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Role of zooplanktonic functional groups in a shallow mesotrophic reservoir

Papel dos grupos funcionais zooplanctônicos em um reservatório mesotrófico raso

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Abstract: Aim: Zooplankton functional groups play an important role in lake functioning and can readily respond to environmental changes and may be associated with phytoplankton changes. In warmer regions, zooplankton species have a smaller body size, which decreases their grazing capacity, attenuating top-down control throughout phytoplankton. We evaluated changes in density and biomass of zooplankton functional groups and their relationship with algal groups in horizontal reservoir zonation (pelagic, sublittoral, and eulittoral zones) of the shallow reservoir. We hypothesize that the density and biomass of zooplankton functional groups are associated with fluctuations in the phytoplankton groups in horizontal reservoir zonation. **Methods:** Changes in the structure of the zooplankton functional group and the controlling limnological variables were verified at three sampling stations: pelagic, sublittoral, and eulittoral zones in a mesotrophic reservoir. **Results:** Zooplankton species were distributed in seven functional groups. The density and biomass of zooplankton functional groups were not clearly associated with biomass variations of phytoplankton groups. However, the zooplankton functional groups were associated with horizontal reservoir zonation, where specific groups were found in the pelagic, sublittoral, and eulittoral zones. **Conclusions:** The zooplankton functional groups were related to the horizontal zonation of the reservoir but were not associated with changes in the phytoplankton groups due to the dominance of small organisms.

Keywords: potential grazing pressure; body size; omnivores; functional traits.

Resumo: Objetivo: Os grupos funcionais do zooplâncton desempenham um papel importante no funcionamento dos lagos, são capazes de responder prontamente às mudanças ambientais e podem estar associados às mudanças no fitoplâncton. Em regiões mais quentes, as espécies de zooplâncton apresentam pequeno tamanho corporal, o que diminui sua capacidade de pastejo e atenua o controle de cima para baixo sobre o fitoplâncton. Avaliamos as mudanças na densidade e biomassa de grupos funcionais do zooplâncton e sua relação com grupos de algas na zonação horizontal de um reservatório raso (zona pelágica, sublitoral e eulitoral). Nossa hipótese é que a densidade e biomassa dos grupos funcionais do zooplâncton estão associadas a flutuações nos grupos do fitoplâncton no zoneamento horizontal do reservatório. **Métodos:** Em um reservatório mesotrófico, as alterações na estrutura do grupo funcional do zooplâncton e nas variáveis limnológicas foram avaliadas em três zonas de amostragem: pelágica, sublitoral e eulitoral. **Resultados:** As espécies de zooplâncton foram distribuídas em sete grupos funcionais. Evidenciou-se que a densidade e a biomassa dos grupos funcionais do zooplâncton não foram claramente associadas às variações da biomassa dos grupos do fitoplâncton. No entanto, os grupos funcionais do zooplâncton foram associados à zonação horizontal do reservatório, onde grupos específicos foram encontrados na zona pelágica, sublitoral e eulitoral.

Conclusões: Os grupos funcionais do zooplâncton foram relacionados com a zonação horizontal do reservatório, mas não foram associados às mudanças nos grupos do fitoplâncton devido à dominância de organismos de pequeno porte.

Palavras-chave: pressão potencial de pastejo; tamanho do corpo; onívoros; traços funcionais.

1. Introduction

Studies have reported the sensitivity responses of zooplanktonic assemblages to environmental changes (Branco et al., 2007; Hébert et al., 2017; Vignatti et al., 2017; Oh et al., 2017). Considering the attributes of ecologically relevant species, functional diversity is a good predictor of processes and ecosystem functioning (Tilman et al., 1997; Barnett et al., 2007; Hébert et al., 2017), since this measure considers the attributes of a species and the impact thereof on the local ecosystem (Hébert et al., 2017). Functional traits in zooplankton communities can be grouped based on morphological, physiological, behavioral, and life-history traits, which may comprise different ecological functions (Litchman et al., 2013; Gomes et al., 2019). Some studies have demonstrated the predictive potential of zooplankton functional groups for environmental changes in lakes, highlighting the important role the community has in environmental monitoring (Oh et al., 2017; Rusak et al., 2002; Sodré & Bozelli, 2019; Goździejewska et al., 2021). Based on functional traits, the responses of functional groups to variations in limnological conditions is an issue explored in various biological communities, such as phytoplankton (Reynolds et al., 2002; Salmaso et al., 2015; Cupertino et al., 2019), periphyton (Dunck et al., 2013, 2015), and macroinvertebrates (Bonsdorff & Pearson, 1999; Cummins, 2016; Li et al., 2021). Although the number of studies on the functional traits of zooplankton communities has been gradually increasing, there is a gap in functional-approach studies worldwide (Gomes et al., 2019), especially when considering tropical lakes and reservoirs.

