







## Species-specific response of phytoplankton to zooplankton grazing in tropical eutrophic reservoirs

Resposta espécie-específica do fitoplâncton ao pastejo do zooplâncton em reservatórios eutróficos tropicais

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**Abstract: Aim:** To test the hypothesis that zooplankton changes the structure of phytoplankton in tropical reservoirs by reducing the biomass of algal species susceptible to herbivory. **Methods:** We experimentally evaluated the species-specific responses of phytoplankton to zooplankton within eutrophic reservoirs with different phytoplankton community structure in northeastern of Brazil. Water samples were collected from the subsurface in coastal regions of the Apipucos and Mundaú reservoirs in January/2012 and November/2014, respectively, and transported to the laboratory. The experiments were performed in Erlenmeyer flasks (1 liter) filled with water from the sample sites and were maintained for five days in the laboratory conditions. Two treatments were maintained (1) with phytoplankton and the presence of the native zooplankton and (2) without native zooplankton. **Results:** Zooplankton proved to be an important factor, modifying the structure of the phytoplankton community, especially in the Apipucos reservoir. In this reservoir, we observed a significant reduction of biomass in diatom *Cyclotella meneghiniana*, and the chlorophyte *Chlamydomonas* sp., and an increase in the biomass of *Raphidiopsis raciborskii*. In the Mundaú reservoir, we observed a significant reduction of *C. meneghiniana* and *R. raciborskii*, while cyanobacteria *Microcystis aeruginosa* increased their biomasses in the presence of zooplankton. **Conclusions:** These results show the importance of the microalgae community structure in phytoplankton-zooplankton interactions for food webs in tropical environments, as well as support the role of zooplankton in fostering cyanobacterial growth and maintain algal blooms.

**Keywords:** cyanobacterial blooms; *Thermocyclops*; top-down control; food webs.

**Resumo: Objetivo:** Testar a hipótese de que o zooplâncton altera a estrutura do fitoplâncton em reservatórios tropicais, reduzindo a biomassa de espécies de algas susceptíveis a herbivoria. **Métodos:** Avaliamos experimentalmente as respostas espécie-específicas do fitoplâncton ao zooplâncton em reservatórios eutróficos com diferentes estruturas da comunidade fitoplânctônica no nordeste do Brasil. Amostras de água foram coletadas da subsuperfície nas regiões costeiras dos reservatórios



Apipucos e Mundaú em janeiro/2012 e novembro/2014, respectivamente, e transportadas para o laboratório. Os experimentos foram realizados em frascos Erlenmeyer (1 litro) cheios de água dos locais das amostras e mantidos por cinco dias nas condições laboratoriais. Dois tratamentos foram mantidos (1) com fitoplâncton e presença do zooplâncton nativo e (2) sem zooplâncton nativo.

**Resultados:** O zooplâncton provou ser um fator importante, modificando a estrutura da comunidade fitoplanctônica, principalmente no reservatório de Apipucos. Neste reservatório, observamos uma redução significativa na biomassa de *Cyclotella meneghiniana* e *Chlamydomonas* sp., e um incremento na biomassa de *Raphidiopsis raciborskii*. No reservatório Mundaú, observamos uma redução significativa de *C. meneghiniana* e *R. raciborskii*, enquanto a cianobactéria *Microcystis aeruginosa* aumentou sua biomassa na presença de zooplâncton. **Conclusões:** Estes resultados mostram a importância da estrutura da comunidade de microalgas nas interações fitoplâncton-zooplâncton para as cadeias alimentares em ambientes tropicais, bem como, apoiam o papel do zooplâncton na promoção do crescimento de cianobactérias e na manutenção da proliferação de algas.

**Palavras-chave:** florações de cianobactérias; *Thermocyclops*; controle top-down; teia alimentar.

## 1. Introduction

In freshwater aquatic ecosystems, the intensity of phytoplankton-zooplankton interactions is driven by environmental trophic state. In eutrophic reservoirs, especially those located in tropical and subtropical areas, the zooplankton exerts a weak influence on the structure of the phytoplankton community, due to the frequent dominance of unpalatable algae for grazing (Ger et al., 2014) and small zooplankton organisms that are considered inefficient in controlling of algae biomass (Zhang et al., 2013).

The phytoplankton group with advantages in eutrophic reservoirs is cyanobacteria, which often forms intense blooms with a dominance of species belonging to genera such as, *Anabaena*, *Raphidiopsis* (*Cylindrospermopsis*), *Dolichospermum*, *Microcystis*, and *Planktothrix* (Paerl et al., 2001). Haney (1987) describes two important relationships between the cyanobacteria and zooplankton communities in aquatic freshwater ecosystems: (1) direct relation, when the zooplankton reduces the cyanobacteria biomass through grazing or increases the phytoplankton biomass through nutrient release in excreta; (2) indirect relation, when the zooplankton provides a competitive advantage for cyanobacteria by consuming other algae species.

The direct relationship between zooplankton grazing on cyanobacteria can be accompanied by deleterious effects for zooplankton, however, such effects are associated with toxin-producing strains (Wilson et al., 2006). In addition to toxins, cyanobacteria have morphological characteristics that can clog feeding apparatus (Gliwicz & Lampert, 1990), and are deficient in nutrients that are essential for zooplankton growth (Müller-Navarra et al., 2000). Furthermore, other species feature low susceptibility to grazing, such as many chrysophytes,

that have a siliceous exoskeleton which makes ingestion by zooplankton difficult, i.e. the genus *Dinobryon* (Colina et al., 2016).

