

## Zooplankton communities show contrasting productivity variables thresholds in dammed and undammed systems

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### ABSTRACT

#### Zooplankton communities show contrasting productivity variables thresholds in dammed and undammed systems

Reservoir construction is one of the main threats to large rivers because they alter various ecological aspects downstream of the dam such as hydrodynamics and the concentration of productivity variables. In this context, our study aimed to i) compare zooplankton community responses (composition) to the concentration of productivity variables (chlorophyll *a*, phosphate and nitrate concentrations) in dammed and undammed systems, ii) indicate which concentrations of the productivity variables represent thresholds for changes in the community and iii) verify if the body sizes of the species with greater magnitudes of environmental community change are different between these systems. Samples were collected in six habitats of the upper Paraná River floodplain between 2000 and 2015. We tested for variation in the abundance and frequency of the zooplankton community in both systems using a TITAN analysis. We registered 256 taxa in the undammed system and 239 in the dammed system. A PERMANOVA analysis showed that the composition of zooplankton species differed significantly ( $p = 0.001$ ) among the studied systems. The TITAN analysis identified significant positive and negative thresholds for phosphate and nitrate in higher concentrations in the unpreserved system, contrary to what was found for chlorophyll *a*. According to the size spectrum, smaller species are indicators of thresholds in the undammed system. In general, our results indicate that productivity variables differentially affect the frequency and abundance of the community according to the type of system evaluated.

**Key words:** oligotrophication, rivers, zooplankton, flood Plain

### RESUMO

#### Comunidades zooplancônicas mostram limiares de variáveis de produtividade contrastantes em sistemas barrados e não-barrados

A construção de reservatórios é uma das principais ameaças em rios de grande ordem, uma vez altera inúmeros aspectos ecológicos a jusante das barragens, como a hidrodinâmica e a concentrações das variáveis de produtividade. Nesse contexto, nosso estudo teve como objetivos i) comparar a resposta da comunidade zooplancônica (composição) em função da concentração das variáveis de produtividade em um sistema barrado e um não barrado, ii) apontar em quais concentrações das variáveis de produtividade ocorre o ponto de mudança da comunidade nesses sistemas e ainda, iii) verificar se o tamanho corporal das espécies com maior potencial de indicação de mudança da comunidade são distintos nesses sistemas. As amostragens foram realizadas em seis ambientes da planície de inundação do alto rio Paraná, entre os anos de 2000 e 2015. A variação da abundância e frequência da comunidade de zooplancônica entre os sistemas foi testada através da análise

*TITAN*. Foram registrados 256 táxons para o sistema não barrado e 239 para o barrado. A análise PERMANOVA indicou que a composição de espécies diferiu significativamente ( $p = 0.001$ ) entre os sistemas. Com exceção da clorofila-*a* a *TITAN* identificou que os pontos de mudança positivos e negativos significativos de fosfato e nitrato foram registrados em maiores concentrações no sistema não barrado. De acordo com o espectro de tamanho, foram observadas espécies menores como indicadoras de mudança no sistema não barrado. Em geral, os resultados indicam que as variáveis de produtividade afetam de maneira distinta a frequência e a abundância da comunidade de acordo com o tipo de sistema avaliado.

**Palavras chave:** oligotrofização, rios, zooplâncton, planície de inundação

## INTRODUCTION

Anthropic impacts constantly threaten the ecological integrity of aquatic ecosystems (Dudgeon *et al.*, 2003). Reservoir construction is considered one of the main impacts on large rivers (Agostinho *et al.*, 2008). These systems, mainly when they are disposed in cascades, affect various ecological aspects downstream of the dams through a reduction in suspended solid transportation, an increase in water transparency and a decrease in the concentration of productivity variables (i.e. nutrients and algal biomass) (Ney, 1996; Agostinho *et al.*, 1995). Consequently, all aquatic organisms are also affected (Matsumura-Tundisi *et al.*, 1986; Ortega-Mayagoitia *et al.*, 2011; Onandia *et al.*, 2014).

Studies on aquatic ecosystems have demonstrated that variations in species numbers are driven by productivity (Schmid, 2002; Cardinale *et al.*, 2009), especially in relation to the concentrations of the productivity variables chlorophyll *a*, phosphate and nitrate (Pagioro *et al.*, 2005; Esteves *et al.*, 2011). Thus, productivity variables act as environmental filters (Arrieira *et al.*, 2015) by selecting only the most suitable species to survive in environments with certain concentrations of these variables (Armynot du Châtelet *et al.*, 2004; Cardinale *et al.*, 2009). In this sense, a group of species can be used to indicate the range of environmental variation that supports these organisms (Simões *et al.*, 2012), and can therefore serve as tools for environmental management activities (Palmer *et al.*, 2013)

Besides the number of species, aquatic organisms also respond to changes in productivity through their body size spectrum (Masson *et al.*, 2004; Havens *et al.*, 2015). In less productive environments, organisms allocate energy to their