Zooplankton are morphologically and taxonomically diverse groups with large variations in body length that are determinant for biomass and herbivory pressure (Kiorbe, 2011). Feeding habits, habitat preference, form of food capture, reproduction and growth rates are the functional traits commonly used to determine functional groups (Barnett et al., 2007; Litchman et al., 2013), which may be associated with changes in algal communities (Becker et al., 2009). In tropical and subtropical aquatic ecosystems, the control of the zooplankton over phytoplankton development is less evident than in temperate regions, because in tropical and subtropical aquatic ecosystems the interaction is more complex (Meerhoff et al., 2007). In warmer regions, zooplankton have a smaller body size (Gillooly & Dodson, 2000), which reduces their grazing capacity by attenuating the top-down control over the phytoplankton. In addition, the continuous reproduction of omnivorous fish throughout the year and zooplankton's association with submerged vegetation can exert strong predation pressure on phytoplankton and zooplankton, being responsible for the small size of the animals (Jeppesen et al., 2005; Iglesias et al., 2007). Thus, the effects of zooplankton grazing on phytoplankton can be reduced or eliminated in shallow tropical lakes (Jeppesen et al., 2005; Meerhoff et al., 2007).

In the present study, we evaluated changes in density and biomass of zooplankton functional groups and their relationship with algal communities in horizontal zonation (pelagic, sublittoral, and eulittoral zones) of a shallow reservoir. Considering that pelagic, sublittoral and eulittoral zones have different environmental characteristics (Santos et al., 2020), our hypothesis is zooplankton functional groups are associated positively with fluctuations in the total and relative biomass of phytoplankton groups in horizontal reservoir zonation. The present study contributes to elucidating the role of zooplankton functional groups in lakes and shallow tropical reservoirs, especially as an indicator of environmental changes.

2. Materials and Methods

2.1. Study area

The environment selected for the study, Ninfeias reservoir, is located at Parque Estadual das Fontes do Ipiranga (PEFI) (23°38' S, 46°37' W) and in the urban area of São Paulo (Brazil) (Figure 1). The regional climate is considered tropical altitude (Conti & Furlan, 2003). This reservoir is formed by the Pirarungaua stream dam and serves a landscaping purpose in the São Paulo Botanical Garden. It is a small, shallow, mesotrophic reservoir with an area of 5,433 m^2, a maximum depth of 3.6 m, an average depth of 1.3 m, and a residence time of 7.2 days.

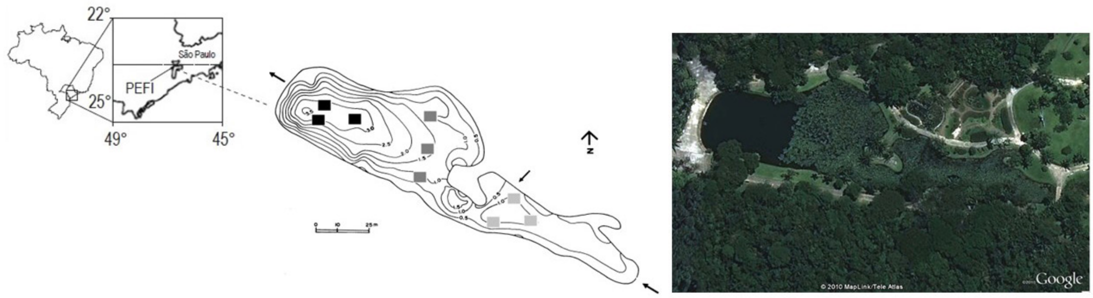

Figure 1. Sampling site location on bathymetric map of Ninfeias Reservoir (black squares pelagic zone, gray squares sublittoral zone; light gray squares eulittoral zone). Modified from Bicudo et al. (2007) and Santos et al. (2020). Reservoir image from Google (December/2010).

