

Cyanobacteria dominance drives zooplankton functional dispersion

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Abstract Accelerated eutrophication reduces water quality and shifts plankton communities. However, its effects on the aquatic food web and ecosystem functions remain poorly understood. Within this context, functional ecology can provide valuable links relating community traits to ecosystem functioning. In this study, we assessed the effects of eutrophication and cyanobacteria blooms on zooplankton functional diversity in a tropical hypereutrophic lake. Phytoplankton and zooplankton communities and

limnological characteristics of a tropical Brazilian Lake (Southeast, Brazil) were monitored monthly from April 2013 to October 2014. Lake eutrophication indicators were total phosphorus, total chlorophyll-a, and chlorophyll-a per group (blue, green, and brown). The variation of major phytoplankton taxonomic group biomass was calculated and used as a proxy for changes in phytoplankton composition. Zooplankton functional diversity was assessed through functional dispersion and the community-weighted mean trait value. Regressions were performed between the lake eutrophication indicators, the phytoplankton biomass variation, and zooplankton functional dispersion. Our results suggest that eutrophication and cyanobacterial dominance change the composition of zooplankton traits and reduce functional dispersion, leading to zooplankton niche overlap. These findings

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are important because they provide a meaningful view of phytoplankton-zooplankton trophic interactions and contribute to an improved understanding their functional effects on aquatic ecosystems.

Keywords Plankton · Freshwater · Biodiversity · Eutrophication · Microbial food quality

Introduction

Eutrophication is a globally recurrent problem in aquatic ecosystems due to increased nutrient inputs (Paerl et al., 2001). For instance, nitrogen and phosphorus enrichment coupled with rising water temperatures can especially favor cyanobacteria blooms, which may negatively impact ecosystem functioning and services (Moss et al., 2011; Paerl & Paul, 2012). These impacts are related to changes in water physical and chemical conditions, such as oxygen depletion, the presence of toxins, and also changes in aquatic community structure and food webs disruption (Paerl & Huisman, 2009).

Cyanobacterial blooms represent a decrease in the overall food quality for herbivorous zooplankton and often reduce zooplankton fitness (Ghadouani et al., 2003). Cyanobacteria are a nutritionally inadequate food source for zooplankton due to their low concentration of fatty acids and sterols (Müller-Navarra et al., 2000). During blooms, a decrease in the biomass of edible eukaryotic phytoplankton likely reduces the quantity of good quality prey for herbivorous zooplankton (Ahlgren et al., 1992). In high abundance, cyanobacteria are known to negatively affect zooplankton fitness by the obstruction of their filtering apparatus (DeMott et al., 2001) or acute toxicity (DeMott et al., 1991; Soares et al., 2009). Cyanobacteria may also have negative sub-lethal effects on the fitness of herbivorous zooplankton (Lüring, 2003; Engström-Öst et al., 2015; Kosiba et al., 2018). However, due to the large genotypic and phenotypic variability in responses, some zooplankton species can be tolerant to cyanobacteria toxins or even benefit from their presence (Wilson et al., 2006). Moreover, some mixotrophic protozoan grazers are resistant to cyanobacterial toxins and can upgrade the food quality of cyanobacterial detritus for metazoan zooplankton (Bec et al., 2006; Yang et al., 2006). Finally, previous

exposure to blooms has been linked to genotypic and phenotypic adaptations for improved zooplankton tolerance, highlighting the role of local adaptation of zooplankton to cyanobacterial blooms (Hairston et al., 2001; Sarnelle & Wilson, 2005). Consequently, the response of zooplankton to cyanobacteria is expected to vary depending on bloom history.

Phytoplankton is generally considered to be the most important environmental filter for the determination of zooplankton community distribution (Vogt et al., 2013). The complexity of cyanobacteria-zooplankton interactions, however, makes it difficult to predict the effect of blooms on zooplankton communities, especially in warmer climates where blooms can be permanent (Bouvy et al., 2001). In general, longer duration of cyanobacteria blooms has been associated to zooplankton communities dominated by small and selective grazing species in detriment of large generalist herbivores like *Daphnia* (Panosso et al., 2003; Hansson et al., 2007, Rangel et al. 2016). Yet, the effect of cyanobacteria blooms on the overall structure and function of zooplankton communities is poorly understood.

Recently, functional traits have been a promising approach for studying the link between communities and their ecological function (Hébert et al., 2016, 2017). Functional traits can be any morphological, physiological or behavioral characteristic describing an organisms' response to environmental interactions or conditions (i.e. response traits; Díaz & Cabido, 2001; Violle et al., 2007) or those related to the role of organisms in the ecosystem processes (i.e., effect traits; Violle et al., 2007). Among the multitude of functional traits in zooplankton, body size, grazing mode, and trophic position are considered as key traits because they regulate multiple ecological functions including nutrient cycling, respiration, herbivory rates, and cascading top-down control of phytoplankton biomass (Litchman et al., 2013; Hébert et al., 2016, 2017).