The phytoplankton-zooplankton interaction is even more complex when considering other common eukaryotic algae species, besides cyanobacteria, in eutrophic water bodies. In this respect, chlorophytes also stand out since many species are considered less “palatable” due to their long spines and/or processes. Lürling & van Donk (2000) and Lürling (2003) showed that species of the genera *Scenedesmus* and *Desmodesmus* can inhibit predation by increasing the number of cells in the colony.

The zooplankton community in tropical reservoirs is mainly composed of rotifers and crustaceans, the latter represented by copepods and cladocerans (Sipaúba-Tavares et al., 1994; Almeida et al., 2009; Almeida et al., 2012). Studies show that the eutrophication process can directly influence the structure of the zooplankton community in reservoirs, causing significant effects on body size and biomass of zooplankton (Pinto-Coelho et al., 2005). According to Jeppesen et al. (2011), increased eutrophication positively affects zooplankton biomass, but negatively affects species richness and size, with large cladocerans being replaced by Cyclopid copepods and rotifer.

The low number of Cladocera in the tropics has been justified by the strong top-down control by fish in the water bodies of this region (Hansson et al., 2007; Iglesias et al., 2008). Since Cladocera has a significantly higher average body size as compared to the representatives of the other zooplankton groups, they are easily seen by fish and were more strongly affected by predation compared to rotifers, for example (Scasso et al., 2001; Silveira et al., 2010). Studies indicate that the occurrence of cyanobacterial blooms in the water bodies may

also contribute to the reduction of Cladocera biomass, since, in general, these organisms are not very selective about the type of food they consume as compared to other zooplankton groups, and are most affected when exposed to cyanobacteria (Hansson et al., 2007; Ger et al., 2014).

Zooplankton groups have different grazing mode and food types, thus, changes in the zooplankton community have direct effects on the phytoplankton. Rotifers fill the ecological niche of small filter feeders, which, in general, consume small phytoplankton organisms and bacteria (Melo Júnior et al., 2007). Cladocerans are also filter feeders; however, due to their large size about rotifers, they consume prey with a wider range of sizes (Hill et al., 2016). Copepods select and manipulate their prey and can feed on larger algae (Reynolds, 2006; Hill et al., 2016).

Although phytoplankton-zooplankton interactions have been widely discussed by many researchers in recent decades (Yang et al., 2006; Urrutia-Cordero et al., 2015; Li et al., 2020), few studies have evaluated the species-specific response of phytoplankton to zooplankton in natural communities. Furthermore, most studies have focused on eutrophic reservoirs with cyanobacterial blooms, while few studies have explored this interaction in other water bodies where cyanobacteria do not dominate, where other algal groups with defense mechanisms against herbivores dominate (i.e., Diniz et al., 2019).

In this study, we evaluated the species-specific response of phytoplankton to zooplankton grazing pressure using the native communities of two tropical reservoirs (the Apipucos and Mundaú reservoirs) in northeastern Brazil. These water bodies were eutrophic and presented different phytoplankton community structures. In the Apipucos reservoir, the community consisted of many taxa (about 50) (Almeida et al., 2012), with quantitative dominance of diatoms and Chlorophyceae. Meanwhile, in the Mundaú reservoir, the number of taxa was around 15 and with a dominance of the cyanobacteria species *Raphidiopsis (Cylindrospermopsis) raciborskii* (Woloszynska) Aguilera, Berrendero Gómez, Kastovsky, Echenique & Salerno (Dantas et al., 2008; Bittencourt-Oliveira et al., 2011). Therefore, this study aimed to test the hypothesis that zooplankton changes the structure of phytoplankton in tropical reservoirs by reducing the biomass of algal species susceptible to herbivory, such as chlorophytes, diatoms, and flagellates, and these

effects are more expressive in reservoirs with a high diversity of phytoplankton.

## 2. Materials and Methods

### 2.1. Study sites and field procedures

Apipucos (8°01'14"S, 34°56'00"W) and Mundaú (08°56'47"S, 36°29'33"W) reservoirs are located in the State of Pernambuco, northeastern Brazil. Apipucos reservoir has a total area of 2.9 km<sup>2</sup>, a volume of 556,375 m<sup>3</sup>, and a mean depth of 2.5 m (Neumann-Leitão et al., 1989; Almeida et al., 2012). This reservoir was built for flood containment and recreation. Recently, due to the intense urbanization of surrounding areas, this water body has received domestic and industrial sewage (Silva et al., 2009), being classified as hypereutrophic (Oliveira et al., 2014). *Eichhornia crassipes* (Mart.) Solms is the most common macrophyte that forms large floats at the water surface, especially in the coastal region (Pereira & Nascimento, 2009; Almeida et al., 2012).

Mundaú reservoir has an area of 4 km<sup>2</sup>, a volume of 1,900,000 m<sup>3</sup>, and 11 m mean depth (Lira et al., 2014). This reservoir was classified as eutrophic (Moura et al., 2007), and built for public water supply to the population in Garanhuns City, however, currently receives urban drainage (SHR, 2000). The occurrence of macrophytes is not expressive, but some inexpressive individuals of *Nymphaea* spp. have been observed (Lira et al., 2014).

