (Mitsuka & Henry, 2002).

Therefore, although the hydrodynamics was considered the main factor influencing the occurrence and dominance of copepod groups, the results obtained in our study also indicate the relevance of the trophic degree as a structuring factor for this assemblage, when comparing the Paraná River (oligotrophic) with the adjacent mesotrophic lakes. In summary, the results obtained in our study evidenced a decrease in the copepod abundance along the longitudinal axis of the Paraná River, from upstream to downstream, refuting our first hypothesis. This was likely due to the influence of fauna coming from the reservoir in the organization of the copepod assemblage in the upstream stretch of the study area.

Our second hypothesis was partially refuted considering that the highest copepod diversity, contrary to our expectations, was registered in the Paraná River, although the highest abundance was verified in the floodplain lakes. Finally, the third hypothesis was corroborated, since the abundance and composition patterns of copepods were related to the environmental gradient.

Thus, we highlight the importance of the maintenance of the ecological integrity of the Upper Paraná River floodplain, in order to maintain the high biodiversity registered in the last undammed stretch of this important tropical river. We emphasize the importance of the regulation of outflow from reservoirs located upstream this stretch, which is a necessary condition to the existence of hydrological connectivity between the floodplain habitats and the main river, fundamental for the biodiversity of river-floodplain systems.

Acknowledgements

We thank the doctoral students Diogo Castanho Amaral and Vanessa Tibúrcio and the undergraduate student Junior Bueno for help with species identification, Dr. Geziele M. Alves for valuable suggestions, the National Council of Scientific and Technologic Development (CNPq) – Process Number 478629/2012-5-CNPq, the State University of Maringá (Nupelia/UEM), the Intermunicipal Consortium for the Conservation of the Remaining of the Paraná River and its influence areas (Coripa), and other collaborators of the project 'Upper Paraná River: longitudinal gradient of environmental variables and aquatic communities in the last undammed stretch between Porto Primavera UHE and Itaipu Reservoir for logistic, intellectual and financial support.

References

AGOSTINHO, A.A. Considerações sobre a ictiofauna das principais bacias hidrográficas brasileiras. In: *Resumos do 10º Encontro Brasileiro de Ictiologia*. São Paulo: Universidade de São Paulo, 1993, pp. 301.

AGOSTINHO, A.A., GOMES, L.C. and PELICICE, F.M. *Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil*. Maringá: Eduem, 2007, 501 p.

AGOSTINHO, A.A., GOMES, L.C., SANTOS, N.C.L., ORTEGA, J.C.G. and PELICICE, F.M. Fish assemblages in Neotropical reservoirs: Colonization patterns, impacts and management. *Fisheries Research*, 2016, 173(1), 26-36. http://dx.doi.org/10.1016/j.fishres.2015.04.006.

AGOSTINHO, A.A., GOMES, L.C., THOMAZ, S.M. and HAHN, N.S. The Upper Paraná river and its floodplain: main characteristics and perspectives for management and conservation. In: S.M. THOMAZ, A.A. AGOSTINHO and N.S. HAHN, orgs. *The upper Paraná River and its floodplain – physical aspects, ecology, and conservation*. Leiden: Backhuys Publishers, 2004a, pp. 381-393.

AGOSTINHO, A.A., GOMES, L.C., VERÍSSIMO, S. and OKADA, E.K. Flood regime, dam regulation and fish in the upper Paraná river: effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries*, 2004b, 14(1), 11-19. http://dx.doi.org/10.1007/s11160-004-3551-y.

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

BARBOSA, F.A.R., PADISÁK, J., ESPINDOLA, E.L.G., BORICS, G. and ROCHA, O. The cascading reservoir continuum concept (CRCC) and its application to the river Tietê-Basin, São Paulo State, Brazil. In: J.G. TUNDISI and M. STRASKRABA, orgs. *Theoretical reservoir ecology and its applications*. Leiden: International Institute of Ecology, 1999, pp. 425-437.