Although various theoretical or experimental studies have evaluated the effects of cyanobacteria on zooplankton, most of these are at the individual or population level (Panosso et al., 2003; Ger et al., 2011, 2016). Hence, how cyanobacteria dominance affects the community functional diversity of zooplankton remains poorly understood. Accordingly, the goal of this study is to better understand how zooplankton functional diversity responds to temporal

shifts in phytoplankton resources and especially the dominance of cyanobacteria in a tropical hypertrophic tropical lake. We tested the hypothesis that higher phytoplankton homogeneity due to cyanobacteria dominance would reduce the functional trait diversity of the zooplankton community and also increase zooplankton functional trait dispersion.

Materials and methods

Study area

Lake Mariano Procópio (21°44'S, 43°21'W) is a small (area of 1.1 ha) and shallow (maximum depth 1.2 m) pond in the urban area of Juiz de Fora, Minas Gerais state, Brazil. The regional climate is classified as Cwa in the Köppen's climate classification system (Alvares et al., 2014), with hot-rainy summers and cool-dry winters. The mean annual rainfall is 1536 mm, and the mean annual temperature is 18°C (data from the Laboratory of Climatology and Environmental Analysis—Department of Geosciences/UFJF). The lake is classified as hypereutrophic, with the dominance of cyanobacteria *Microcystis* spp. and sporadic blooms of *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju (Miranda et al., 2017). In the lake, we found the occurrence of fish of the genera *Cyprinus* sp. (herbivorous), *Prochilodus* sp. (detritivorous), and *Hoplias* sp. (carnivorous).

Sampling and analytical methods

Samples of phytoplankton and zooplankton communities and limnological attributes were monthly taken from April 2013 to October 2014 in two stations within the Lake Mariano Procópio: station 1—located in a canal-like region and station 2—located in central and deepest area of the lake (for more details see Miranda et al., 2017).

Water temperature, turbidity, and dissolved oxygen (DO) were measured in situ using a YSI 6920A probe, and water transparency using a Secchi disk (SD). The euphotic zone (zeu) was estimated as 2.7 times the Secchi disk extinction depth. Water samples for analysis of total phosphorus (TP), dissolved phosphorus (soluble reactive phosphorus—SRP, filtered through Whatman GF/C filters) were collected and frozen at −4°C until the analysis. Laboratory analysis

for TP and SRP were performed according to standard spectrophotometric techniques (Wetzel & Likens, 1990). Total cyanobacterial and eukaryotic algae chlorophyll-a were measured in situ using a phytoplankton analyzer (PHYTO-PAM). Chlorophyll-a concentration was measured for the total chlorophyll-a (total Chl a) and the main algal groups, blue-green (Blue Chl a), green (Green Chl a), and brown (Brown Chl a) as determined by the fluorescence readings at four wavelengths (470, 520, 645, and 665 nm, respectively) (Schreiber, 1998).

Phytoplankton was sampled at the subsurface (~0.10 m) of the water column using a vial of 100 ml capacity. And the samples were immediately preserved with Lugol's solution. The phytoplankton abundance was estimated using an Olympus IX71 inverted microscope using the settling technique (Utermöhl, 1958). The units (cells, filaments, and colonies) were counted at 400× magnification in random fields at least to 100 specimens of the most frequent species (error < 20%, $P < 0.05$, Lund et al., 1958). Colonies and filaments were multiplied by the mean number of cells per colony or filament to estimate the cell numbers. Phytoplankton was identified at the species level and categorized as major taxonomic groups: according to Komárek and Anagnostidis (1998, 2005) to cyanobacteria and van den Hoek et al. (1995) to others phytoplankton groups. Phytoplankton specific biomass was expressed as fresh weight (mg l^{-1}), estimated from the product of the population and the mean unit volume of each species (Hillebrand et al., 1999), assuming a specific density of phytoplankton cells of 1 g cm^{-3} . The mean cell size was based on measurements of at least 30 individuals. Phytoplankton monthly heterogeneity was assessed by the phytoplankton biomass variation (PBV), that is, the variance of the biomass of the main phytoplankton groups found in each month (i.e., Cyanobacteria, Bacillariophyceae, Chrysophyceae, Cryptophyceae, Xanthophyceae, Euglenophyceae, Chlorophyceae, and Zygnematophyceae). The variance was calculated according to Eq. 1. Lower PBV represents greater phytoplankton community heterogeneity while greater PBV represents the dominance of some phytoplanktonic group.

$$\text{Variance} = \sum (x - \bar{x})^2 / (n - 1) \quad (1)$$

where x is the sample, \bar{x} is the mean and n is the sample size.

Zooplankton community was sampled from 100 l of water poured into a plankton net (68 μm mesh) with the help of a bucket with 10 l capacity. Zooplankton samples were preserved in the field with 4% formalin solution. In the laboratory, zooplankton samples were counted in a Sedgewick-Rafter chamber under a microscope (Olympus BX41) and were identified as the lowest possible taxonomic units. Immature copepods (nauplii and copepodites) were classified only in Cyclopoida or Calanoida. Zooplankton density (ind. l^{-1}) was estimated by triplicate aliquots of samples counted in Sedgewick–Rafter chambers and species richness according to the number of species in a sample. The mean body size of each species was based on measurements of at least 20 individuals. Rotifera biomass was expressed as dry weight and estimate according to Ruttner-Kolisko (1977), and both Copepoda and Cladocera biomass were estimated according to Dumont et al. (1975).

