







Drivers of zooplankton spatial dynamics in a small neotropical river

Condutores da dinâmica espacial do zooplâncton em um pequeno rio neotropical

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Cite as: Picapedra, P.H.S. Drivers of zooplankton spatial dynamics in a small neotropical river. *Acta Limnologica Brasiliensia*, 2022, vol. 34, e13.

Abstract: Aim: Our objective was to describe the structure and spatial patterns of the zooplankton community in a small Brazilian river system (Paranaíba River sub-basin) and evaluate the role of an oxbow lake in the dynamics of this community. **Methods:** Zooplankton samples were collected from sites located in an oxbow lake and the Aporé River bed during the rainy and dry seasons. We collected these samples from the surface and bottom levels of two different zones (littoral and channel). For each hydrological season, analysis of variance was conducted to determine the differences in species richness and abundance of zooplankton among different sites (longitudinal), zones (lateral), and depths (vertical). Cluster analysis was performed to assess the similarity in species composition. In addition, a canonical correspondence analysis was used to select the environmental variables that best explained the variation in zooplankton abundance data. **Results:** We recorded 152 species: 70 rotifers, 53 testate amoebae, 20 cladocerans, and 9 copepods. We observed changes in the species richness and abundance of zooplankton along the longitudinal axis of the river in both the rainy and dry seasons. However, we did not detect any lateral or vertical changes in these attributes. Cluster analysis also indicated that the greatest differences in species composition were in the longitudinal axis of the river. The longitudinal variability of zooplankton was mainly associated with the influence of an upstream oxbow lake, as well as the changes in water flow velocity, turbidity, and concentrations of suspended solids downstream. **Conclusions:** Our results demonstrate the importance of a heterogeneity of hydrological characteristics as a structuring factor of the zooplankton community in the Aporé River. Thus, we highlight the relevance of actions to protect and maintain the natural characteristics of these environments.

Keywords: Aporé river; meander; microhabitat; potamoplankton; taxonomic composition.

Resumo: Objetivo: Nosso objetivo foi descrever a estrutura e os padrões espaciais da comunidade zooplanctônica em um pequeno sistema fluvial brasileiro (sub-bacia do rio Paranaíba) e avaliar o papel de um meandro na dinâmica dessa comunidade. **Métodos:** Amostras de zooplâncton foram coletadas em pontos localizados em um meandro e no leito do rio Aporé durante os períodos chuvoso e seco. Coletamos essas amostras na superfície e fundo de duas zonas diferentes (litorânea e canal).



Para cada período hidrológico, a análise de variância foi conduzida para determinar as diferenças na riqueza de espécies e abundância do zooplâncton entre os diferentes pontos (longitudinal), zonas (lateral) e profundidades (vertical). A análise de cluster foi realizada para avaliar a similaridade na composição de espécies. Além disso, uma análise de correspondência canônica foi usada para selecionar as variáveis ambientais que melhor explicaram a variação nos dados de abundância do zooplâncton.

Resultados: Registramos 152 espécies: 70 de rotíferos, 53 de amebas testáceas, 20 de cladóceros e 9 de copépodes. Observamos mudanças na riqueza de espécies e abundância do zooplâncton ao longo do eixo longitudinal do rio tanto no período chuvoso quanto no seco. No entanto, não detectamos nenhuma mudança lateral ou vertical nesses atributos. A análise de cluster também indicou que as maiores diferenças na composição de espécies estavam no eixo longitudinal do rio. A variabilidade longitudinal do zooplâncton foi associada principalmente a influência de um meandro a montante, bem como a mudanças na velocidade de fluxo d'água, turbidez e concentrações de sólidos suspensos à jusante. **Conclusões:** Nossos resultados demonstraram a importância de uma heterogeneidade de características hidrológicas como fator estruturante da comunidade zooplânctônica no rio Aporé. Assim, destacamos a relevância de ações para proteger e manter as características naturais desses ambientes.

Palavras-chave: rio Aporé; meandro; micro-habitat; potamoplâncton; composição taxonômica.

1. Introduction

In river systems, hydrology, connectivity, and geomorphology create a variety of habitats with different environmental conditions. These characteristics reveal that rivers are highly dynamic and heterogeneous environments, exhibiting gradual changes in physical (flow, turbidity, slope, substrate) and chemical (nutrients, dissolved oxygen) variables, which induce habitat preferences and influence the migration and dispersion of aquatic organisms (Pace et al., 1992; Baranyi et al., 2002; Bomfim et al., 2017; Ramos et al., 2021).

Zooplankton in river systems occupy an important level of the food web in which they contribute to secondary production and allow for the flow of energy from primary producers to higher organisms (Thorp & Casper, 2003; Sluss et al., 2011). Rivers are generally considered inhospitable for the development of zooplankton because of the challenge of swimming against the currents (Hynes, 1970; Kobayashi et al., 1998; Viroux, 2002). However, some studies have reported considerable development of zooplanktonic populations in river parts with reduced water flow caused by irregularities in channel morphology, such as anastomosis, backwaters, or depth variations (Basu et al., 2000a; Thorp & Mantovani, 2005; Zimmermann-Timm et al., 2007; Picapedra et al., 2018). Furthermore, the “extreme expression” of irregularities in river channel can be found in marginal environments, such as meanders (oxbow lakes). These parts recreate true lentic conditions that provide zooplankton populations for inoculation of riverine stretches downstream (Spaank et al., 1998; Viroux, 2002).

However, understanding of factors controlling the structure of riverine zooplankton and their

ecological importance is lacking when compared with that of lentic systems (Picapedra et al., 2019; Padovesi-Fonseca et al., 2021). Previous studies characterized the zooplankton from streams and small rivers (e.g. Picapedra et al., 2019; Gomes et al., 2020; Godfrey et al., 2020), as well as large rivers (e.g. Bum & Pick, 1996; Basu & Pick, 1997; Paggi et al., 2014; Portinho et al., 2016), as having a low density and a predominance of protozoa or rotifers and small-sized microcrustaceans. Moreover, they identified downstream advection and spatiotemporal changes in turbulence, water residence time, turbidity, and food availability as the main factors that regulate these organisms.

Furthermore, most studies describe zooplankton dynamics based only on point samples, normally taken from the middle of the channel, with the lateral and vertical dimensions largely neglected (Viroux, 1999; Sluss et al., 2011; Appel et al., 2019). The rare studies that have focused on analyzing the possible heterogeneity in zooplankton distribution, such as laterally and vertically, have indicated the existence of some spatial variations in one or all dimensions (e.g. Viroux, 1999; Thorp et al., 1994; Jack et al., 2006; Casper & Thorp, 2007), although no consistent pattern has been observed. However, it should be noted that the zooplankton community of large rivers is better understood than that of small rivers or streams, especially in the tropical region. Investigating the factors that control the zooplankton community structure can be an important step toward establishing protection and conservation measures for the natural characteristics of these environments.

This study aimed to determine the structure and describe the spatial patterns (longitudinal, lateral, and vertical) of the zooplankton community in a

small neotropical river during different hydrological seasons (rainy and dry), as well as to assess the role of an oxbow lake on the zooplankton dynamics of the main river channel. We hypothesized the following: (i) Zooplankton of the main river channel will essentially consist of testate amoebae and rotifers, which can develop in dynamic fluvial environments; in the oxbow lake, the zooplankton will consist of planktonic species and/or individuals of microcrustaceans (cladocerans and copepods), owing to their typical lacustrine conditions; (ii) Because of the natural advection process of riverine zooplankton, higher abundances will be observed in the oxbow lake; the higher flow velocities in the main river channel will be related to greater species richness, facilitated by stronger lateral and vertical mixing of water; (iii) Changes in zooplankton structure will be clearer for longitudinal dimension in comparison to lateral and vertical dimensions in the river, as a result of greater heterogeneity of environmental characteristics; (iv) Seasonal differences in spatial distribution patterns of riverine

zooplankton will be evident, owing to the variation in the rainfall regime that affects water flow, turbidity, and nutrient input into environments.

2. Material and Methods

2.1. Study area

The Aporé River, located in the Midwest region of Brazil, is a tributary of the Paranaíba River sub-basin. The course of the river flows west/east and stretches between the states of Goiás and Mato Grosso do Sul as a natural border. Finally, the Aporé River flows into the Paranaíba River, which together with the Grande River form the Paraná River.

