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ECOLOGY

Responses of the zooplankton community to the formation of a small reservoir on the Caveiras River, southern Brazil

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ABSTRACT. We investigated changes in the species richness, abundance, and composition of the zooplankton community in response to the formation of a small reservoir in the Caveiras River, southern Brazil. Zooplankton were collected using a motor-pump and a plankton net (68 µm mesh), with 600 L of water filtered per sample. Sampling occurred during the pre- (April, August, and December 2011) and post-impoundment (July and October 2013, and January 2014) phases of the Caveiras River. We identified 86 taxa in this study, and rotifers were the predominant group. The species richness and abundance of the zooplankton increased after the filling of the reservoir. Furthermore, the zooplankton community showed a clear change in the species composition between the phases before and after the formation of the reservoir, with the emergence of typical planktonic species. Changes in the structure of the zooplankton community were related to changes in limnological characteristics due to the impoundment of the river, mainly in the availability of food and in the concentration of nutrients.

Keywords: cladocerans; copepods; dam construction; João Borges reservoir; rotifers; Santa Catarina State.

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Introduction

Zooplankton communities are an essential component of aquatic environments and are formed by different groups of invertebrates (*e.g.*, rotifers, cladocerans, and copepods) that have a water column as their main habitat; they are a key element for understanding the natural processes in freshwater ecosystems (Padovesi-Fonseca & Rezende, 2017). These organisms play an important role in nutrient cycling and energy flow. Due to their short life cycles, they are widely recognized for responding quickly to changes in the environment (Kozlowsky-Suzuki & Bozelli, 2002; Matsumura-Tundisi & Tundisi, 2005), such as the formation of a reservoir. Once formed, the reservoir blocks the free flow of the river and creates a semi-lentic or lentic habitat (Baxter, 1977), and changes important factors such as the quantity and quality of water, habitat, and transport of nutrients and sediments (Loken et al., 2018). Likewise, considerable changes occur in the structure of the riverine zooplankton, especially in their abundance, species composition, and in the orientation of trophic nets (Kobayashi, Shiel, Gibbs, & Dixon, 1998; Zhou, Tang, Wu, Fu, & Cai, 2008).

Currently, reservoirs are inseparable components of the Brazilian landscape and are present in all the main hydrographic basins, the result of the choice made by the country to generate electricity (Takahashi, Lansac-Tôha, Dias, Bonecker, & Velho, 2009). There has been a proliferation of these engineering works, especially of small hydroelectric plants (SHPs), which are important for the national energy matrix (International Energy Agency [IEA], 2013). In this context, SHPs have advantages because they can take advantage of the great hydro energy potential of Brazil, being suitable for smaller rivers in isolated locations (Latini & Pedlowski, 2016).

However, it is important to emphasize that despite the great potential of SHPs in Brazil and their image of being a low environmental impact energy source, the option for this type of enterprise should be analyzed more cautiously. Often the operational design of the SHPs gives the 'false idea' that these developments cause little change in the natural characteristics of the flow of the rivers, this fact being attributed to their smaller size and that many follow the run-of-river system (Premalatha, Abbasi, Abbasi, & Abbasi, 2014), which means they can accumulate a limited amount of water, if any (Perbiche-Neves & Nogueira, 2013).

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In this context, we evaluated the effects of the construction of a small reservoir on the zooplankton community. Our main objective was to evaluate whether the attributes (richness, abundance, and composition) of the zooplankton community differed between the period before and after the formation of the João Borges Reservoir on the Caveiras River. We hypothesized that even the construction of a small dam in a newly formed environment will significantly affect the zooplankton community. There will probably be a rapid increase in the species richness and the abundance of zooplankton, due to the decrease water flow and increase food availability after the impoundment of the river. In addition, the composition of the community will also be affected, with the appearance of planktonic species.

