

Does artificial drawdown affect zooplankton structure in shallow lakes? A short-term study in a tropical reservoir

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Received: 8 May 2016 / Revised: 24 March 2017 / Accepted: 9 April 2017 / Published online: 19 April 2017
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Abstract Water level fluctuation by artificial drawdown is one management activity that has the potential to control macrophyte growth, but there is little knowledge of how this operational procedure affects other biotic components of the ecosystem. This study investigated zooplankton dynamics in response to artificial drawdown over a short timeframe (13 days) in a Brazilian reservoir, by examining the impact on zooplankton communities in two shallow lakes (Lake Pedra Branca-LPB, and Guaritá-LG) connected to a reservoir (Salto Grande) that undergo sudden and remarkable fluctuations in their water levels. Zooplankton communities were sampled in both lakes before (pre-drawdown), during (low water), and after (post-drawdown) the artificial drawdown procedure. In LPB, drawdown resulted in an increase in zooplankton density, and temporarily changed the community in association with an increase in water conductivity and presence of non-planktonic

organisms during the low water phase. In LG, drawdown had no significant effect on zooplankton community between the phases before and during the drawdown event. The results from this study suggest that artificial drawdown over a short timeframe in reservoir systems do not negatively affect the overall density, richness, and diversity of zooplankton communities in marginal shallow lakes.

Keywords Biodiversity · Microcrustaceans · Rotifers · Regulated rivers · Remedial measures · Submerged plants

Introduction

The excessive growth of aquatic macrophytes poses a major threat to the management of many river systems around the world (Hershner & Havens, 2008; Monterroso et al., 2011). Aquatic plants can become a nuisance in highly regulated river systems where reservoirs have been constructed and the hydrology has been dramatically altered (Boschilia et al., 2012). The massive occurrence of macrophytes can result in a number of ecological, social, and/or economic impacts on river systems (Thomaz, 2002). For example, two Hydrocharitaceae species native to South America, *Egeria densa* Planch. and *Egeria najas* Planch. (Cook & Urmi-Köning, 1984), have been implicated in the clogging of hydropower intake turbines, and disrupting navigation and recreational activities in tropical

Electronic supplementary material The online version of this article (doi:10.1007/s10750-017-3193-4) contains supplementary material, which is available to authorized users.

Handling editor: Mariana Meerhoff

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reservoirs (Bini & Thomaz, 2005; Boschilia et al., 2012).

The difficulties associated with the management of aquatic macrophytes in reservoir systems have increased the need for the development and implementation of novel and specific solutions to control their growth (Thomaz, 2002). Herbicides and mechanical methods of harvesting and cutting have both been used to control macrophytes in reservoir systems (Velini et al., 2005; Richardson, 2008), but such methods often adversely affect water quality, and subsequently have negative impacts on the aquatic biota (Pieterse & Murphy, 1990; Monahan & Caffrey, 1996; Richardson, 2008). Another potential method of dealing with these challenges is through artificial water level drawdown (Thomaz, 2002; Thomaz et al., 2006; Cook et al., 2012). This involves the management of water level regimes in reservoirs during a winter season, in order to expose shore macrophytes to dehydration with the aim of decreasing their biomass (Pieterse & Murphy, 1990; Rørslett & Johansen, 1996). The dead plants are partially removed before restoration of the normal water level (Pieterse & Murphy, 1990; Rørslett & Johansen, 1996), thereby maintaining ecological values with minimal impact on the aquatic biodiversity (Thomaz, 2002; Cook et al., 2012).

The management of water level regimes by artificial drawdown often occurs much more rapidly than a natural drying event in tropical regions, and may directly affect physical processes (e.g., geomorphologic processes of erosion and sedimentation) and water quality, and in turn, negatively impact on the aquatic biota (Leira & Cantonati, 2008; Wantzen et al., 2008). The impact of water level drawdown events on aquatic macrophytes has been a topic of considerable research (Rørslett and Johansen, 1996; Thomaz et al., 2006; Boschilia et al., 2012; Ning et al., 2012); however, the effects on many other biotic components are less known. Previous studies have shown that lake level changes may affect littoral biota, such as periphyton (Hawes & Smith, 1993) and benthic macroinvertebrates (Baumgärtner et al., 2008). Unpredictable and extreme changes to water levels over a short time period can affect phytoplankton biomass and species composition by influencing both light availability (Valeriano-Riveiros et al., 2014; Da Costa et al., 2016) and nutrient dynamics (Kimmel et al.,

1990). Such water level changes may also affect zooplankton by influencing their water quality conditions (Duggan et al., 2002; Watkins et al., 2013; Perbiche-Neves et al., 2013a), competition for resources, and vulnerability to predation by fish and invertebrates during the low water phase (Havens et al., 2007). Indeed, these processes can interactively affect the taxonomic structure of zooplankton communities, with subsequent changes to species dominance and community composition (Danielsdottir et al., 2007; Deboer et al., 2016).

Artificial drawdowns are now commonly used for the management of aquatic macrophytes in many tropical reservoirs (Thomaz, 2002; Thomaz et al., 2006), and studies evaluating the success of applying these practices have warranted greater attention in recent years (Havens et al., 2007; Deboer et al., 2016). This study assessed the broader ecological implications of using an artificial drawdown over a short timeframe (13 days) to reduce the abundance and distribution of *Egeria* in a reservoir. Specifically, it examined the impact of artificial drawdown on the zooplankton communities in two shallow lakes connected to the reservoir, which undergo fluctuations in their water levels mainly caused by the operation of the dam. It focused on the response of zooplankton, since firstly they are usually the most important food source for invertebrates and juvenile fish; and secondly they respond rapidly to short-term changes in hydrology, and thus are useful indicators of the trophic status and water quality of aquatic systems (Fernando, 1994; Perbiche-Neves et al., 2013a).

The specific objective of this study was to examine temporal changes in the density, taxon richness, diversity, and structure of the zooplankton communities in the two marginal shallow lakes, by assessing changes in these attributes before drawdown (i.e., the pre-drawdown phase), during drawdown (i.e., the low water phase), and after re-filling (i.e., the post-drawdown phase). Physical and chemical characteristics of water were also assessed to examine the environmental changes in both lakes that may have been affecting the zooplankton communities during the drawdown. We predicted that the artificial drawdown over a short timeframe would cause a decrease in the density, richness, and diversity of zooplankton, and alter the community structure by causing losses as a result of advection and water quality alterations.