It has an extensive littoral region and a large abundance of aquatic macrophytes, such as *Nymphaea* spp. (rooted with floating leaves), *Utricularia foliosa* L. (free-floating) and *Panicum repens* L. (rooted plant) (Santos et al., 2020).

2.2. Sampling design

Changes in the zooplankton community structure and the controlling limnological variables were examined at three sampling stations (pelagic zone, sublittoral and eulittoral) to encompass the complete spatial heterogeneity at the Ninfeias reservoir. Triplicate samples were performed at each station, pelagic (2.5-3.5m deep), sublittoral (1 to 2 m deep) and eulittoral (<1 m deep), totaling nine samples per month sampled. The littoral classification is followed by Esteves & Caliman (2011). Water samples for abiotic and phytoplankton analysis were collected using the van Dorn bottle at three different depths: subsurface, middle, and bottom; they were then manually integrated for evaluation of the whole water column, except in the eulittoral (subsurface). Sampling was done from January to December 2014 and included the rainy season (January to April and November to December) and the dry season (May to October), according to the monthly average rainfall in 2014 (Figure 2).

The separation of algae into metaphytic and planktonic habitats is difficult, especially when there is no visible algal mass. As the threshold between algal habitats is very tenuous (Margalef, 1998), we opted for the term phytoplankton as we did not observe an algal mass at the sampling sites during the study period. Thus, algae sampled in the water column were designated phytoplankton.

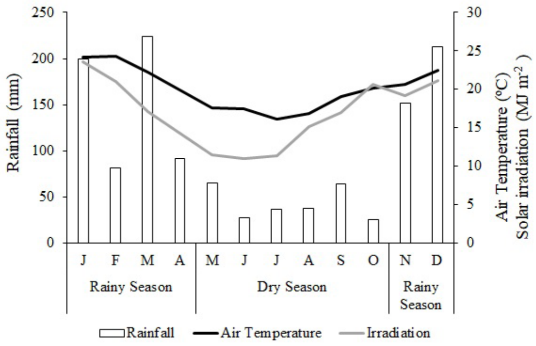

Figure 2. Climate variables (rainfall, air temperature and irradiation) recorded during the study period.

2.3. Climatic and abiotic variables

The climate data were provided by the CIENTEC Meteorological Station (IAG/USP, 2014), which is located at approximately 1000 meters from the studied reservoir.

At the sampling sites, the abiotic variables determined were water transparency (Secchi disc, Z_{ds}), temperature, column depth (Z_{max}), electrical conductivity, pH (multiparameter underwater probe), and underwater radiation (luximeter Li- COR 250A). In addition, the vertical light attenuation coefficient ($k = (\ln Io - \ln I)/z$), where Io is the surface radiation, I is the radiation at a given depth, z is the depth in meters (distance between the two depths) and ln the neperian or natural logarithm (Padial & Thomaz, 2008) was calculated. The euphotic zone ($_{Zeu}$) was estimated by multiplying Secchi depth by 2.7 (Cole, 1994). The concentration of the dissolved oxygen (Golterman et al., 1978), dissolved inorganic carbon forms (Mackereth et al., 1978), total nitrogen and total phosphorus (Valderrama, 1981) were determined. The suspended material concentration was determined using the gravimetric method (Golterman et al., 1978).

2.4. Macrophyte and phytoplankton

The percentage of macrophyte coverage was determined monthly at the littoral sampling sites (Thomaz et al., 2004).

Chlorophyll-*a* concentrations (corrected for pheophytin) were determined from water subsamples filtered through glass-fiber filters (GF/F Whatman, Maidstone, UK) according to Sartory & Grobbelaar (1984). Water samples were preserved with a 4% formalin solution for qualitative analysis and with an acetic Lugol solution for quantitative analysis. Phytoplankton counting was performed using a Zeiss Axiovert microscope (400x) according to Utermöhl (1958). Phytoplankton was counted on transects and the count limit was determined via the species rarefying curve. Density (ind mL^{-1}) was calculated according to Ros equation (1979). Biovolume was obtained from Fonseca et al. (2014) or estimated from Hillebrand et al. (1999). Phytoplankton biovolume ($\mu m^3\ mL^{-1}$) was converted to $mm^3\ L^{-1}$ (= mg L^{-1}). Phytoplankton species were classified into algal classes (Bicudo & Menezes, 2018). An algal class was considered dominant when it presented more than 50% of the total biomass in the sample.