The region has a tropical climate (Aw, Köppen climate classification), with an average annual temperature of approximately 22.5 °C and rainfall ranging from 60 to 1,700 mm, with rainy and dry seasons. The phytophysiognomy of the basin is located in an area of intersection between two biomes, the Cerrado and the Atlantic Forest (Ramalho et al., 2014). This study was conducted in the lower stretch of the Aporé River (Figure 1). This

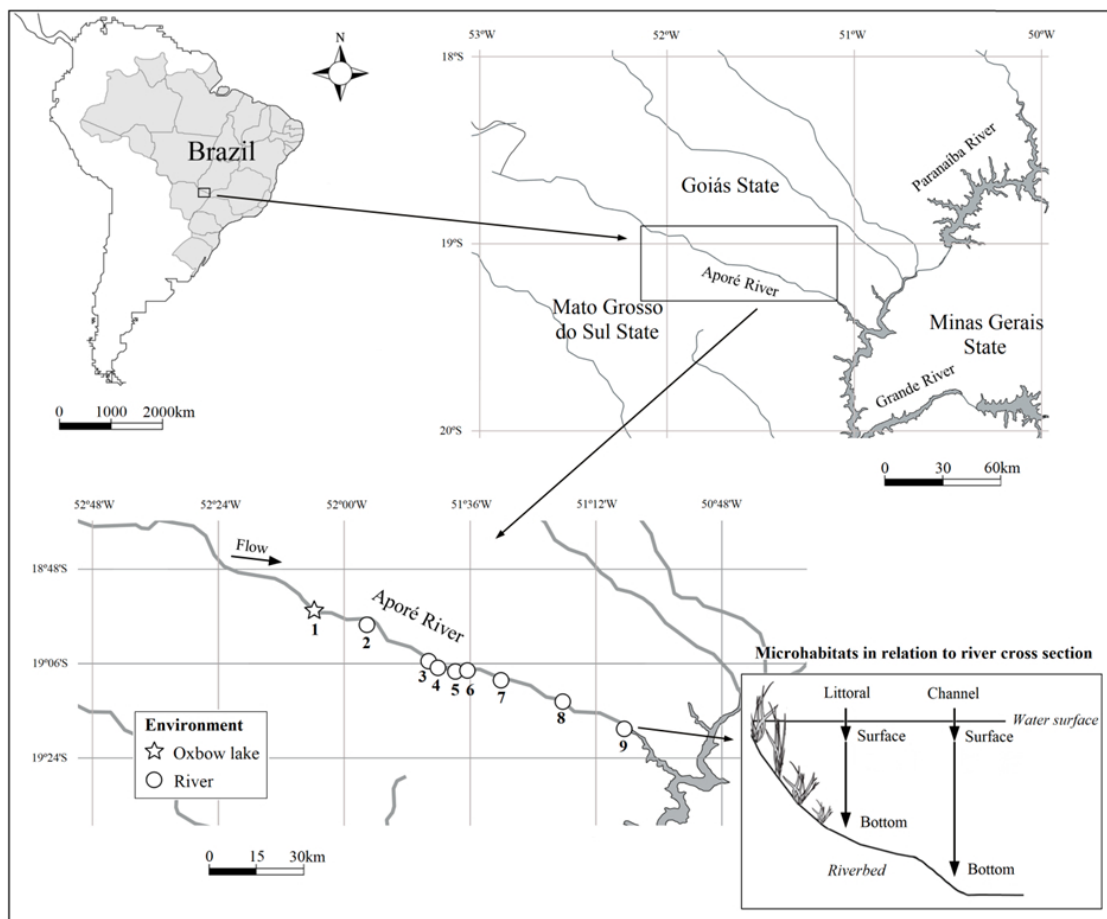


Figure 1. Map showing the location of the sampling sites and a schematic view of where microhabitats were sampled at each site on the Aporé River, Paranaíba River basin.

stretch presents a great heterogeneity of hydrological characteristics (e.g. flow and depth), provided by the high sinuosity and the presence of oxbow lakes, waterfalls, rapids, boulders, and littoral vegetation (Table 1; Figure 2).

2.2. Sampling

Diurnal collections were conducted during the rainy (December 2018) and dry (July 2019) seasons. Nine sampling sites were established, one of which was located in an oxbow lake (Site 1) and the other eight were on the Aporé River bed (Sites 2-9). Four samples were taken from each site, comprising two zones: littoral (sublittoral) and channel (middle of the river), and two depths: surface and bottom (Figure 1). A total of 72 samples were collected in the two seasons.

Zooplankton samples were obtained using a motor pump. We filtered 200 L of water per sample using a conical plankton net with a mesh size of 68 μm . Subsequently, the collected material was placed in polyethylene bottles (500 mL), labeled, and fixed in 4% formaldehyde buffered with sodium borate (Na_3BO_3).

The following environmental variables were also measured: electrical conductivity ($\mu\text{S cm}^{-1}$; portable

conductivity meter, Digimed® DM-3P), dissolved oxygen (mg L^{-1} ; portable oximeter, YSI 550A), pH (portable pH meter, Digimed® DM-2P), water temperature ($^{\circ}\text{C}$; mercury bulb thermometer), total phosphorus (mg L^{-1} ; APHA, 2005), total suspended solids (mg L^{-1} ; APHA, 2005), turbidity (NTU; portable turbidimeter, LaMotte® 2020i), and water flow velocity (m s^{-1} ; mechanical flow meter, General Oceanics™).

2.3. Data processing and statistical analysis

In the laboratory, samples were concentrated to 50 mL, 10 subsamples were taken with a Hensen-Stempel pipette (2.5 mL), and 25 mL of each sample was evaluated. Sedgewick-Rafter chambers were used to quantify zooplankton under an optical microscope at magnifications from $\times 10$ to $\times 100$. Total density was expressed as individuals per m^{-3} . The species were identified using: Koste (1978), Elmoor-Loureiro (1997, 2010), Lansac-Tõha et al. (2002), Souza (2008), and Perbiche-Neves et al. (2015).

For each hydrological season (rainy and dry), we performed principal component analysis (PCA) with a correlation matrix to characterize the environmental conditions of the Aporé River.



Figure 2. Collection sites in the Aporé River, Paranaíba River basin. Lentic (Site 1) and lotic (Sites 2-9) environments.

Table 1. Environmental characteristics and physicochemical water variables (mean \pm standard deviation) measured along the Aporé River, Paranaíba River basin, during the different hydrological seasons.

Variables	Site								
	1	2	3	4	5	6	7	8	9
General									
Latitude (S)	18°56'05"	18°58'35"	19°06'47"	19°06'56"	19°07'58"	19°08'12"	19°09'10"	19°13'15"	19°18'27"
Longitude (W)	52°05'58"	51°55'40"	51°42'25"	51°42'14"	51°39'48"	51°39'30"	51°30'05"	51°18'18"	51°06'35"
Width (m)	20	20	60	30	35	40	60	60	80
Maximum depth (m)	2.6	1.5	1.5	1.7	1.7	1.6	1.5	1.5	1.5
Boulders	-	-	-	Presence	Presence	Presence	-	Presence	-
Submerged plants	Presence	Presence	-	-	-	-	-	-	-
Emergent plants	Presence	Presence	-	-	-	-	-	-	-
Floating plants	-	-	-	-	-	-	-	Presence	Presence
Rainy									
Electrical conductivity ($\mu\text{S cm}^{-1}$)	16.1 (± 1.0)	10.3 (± 0.7)	14.7 (± 0.3)	16.7 (± 1.2)	17.1 (± 0.6)	18.2 (± 1.0)	23.1 (± 1.3)	28.5 (± 1.3)	34.0 (± 2.5)
Dissolved oxygen (mg L^{-1})	3.9 (± 0.1)	6.5 (± 0.5)	6.1 (± 0.1)	5.3 (± 0.3)	8.2 (± 0.4)	8.2 (± 0.2)	7.7 (± 0.1)	7.4 (± 0.2)	7.7 (± 0.1)
pH	6.8 (± 0.1)	7.2 (± 0.3)	7.7 (± 0.1)	7.4 (± 0.3)	7.5 (± 0.3)	7.6 (± 0.2)	8.0 (± 0.0)	7.2 (± 0.3)	7.6 (± 0.2)
Temperature ($^{\circ}\text{C}$)	25.8 (± 0.3)	25.7 (± 0.3)	26.3 (± 0.1)	26.4 (± 0.4)	27.8 (± 0.1)	27.7 (± 0.2)	25.7 (± 0.5)	27.3 (± 0.3)	27.8 (± 0.1)
Total phosphorus (mg L^{-1})	0.05 (± 0.00)	0.01 (± 0.00)	0.01 (± 0.00)	0.02 (± 0.00)	0.54 (± 0.05)	0.26 (± 0.03)	0.25 (± 0.04)	0.05 (± 0.01)	0.04 (± 0.01)
Total suspended solids (mg L^{-1})	55.8 (± 4.2)	68.3 (± 4.7)	66.9 (± 4.4)	67.8 (± 5.2)	42.6 (± 2.9)	48.3 (± 1.6)	52.8 (± 3.9)	55.8 (± 3.0)	55.5 (± 2.6)
Turbidity (NTU)	8.4 (± 0.6)	14.3 (± 0.6)	14.2 (± 0.7)	12.9 (± 0.9)	12.5 (± 1.3)	13.2 (± 0.9)	17.3 (± 1.6)	12.6 (± 1.2)	14.1 (± 0.7)
Water flow velocity (m s^{-1})	0.00 (± 0.00)	0.71 (± 0.16)	0.76 (± 0.32)	0.71 (± 0.14)	1.09 (± 0.28)	0.98 (± 0.18)	0.73 (± 0.63)	0.88 (± 0.27)	0.81 (± 0.37)
Dry									
Electrical conductivity ($\mu\text{S cm}^{-1}$)	16.2 (± 0.5)	11.7 (± 1.0)	24.4 (± 4.6)	18.6 (± 1.1)	17.5 (± 1.0)	18.0 (± 0.8)	21.1 (± 0.6)	25.6 (± 1.3)	32.7 (± 1.7)
Dissolved oxygen (mg L^{-1})	5.6 (± 0.1)	8.6 (± 0.1)	8.6 (± 0.2)	8.3 (± 0.2)	8.9 (± 0.0)	9.2 (± 0.4)	8.2 (± 0.1)	7.9 (± 0.0)	8.0 (± 0.1)
pH	6.1 (± 0.1)	6.8 (± 0.1)	6.5 (± 0.2)	7.3 (± 0.1)	7.4 (± 0.2)	7.7 (± 0.0)	6.5 (± 0.2)	6.6 (± 0.2)	6.8 (± 0.1)
Temperature ($^{\circ}\text{C}$)	20.8 (± 0.6)	20.3 (± 0.5)	18.0 (± 0.1)	20.8 (± 0.5)	20.6 (± 0.1)	20.7 (± 0.2)	18.1 (± 0.1)	18.4 (± 0.2)	18.5 (± 0.4)
Total phosphorus (mg L^{-1})	0.01 (± 0.00)	0.02 (± 0.01)	0.01 (± 0.00)	0.01 (± 0.00)	0.02 (± 0.00)	0.01 (± 0.00)	0.02 (± 0.00)	0.02 (± 0.00)	0.02 (± 0.01)
Total suspended solids (mg L^{-1})	38.0 (± 5.2)	19.6 (± 2.3)	15.1 (± 2.0)	17.4 (± 0.9)	25.5 (± 1.3)	28.0 (± 1.8)	25.8 (± 1.7)	34.4 (± 1.1)	28.6 (± 2.2)
Turbidity (NTU)	3.2 (± 1.0)	6.3 (± 1.0)	7.4 (± 1.4)	6.8 (± 0.5)	6.3 (± 0.5)	7.1 (± 1.0)	6.9 (± 0.8)	7.3 (± 0.7)	7.9 (± 0.7)
Water flow velocity (m s^{-1})	0.00 (± 0.00)	0.67 (± 0.14)	0.75 (± 0.77)	0.94 (± 0.15)	0.90 (± 0.35)	1.26 (± 0.49)	0.91 (± 0.54)	0.86 (± 0.24)	0.79 (± 0.19)