Zooplankton functional diversity was calculated using indexes based on four traits: adult body size (continuous), trophic group (herbivorous, carnivorous, detritivore, or omnivorous; categorical), feeding type (raptorial, microphagous filter-feeders, Bosminidae filter-feeders, or stationary suspension-feeders; categorical), and reproduction form (sexual or asexual) (see supplementary material). Zooplankton traits were selected based on literature reviews synthesizing laboratory and observational work on feeding and life history of zooplankton (Kiørboe, 2011; Obertegger et al., 2011; Litchman et al., 2013). These selected traits represent the community functional organization as a response to changes in the phytoplanktonic food resource, as well as changes in zooplanktonic performance in ecosystem processes such as top-down phytoplankton control and nutrient cycling among trophic levels (Hébert et al., 2016, 2017). Zooplankton body size was measured during sample counting, and a mean body size value was used to each zooplankton species. Others traits of zooplankton species were taken from the literature.

Data analysis

The functional diversity index used was functional dispersion (FDis) which is the average distance of

each species to the centroid of all species in the multidimensional trait space taking into account the relative abundances of species. FDis index was calculated using Gower dissimilarity method modified by Pavoine et al. (2009). The community-weighted mean of functional traits (CWM) was also calculated to synthesize changes in mean values of traits within communities associated with changes in environmental conditions. CWM represents the average for each trait weighted by its relative abundance in the community (Pla et al., 2011). Functional diversity measures (FDis and CWM) were performed using R programming version 3.2.2 (R Core Team 2015) using packages FD (Laliberté & Legendre, 2010; Laliberté et al., 2014).

Linear regressions were performed to test the influence of TP concentrations on phytoplankton total Chl a, and Ch a per group. In addition, a series of linear regressions were done to test TP influence on zooplankton biomass. To relate phytoplankton monthly heterogeneity with zooplankton functional diversity we regressed PBV (predictive variable) against FDis (response variable) to evaluate the occurrence of linear or quadratic relationships. Regressions were performed using Sigmaplot version 12.2 (Systat Software, Inc).

Results

Along the period sampled, the hypereutrophic lake exhibited stable thermal and DO conditions. Water temperature average was $20.87 \pm 2.85^\circ\text{C}$ (mean \pm standard deviation) with higher values in January 2014 (26°C) and lower in July 2013 (16°C). DO concentrations varied to 5.10 mg l^{-1} (January 2014) to 9.65 mg l^{-1} (October 2013) with an average of $7.07 \pm 1.18 \text{ mg l}^{-1}$. TP concentrations ranged from $155.53 \mu\text{g l}^{-1}$ (January 2014) to $452.22 \mu\text{g l}^{-1}$ (October 2014) and SRP from $5.46 \mu\text{g l}^{-1}$ (April 2013) to $121.59 \mu\text{g l}^{-1}$ (August 2014). Total Chl a ranged from $124.85 \mu\text{g l}^{-1}$ (September 2014) to $626.76 \mu\text{g l}^{-1}$ (October 2014) and Chl a for Blue (cyanobacteria) had the highest values, ranging from $58.93 \mu\text{g l}^{-1}$ to $569.75 \mu\text{g l}^{-1}$ (Table 1).

Phytoplankton total biomass varied from 26.60 to 90.38 mg l^{-1} (Table 1). Cyanobacteria was dominant along most of the period, except in July 2013, when diatoms dominated (Fig. 1A). The percentage of

Table 1 Minimum, maximum, mean and standard deviation (SD) values of limnological characteristics, total chlorophyll-a concentration (Total Chl a), chlorophyll-a per groups (Blue Chl a, Green Chl a, and Brown Chl a), zooplankton total biomass,

phytoplankton total biomass and phytoplankton groups biomass variation (PBV) in the Lake Mariano Procópio from April 2013 to October 2014

	Minimum	Maximum	Mean \pm SD
Maximum depth (m)	0.75	1.00	0.92 \pm 0.78
Euphotic zone (m)	0.30	0.75	0.57 \pm 0.11
Water temperature ($^{\circ}$ C)	16.03	26.04	20.87 \pm 2.85
DO (mg l $^{-1}$)	5.10	9.65	7.07 \pm 1.18
TP (μ g l $^{-1}$)	155.53	452.22	256.62 \pm 57.85
SRP (μ g l $^{-1}$)	5.46	121.59	27.78 \pm 33.14
Total Chl a (μ g l $^{-1}$)	124.85	626.76	247.29 \pm 114.13
Blue Chl a (μ g l $^{-1}$)	58.93	569.75	170.62 \pm 116.23
Green Chl a (μ g l $^{-1}$)	< 0.001	90.02	33.78 \pm 13.69
Brown Chl a (μ g l $^{-1}$)	10.03	57.01	45.23 \pm 21.72
Phytoplankton total biomass (mm 3 l $^{-1}$)	26.60	90.38	48.46 \pm 14.58
PBV of phytoplankton biomass	20.15	279.73	109.03 \pm 85.17
Zooplankton total density (ind. l $^{-1}$)	50.85	1373.67	434.49 \pm 355.40
Zooplankton total biomass (mg DW. l $^{-1}$)	22.00	858.27	117.95 \pm 185.61
Zooplankton functional dispersion (FDis)	0.02	0.46	0.23 \pm 0.14