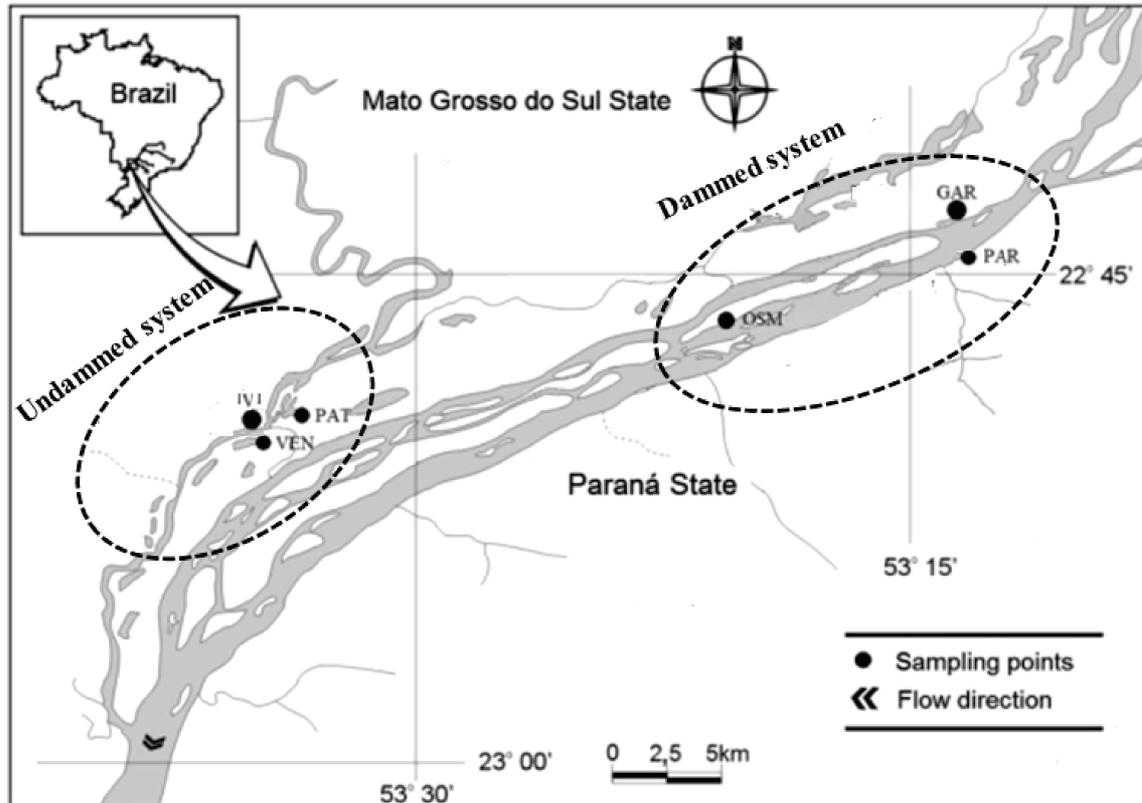
own body development and increase in size instead of investing in offspring that have little or no chance of survival (Havens, 1998). Therefore, body size is an attribute that can be used as an indicator of the importance of productivity variables in the bioenergetic relationships between aquatic organisms (Sorf *et al.*, 2015).

The zooplankton community, which is mainly comprised of rotifers, cladocerans and copepods, is influenced by variations in productivity (Schwind *et al.*, 2017; Braghin *et al.*, 2016). Once predated, the energy present in these producers is transferred to higher trophic levels (Lemke & Benke, 2009). Furthermore, due to their short life cycle and high reproductive efficiency, zooplankton species are considered excellent bioindicators in aquatic ecosystems. They are able to indicate changes in the productivity of the ecosystem (Wojciechowski *et al.*, 2017) through changes in their frequency, abundance (Schwind *et al.*, 2017) and body size (Bonecker *et al.*, 2011).

Considering the importance of productivity variables (chlorophyll *a*, nitrate and phosphate) for aquatic communities, this study aimed to i) compare the response of the zooplankton community (composition) of dammed and undammed systems, ii) indicate which concentrations of the productivity variables represent thresholds for changes in the community in each system and iii) verify if the body size of indicator species to changes in productivity variables is different between these systems.

## MATERIAL AND METHODS

The study was performed in the floodplain environments of the Upper Paraná River (22° 400 – 22° 500 S; 53° 100 – 53° 240 W). This floodplain is located downstream (230 Km) of the reservoir



**Figure 1.** Map presenting the location of the sampling stations in the upper Paraná River floodplain in the undammed system (IVI = Ivinhema river; PAT = Patos lake; VEN = Ventura lake) and dammed (PAR = Paraná river; GAR = Garças lake; OSM = Osmar lake). *Mapa apresentando a localização das estações de amostragem na planície de inundação do alto rio Paraná no sistema não represado (IVI = rio Ivinhema; PAT = lagoa dos Patos; VEN = lagoa Ventura) e represado (PAR = rio Paraná; GAR = lagoa Garças; OSM = lagoa Osmar).*

of Porto Primavera (State of São Paulo) and the upstream Itaipu (State of Paraná), both of which are located on the Paraná River, which is the main river of this ecosystem and is largely regulated by a series of upstream dams. The sampling point of the Paraná River is located downstream from the reservoir of Porto Primavera while the river Ivinhema is located in the legally protected area belonging to Ivinhema State Park. The systems evaluated in this study was Paraná system (dammed) (Paraná river, Osmar Lake and Garças Lake) and Ivinhema (undammed) (Ivinhema river, Patos Lake and Ventura lake) (see Table S1, <http://www.limnetica.net/en/limnetica>). Both affect the floodplain dynamics through their hydrology and cause floods in December and March. The Ivinhema River has a mean flow

velocity of 0.85 m/s, whereas in the Paraná River, the mean flow velocity changed from 0.88 to 0.60 m/s after damming (Rodrigues *et al.*, 2009). Additionally, the Ivinhema River, which is free of dams, is considered the main tributary on the right side of the Paraná River (Braghin *et al.*, 2015) (Fig. 1).