The data used for this analysis were transformed into $\log(x+1)$, except for pH. Subsequently, we applied a one-way permutational multivariate analysis of variance (PERMANOVA), based on Euclidean distance, to determine the differences between the environments, i.e., sites (longitudinal), zones (lateral), and depths (vertical). Additionally, we used two-way PERMANOVA to determine the differences in environments between seasons (site \times season, zone \times season, and depth \times season).

We performed one-way analysis of variance (ANOVA) to compare the changes in species richness (number of species) and abundance of zooplankton (Total, Testate amoebae, Rotifera, Cladocera, and Copepoda) among sites, zones, and depths for each season. We used two-way ANOVA to verify spatial changes in these attributes between seasons. Normality and homoscedasticity (homogeneity of variance) were verified using the Shapiro-Wilk and Levene tests, respectively. When ANOVA was significant ($p < 0.05$), we used Tukey's post-hoc test to investigate the differences between pairs. A cluster analysis was performed using the Jaccard similarity coefficient (presence/absence) to analyze the spatial similarity in species composition for each season.

The relationship between environmental variables and zooplankton species was explored using canonical correspondence analysis (CCA) (Ter Braak, 1986). For this analysis, the most common species ($\geq 25\%$ occurrence) in the samples from each season were used to avoid the effects of rare species. The data used for this analysis were transformed into $\log(x+1)$. Additionally, the effect of multicollinearity among environmental variables was analyzed using

variance inflation factors. The statistical significance of the eigenvalues and species-environment correlations for the axes generated by the CCA were tested using the Monte Carlo method, based on 999 permutations and a significance level of $p < 0.05$ (Legendre et al., 2011).

All analyses were performed using the statistical environment R version 3.5.0 (R Development Core Team, 2018).

3. Results

3.1. Environmental variables

Environmental heterogeneity was observed only between the Apore River sites during the rainy (one-way PERMANOVA, $df = 8$, pseudo-F = 10.9, $p < 0.001$) and dry (one-way PERMANOVA, $df = 8$, pseudo-F = 34.5, $p < 0.001$) seasons. Moreover, environmental changes were noticed at the sites in relation to the two hydrological seasons (two-way PERMANOVA, $df = 1$, pseudo-F = 13.8, $p < 0.001$). The environmental characteristics of the Apore River sites during the different hydrological seasons are described in Table 1.

The first two PCA axes generated for the rainy season explained 68.1% of environmental variability. PC 1 showed that Sites 5-9 had high dissolved oxygen. PC 2 showed that Sites 2, 3, 4, 7, and 9 had high turbidity and total suspended solids. For the dry season, the first two PCA axes explained 67.2% of environmental variability. PC 1 showed that Sites 2-9 had high dissolved oxygen, turbidity, and water flow velocity. PC 2 showed that Sites 3, 7, 8, and 9 had high electrical conductivity and total phosphorus contents. Sites 1, 2, 4, 5, and 6 were associated with low temperature values (Figure 3).

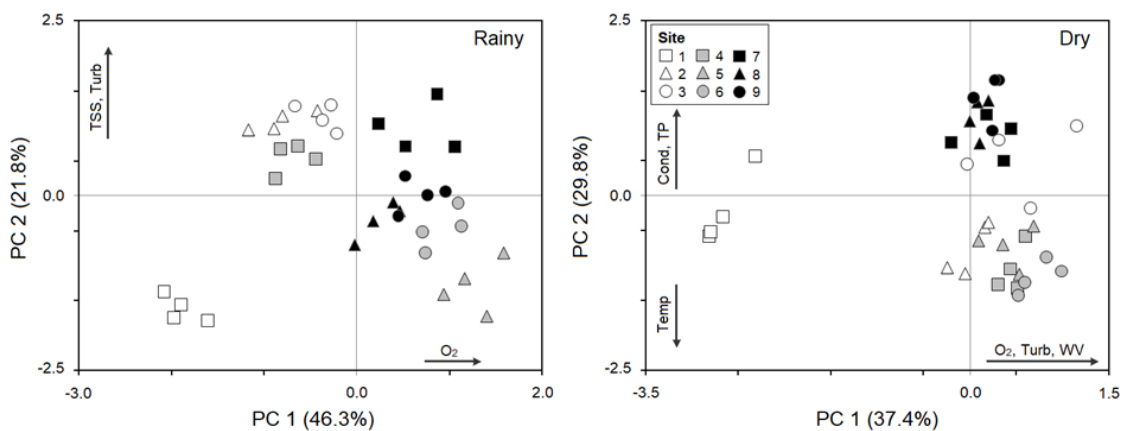


Figure 3. Principal component analysis (PCA) ordination showing the environmental differences for each site in the Apore River, Paranaíba River basin, during the different hydrological seasons. Abbreviations: Cond, electrical conductivity; O_2 , dissolved oxygen; Temp, temperature; TP, total phosphorus; TSS, total suspended solids; Turb, turbidity; WV, water flow velocity.

3.2. General scenario of the zooplankton community

The zooplankton community comprised 152 taxa. Rotifera was the richest group in number of species (70 species), followed by testate amoebae (53 species), Cladocera (20 species), and Copepoda (9 species). Testate amoebae were represented by nine families, with Diffugiidae being the richest, with 24 species. The rotifers were distributed in 17 families, of which Lecanidae (17 species) and Brachionidae (15 species) were the most representative in terms of number of species. Among microcrustaceans, cladocerans were represented by seven families, with Chydoridae having the greatest number of species (11). In turn, copepods were distributed into two families, with Cyclopidae being the most representative, with six species. Some taxa occurred in all studied sites: *Arcella costata*, *A. discoides*, *A. vulgaris*, *Centropyxis aculeata*, *Diffugia* sp., *Cephalodella* sp., *Collotheca* sp., *Filinia terminalis*, *Lecane bulla*, *L. lunaris*, *Notommata* sp., and nauplii of cyclopoid and calanoid copepods. In addition, we observed that 28 taxa were frequent ($\geq 25\%$ occurrence) in the samples, as shown in Table 2.

The density of the zooplankton community was mainly driven by rotifers, with *Cephalodella* sp., *F. terminalis*, and *Notommata* sp. as the most abundant taxa. Testate amoebae represented the second most abundant group in the study, with species of the genus *Centropyxis* dominating. In turn, *Bosminopsis deitersi* and *Alonella dadayi* were the most abundant species among cladocerans, and nauplii among copepods.

