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ECOSSYSTEMS

# Temporal and vertical variation of phytoplankton and zooplankton in two tropical reservoirs with different trophic states

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**Abstract:** In tropical reservoirs, limnological factors are responsible for changes in plankton and vary at temporal and vertical scales. The aim of this study was to evaluate the effects of temporal and vertical variation of the water column on phytoplankton and zooplankton dynamics in two tropical reservoirs (mesotrophic and supereutrophic) in Northeastern Brazil. Monthly collections from three depths in the limnetic region of the reservoirs were performed to analyze the phytoplankton, zooplankton, and limnological variables. The temporal and vertical variation of the physical and chemical water variables, including their interactions, influenced the phytoplankton and zooplankton community. In the supereutrophic reservoir, decreased nitrogen and increased phosphorus and temperature contributed to the dominance of *Microcystis panniformis* Komárek, Komárková-Legnerová, Sant'Anna, M.T.P.Azevedo & P.A.C.Senna. Conversely, *Planktothrix agardhii* (Gomont) Anagnostidis & Komárek was dominant under high nitrogen concentrations and low temperatures. In the mesotrophic reservoir, the desmids were dominant and showed a positive relationship with nitrogen. Copepoda Calanoida was dominant and correlated to phytoplankton in both reservoirs. The results showed that nitrogen forms directly influenced phytoplankton, and the importance of nitrogen for management strategies of tropical reservoirs, as well as demonstrated the ability of Calanoida to adapt to different trophic conditions and phytoplankton compositions.

**Key words:** Calanoida, cyanobacteria, desmids, eutrophication, nitrogen.

## INTRODUCTION

Climate change and eutrophication have caused strong changes in aquatic ecosystems. With the consequent increase in temperature, reduction of water levels, and nutrient enrichment (Van Zuiden et al. 2016), many shallow reservoirs around the world have gone from a clear state dominated by aquatic macrophytes to a turbid state dominated by cyanobacteria blooms (Dong et al. 2018). Although some studies have been conducted about this topic, the main factors influencing phytoplankton and cyanobacteria dynamics still need to be studied further (Jeppesen et al. 2010, Elliott 2012, Rigosi et al. 2014).

Increased temperature and nutrient concentrations are two factors responsible for increased cyanobacterial blooms (Lürling et al. 2018). Long-term monitoring studies suggest that phosphorus (P) is the main nutrient responsible for cyanobacteria blooms in temperate and tropical regions (Downing et al. 2001, Anneville et al. 2005), however, according to Kosten et al. (2012), high temperatures are also important factors for algae growth. Nutrients play a fundamental role in phytoplankton dynamics in oligotrophic lakes, while temperature is the most important factor in mesotrophic lakes, and synergism between temperature and nutrients influence phytoplankton in eutrophic lakes (Rigosi et al. 2014).

In addition to phosphorus (P), the availability of nitrogen (N) forms in the water favors the growth of cyanobacteria and eukaryotic algae (Chaffin et al. 2013, Davis et al. 2015). Among cyanobacteria, non-diazotrophic filamentous species are favored under increasing nitrogen concentrations (Paerl & Otten 2016); and among eukaryotic algae, desmids are strongly influenced by a variety of nitrogen forms (Mataloni et al. 2015). Generally, most desmids are found in oligotrophic and mesotrophic environments adhered to macrophytes or as part of phytoplankton (Negro et al. 2003). However, some desmids species are adapted to increased nitrogen and phosphorus, such as *Staurastrum leptocladum* Nordstedt, which are found in eutrophic environments (González & Roldán 2019, Bortolini et al. 2019). Mataloni et al. (2015) verified that planktonic desmids showed a preference for minerotrophic water conditions in swamp pools.

Phytoplankton species show different morphophysiological strategies in response to environmental conditions, such as the presence of gaseous vesicles in cyanobacteria (Harke et al. 2016), or active displacement in the water column by phytoflagellates (Shikata et al. 2015). Along with composition and structure, the vertical distribution of phytoplankton in the water column can be regulated by environmental factors (Rao et al. 2018), such as availability of light and nutrients, mixing zone, dissolved oxygen and wind speed (Cao et al. 2006, Sevindik et al. 2017).

Similarly, the vertical composition and dynamics of zooplankton in the water column respond to changes in phytoplankton composition and water conditions (Hampton et al. 2014, Simoncelli et al. 2019), which has recently aroused the interest of researchers from around the world (Hansson & Hylander 2009, Vadadi-Fülöp et al. 2012). Studies show that temperature and luminosity are the main factors influencing the vertical dynamics of zooplankton (Tiberti & Barbieri 2011, Simoncelli et al. 2019). However, the reason why zooplankton continues to migrate in the water column is multifactorial, what is not fully understood, and still needs to be further assessed, since these organisms are important in trophic networks.