BORTOLINI, J.C., MORESCO, G.A., PAULA, A.C.M., JATI, S. and RODRIGUES, L.C. Functional approach based on morphology as a model of phytoplankton variability in a subtropical floodplain lake: a long-term study. *Hydrobiologia*, 2016, 767(1), 151-163. http://dx.doi.org/10.1007/s10750-015-2490-z.

BOTTRELL, H.H., DUNCAN, A., GLIWICZ, Z.M., GRYIEK, E., HERZIG, A., HILLBRICHT-ILKOWSKA, A., KURASAWA, H., LARSSON, P. and WEGLENSKA, T.A. Review of some problems in zooplankton production studies. *Norwegian Journal of Zoology*, 1976, 24, 419-456.

CASANOVA, S.M.C. and HENRY, R. Longitudinal distribution of copepoda populations in the transition zone of Paranapanema river and Jurumirim reservoir (São Paulo, Brazil) and interchange with two lateral lakes. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2004, 64(1), 11-26. PMid:15195360. http://dx.doi.org/10.1590/S1519-69842004000100003.

CHANG, K.H., DOI, H., IMAI, H., GUNJI, F. and NAKANO, S. Longitudinal changes in zooplankton distribution below a reservoir outfall with reference to river planktivory. *Limnology*, 2008, 9(2), 125-133. http://dx.doi.org/10.1007/s10201-008-0244-6.

ESKINAZI-SANT'ANNA, E.M., MENEZES, R., COSTA, I.S., ARAÚJO, M., PANOSSO, R. and ATTAYDE, J.L., Zooplankton assemblages in eutrophic reservoirs of the Brazilian semi-arid. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2013, 73(1), 37-52. http://dx.doi.org/10.1590/S1519-69842013000100006.

FERRAREZE, M. and NOGUEIRA, M.G. Importance of Lateral Lagoons for the Zooplankton Assemblages (Cladocera and Copepoda) in a Large Tropical Reservoir. *Oecologia Australis*, 2011, 15(3), 522-536. http://dx.doi.org/10.4257/oeco.2011.1503.07.

GOLTERMAN, H.L., CLYMO, R.S. and OHMSTAD, M.A.M. *Methods for physical and chemical analyses of freshwaters*. Oxford: Blackwell Scientific Publication, 1978, 213 p.

GRABOWSKA, M., EJSMONT-KARABIN, J. and KARPOWICZ, M. Reservoir-River relationships in Lowland, Shallow, Eutrophic Systems: an impact of Zooplankton from Hypertrophic Reservoir on River Zooplankton. *Polish Journal of Ecology*, 2013, 61(4), 759-768.

ISTVÁNOVICS, V.M., HONTI, M., VOROS, L. and KOZMA, Z. Phytoplankton dynamics in relation to connectivity, flow dynamics and resource availability - the case of a large, lowland river, the Hungarian Tisza. *Hydrobiologia*, 2010, 637(1), 121-141. http://dx.doi.org/10.1007/s10750-009-9991-6.

LANDA, G.G., BARBOSA, F.A.R., RIETZLER, A.C. and MAIA-BARBOSA, P.M. *Thermocyclops decipiens* (Kiefer, 1929) (Copepoda,Cyclopoida) as Indicator of Water Quality in the State of Minas Gerais, Brazil. *Brazilian Archives of Biology and Technology*, 2007, 50(4), 695-705. http://dx.doi.org/10.1590/S1516-89132007000400015.

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

LANSAC-TÔHA, F.A., BONECKER, C.C., VELHO, L.F.M., TAKAHASHI, E.M. and NAGAE, M.Y. Zooplankton in the upper Paraná river floodplain: composition, richness, abundance and relationships with the hydrological level and the connectivity. In: A.A. AGOSTINHO, L. RODRIGUES, L.C. GOMES, S.M. THOMAZ and L.E. MIRANDA, orgs. *Structure and functioning of the Paraná river and its floodplain*. Maringá: Eduem, 2004, pp. 75-84.

