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Microcrustaceans structure determined by the type and trophic state of lakes

Estrutura de microcrustáceos determinada pelo tipo e estado trófico dos lagos

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Abstract: Aim: In this study, we investigated the response of microcrustaceans composition, diversity and abundance (Cladocera and Copepoda) to the lake’s origin (natural and man-made) and trophic state (mesotrophic and eutrophic, with natural eutrophication and artificial eutrophication). We tested the following hypotheses: (I) the increase in the abundance of certain microcrustacean species may indicate a rise in the trophic level; (II) the richness and abundance vary amongst lakes and are higher in the lake with natural eutrophication; and (III) the microcrustaceans abundance is associate with high primary productivity, being higher in the eutrophic environment with artificial eutrophication. **Methods:** The study was conducted in a segment of the Paranapanema River basin, in southeastern Brazil, focusing on five lakes spanning an eight-kilometer stretch, to understand the different organisms’ responses to distinct conditions of aquatic environments. Sampling was carried out bimonthly over the course of a year. **Results:** A principal component analysis (PCA) separated three types of lakes: eutrophic (natural and man-made) to mesotrophic. Additionally, 25 taxa were found. SIMPER analysis filtered six species with more than 70% dissimilarity contribution. Five species exhibited differences amongst the lakes, one species correlated with natural variables as depth. The redundancy analysis associated the *Bosminopsis deitersi* abundance with man-made eutrophic lakes and with the variables electrical conductivity, phosphorus, nitrogen, chlorophyll-a, and hardness. High abundances of *B. deitersi* indicated artificial eutrophication especially in man-made lakes, while natural lakes with natural eutrophication were not favorable environments for the increase of *B. deitersi* abundance. **Conclusions:** This study highlights the neotropical oxbow lakes, emphasizing the significance of physicochemical characterization, detailed temporal sampling, and lake classification by origin and trophic level.

Keywords: anthropic impacts; oxbow lakes; Neotropical region; zooplankton.

Resumo: Objetivo: Neste estudo, nós investigamos a resposta da composição, diversidade e abundância de microcrustáceos (Cladocera e Copepoda) à origem do lago (natural e artificial) e ao estado trófico (mesotrófico e eutrófico, com eutrofização natural e eutrofização artificial). Testamos as seguintes hipóteses: (I) o aumento na abundância de certas espécies de microcrustáceos pode indicar um aumento no nível trófico; (II) a riqueza e a abundância variam entre os lagos e são maiores no lago com eutrofização natural; e (III) a abundância de microcrustáceos está associada à alta produtividade primária, sendo maior no ambiente eutrófico com eutrofização artificial. **Métodos:** O estudo foi realizado em um segmento da bacia do rio Paranapanema, no sudeste do Brasil, com foco em cinco lagos em um trecho de oito quilômetros, para entender as respostas dos diferentes organismos em condições distintas de ambientes aquáticos. A amostragem foi realizada bimestralmente ao longo de um ano. **Resultados:** Uma análise de componentes principais (PCA) separou três tipos de lagos: eutróficos (naturais e artificiais) a mesotróficos. Adicionalmente, 25 táxons foram encontrados. A análise SIMPER filtrou seis espécies com mais de 70% de contribuição de dissimilaridade. Cinco espécies apresentaram diferenças entre os lagos, uma espécie correlacionada com variáveis naturais, como profundidade. A análise de redundância associou a abundância de *Bosminopsis deitersi* com lagos eutróficos artificiais e com as variáveis condutividade elétrica, fósforo, nitrogênio, clorofila-*a* e dureza. Altas abundâncias de *B. deitersi* indicaram eutrofização artificial especialmente em lagos artificiais, enquanto lagos naturais com eutrofização natural não foram ambientes favoráveis para o aumento da abundância de *B. deitersi*. **Conclusões:** Este estudo destaca os lagos de meandros neotropicais, enfatizando a importância da caracterização físico-química, da amostragem temporal detalhada e da classificação dos lagos por origem e nível trófico.

Palavras-chave: impactos antrópicos; lagos de meandros; região Neotropical; zooplâncton.

1. Introduction

The zooplankton community, a key heterotrophic component of aquatic ecosystems, consists of various groups including protozoans, rotifers, cnidarians, microcrustaceans, and others, with microcrustaceans being the most abundant. These organisms perform essential ecological functions, such as nutrient cycling and facilitating energy flow between primary producers and higher trophic levels, which are crucial for maintaining the dynamics of aquatic ecosystems (Landa et al., 2007; Karpowicz et al., 2020). Microcrustaceans (Copepoda and Cladocera) are numerically important in rivers and lakes where they also present notable biomass related to environmental conditions (Sendacz et al., 2006; Bonecker et al., 2007). These organisms have many proles and short life cycles (Rietzler et al., 2002) with the ability to quickly respond to environmental disturbances, what is especially demonstrated by the changes in ecological attributes such as composition, richness, and abundance (Perbiche-Neves et al., 2007, 2013).

Some species are widely known as bioindicators of water quality, providing insights into their interactions with the physical, chemical, and biological processes of aquatic environments (Ghidini et al., 2009; Perbiche-Neves et al., 2016; Muñoz-Colmenares et al., 2021). Several species, particularly those within genera of Copepoda like *Thermocyclops*, *Acanthocyclops*, and *Metacyclops*, as well as cladocerans of the family Bosminidae, have been commonly used for water quality assessment (Ghidini et al., 2009; Silva, 2011; Perbiche-Neves et al., 2016).