Zooplankton is a fundamental part of the trophic chain, as it is a link between primary producers, i.e. phytoplankton, and secondary consumers such as planktivorous fish (Koel et al. 2019), and acts in energy transfer to higher trophic levels. The presence of planktivorous fish also affects the vertical distribution patterns of zooplankton, because zooplankton tends to migrate vertically in the water column to escape predators (Rhode et al. 2001, Tiberti & Iacobuzio 2013), which majorly impacts the trophic network.

We conducted a monitoring study that analyzed the factors that influence temporal and vertical variation of phytoplankton and zooplankton in two tropical reservoirs with different trophic states. The hypotheses tested were: (i) the composition and biomass of phytoplankton differ temporally and spatially in waters enriched with nitrogen or phosphorus, with the dominance of non-diazotrophic filamentous cyanobacteria under high nitrogen concentrations; (ii) the temporal and vertical dynamics of Copepoda Calanoida are negatively associated with Cyanobacteria and positively with Chlorophyta dominance in phytoplankton.

## MATERIALS AND METHODS

### Study area

Tapacurá (8° 02’31.9”S, 35° 11’46.5”W) and Tabocas (8° 14’58.3”S, 36° 22’42.1”W) reservoirs are located in Pernambuco State, Northeastern, Brazil (Figure 1). The reservoirs are located in the “As” climate region, according to the Köppen climate classification (Alvares et al. 2013). The Tapacurá reservoir is supereutrophic and has a maximum depth of approximately 12 m (Diniz et al. 2019) and maximum accumulation capacity of 94,200,000 $m^3$, with the rainy season occurring from March to August, and dry season from September to February (APAC 2017). This reservoir has a history of perennial blooms of the cyanobacteria *Raphidiopsis* (previously *Cylindrospermopsis*) *raciborskii* (Woloszynska) Aguilera, Berrendero Gómez, Kastovsky, Echenique & Salerno (Aguilera et al. 2018), *Microcystis aeruginosa* (Kützing) Kützing, *Microcystis panniformis* Komárek, Komárková-Legnerová, Sant’Anna, M.T.P.Azevedo, & P.A.C.Senna and *Planktothrix agardhii* (Gomont) Anagnostidis & Komárek (Moura et al. 2018).

Tabocas reservoir is mesotrophic with chlorophytes dominance (Diniz et al. 2019) and has dense banks of submerged macrophyte *Egeria densa* Planchon (in the present study). Its maximum depth is 4 m (Diniz et al. 2019), maximum accumulation capacity is 1,168,000 $m^3$. The rainy season occurs from March to July, and the dry season occurs from August to February (APAC 2017). These ecosystems are primarily used for public supply and recreational activities.

### Sampling and laboratory procedures

Water samples were collected during the rainy (July/2016 and March/2017) and dry (September/2016 and January/2017) seasons from both reservoirs at a single sampling station located in the limnetic region and at three depths