2.5. Zooplankton

Zooplankton samples were collected with a suction motor, integrating the water column, using a 50 µm plankton net and anesthetized by CO_2 (soda water) and preserved in 4% formalin. Organisms were identified and counted microscopically. Five functional attributes were selected: body length, habitat, trophic level, eating habits, and type of reproduction, based on the literature for the classification of Zooplankton Functional Groups (Barnett et al., 2007; Litchman et al., 2013; Gomes et al., 2019).

To calculate the biomass, the most representative species were used, that is, those present in more than 50% of the samples, in relation to the frequency of occurrence, and with a contribution greater than 20% of the total density (ind m^{-3}) of the sample. For calculation purposes, the body size of about 30 organisms from each species were measured. To calculate the biomass of the Rotifera populations, the technique described by Ruttner-Kolisko (1974) was used. The linear regression established by Bottrell et al. (1976) for calculating the biomass of Cladocera and Copepoda populations was used. Measurements of zooplankton species to obtain biomass were carried out bimonthly.

The zooplankton biomass (µg DW L^{-1}) / phytoplankton biomass ratio (Chl.*a* multiplied by 66 to convert ug/L to µg DW L^{-1}) was used as an approximation for grazing pressure (Jeppesen et al., 2005). For this calculation, it is assumed that zooplankton use phytoplankton as the sole source of food and that all phytoplankton biomass is consumed each day. Thus, this ratio gives an indication of the proportion of the phytoplankton stock that is consumed per day (Jeppesen et al., 1994).

Based on habitat attributes and feeding habits, the species were classified into functional groups. The zooplanktonic species were distributed into the following functional groups: scrapers herbivores littoral (G1), filtering suspension-feeder herbivores pelagic (G2), suspension-feeders with mouthparts herbivores pelagic (G3), raptorial omnivores (G4), suspension-feeder ciliates herbivores pelagic (G5), sucking herbivores pelagic (G6) and suspension-feeders ciliates herbivores littoral (G7). For the data referring to the density of the functional groups, all zooplankton species present in the study were considered, with monthly records. While for the data referring to biomass, and consequently for potential grazing, only the most abundant species were used, with records every two months, according to the data referring to phytoplanktonic biomass.

2.6. Data analysis

The permutational multivariate analysis of variance (two-way PERMANOVA; $\alpha = 0.05$) was used to evaluate the influence of seasonality and reservoir zone (spatial scale) on zooplankton functional group variability. This analysis was performed using the Bray-Curtis similarity and 9999 permutations in PAST 3.25 (Hammer et al., 2001).

A redundancy analysis (RDA) was performed to evaluate the environmental variables (dissolved oxygen, depth, particulate matter, light, TP, TN, chlorophyll-a, and macrophyte cover) and a matrix of the density of the zooplankton functional groups in the pelagic and littoral zones (sublittoral and eulittoral) in the year studied. For RDA, environmental variables were selected based on principal component analysis (PCA). The abiotic and biotic data were log-transformed [log (x + 1)]. Pearson correlation between ordination axes and functional group density and environmental variables was calculated ($r < 0.5$). In addition, the significance of the RDA axes was determined by the Monte Carlo Test, determining the degree of interpretability of the axes ($p < 0.05$).

The analysis was performed in the PC-ORD 6.0 software (McCune & Mefford, 2011).

3. Results

The highest Z_{ds}/Z_{max} ratio values and the lowest attenuation underwater radiation values were recorded during the dry period (Table 1). During the rainy season, we recorded the highest macrophyte coverage, phytoplankton chlorophyll *a*, TP concentrations, suspended material and conductivity (Table 1).

Significant differences were found in the composition of the zooplankton functional groups between months and studied zones (two-way PERMANOVA: F = 75.01; p = 0.0001; F =38.67; p = 0.0001, respectively). The interaction among factors (seasonality and zones) was significant (two-way PERMANOVA: F = 34.67; p = 0.0001).

The G5 functional group (suspension-feeder ciliates herbivores pelagic), which includes rotifers such as *Kellicottia bostoniensis* (Rousselet, 1908), was the most abundant in the pelagic zone, with high densities from May (70% total density) until December (67%) (Figure 3). The G3 group (suspension-feeders with mouthparts herbivores pelagic), composed of Calanoida copepods, was more abundant in April (62%) but showed little representation in May (2.5%). The G5 group was also the most abundant in the sublittoral from April to June and from October to December, accounting for 48% to 62% of zooplankton total density (Figure3). The G6 group (sucking herbivores pelagic), which includes rotifers *Polyarthra*, was dominant in January (87%), and from July to September (57% to 75%). The G1 group (scrapers herbivores littoral), which includes littoral Cladocerans, such as *Chydorus*, which was most representative in February and March, with almost 20% of total density.