DO dissolved oxygen, TP total phosphorus, SRP soluble reactive phosphorus (PO $_4^{3-}$)

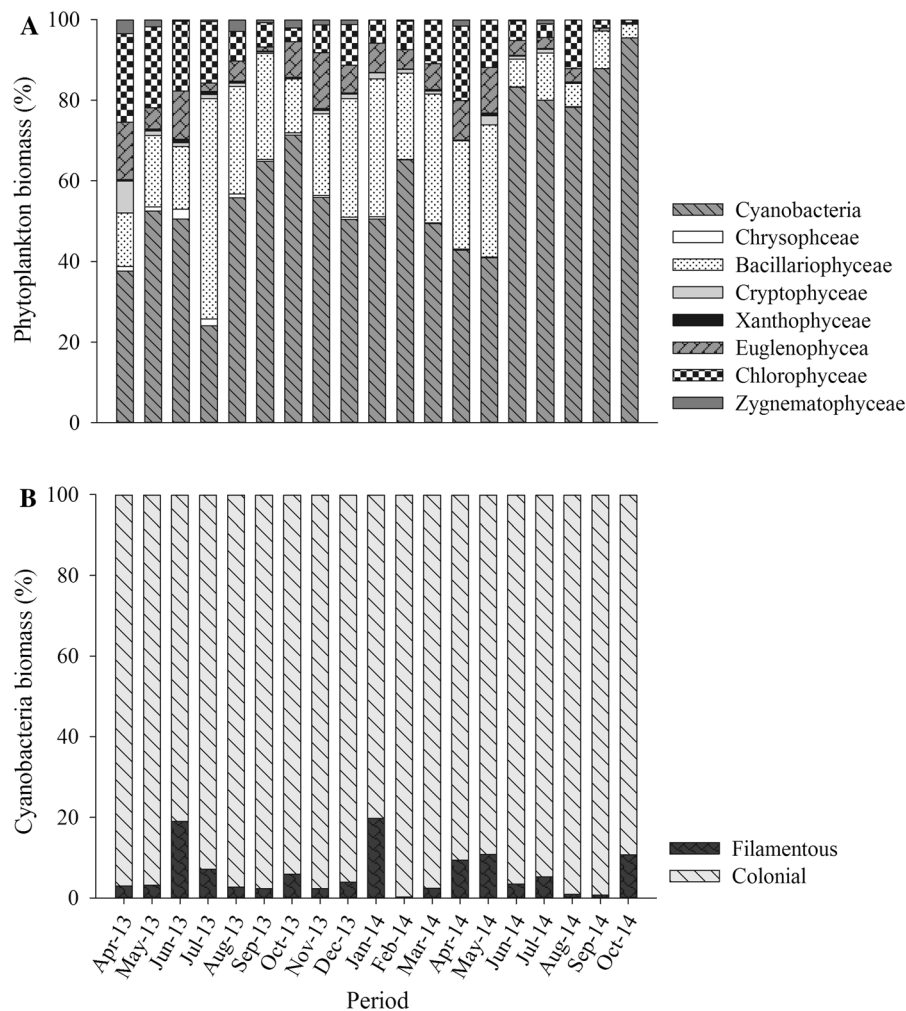
cyanobacteria biomass in relation to the other phytoplankton groups varied of 38% (April 2013) to 95% (October 2014). Nine species of colonial and filamentous cyanobacteria were registered during the study, with main contribution of *Microcystis aeruginosa* Kützing, *Merismopedia tenuissima* Lemmermann, *Aphanocapsa delicatissima* West and West, and *Synechococcus nidulans* (Pringsheim) Komárek in Bourrelly. The biomass of colonial cyanobacteria species was higher than filamentous species along the entire period (> 80%; Fig. 1B). The total Cyanobacteria PBV value varied along sampled months and ranged from 20.16 to 279.73 (Table 1). PBV and was mostly biased by cyanobacteria biomass. Lower PBV values were related to a greater distribution of the phytoplanktonic biomass between the different groups.