Since the 1970s, microcrustaceans have been used as bioindicators of water quality in Brazil, particularly for assessing environmental conditions and eutrophication levels in lentic, lotic or aquatic ecosystems water bodies such as rivers, ponds, lakes, and reservoirs (Sendacz et al., 2006; Picapedra et al., 2020; Silva et al., 2020). However, there has been limited research conducted in natural oxbow lakes (Neves et al., 2003; Keppeler & Hardy, 2004). The expansion of urban and agricultural areas, as well as intensive livestock production, along with the discharge of residential and industrial wastewater, has led to pollution and disruption of water dynamics and quality in lakes (Hébert et al., 2021; Paquette et al., 2022).

While spatial compartmentalization, water retention time, and trophic level are the most important drivers of the zooplankton community in reservoirs (Perbiche-Neves & Nogueira, 2010, 2013), the connection events between oxbow lakes and the main river are important to the diversity variation of zooplankton (Güntzel et al., 2010; Napiórkowski & Napiórkowska, 2017). For lakes, there are records that zooplankton respond quickly to pulses, in addition to other relationships between abiotic features (Zhou et al., 2023). Another factor is macrophytes, which can determine the abundance and diversity of zooplankton (Choi et al., 2014). Nonetheless, research focusing on natural lakes, particularly oxbow lakes, and comparative studies with artificial ones, remains limited in the Neotropical Region.

Our study aims to investigate potential differences in the composition, diversity, and abundance of microcrustacean assemblages amongst five lakes located in close proximity within the same river basin. These lakes exhibit variations in their origins (man-made or natural), trophic state (mesotrophic or eutrophic), and types of eutrophication (artificial or natural). By analyzing the ecological attributes of these assemblages (composition, diversity, and abundance), we intend to determine whether microcrustacean species can serve as bioindicators of water quality, particularly in contrasting lake origins and trophic states.

We tested the following hypotheses: (I) the increase in the abundance of certain microcrustacean species may indicate a rise in the trophic state; (II) the richness and abundance vary amongst lakes and are higher in the lake with natural eutrophication (due to the cumulative richness and slow eutrophication process, in contrast to the artificial, which is characterized by rapid nutrients increase, especially by sewage input); and (III) the microcrustaceans abundance is associate with high primary productivity, being higher in the eutrophic environment with artificial eutrophication.

2. Material and Methods

2.1. Study area

The study was developed in a section of the Paranapanema River basin, which constitutes one of the most important tributaries of the Upper Paraná River Basin. Five lakes were examined within an eight-kilometer stretch (Figure 1). Amongst these lakes, three were of natural origin (meander lakes, oxbow lakes), one was extensively modified (classified as artificial) for recreational fishing and leisure activities, and the remaining lake was designated for silt disposal from mining operations (also classified as artificial). These lakes were strategically selected due to their diverse origins, trophic states, and varied anthropogenic influences in their surroundings. This selection was crucial for comprehending how microcrustacean assemblages respond to different environmental conditions.

The Itapetininga (Ita) Lake (23° 36’ 16.48” S, 48° 27’ 25.34” W; area of 10.268 m^2) is located on the left bank of the Itapetininga River – a tributary of Upper Paranapanema River, with riparian forest and no potential impacts on the surroundings. The Capaúva (Capa) Lake (23º 36’ 10.40” S, 48º 28’ 48.15” W; area of 21.313 m^2) appears to be an old, modified oxbow lake in a fairly eutrophic reservoir

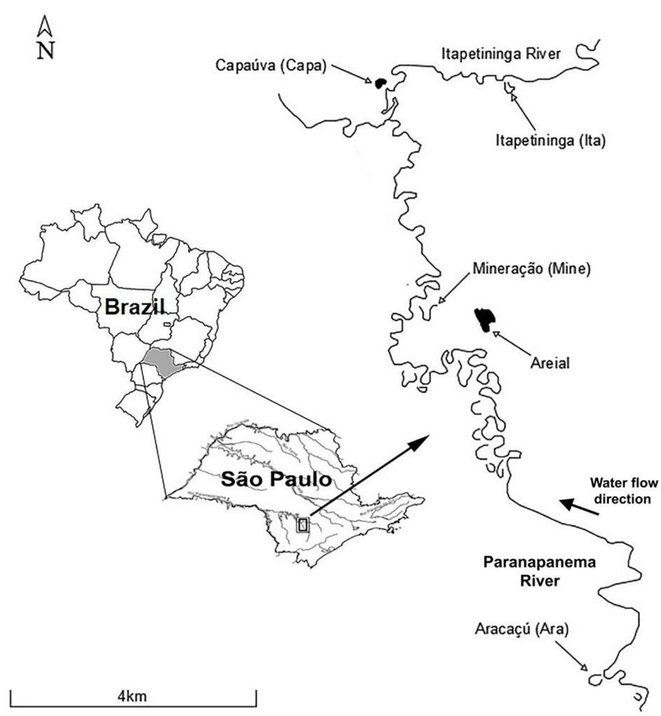

Figure 1. Map of the sampling sites in the five studied lakes: Itapetininga (Ita), Capaúva (Capa), Mineração (Mine), Aracaçu (Ara) – all natural lakes, and Areial – an artificial lake, State of São Paulo. The water direction is Aracaçú to downstream.

with frequent cyanobacterial blooms, which receives water from the central lake of the Municipality of Campina do Monte Alegre (two kilometers upstream) and sewage sources. The Mineração (Mine) Lake (23° 38' 31.50" S, 48° 28' 19.62" W; area of 21.286 m^2) is a natural oxbow lake, with few influences in the surrounding landscape. The Areial Lake (23º 38' 33.80" S, 48º 27' 28.56" W; area of 21.264 m^2), which is an artificial and deeper lake, is formed by the activity of sand mining and receives the washing water from the sand extraction. Finally, the Aracaçu Lake (Ara) (23° 41' 56.71" S, 48° 26' 16.30" W; area of 21.626 m^2) is an old, natural and quite shallow oxbow lake, with a strong siltation, eutrophication and many aquatic macrophytes.