LANSAC-TÔHA, F.A., VELHO, L.F.M., HIGUTI, J. and TAKAHASHI, E.M. Cyclopidae (Crustacea, Copepoda) from the upper Paraná river floodplain, Brazil. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2002, 62(1), 125-133. PMid:12185912. http://dx.doi.org/10.1590/S1519-69842002000100015.

LEGENDRE, P. and GALLAGHER, E.D. Ecologically meaningful transformations for ordination of species data. *Oecologia*, 2001, 129(2), 271-280. PMid:28547606. http://dx.doi.org/10.1007/s004420100716.

LEGENDRE, P. and LEGENDRE, L. *Numerical ecology*. Amsterdam: Elsevier Science Ltd, 1998, 839 p.

LOPES, R.M., LANSAC-TÔHA, F.A., VALE, R. and SERAFIM-JUNIOR, M. Comunidade zooplanctônica do reservatório de Segredo. In: A.A. AGOSTINHO and L.C. GOMES, orgs. *Reservatório de Segredo – bases ecológicas para o manejo*. Maringá: Eduem, 1997, 387 p.

MACKERETH, F.J.H., HERON, J. and TALLING, J.F. *Water analysis: some revised methods for limnologists*. Far Sawrey, Ambleside: Freshwater Biological Association Scientific Publication, 1978, 120 p.

MAIA-BARBOSA, P.M., BRITO, S., RIETZLER, A.C. and ESKINAZI-SANT'ANNA, E.M., 2006. Diversidade do zooplâncton de Minas Gerais. *Ciência Hoje*, vol. 38, no. 227, pp. 67-69.

MANTOVANO, T., ARRIEIRA, R.L., SCHWIND, L.T.F., BONECKER, C.C. and LANSAC-TÔHA, F.A. Rotifer community structure along a stretch under the influence of dams in the Upper Paraná River floodplain. *Acta Scientiarum. Biological Sciences*, 2015, 37(3), 281-289. http://dx.doi.org/10.4025/actascibiolsci.v37i3.27759.

MATSUMURA-TUNDISI, T. and TUNDISI, J.G. Calanoida (Copepoda) species composition changes in the reservoirs of São Paulo State (Brazil) in the last twenty years. *Hydrobiologia*, 2003, 504(1-3), 215-222. http://dx.doi.org/10.1023/B:HYDR.0000008521.43711.35.

MITSUKA, P.M. and HENRY, R. The fate of copepod populations in the Paranapanema River (São Paulo), downstream from the Jurumirim Dam. *Brazilian Archives of Biology and Technology*, 2002, 45(4), 479-490. http://dx.doi.org/10.1590/S1516-89132002000600012.

NADAI, R. and HENRY, R. Temporary fragmentation of a marginal lake and its effects on zooplankton community structure and organization. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2009, 69(3), 819-835. PMid:19802441. http://dx.doi.org/10.1590/S1519-69842009000400009.

NAPIÓRKOWSKI, P., KENTZER, A. and DEMBOWSKA, E. Zooplankton of the lower Vistula River: the effect of Włocławek Dam Reservoir (Poland) on community structure. *Verhandlungen des Internationalen Verein Limnologie*, 2006, 29, 2109-2114.

NETO, A.J.G., SILVA, L.C., SAGGIO, A.A. and ROCHA, O. Zooplankton communities as eutrophication bioindicators in tropical reservoirs. *Biota Neotropica*, 2014, 14(4), 1-12.

NEY, J.J. Oligotrophication and its discontents: effects of reduced nutrient loading on reservoir fisheries. In L.E. MIRANDA and D.R. VRIES, orgs. Multidimensional Approaches to Reservoir Fisheries Management. *American Fisheries Society Symposium*, 1996, 16, 285-295.