Zooplankton density varied from 50.85 to 1373.67 ind l $^{-1}$ and zooplankton biomass varied from 22.00 mg DW l $^{-1}$ to 858.27 mg DW l $^{-1}$ (Table 1). In general, there was a dominance of immature Copepoda Cyclopoida and Rotifera species, both in density and biomass (Fig. 2), with the main contribution of nauplii and Cyclopoida copepodite, and

Rotifera species *Brachionus falcatus* Zacharias, 1898; *Filinia opoliensis* Zacharias, 1898; and *Epiplanes* sp. Zooplankton CWM values, obtained for each functional trait, were very similar in the first four months (April, May, June, and July 2013) of sampling but showed substantial variation in the rest of the period (Fig. 3). There was a dominance of zooplankton species with small body sizes, except in the last month (October 2014), when organisms with high body sizes were found (Fig. 3A). Zooplankton species mostly belonged to omnivorous, herbivorous and detritivore trophic groups (Fig. 3B). Zooplankton feeding types were mostly raptorial and microphagous filter-feeders, except for the last three months, when Bosminidae filter-feeders and copepods stationary suspension-feeders were present (Fig. 3C). FDis was very similar in the first four sampled months, as a result of the CWM's distribution of functional traits in these months. FDis values ranged from 0.02 (June and April 2013) to 0.45 (April 2014; Table 1).

Regressions of TP and total Chl a and Chl a per group demonstrated that TP concentration was significantly and positively correlated with total Chl a and Blue Chl a (Table 2). The phytoplankton biomass

Fig. 1 Relative contribution of phytoplankton biomass in Lake Mariano Procópio from April 2013 to October 2014. **A** Biomass per phytoplankton taxonomic groups and **B** Cyanobacteria biomass per colonial and filamentous morphotypes



variation was also significantly related to zooplankton FDis (Fig. 4). A linear increase in FDis with PBV was found for most of the data points. However, in months where the PBV was greater than 110.68, the FDis decreased. It was the case in February (244.18), June (279.73), July (251.18), and September (254.35) 2014 (Fig. 4). These sampling months showed a high cyanobacteria dominance and, in general, low Chrysophyceae and Cryptophyceae biomass.

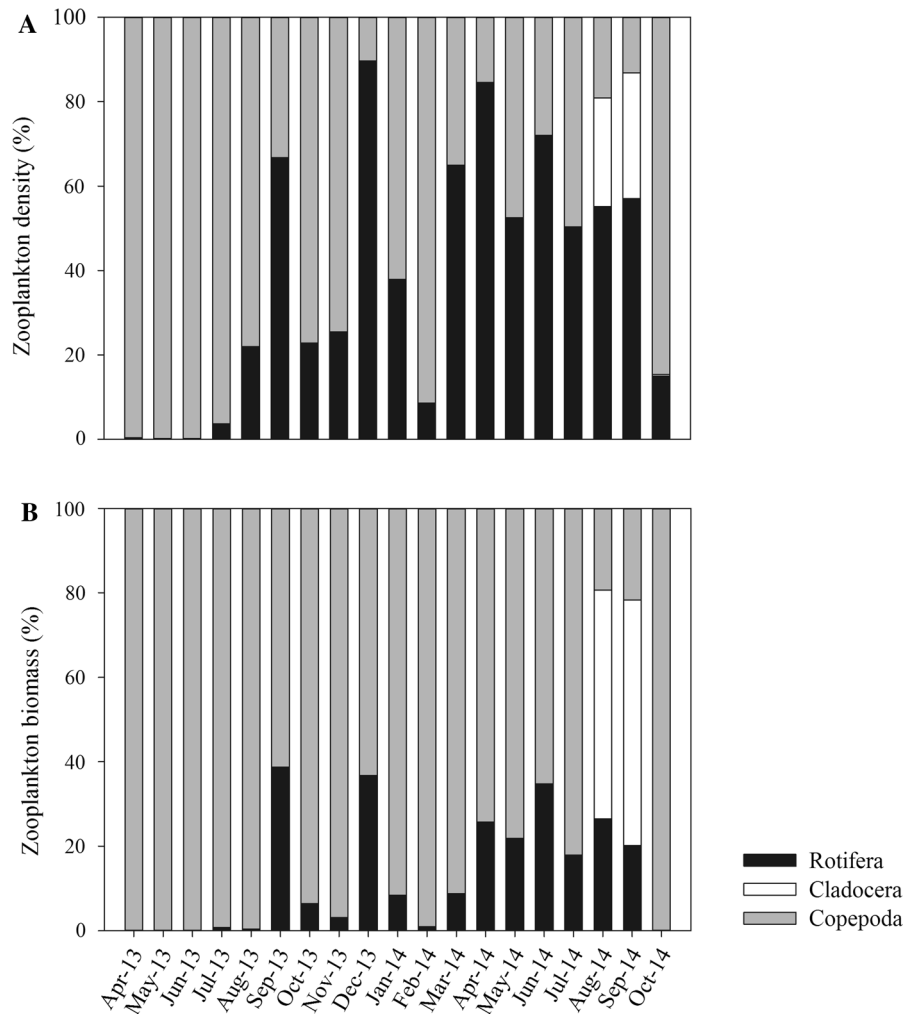
Discussion

Changes in phytoplankton quality and availability may reflect on zooplankton functional diversity (Chapin et al., 2000) since zooplankton species diversity can be closely related to resources usage

and supply (Ptacnik et al., 2008). In our study, we found the phytoplankton composition was significantly related to zooplankton traits and FDis. Our results suggest that blooms of colonial cyanobacteria (*M. aeruginosa*, *M. tenuissima*) favor specific zooplankton traits, including selective grazing (i.e., active prey selection) and omnivorous or detritivores trophic groups, causing an increase in zooplankton FDis, confirming our main hypothesis.