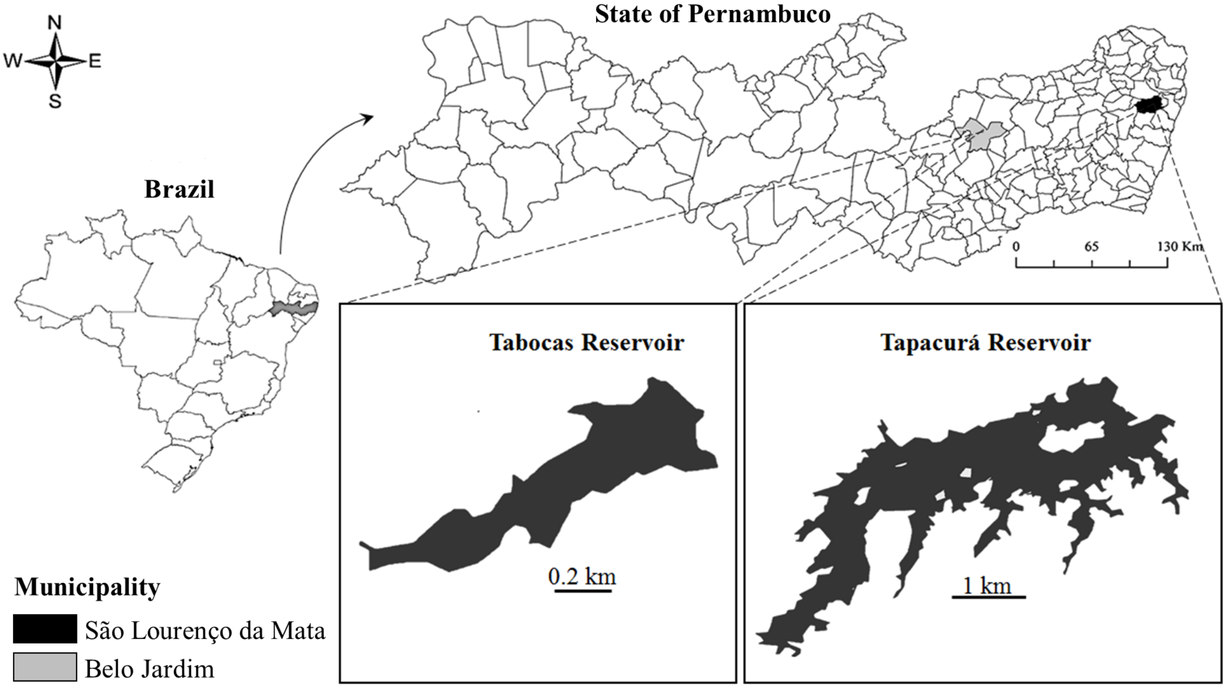

**Figure 1.** Location of the Tapacurá (supereutrophic) and Tabocas (mesotrophic) reservoirs in the municipalities of São Lourenço da Mata and Belo Jardim in the State of Pernambuco, Northeast, Brazil.

using a *van Dorn* bottle: surface, euphotic zone limit ($Z_{eu}$) and bottom. The $Z_{eu}$ was estimated by multiplying the value of the water transparency (m), determined with the Secchi disc, by factor 2.7 (Esteves 2011) and the maximum depth ($Z_{max}$) (called bottom) was determined with a portable ecobatimeter (Hondex PS-7 model). The $Z_{eu}$:$Z_{max}$ ratio was used as the availability of light in the water column (Jensen et al. 1994).

The abiotic variables of water, temperature (ºC), dissolved oxygen (mg $L^{-1}$), pH, dissolved total solids (mg $L^{-1}$), and electrical conductivity (µS $cm^{-1}$) were analyzed *in situ* with a multiparametric probe (model HANNA HI 9829). Water transparency (m) was measured by the disappearance of the Secchi disc and the luminous intensity (µmol photons $m^{-2}$ $s^{-1}$) was measured with a photometer (model LI-250A). Precipitation data (mm) was obtained from the National Meteorological Institute database (INMET 2017).

Samples were collected to determine nutrient concentrations from the three depths with a *van Dorn* bottle and stored in 300 mL plastic containers, transported under refrigeration, and frozen to -4°C in the laboratory until analysis. Total phosphorus (TP; µg $L^{-1}$) and orthophosphate ($P\text{-}PO_4^{3-}$; µg $L^{-1}$) (Strickland & Parsons 1972), nitrite ($N\text{-}NO_2^-$; µg $L^{-1}$) and nitrate ($N\text{-}NO_3^-$; µg $L^{-1}$) (Mackereth et al. 1978), and ammoniacal nitrogen ($N\text{-}NH_4^+$; µg $L^{-1}$) (Koroleff 1976) were analyzed. The dissolved inorganic nitrogen (DIN; µg $L^{-1}$) concentrations were estimated by the sum of nitrate, nitrite, and ammoniacal nitrogen.

## Phytoplankton analysis

Phytoplankton was quantified using samples collected at the three depths using a *van Dorn* bottle, and fixed with 1% acetic lugol. Taxa were identified using taxonomic bibliographies for each phytoplankton group, such as Prescott & Vinyard (1982), Komárek & Anagnostidis (1999, 2005), Popovský & Pfiester (1990), Krammer & Lange-Bertalot (1991), John et al. (2002) and Komárek (2013), to the lowest taxonomic level possible. The phytoplankton density (ind $mL^{-1}$) was determined by counting organisms in sedimentation chambers using an inverted microscope (Zeiss, Axiovert) according to Utermöhl (1958), and the cell volume was calculated from geometric models according to the shape of the cells (Hillebrand et al. 1999). Phytoplankton species biomass was determined by multiplying the density by the mean algal volume of the species, and expressed in mg $L^{-1}$, admitting that the volume of 1 $mm^3$ is equivalent to 1 mg of fresh weight of phytoplankton (Wetzel & Likens 2000). The dominance was determined according to (Lobo & Leighton 1986).