Material and methods

Study area

This study was conducted in the Caveiras River, which belongs to the Uruguay River basin (Figure 1). The Caveiras River starts at an altitude of approximately 1,300 m in the mountain region of Santa Catarina State. The course of the river follows an east/west direction and flows into the Canoas River, which in turn flows into the Uruguay River (Rafaeli-Neto, Becegato, & Cabral, 2013). The predominant climate in the region is temperate subtropical (Cfb, Köppen climate classification), with an average annual temperature of 16° C, precipitation varying between 1,500 and 2,100 mm, and no dry period. The reservoir studied is the João Borges Reservoir ($25^{\circ}43'40'S$, $50^{\circ}39'30'W$), which is one of several reservoirs located on the Caveiras River with the objective of generating electricity. The construction of the reservoir was completed in April 2013 and it is located in the upper stretch of the Caveiras River. The reservoir has a surface area of $3.41 \, \mathrm{km}^2$, with an average annual flow of $1,571 \, \mathrm{m}^3 \, \mathrm{s}^{-1}$. The average water retention time of the reservoir is $10 \, \mathrm{days}$, and the maximum depth is $17 \, \mathrm{m}$. Collections were carried out in the pre- (April, August, and December 2011) and postimpoundment (July and October 2013, and January 2014) phases of the Caveiras River. The sampling sites were predetermined based on the possible changes in the flow characteristics that would occur with the impoundment (Figure 1).

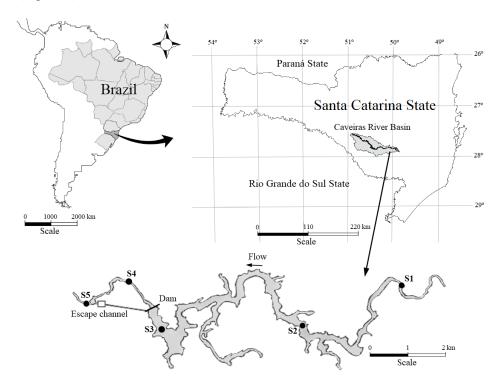


Figure 1. Map of the João Borges Reservoir and the sampling sites on the Caveiras River, Santa Catarina, Brazil.

Sampling and quantification of environmental variables

Dissolved oxygen (mg L⁻¹; portable oximeter, YSI 550A), electrical conductivity (µS cm⁻¹; portable conductivity meter, Digimed® DM-3P), pH (portable pH meter, Digimed® DM-2P), water temperature (°C; mercury bulb thermometer), and turbidity (NTU; portable turbidity meter, LaMotte® 2020i) were measured *in*

situ. We also determined the transparency of the water column using a Secchi disk (m). Total concentrations of phosphorus (mg L^{-1}) and suspended solids (mg L^{-1}) were obtained according to American Public Health Association [APHA] (2005). In addition, concentrations of chlorophyll a (µg L^{-1}) were obtained according to Golterman, Clymo, and Ohnstadt (1978).

Sampling, identification, and quantification of zooplankton

Zooplankton samples (30 in total) were taken at each site using a conical plankton net with a mesh size of 68 μ m. We filtered 600 L of water per sample using a motor pump. The collected material was placed in polyethylene bottles (500 mL), labeled, and fixed in 4% formaldehyde buffered with sodium borate (Na₃BO₃). Sedgewick-Rafter chambers were used to quantify the zooplankton. Standardized volume (50 mL) aliquots were removed from the samples using a Hensen-Stempell pipette (2.5 mL) and used to count the zooplankton. At least 50 rotifers, cladocerans, immature forms (nauplii and copepodites), and adult copepod individuals were counted (modified from Bottrell et al., 1976) under an optical microscope with a magnification range of $10 \times to 100 \times$. The density was expressed in terms of individuals per m⁻³. The species were identified using Koste (1978), Segers (1995), Elmoor-Loureiro (1997; 2010), Lansac-Tôha, Velho, Higuti, and Takahashi (2002), and Perbiche-Neves, Boxshall, Previatelli, Rocha, and Nogueira (2015).