3.3. Spatial distribution of zooplankton community

We only observed significant differences (ANOVA, $p < 0.05$) in the attributes (species richness and abundance) of the zooplankton community among the Aporé River sites. We also observed that the richness of cladocerans and abundance of testate amoebae and rotifers showed significant differences in their spatial distribution (sites) between the two hydrological seasons (Table 3).

In terms of species richness, the rainy season was characterized by higher values of total zooplankton and rotifers at Sites 9 and 4, testate amoebae at Sites 6, 9, and 4, and cladocerans and copepods at Sites 4 and 1, respectively. In turn, the dry season was characterized by higher values of total zooplankton and rotifers at Site 4, testate amoebae at Sites 7 and 9, and cladocerans and copepods at Sites 1 and 2. Notably, the distribution of zooplankton species

richness among different zones and depths were homogeneous during the two hydrological seasons (Figure 4).

In terms of abundance, the rainy season showed higher values of total zooplankton and copepods at Site 1, whereas testate amoebae showed higher values at Site 4. The distribution of rotifers and cladocerans was found to be homogenous in the sites. In turn, the dry season exhibited higher values of total zooplankton, cladocerans, and copepods at Site 1, whereas testate amoebae and rotifers showed higher values at Sites 8 and 4, respectively. We observed homogeneity in the distribution of zooplankton abundance among different zones and depths of the Aporé River during the two hydrological seasons (Figure 5).

Cluster analysis based on species occurrence indicated a distinct environmental separation of the Aporé River during different hydrological seasons. During the rainy season, we observed a greater similarity in zooplankton species composition according to the lentic and lotic characteristics of the environments, separating the oxbow lake (A) from the river (B). However, a smaller similarity was noticed between environments during the dry season, as the first group (A) was formed by the oxbow lake and the upstream site of the river (Site 2, channel zone), whereas the other groups (B, C, and D) were formed by the river sites (Figure 6).

3.4. Relationship between environmental variables and zooplankton

According to the CCAs, the first two axes explained 64.4% and 69.0% of data variability during the rainy and dry seasons, respectively. Furthermore, the species-environment correlation in the first two axes was significant for the rainy (CCA 1, $p = 0.001$; CCA 2, $p = 0.013$) and dry (CCA 1, $p = 0.001$; CCA 2, $p = 0.01$) seasons, according to the Monte Carlo permutation test (Figure 7).

For the rainy season, we found a positive correlation of dissolved oxygen, pH, turbidity, and water flow velocity with the first axis of the CCA, showing that these variables were correlated with the distribution of some species of testate amoebae (e.g. *Arcella rotundata*, *A. discoides*, *Diffugia acuminata*, and *D. corona*) and rotifers (*Cephalodella* sp., *Notommata* sp., and *Trichocerca similis*) at Sites 3, 5, 6, and 7. The second axis represented the electrical conductivity and total phosphorus. The conductivity was found to be negatively correlated with the abundance of some species of

Table 2. Taxonomic composition, site occurrence and frequency of occurrence (FO%) of zooplankton in the Aporé River, Paranaíba River basin.

Taxa	Site	FO%
Testate amoebae		
Arcellidae		
<i>Arcella brasiliensis</i> Cunha, 1913	2, 4, 7, 9	7
<i>Arcella conica</i> (Playfair, 1918)	3, 4, 7, 8, 9	10
<i>Arcella costata</i> Ehrenberg, 1847	1, 2, 3, 4, 5, 6, 7, 8, 9	44
<i>Arcella crenulata</i> Deflandre, 1928	2, 3, 4, 6, 9	8
<i>Arcella dentata</i> Ehrenberg, 1830	2, 4, 5, 6, 7, 8, 9	15
<i>Arcella discoides</i> Ehrenberg, 1843	1, 2, 3, 4, 5, 6, 7, 8, 9	56
<i>Arcella gibbosa</i> Pénard, 1890	6, 9	4
<i>Arcella hemisphaerica</i> Perty, 1852	2, 3, 4, 5, 6, 7, 8, 9	40
<i>Arcella megastoma</i> Pénard, 1902	4, 6, 7, 8, 9	24
<i>Arcella rotundata</i> Playfair, 1918	1, 2, 4, 5, 6, 7, 8, 9	24
<i>Arcella vulgaris</i> Ehrenberg, 1830	1, 2, 3, 4, 5, 6, 7, 8, 9	81
Centropyxidae		
<i>Centropyxis aculeata</i> (Ehrenberg, 1830)	1, 2, 3, 4, 5, 6, 7, 8, 9	90
<i>Centropyxis cassis</i> (Wallich, 1864)	2, 3, 4, 5, 6, 7, 8, 9	35
<i>Centropyxis constricta</i> Pénard, 1890	1, 2, 3, 6, 7, 8, 9	15
<i>Centropyxis discoides</i> Pénard, 1890	2, 3, 4, 5, 6, 7, 8, 9	21
<i>Centropyxis ecornis</i> (Ehrenberg, 1841)	2, 3, 4, 5, 6, 7, 8, 9	56
<i>Centropyxis gibba</i> (Deflandre, 1929)	2, 3, 4, 5, 6, 7, 8, 9	39
<i>Centropyxis platystoma</i> Pénard, 1890	3, 4, 5, 6, 7	13
Cyphoderidae		
<i>Cyphoderia ampulla</i> Ehrenberg, 1840	8, 9	3
Diffugiidae		
<i>Cucurbitella dentata quinquelobata</i> Gauthier-Lièvre & Thomas, 1960	1, 4, 7, 9	7
<i>Diffugia acuminata</i> Ehrenberg, 1838	2, 3, 4, 5, 6, 7, 9	31
<i>Diffugia brevicolla</i> Cash & Hopkinson, 1909	2	1
<i>Diffugia capreolata</i> Pénard, 1902	8	1
<i>Diffugia corona</i> Wallich, 1864	1, 2, 3, 4, 5, 6, 7	21
<i>Diffugia cylindrus</i> Ogden, 1983	2, 3, 4, 7, 8, 9	14
<i>Diffugia difficilis</i> (Thomas, 1955)	8	1
<i>Diffugia distenda</i> Ogden, 1983	3, 7	3
<i>Diffugia elegans</i> Pénard, 1890	5, 8, 9	4
<i>Diffugia gramen</i> (Pénard, 1899)	1, 4, 7, 9	15
<i>Diffugia limnetica</i> Pénard, 1912	1, 2, 3, 4, 6, 7, 9	11
<i>Diffugia linearis</i> Gauthier & Lièvre, 1958	5	1
<i>Diffugia litophila</i> Pénard, 1902	3, 6, 7, 8, 9	10
<i>Diffugia lobostoma</i> Leidy, 1879	1, 2, 3, 5, 7, 9	13
<i>Diffugia minuta</i> Rampi, 1950	2, 3, 4, 5, 6, 7, 8, 9	18
<i>Diffugia muriformis</i> Gauthier-Lièvre & Thomas, 1958	3, 7	3
<i>Diffugia oblonga</i> Ehrenberg, 1838	6, 9	4
<i>Diffugia penardi</i> Hopkinson, 1909	2, 8, 9	4
<i>Diffugia pseudogramen</i> Gauthier-Lièvre & Thomas, 1958	7	1
<i>Diffugia pyriformis</i> Perty, 1849	1, 3, 4, 6, 9	7
<i>Diffugia</i> sp.	1, 2, 3, 4, 5, 6, 7, 8, 9	46
<i>Diffugia urceolata</i> Carter, 1864	3, 7, 9	4
<i>Pontigulasia compressa</i> (Carter, 1864)	9	1
<i>Pontigulasia elisa</i> Pénard, 1893	3, 4, 6, 7, 8	17
Euglyphidae		
<i>Euglypha acanthophora</i> (Ehrenberg, 1841)	1, 2, 4, 6, 7	7

Table 2. Continued...