## Zooplankton analysis

Fifty liters of water were collected from each reservoir at the three depths with a *van Dorn* bottle and filtered with a 68 µm mesh plankton net to collect zooplankton. The samples were fixed with 4% formaldehyde. The species were identified according to Koste (1978), Montú & Goeden (1986) and Elmoor-Loureiro (1997), to the lowest taxonomic level possible. To quantify the density of organisms (ind $L^{-1}$), samples were concentrated and diluted to 100 mL with distilled water and three subsamples (2 mL) were counted in a Sedgwick-Rafter chamber. The biovolume of the taxa was calculated according to the geometric formulas of Ruttner-Kolisko (1977) for rotifers and Dumont et al. (1975) for cladocerans and copepods. Zooplankton biomass (µg PS $m^{-3}$) was estimated using density and average biovolume of the taxa. Species dominance was calculated according to Lobo & Leighton (1986).

### Statistical analyses

PERMANOVA was performed to verify the differences in abiotic, phytoplankton, and zooplankton variables between reservoirs. ANOVA *two-way* was performed to verify the differences in abiotic, phytoplankton, and zooplankton variables between depths and months in each reservoir, and verify differences in the biomass of diazotrophic filamentous, non-diazotrophic filamentous, and colonial cyanobacteria between months and depths in each reservoir. The Tukey's HSD test was performed when significant difference was observed between the variables. Variance analyses were preceded by the Kolmogorov-Smirnov normality test and Bartlett's homoscedasticity test. The non-parametric Kruskal-Wallis test (test H) was used for non-homoscedastic data.

Principal component analysis (PCA) was performed to evaluate the ordination of environmental abiotic factors (electrical conductivity, luminous intensity, dissolved oxygen, pH, total dissolved solids, water temperature, nitrate, nitrite, ammoniacal nitrogen, DIN, orthophosphate, total phosphorus, $Z_{eu}$, and $Z_{eu}$:$Z_{max}$) between reservoirs, based on a correlation matrix. Redundancy Analyses (RDA) were used to identify the relationships between phytoplankton and zooplankton with abiotic variables aforementioned, assuming that phytoplankton influence zooplankton and vice versa. RDA was applied based on the length of the first axis of the Detrended Correspondence Analysis (DCA). The dependent variables were log-transformed, and the explanatory variables were standardized by the "decostand" function. The explanatory variables were selected by the Forward procedure using the Ordistep function with 999 permutations ($p < 0.05$), and the collinearity of the variables through the variance of inflation factor (VIF < 20). For phytoplankton, species with biomass above 1% total biomass were considered, for zooplankton the biomasses of all species were considered. All statistical analyses were performed with the vegan package in the R program (R Development Core Team 2015) with a significance of $p < 0.05$.

## RESULTS

The highest precipitation values were observed in March/2017 for both reservoirs, with the supereutrophic reaching 156.2 mm and the mesotrophic at 17.5 mm. In the mesotrophic reservoir, the highest water transparency was recorded in July/2016 compared to the supereutrophic reservoir, with high Secchi disc value (2.2 m). The pH ranged from 4.4 (acid) to 12.5 (alkaline) between July/2016 and January/2017 in the mesotrophic reservoir, while water pH remained alkaline in the supereutrophic reservoir, ranged from 7.8 to 12.6 (Table I). In addition to pH, other variables, such as water temperature, conductivity, total dissolved solids and nutrients (nitrite and nitrate) varied over time in both reservoirs (Table II). Ammoniacal nitrogen, dissolved inorganic nitrogen, and total phosphorus showed temporal variation in the mesotrophic reservoir only (Table II).

The physical and chemical water variables varied significantly between the reservoirs (PERMANOVA: F = 0.49 and $p = 0.001$) throughout the study period and between the depths (surface, $Z_{eu}$, and bottom). The availability of luminous intensity and dissolved oxygen were higher at the water surface of the reservoirs. A hypoxia condition was detected at the maximum depth in the supereutrophic reservoir (Table I and II). The PCA explained 68.5% of the variation of environmental variables in the two first ordination axes (first axis: 43.66%, second axis: 24.84%) (Figure 2). Two groups with different patterns for the physical and