Materials and methods

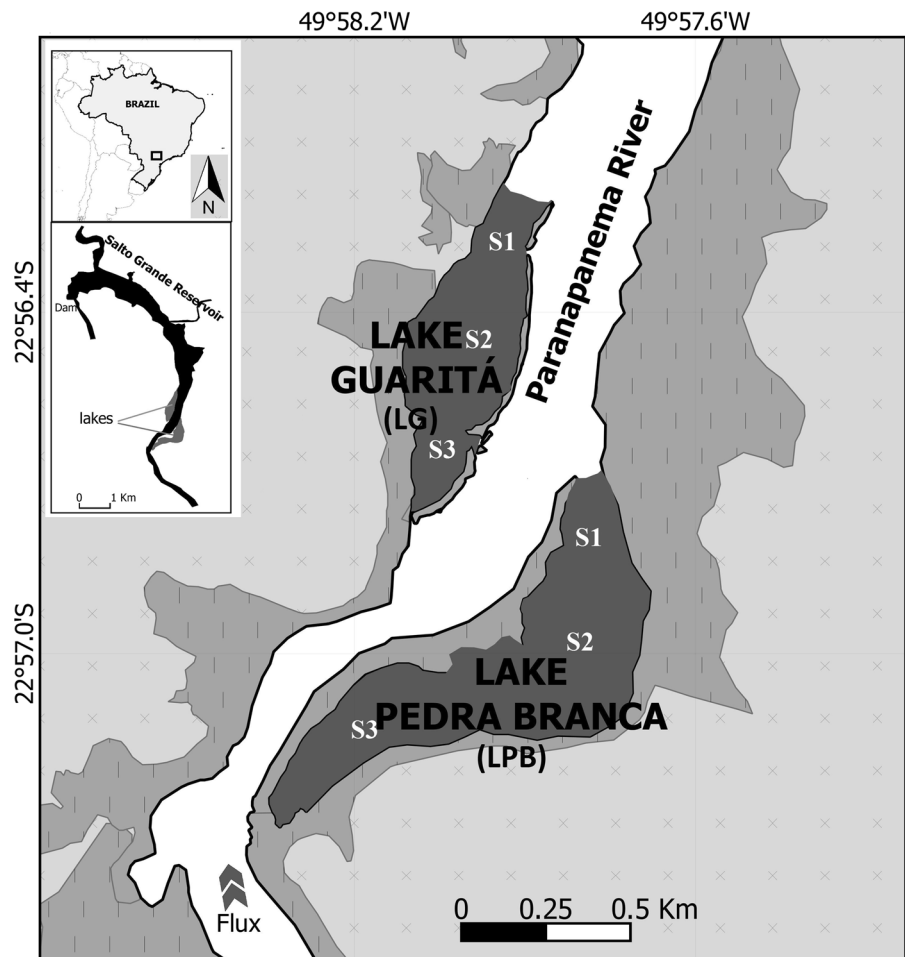
Study sites

The study was conducted in Salto Grande Reservoir watershed (Fig. 1) (22°57′S/49°57′W). The Salto Grande Reservoir is located on the Paranapanema River (southeast Brazil), and has an area of 12 km², a volume of 44.2 hm³, a mean water retention time of 1.5 days, and a mean water discharge of 395 m³ s⁻¹ (Nogueira et al., 2012). The land in the Salto Grande Reservoir watershed is intensively used for agricultural activities (corn (*Zea mays*), sugarcane (*Saccharum* spp.), soy beans (*Glycine max*)), and livestock grazing. As a consequence, the tributaries of this reservoir are highly turbid and transport considerable nutrient loads (a detailed limnological description can be found in Nogueira et al., 2012).

Two shallow lakes, connected to Salto Grande Reservoir, were selected for sampling to evaluate the effects of artificial drawdown on the zooplankton community (Fig. 1). There are only two shallow lakes connected to this reservoir, and they are strategically important for the maintenance of the regional vertebrate and invertebrate diversity in this river basin (Ferrareze & Nogueira, 2011). The first, Lake Pedra Branca (LPB), has a surface area of 0.44 km² and a mean depth of 2 m, which varies in response to the water levels in the reservoir. The second, Lake Guaritá (LG), has a surface area of 0.23 km² and a mean depth of 2.5 m, which also varies in response to the water level in the reservoir. There are dense stands of emergent aquatic macrophytes in both lakes, but they are particularly dense in LPB.

The management of water levels by artificial drawdown in the Salto Grande Reservoir is currently

Fig. 1 Geographic location of the study area showing the position of Lakes Pedra Branca (LPB) and Guaritá (LG) and Salto Grande Reservoir



being undertaken as part of a long-term management program by the hydropower energy company to mitigate the detrimental effects of the *Egeria* stands. This procedure often causes declines in the water level of the reservoir and associated declines in the water levels of the two lakes. Indeed, although the two lakes undergo climatically-driven annual fluctuations in their water levels, their water levels are still predominantly influenced by the operation of the Salto Grande Reservoir (Fig. 2a–c).

The Salto Grande Reservoir was drawn down by ~2 m over a period of 13 days, between August 21, 2011 and September 2, 2011 (Fig. 2b). Water levels in both LG and LPB changed rapidly during the drawdown (Fig. 2c), but LG still remained connected to the main channel river over the course of the drawdown event, whereas LPB became disconnected following three days of drawdown.

Zooplankton sampling and identification

Samples were collected from each lake on sampling days undertaken during the pre-drawdown phase (August 19, 2011), low water phase (23 and 30 August), and post-drawdown phase (September 2 and 19, 2011, and October 22, 2011). Zooplankton samples and environmental variables were collected from three sites at different locations in the limnetic region of each lake (Fig. 1). These sites were selected to represent different ecosystem conditions of the lakes. For both lakes, site 1 was located in an open area,

which had a relatively narrow permanent connection to the river. Site 2 was located in the middle of each lake, which was densely colonized by submerged aquatic macrophytes, especially *E. densa* and *E. najia* (though LPB had a higher density of these plants than LG). Site 3 was more isolated from each lake's connection to the river, represented preferential fish habitat, and was characterized by the presence of different physiognomic macrophytes groups in the littoral region (e.g., floating, submerged), mainly in LPB. The three sites in each lake were distributed approximately 0.40 km from one another.

Zooplankton samples were collected at each site with a 20-L bucket, with five samplings undertaken on each sampling occasion to form a 100 L composite sample. The samples were filtered through a zooplankton net (55 μ m) and preserved in 4% formalin. All zooplankton were identified using specialized identification guides (e.g., Koste, 1978; Reid, 1985; Elmoor-Loureiro, 1997). A minimum of 200 individuals were quantified per replicate, and the final density was expressed as individuals per cubic meter. Samples with low zooplankton densities were counted in full and not subsampled.