2.2. Zooplankton sampling, analysis of microcrustaceans, and statistical analysis

The samplings were conducted bimonthly during a year, in all lakes, covering the following months: September 2017, November 2017, January 2018, March 2018, May 2018, and July 2018. Limnological variables such as alkalinity and total hardness ($mg.L^{-1}$) were measured with Alfakit®. Water transparency (m) was determined by observing the disappearance of the Secchi Disk (SD). Additionally, pH, turbidity (NTU), dissolved oxygen ($mg.L^{-1}$), water temperature (C°), and electrical conductivity ($\mu S.cm^{-1}$) were determined using the Hanna® multiparameter probe. The depth (m) was determined by lowering a measuring line to the bottom of each lake.

Water samples were collected for laboratory analysis of total phosphorus ($\mu g.L^{-1}$), total nitrogen ($\mu g.L^{-1}$), and total chlorophyll-a ($\mu g.L^{-1}$) (Goltermann et al., 1978; Mackereth et al., 1978; Valderrama, 1981; CETESB, 2014). Subsequently, the modified Carlson Trophic State Index - TSI was calculated (Lamparelli, 2004), using water transparency, total phosphorus and total chlorophyll-a.

Principal component analysis (PCA) was used to ordinate the lakes based on their spatial and temporal physical and chemical variables. All variables, except pH, were log-transformed. A Pearson correlation was used to standardize the data, and in case of highly correlated variables, one variable was excluded from the analysis.

The quantitative and qualitative zooplankton samples were collected by diagonal hauls in the water column, with a conical plankton net of 68 µm mesh size, filtering a volume of 400 liters of water per sample (Wetzel & Likens, 2000). The net was towed along a diagonal path from the bottom towards the surface, covering various depths. The retained material was stored in High-Density Polyethylene bottles with airtight screw caps, containing four percent formaldehyde buffered with calcium tetraborate for fixation of the collected samples.

Specimens were identified with microscope, stereoscope, and specialized bibliographies, Reid (1985), Elmoor-Loureiro (1997), Ueda & Reid (2003), and Perbiche-Neves et al. (2015). The samples were qualitatively analyzed until the stabilization of a rarefaction curve, approximately with 200 individuals per sample. The zooplankton samples were deposited in the Plankton Museum of the Hydrobiology Department, Federal University of São Carlos, São Carlos, Brazil. For the quantification of the organisms, an acrylic chamber with a capacity of five mL was used. Homogenized samples were added to the chamber, and a minimum of 200 individuals per sample were counted (Goswami, 2004).

Species richness (S), alpha diversity using the Shannon-Wiener index (H) and evenness (H/S) were calculated using PAST software, version 4.03 (Hammer et al., 2001). Abundance was quantified as individuals per cubic meter. These ecological metrics were compared across the lakes using analysis of variance (ANOVA) or the Kruskal-Wallis test, with normality assessed using the Shapiro-Wilk test. *Post hoc* analysis was conducted using Tukey's honestly significant difference (HSD) test for ANOVA and Dunn's test for the Kruskal-Wallis test. A Principal Coordinate Analysis (PCoA) and Permutational Multivariate Analysis of Variance (PERMANOVA) were used to assess whether species composition differed amongst the lakes. The species composition data was based on an abundance matrix, and Bray-Curtis dissimilarity was used as the distance metric for both analyses.

In terms of frequency in the lakes studied, for each species, the number of sites where it was recorded was divided by the total number of sites sampled, regardless of how many times the species was found. The value obtained was then multiplied by 100 to express the frequency in percentage terms.

Aiming to identify potential bioindicators of water quality amongst zooplankton species, we employed a statistical approach similar to that of Saito et al. (2015) and Perbiche-Neves et al. (2016), following a four-step procedure.

First, a Similarity Percentage (SIMPER) analysis based on Bray-Curtis dissimilarity was applied to filter species contributing over 70 percent of importance during our samplings, employing free permutations. Next, comparative analyzes (ANOVA and Kruskal-Wallis, depending on data normality) were used to assess if the species identified by SIMPER varied amongst lakes categorized by their origin and trophic level. Subsequently, a Spearman correlation was employed between the SIMPER-identified species and natural variables to account for potential confounding effects on microcrustacean species. Water temperature and depth were considered natural variables because they fluctuate independently of other factors and are therefore unaffected by human interference.

Finally, the species identified by SIMPER that exhibited differences in comparative analyses but showed no correlation with natural variables were subjected to redundancy analysis (RDA), comparing them with the remaining limnological variables, to understand the possible associations and patterns in the lakes categorized, according to Trophic State Index (TSI).

All the analyses were carried out in the R software, the vegan package (Oksanen et al., 2018) was used for the PERMANOVA, SIMPER, and RDA analyses.

3. Results

3.1. Abiotic variables

The analysis of the limnological variables and the trophic state index (Table 1) confirmed that Capaúva and Aracaçu Lakes are classified as eutrophic, while the remaining three lakes (Itapetininga, Mineração, and Areial) are mesotrophic.

The lakes were classified as: I. natural mesotrophic – NM (Mineração and Itapetininga), II. man-made mesotrophic – MM (Areial), III. natural eutrophic with natural eutrophication (absence of visible cyanobacteria blooms, shallow, with macrophytes) – NE (Aracaçu) and IV. man-made eutrophic with artificial eutrophication – ME (Capaúva).