Taxa	Site	FO%
<i>Euglypha denticulata</i> Brown, 1912	2	3
<i>Euglypha laevis</i> Perty, 1849	1, 8, 9	4
Lesquereusidae		
<i>Lesquereusia globulosa</i> Gauthier-Lièvre & Thomas, 1959	2, 3, 4, 7, 8, 9	14
<i>Lesquereusia spiralis</i> (Ehrenberg, 1840)	2, 3, 4, 5, 6, 7, 8, 9	33
<i>Netzelia oviformis</i> Ogden, 1979	2, 4, 5, 7	8
Paraquadrulidae		
<i>Quadrulella symmetrica tubulata</i> (Gauthier-Lièvre, 1953)	5, 7, 8, 9	6
Plagiopyxidae		
<i>Plagiopyxis</i> sp.	8	1
Trigonopyxidae		
<i>Cyclopyxis impressa</i> (Daday, 1905)	2, 3, 4, 6, 7, 8, 9	21
<i>Cyclopyxis kahli</i> (Deflandre, 1929)	2, 3, 4, 5, 6, 7, 8, 9	38
Rotifera		
Asplanchnidae		
<i>Asplanchna sieboldii</i> (Leydig, 1854)	4, 5, 6	4
Brachionidae		
<i>Anuraeopsis navicula</i> Rousselet, 1911	1, 3, 4, 7, 8	8
<i>Brachionus angularis</i> Gosse, 1851	3, 7, 8, 9	21
<i>Brachionus bidentata</i> Anderson, 1889	8	1
<i>Brachionus calyciflorus</i> Pallas, 1766	6	1
<i>Brachionus caudatus</i> Ahlstrom, 1940	5, 7, 9	6
<i>Brachionus dolabratus</i> Harring, 1914	4, 5	4
<i>Brachionus falcatus</i> Zacharias, 1898	5, 7, 8, 9	8
<i>Brachionus quadridentatus</i> Hermann, 1783	7, 8	7
<i>Kellicottia bostoniensis</i> (Rousselet, 1908)	2, 4, 7, 9	7
<i>Keratella americana</i> Carlin, 1943	4, 5, 6, 8, 9	10
<i>Keratella cochlearis</i> Gosse, 1851	2, 4, 5, 7, 9	10
<i>Keratella tropica</i> (Apstein, 1907)	1, 2, 4, 5, 7, 9	24
<i>Notholca</i> sp.	2	3
<i>Plationus patulus</i> (Müller, 1786)	1, 4	6
<i>Platylabus quadricornis</i> (Ehrenberg, 1832)	2, 3, 4, 9	13
Collotheceidae		
<i>Collotheca</i> sp.	1, 2, 3, 4, 5, 6, 7, 8, 9	53
Conochilidae		
<i>Conochilus coenobasis</i> (Skorikow, 1914)	1, 2, 3, 7	8
Euchlanidae		
<i>Beauchampiella eudactylota</i> (Gosse, 1886)	1, 6	3
<i>Dipleuchlanis propatula</i> (Gosse, 1886)	4, 6, 7, 9	7
<i>Euchlanis dilatata</i> Ehrenberg, 1832	1, 3, 4, 6, 9	10
<i>Tripleuchlanis plicata</i> (Levander, 1894)	2, 3, 4, 5, 7, 9	17
Flosculariidae		
<i>Ptygura</i> sp.	1, 2, 4, 5	15
<i>Sinantherina ariprepes</i> Edmondson, 1939	4, 5, 6, 8, 9	10
Hexarthridae		
<i>Hexarthra mira</i> (Hudson, 1871)	8	1
Lecanidae		
<i>Lecane aculeata</i> (Jakubski, 1912)	4	1
<i>Lecane bulla</i> (Gosse, 1851)	1, 2, 3, 4, 5, 6, 7, 8, 9	78
<i>Lecane cornuta</i> (Müller, 1786)	4	1
<i>Lecane decipiens</i> (Murray, 1913)	4	1
<i>Lecane elsa</i> Hauer, 1931	7	1
<i>Lecane grandis</i> (Murray, 1913)	3, 4	4

Table 2. Continued...

Taxa	Site	FO%
<i>Lecane hastata</i> (Murray, 1913)	4, 8	3
<i>Lecane leontina</i> (Turner, 1892)	1, 2, 3, 6, 8, 9	18
<i>Lecane ludwigi</i> (Eckstein, 1883)	1, 2, 4, 5, 7, 8, 9	15
<i>Lecane luna</i> (Müller, 1776)	1, 2, 3, 4, 5, 6, 8, 9	31
<i>Lecane lunaris</i> (Ehrenberg, 1832)	1, 2, 3, 4, 5, 6, 7, 8, 9	47
<i>Lecane murrayi</i> (Hauer, 1965)	4, 7, 8	7
<i>Lecane obtusa</i> (Murray, 1913)	4, 7	4
<i>Lecane quadridentata</i> (Ehrenberg, 1832)	9	1
<i>Lecane signifera</i> (Jennings, 1896)	1, 4	6
<i>Lecane</i> sp.	1, 2, 3, 4, 5, 6, 7, 8, 9	44
<i>Lecane stenroosi</i> (Meissner, 1908)	4, 9	3
Lepadellidae		
<i>Lepadella ovalis</i> (Müller, 1786)	1, 2, 3, 4, 5, 6, 7, 8, 9	44
<i>Lepadella patella</i> (Müller, 1773)	2, 3, 4, 8, 9	10
<i>Lepadella pumilo</i> Hauer, 1931	3, 4, 5	4
<i>Paracolurella logima</i> (Myers, 1934)	3	1
Mytilinidae		
<i>Mytilina crassipes</i> (Lucks, 1912)	2, 4	3
<i>Mytilina mucronata</i> (Müller, 1773)	9	1
Notommatidae		
<i>Cephalodella gibba</i> (Ehrenberg, 1830)	2, 3, 7, 8, 9	10
<i>Cephalodella</i> sp.	1, 2, 3, 4, 5, 6, 7, 8, 9	94
<i>Monommata</i> sp.	1, 3, 4, 5, 6, 7, 8, 9	49
<i>Notommata copeus</i> Ehrenberg, 1834	4, 8	3
<i>Notommata</i> sp.	1, 2, 3, 4, 5, 6, 7, 8, 9	69
Philodinidae		
<i>Dissotrocha aculeata</i> (Ehrenberg, 1832)	2, 3, 4, 5, 6, 7, 8, 9	33
<i>Dissotrocha</i> sp.	1, 3, 4, 5, 6, 7, 8, 9	24
Synchaetidae		
<i>Polyarthra dolichoptera</i> Idelson, 1925	1, 2, 3, 4, 5, 6, 7, 8	24
<i>Synchaeta stylata</i> Wierzejski, 1893	1	1
Testudinellidae		
<i>Pompholyx complanata</i> Gosse, 1851	4, 6, 7, 9	11
<i>Testudinella patina</i> (Hermann, 1783)	1, 2, 3, 5, 8	8
Trichocercidae		
<i>Trichocerca bidens</i> (Lucks, 1912)	2, 3, 4, 5, 7	14
<i>Trichocerca cylindrica</i> (Imhof, 1891)	2, 3, 4, 5, 6, 7, 9	18
<i>Trichocerca fusiformis</i> (Levander, 1894)	5, 6	3
<i>Trichocerca insulana</i> (Hauer, 1937)	2, 3, 5, 7	6
<i>Trichocerca similis</i> (Wierzejski, 1893)	2, 3, 4, 5, 6, 7, 8, 9	44
<i>Trichocerca</i> sp.	1, 2, 4, 5, 8, 9	14
<i>Trichocerca tigris</i> (Müller, 1786)	2	1
Trichotriidae		
<i>Macrochaetus sericus</i> (Thorpe, 1893)	2, 3, 4, 5, 6, 9	24
<i>Trichotria tetractis</i> (Ehrenberg, 1830)	3, 4, 8, 9	10
Trochosphaeridae		
<i>Filinia opoliensis</i> (Zacharias, 1898)	2, 3, 5, 6, 8, 9	8
<i>Filinia terminalis</i> (Plate, 1886)	1, 2, 3, 4, 5, 6, 7, 8, 9	46
Cladocera		
Bosminidae		

Table 2. Continued...

Taxa	Site	FO%
<i>Bosmina haggmani</i> Stingelin, 1904	1, 2, 3, 4, 5, 6, 7, 8	11
<i>Bosminopsis deitersi</i> Richard, 1895	1, 2, 5, 9	26
Chydoridae		
<i>Acroperus tupinamba</i> Sinev & Elmoor-Loureiro, 2010	2, 4, 9	6
<i>Alona guttata</i> Sars, 1862	4, 8	3
<i>Alonella dadayi</i> Birge, 1910	1, 2, 4, 7, 8, 9	26
<i>Biapertura ossiani</i> (Sinev, 1998)	4, 5, 6, 8	8
<i>Chydorus eurynotus</i> Sars, 1901	1, 4, 7, 9	10
<i>Euryalona orientalis</i> (Daday, 1898)	8	1
<i>Leydigiopsis curvirostris</i> Sars, 1901	2, 7, 8, 9	7
<i>Magnospina dentifera</i> (Sars, 1901)	4, 7, 8	4
<i>Nicsmirnovius paggii</i> Souza & Elmoor-Loureiro, 2017	4	3
<i>Notoalona sculpta</i> (Sars, 1901)	5	1
<i>Ovalona glabra</i> (Sars, 1901)	4, 8	4
Daphniidae		
<i>Ceriodaphnia silvestrii</i> Dadayi, 1902	9	3
<i>Daphnia gessneri</i> Herbst, 1967	1, 2, 5, 7	7
<i>Simocephalus mixtus</i> Sars, 1903	3	1
Ilyocryptidae		
<i>Ilyocryptus spinifer</i> Herrick, 1882	1, 9	4
Macrothricidae		
<i>Macrothrix squamosa</i> Sars, 1901	1, 4, 9	6
Moinidae		
<i>Moina minuta</i> Hansen, 1899	1	1
Sididae		
<i>Diaphanosoma spinulosum</i> Herbst, 1975	6	1
Copepoda		
Young stages		
Nauplii Cyclopoida	1, 2, 3, 4, 5, 6, 7, 8, 9	72
Nauplii Calanoida	1, 2, 3, 4, 5, 6, 7, 8, 9	46
Copepodit Cyclopoida	1, 2, 3, 4, 8, 9	22
Copepodit Calanoida	1, 2, 3, 5, 6, 8, 9	22
Cyclopidae		
<i>Acanthocyclops robustus</i> (Sars, 1863)	1, 6	3
<i>Mesocyclops meridianus</i> (Kiefer, 1926)	1, 9	3
<i>Mesocyclops</i> sp.	1, 2, 9	10
<i>Paracyclops chiltoni</i> (Thomson, 1882)	1, 6	6
<i>Thermocyclops decipiens</i> (Kiefer, 1929)	1, 2, 3, 6, 7, 9	19
<i>Thermocyclops minutus</i> (Lowndes, 1934)	1, 2, 3, 4, 8, 9	15
Diaptomidae		
<i>Argyrodiaptomus azevedoi</i> (Wright, 1935)	1, 9	3
<i>Argyrodiaptomus furcatus</i> (Sars, 1901)	1, 2, 6	6
<i>Notodiaptomus</i> sp.	1, 2, 6	11