Environmental variables

The environmental conditions within each lake were also assessed at each site and on each sampling day. The depth of each lake was measured using a Speedtech sonar (depthmate Portable Sounder), and

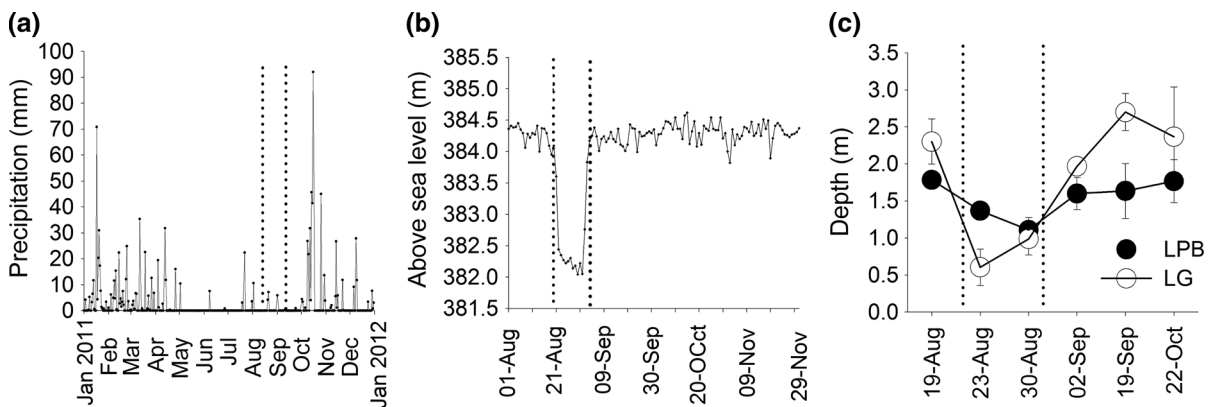


Fig. 2 **a** Daily precipitation, **b** water level fluctuation in Salto Grande Reservoir during drawdown, and **c** temporal water depth changes in Lakes Pedra Branca (LPB) and Guaritá (LG). The

dotted line indicates the timing of drawdown for the low water phase (23 August and 30 August)

water transparency was determined using a Secchi disk. Water temperature, pH, conductivity, and dissolved oxygen were measured using a calibrated Multiprobe Horiba (Model U22- Horiba Ltd. Japan) water analyzer. Water samples were obtained from the surface (Van Dorn bottle) for assessing the concentrations of pelagic phytoplankton—chlorophyll-*a* (Talling & Driver, 1963), total nitrogen (Mackereth et al., 1978), total phosphorus (Strickland & Parsons, 1960), and suspended matter (mineral and organic) (Cole, 1979).

Data analysis

All analyses were undertaken separately for each lake because of their distinct zooplankton communities, and differences in their morphology and degree of physical connection to the main channel (Debastiani-Júnior & Nogueira, 2015).

Since measurements taken in each lake over time violated the ANOVA assumption of independence (see online resource 1—Table S1), we performed a repeated measures ANOVA (RM-ANOVA) to examine the effects of drawdown on the zooplankton community and environment variables. Repeated measures designs assume that observations on the same unit are correlated, with measures taken close together in time being more highly correlated than measures taken further apart in time (Field, 2013).

Prior to performing all analyses, all environmental variables were $\log_{10}(x + 1)$ transformed data (except pH). With the exception of the taxon richness data, which were already normally distributed, all density and diversity data were square-root transformed to reduce the influence of outliers and to fulfill the requirements of parametric ANOVA. The normality of the data was assessed using the Shapiro–Wilks Test, and homogeneity of variances was assessed using Levene's Test. Secchi transparency was found to be 100% of total depth during all sampling phases, and consequently, this variable was excluded from the statistical analyses.

Difference between means of the density, taxon richness, and Shannon–Wiener diversity index of the total zooplankton, rotifer, and microcrustacean communities for each lake were tested using one-way RM-ANOVA, with the sampling day (19 August, 23 and 30 August, 02 and 19 September, and 22 October) as the

repeated factor. Environmental variables were analyzed using the same RM-ANOVA model. Data were also evaluated by the Mauchly sphericity test to validate RM-ANOVAs (Field, 2013). If there was a significant violation of sphericity, an adjustment (Greenhouse–Geisser) univariate procedure for repeated measures was used (Field, 2013). Where significant factors were identified, post hoc tests were carried out using Bonferroni pairwise comparisons. Statistical analyses were undertaken using SPSS version 20.0 (SPSS Inc., Chicago, IL, U.S.A.).

Variation in zooplankton community structure among the pre-drawdown (August 19, 2011), low water (23 and 30 August), and post-drawdown (September 2 and 19, 2011, and October 22, 2011) phases was assessed using Principal Coordinates Analyses (PCoA) [PERMANOVA + for PRIMER (Anderson et al., 2008)] on the basis of Bray–Curtis similarities derived from square-root transformed density data (Anderson et al., 2008). PERMANOVA was then used to determine whether the variation in zooplankton community structure was significant. The Distance-based Linear Model routine [DistLM in PERMANOVA + for PRIMER (Anderson et al., 2008)] was performed (Clarke & Warwick, 2001; Anderson et al., 2008) to analyze and model the relationship between zooplankton community structure and the environmental variables. The DistLM model was constructed using the stepwise selection procedure and the adjusted R^2 as a selection criterion, to enable the fitting of the best explanatory variables to the model (Anderson et al., 2008). Prior to undertaking DistLM, the full set of nine available environmental variables was tested for collinearity using Draftsman plots and Spearman correlation matrices, and redundant variables with correlations (r^2) > 0.8 were omitted from the analysis. For LPB, the environmental variables selected included depth, water temperature, water transparency, suspended matter, conductivity, chlorophyll-*a*, total nitrogen, and total phosphorus, while for LG, all nine environmental variables were selected. Finally, the similarity percentage procedure (SIMPER in PRIMER v6.0 (Clarke & Warwick, 2001)) was used to identify those taxa contributing most to similarities within each phase of the drawdown. All analyses were undertaken on site averages from each lake within each sampling day. Significant differences were inferred at an α -level of 0.05.

Results

Environmental variables

In LPB, pH and dissolved oxygen (30 August) increased significantly during the low water phase before declining during the post phase (Tables 1 and 2; see Bonferroni post hoc analysis $P < 0.05$ in Online resource 2—Table S2). Also, conductivity was significantly greater during the low water phase and soon after artificial drawdown (2 September) than pre-drawdown event (Tables 1 and 2; Table S2).