The greatest depths were observed in Areial, Itapetininga, and Mineração Lakes. In terms of electrical conductivity and nutrient levels, the highest values were recorded in the Aracaçu, Capaúva, and Itapetininga meanders, respectively (Table 1). Itapetininga, Mineração, and Areial Lakes were categorized as mesotrophic, presenting low limnological variability and seasonal influence compared to the other two lakes, which were classified as eutrophic (Table 1). Amongst the eutrophic lakes, Aracaçu Lake (natural eutrophication) exhibited lower electrical conductivity, while Capaúva Lake (artificial eutrophication) showed higher values. However, other variables such as total phosphorus, total nitrogen, and chlorophyll-a levels were similar across these lakes.

In the PCA (Figure 2), 38.16% of limnological variables' variance in a spatial temporal scale was explained, with 20.86% attributed to the first component and 17.3% to the second component. The correlation coefficients of the variables with the

Table 1. Mean values of the limnological variables obtained in Itapetininga (Ita), Capaúva (Capa), Mineração (Mine), Areial, and Aracaçu (Ara) lakes from bimonthly sampling.

LAKES	ITA	CAPA	MINE	AREIAL	ARA
Classification	NM	ME	NM	MM	NE
pH	6.0	6.2	5.6	5.4	6.0
Hard ($mg.L^{-1}$)	35	42	25	27	26
Alca ($mg.L^{-1}$)	32	41	31	55	38
Transp (m)	0.89	0.59	0.96	0.35	0.46
Turb (NTU)	9.6	36.7	10.8	48.2	38.8
DO ($mg.L^{-1}$)	4.8	5	5.7	6.1	5.2
Temp (C°)	23.0	23.2	22.8	24.2	23.0
Cond ($\mu S.cm^{-1}$)	40.8	71.0	38.0	44.5	26.0
TP ($\mu g.L^{-1}$)	47	60	26	43	62
TN ($\mu g.L^{-1}$)	457	626	273	177	627
Chlor ($\mu g.L^{-1}$)	16	40	38	21	41
Dep (m)	3.4	3	3.4	5	0.83
TSI Index	M	E	M	M	E
TSI value	40	50	44	44	51

Codes: pH = Hydrogen potential, Hard = total hardness, Alca = total alkalinity, Transp = water transparency, Turb = turbidity, DO = dissolved oxygen, Temp = water temperature, Cond = conductivity; TP = total phosphorus; TN = total nitrogen; Chlor = total chlorophyll-*a*; TSI = Trophic State Index; Dep = Depth; NM = natural mesotrophic; ME = man-made eutrophic; MM = man-made mesotrophic; NE = natural eutrophic; M = mesotrophic; E = eutrophic.

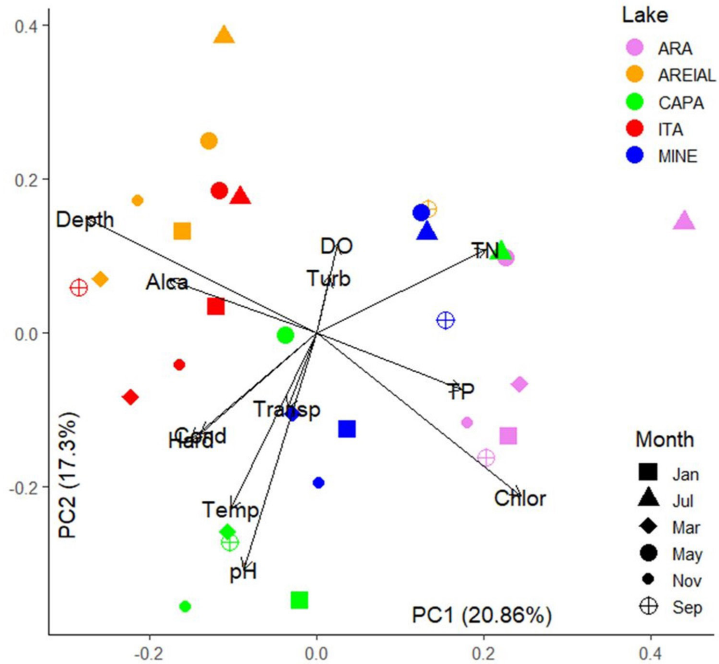

Figure 2. Biplot of Principal Component Analysis (PCA) used to order the limnological variables measured in the studied lakes: Itapetininga (ITA), Capaúva (CAPA), Mineração (MINE), Areial and Aracaçu (ARA), during 2017 and 2018. Codes: pH = Hydrogen potential, Hard = total hardness, Alca = total alkalinity, Transp = water transparency, Turb = turbidity, DO = dissolved oxygen, Temp = water temperature, Cond = conductivity; TP = total phosphorus; TN = total nitrogen; Chlor = total chlorophyll-*a*; Depth = Depth; Jan = January; Mar = March; Jul = July; Sep = September; Nov = November.

Table 2. Loading of the first six principal components generated in the PCA used to ordering the limnological variables measured.

	PC1	PC2	PC3	PC4	PC5	PC6
pH	-0.16	-0.56	-0.04	-0.04	0.08	0.21
Hard	-0.27	-0.25	-0.33	0.42	-0.06	-0.17
Alca	-0.32	0.13	-0.38	-0.14	0.05	0
Transp	-0.06	-0.18	0.55	0.2	-0.18	-0.11
Turb	0.03	0.13	-0.54	-0.34	-0.19	0.1
DO	0.05	0.21	0.01	-0.02	0.78	-0.48
Temp	-0.19	-0.42	0.07	-0.27	0.4	0.26
Cond	-0.25	-0.24	-0.25	0.36	-0.04	-0.41
TP	0.32	-0.13	-0.19	0.34	0.36	0.5
TN	0.37	0.2	-0.14	0.51	-0.01	0.16
Chlor	0.45	-0.39	-0.17	-0.09	-0.11	-0.32
Dep	-0.5	0.27	0.07	0.25	0.05	0.26

Codes: pH = Hydrogen potential, Hard = total hardness, Alca = total alkalinity, Transp = water transparency, Turb = turbidity, DO = dissolved oxygen, Temp = water temperature, Cond = conductivity; TP = total phosphorus; TN = total nitrogen; Chlor = total chlorophyll-*a*; Dep = Depth.