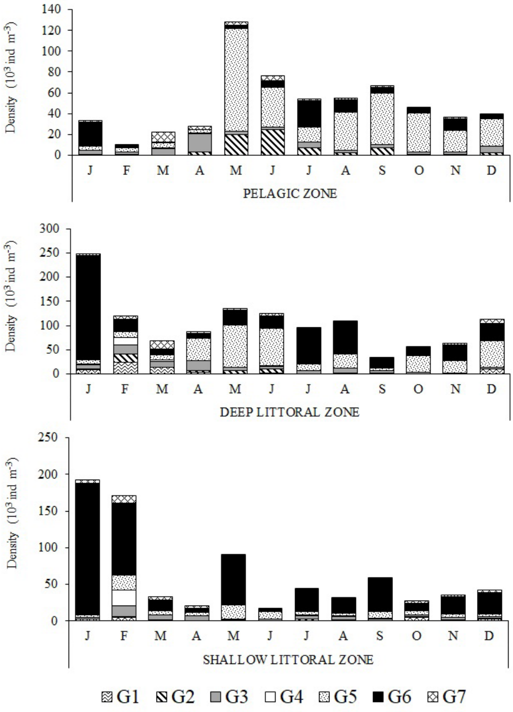

Figure 3. Total density of zooplankton functional groups (ind.m^{-3}) in the pelagic, sublittoral, and eulittoral zones of the Ninfeias Reservoir from January to December 2014.

Table 1. Mean and standard deviation of the environmental variables measured during the dry and rainy periods in the Ninfeias reservoir from January to December 2014. Modified from Santos et al. (2020).

	Rainy period			Dry period		
	Pelagic	**Sublittoral**	**Eulittoral**	**Pelagic**	**Sublittoral**	**Eulittoral**
Conductivity (µS cm^{-1})	73.2 ± 26.5	49.6 ± 6.0	52.0 ± 6.0	53.7 ± 5.2	50.4 ± 6.4	48.5 ± 3.0
Dissolved oxygen (mg L^{-1})	5.5 ± 1.3	6.1 ± 1.1	6.4 ± 1.5	6.0 ± 1.0	6.5 ± 1.4	6.7 ± 1.1
Depth (m)	2.85±0.34	1.19±0.20	0.71±0.25	2.84±0.36	1.07±0.16	0.68±0.19
Free CO_2 (mg L^{-1})	11.4 ± 8.8	6.9 ± 4.7	7.1 ± 3.9	5.9 ± 1.9	6.3 ± 3.4	6.4 ± 2.4
Light (µmol m^{-2} s^{-2})	4448 ± 2478	6022 ± 4296	4661 ± 3680	2674 ± 2046	3910± 3126	4453± 1863
pH	6.7 ± 0.3	6.8 ± 0.3	6.8 ± 0.3	6.8 ± 0.2	6.8 ± 0.2	6.8 ± 0.2
Z_{eu} (m)	3.3±0.4	2.6±0.4	1.8±0.3	4.5±1.3	2.8±0.5	1.8±0.4
Z_{eu}/Z_{max} ratio	1.2±0.2	2.3±0.4	2.7±0.5	1.6±0.6	2.6±0.2	2.7±0.1
Z_{ds}/Z_{max} ratio	0.4 ± 0.1	0.8 ± 0.2	0.9 ± 0.2	0.6 ± 0.2	1.0	1.0 ± 0.1
Suspended matter (mg L^{-1})	7.0 ± 3.4	6.4 ± 2.5	7.8 ± 6.5	3.0 ± 1.0	3.5 ± 0.9	3.7 ± 1.1
Temperature (ºC)	22.0 ± 0.9	23.3 ± 1.5	22.9 ± 2.2	17.8 ± 2.0	18.6 ± 2.4	18.8 ± 2.6
Total Nitrogen (µg L^{-1})	299.9±346.7	196.0±231.9	185.4±195.9	33.0 ± 51.6	20.0 ± 10.6	25.6 ± 8.7
Total Phosphorus (µg L^{-1})	19.8 ± 10.0	23.6 ± 6.5	27.6 ± 11.0	13.2 ± 4.4	13.0 ± 3.9	12.3 ± 4.9
Macrophyte coverage (%)		48.3 ± 8.7	68.2 ± 13.5		28.7 ± 12.0	49.1 ± 17.7
Phytoplankton Chlorophyll-*a* (ug L^{-1})	20.4 ± 16.6	19.1 ± 8.9	24.9 ± 4.2	8.8 ± 6.4	12.3 ± 11.2	8.7 ± 5.4