In LG, water temperature increased during the low water phase (30 August) before declining during the post-drawdown phase (Tables 1 and 2; Table S2). Dissolved oxygen increased during the low water phase (23 August) before declining during the post-drawdown phase and remained at concentrations similar to those prior to artificial drawdown, while chlorophyll-*a* concentration increased during the post-drawdown phase (22 October), eight weeks after the artificial drawdown was applied (Table 1 and 2; Table S2).

Zooplankton community in the Lake Pedra Branca

RM-ANOVA indicated that there were significant differences in the density of total zooplankton, microcrustaceans, and rotifers among sampling days in LPB (Table 2). Total zooplankton and microcrustacean densities increased significantly during the low water and post-drawdown phase (Fig. 3a; see Bonferroni post hoc analysis $P < 0.05$ in Online resource 2—Table S3). Rotifer densities were uniform during the pre-drawdown and low water phases, but they were significantly greater in post-drawdown (19 September) than pre-drawdown events (Fig. 3a; Table S3).

Total zooplankton and rotifer taxon richness differed significantly among sampling days (Table 2). Total zooplankton richness was similar among sampling days during the pre-drawdown and low water phases, but was greater soon after artificial drawdown (2 September) than pre-drawdown event (Fig. 3a; Table S3). Rotifer richness increased significantly during the low water (23 August) and post-drawdown (2 and 19 September) phases than pre-drawdown event

Table 1 Mean values and standard deviation (SD) of limnological variables measured in Lakes Pedra Branca (LPB) and Guaritá (LG) during the pre-drawdown (August 19, 2011), low

water (23 and 30 August), and post-drawdown (September 2 and 19, 2011, and October 22, 2011) phases

	19-Aug	23-Aug	30-Aug	2-Sep	19-Sep	22-Oct
LPB						
WT	22.06 (1.27)	22 (1.00)	22.93 (0.42)	18.96 (1.03)	23.63 (0.70)	24 (1.00)
SM	1.18 (0.08)	1.06 (0.30)	5.06 (2.35)	2.041 (0.40)	3.15 (0.82)	3.17 (1.69)
pH	7.46 (0.34)	8.37 (0.06)	7.29 (0.34)	6.41 (0.15)	6.64 (0.40)	6.79 (0.27)
Cond	61.67 (2.05)	70.67 (2.86)	93.00 (5.23)	100.33 (10.50)	73.33 (5.77)	66.66 (5.77)
DO	12.40 (0.21)	13.33 (0.23)	8.23 (0.25)	8.27 (0.60)	8.83 (0.76)	9.3 (0.92)
Chlo <i>a</i>	1.30 (0.66)	1.09 (0.06)	2.86 (2.22)	1.51 (0.48)	3.20 (2.19)	1.83 (1.00)
TN	288.41 (51.83)	282.96 (33.44)	413.8 (41.04)	464.03 (22.23)	309.88 (42.12)	319.4 (87.12)
TP	17.52 (7.68)	20.60 (0.17)	34.23 (5.44)	34.05 (9.22)	25.725 (6.02)	25.74 (11.44)
LG						
WT	20.23 (0.45)	20.66 (0.21)	25.36 (0.92)	20.8 (0.20)	21.56 (0.42)	22.86 (0.35)
SM	1.04 (0.03)	2.46 (1.15)	1.53 (0.10)	3.18 (0.48)	0.69 (0.21)	1.41 (0.16)
pH	6.26 (0.11)	7.05 (0.20)	7.23 (0.38)	6.67 (0.06)	6.12 (0.22)	6.63 (0.31)
Cond	60 (0)	70 (0)	70 (0)	70 (0.02)	70 (0.03)	70 (0.02)
DO	10.26 (0.55)	13.73 (0.49)	9.07 (0.26)	9.53 (0.05)	9.33 (0.38)	9.10 (0.44)
Chlo <i>a</i>	0.77 (0.24)	0.64 (0.41)	0.32 (0.17)	0.66 (0.37)	1.48 (0.44)	1.78 (0.71)
TN	349.65 (55.40)	262.4 (66.54)	271.38 (52.08)	335.56 (34.50)	254.6 (45.49)	418.41 (33.41)
TP	14.50 (2.15)	25.60 (6.99)	26.89 (8.68)	23.01 (3.35)	29.36 (10.70)	19.99 (1.96)

Code: *WT* Water temperature ($^{\circ}\text{C}$), *SM* suspended matter (mg l^{-1}), *Cond* conductivity ($\mu\text{S cm}^{-1}$), *DO* dissolved oxygen (mg l^{-1}), *Chlo a* chlorophyll-*a* ($\mu\text{g l}^{-1}$), *TN* total nitrogen ($\mu\text{g l}^{-1}$), *TP* total phosphorus ($\mu\text{g l}^{-1}$)

Table 2 *F* values and significance level results from repeated measures ANOVA (RM-ANOVA) on the environmental and zooplankton response variables observed in Lakes Pedra Branca (LPB) and Guaritá (LG) during the study period of artificial drawdown

	LPB		LG	
	<i>F</i> values	<i>P</i>	<i>F</i> values	<i>P</i>
Environmental variables				
Depth	15.574	0.001	4.751	0.005
Water temperature	11.331	0.051	43.355	0.020
Suspended matter	3.641	0.145	8.411	0.079
pH	13.810	0.001	5.529	0.108
Conductivity	15.879	0.016	0.020	0.990
Dissolved oxygen	70.351	0.009	65.111	0.002
Chlorophyll- <i>a</i>	1.285	0.375	6.072	0.008
Total nitrogen	3.610	0.145	3.214	0.149
Total phosphorus	1.937	0.260	1.358	0.356
Zooplankton community				
Density				
Total Zooplankton	10.422	0.001	3.280	0.051
Microcrustacean	6.316	0.007	3.777	0.064
Rotifera	10.815	0.003	3.862	0.041
Total richness				
Total Zooplankton	9.358	0.000	7.120	0.000
Microcrustacean	2.930	0.065	9.758	0.000
Rotifera	13.866	0.000	1.949	0.197
Diversity index				
Total Zooplankton	15.663	0.004	9.910	0.001
Microcrustacean	3.631	0.049	9.933	0.000
Rotifera	4.000	0.000	7.181	0.000

Bold *P* values indicate statistically significant effects ($P < 0.05$)

The *F* value and *P* value results were obtained after Greenhouse-Geisser correction. Post hoc tests on pairwise comparisons were carried out using Bonferroni correction

(Fig. 3a; Table S3). Microcrustacean richness did not vary significantly over time (Table 2; Fig. 3a).