PCA axes are shown in Table 2. Capaúva and Aracaçu Lakes (both eutrophic) were related especially in terms of turbidity, nitrogen, phosphorus, and chlorophyll-*a*. Areial Lake (man-made mesotrophic) also showed a significant correlation with turbidity. Mineração and Itapetininga (both natural mesotrophic) were associated with water transparency. Moreover, Areial and Itapetininga Lakes were correlated with depth, while nearly all lakes were correlated with electrical conductivity.

3.2. Biological community

For zooplankton, 25 taxa were identified (Table 3). Copepods comprised eight taxa (32%

Table 3. List of species with occurrence and frequency in the lakes studied, Itapetininga (ITA), Capaúva (CAPA), Mineração (MINE), Areial and Aracaçu (ARA).

Taxa	Occurrence of Taxa in each lake					Frequency (%)
COPEPODA						
Diaptomidae	**ITA**	**CAPA**	**MINE**	**AREIAL**	**ARA**	
Notodiaptomus henseni (Dahl F., 1894)	1	1	1	1	1	100
Notodiaptomus iheringi (Wright S., 1935)	1	1	1	1	0	80
Cyclopidae						
Thermocyclops inversus Kiefer, 1936	1	1	1	1	1	100
Mesocyclops longisetus (Thiébaud, 1912)	0	0	1	1	0	40
Microcyclops anceps (Richard, 1897)	0	0	0	0	1	20
Microcyclops ceibaensis (Marsh, 1919)	0	0	0	0	1	20
Eucyclops serrulatus (Fischer, 1851)	0	0	0	0	1	20
Paracyclops chiltoni (Thomson G.M., 1883)	0	0	0	0	1	20
CLADOCERA						
Chydoridae						
Oxyurella ciliata Bergamin, 1939	0	0	0	0	1	20
Alona rustica Scott, 1895	0	0	0	0	1	20
Magnospina dentifera (G.O. Sars, 1901)	1	1	0	0	1	60
Bosminidae						
Bosminopsis deitersi Richard,1895	1	1	1	0	1	80
Bosmina freyi De Melo & Hebert, 1994	1	1	0	0	0	40
Bosmina hagmanni Stingelin, 1904	1	1	0	0	0	40
Daphniidae						
Ceriodaphnia silvestrii Daday, 1902	0	0	1	1	0	40
Ceriodaphnia cornuta G.O. Sars, 1885	0	0	0	1	0	20
Daphnia gessneri Herbst, 1967	0	1	0	0	0	20
Sididae						
Diaphanosoma brevireme G.O. Sars, 1901	0	0	1	1	0	40
Diaphanosoma birgei Korínek, 1981	0	1	1	0	1	60
Diaphanosoma spinulosum Herbst, 1975	1	1	1	1	1	100
Moina minuta Hansen,1899	1	1	1	1	1	100
Simocephalus serrulatus (Koch, 1841)	0	0	0	0	1	20
Macrothricidae						
Macrothrix paulensis (G.O. Sars, 1900)	0	0	0	0	1	20
Macrothrix spinosa King, 1853	0	1	0	1	1	60
Macrothrix elegans G.O. Sars, 1901	1	0	0	1	1	60

of the total species), while Cladocera accounted for 17 taxa (68% of the total species), distributed amongst the families Sididae (three species), Bosminidae (three species), Moinidae (one specie), Macrothricidae (three species), Chydoridae (three species), and Daphniidae (four species).

Comparing richness, diversity (H´), evenness, and total abundance, only total abundance was different amongst the lakes (Table 4) and higher in the man-made eutrophic lake.

In the PCoA (Figure 3), we delineated the species composition, determining how the different lakes are grouped and dispersed in relation to each other. This analysis revealed both similarities and significant differences in species diversity among the lakes. The first axis explained 28.1% of the total variance, while the second axis explained 17.48%. In addition, the PERMANOVA test indicated significant differences in species composition between the lakes, resulting in a p-value < 0.001 and an $R^2 = 0.36$.

Using a SIMPER analysis, six species presented in Table 3 were identified as collectively contributing to 70% of the dissimilarity observed amongst the lakes, making them significant candidates for use as bioindicators. *Bosminopsis deitersi* emerged as important in eutrophic lakes, regardless of their origin, while *N. henseni* predominated in mesotrophic lakes.