Data analysis

To investigate the temporal and spatial changes in the zooplankton richness (number of species) and abundance as well as in environmental variables, an analysis of variance (two-way ANOVA) was applied, with a significance level of p < 0.05. The analyses were performed considering the following factors: phase (post and pre-impoundment) and environment (S1, S2, S3, S4, and S5). We also performed non-metric multidimensional scaling (NMDS) with a Bray-Curtis distance matrix to determine similarities in the zooplankton community based on the density data (Oksanen et al., 2016). The position of the samples in relation to the phases was used as a factor. Subsequently, a similarity analysis (ANOSIM) was used to verify the statistical significance of the groups found in the NMDS. In addition, a similarity percentage test (SIMPER) was used to assess the contribution of each species in separating the groups found in the NMDS. Finally, a canonical correspondence analysis (CCA) was used to select the predictors that best explained the variation in the zooplankton density data. For the CCA, only the density data of the species that contributed most to the variation in the community between the pre- and post-impoundment phases, according to the SIMPER test, were used. The statistical significance of the eigenvalues and species-environment correlations for the axes generated by the CCA was tested using the Monte Carlo method, based on 999 permutations (Legendre, Oksanen, & Ter-Braak, 2011), with a significance level of p < 0.05.

All data (except pH) were $\log (x + 1)$ transformed prior to the analysis to reduce the influence of outliers. The ANOVA, NMDS, ANOSIM, SIMPER, and CCA analyses were performed by the statistical environment in R version 3.0.2 (R Development Core Team, 2011).

Results

Environmental variables

Spatial heterogeneity was not observed for all environmental variables, both before and after the formation of the reservoir (ANOVA; p > 0.05). Contrarily, after the formation of the reservoir, there were significant changes (ANOVA; p < 0.05) for some environmental variables. There was an increase in the concentrations of total phosphorus and chlorophyll a with the river impoundment, while the concentration of total suspended solids decreased (Table 1).

Table 1. Mean values (± Standard Deviation) of the environmental variables in the pre- and post-impoundment phases of the Caveiras River, Santa Catarina, Brazil. ANOVA results (P values) are also provided, and the values in bold are considered significant (p < 0.05).

Environmental variables	Pre	Post	P values
Chlorophyll a (µg L^{-1})	1.7 (±1.5)	9.4 (±12.1)	0.026
Dissolved oxygen (mg L ⁻¹)	8.9 (±1.3)	7.9 (±1.5)	0.118
Electrical conductivity (µS cm ⁻¹)	37.9 (±7.7)	34.8 (±5.5)	0.307
pН	6.5 (±0.3)	6.9 (±0.9)	0.200
Total suspended solids (mg L ⁻¹)	136.9 (±60.9)	68.9 (±38.9)	0.009
Total phosphorus (mg L^{-1})	0.04 (±0.01)	0.09 (±0.06)	0.016
Turbidity (NTU)	13.4 (±7.4)	17.2 (±6.7)	0.132
Water temperature (°C)	18.1 (±4.1)	18.7 (±4.2)	0.749
Water transparency (m)	0.81 (±0.35)	0.80 (±0.28)	0.967

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Zooplankton community

The zooplankton community was composed of 86 taxa, with Rotifera being the richest group in terms of number species (60 species), followed by Cladocera (18 species) and Copepoda (eight species). A greater number of zooplankton taxa were recorded in the post-impoundment phase (71 species) compared with the pre-impoundment phase (46 species). In addition, rotifers were the most specious group both before and after the formation of the reservoir (Table 2; Figure 2a). The abundance of the zooplankton community in the pre-impoundment phase was mainly driven by rotifers and immature stages of copepods (nauplii and copepodites), whereas in the post-impoundment phase, the abundance of the community was dominated mainly by cladocerans and immature stages of copepods (Figure 2b).

Table 2. Full list of zooplankton taxa sampled in the pre- and post-impoundment phases of the Caveiras River, Santa Catarina, Brazil.