There were significant differences in the diversity of total zooplankton, microcrustaceans, and rotifers among sampling days in LPB (Table 2). Total zooplankton diversity did not differ significantly among sampling days during the pre-drawdown and low water phases; however, it increased significantly soon after artificial drawdown on 2 September, and was greater on that day than on 19 September or on 22 October (Fig. 3a; Table S3). Rotifer diversity was significantly greater during the low water phase (23 August) and after re-filling of the lake on 2 September

than pre-drawdown phase (Fig. 3a; Table S3). Although microcrustacean diversity varied significantly over time, the variation could not be detected using Bonferroni post hoc analysis (Fig. 3a; Table S3).

Results from the PCoA plot corroborated the differences among phases in LPB (Fig. 4a). The two first axes explained 49.6% of the variation in zooplankton community structure. Plots of the first two axes showed separation of treatments before drawdown (pre-drawdown = 19 August) to the treatments after the drawdown event (low water = 23 August and 30 August; post-drawdown phase = 2 September, 19 September and 22 October). PERMANOVA indicated that zooplankton community structure during the pre-drawdown phase differed significantly from that during the low water and post-drawdown phases in LPB (Table 3). Marginal tests from the DistLM analysis revealed that depth and conductivity were both significant in explaining the variation in community structure among drawdown phases (Table 4). The sequential (i.e., cumulative) test from the DistLM analysis showed that depth and water temperatures were responsible for explaining 27% of the variation in zooplankton community structure (Table 4). Three taxa (bolded in Table 5) accounted for up to 36.53% of the community similarity during the pre-drawdown phase; namely *Polyarthra vulgaris* Carlin, 1943, *Collotheca* sp. and *Euchlanis* sp. In comparison, *Bosmina freyi* De Melo & Hebert, 1994, *Thermocyclops decipiens* Kiefer, 1929, and *Ceriodaphnia silvestrii* Daday, 1902 were dominant during the low water phase, and the former two species remained dominant during the post-drawdown phase (along with *Polyarthra vulgaris*) (Table 5).

Zooplankton community in the Lake Guaritá

Total zooplankton and microcrustacean densities did not vary significantly during the artificial drawdown in LG (Table 2; Fig. 3b). Rotifer densities varied significantly over time and were uniform during the pre-drawdown and low water phases; however, they were greater during post-drawdown phase (2 and 19 September) than low water phase (Table 2; Fig. 3b; see Bonferroni post hoc analysis $P < 0.05$ in Online resource 2—Table S3).

RM-ANOVA indicated that there were significant differences in the taxon richness of total zooplankton

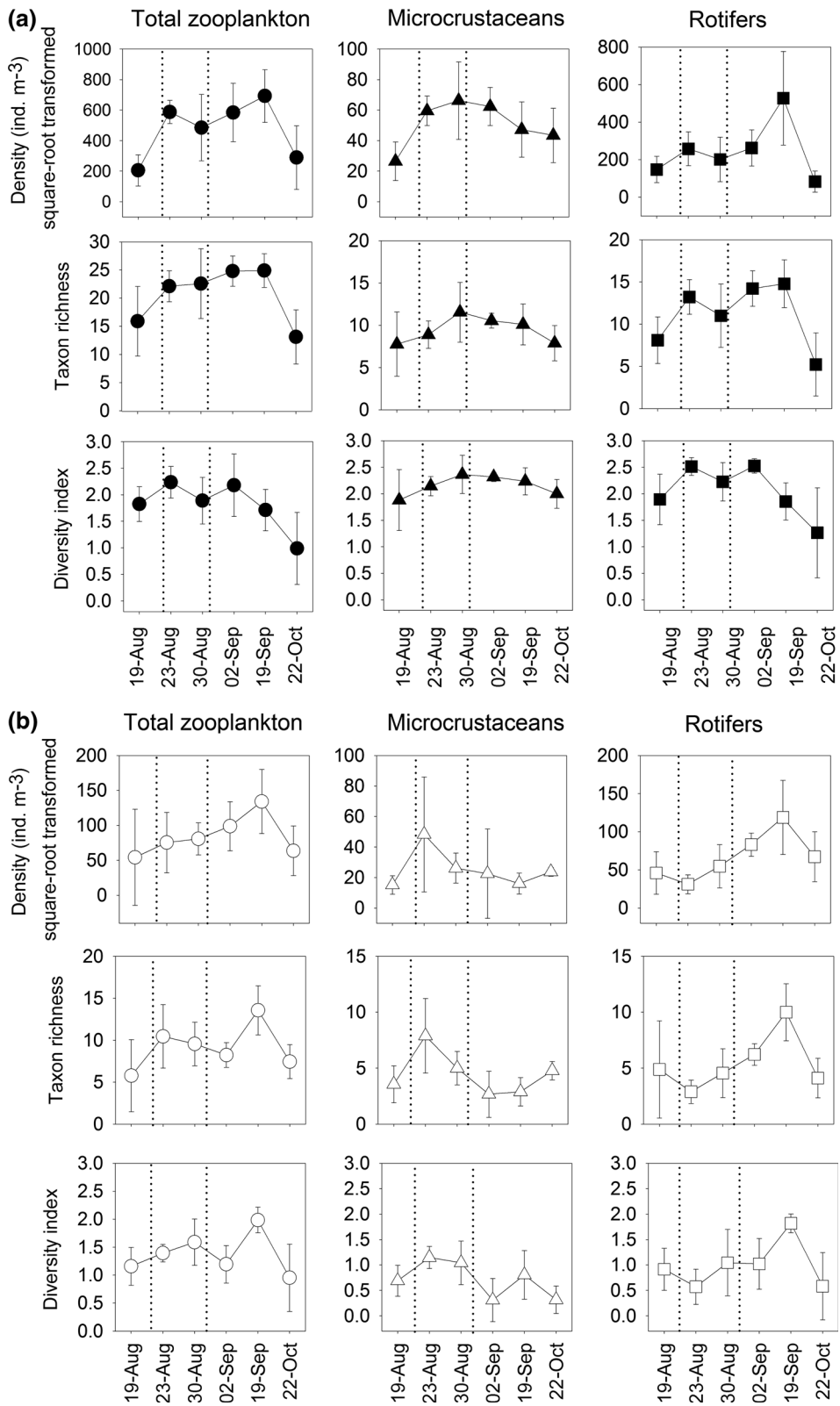


Fig. 3 Mean (SD) density, taxon richness, and diversity of total zooplankton (filled circle), microcrustaceans (filled triangle), and rotifers (filled square) during artificial drawdown in (a) LPB (shaded symbols) and (b) LG (unshaded symbols). Note, the dotted line indicates the timing of drawdown for the low water phase (23 August and 30 August)

and microcrustaceans among sampling days in LG (Table 2). Total zooplankton richness was uniform during the pre-drawdown and low water phases; however, it was significantly greater during post-drawdown (19 September) than pre-drawdown phase,