Water samples were collected from the subsurface in coastal regions of the Apipucos and Mundaú reservoirs in January/2012 and November/2014, respectively. Samples were conditioned in plastic bottles and transported to the laboratory at natural temperature conditions (about 27°C). After the reservoirs waters has been collected and transported to the laboratory, grazing assays were carried out. Therefore, the phytoplanktonic and zooplanktonic communities of the initial conditions of the experiments were the same as the natural communities of the reservoirs.

### 2.2. Experimental design

The phytoplankton community of the Apipucos and Mundaú reservoirs was maintained under two conditions, with (n=3) and without zooplankton (n=3). For this, samples were filtered with plankton net (68 µm mesh) for treatments without zooplankton and placed in three Erlenmeyer flasks (1 liter) maintained closed for five days in laboratory conditions: temperature of 25±1°C, artificial lighting with 20-W fluorescent lamps

( $80 \pm 2 \mu\text{mol.photons m}^{-2} \text{s}^{-1}$ ), a 12-h photoperiod, and constant aeration using an aquarium aerator. In the other three flasks, we put the native zooplankton organisms directly collected from Apipucos reservoir water which were acclimatized in laboratory conditions for 12 hours as described above. The same procedure was done for samples from the Mundaú reservoir.

## 2.2. Phytoplankton and zooplankton analysis

For quantitative studies of phytoplankton and zooplankton in the experiments, samples were collected from all treatments at the beginning (Day 1;  $T_{\text{Initial}}$ ) and the end (Day 5;  $T_{\text{Final}}$ ) of the experiment. Aliquots of 10 mL to counting of phytoplankton of each treatment were sampled and preserved using a solution of acetic Lugol at 1%. The biomass ( $\text{mg.L}^{-1}$ ) was estimated using the density ( $\text{ind.mL}^{-1}$ ) data (Utermöhl, 1958) and mean cell biovolume of each taxon (Hillebrand et al., 1999). Zooplankton samples were preserved using formalin solution at 4% and the analyses were carried out under an optical microscope with a Sedgwick-Rafter counting chamber of 1 mL. The biomass ( $\text{mg.L}^{-1}$ ) was estimated by mean biovolume of taxa, according to Ruttner-Kolisko (1977) for rotifers, and Pinto-Coelho (2004) for microcrustaceans.

The standard error of the mean biomasses ( $\pm$  SEM) of phytoplankton and zooplankton was calculated. The dominance of phytoplankton and zooplankton taxa at the beginning of the experiment was determined according to Lobo & Leighton (1986), the taxa with biomass higher than 50% of total biomass were considered dominant.

## 2.3. Statistical analysis

The taxonomic diversity of phytoplankton in the Apipucos and Mundaú reservoirs at  $T_{\text{Initial}}$  and in the zooplankton treatment at the end of the experiment was analyzed based on species abundance, using the Shannon diversity index ( $H'$ ) (Shannon, 1948) and the Pielou equitability index ( $J'$ ) (Pielou, 1966). The Pielou  $J'$  index ranges from 0 to 1, indicating homogeneity or highest heterogeneity, respectively. To assess the significant differences in total phytoplankton biomass and biomass of species in the  $T_{\text{Initial}}$  and treatments with and without zooplankton, we performed an ANOVA *one-way* and Kruskal-Wallis test for parametric and non-parametric residues, respectively. Tukey's *post hoc* test was applied to discriminate the significant differences in biomasses of phytoplankton

species between  $T_{\text{Initial}}$  and treatments with and without zooplankton at  $T_{\text{Final}}$ . Normality and homoscedasticity of residues was previously determined using the Kolmogorov-Smirnov and Bartlett tests, respectively. The statistical analyses were performed with a 5% significance level using the R software (R Core Team, 2016). In the results, we included phytoplankton taxa that presented biomass greater than 1% in the tested treatments.

## 3. Results

Higher diversity was observed at  $T_{\text{Initial}}$  in the Apipucos reservoir ( $H' = 3.78$  bits,  $J' = 1.00$ ) compared to the Mundaú reservoir ( $H' = 2.40$  bits,  $J' = 1.00$ ). At the end of the experiment, it was verified that zooplankton negatively affected phytoplankton diversity in Apipucos ( $H' = 3.76$  bits,  $J' = 1.00$ ), while the opposite was observed in Mundaú ( $H' = 2.49$  bits,  $J' = 1.00$ ). At the beginning of the experiment, the zooplankton biomass was similar to that observed during samplings from the reservoirs, with an abundance of  $152.27 (\pm 11.97) \text{ mg.L}^{-1}$  and  $1003.90 (\pm 155.89) \text{ mg.L}^{-1}$  for Apipucos and Mundaú, respectively.

### 3.1. Apipucos reservoir

At the beginning of the experiment ( $T_{\text{Initial}}$ ), the zooplankton community was composed of 10 taxa belonging to Rotifera (82%), Cladocera (9%), and Copepoda (9%, adults and nauplii). The total biomass was  $152.27 \pm 34.74 \text{ mg.L}^{-1}$ , with dominance of *Thermocyclops* ( $51.54 \pm 3.81 \text{ mg.L}^{-1}$ ) and nauplii ( $74.32 \pm 4.89 \text{ mg.L}^{-1}$ ) (Figure 1a). At the end of the experiment ( $T_{\text{Final}}$ ), total biomass was  $107.13 \pm 34.74 \text{ mg.L}^{-1}$ . We observed an increase in *Brachionus* biomass and a reduction in *Thermocyclops* and nauplii biomass (Figure 1a).