NOGUEIRA, M.G., OLIVEIRA, P.C.R. and BRITTO, Y.T. Zooplankton assemblages (Copepoda and Cladocera) in a cascade of reservoirs of a large tropical river (SE Brazil). *Limnetica*, 2008, 27(1), 151-170.

OKSANEN, J., BLANCHET, F.G. and KINDT, R. *Vegan: community ecology package. R package version 2.0-6* [software]. Vienna: The R Foundation for Statistical Computing, 2012 [viewed 5 Jan. 2017]. Available from: http://vegan.r-forge.r-project.org/

PAGGI, J.C. and PAGGI, S.J. Zooplâncton de ambientes lóticos e lênticos do Rio Paraná Médio. *Acta Limnologica Brasiliensia*, 1990, 3, 685-719.

PEDROZO, C.S. and ROCHA, O. Zooplankton and water quality of lakes of the Northern Coast of Rio Grande do Sul State, Brazil. *Acta Limnologica Brasiliensia*, 2005, 17(4), 445-464.

PERBICHE-NEVES, G., BOXSHALL, G., PREVIATTELLI, D., ROCHA, C.E.F. and NOGUEIRA, M.G. Identification guide to some Diaptomid species (Crustacea, Copepoda, Calanoida, Diaptomidae) of de la Plata-River Basin (South America). *ZooKeys*, 2015, 197, 1-111. PMid:25931959. http://dx.doi.org/10.3897/zookeys.497.8091.

PERBICHE-NEVES, G., NOGUEIRA, M.G., OLIVEIRA, P. and SERAFIM-JUNIOR, M. Sobre alguns Atributos Ecológicos de Copépodes (Crustacea) Planctônicos de dois reservatórios profundos. *Brazilian Journal of Aquatic Science and Technology*, 2014, 18(1), 1-8. http://dx.doi.org/10.14210/bjast.v18n1.p1-8.

PERBICHE-NEVES, G., SERAFIM-JUNIOR, M., GHIDINI, A.R. and BRITO, L. Spatial and temporal distribution of Copepoda (Cyclopoida and Calanoida) of an eutrophic reservoir in the basin of upper Iguaçu river, Paraná, Brazil. *Acta Limnologica Brasiliensia*, 2007, 19(4), 393-406.

PERBICHE-NEVES, G., SERAFIM-JÚNIOR, M., PORTINHO, J.L., SHIMABUKURO, É.M., GHIDINI, A.R. and BRITO, L.D. Effect of atypical rainfall on lotic zooplankton: comparing downstream of a reservoir and tributaries with free stretches. *Tropical Ecology*, 2012, 53(2), 149-162.

PIELOU, E.C. *Ecological diversity*. New York: Ed. John Wiley, 1975, 165 p.

PORTINHO, J.L., PERBICHE-NEVES, G. and NOGUEIRA, M.G. Zooplankton community and tributary effects in free-flowing section downstream a large tropical reservoir. *International Review of Hydrobiology*, 2016, 101(1-2), 48-56. http://dx.doi.org/10.1002/iroh.201501798.

POURRIOT, R., ROUGIER, C. and MIQUELIS, A. Origin and development of river zooplankton: example of the Marne. *Hydrobiologia*, 1997, 345(2), 143-148. http://dx.doi.org/10.1023/A:1002935807795.

R DEVELOPMENT CORE TEAM. *R: A language and environment for statistical computing. Version 3.1.3* [software]. Vienna: R Foundation for Statistical Computing, 2015.

SANTOS-SILVA, E.M. *Revisão das espécies do "complexo nordestinus" (Wright, 1935) de Notodiaptomus Kiefer, 1936 (Copepoda: Calanoida: Diaptomidae)* [Tese de Doutorado em Zoologia]. São Paulo: Universidade de São Paulo, Instituto de Biociências da Universidade de São Paulo, 2000.

SARTORI, L.P., NOGUEIRA, M.G., HENRY, R. and MORETTO, E.M. Zooplankton fluctuations in Jurumirim Reservoir (São Paulo, Brazil): a three-year study. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2009, 69(1), 1-18.