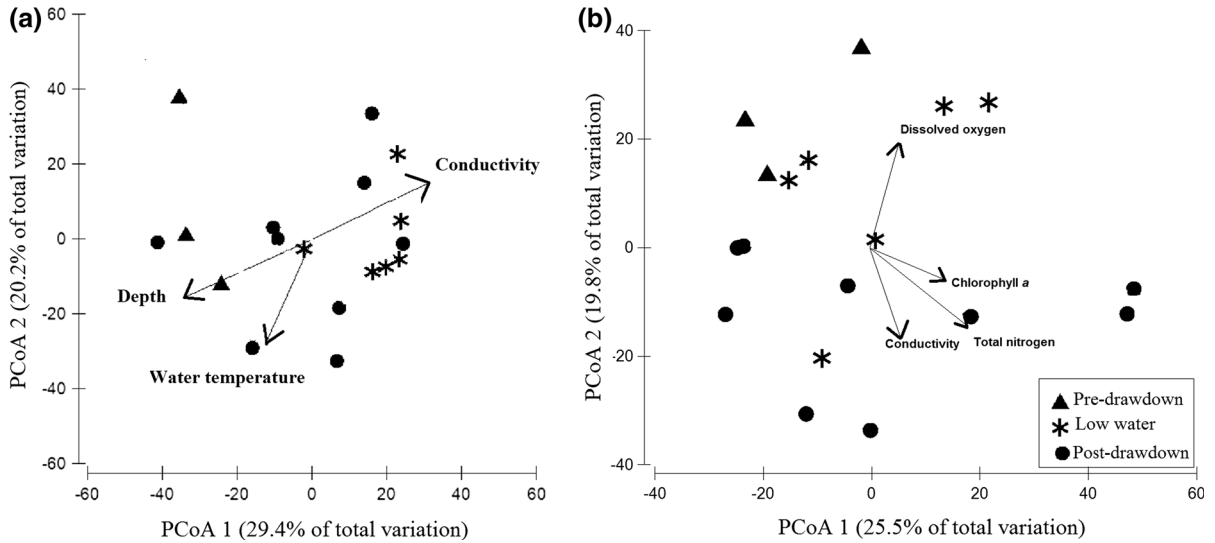


Fig. 4 PCoA plots showing ordinated sampling phases and sampling days based on community structure and composition data in (a) LPB (Lake Pedra Branca) and (b) LG (Lake Guaritá).

Vectors visualize the fitted environmental variables as suggested by the DistLM model. Symbols represent average PCoA scores for replicates of each site by sampling day

Table 3 PERMANOVA of the effects of drawdown on the temporal patterns of zooplankton community abundance and composition

PERMANOVA test								
	df	SS	MS	Pseudo-F	<i>P</i> (perm)	Pairwise test	<i>t</i>	<i>P</i> (perm)
LPB								
Zooplankton community								
Phases	2	7,564.1	3,782.1	2.633	0.005	Pre vs Low water	2.172	0.011
Residual	15	21,545	1,436.4			Pre vs Post	1.504	0.034
Total	17	29,109				Low water vs Post	1.400	0.06
LG								
Zooplankton community								
Phases	2	6,906.2	3,453.1	1.845	0.019	Pre vs Low water	1.099	0.322
Residual	14	26,190	1,870.7			Pre vs Post	1.34	0.036
Total	16	33,096				Low water vs Post	1.485	0.027

LPB Lake Pedra Branca, LG Lake Guaritá

Bold *P* values indicate statistically significant effects ($P < 0.05$)

Table 4 Results of distance-based linear model (DistLM) analysis

Variables	SS (trace)	Pseudo-F	P	Prop.
LPB				
Marginal test				
Depth	4,984.2	3.310	0.000	0.17
Conductivity	4,736.5	3.110	0.001	0.16
Sequential test				
Depth	4,984.2	3.310	0.000	0.17
Water temperature	2,984.1	2.160	0.004	0.10
LG				
Marginal test				
Total nitrogen	3,924.5	2.020	0.030	0.12
Dissolved oxygen	3,725.3	1.900	0.050	0.11
Chlorophyll- <i>a</i>	3,421.5	1.730	0.040	0.10
Sequential test				
Total nitrogen	4,420.6	3.060	0.020	0.13
Conductivity	3,715.3	1.880	0.050	0.11

Results of the marginal test show the influence of each parameter in isolation, whereas results of the sequential test show the effect of environmental variables on zooplankton community structure in the combined model (Selection procedures Step-wise, selection criterion, *adjusted R*²). *Prop.* proportion of total variation explained, *LPB* Lake Pedra Branca and *LG* Lake Guaritá. Bold P values indicate statistically significant effects ($P < 0.05$)

whereas microcrustacean richness increased during low water (23 August) than post-drawdown phase (2 and 19 September) (Fig. 3b; Table S3). Rotifer richness did not vary significantly over time (Table 2; Fig. 3b).

There were significant differences in the diversity of total zooplankton, microcrustaceans, and rotifers among sampling days in LG (Table 2; Fig. 3b). Overall total zooplankton, microcrustacean, and rotifer diversities were uniform during pre-drawdown and low water phases (Fig. 3b). Nevertheless, total zooplankton and rotifer diversity were significantly greater on 19 September than on 19 August, 23 August, and 22 October (Fig. 3b; Table S3), whereas microcrustacean diversity was greater during low water phase than soon after artificial drawdown on 2 September (Fig. 3b; Table S3).

The first two axes of the PCoA plot explained 45.3% of the total variation, and showed how zooplankton community structure and composition varied during the drawdown event in LG (Fig. 4b). PERMANOVA analysis indicated that zooplankton

community structure during the post-drawdown phase differed significantly from that during the pre-drawdown and low water phases (Table 3). The DistLM analyses revealed that total nitrogen, dissolved oxygen, and chlorophyll-*a* concentrations were all significant in explaining the variation in community structure among drawdown phases (Table 4, marginal tests). The influence of total nitrogen concentration remained significant in the sequential DistLM tests, along with conductivity (Table 4). The pre-drawdown phase zooplankton community was mainly characterized by *Chydorus pubescens* Sars, 1901, *Euchlanis* sp. and *Polyarthra vulgaris*; whereas the low water phase community was mainly characterized by *Cephalodella* sp., *Chydorus pubescens* and *Lepadella* sp. By contrast, the post-drawdown phase community was mainly characterized by the rotifers, Bdelloidea, *Trichotria tetractis* (Ehrenberg, 1830), and *Lecane bula* (Gosse, 1851) (Table 5).