### Sampling design

Three environments with different degrees of connection (river, one permanently connected lake and one lake isolated from the river) were selected in one dammed and three undammed systems (Table S1). Although the environments are hydrologically distinct, we aimed to evaluate heterogeneous communities, with a gradient of

species abundance and frequency. The zooplankton community was always sampled in the morning in the limnetic region at a depth of 0.5–1.5 m four times a year in two different hydrological periods (March and December, which are flood periods and June and September, which are dry periods) between 2000 and 2015. For each sample, 600 L of water were filtered using a motor pump (200 L/s) and plankton net of 68  $\mu\text{m}$  mesh size. The samples were preserved in a 4 % formaldehyde solution buffered with calcium carbonate in 100 ml glass bottles.

Species of rotifers, cladocerans and copepods were identified based on specialized literature (Koste, 1978; Sendacz & Kubo, 1982; Segers, 1995; Elmoor-Loureiro, 1997). The abundance of individuals was estimated by analysing a minimum of three subsamples (Bottrell *et al.*, 1976) in a Sedgewick-Rafter chamber using an optical microscope Bottrell *et al.* (1976).

At the same time that the zooplankton was sampled, we collected 5 L of water at the subsurface of the limnetic region with a van Dorn bottle to measure the concentration of chlorophyll *a*, phosphate ( $\text{PO}_4$   $\mu\text{g/L}$ ) and nitrate ( $\text{NO}_3$   $\mu\text{g/L}$ ) in each sample from The phosphate and nitrate was measured in dissolved (filtered water). The N-nitrate ( $\mu\text{g/L}$ ) analysis was performed using the flow injection method (Giné *et al.*, 1980), following the same procedure that converts nitrate to nitrite (used for total nitrogen). The chlorophyll *a* concentration was determined by filtering aliquots of water in glass fibre filters (Whatman GF / F), extracting the pigments with 90 % acetone and reading a spectrophotometer (663 and 775 nanometers), and was processed according to the methodology presented by Golterman *et al.* (1969). Calculations were performed according to the formula described in Wetzel & Likens (1991).

Body size of the zooplankton species was obtained using an optic microscope with a precision of 10  $\mu\text{m}$ . These measurements were obtained for the species of each environment and system and were then averaged to capture all variation in the body size of zooplankton species. For the rotifers and cladocerans, body size was estimated as the distance between the superior extreme of the head (without elm and spines) and the end of the carapace (Hardy, 1989). For cope-

**Table 1.** Classification of body size of zooplankton species categorized according to an adaptation of Bonecker *et al.*, (2011). *Classificação do tamanho corporal de espécies zooplanctônicas categorizadas de acordo com a adaptação de Bonecker et al., (2011).*

Rotifera	Cladocera	Copepoda	Body size
0-200	0-400	<880	Small
201-300	401-600	881-1430	Medium
> 300	> 601	> 1431	Large

pods, we used the distance between the head and the last abdominal segment (Azevedo *et al.*, 2012). Finally, indicator species were categorized according to the minimum and maximum values found for all rotifers, cladocerans and copepods in the analysed samples (Table 1).

### Data analysis

To test whether the composition of the zooplankton communities differed significantly between the systems studied (dammed and undammed), we performed a multivariate analysis of permutational variance (PERMANOVA). For this analysis, a dissimilarity matrix was calculated from the Jaccard method. The PERMANOVA was implemented using R 3.4 software (R Development Core Team, 2017) using the ADONIS command of the Vegan package (Oksanen *et al.*, 2018).

We used a Threshold Indicator Rate Analysis (TITAN) to evaluate the frequency and abundance of zooplankton in the community along the productivity gradient (phosphate, nitrate and chlorophyll *a*) for the undammed and dammed environments (Baker & King, 2010). This statistical analysis was performed using the "mvpart" package (De'ath, 2014) of the R Software (R Core Team, 2017).

TITAN allowed us to identify the limits or points of change for each taxon and for the whole community along the environmental gradient and detected changes in the distributions of the species. This analysis uses the value IndVal (Value Indicator) to identify these points of change. When the value obtained by IndVal is less than 0.05 and values of purity and reliability

are greater than 0.95 a species is considered significantly associated with a positive (z+) or negative (z-) response. To determine the significant indicator taxa with high precision, the data were permuted by means of 500 randomizations, and  $IndVal < 0.05$  were retained.

**RESULTS**

We identified 297 species, including 201 rotifers, 66 cladocerans and 30 copepods. The undammed system had the highest number of taxa (256), of which 171 were rotifers, 62 were cladocerans and 23 were copepods. We recorded 239 taxa in the dammed system, of which 162 were rotifers, 46 were cladocerans and 28 were copepods (Table S2, available at <http://www.limnetica.net/en/limnetica>). In addition, the PERMANOVA showed that the composition of zooplankton species differed significantly ( $p = 0.001$ ) among the systems studied.