Rotifera	Pre	Post	Rotifera (continued)	Pre	Post
Ascomorpha ecaudis Perty, 1850		×	Polyarthra vulgaris (Carlin, 1943)	×	×
Asplanchna sieboldii (Leydig, 1854)		×	Pompholyx triloba Pejler, 1957	×	
Brachionus angularis Gosse, 1851		×	Ptygura sp.		×
Brachionus calyciflorus Pallas, 1776	×	×	Synchaeta pectinata Ehrenberg, 1832	×	
Brachionus caudatus Barrois & Daday, 1894	×	×	Synchaeta stylata Wierzejski, 1893	×	×
Brachionus dolabratus Harring, 1914	×	×	Testudinella mucronata (Gosse, 1886)	×	
Brachionus falcatus Zacharias, 1898	×	×	Testudinella patina (Hermann, 1783)		×
Brachionus forficula Wierzejski, 1891		×	Trichocerca bicristata (Gosse, 1887)		×
Cephalodella gibba (Ehrenberg, 1830)	×		Trichocerca bidens (Lucks, 1912)		×
Cephalodella sp.	×	×	Trichocerca cylindrica (Imhof, 1891)	×	
Collotheca sp.		×	Trichocerca insignis (Herrick, 1885)	×	
Colurella sp.	×		Trichocerca similis (Wierzejski, 1893)		×
Conochilus coenobasis (Skorikow, 1914)	×	×	Trichocerca sp.	×	×
Conochilus dossuarius Hudson, 1885		×	Trichotria tetractis (Ehrenberg, 1830)	×	×
Conochilus unicornis Rousselet, 1892	×	×	Cladocera		
Dipleuchlanis propatula (Gosse, 1886)	×	×	Acroperus tupinamba Sinev & Elmoor-Loureiro, 2010	×	×
Dissotrocha sp.		×	Alonella dadayi Birge, 1910	×	×
Epiphanes sp.	×		Bosmina cf. freyi De Melo & Hebert, 1994	×	×
Euchlanis dilatata Ehrenberg, 1832	×	×	Bosmina hagmanni Stingelin, 1904	×	×
Filinia longiseta (Ehrenberg, 1834)	×	×	Bosminopsis deitersi Richard, 1895	×	×
Filinia opoliensis (Zacharias, 1898)		×	Ceriodaphnia cornuta Sars, 1886	×	×
Filinia terminalis (Plate, 1886)	×	×	Ceriodaphnia silvestrii Dadayi, 1902		×
Hexarthra mira (Hudson, 1871)		×	Chydorus eurynotus Sars, 1901		×
Kellicottia bostoniensis (Rousselet, 1908)	×	×	Coronatella cf. poppei (Richard, 1897)	×	×
Keratella americana Carlin, 1943	×	×	Daphnia laevis Birge, 1878		×
Keratella cochlearis (Gosse, 1851)	×	×	Diaphanosoma spinulosum Herbst, 1975		×
Keratella tropica (Apstein, 1907)	×	×	Euryalona orientalis (Daday, 1898)		×
Lecane aculeata (Jakubski, 1912)		×	Ilyocryptus spinifer Herrick, 1882		×
Lecane bulla (Gosse, 1851)	×	×	Leydigiopsis sp.	×	
Lecane cornuta (Müller, 1786)	×		Magnospina dentifera (Sars, 1901)	×	
Lecane ludwigii (Eckstein, 1883)	×		Moina minuta Hansen, 1899	×	×
Lecane luna (Müller, 1776)		×	Ovalona glabra (Sars, 1901)		×
Lecane lunaris (Ehrenberg, 1832)		×	Simocephalus vetulus (Müller, 1776)		×
Lecane quadridentata (Ehrenberg, 1830)		×	Copepoda		
Lecane sp.	×		Nauplii Cyclopoida	×	×
Lecane stenroosi (Meissner, 1908)		×	Nauplii Calanoida		×
Lepadella cristata (Rousselet, 1893)		×	Copepodit Cyclopoida	×	×
Lepadella ovalis (Müller, 1786)	×		Copepodit Cycloponda Copepodit Calanoida		×
Macrochaetus collinsi (Gosse, 1867)		×	Acanthocyclops robustus (Sars, 1863)		×
Mytilina mucronata (Müller, 1773)		×	Acuminocyclops robustus (sais, 1805) Argyrodiaptomus sp.		×
Notommata copeus Ehrenberg, 1834	×	•	Mesocyclops aspericornis (Daday, 1906)		×
Notommata sp.	×		Mesocyclops meridianus (Kiefer, 1926)		×
Plationus patulus (Müller, 1786)	^	×	Mesocyclops mendianus (Kielel, 1926) Mesocyclops sp.		×
Platyias quadricornis (Ehrenber, 1832)	×	×	Notodiaptomus sp.		×
Platylas quadricornis (Efficience, 1832) Ploesoma hudsoni (Imhof, 1891)	^	×	Thermocyclops decipiens (Kiefer, 1929)		×
Polyarthra dolichoptera Idelson, 1925		×	Thermocyclops minutus (Lowndes, 1934)		×