Discussion

In disagreement with hypothesis, artificial drawdown over a short timeframe (13 days) significantly increased the density, taxon richness, and diversity of total zooplankton, microcrustaceans, and rotifers in LPB, and the composition of the zooplankton during the pre-drawdown phase differed significantly from that during the low water and post-drawdown phases. In comparison, no significant drawdown alterations to total zooplankton, microcrustacean, and rotifer density, taxon richness, and diversity were detected in LG; however, zooplankton community composition differed during the post-drawdown phase from that during the pre-drawdown and low water phases, which partially supports the hypothesis for this lake. Nevertheless, the overall collection of taxa present in both lakes during the pre-drawdown phase was not significantly affected in subsequent phases of the drawdown event (as shown in Table 5). The results from this study suggest that artificial drawdown could potentially be used to control the excessive growth of *E. densa* and *E. najas* in reservoir systems without negatively affecting the overall density, richness, and diversity of zooplankton communities in marginal shallow lakes.

Although both lakes were exposed to identical drawdown regimes, their zooplankton communities

Table 5 SIMPER analysis identifying which zooplaknton taxa contribute mostly strongly towards differences among drawdown phases

Taxa	LPB						LG					
	Pre		Low water		Post		Pre		Low water		Post	
	Average similarity 42.85%		Average similarity 58.40%		Average similarity 42.42%		Average similarity 31.57%		Average similarity 45.85%		Average similarity 39.49%	
	Density	%	Density	%	Density	%	Density	%	Density	%	Density	%
Cladocera												
<i>Alona</i> sp.			16.9		3.31							
<i>Bosmina freyi</i>	4.78	4.31	71.26	19.77	69.13	26.66			3.69	4.88	6.55	3.58
<i>Ceriodaphnia silvestrii</i>	5.74	7.12	41.37	9.87	27.12	4.72			3.85	5.8		
<i>Chydorus pubescens</i>							9.78	36.35	9.87	15.46		
<i>Daphnia gessneri</i>	5.96	5.72	9.63	1.91	15.9	5.54						
<i>Macrothrix</i> sp.			13.59	2.02	8.33	2.64	2.87	11.5	3.03	4.04		
<i>Moina minuta</i>					16.92	1.96						
Copepoda												
<i>Microcyclops</i> sp.					9.81	2.46						
<i>Notodiptomus henseni</i>	5.65	5.56	38.07	7.24	15.4	3.88			6.06	7.15	4.1	6.47
<i>Thermocyclops decipiens</i>			49.1	12.21	20.71	7.3			2.4	5.08		
Rotifera												
Bdelloidea					7.44	1.81					9.18	14.77
<i>Brachionus</i> sp.									6.93	7.47	6.61	3.99
<i>Cephalodella</i> sp.									6.99	18.1	6.38	5.94
<i>Collotheca</i> sp.	18.25	9.3	10.12	2.23								
<i>Conochilus unicornis</i>	10.71	6.11									4.57	3.36
<i>Euchlanis</i> sp.	11.28	10.95	30.66	5.69	15.63	3.5	9.58	22.01			5.93	3.67
<i>Keratella cochlearis</i>			12.19	3.18	8.88	2.31						
<i>Lecane</i> cf. <i>leontina</i>			20.59	5.08								
<i>Lecane arcula</i>			13.25	3.04	6.73	2.27						
<i>Lecane bulla</i>											10.07	13.01
<i>Lecane decipiens</i>			10.97	2.82	13.61	3.46						
<i>Lecane</i> cf. <i>elsa</i>			13.63	1.91	11.75	3.13						
<i>Lecane lunaris</i>											4.38	3.95
<i>Lepadella</i> sp.	5.46	4.9			10.42	2.87			4.72	7.56	5	3.97
<i>Macrochaetus</i> sp.	7.13	4.09	12.66	3.21								
<i>Polyarthra vulgaris</i>	19.65	16.28	15.92	4.12	34.08	13.56	6.69	22.01	4.34	6.48	6.6	9.62
<i>Trichocerca</i> sp.	6.08	6.44			9.93	2.56			5.19	6.29		
<i>Trichotria tetractis</i>	5.74	7.88	14	3.07					5.64	4.08	12.71	14.32

This analysis assesses the average density and percent contribution (%) of each taxon to the observed similarity within sampling phases. Bolded text is used to represent the three main taxa that contribute most to the similarity within sampling phases

LPB Lake Pedra Branca, LG Lake Guaritá. *Cut-off for low contributions: 90%

* Due to ubiquitous nature of some species within sites, a cut-off criterion was applied to allow for the identification of a subset of species whose cumulative percentage contribution reached 90% of the similarity value

differed in their response patterns. The most likely explanation for this variation relates to the morphology of these marginal lakes and their associated differences in water quality (Debastiani-Júnior & Nogueira, 2015). LPB becomes completely disconnected from the main channel of the Paranapanema River during a drawdown event, whereas LG still maintains water exchange with the main channel of the river. Hydrological connectivity and disturbance caused by water level fluctuations are important drivers of zooplankton population dynamics via their influence on abiotic and biotic factors, such as water quality, competition, and predation (Baranyi et al., 2002; Paggi & Paggi, 2008).

Changing water levels typically influence complex processes observed in shallow lakes, especially those involving nutrients and biological productivity (Leira & Cantonati, 2008; Wantzen et al., 2008; Lake, 2011). Artificial drawdown had a significant effect on the water quality in LPB. During the period of declining water levels, there was an increase in conductivity, combined with a decline in dissolved oxygen and a deviation from non-neutral pH (from 8.37 to 6.41) toward the post-drawdown phase. These results may be explained by the biological processes associated with submerged macrophytes that were not removed during periods of low water levels, such as their intense respiration and the decomposition of their labile organic matter (Carvalho et al., 2005). After lakes refill, the dead biomass from macrophytes becomes rehydrated, releasing organic matter and nutrients from the dead portion of the plants back into the system (Carvalho et al., 2005). All these water quality changes are therefore potential factors relating to the environmental trophic status (Pinto-Coelho et al., 2005) and food resource availability, which influence the zooplankton species composition in LPB.