PMid:19347141. http://dx.doi.org/10.1590/S1519-69842009000100002.

SHAH, J.A., PANDIT, A.K. and SHAH, G.M. Distribution, diversity and abundance of copepod zooplankton of Wular Lake, Kashmir Himalaya. *Journal of Ecology and the Natural Environment*, 2013, 5(2), 24-29. http://dx.doi.org/10.5897/JENE12.100.

SILVA, W.M. *Diversidade dos Cyclopoida (Copepoda, Crustacea) de água doce do estado de São Paulo: taxonomia, ecologia e genética* [Tese de Doutorado em Ecologia e Recursos Naturais]. São Carlos: Universidade Federal de São Carlos, 2003.

SIMÕES, N.R., NUNES, A.H., DIAS, J.D., LANSAC-TÔHA, F.A., VELHO, L.F.M. and BONECKER, C.C. Impact of reservoirs on zooplankton diversity and implications for the conservation of natural aquatic environments. *Hydrobiologia*, 2015, 758(1), 3-17. http://dx.doi.org/10.1007/s10750-015-2260-y.

SMITH, G.A., FITZPATRICK, L.C. and PEARSON, W.D. Structure and Dynamics of a Zooplankton Community in a Small North-Central Texas Pond Ecosystem. *The Southwestern Naturalist*, 1979, 24(1), 1-16. http://dx.doi.org/10.2307/3670620.

SOKAL, R.R. and ROHLF, F.J. *Biometry: the principles and pratice of statistics in biological research*. New York: Freeman and Company, 1991, 859 p.

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

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

STATSOFT INC. *Statistica for Windows: data analysis software system. Version 7.1* [software]. Tulsa: Statsoft Inc., 2005.

SUGUMARAN, J. Influence of Seasons on Copepods of Agniyar Estuary, Palk Strait, Tamil Nadu, India. *International Journal of Zoology and Applied Biosciences*, 2016, 1(1), 40-45.

VANNOTE, R.L., MINSHALL, G.W., CUMMINS, K.W., SEDELL, J.R. and CUSHING, C.E. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 1980, 37(1), 130-137. http://dx.doi.org/10.1139/f80-017.

VELHO, L.F.M., BINI, L.M. and LANSAC-TÔHA, F.A. Testate amoeba (Rhizopoda) diversity in plankton of the Upper Paraná River floodplain, Brazil. *Hydrobiologia*, 2004, 523(1), 103-111. http://dx.doi.org/10.1023/B:HYDR.0000033098.46753.9f.

VELHO, L.F.M., LANSAC-TÔHA, F.A., TAKEDA, A.M., HIGUTI, J. and FRANCO, G.M.S. Structure and dynamics of the cyclopoid copepod (Crustacea) assemblage associated with aquatic macrophytes in two lotic environments of the Upper Paraná river basin, Brazil. *Acta Scientiarum*, 2001, 23, 349-356.

VIROUX, L. Zooplankton development in two large lowland rivers, the Moselle (France) and the Meuse (Belgium), in 1993. *Journal of Plankton Research*, 1997, 19(11), 1743-1762. http://dx.doi.org/10.1093/plankt/19.11.1743.

WARD, J.V. and STANFORD, J.A. The serial discontinuity concept: Extending the model to floodplain rivers. *Regulated Rivers: Research and Management*, 1995, 10(2-4), 159-168. http://dx.doi.org/10.1002/rrr.3450100211.

WARD, J.V. The structure and dynamics of lotic ecosystems. In: R. MARGALEF, orgs. *Limnology now: a paradigm of planetary problems*. New York: Elsevier Science, 1994, pp. 195-218.

WETZEL, R.G. and LIKENS, G.E. *Limnological analyses*. New York: Springer-Verlag, 1991, 429 p.

Received: 05 January 2017
Accepted: 29 May 2017