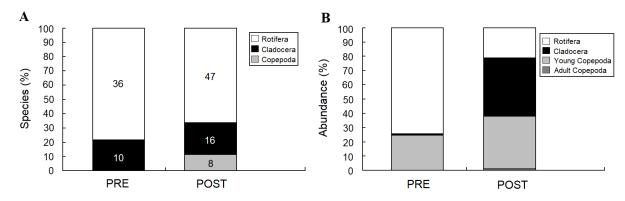


Figure 2. Proportion (%) of the number of species (A) and the abundance (B) of rotifers, cladocerans and copepods in the pre- and post-impoundment phases of the Caveiras River, Santa Catarina, Brazil.

In general, no spatial heterogeneity was observed for the attributes of species richness and abundance of zooplankton during the pre- and post-impoundment phases of the Caveiras River (ANOVA; p > 0.05) (Figure 3). However, significant changes were observed in the attributes of the community between the pre- and post-impoundment phases. There was an increase in the species richness of zooplankton (ANOVA; total, p < 0.001; Rotifera, p = 0.009; Cladocera, p < 0.001; Copepoda, p < 0.001) after reservoir formation (Figure 3a and 3c). In turn, the abundance also significantly increased after the river impoundment (ANOVA; Total, p < 0.001; Rotifera, p = 0.041; Cladocera, p < 0.001; Copepoda, p < 0.001) (Figure 3b and 3d).

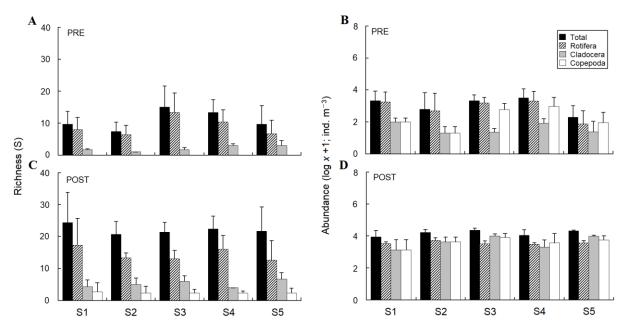


Figure 3. Spatial variation of the mean values (bars = standard error) of species richness (A and C) and abundance (B and D) of total zooplankton, rotifers, cladocerans and copepods in the pre- and post-impoundment phases of the Caveiras River, Santa Catarina, Brazil.

Ordination of the zooplankton community

The NMDS ordination summarized the structure of the zooplankton community and separated the preand post-impoundment phases of the Caveiras River. The ANOSIM results also showed that the structure of the zooplankton community was significantly different between these two phases (Figure 4a). According to the SIMPER test, the species that contributed to 48.7% of the differences in the composition between the phases were: the rotifers *Keratella americana*, *K. cochlearis*, *Conochilus coenobasis*, *Kellicottia bostoniensis*, *Asplanchna sieboldii*, *Polyarthra vulgaris*, *Synchaeta stylata*, and *Filinia terminalis*; the cladocerans *Bosminopsis deitersi*, *Bosmina hagmanni*, and *Ceriodaphnia silvestrii*; and the copepods *Thermocyclops decipiens* and immature stages (nauplii and copepodites) of Calanoida.