The water quality changes occurred in such a way that contributed to peaks in the densities of rotifer populations and the populations of some microcrustacean taxa in LPB. The zooplankton community was numerically dominated by small zooplankton organisms, including *Bosmina freyi* and *Thermocyclops decipiens*, *Polyarthra vulgaris*, *Keratella cochlearis*, and species of the Lecanidae family. Based on records and comparisons of lakes of differing trophic status, several workers suggested that more eutrophic conditions favor the dominance of these taxa (Gannon & Stemberger, 1978; Duggan et al., 2002; Perbiche-

Neves et al., 2013a), owing to their ability to effectively avoid typically abundant cyanobacteria and feed on smaller algal particles (Danielsdottir et al., 2007). DeBoer et al. (2016) similarly observed a rapid increase in total zooplankton density (especially *Bosmina* spp.) and changes in zooplankton community structure following a water level drawdown at Red Willow Reservoir, and they attributed this response to a decline in the dissolved oxygen concentration and an increase in algal biomass (as estimated by chlorophyll-*a* concentration). In this study, the high variability of abiotic conditions similarly led to changes in species dominance and community composition and contributed to the high variability of zooplankton communities, which continued until soon after the refilling of LPB Lake on 2 September. It is possible that the artificial drawdown over a short timeframe produced a temporary disturbance effect, which the water quality changes enhanced the availability of resources, increasing community variability between the phases before and during the drawdown event (Connell, 1978; Dodson et al., 2000; Angeler & Moreno, 2007). However, zooplankton community structure appeared altered again after drawdown was applied (22 October), which could be associated with seasonal variation by changes in precipitation (Nogueira et al., 2006).

Moreover, analyses of fish assemblages in tropical reservoirs of Brazil (Pelicice et al., 2005; Pelicice & Agostinho, 2006) have shown that *Egeria* spp. support a particular fish fauna composed of small-sized individuals (<5 cm), many of which feed almost exclusively medium and large-sized zooplankton (Iglesias et al., 2011). Even though there is no fish data in this study, this may also explain the development, maintenance and high abundance of small zooplankton species, such as *Bosmina freyi*, in LPB during the low water and post-drawdown phases.

Most taxa recorded during the low water phase in LPB are commonly linked to aquatic macrophytes in tropical lakes (Maia-Barbosa & Guimarães, 2008; Lansac-Tôha et al., 2009; Nadai & Henry, 2009). The increase in zooplankton taxon richness and consequent change in composition could have also been at least partly due to the dispersal of non-planktonic species during the low water phase. This was supported by the presence of non-planktonic species, such as *Alona* sp., *Macrothrix* sp., *Lecane* cf. *leontina*, *Lecane arcuata* Harring, 1914, *Lecane decipiens* (Murray, 1913),

Lecane cf. *elsa*, *Macrochaetus* sp. and *Trichotria tetractis* (Ehrenberg, 1830) in LPB during the low water phase (Table 5). These taxa together contributed to >25% to the total similarity of community composition (58%) during the low water phase. In shallower water, light conditions at the lake bottom are better; some rooted emergent macrophytes (e.g., *Egeria* sp.) can more easily grow to the surface layer of the water, thus reducing the separation between macrophyte beds and open water (pelagic) within the lake (as shown in the pictures of lakes in the Online resource 3). Many epiphytic and benthic zooplankton organisms often exhibit vertical movements in subtropical vegetated shallow lakes to avoid unsuitable physical and chemical features, such as low dissolved oxygen within macrophytes stands and potentially also to avoid predation (Meyers, 1980; Miranda & Hodges, 2000; Tavşanoğlu et al., 2012). In addition, non-planktonic rotifers would be able to vertically migrate to upper layers, where phytoplankton is abundant and available to feed on (José de Paggi, 1995). Thus, we cannot discard the possibility that the reduced separation between macrophyte beds and open water probably led to a more active replacement of species and allowed for a great number of non-planktonic species in the water column throughout our sampling period. A similar situation has been observed in other shallow subtropical lakes on the Paraná River floodplain (José de Paggi, 1993; José de Paggi et al., 2012), where *Panicum elephantipes*, *Cyperus alternifolius*, *Thypha* sp., and *Paspalum repens* were the dominant macrophytes and they supported the diversity of non-planktonic organisms in the open water regions of these lakes.

In LG, the density and diversity of microcrustacean and rotifer communities remained similar during the pre-drawdown and low water phases, and were largely influenced by the resident populations of the main channel of the Paranapanema River, inhabiting in the Salto Grande Reservoir (Nogueira et al., 2008; Perbiche-Neves & Nogueira, 2010; Perbiche-Neves & Nogueira, 2013b). In agreement with the ecological attribute results, overall community structure did not vary significantly between the pre-drawdown and low water phases. Watkins et al. (2013) also found no effect of water level drawdown on zooplankton communities. Their results indicated that a management regime involving a partial drawdown did not compromise zooplankton diversity in

experimental wetlands located on the floodplain of a temperate Australian river (Watkins et al., 2013). In this study, changes in the post-drawdown phase zooplankton community varied with nutrient (total nitrogen), dissolved oxygen, and chlorophyll-*a* concentrations, in addition to conductivity. The water quality and associated zooplankton community changes occurred approximately eight weeks after the artificial drawdown was applied (Fig. 4b), coinciding with the increasing trophic status of Paranapanema Reservoir at the beginning of the rainy season (Fig. 2a) which typically occurs in early October (Nogueira et al., 2006; Minuzzi et al., 2007). Thus, the temporary changes to zooplankton community structure observed may have been solely due to direct and indirect effects of seasonal variation on the limnological conditions rather than artificial drawdown.

Conclusion

Our results suggest that artificial drawdown over a short timeframe may have enhanced zooplankton richness and diversity in one shallow, less-connected lake, but had no significant impact on zooplankton community structure in the other also shallow, but more-connected lake. However, other effects might be considered when the community interactions are measured over a long term (Lake, 2011). Havens et al. (2007) observed significantly changes in zooplankton community composition in Lake Okeechobee between the pre- to the post-drawdown periods, which persisted for five years after the drawdown event. They argued that the water level drawdown had positive effects on plant growth of the macrophyte, *Chara*, in Lake Okeechobee, which became more favorable for the survival of small planktivorous fish and contributed to their predation on zooplankton among the plants. Environmental consequences of an artificial drawdown can appear in very different timescales, ranging from days to seasons or even years (Hellsten et al., 1996; Leira & Cantonati, 2008). All these findings support the need for more research on the effects of drawdown to macrophyte growth/communities into the response of zooplankton and other communities to drawdown events—particularly in relation to their extent, frequency, and duration.

Acknowledgements We are grateful to CNPq (Brazilian National Council of Technological and Scientific Development) for the scholarship to JLP (CNPq process 152109/2012-9) and Duke Energy for financial support. We also thank Virginia Sanches Uieda, Raoul Henry, Gilmar Perbiche-Neves, Daryl Nielsen, and Nathan Ning for constructive comments on earlier versions of the manuscript, as well as Danilo A.O. Naliato and Diogo F. Souza for help with the fieldwork. Dr. Douglas D. Kane improved the grammar of the final manuscript. We thank the anonymous reviewers for their careful reading of our manuscript and their many insightful comments and suggestions.

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