Forty-eight phytoplankton taxa were identified at  $T_{\text{Initial}}$  belonging to Cyanophyceae (15%), Bacillariophyceae (8%), Chlorophyceae (60%), Euglenophyceae (8%), and Cryptophyceae (8%) (Table 1). Total biomass was  $23.70 \pm 2.94 \text{ mg.L}^{-1}$ , with no dominant taxa registered (Table 1). The total phytoplankton biomass was significantly higher in the without zooplankton treatment compared to treatment with zooplankton and the  $T_{\text{Initial}}$  ( $F = 10.93$  and  $p = 0.00998$ ) (Figure 1b). A reduction in the relative biomass of Bacillariophyceae was observed in the treatment with zooplankton at the end of the experiment ( $T_{\text{Final}}$ ), while there was an increase in the relative biomasses of Cyanophyceae and Chlorophyceae (Figure 1c).

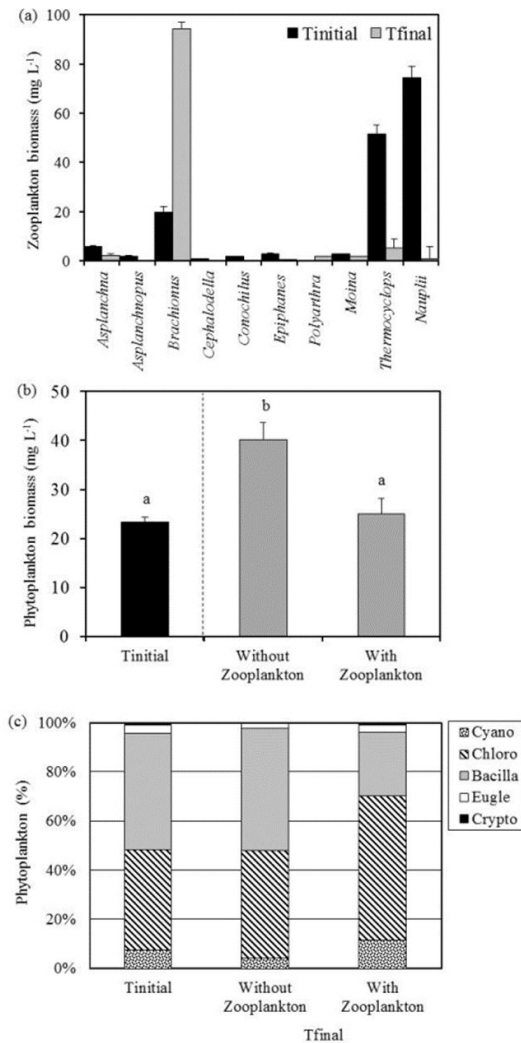


In zooplankton treatment, we observed a significant reduction in biomass of diatom *Aulacoseira granulata* (Ehrenberg) Simonsen and *Cyclotella meneghiniana* Kützing, and the chlorophyte *Chlamydomonas* sp. (Table 1). The chlorophytes *Dictyosphaerium pulchellum* H.C. Wood and *Micractinium pusillum* Fresenius, and the cryptophyceae *Cryptomonas erosa* Ehrenberg also presented reduced biomasses in the presence of zooplankton but was not significant (Table 1). On the other hand, we observed a significant

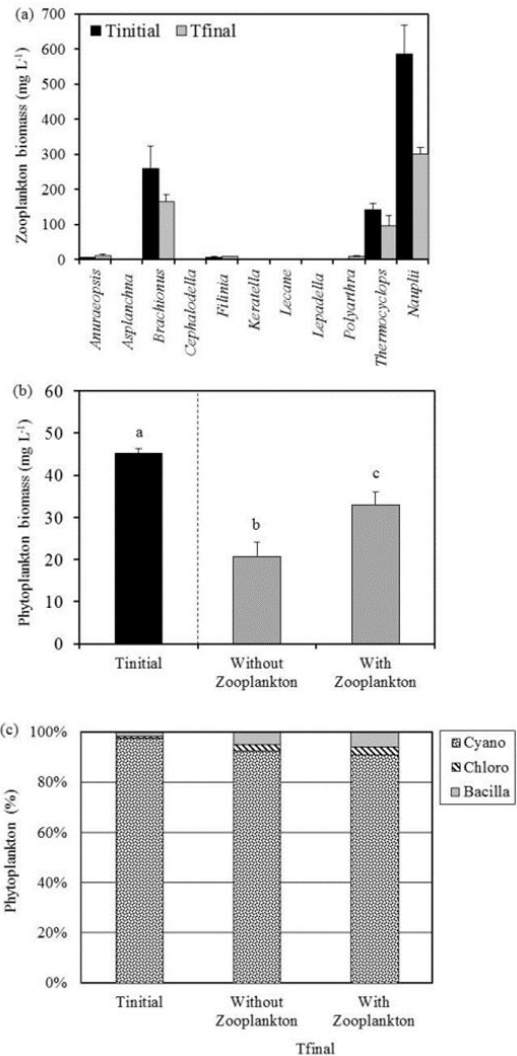
increase in biomass of cyanobacteria *Raphidiopsis raciborskii* in the presence of zooplankton.