The G6 Group (sucking herbivores pelagic) was dominant in the eulittoral zone throughout the year, reaching 93% of total density in January. June was an exception to this; in June the G5 group, suspension-feeder ciliates herbivores pelagic, was the largest with 63% (Figure 3).

Redundancy analysis was performed with seven environmental variables and the density of seven zooplankton functional groups (Figure 4). A Monte Carlo randomization test showed that both axes are interpretable ($p < 0.01$). The eigenvalues for axis 1 ($\lambda = 1.237$) and 2 ($\lambda = 0.343$) explained 22.6% of the total data variability. Pearson's species-environment correlation for axis 1 (0.882) indicated a high relationship between species distribution and environmental variables. On the positive side of axis 1, all pelagic zone scores were correlated with the highest depth values (Pearson: $r = 0.950$). Functional groups G2 and G5 were significantly correlated with pelagic zone (Pearson: $r = 0.498$; $r = 0.295$, respectively). In contrast, most of the sublittoral and eulittoral zone sampling units were correlated with high macrophyte coverage (Pearson: $r = -0.897$) and a higher light attenuation coefficient (Pearson: $r = -0.763$). The functional groups G3, G4, G6, and G7 were more associated with the environmental conditions of the littoral zone, especially the G6 group (Pearson: $r = -0.539$). Thus, RDA axis 1 represented the spatial variability of the zooplankton functional groups.

In the pelagic zone, the functional groups differed in biomass ($p = 0.0008$) and the G2 group was the most representative in June (Figure 5B). In the littoral zone (sublittoral and eulittoral), group G6 (rotifers like *Polyarthra*) was most representative (Figure 5B).

Groups G3 and G4, G7 and G3, G4 and G5, G7 and G5, G7 and G6 differed in biomass in the sublittoral zone ($p = 2.27e\text{-}16$). Groups G2 ($p = 0.0135$) and G6 ($p = 0.0074$) presented higher biomass in the dry and rainy periods, respectively.

The highest potential grazing pressure values were obtained in the dry season (June and August) in the pelagic zone, where group G2 (cladocerans like *Daphnia*) accounted for the highest grazing (Figure 6).

In the pelagic zone, the highest phytoplankton biomass was found in August (dry period), when Chrysophyceae was dominant. In the sublittoral zone, the highest biomass was found in April and August, when Chrysophyceae was dominant (Figure 6). Different from other zones, Chrysophyceae, Dinophyceae, and Zygnematophyceae in February (rainy period) contributed similarly to the phytoplankton structure in the sublittoral zone. However, Chrysophyceae was also dominant in April (rainy period).

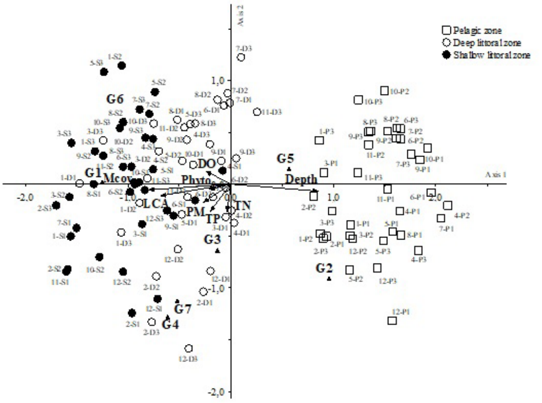

Figure 4. RDA for zooplankton functional groups in pelagic, sublittoral, and eulittoral zones. Scores: the first number indicates the month; the letter indicates the sampled zone, and the last number indicates the sampling site in each zone. Vectors: Mcov: macrophyte coverage; PM: particulate matter; DO: dissolved oxygen; TP: total phosphorus; TN: total nitrogen; Depth: depth; Phyto: phytoplankton chlorophyll-a; LCA: light attenuation coefficient. G1: scrapers herbivores littoral; G2: filtering suspension-feeder herbivores pelagic; G3: suspension-feeders with mouthparts herbivores pelagic; G4: raptorial omnivores; G5: suspension-feeder ciliates herbivores pelagic; G6: sucking herbivores pelagic; G7: suspension-feeders ciliates herbivores littoral.