During the whole study period, both the dammed and the undammed systems presented a large variation in the environmental variables related to productivity. According to the coefficients of variation, the chlorophyll *a* concentration showed the highest variation, followed by phosphate and nitrate (Table 2).

TITAN identified significant thresholds ( $p < 0.05$ ) in response to the frequency and abundance

of the zooplankton community to chlorophyll *a* in both systems (Table 3). The negative (z-) and positive thresholds (z+) were identified at higher chlorophyll *a* concentrations in the dammed (1.01 µg/L; 4.69 µg/L) than in the undammed system (0.54 µg/L; 2.65 µg/L) (Table 3). Furthermore, 109 taxa were registered as indicators of change in the zooplankton community in the undammed system (Fig. 2b) and 110 in the dammed system (Fig. 2d) with significant values for the chlorophyll *a* gradient ( $p < 0.05$ ).

The majority of the taxa in the community showed a positive response (z+) to chlorophyll *a* concentration in both the undammed (79 taxa) and in the dammed systems (98 taxa). The taxa with higher magnitudes of positive responses (z+) in the undammed system were *Chydorus eurynotus*, *Cephalodella gibba*, *Brachionus mirus*, *Alonella dadayi* and *Euchlanis dilatata* (Fig. 2b), and in the dammed system were *Diaphanosoma brevireme*, *Dipleuchlanis propatula* and *Notomata copeus* (Fig. 2d). The abundance and frequency of taxa indicators with positive responses (z+) started to grow in the undammed system in concentrations of 0.2 µg/L until 0.6 µg/L, at which point there was a rapid decline, and a subsequent increase until 42 µg/L (Fig. 2a). Also, in the dammed river there was a slow decrease between concentrations of 0.1 µg/L and 100 µg/L.

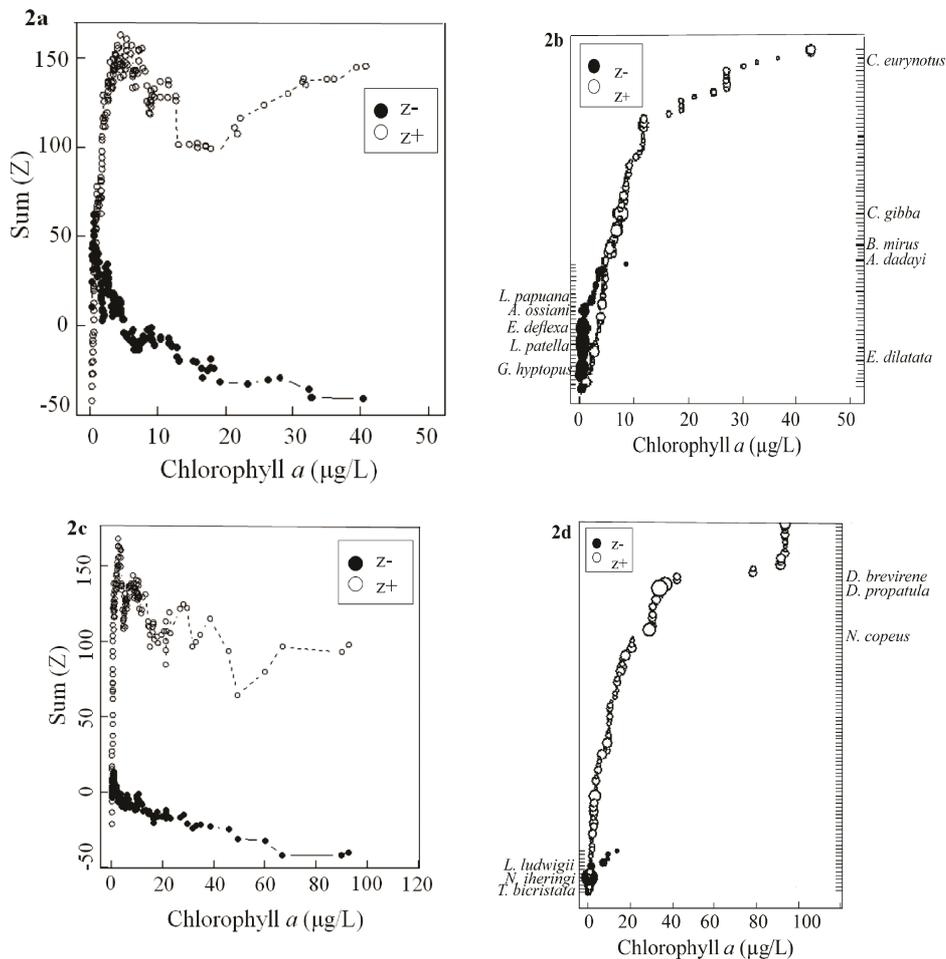
**Table 2.** Mean values and coefficient of variation (CV %) of the environmental variables in the undammed (IVI = Ivinhema river, PAT = Patos lake, VEN = Ventura lake) and dammed (PAR = Paraná river, GAR = Garças lake, OSM = Osmar lake) system during the study period. *Valores médios e coeficiente de variação (CV %) das variáveis ambientais no sistema não barrado (IVI = rio Ivinhema, PAT = lagoa dos Patos, VEN = lagoa Ventura) e barrado (PAR = rio Paraná, GAR = lagoa das Garças, OSM = lagoa Osmar) represado durante o período do estudo.*