### 3.2. Mundaú reservoir

Twelve zooplankton taxa were identified at  $T_{\text{Initial}}$  of the experiment, belonging to Rotifera (92%), and Copepoda (8%, adults and nauplii). Total biomass was  $1003.90 \pm 171.17 \text{ mg.L}^{-1}$ , with dominance of *Brachionus* ( $259.60 \pm 64.15 \text{ mg.L}^{-1}$ ), *Thermocyclops* ( $142.40 \pm 18.84 \text{ mg.L}^{-1}$ ), and nauplii ( $585.95 \pm 83.33 \text{ mg.L}^{-1}$ ) (Figure 2a). At  $T_{\text{Final}}$  we



**Figure 1.** Zooplankton biomass (a), total phytoplankton biomass (b), and relative biomass of phytoplankton classes (c) in experiments at Apipucos reservoir.  $T_{\text{Initial}}$  = Begin of experiment;  $T_{\text{Final}}$  = End of experiment. Bars represent standard errors of the mean ( $\pm$ SEM). In Figure b, columns with the same letter do not differ significantly ( $p < 0.05$ ). Cyano = Cyanophyceae, Chloro = Chlorophyceae, Bacilla = Bacillariophyceae, Eugle = Euglenophyceae, Crypto = Cryptophyceae.



**Figure 2.** Zooplankton biomass (a), total phytoplankton biomass (b), and relative biomass of phytoplankton classes (c) in experiments at Mundaú reservoir.  $T_{\text{Initial}}$  = Begin of experiment;  $T_{\text{Final}}$  = End of experiment. Bars represent standard errors of the mean ( $\pm$ SEM). In Figure b, columns with the same letter do not differ significantly ( $p < 0.05$ ). Cyano = Cyanophyceae, Bacilla = Bacillariophyceae, Chloro = Chlorophyceae.

observed total biomass of  $190.24 \pm 58.03 \text{ mg.L}^{-1}$  and a reduction of *Brachionus* ( $p = 0.04071$ ) and nauplii biomass ( $p = 0.002151$ ) (Figure 2a).

The phytoplankton community was composed of 11 taxa belonging to Cyanophyceae (46%), Chlorophyceae (27%), and Bacillariophyceae (27%) (Table 2). The total biomass was  $45.31 \pm 0.85 \text{ mg.L}^{-1}$ , with the dominance of cyanobacteria *R. raciborskii* (Table 2). The total biomass of phytoplankton showed a significant difference between treatments ( $F = 30.53$  and  $p = 0.00072$ ) (Figure 2b). The relative biomass showed that Cyanophyceae dominated over the other phytoplankton classes at  $T_{\text{Initial}}$  and in treatments with and without zooplankton at  $T_{\text{Final}}$ , however, there was a slight reduction in Cyanophyceae biomass at the  $T_{\text{Final}}$  compared to  $T_{\text{Initial}}$  (Figure 2c).

Regarding the phytoplankton species, we observed a significant reduction in biomass

of cyanobacteria *R. raciborskii*, *Geitlerinema amphibium* (C.Agardh ex Gomont) Anagnostidis, *Merismopedia tenuissima* Lemmermann, and the diatom *C. meneghiniana* at  $T_{\text{Final}}$  in the presence and absence of zooplankton compared to  $T_{\text{Initial}}$  (Table 2). Although no significant results were observed in the *R. raciborskii* biomass between treatments with and without zooplankton, an increase in the biomass of this cyanobacteria has been verified in the presence of zooplankton at the end of the experiment (Table 2). Differently, the cyanobacteria *Microcystis aeruginosa* (Kützing) Kützing, the chlorophyte *Monoraphidium griffithii* (Berkeley) Komárková-Legnerová and other chlorophytes, and the diatom *A. granulata* had their biomass increased in the presence of zooplankton, as compared to treatment without zooplankton at the end of the experiment (Table 2).

**Table 1.** Phytoplankton biomass ( $\text{mg.L}^{-1}$ ) and standard error of the mean ( $\pm\text{SEM}$ ) at the beginning of the experiment ( $T_{\text{Initial}}$ ) and the end of the experiment with and without zooplankton ( $T_{\text{Final}}$ ) at Apipucos reservoir.