In our study zooplankton was basically composed by immature stages of cyclopoid copepods (Nauplii and copepodites) and rotifers, which were both dominant in density and biomass species. Rotifers group includes species with omnivorous food habit and therefore has low food dependency on phytoplankton, mainly because they also feed on bacteria, flagellates and organic detritus (Arndt, 1993). Overall,

Fig. 2 Relative contribution of zooplankton **A** density and **B** biomass in lake Mariano Procópio from April 2013 to October 2014



the group food selection abilities enabling them to handle and differentiate particles by size and taste (DeMott, 1986; DeMott & Moxter, 1991). This functional trait likely allowed a high range of food resources such as protists and bacteria for rotifers. Cyclopoid copepods are also highly selective raptorial grazers known to graze on mobile heterotrophic prey including ciliates and flagellates (Kiørboe, 2011). Taken together, these traits may represent a weaker link and lower trophic transfer efficiency between phytoplankton and zooplankton (Ersoy et al., 2017).

Throughout the study, it was observed greater abundances of zooplankton species with small body size, omnivorous trophic group, and microphagous feeding mode. However herbivorous organisms were also present at high densities in some sampling periods (e.g., September and December 2013; April, July,

August, September, and October 2014). The presence of herbivorous zooplankton species should represent greater zooplankton top-down control on phytoplankton. However, these organisms when present had in majority small body size. Further, we found a negative relationship between zooplankton biomass and total chlorophyll-a, suggesting there is lower efficiency in this zooplankton function. Conversely, the dominance of zooplankton small forms and selective raptorial feeders point to a strong bacteria, flagellates, and organic detritus grazing. And an intensive microbial grazing might decrease bacterial influence in eutrophic systems (Gasol & Duarte, 2000; Cotner & Biddanda, 2002).

The zooplankton feeding mode “microphagous filter-feeders” as found here presents costs and benefits because it allows a lower energy expenditure