According to the CCA, the abundance of zooplankton was correlated with environmental variables as well as with the environment (Permutest, p = 0.001). Furthermore, the analysis results illustrated that the

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environmental variables influenced 74.2% of the variation in the zooplankton abundance. The significant correlations for the pre-impoundment phase are as follows: *K. americana*, *K. cochlearis*, *F. terminalis*, and *P. vulgaris* were positively correlated with electrical conductivity; *K. bostoniensis* and Cyclopoid nauplii were positively correlated with dissolved oxygen and total suspended solids. In turn, the correlations for the post-impoundment phase were as follows: *A. sieboldii*, *B. deitersi*, *C. coenobasis*, and immature (nauplii and copepodites) Calanoida were positively correlated with the concentrations of chlorophyll *a* and total phosphorus; *B. hagmanni*, *C. silvestrii*, *S. stylata*, and *T. decipiens* were negatively correlated with electrical conductivity (Figure 4b).

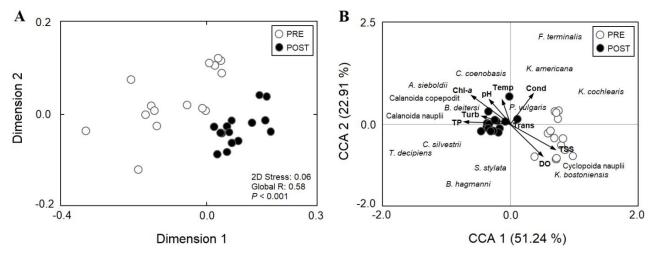


Figure 4. Non-metric multidimensional scaling (NMDS) based on zooplankton species composition (A) and canonical correspondence analysis (CCA) ordering diagram of zooplankton taxa and environments (B) in the pre- and post-impoundment phases of the Caveiras River, Santa Catarina, Brazil. Abbreviations of environmental variables: Chl-*a* = chlorophyll *a*, Cond = electrical conductivity, TP = total phosphorus, DO = dissolved oxygen, TSS = total suspended solids, Temp = water temperature, Trans = water transparency, and Turb = turbidity.

Discussion

Before and after the formation of the João Borges Reservoir, spatial heterogeneity was not observed for the different limnological variables of the Caveiras River. This fact may be linked to the formation of a low longitudinal gradient after the impoundment of the river. In general, the formation of longitudinal gradients is not as clear in run-of-river reservoirs when compared to storage reservoirs. In run-of-river reservoirs, modifications due to the entry of tributaries are minimal and are associated with the semi-lotic conditions of these systems, such as the greater speed of water flow and the lower depth (Nogueira, Perbiche-Neves, & Naliato, 2012; Picapedra, Fernandes, Taborda, Baumgartner, & Sanches, 2020). However, after the formation of the reservoir, there were significant changes in the water quality, such as a decrease in the concentration of total suspended solids and an increase in the concentrations of chlorophyll a and total phosphorus. Probably, the decrease in the flow speed and the increase in the water retention time with the impoundment provided greater sedimentation of the suspended solids. In turn, the increase in the total phosphorus was related to the increased decomposition of the flooded organic matter, which occurs mainly in the first months after the formation of a reservoir (Mendonça et al., 2012). Consequently, the greater availability of nutrients favored the greater productivity of phytoplankton, as indicated by the concentrations of chlorophyll a.

Regarding zooplankton, rotifers contributed the most to the total richness both before and after the formation of the reservoir. The high diversity of rotifers in reservoirs has been a recurring pattern in Brazil (Lansac-Tôha, Bonecker, & Velho, 2005; Takahashi et al., 2009; Serafim-Júnior, Lansac-Tôha, & Perbiche-Neves, 2016). This fact is linked to the great versatility of rotifers in inhabiting different environments, such as a newly formed reservoir, and to the opportunistic characteristics of these organisms, such as great food plasticity, high reproductive rates, asexual reproduction, and the production of resistant eggs (Allan, 1976; Lansac-Tôha et al., 2009). Regarding density, rotifers were more abundant before the formation of the reservoir, while microcrustaceans were more abundant after. This fact can be explained by the decrease in the river turbulence after the operation of the dam, resulting in less suspension of organic and inorganic particles in the water, which generally causes mechanical disturbances in the filtering appendages of microcrustaceans, such as obstruction and/or clogging, reducing the feeding and growth rates of these organisms (Claps,