Taxa	$T_{\text{Initial}}$	Treatments ( $T_{\text{Final}}$ )		p-value
		Without Zooplankton	With Zooplankton	
<b>Cyanophyceae</b>				
<i>Raphidiopsis raciborskii</i>	$0.19 \pm 0.12^a$	$0.19 \pm 0.11^a$	$1.01 \pm 0.20^b$	0.0124
<i>Geitlerinema amphibium</i>	$0.16 \pm 0.02^a$	$0.77 \pm 0.16^b$	$0.22 \pm 0.07^a$	0.00943
<i>Merismopedia tenuissima</i>	$1.37 \pm 0.18$	$0.64 \pm 0.22$	$1.64 \pm 0.44$	n.s.
<i>Sphaerospermopsis aphanizomenoides</i>	$0.00 \pm 0.00$	$0.04 \pm 0.04$	$0.00 \pm 0.00$	n.s.
Others Cyanophyceae	$0.04 \pm 0.02$	$0.05 \pm 0.01$	$0.03 \pm 0.01$	n.s.
<b>Bacillariophyceae</b>				
<i>Aulacoseira granulata</i>	$0.33 \pm 0.07$	$0.40 \pm 0.23$	$0.13 \pm 0.07$	n.s.
<i>Cyclotella meneghiniana</i>	$10.58 \pm 0.98^a$	$19.16 \pm 1.73^b$	$5.50 \pm 1.62^a$	0.00179
<i>Ulnaria ulna</i>	$0.28 \pm 0.04$	$0.72 \pm 0.10$	$0.83 \pm 0.01$	n.s.
Others Bacillariophyceae	$0.07 \pm 0.05$	$0.00 \pm 0.00$	$0.00 \pm 0.00$	n.s.
<b>Chlorophyceae</b>				
<i>Chlamydomonas</i> sp.	$0.13 \pm 0.01^a$	$0.11 \pm 0.02^a$	$0.04 \pm 0.01^b$	0.00195
<i>Desmodesmus protuberans</i>	$1.29 \pm 0.14^a$	$2.66 \pm 0.41^{ab}$	$3.04 \pm 0.45^b$	0.031
<i>Desmodesmus quadricauda</i>	$1.68 \pm 0.53^a$	$5.57 \pm 1.50^b$	$2.44 \pm 0.19^{ab}$	0.0537
<i>Dictyosphaerium pulchellum</i>	$0.08 \pm 0.03$	$0.07 \pm 0.01$	$0.06 \pm 0.02$	n.s.
<i>Micractinium pusillum</i>	$0.29 \pm 0.06$	$0.71 \pm 0.24$	$0.23 \pm 0.02$	n.s.
<i>Pediastrum duplex</i>	$4.83 \pm 0.23$	$6.50 \pm 1.41$	$7.29 \pm 1.10$	n.s.
<i>Scenedesmus acuminatus</i>	$0.59 \pm 0.06^a$	$1.07 \pm 0.12^b$	$0.83 \pm 0.01^{ab}$	0.0134
Others Chlorophyceae	$0.82 \pm 0.04$	$1.29 \pm 0.23$	$0.95 \pm 0.07$	n.s.
<b>Euglenophyceae</b>				
<i>Phacus</i> sp.	$0.13 \pm 0.07$	$0.20 \pm 0.12$	$0.13 \pm 0.07$	n.s.
<i>Trachelomonas volvocina</i>	$0.53 \pm 0.05$	$0.50 \pm 0.06$	$0.51 \pm 0.12$	n.s.
Others Euglenophyceae	$0.12 \pm 0.10$	$0.12 \pm 0.10$	$0.11 \pm 0.10$	n.s.
<b>Cryptophyceae</b>				
<i>Cryptomonas erosa</i>	$0.07 \pm 0.01$	$0.09 \pm 0.02$	$0.02 \pm 0.01$	n.s.
Others Cryptophyceae	$0.12 \pm 0.12$	$0.00 \pm 0.00$	$0.22 \pm 0.21$	n.s.

P-values represent statistical results of ANOVA *one-way*. Different letters indicate significant differences between the means ( $p < 0.05$ ). "n.s. = no significative".

**Table 2.** Phytoplankton biomass (mg.L<sup>-1</sup>) and standard error of the mean ( $\pm$ SEM) at the beginning of the experiment (T<sub>Initial</sub>) and the end of the experiment with and without zooplankton (T<sub>Final</sub>) at Mundaú reservoir.

Taxa	T <sub>Initial</sub>	Treatments (T <sub>Final</sub> )		p-value
		Without Zooplankton	With Zooplankton	
<b>Cyanophyceae</b>				
<i>Raphidiopsis raciborskii</i>	42.34 $\pm$ 0.68 <sup>a</sup>	18.53 $\pm$ 3.97 <sup>b</sup>	27.79 $\pm$ 0.82 <sup>b</sup>	0.022651
<i>Geitlerinema amphibium</i>	0.85 $\pm$ 0.06 <sup>a</sup>	0.21 $\pm$ 0.05 <sup>b</sup>	0.14 $\pm$ 0.04 <sup>b</sup>	0.000129
<i>Merismopedia tenuissima</i>	0.11 $\pm$ 0.01 <sup>a</sup>	0.04 $\pm$ 0.02 <sup>b</sup>	0.01 $\pm$ 0.01 <sup>b</sup>	0.00248
<i>Microcystis aeruginosa</i>	0.95 $\pm$ 0.03 <sup>a</sup>	0.11 $\pm$ 0.04 <sup>b</sup>	2.16 $\pm$ 0.44 <sup>c</sup>	0.02651
<i>Sphaerospermopsis aphanizomenoides</i>	0.00 $\pm$ 0.00	0.24 $\pm$ 0.24	0.00 $\pm$ 0.00	n.s.
Others Cyanophyceae	0.01 $\pm$ 0.00	0.01 $\pm$ 0.00	0.01 $\pm$ 0.00	n.s.
<b>Chlorophyceae</b>				
<i>Coelastrum microporum</i>	0.00 $\pm$ 0.00	0.09 $\pm$ 0.09	0.17 $\pm$ 0.17	n.s.
<i>Monoraphidium griffithii</i>	0.00 $\pm$ 0.00 <sup>a</sup>	0.00 $\pm$ 0.00 <sup>a</sup>	0.08 $\pm$ 0.03 <sup>b</sup>	0.02113
<i>Scenedesmus acuminatus</i>	0.10 $\pm$ 0.00	0.36 $\pm$ 0.14	0.43 $\pm$ 0.04	n.s.
Others Chlorophyceae	0.11 $\pm$ 0.02 <sup>a</sup>	0.11 $\pm$ 0.06 <sup>a</sup>	0.38 $\pm$ 0.06 <sup>b</sup>	0.0137
<b>Bacillariophyceae</b>				
<i>Aulacoseira granulata</i>	0.26 $\pm$ 0.02 <sup>a</sup>	0.06 $\pm$ 0.06 <sup>a</sup>	0.71 $\pm$ 0.10 <sup>b</sup>	0.00177
<i>Cyclotella meneghiniana</i>	0.28 $\pm$ 0.01 <sup>a</sup>	0.06 $\pm$ 0.06 <sup>b</sup>	0.02 $\pm$ 0.02 <sup>b</sup>	0.00696
<i>Ulnaria ulna</i>	0.31 $\pm$ 0.01	0.91 $\pm$ 0.30	1.27 $\pm$ 0.27	n.s.