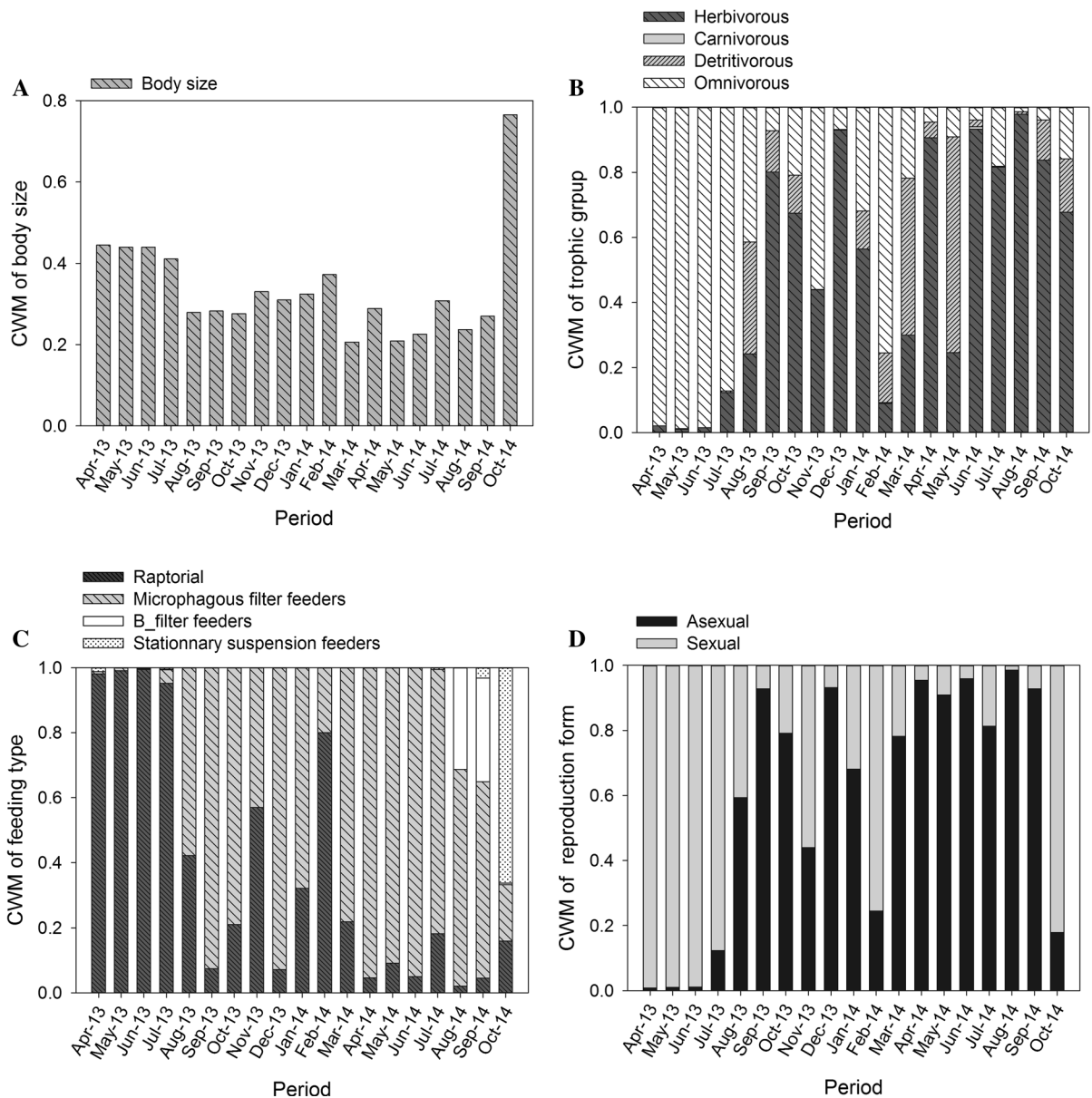


Fig. 3 Total community-weighted mean trait values (CWM) of zooplankton community in Mariano Procópio lake from April 2013 to October 2014. **A** Body size; **B** trophic group (herbivorous, carnivorous, detritivores, omnivorous); **C** feeding

type (Raptorial, Microphagous filter-feeders, Bosminidae filter-feeders and Stationary suspension-feeders) and **D** reproduction form (Asexual or sexual)

and the ability to survive low food consumption conditions. The presence of a greater number of zooplankton organisms with this functional trait also suggests a strong microbial grazing, an important mechanism for nutrients cycling in the ecosystem (Gasol & Duarte, 2000). Zooplankton body size is a functional trait which allows relating multiple

organismal roles with their respective impacts at the ecosystem scale, such as secondary productivity, carbon cycling and nutrient and energy transfer (Litchman et al., 2013; Hébert et al., 2017). These functional traits can potentially influence the primary production by changing zooplankton excretion and

Table 2 Summary of regressions between (a) Total phosphorus concentration (TP $\mu\text{g l}^{-1}$) versus total chlorophyll-a (Total Chl a) and chlorophyll-a per groups (Blue, Green, Brown); (b) total phosphorus, total chlorophyll-a, and chlorophyll-a per groups versus zooplankton biomass (mg DW. l^{-1})

	β_0 (Intercept)	β_1 (Slope)	R^2	R^2_{adj}	P
(a)					
TP \times Total Chl a	- 115.39	1.41	0.51	0.48	< 0.001
TP \times Blue Chl a	- 180.85	1.36	0.46	0.43	0.001
TP \times Green Chl a	12.96	0.14	0.07	0.01	0.294
TP \times Brown Chl a	3.73	0.11	0.24	0.20	0.031
(b)					
TP \times Zooplankton biomass	- 555.73	2.62	0.70	0.68	< 0.001
Total Chl a \times Zooplankton biomass	111.76	- 0.15	0.05	0.00	0.349
Blue Chl a \times Zooplankton biomass	107.87	- 0.20	0.09	0.03	0.218
Green Chl a \times Zooplankton biomass	113.77	- 0.77	0.09	0.04	0.206
Brown Chl a \times Zooplankton biomass	- 3.19	2.46	0.43	0.40	0.002

Bold values represent significant relationships

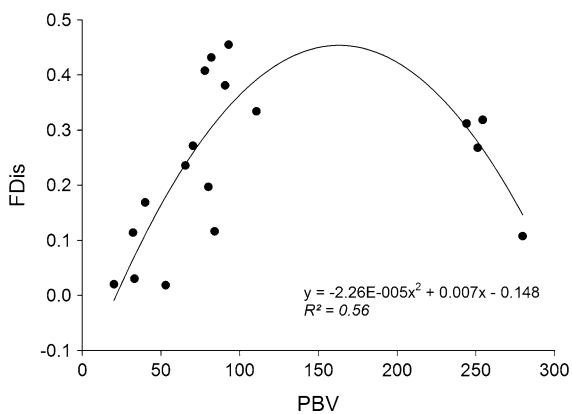


Fig. 4 Relationship between phytoplankton biomass variation per phytoplankton groups (PBV) and zooplankton functional dispersion (FDis) in lake Mariano Procópio from April 2013 to October 2014. The relationship between PBV and FDis has a polynomial quadratic relationship (R^2 adjusted = 0.56, $P < 0.001$, $n = 18$)

hence the nutrient recycled back to phytoplankton, for example (Carpenter et al., 1985).