testate amoebae (e.g. *Arcella costata*, *Diffugia* sp.), rotifers (e.g. *Filinia terminalis*, *Keratella tropica*, and *Polyarthra dolichoptera*), and copepodites of calanoid copepods at Sites 1 (channel-bottom and littoral-surface) and 2. Total phosphorus was negatively correlated with the abundance of some species of testate amoebae (e.g., *Arcella vulgaris*, *A. megastoma*, *Centropyxis eornis*, *Lesquereusia spiralis*), rotifers (e.g., *Brachionus angularis*, *Lecane bulla*, and

Lepadella ovalis), and the cladoceran *Alonella dadayi* at sites 4, 8, and 9.

For the dry season, we observed a positive correlation of electrical conductivity, dissolved oxygen, pH, turbidity, and water flow velocity with the first axis of the CCA, indicating their influence on the abundance of some species of testate amoebae (e.g. *Arcella vulgaris*, *Centropyxis cassis*, *C. constricta*, and *Cyclopyxis kahli*) and rotifers (e.g. *Dissotrocha*

Table 3. Analysis of variance (ANOVA) of zooplankton richness and abundance by sites (1-9), zones (littoral and channel), and depths (surface and bottom) within and between the hydrological seasons (rainy and dry).

Factor	Zooplankton	Richness F value			Abundance F value		
		Rainy	Dry	Rainy*Dry	Rainy	Dry	Rainy*Dry
Site (df = 8)	Total	5.6 (***)	5.6 (***)	2.0 (ns)	3.2 (*)	20.3 (***)	0.2 (ns)
	Testate amoebae	5.7 (***)	6.4 (***)	1.8 (ns)	17.2 (***)	10.0 (***)	5.6 (***)
	Rotifera	3.3 (**)	6.1 (***)	1.6 (ns)	2.0 (ns)	5.1 (**)	3.3 (**)
	Cladocera	6.8 (***)	6.1 (***)	5.6 (***)	1.8 (ns)	2.9 (*)	1.1 (ns)
	Copepoda	6.4 (***)	13.5 (***)	2.1 (ns)	5.1 (**)	82.5 (***)	0.4 (ns)
Zone (df = 1)	Total	0.0 (ns)	0.1 (ns)	0.0 (ns)	0.5 (ns)	0.0 (ns)	0.3 (ns)
	Testate amoebae	0.1 (ns)	0.1 (ns)	0.3 (ns)	0.0 (ns)	0.1 (ns)	0.0 (ns)
	Rotifera	0.4 (ns)	0.0 (ns)	0.1 (ns)	0.4 (ns)	0.0 (ns)	0.2 (ns)
	Cladocera	0.1 (ns)	0.0 (ns)	0.0 (ns)	0.5 (ns)	0.5 (ns)	0.3 (ns)
	Copepoda	0.1 (ns)	0.0 (ns)	0.0 (ns)	0.4 (ns)	0.0 (ns)	0.2 (ns)
Depth (df = 1)	Total	0.1 (ns)	2.1 (ns)	0.7 (ns)	0.2 (ns)	0.1 (ns)	0.1 (ns)
	Testate amoebae	0.1 (ns)	0.8 (ns)	0.1 (ns)	0.0 (ns)	0.2 (ns)	0.0 (ns)
	Rotifera	0.0 (ns)	1.7 (ns)	1.2 (ns)	0.1 (ns)	1.6 (ns)	0.3 (ns)
	Cladocera	0.1 (ns)	0.2 (ns)	0.2 (ns)	0.3 (ns)	0.9 (ns)	0.1 (ns)
	Copepoda	0.6 (ns)	0.0 (ns)	0.0 (ns)	0.2 (ns)	0.1 (ns)	0.3 (ns)

Significance levels are: (ns) non-significant, $p > 0.05$; (*) $0.01 < p \leq 0.05$; (**) $0.001 < p \leq 0.01$; (***) $p \leq 0.001$. Abbreviation: df, degrees of freedom.

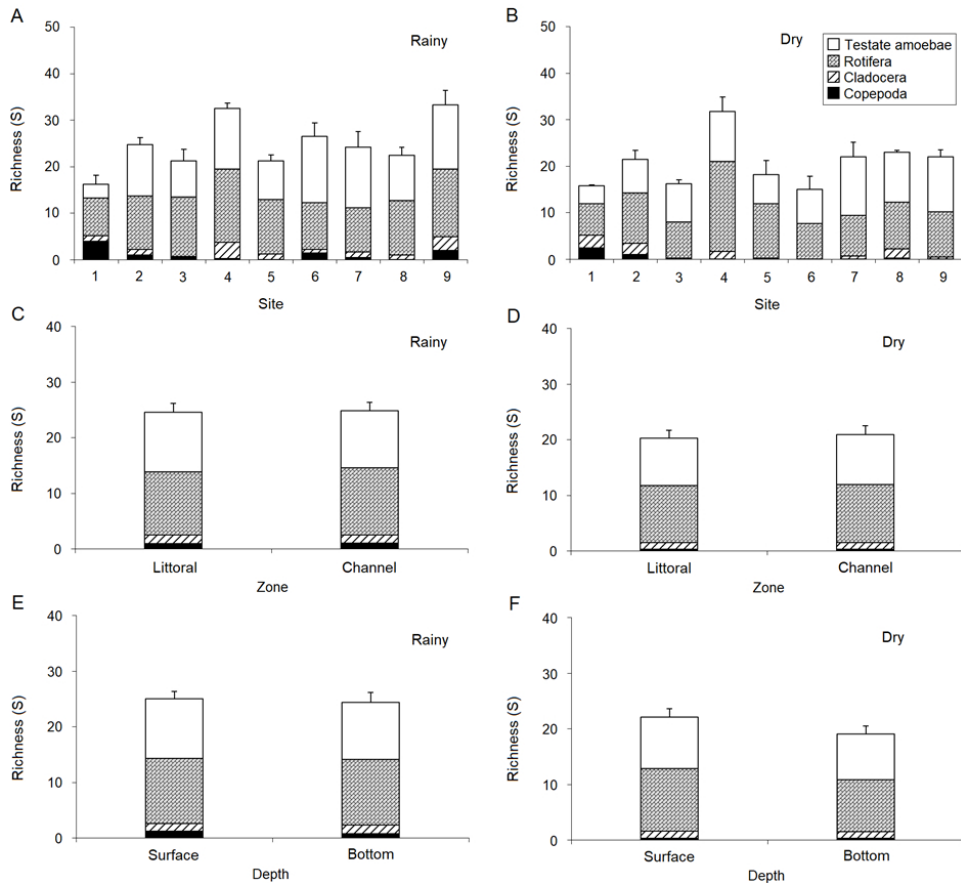


Figure 4. Zooplankton species richness of sites (A and B), zones (C and D), and depths (E and F) of the Aporé River, Paranaíba River basin, during the different hydrological seasons. Data were represented as mean ± standard error.