P-values represent statistical results of ANOVA *one-way*. Different letters indicate significant differences between the means ( $p < 0.05$ ). "n.s. = no significative".

#### 4. Discussion

In the present study, we observed zooplankton from tropical reservoirs controlling phytoplankton biomass. Zooplankton proved to be an important factor in modifying the structure of the phytoplankton community, especially in the Apipucos reservoir, where the presence of zooplankton reduced the total phytoplankton biomass and increased biomass of *R. raciborskii*. Even though the Mundaú reservoir had higher phytoplankton and zooplankton biomass, it showed weak trophic links between these communities, since the presence of the zooplankton doesn't significantly reduce any phytoplankton taxon. However, zooplankton showed positive effects on *M. aeruginosa* biomass.

Despite the high biomass of zooplankton in the Mundaú reservoir, the occurrence of cyanobacterial blooms certainly explains the slight effect of predation on phytoplankton in this environment during the experiment. Studies show that cyanobacteria are not a good food source for zooplankton (Chalar, 2009), this can weaken trophic relationships (Heathcote et al., 2016). The size of filaments or colonies are factors that can suppress the top-down control of zooplankton over cyanobacteria by reducing the feeding efficiency of consumers (Lampert, 1987), mainly when zooplankton is dominated by rotifers. Moreover,

the cyanobacteria reduce both the phytoplankton diversity in aquatic ecosystems where they form blooms and the heterogeneity of food that can be used by zooplankton (Wang et al., 2009). Under these conditions, zooplankton directly affects the trophic web because it uses other food sources such as microzooplankton (heterotrophic protozoa – ciliates, heterotrophic flagellates, and other heterotrophic organisms) under high biomass of non-nutritive algae, e.g., cyanobacteria (Ger et al., 2016).

Unlike cyanobacteria, heterotrophic protozoa produce high amounts of fatty acids, implying the inhibition of zooplankton grazing on phytoplankton, and consequent increase in algae biomass and reduction in heterotrophic protozoa (Stoecker & Pierson, 2019). Moreover, heterotrophic protozoa can ingest toxic cyanobacteria (e.g., *Microcystis*) since they can coexist with them, and promote increased biodiversity of the phytoplankton community (Zhang et al., 2020). Thus, microzooplankton plays a fundamental role in the trophic web and the microbial loop.

In the Apipucos reservoir, the high diversity of phytoplankton species with high biomass taxa that is highly susceptible to herbivores such as *C. meneghiniana* (James & Forsyth, 1990), and the presence of taxa with high nutritional quality for zooplankton, as *Chlamydomonas* sp. (Santer

& van den Bosch, 1994) and *Cryptomonas erosa* (von Ruckert & Giani, 2008), was important for establishing the high degree of zooplankton coupling in this environment. Therefore, as reported by Danielsdottir et al. (2007) and von Ruckert & Giani (2008), both the concentration, in terms of density or biomass, and the phytoplankton composition, containing taxa with different nutritional quality, are essential for maintaining the zooplankton populations and natural processes of energy transfer in aquatic food webs.

The increase in phytoplankton biomass, especially cyanobacteria in treatments with zooplankton, demonstrates the importance of the indirect effect of herbivory in tropical reservoirs, as shown by Hong et al. (2013) and Leitão et al. (2018). Such approach has been the focus of many studies, especially those which advocate the hypothesis that states the maintenance of perennial cyanobacteria blooms in tropical reservoirs is partially due to competitive advantage for nutrients by cyanobacteria with a reduction in the biomass of other algal species that are preferably predated by zooplankton in that region (Mitra & Flynn, 2006; Wang et al., 2010; Ger et al., 2014).