In the eutrophic lakes, with natural and artificial eutrophication, *B. deitersi* accounted for 38%, followed by *N. henseni* at 18%, and *D. spinulosum* at 14%. Similarly, in comparisons amongst natural mesotrophic and artificial eutrophic lakes, *B. deitersi* remained prominent at 39%, with *N. henseni* at 18% and *D. spinulosum* at 11%. This trend

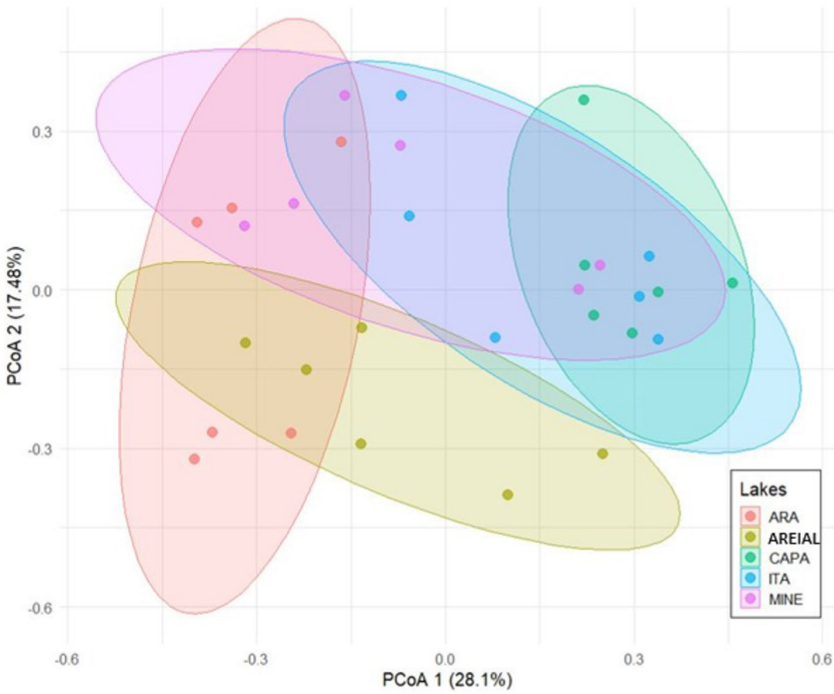

Figure 3. Principal Component Analysis (PCoA) of species composition in lakes ARA, AREIAL, CAPA, ITA, and MINE. The points represent the samples collected, while the ellipses outline the dispersion and grouping of the species communities in each lake.

Table 4. Results of comparative tests (ANOVA-F and *p* value; and Kruskal-Wallis H and *p* value) for ecological attributes and species abundance amongst the four types of lakes, natural mesotrophic, man-made mesotrophic, natural eutrophic with natural eutrophication and man-made eutrophic with artificial eutrophication. In bold significant differences ($p<0.05$).

Ecological attributes	F	*p*	Species abundance	H	*p*
Richness (S)	3.63	0.30	*N. henseni*	11.20	**0.01**
Evenness	1.82	0.60	*T. inversus*	10.57	**0.01**
	H	***p***	*B. deitersi*	20.33	**<0.01**
Total Abundance	6.05	**<0.01**	*M. minuta*	3.86	0.26
Alpha Diversity (H´)	1.69	0.19	*D. spinulosum*	7.90	**0.04**
			M. spinosa	7.53	**0.05**

persisted when contrasting man-made mesotrophic with man-made eutrophic lakes, with *B. deitersi* at 39%, *N. henseni* at 18%, and *D. spinulosum* at 11%. In natural eutrophic lakes *versus* man-made mesotrophic lakes, *N. henseni* led at 22%, followed by *M. minuta* at 19%, *T. inversus* and *D. spinulosum* both at 11%, and *M. spinosa* at 8%. Amongst mesotrophic lakes, both man-made and natural, *N. henseni* took the lead at 22%, followed by *B. deitersi* at 20%, *T. inversus* at 17%, and *M. minuta* at 15%.

The abundance of the species filtered by SIMPER was compared across the four lake types (Figure 4). Amongst the species examined, only *M. minuta* showed no significant differences across the lakes. In contrast, *B. deitersi* exhibited higher abundance in the man-made eutrophic lake (Figure 4e), while *N. henseni*, *T. inversus*, and *D. spinulosum* were more abundant in both the man-made eutrophic and natural mesotrophic lakes (Figure 4b, 4c, and 4d, respectively). *Macrothrix spinosa*, on the other hand, was found to be abundant only in the natural eutrophic lake (Figure 4f).

Spearman correlation was conducted using the four species identified through SIMPER analysis (Table 5) and two variables (depth and temperature). The results revealed that only *N. henseni* exhibited a significant correlation with depth, whereas *M. spinosa* demonstrated a nearly significant negative correlation with depth. Thus, these two species were deemed less useful for indicating water quality,

Table 5. Spearman correlations amongst the species identified through SIMPER analysis and two environmental variables: depth and water temperature. Correlations with *p*-values below 0.05 are denoted in bold, while correlations with a p-value of 0.08 are marked with bold asterisks*.

	Depth	Temperature	*N. henseni*	*T. inversus*	*D. spinulosum*	*M. spinosa*
Depth	1	0.04	**0.46**	0.02	0.11	**-0.32***
Temperature	0.04	1	0.02	0.14	0.18	0.09