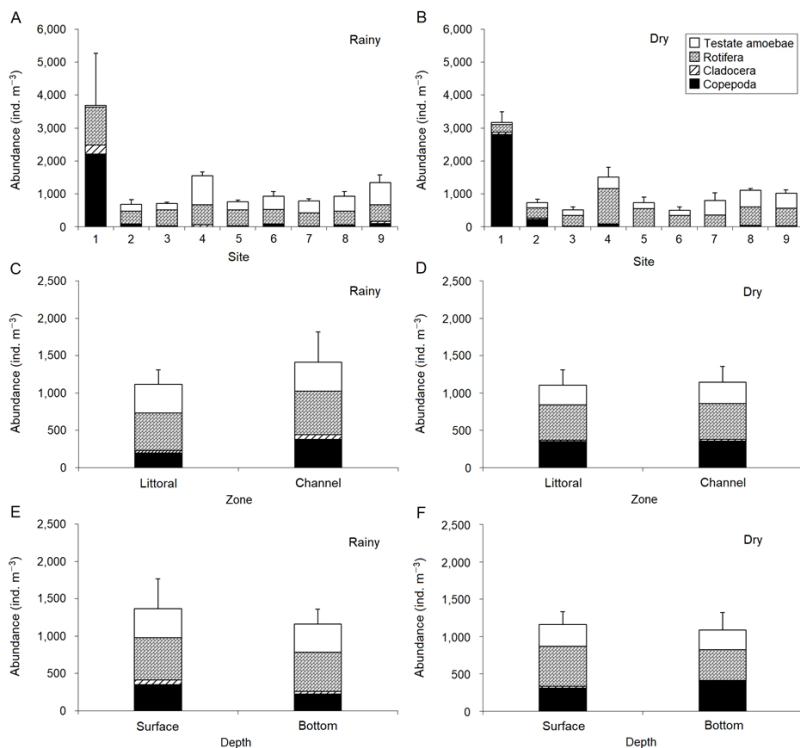


Figure 5. Zooplankton abundance of sites (A and B), zones (C and D) and depths (E and F) of the Aporé River, Paranaíba River basin, during the different hydrological seasons. Data were represented as mean ± standard error.

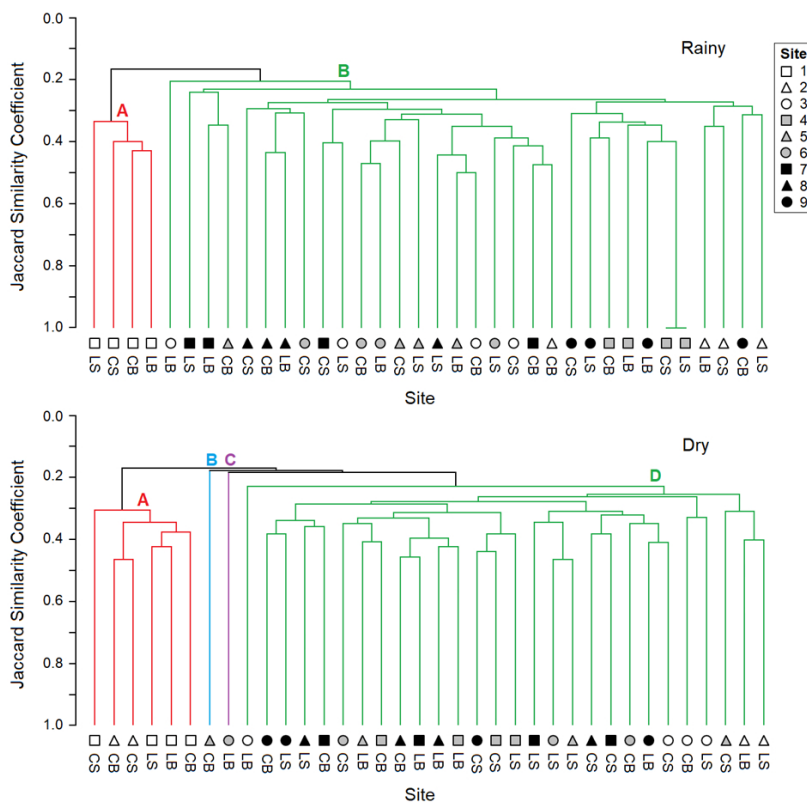


Figure 6. Cluster analysis dendrogram showing the similarity between zooplankton-sampled environments in the Aporé River, Paranaíba River basin, during the different hydrological seasons. Abbreviations: CS, channel-surface; CB, channel-bottom; LS, littoral-surface; LB, littoral-bottom. Different letters (A-D) indicate the formation of different groups.

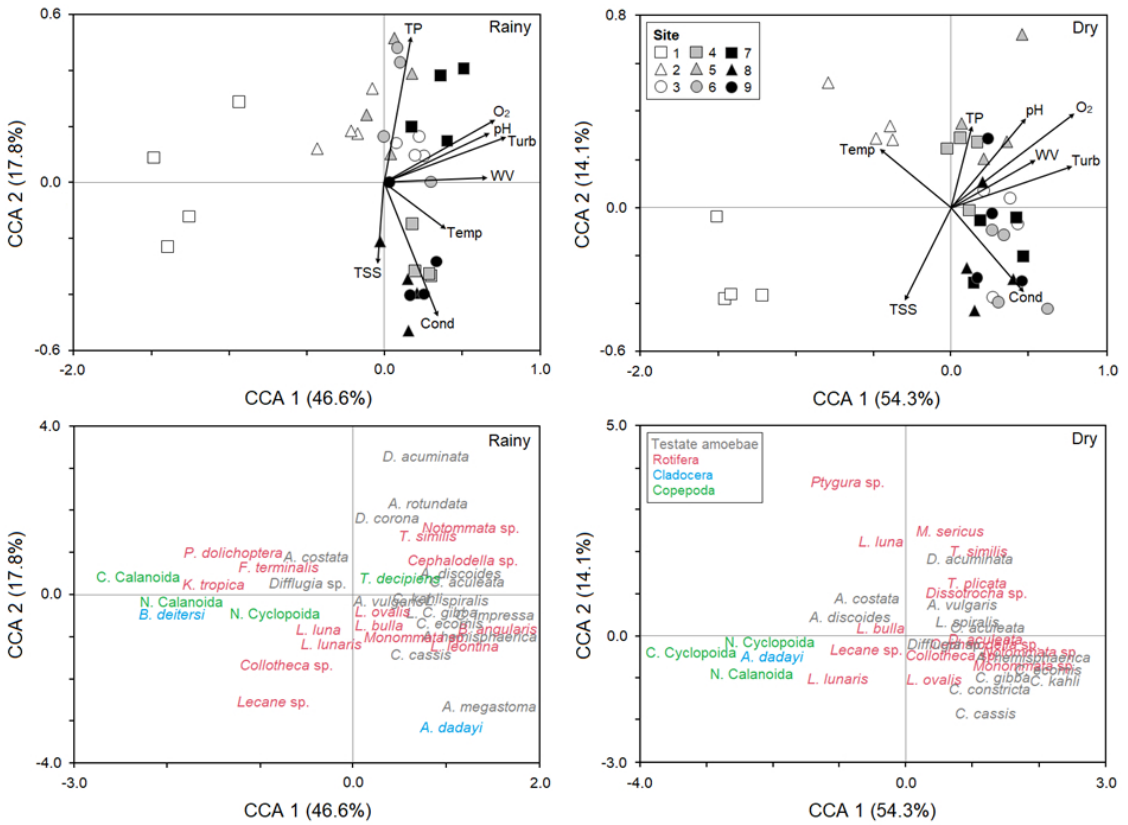


Figure 7. Canonical correspondence analysis (CCA) ordination showing the relationships between the environmental variables and the environments, and zooplankton taxa of the Aporé River, Paranaíba River basin, during the different hydrological seasons. Abbreviations: Cond, electrical conductivity; O₂, dissolved oxygen; Temp, temperature; TP, total phosphorus; TSS, total suspended solids; Turb, turbidity; WV, water flow velocity.

aculeata, *Macrochaetus sericus*, *Tripleuchlanis plicata*, and *Lepadella ovalis*) on Sites 3-9. On the first axis, we found a positive correlation between temperature and the abundance of some species of testate amoebae of the genus *Arcella* and rotifers (*Lecane bulla*, *L. luna*, and *Ptygura sp.*) at Site 2. The second axis showed a positive correlation between the concentration of total suspended solids and the abundance of some species of rotifers of the genus *Lecane* and microcrustaceans (nauplii and copepodites of copepods, and cladoceran *Alonella dadayi*) at Site 1.

4. Discussion

In our study, we found a high species richness of zooplankton when compared to studies in large rivers (e.g. Matsumura-Tundisi et al., 2015; Picapedra et al., 2017; Branco et al., 2018). This fact can be explained by our sampling effort, which sampled different microhabitats, and by the heterogeneity of habitats found along the Aporé River, which differed in their abiotic

characteristics. Allied to this, changes in the surrounding characteristics (presence of rural, urban, and preserved areas) along the studied section of the river may also have contributed to the occurrence of a large number of taxa. Topographic features such as stability of the margins and sinuosity of the bed, in addition to the use and occupation of the surroundings, can contribute to a greater or lesser entry of allochthonous material into the bodies of small rivers, imposing different environmental pressures on the organisms that live there (Hepp et al., 2010).