The substitution of cladocerans and Calanoid copepods for rotifers can occur because of increased eutrophication, which consequently favors increased cyanobacteria (Borges et al., 2010). Furthermore, eutrophication can also lead to the dominance of Cyclopoid copepods in several reservoirs (Jeppesen et al., 2000) as a result of their feeding habits (Soto & Hurlbert, 1991; Hansson et al., 2007). In addition to the ability to consume algae (Tønno et al., 2016) and other zooplankton (Andrade & López, 2005) through their ambush feeding habit, cyclopoid copepods show better performance in food activity under low light availability (Kandathil Radhakrishnan et al., 2020). This may explain the success of cyclopoid copepods in coexisting with cyanobacterial blooms, which commonly reduce the penetration of light into the water column. In our study, the rotifer *Brachionus* and cyclopoid copepod *Thermocyclops* (in the nauplii and adult stages) were the most abundant zooplankton taxa in the Mundaú and Apipucos reservoirs, respectively.

*Brachionus* species can simultaneously collect food particles of small size and process larger cells individually (Pagano, 2008), as well as select or reject particles according to their quality and quantity (Gilbert & Starkweather, 1977). Studies by Starkweather & Kellar (1983), Soares et al. (2010),

and Kâ et al. (2012) show that *Brachionus* species, typical to tropical environments (*B. angularis*, *B. calyciflorus*, and *B. falcatus*), can consume filamentous cyanobacteria, such as *R. raciborskii* and *Anabaena flos-aquae* Brébisson ex Bornet & Flauhault. Regarding colonial cyanobacteria, such as *Microcystis aeruginosa*, Kâ et al. (2012) showed that zooplankton of different taxonomic groups, including *Brachionus*, were not able to consume this cyanobacteria. Such results are similar to those found in Mundaú, where the dominant zooplankton (*Brachionus*) favored the *M. aeruginosa* biomass and reduced the *R. raciborskii* biomass. In contrast, Soares et al. (2010) showed the potential of *B. calyciflorus* to ingest *Microcystis*, even though population growth was not supported when exposed to a diet made of only these cyanobacteria.

In turn, the copepod *Thermocyclops* shows several eating habits depending on its life stage and is a filter feeder during the nauplii stadium, consuming small algae, while as an adult is omnivorous with the raptorial eating habit (Gliwicz, 2004). However, Hopp et al. (1997) showed experimentally that many adult cyclopoids, including *Thermocyclops*, manage to survive on a diet composed of only algae, and present higher reproductive performance and longevity when exposed to a mixed diet, consisting of rotifers, copepod nauplii, small copepodites, and large phytoplankton forms.

In our study, we observed an increase of *R. raciborskii* in the presence of zooplankton in the Apipucos experiment, with *Thermocyclops* as the dominant species. Leitão et al. (2018) showed that copepods can promote the dominance of cyanobacteria, however, this study evaluated the effects of the Calanoid copepod *Notodiaptomus iheringi* (Wright, 1935) on *M. aeruginosa*. Differently, Leitão et al. (2020) showed that *N. iheringi* can efficiently control the biomass of *R. raciborskii*, while *Thermocyclops decipiens* (Kiefer, 1929), although not have a top-down effect on the biomass of *R. raciborskii*, can reduce the length of filaments, facilitating the top-down control of *N. iheringi*.

In the Mundaú reservoir, the high biomass of *R. raciborskii* negatively affected the *Thermocyclops* biomass, nevertheless, at the end of the experiment there was a small reduction in Cyanophyceae biomass in the zooplankton treatment. According to Gebrehiwot et al. (2019), *T. decipiens* can ingest *R. raciborskii* through the fragmentation of long filaments but can negatively affect the survival and growth of zooplankton when cyanobacteria are



the only food source. Meanwhile, the reduction of *Thermocyclops* observed in our results may not have been related to poor food (cyanobacteria), but rather to acclimatization time. Also, treatment with edible prey for zooplankton was not maintained during the experiment, making it impossible to analyze the direct effects of cyanobacteria on zooplankton.

In the Pampulha reservoir, located in the Southeastern region of Brazil, von Rückert & Giani (2008) observed a weak interaction between phytoplankton and zooplankton, possibly due to the use of other non-algal food sources by *T. decipiens*, the dominant zooplankton species. The reduction of *Thermocyclops* biomass in nauplii stadium herein may be due to predation by adult organisms of this taxon, as noted by Carvalho (1984). Furthermore, *Thermocyclops* can consume the nauplii of its species, even when offered other food types, like other zooplankton species and microalgae. However, these results are not conclusive and were unable to determine a predation interaction between these taxa. Moreover, we cannot rule out the possibility that the laboratory conditions could have influenced our results. Therefore, further studies are required to evaluate the direct relationship between these taxa.

In conclusion, the zooplankton reduced the phytoplankton biomass in the reservoir with the dominance of diatoms and green algae, which supports the importance of the phytoplankton community structure on the strength of trophic interactions in the tropics. Phytoplankton biomass reduction was observed for the taxa of diatoms, green algae, and unicellular or colonial cryptomonads of small size. On the other hand, cyanobacteria and large colonial chlorophytes were not adversely affected when exposed to zooplankton. *R. raciborskii* and *M. aeruginosa* commonly formed blooms in the reservoirs and increased biomass in the presence of zooplankton. These results emphasize the framework of other studies (Wang et al., 2010; Leitão et al., 2018), which support that tropical zooplankton plays an important role in maintaining cyanobacterial blooms.

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