Gabellone, & Benítez, 2011). Some authors (Thorp & Mantovani, 2005; Sluss, Cobbs, & Thorp, 2008) associated the increase in the abundance and growth rate of microcrustaceans with the decrease in turbulence. In general, high turbulence favors species of rotifers, which have a short generation time and preferentially feed on suspended particles (Sluss et al., 2008; Zhou et al., 2009). In addition, the greater abundance of immature stages of copepods (nauplii and copepodites) compared to adults in this study indicates an adaptive strategy to compensate for the high mortality of these phases before they become adults (De-Carli, Albuquerque, Moschini-Carlos, & Pompêo, 2018).

The homogeneity in the spatial distribution of species richness and zooplankton abundance, both before and after the formation of the reservoir, can be explained by the high export rates of organisms between environments and the great capacity for the natural dispersion of zooplankton (Perbiche-Neves & Nogueira, 2013). In addition, the low flow variability between the environments may have helped to promote the absence of a gradient between environments. In turn, filling the reservoir led to an increase in the species richness and abundance of zooplankton, both in environments located upstream and downstream of the dam. The increase in these attributes can be explained by the new physical characteristics of the environment, such as the reduction in water velocity, which can favor these organisms, especially filtering species (Rocha, Tundisi, Espíndola, Roche, & Rietzler, 1999).

According to NMDS, the species composition of zooplankton changed in the post-impoundment phase, being a mix of non-planktonic and planktonic species. The presence of non-planktonic species in the reservoir can be explained by the incorporation of organisms from other compartments (e.g., benthic and littoral areas) or environments located upstream of the reservoir (e.g., tributaries) (Zhou et al., 2008). Similar results were observed by Pedrozo, Schnek, Schwarzbold, and Farias (2012) in the Dona Francisa Reservoir, Jacuí River, highlighting the significant contribution of non-planktonic species at the beginning of reservoir formation. The changes in the zooplankton composition coincided with expected changes in the total concentrations of suspended solids, phosphorus, and chlorophyll a. According to the CCA, most species of zooplankton that occurred in the pre-impoundment phase appeared to be tolerant of the river's unstable hydrological conditions, such as the rotifers Kellicottia bostoniensis, Keratella americana, and K. cochlearis, which mainly feed on suspended particles (Serafim-Júnior, Perbiche-Neves, Brito, Ghidini, & Casanova, 2010; De-Carli et al., 2018). Often, the consumption of suspended particles is more important for zooplankton than the consumption of live biomass. In addition, organic compounds and/or bacteria that are an adequate source of nutrients can adhere to the surface of suspended particles (Lind & Davalos-Lind, 1991). Contrarily, the increase in phosphorus after the river was dammed led to an increase in the primary productivity of the phytoplankton. Consequently, it favored the appearance of microcrustaceans in the zooplankton, such as calanoid copepods and cladocerans (e.g., Bosminopsis deitersi and Bosmina hagmanni), which often consume these algae and are favored by the recently established lentic conditions (Pedrozo et al., 2012).

Conclusion

The analysis of the results obtained in this study allowed us to conclude that even a small run-of-the-river dam has a significant effect on the riverside zooplankton community. The impact of the dam on the attributes of the zooplankton community was observed in the dammed stretch as well as downstream. After the construction of the dam, a rapid increase in the number of species and the abundance of zooplankton was observed. In addition, important changes in the composition of zooplankton were observed, with the appearance of typically planktonic species. This fact was related to the decrease in the flow speed, longer water retention times, and an increase in food availability after the impoundment of the river. Thus, these observations support the use of zooplankton as a useful tool for understanding environmental changes in freshwater ecosystems.

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