	Undammed						Dammed					
	IVI		PAT		VEN		PAR		GAR		OSM	
	CV%	Mean	CV%	Mean	CV%	Mean	CV%	Mean	CV%	Mean	CV%	Mean
<b>Chlorophyll <i>a</i></b>	144.1	1.5	103.8	8.3	121.8	10.3	165.8	1.6	129.1	10.7	180.2	29.6
<b>Phosphate</b>	16.5	42.8	60.2	10.1	17.1	89.5	142.3	4.9	131.7	53.3	120.4	18.69
<b>Nitrate</b>	51.1	106.5	144.8	22.4	159.1	89.1	352.6	160.3	122.4	6.9	196.3	30.1

A negative response (z-) to chlorophyll *a* concentration was observed for 30 taxa in the undammed system and for 12 taxa in the dammed system along the environmental gradient. The taxa with higher magnitudes of negative responses in the undammed system were *Lecane papuana*, *Alona ossiani*, *E. deflexa*, *Lepadella patella* and *Gastropus hyptopus* (Fig.2b), and in the dammed system were *Lecane ludwigii*, *Notodiptomus iheringi* and *Trichocerca bicristata* (Fig.

2d). In the undammed system, the abundance and frequency of taxa indicators with negative responses (z-) initially presented an increase until 6.0 µg/L (Fig. 2a), from which there was a rapid decline until 19 µg/L, and again an increase until 40 µg/L. On the other hand, in the undammed system, we observed an expressive decline from 0.1 µg/L until 40 and 96 µg/L (Fig. 2a).

TITAN identified significant thresholds in the frequency and abundance of the zooplankton



**Figure 2.** TITAN results in response to changes in zooplankton frequency and abundance along the gradient of chlorophyll *a* concentration in the undammed (2a) dammed (2c) systems. The negative (z-) and positive (z+) indicator taxa (white circles) suggest a negative and positive response to increasing concentrations of chlorophyll *a* (black circles), respectively to the undammed (2b) and dammed (2d). *Resultados da TITAN em resposta às mudanças na frequência e abundância do zooplâncton ao longo do gradiente de concentração de clorofila-a no sistema não barrado (2a) e barrado (2c). Os táxons indicadores negativos (z-) (círculos pretos) e positivos (z+) (círculos brancos) sugerem resposta negativa e positiva ao aumento das concentrações de clorofila-a (círculos pretos), respectivamente ao sistema não barrado (2b) e barrado (2d).*

**Table 3.** TITAN results for the zooplankton community in response to chlorophyll-*a*, phosphate and nitrate concentration in the dammed and undammed system. Obs. = Observed change point; 5 % and 95 % = quartiles thresholds. Direction of the response given by z- (negative) and z+ (positive). *Resultados da TITAN para a comunidade zooplanctônica em resposta à concentração de clorofila a, fosfato e nitrato no sistema barrado e não-barrado. Obs. = Ponto de mudança observado; 5 % e 95 % = limiares de quartis. Direção da resposta dada por z- (negativo) e z+ (positivo).*

	Environmental variables	Method	Change point		
			Obs.	5%	95%
Undammed	Chlorophyll <i>a</i>	z-	0.54	0.32	3.64
		z+	4.69	3.27	17.51
	Phosphate	z-	12.9	4.07	13.82
		z+	39.7	12.8	39.7
	Nitrate	z-	91.8	5.25	115.8
		z+	234.2	68.05	223.6
Dammed	Chlorophyll <i>a</i>	z-	1.01	0.34	9.15
		z+	2.65	2.35	42.1
	Phosphate	z-	3.76	2.38	5.29
		z+	12.1	5.29	22.9
	Nitrate	z-	4.5	4.21	61.2