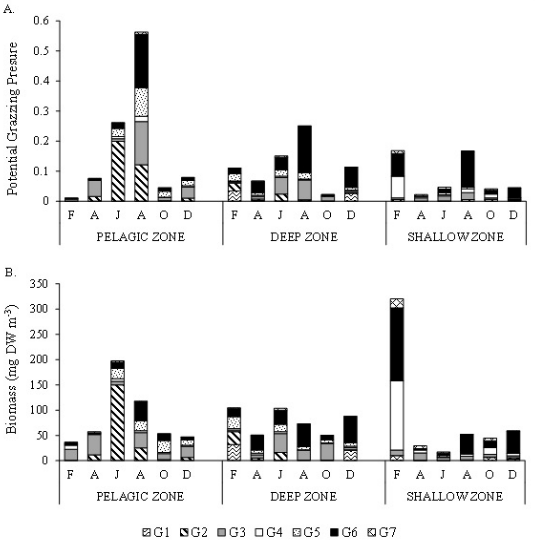

Figure 5. Bimonthly variations in potential grazing pressure (A) and biomass (B) of zooplankton functional groups in pelagic, sublittoral, and eulittoral zones.

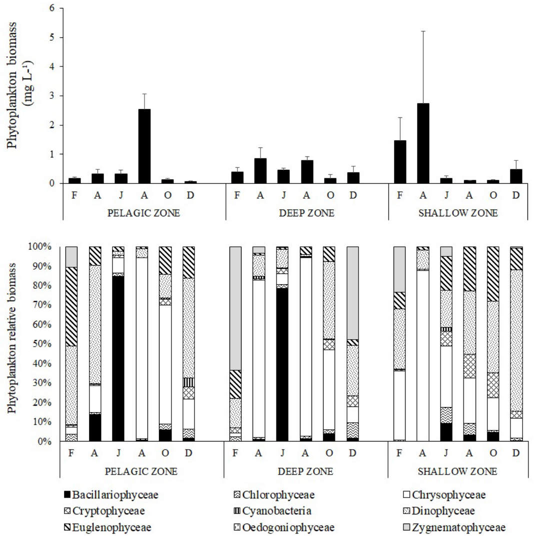

Figure 6. Bimonthly variations in phytoplankton total biomass and relative biomass of the algal groups in pelagic, sublittoral, and eulittoral zones.

4. Discussion

Our results showed seasonal fluctuations in the limnological variables for the three reservoir zones. Compared to the dry season, the rainy season was characterized by high TN and TP concentrations, electrical conductivity, and suspended material, as well as high macrophyte coverage and phytoplankton chlorophyll-*a*. The dry period was characterized by the increased depth of the euphotic zone and decreased light attenuation, especially in the littoral zone. The results of this study showed that the density and biomass of the zooplankton functional groups changed with environmental conditions of the dry and rainy periods in shallow reservoir studied.

The seven zooplankton functional groups reflected their type of habitat and manner of feeding, as described in other studies (Sodré et al., 2017; Gomes et al., 2019). Based on RDA, changes in zooplankton functional groups were mainly explained by spatial variation in the whole reservoir. Our findings evidenced the strong association of the G2 and G5 groups with the pelagic zone. The G2 group (pelagic cladocerans such as *Daphnia)* is typically filtering and tends to exert strong grazing pressure. In the littoral, we found a strong association for between G1, G3, and G6 groups with environmental conditions of sublittoral and eulittoral. The G3 group was associated with the sublittoral zone and Copepoda nauplii (G3) were abundant, contributing with high biomass, which explains their high grazing pressure. Although they have a short body length, poor swimming and sensory abilities and a rudimentary feeding apparatus at this stage, they can consume phytoplankton, microzooplankton, debris, and bacteria (Meyer et al., 2002). The zooplankton functional group most associated with the sublittoral zone was the G6 group, which is represented by sucking herbivore rotifers, such as *Polyarthra*.