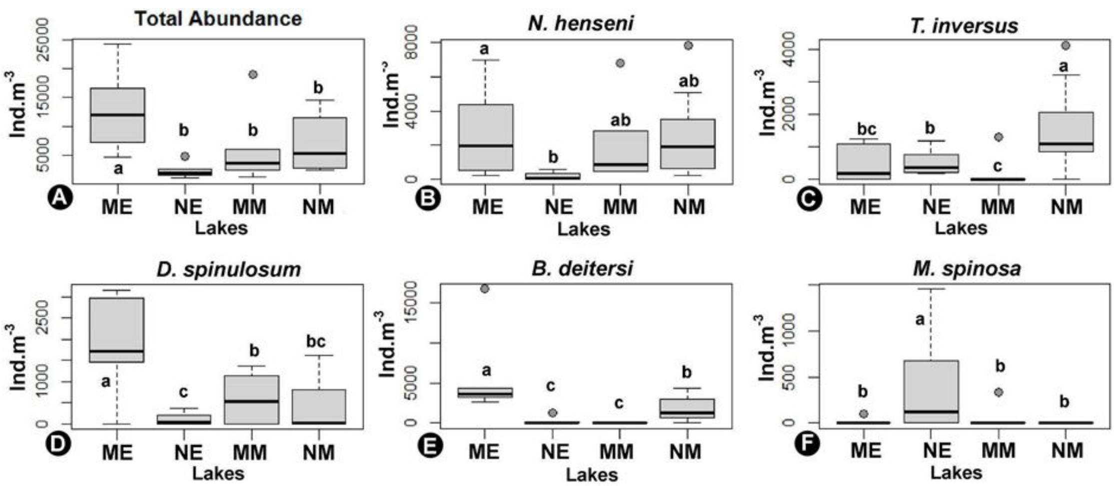

Figure 4. Box-plots of species' abundances with significant differences pointed by ANOVA or Kruskal-Wallis analyzes amongst the four categories of lakes in our study: natural mesotrophic (NM), man-made mesotrophic (MM), natural eutrophic with natural eutrophication (NE), and man-made eutrophic with artificial eutrophication (ME). (a) Total abundance; (b) *N. henseni*; (c) *T. inversus*; (d) *D. spinulosum*; (e) *B. deitersi*; (f) *M. spinosa*. Letters point to homogeneous groups.

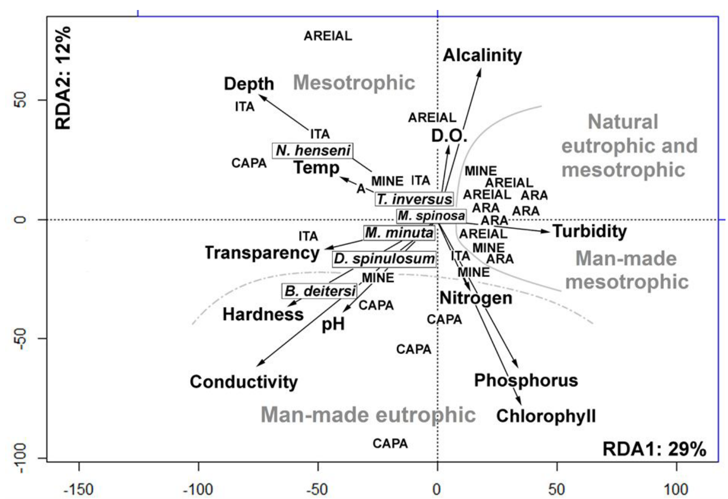

Figure 5. Redundancy Analysis biplot depicting the relationship between microcrustacean species and limnological variables across lakes categorized as man-made mesotrophic (Areial), natural mesotrophic (Itapetininga - ITA and Mineração - MINE), man-made eutrophic (Capaúva - CAPA), and natural eutrophic with natural eutrophication (Aracaçu - ARA). Legend: Conductivity = Electrical Conductivity, D.O. = Dissolved Oxygen, pH = Hydrogen Potential, Temp = Water Temperature, Transparency = Water Transparency.

since they have correlations with natural variables, such as depth, which are not directly influenced by anthropogenic factors. Therefore, they will not be exclusive indicators of other processes related to water quality.

The RDA accounted for 41% of the relationship between zooplankton and limnological variables, with 29% attributed to the first component and 12% to the second (Figure 5). This analysis categorized species, variables, and lakes into three distinct groups: turbidity, natural and man-made mesotrophic lakes, along with natural eutrophic lakes; *N. henseni* and *T. inversus* with depth, dissolved oxygen, alkalinity, and water temperature in both mesotrophic lakes; and *B. deitersi* with electrical conductivity, hardness, pH, nitrogen, phosphorus, and chlorophyll-a. The species *M. minuta* and *M. spinosa* showed weaker correlations and were positioned centrally in the biplot. Consequently, based on the second component, *N. henseni* could be linked to natural and man-made mesotrophic lakes.

4. Discussion

Our findings substantiated all three hypotheses under examination. We observed higher richness and abundance in eutrophic environments, with richness being greater in the natural eutrophic lake and abundance in the man-made eutrophic lake. Each lake exhibited traits reflective of its trophic status, with microcrustacean species displaying varying levels of tolerance or sensitivity to these conditions. This underscores how microcrustaceans respond to limnological variables and trophic gradients, particularly exemplified by *B. deitersi*.

Based on the environmental analysis, the lakes exhibited a diverse range of trophic conditions, varying from mesotrophic states in Mineração, Areial, and Itapetininga Lakes to eutrophic levels in Capaúva and Aracaçu Lakes. Additionally, the eutrophication processes differed between these last lakes, with artificial eutrophication occurring rapidly and intensely in the former and natural eutrophication progressing at a slower pace in the latter. While indicators such as nutrients, turbidity, and chlorophyll-a levels clearly indicated the pronounced trophic conditions of Capaúva and Aracaçu Lakes, our findings diverged from those of Matsumura-Tundisi & Tundisi (2003, 2005) regarding the efficacy of electrical conductivity as a marker of human influence, such as sewage contamination. This discrepancy can be attributed to the calcareous soil composition prevalent in the area (Moroz-Caccia Gouveia, 2018), which leads to elevated levels of hardness and alkalinity in the lakes, thereby facilitating an increase in heavy ion concentrations in the water.

The natural eutrophication observed in Aracaçu Lake is evident from its age and the resulting sedimentation, siltation, and loss of depth over time. These conditions have facilitated the growth of numerous aquatic macrophytes in the lake, as pointed out previously by Dubey & Dutta (2020). Aquatic macrophytes have been found to enhance the species richness of both copepods (Perbiche-Neves et al., 2014) and cladocerans (Debastiani-Júnior et al., 2015), primarily by increasing habitat complexity. This effect is particularly notable in floating macrophytes, whose root structures also contribute significant amounts of organic matter. Consequently, our hypothesis regarding greater diversity in natural lakes with natural eutrophication was confirmed upon analyzing species richness using descriptive statistics for each lake individually. However, when grouped into categories, no significant difference was observed.