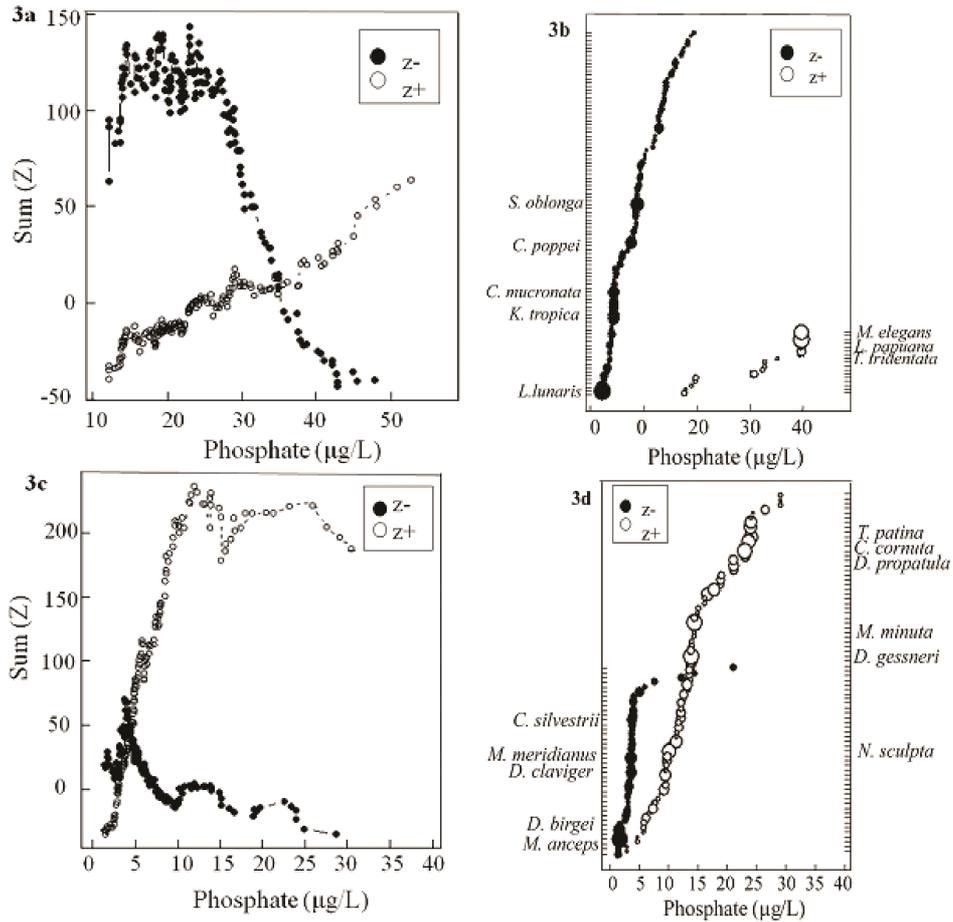
community in response to phosphate concentration along the environmental gradient in both systems. Negative (z-) and positive (z+) thresholds were registered at higher concentrations in the undammed (12.9 µg/L and 39.7 µg/L) than in the dammed system (3.76 µg/L and 12.1 µg/L) (Table 3). Furthermore, 113 taxa were considered indicators of community change in the undammed system, and 116 in the dammed system, with significant values for the environmental gradient related to phosphate concentration ( $p < 0.05$ ).

In total, 17 taxa showed a positive response to phosphate concentration in the undammed system and 76 in the dammed system. In the undammed system, the taxa with highest magnitudes of positive responses were *Macrothrix elegans*, *Lecane papuana* and *Testudinella tridentata* (Fig. 3b) and in the dammed system were *Testudinella patina*, *Ceriodaphnia cornuta*, *Dipleuchlanis propatula*, *Moina minuta*, *Daphnia gessneri* and *Notoalona sculpta* (Fig. 3d). A negative response to phosphate concentration was observed for 96 taxa in the undammed system and 40 in the dammed system. Among them, in the preserved system, *Synchaeta oblonga*, *Coronatella poppei*, *Cephalodella mucronata*, *Keratella tropica* and *Lecane lunares* (Fig. 3b)

presented the highest magnitude responses, while in the dammed system, the highest magnitude responses were observed for *Mesocyclops meridianus*, *Dicranophoroides claviger*, *Diaphanosoma birgei*, *Microcyclops anceps* and *Ceriodaphnia silvestrii* (Fig. 3d).

Negative (z-) and positive (z+) thresholds were identified at higher concentrations of nitrate in the undammed system (91.8 µg/L; 4.5 µg/L) than in the dammed system (234.2 µg/L; 218.4 µg/L) (Table 3). Furthermore, 111 taxa were considered community change indicators in the preserved system and 96 in the dammed system, with significant values ( $p < 0.05$ ).

The majority of the taxa showed a negative response (z-) to nitrate concentration in the undammed (70 taxa) and dammed systems (95 taxa). Taxa with the highest magnitude negative responses in the undammed system were *Trichocerca stylata*, *Euchlanis deflexa*, *Lecane elsa*, *Ascomorpha ecaudis* and *Hexarthra mira* (Fig. 4b), while in the dammed system were *Ceriodaphnia silvestrii*, *Notodiaptomus henseni*, *Ploesoma lenticulare* and *Dipleuchlanis propatula* (Fig. 4d). In the undammed system, the frequency and abundance of taxa that were indicators of negative responses (z-) started to oscillate until a concentration of 131 µg/L, from which there was