Regarding temporal scale, the presence of these large filters is explained by the reduced availability of food, as large amounts of filamentous algae or material suspended in the water column may clog the filter apparatus in the dry season. The high potential grazing pressure recorded for G2 in June is due to *Daphnia*'s large contribution to the biomass. According to the size efficiency hypothesis proposed by Brooks & Dodson (1965), species with a larger body size excel in small particle filtration (1-15µm), being competitively superior to smaller species. Thus, species with a larger body can monopolize resources, excluding smaller species. These species are also more efficient grazers and have a greater impact on energy transfer in aquatic ecosystems (Fernández & Rejas, 2017). In August, the contribution of *Daphnia* to the biomass decreased, probably opening a niche space, which was occupied by opportunistic rotifers (G3, G4, G5, and G6), contributing to the increased grazing potential of these groups. In addition, G6 group (rotifers like *Polyarthra*) was highly representative in density and biomass throughout the study, explaining their high contribution to the calculated potential grazing pressure. These organisms participate in the energy flow by consuming microalgae, debris and bacteria in a shallow environment influenced by the colonization of aquatic macrophytes (Branco et al., 2007).

Considering the effect zooplankton grazing has on phytoplankton, there was dominance of taxa with small body size, as *Polyarthra vulgaris* (G6 group), *Kellicotia bostoniensis* (G5 group), *Bosminopsis deitersi* (G2 group) and the young forms of Cyclopoida (G4 group), which were the most representative taxa in abundance and biomass during the study. These species have a low grazing rate (Mourelatos & Lacroix, 1990; Lionard et al., 2005). Castro et al. (2018) recorded the presence of two fish species, *Geophagus brasiliensis,* and *Hoplias malabaricus,* in the Ninfeias Reservoir, the first being the most abundant. The pressure exerted by the omnivore *G. brasiliensis*, as reported in studies on tropical and subtropical regions (Meerhoff et al., 2007) may explain the dominance of taxa with small body size. Added to this, the low tolerance that filter cladocerans with longer body lengths have to UV radiation, as reported in some studies (De Los Ríos, 2005; Fernández & Rejas, 2017) could also explain the small effect zooplankton grazing has on phytoplankton in tropical and subtropical ecosystems. In these environments, underwater radiation is more intense than in temperate environments, which compromises the grazing rate of organisms such as *Daphnia* (Fernández & Rejas, 2017). Although our results suggested low grazing pressure, the adaptive strategies of phytoplankton against grazing should not be underestimated in the community structure (Lürling, 2021).

The G1 group (scrapers cladocerans littoral) was associated with macrophyte coverage, especially during the rainy season. In tropical and subtropical environments, cladocerans may avoid macrophytes as they can be a refuge for young and invertebrate fish that eat zooplankton (Meerhoff et al., 2006; Iglesias et al., 2007). The cladoceran community in the littoral zone was predominantly composed of scrapers (G1), and these organisms were rare in the pelagic zone, which explains the spatial variation in their potential grazing rate contribution.

Our findings showed that zooplanktonic functional groups composed of organisms with a small body size are predominant throughout the year in reservoir zones. These tiny organisms do not exert strong grazing pressure on phytoplankton, which had high biomass with a dominance of Chrysophyceae and Dinophyceae. These algal classes were predominantly constituted of flagellated species, such as *Mallomonas* sp., *Chromulina* spp., *Peridinium gatunense* Nygaard, *Parvodinium umbonatum* (F.Stein) Carty (Santos et al., 2020), which have specific predation strategies (Wehr & Sheath, 2003). However, the G2 group (filter cladocerans), abundant in the dry period in the pelagic zone, seems to exert significant herbivory pressure on algae when diatom dominance occurred. Despite diatoms having a siliceous frustule that provides protection against predation, the biogenic silica concentration may vary among species (Hamm et al., 2003; Liu et al., 2016). In addition, even though zooplankton grazing seems to have little impact on phytoplankton, more studies are needed, especially in relation to the G2 group.

In summary, we evidenced that neither the density nor the biomass of zooplankton functional groups was clearly associated with algal class variations due to the dominance of organisms with small body sizes. However, an increase in grazing pressure on phytoplankton was found to occur in the dry season (May, June). In addition, the zooplankton functional groups were associated with horizontal reservoir zonation, where specific groups were found in the pelagic, sublittoral, and eulittoral zones. Therefore, our findings suggest that zooplankton functional groups can be used as indicators for environmental changes, especially on a spatial scale, in reservoirs, as it was seen in present mesotrophic reservoir.

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