The artificial eutrophication of Capaúva Lake, a man-made reservoir, was evident due to the significant influence of urban discharges from the upstream drainage basin. These inputs, containing domestic effluents, contribute to elevated levels of chlorophyll-a, conductivity, and nutrients, creating favorable conditions for the proliferation of cyanobacteria (Wurtsbaugh et al., 2019). Extensive literature documents these eutrophic conditions, highlighting irregular fluctuations in the zooplankton community and the impacts of toxic algae (Illyová & Pastuchová, 2012; Ejsmont-Karabin & Karabin, 2013; Ochocka & Pasztaleniec, 2016). Although this Lake exhibits high levels of total hardness compared to other lakes, statistical analysis indicates that this variable is not significant for zooplankton organisms in this context.

The elevated levels of electrical conductivity also observed in Capaúva Lake can be attributed in part to local soil conditions, although sewage contamination certainly exacerbated this factor. The detrimental effects of a substantial increase in conductivity were evident in the decline of diversity indices, as reported by Matsumura-Tundisi & Tundisi (2003, 2005) in the reservoirs of the Tietê River, one of Brazil's most polluted rivers.

Our study identified several physicochemical variables that significantly influenced zooplankton responses, consistent with findings from previous research. These variables include nutrients, chlorophyll-a, turbidity, conductivity, water transparency, and depth, as demonstrated in studies by Branco et al. (2002), Nogueira (2001), Nogueira et al. (2008) and Wang et al. (2010). However, limnological variables such as hardness, alkalinity, and water temperature did not appear to play a significant role in determining changes in the conditions and composition of the zooplankton of the lakes.

In mesotrophic Itapetininga, Mineração, and Areial Lakes, the highest values for depth, dissolved oxygen, and water transparency were observed. The zooplankton composition consisted of species commonly found in lakes with oligotrophic and mesotrophic conditions. The high abundance of *N. henseni*, *T. inversus*, and *D. spinulosum* corroborates findings from previous studies by other authors (Matsumura-Tundisi & Tundisi, 2003; Silva, 2011; Perbiche-Neves et al., 2016). Additionally, correlation was found between the abundance of *N. henseni* and depth in the lakes, which discarded its relationship with trophic level. Other studies (Matsumura-Tundisi & Tundisi, 2003; Nogueira et al., 2008; Perbiche-Neves et al., 2015) have also observed this species to be abundant in mesotrophic reservoirs. Bouvy et al. (2001) suggest that this species has the ability to break filaments of cyanobacteria into small particles for food supply, thereby controlling the proliferation of cyanobacteria populations in eutrophic lakes.

In parallel, positive correlations between the cladoceran species *B. deitersi* and eutrophication effects were observed across all statistical filters, consistent with findings from previous studies identifying these species as bioindicators of eutrophication (Pinto-Coelho et al., 2005; Ghidini et al., 2009; Guevara et al., 2009).

Some studies suggest that Calanoida species, such as *N. henseni*, are more closely associated with variations in conductivity (Matsumura-Tundisi & Tundisi, 2003), thermal and climatic variations (Perbiche-Neves et al., 2015), as well as biogeographical ecoregions (Perbiche-Neves et al., 2014). Contrastingly, *M. spinosa* exhibited nearly a significant negative correlation with depth and remained neutral in RDA. This suggests its affinity for shallow habitats and presence of aquatic macrophytes, consistent with findings by Debastiani-Júnior et al. (2016).

In terms of the richness index, the eutrophic lakes, Capaúva and Aracaçu, exhibited a higher number of species, although no significant difference was observed, this could be due to the different species composition, which could explain the variation in richness despite the lack of statistical significance. Previous studies by Barnett & Beisner (2007), Brucet et al. (2009), and Garcia et al. (2012) have highlighted that the diverse habitats within meanders contribute to their high diversity. These habitats offer abundant micro-habitats and ecological niches (Debastiani-Júnior et al., 2016). Moreover, the combination of elevated nutrient levels and prolonged water residence times in lentic environments may result in increased phytoplankton biomass, particularly cyanobacteria. This, in turn, can influence zooplankton population dynamics, as certain species are more tolerated by them (Dantas-Silva & Dantas, 2013; Ger et al., 2014).

The abundance of *B. deitersi* showed a positive correlation with the trophic state of the lakes, with lower abundance observed in mesotrophic lakes (natural and man-made), in line with what was observed by Nogueira et al. (2008) and Brito et al. (2013). *T. inversus* was considered an bioindicator of mesotrophic conditions associated with high concentrations of dissolved oxygen, consistent with findings by Landa et al. (2007), Silva (2011), and Perbiche-Neves et al. (2016). Conversely, *T. decipiens*, for example, typically dominant in eutrophic environments, was not found in high densities here, potentially replaced by other microcrustaceans such as *B. deitersi*, as observed in Capaúva Lake.

This study provided insights into the natural oxbow lakes at the beginning of the subtropical region, highlighting the importance of physicochemical characterization in environmental diagnosis, meticulous temporal sampling, and classification of lakes based on their origin and trophic level. Notably, variations exist amongst eutrophic lakes, contingent upon the origin of eutrophication – whether natural or man-made. Artificial eutrophication in man-made lakes promotes an increase in abundance, particularly of *B. deitersi*.

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Data availabilty

All research data analyzed in the research is available in ZENODO. Access is restricted until June 2025. It can be accessed in https://doi.org/10.5281/zenodo.14041533

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