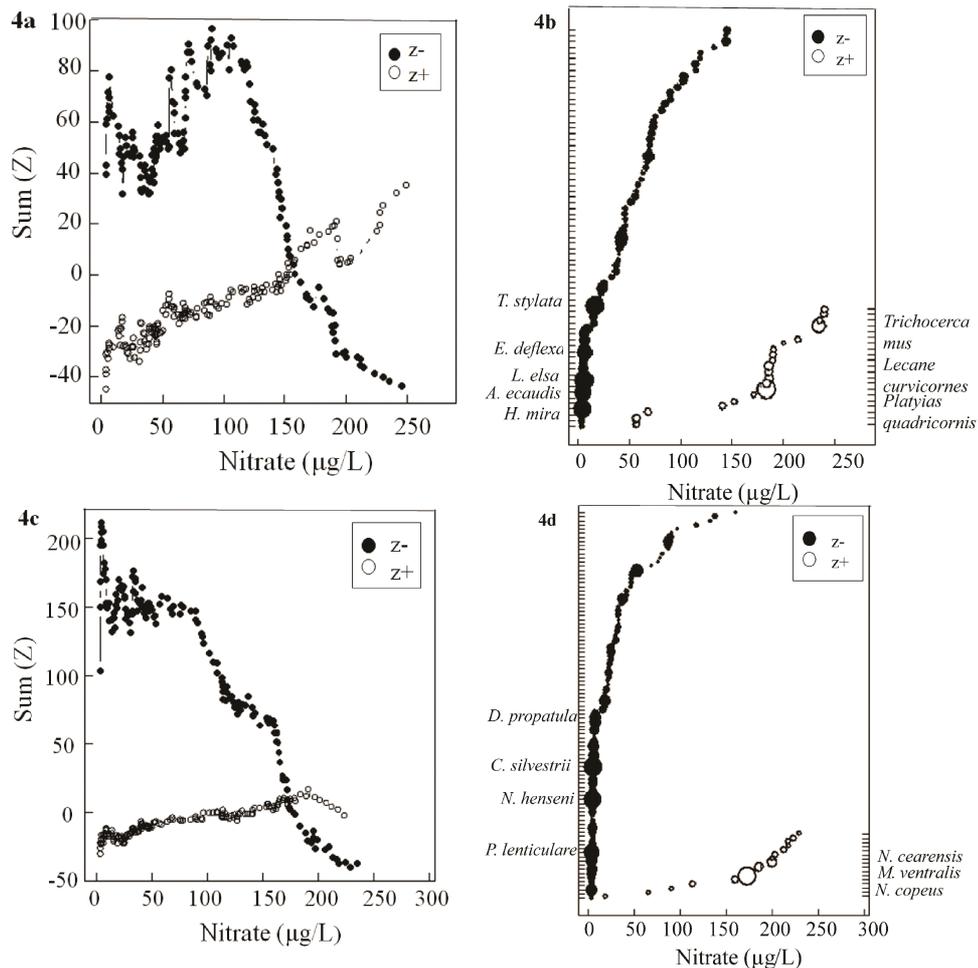
**Figure 3.** TITAN results in response to changes in the frequency and abundance of zooplankton along the gradient of the phosphate concentration in the undammed (3a) and dammed (3c) systems. The negative (z-) and positive (z+) indicator taxa (white circles) suggest a positive and negative response to the increase in phosphate concentrations (black circles), respectively to the undammed (3b) and undammed (3d). *Resultados da TITAN em resposta às mudanças na frequência e abundância do zooplâncton ao longo do gradiente ambiental da concentração de fosfato no sistema não barrado (3a) e barrado (3c). Os táxons indicadores negativos (z-) (círculos pretos) e positivos (z+) (círculos brancos) sugerem resposta negativa e positiva ao aumento das concentrações de fosfato (círculos pretos), respectivamente ao sistema não barrado (3b) e barrado (3d).*

a decrease until 232 µg/L. On the other hand, in the dammed system, the frequency and abundance oscillated until a concentration of 62 µg/L, from which there was a loss of taxa until 250 µg/L.

A positive response (z+) to nitrate concentration was registered in 21 taxa in the undammed system and in 16 taxa in the dammed system. Among them, *Trichocerca mus*, *Platyias quadricornis* and *Lecane curvicornis* (Fig. 4b) presented the highest magnitude positive responses in the undammed system and *Notodiptomus cearensis*,

*Mytilina ventralis* and *Notommata copeus* in the dammed system (Fig. 4d). In the undammed system, from a concentration of 2.0 µg/L of nitrate and up, there was a gain of taxa indicators with positive responses (z+) until 251 µg/L (Fig. 4a), while in the dammed system, this gain occurred between 2.0 µg/L and 231 µg/L (Fig. 4c).

Finally, in the undammed system the taxa with higher potential to indicate changes in the productivity variables generally had a smaller size spectrum in comparison to the largest body size



**Figure 4.** TITAN results in response to changes in the frequency and abundance of zooplankton along the environmental gradient of the nitrate concentration in the undammed (4a) and dammed (4c) systems. The negative (z-) and positive (z+) indicator taxa (white circles) suggest a positive and negative response to the increase in nitrate concentrations (black circles), respectively to the undammed (4b) and dammed (4d). *Resultados da TITAN em resposta às mudanças na frequência e abundância do zooplâncton ao longo do gradiente ambiental da concentração de nitrato no sistema não barrado (4a) e barrado (4c). Os táxons indicadores negativos (z-) (círculos pretos) e positivos (z+) (círculos brancos) sugerem resposta negativa e positiva ao aumento das concentrações de nitrato (círculos pretos), respectivamente ao sistema não barrado (4b) e barrado (4d).*

observed in the taxa found in the dammed system (Table S3, available at <http://www.limnetica.net/en/limnetica>).

## DISCUSSION

Our results provide evidence that productivity-related variables act differently on the frequency and abundance of the zooplankton community in undammed and dammed systems. In these environments, the points of change of the community

are related to higher and lower concentrations of the variables, as evidenced by the gain and loss of zooplankton species, respectively. Thus, these results suggest that changes in the concentrations of productivity variables are determinant for the occurrence of organisms in aquatic ecosystems. Still, productivity variables evidenced that species with a higher potential of indicating changes in the undammed and dammed systems were of smaller and larger size, respectively.