When pooling the data from our study, rotifers clearly dominated the zooplankton community, both in terms of species richness and density. This predominance of rotifers in rivers has been explained by their lower susceptibility to turbidity, short life cycle, and low predation by fish (Pace et al., 1992; Sluss et al., 2008; Bomfim et al., 2017). In terms of species richness, the Lecanidae and Brachionidae families were the most relevant, while in terms of abundance, the species of the Notommatidae (Genera *Cephalodella* and *Notommata*) and

Trochosphaeridae (*Filinia terminalis*) families predominated. This fact is commonly observed in rivers in South America (Paggi et al., 2014; Picapedra et al., 2017; Branco et al., 2018), where there is a mix of good swimmers from true plankton and poor swimmers from the littoral zone, and combined with the opportunistic characteristic of these organisms of having a large food spectrum, favors the simultaneous presence of many species in the same environment or the same species in environments with different characteristics (Lansac-Tôha et al., 2009). The testate amoebae were also important in terms of richness and abundance, particularly the Diffflugidae, Arcellidae, and Centropyxidae families, which are predominant in the plankton of other tropical rivers (e.g. Picapedra et al., 2018; 2019; Gomes et al., 2020), mainly due to the high water turbulence that cause the suspension of these organisms from the sediment into the water column. Furthermore, tolerance to physical stress and competitive capacity seem to be key factors that allow these protozoa to remain in riverine plankton (Branco et al., 2018).

Among microcrustaceans, Chydoridae was especially important for the high degree of richness of cladocerans, with most representatives of this family normally associated with littoral vegetation and the benthic interstitial environment (Lansac-Tôha et al., 2009). In this study, a greater abundance of the littoral cladoceran *Alonella dadayi* was observed in the lentic water of the oxbow lake during the dry season and downstream of the river during the rainy season, indicating that some chydorids prefer lentic water and are probably transported away from their habitat by the increase in river flow during the rainy season. In turn, the planktonic cladoceran *Bosminopsis deitersi* (Bosminidae) was the most abundant species, occurring in both lentic and lotic waters. The presence of bosminids in the main river channel can be attributed to the inoculation of individuals from low-flow environments (Zimmermann-Timm et al., 2007), such as the oxbow lake. In addition, bosminids are favored in river environments because of their shorter generation time, ability to withstand a high sediment rate, and adaptability to feed on detritus and bacteria, which reduces the impact of advection loss (Pace et al., 1992; Casper & Thorp, 2007; Paggi et al., 2014; Matsumura-Tundisi et al., 2015). Copepods, represented mainly by nauplii, were the most abundant group in the oxbow lake, owing to their favorable lentic conditions. The scarcity of copepods, especially adults, in river channels

can be explained by greater water turbulence and downstream advection, which makes it difficult to search for food and partners for reproduction (Dole-Olivier et al., 2001).

Statistical analyses highlighted that the richness, abundance, and composition of zooplankton differed more clearly in the longitudinal axis of the Apuré River, both in the rainy and dry seasons. In our study, there was a predominance of cladoceran and copepod taxa in the oxbow lake, and mainly rotifer and testate amoebae taxa were found along the river. In river systems, different communities appear to have different responses to environmental variables, such as water residence time, turbidity, and flow velocity (Thorp & Mantovani, 2005; Lair, 2006). For example, when the water residence time was short, the rotifers dominated the zooplankton, and when the residence time was long, microcrustaceans were more prevalent (Baranyi et al., 2002). A similar pattern was also observed by Spaink et al. (1998) in the Waal River (Netherlands), with a predominance of microcrustaceans in the oxbow lake and rotifers in the main channel. Furthermore, rotifers are better adapted than microcrustaceans to waters with greater turbidity, as they are less negatively affected by high concentrations of suspended material (Kirk & Gilbert, 1990). High flow velocities are also known to inhibit the reproduction and growth rate of zooplankton populations in rivers. Zooplankton population growth is rarely observed at velocities greater than 0.4 m s^{-1} (Rzoska, 1978). In the Apuré River, the lowest abundances were recorded at sites that exhibited flow velocities greater than 0.5 m s^{-1} . Finally, the increase in species richness in the river channel may be related to drift or resuspension of organisms, especially rotifers and testate amoebae, from littoral and benthic zones. The microfauna that live at the bottom are under constant threat of being dislodged from their microhabitat due to water turbulence and becoming trapped by the flow of the main river channel (Viroux, 2002).

The oxbow lake (Site 1) may have played an important role in structuring the zooplankton of the Apuré River. At the downstream site of the oxbow lake (Site 2), we observed planktonic species of rotifers and microcrustaceans, which might have originated from the lake. Because of their low turbulence, shallow depths, and long retention times, fluvial lakes can act as plankton sources for rivers (Basu et al., 2000b; Viroux, 2002). However, the influence of adjacent lentic environments may be spatially limited and no longer observable at a distance downstream (Viroux, 1999), as verified in

the other sites of the Apuré River channel. In turn, the predominance of nauplii and bosminids over rotifers in the oxbow lake may be linked to the higher grazing rates of these organisms. Although grazing rates are higher in copepod adults than in nauplii (Casper & Thorp, 2007), the high densities of nauplii (approximately 85% of the total copepod abundance), should exert a stronger cumulative grazing effect on phytoplankton in low-flow areas, which are generally more productive. Finally, the scarcity of adult copepods in the oxbow lake may be related to the higher concentration of suspended solids that can cause mechanical disturbances in the filtering apparatus (Jönsson et al., 2011), and to the greater risk of predation in standing water from the higher density of larvae and adult planktivorous fish (Czerniawski & Domagała, 2012; Godfrey et al., 2020).

We did not identify significant differences in zooplankton structure between the littoral zone and the main river channel and between different depths, while other studies have recorded zooplankton variability among these microhabitats. For example, greater species richness and abundance of zooplankton may occur in the littoral zone because of the presence of macrophyte beds or other structures (e.g. rocks, tree trunks, and sandbanks), which reduce the flow velocity and create adequate conditions (backwaters) for the development of planktonic populations (Thorp et al., 1994, Basu et al., 2000b; Sluss et al., 2008). A greater abundance of zooplankton can also be observed at greater depths during the day in the river channel because of daily vertical migration that occurs to avoid predation by fish (Casper & Thorp, 2007). Although shoreline macrophyte banks were present at some sites in our study, the banks were especially small and sparse and did not contribute to hydraulic retention. In addition, we found boulder formations both in the littoral zone and in the river channel, which provided high turbulence. Furthermore, because it is a small river, the lateral and vertical dimensions are closer and allow for a greater mixing of water; therefore, thermal or chemical stratification rarely occurs, with abiotic changes being more evident in large rivers (Baranyi et al., 2002; Thorp et al., 2006). Thus, hydraulic forces probably affected the distribution of organisms in the lateral and vertical dimensions of our study, causing a mix of species and preventing the spatial heterogeneity of zooplankton.

The seasonal changes in spatial distribution of zooplankton were more significant for the species

composition, cladoceran richness, and testate amoebae and rotifer abundances. The smaller similarity in species composition during the dry season may be related to a greater variation in abiotic characteristics (e.g., water flow velocity, electrical conductivity, dissolved oxygen, turbidity) along the longitudinal axis of the river, as indicated by the PCA and CCA. Each season has environmental conditions that influence the distribution of species and that select those with the most similar characteristics, promoting the coexistence of those able to adapt to these conditions (Arriera et al., 2015). In turn, the increase in the abundance of testate amoebae and the richness of cladocerans in the rainy season may have been induced by their resuspension in river water because of the increase in flow and turbulence. Finally, the increase in rotifer density in the oxbow lake during the rainy season, mainly of lecanid species (e.g. *Lecane luna*, *L. lunaris*), may be associated with an increase in the concentration of suspended solids caused by the introduction of allochthonous material. Previous studies have shown that bacteria or organic compounds can adhere to the surface of suspended solids, which may be beneficial for zooplankton species as a food source (Lind & Davalos-Lind, 1991; Melão & Rocha, 2006).

In conclusion, the predominance of rotifers and testate amoebae in the main channel and microcrustaceans in the oxbow lake indicates a distinct adaptive capacity of these organisms to live in these environments. Higher abundance of zooplankton in the oxbow lake was resulted by low water flow velocity and high concentration of suspended material. On the other hand, higher species richness of zooplankton in the river resulted from a high contribution of species with littoral characteristics, owing to considerable mixing of water in the channel. Furthermore, the changes in zooplankton structure were more evident along the longitudinal axis of the river, which can be attributed to a greater influence of the oxbow lake on sites upstream of the river, as well as a greater heterogeneity of abiotic factors in the longitudinal dimension than in the lateral and vertical dimensions. Finally, the spatial and seasonal changes in flow, turbidity, and the concentration of suspended solids seemed to exert an important effect on the attributes, especially the composition and abundance, of riverine zooplankton. Thus, we emphasize the importance of studies in river environments, especially those focused on a high degree of sampling, both spatially and temporally,

which allows for a more accurate assessment and understanding of the structure and dynamics of riverine zooplankton, which are currently lacking.

Acknowledgements

We thank the Grupo de Pesquisas em Recursos Pesqueiros e Limnologia (GERPEL) of the Universidade Estadual do Oeste do Paraná (UNIOESTE) for providing logistical support during collection. We are also grateful to the anonymous reviewers, whose detailed comments and constructive suggestions improved the quality of the manuscript.

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Received: 20 October 2021

Accepted: 09 April 2022

Associate Editor: Priscilla de Carvalho.