Our results showed that zooplankton functional dispersion increased until an intermediate level of PBV, and then decreased with high Cyanobacteria dominance at the end of the sampling period. In an intermediate PBV scenario, we suppose the good food quality to zooplankton is not common, but also not scarce. This condition may prevent the competitive exclusion, hence encompassing different life histories and strategy (MacArthur, 1970; Kassen et al., 2000). Therefore, species adapted to both high and low heterogeneity of phytoplankton resource can coexist (Barnett & Beisner, 2007).

It was also found a positive correlation between phytoplankton Brown Chl a and total zooplankton biomass along the sampling period. Brown Chl a is mainly composed by chrysophytes, cryptophytes, and diatoms species. Cryptophytes and diatoms are phytoplankton groups considered an excellent food source for zooplankton due to their high polyunsaturated fatty acids (PUFA), especially the eicosapentaenoic acid (EPA) (Brett et al., 2009). Those are essential for zooplankton growth and reproduction (Brett & Müller-Navarra, 1997) and when present, even in small densities, may drive changes in zooplankton traits composition and FDis. It may be the case when FDis increased until an intermediate level of PBV, which is also the period with higher contribution of Bacillariophyceae.

The significant relations between PBV and zooplankton FDis demonstrated the importance of an intermediate distribution of phytoplankton resource to zooplankton functional diversity. Similar results were found by Barnett & Beisner (2007), that related spatial heterogeneity of phytoplankton to zooplankton functional diversity estimated by FD index (Petchey & Gaston, 2002). They also found that functional diversity decreased with TP gradient and related that to consequently increases in cyanobacteria concentrations.

Because of its negative effects to zooplankton, the Cyanobacteria dominance at the end of the sampling period may have acted as environmental filters, then reducing the dispersion of zooplankton species and their relative abundances in the trait space. This decrease in FDis may have reflected a reduction of the niche space filled by the community, or a niche

overlap. However, this relation is not yet fully understood and also not a consensus when considering eutrophication. For instance, it has been shown that higher biodiversity may be found in more productive and eutrophic environments (Chase, 2010; Harrison et al., 2011; Bini et al., 2014), both due to stochastic events (Chase, 2010) and deterministic conditions, such as nutrients available in the system (Bini et al., 2014). Further, when considering the cyanobacteria effect, the species response may also vary depending on the ecosystem type. For instance, Kosiba et al. (2018) have found that the effect of microcystins on proto- and meta-zooplankton may be more evident in artificial than natural ponds. Disentangling the effects of cyanobacteria and eutrophication is beyond the scope of this study, but it is important to highlight that both may have acted concomitantly.

In tropical regions, TP concentrations together with climate conditions often lead to a persistent cyanobacterial bloom scenario (Figueredo et al., 2016). This massive cyanobacteria growth has been shown to be influential in changing zooplankton functional trait composition, by favoring the selection of traits such as small body size and selective feed mode (Hansson et al., 2007), and those which allow survival in the scarcity of palatable phytoplankton resources and coexistence with potentially toxic cyanobacteria (Ger et al., 2016; Heathcote et al., 2016). However, it is important to highlight that cyanobacteria-zooplankton relationship may differ in temperate and boreal ecosystems, where food webs may have different structures. For instance, Boyero et al. (2017) when analyzing decomposition in a latitudinal scale found that in the tropics decomposition is mainly microbial, while mostly detritivore-mediated at high latitudes.

In a community, losses or additions of species with certain functional traits can have strong impacts on ecosystem processes, such as those resulting in destabilization of trophic webs (Hooper et al., 2005; Violle et al., 2007). Changes in zooplankton functional traits can influence ecosystems functioning in different ways, such as ecosystem respiration, the bioavailability of nutrients and energy flow (Hébert et al., 2017). It is due to central zooplankton role in aquatic food webs acting on energy flow through interactions such as herbivory, interspecific competition, and predation (Carpenter & Kitchell, 1996). For instance, the feeding mode trait represents the elements transfer through organisms and consequently by the trophic

web (Sterner & Hessen, 1994). Within this context, the presence of low herbivorous zooplankton may directly affect nutrient cycles and energy flows through primary producers to the other trophic levels. The dominance of small body size functional traits, in turn, may influence the biomass stocks and their predator's community structure (Vanni, 2002; Sterner, 2009). However, small body size also favors a higher nutrient turnover rate, increasing nutrient availability in water, and influencing phytoplankton production. Hence, besides the effects of eutrophication on phytoplankton community, we show here that cyanobacteria may also affect zooplankton functional diversity changing community functional traits composition and dispersion, which can contribute to possible changes in the functioning of the aquatic ecosystem with environmental consequences still unknown.

Conclusion

Our results suggest that cyanobacteria dominance changed zooplankton traits composition reducing zooplankton FDis. This fact suggests that changes in phytoplankton resource availability may reduce zooplankton FDis. Lower FDis and the dominance of organisms with similar functional traits might influence zooplankton functional role, potentially changing aquatic ecosystem functioning. Our study indicates that approaches based on functional traits may provide a meaningful view of phytoplankton-zooplankton trophic relationships and contributed to better understand their effects on aquatic ecosystem functioning.

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