The significant difference in the species com-

position between the studied systems may be associated with the different physical and chemical conditions of the water caused by the reservoir cascade located downstream of the dammed system which causes changes in aquatic communities. It is known that reservoirs imply an ecological transformation upstream and downstream of these environments (Renault & Santos 2002). Studies show that less productive systems, such as dammed ones, can limit or cause a marked loss of species and generate a negative effect on the distribution of zooplankton abundance (Yachi & Loreau, 1999; Simões *et al.*, 2015). The lower concentrations of these variables negatively affect planktonic species and indicate species that are less tolerant to environments with higher productivity (Schwind *et al.*, 2017).

The frequency and abundance of the zooplankton community were related to changes in chlorophyll *a* concentration. According to Bastidas-Navarro & Modenutti (2007), variation in the concentration of this variable contributes to the availability of feeding resources and consequently to the distribution of aquatic organisms. Thus, a greater availability of resources positively favours aquatic communities by supporting a higher abundance and frequency of zooplankton organisms (Ward & Stanford, 1995; Schwind *et al.*, 2017).

Moreover, the threshold of zooplankton registered in higher concentrations of chlorophyll *a* in the dammed system may be evidence of the influence of reservoirs on the phytoplankton community. Reservoirs located upstream from habitats associated with the Upper Paraná River floodplain serve as a source of propagules from these organisms because such environments offer ideal conditions of light, nutrients and low turbulence for them to grow in abundance (Bortolini *et al.*, 2017). There is a dispersal of viable inocula from the reservoirs by means of connectivity and unidirectional flux, causing partial homogenization in environments located close together. This means that phytoplankton are carried from the reservoirs to the downstream environments such as the dammed system (Bortolini *et al.*, 2017).

In the same way, variation in the frequency and abundance of the zooplankton community in both dammed and undammed systems was

explained by phosphate and nitrate concentration. These nutrients are considered determinant factors for primary productivity and are thus involved in the impoverishment or enrichment of aquatic ecosystems (Smith *et al.*, 2006; Elser *et al.*, 2007; Mieczan *et al.*, 2009). The increase in phosphate and nitrate concentrations usually leads to a higher abundance and biomass of all the components of the pelagic trophic net, which, supports a higher number of consumer species, such as zooplankton (Berninger *et al.*, 1991; Bovo-Scomparin *et al.*, 2013).

In the undammed system, the threshold of the zooplankton community was identified in higher concentrations of phosphate and nitrate. This pattern could be related to the fact that the Ivinhema River is considered preserved since it maintains its natural flow and presents an elevated load of sediments and nutrients (Agostinho *et al.*, 2004; Roberto *et al.*, 2009). In contrast, in the dammed system the community threshold, which registered lower concentrations of these nutrients, can be justified by the effects of the construction of the Porto Primavera Dam, which is located upstream. Apart from increasing water transparency, the reservoir changed the nutrient dynamics of the habitats of the floodplain associated with the Paraná River (Roberto *et al.*, 2009). Previous studies have shown that the water of the Paraná River, which carries very low nutrient concentrations, is diluting the associated habitats during floods (Roberto *et al.*, 2009). This generates negative consequences for the maintenance of the ecological integrity of this system, as it does for the maintenance and establishment of aquatic species (Roberto *et al.*, 2009), including zooplankton (Bonecker *et al.*, 2009).

The response direction and specific attributes of each taxa aid in our comprehension of the mechanisms that determine community changes due to determinant factors as they are directly associated with the tolerances and demands of each group of organisms (Poff, 1997). Our results suggest that the species with a larger potential response to the analyzed variables differed in body size spectrum because smaller species (i.e. *Lecane curvicornis* and *Trichocerca stylata*) were mainly registered in the undammed system, and medium to large-sized species (i.e. *Diploechlanis*

*proapatula*, *Testudinella patina* and *Daphnia gessneri*) were mainly registered in the dammed system. Studies have demonstrated that there is a relationship between the body size of aquatic organisms and food availability (Jeppesen *et al.*, 2010). Habitats with high productivities generally present a higher quantity of available energetic resources (Ortega-Mayagoitia *et al.*, 2011). In less productive environments, organisms allocate energy to their own body development, thus increasing their size, rather than investing energy in offspring with little or no chance of survival (Havens, 1998). On the other hand, environments with high productivity usually present a greater amount of available energy resources (Ortega-Mayagoitia *et al.*, 2011) and favour the colonization of small planktonic organisms (Havens, 1998) that invest in growth and reproduction, which is reflected in population increase and community diversity (Allan, 1976; Dodson, 1992).

We demonstrated that the TITAN method is effective in analysing environmental variables of productivity since it allows researchers to work with the entire gradient without categorizing them and making it possible to visualize the thresholds of the zooplankton community and its main species. In addition, it allowed us determine where in these gradients the largest changes in the frequency and abundance of populations occur. Also, we observed that higher concentrations of these variables were necessary to change the community structure in undammed environments. Through these responses, knowledge of changes in the structure of indicator communities on different levels of productivity makes it possible to predict the future and dynamic state of aquatic ecosystems and thus, to serve as tools for environmental management activities in dammed rivers, helping to implement strategies for planning and conserving biodiversity.

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