**Table I.** Limnological variables of the mesotrophic (Tabocas) and supereutrophic (Tapacurá) reservoirs between the depths and months. Sur = surface; $Z_{eu}$ = euphotic zone limit; Bot = bottom. Not analyzed (-). $Z_{max}$ = Maximum depth (m); $Z_{eu}$ = Depth of euphotic zone; $Z_{eu}$:$Z_{max}$ = Ratio between euphotic zone:maximum depth; Transparency = Water transparency (cm); WT = Water temperature (°C); Luminous intensity (µmol photons $m^{-2}$ $s^{-1}$); DO = Dissolved oxygen (mg $L^{-1}$); EC = Electrical conductivity (µS $cm^{-1}$); TDS = Total dissolved solids (mg $L^{-1}$); $NO_3^-$ = Nitrate (µg $L^{-1}$); $NO_2^-$ = Nitrite (µg $L^{-1}$); $NH_4^+$ = Ammoniacal nitrogen (µg $L^{-1}$); DIN = Dissolved inorganic nitrogen (µg $L^{-1}$); $PO_4^{3-}$ = Orthophosphate (µg $L^{-1}$); TP = Total phosphorus (µg $L^{-1}$).

| Variables | Mesotrophic Reservoir | | | | | | | | | | | | Supereutrophic Reservoir | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | July/2016 | | | September/2016 | | | January/2017 | | | March/2017 | | | July/2016 | | | September/2016 | | | January/2017 | | | March/2017 | | |
| | Sur | Zeu | Bot | Sur | Zeu | Bot | Sur | Zeu | Bot | Sur | Zeu | Bot | Sur | Zeu | Bot | Sur | Zeu | Bot | Sur | Zeu | Bot | Sur | Zeu | Bot |
| $Z_{max}$ | - | - | 4.0 | - | - | 1.6 | - | - | 1.3 | - | - | 1.9 | - | - | 10.0 | - | - | 11.4 | - | - | 8.6 | - | - | 8.8 |
| Transparency | 2.2 | - | - | 0.6 | - | - | 0.15 | - | - | 0.5 | - | - | 1.2 | - | - | 0.7 | - | - | 0.7 | - | - | 0.6 | - | - |
| $Z_{eu}$ | 2.2 | - | - | 1.6 | - | - | 0.4 | - | - | 1.35 | - | - | 3.2 | - | - | 1.9 | - | - | 1.9 | - | - | 1.6 | - | - |
| $Z_{eu}$:$Z_{max}$ | 0.6 | - | - | 1.0 | - | - | 0.3 | - | - | 0.7 | - | - | 0.3 | - | - | 0.2 | - | - | 0.2 | - | - | 0.2 | - | - |
| WT | 25.3 | 24.4 | 22.5 | 27.8 | 27.5 | 26.9 | 29.5 | 29.3 | 25.8 | 26.7 | 26.3 | 25.5 | 26.9 | 26.8 | 26.6 | 28.5 | 28.0 | 26.7 | 29.5 | 29.4 | 28.5 | 30.5 | 30.5 | 29.0 |
| Luminous intensity | - | - | - | 522.8 | 65.6 | 17.1 | 525.5 | 4.5 | 0.4 | 516.4 | 2.7 | 3.3 | 655.1 | 7.2 | 5.3 | 380.7 | 2.4 | 1.8 | 297.7 | 2.6 | 1.6 | 655.9 | 7.1 | 4.3 |
| DO | 6.0 | 5.5 | 4.3 | 5.8 | 5.4 | 4.5 | 9.3 | 9.7 | 5.0 | 3.7 | 3.9 | 4.1 | 4.8 | 3.5 | 0.0 | 7.9 | 4.7 | 0.0 | 4.8 | 3.8 | 2.5 | 5.4 | 5.00 | 0.0 |
| pH | 4.5 | 4.4 | 4.6 | 8.4 | 8.7 | 8.7 | 11.4 | 11.5 | 12.5 | 10.1 | 10.2 | 11.1 | 8.0 | 7.9 | 7.8 | 9.2 | 8.5 | 8.3 | 9.9 | 8.9 | 7.9 | 12.6 | 12.2 | 11.5 |
| EC | 95 | 94 | 87 | 120 | 132 | 125 | 208 | 207 | 210 | 228 | 227 | 225 | 410 | 410 | 414 | 425 | 425 | 423 | 483 | 483 | 479 | 540 | 538 | 516 |
| TDS | 47 | 47 | 43 | 60 | 66 | 63 | 104 | 104 | 105 | 114 | 113 | 113 | 205 | 205 | 207 | 213 | 213 | 211 | 241 | 241 | 240 | 270 | 269 | 258 |
| $NO_3^-$ | 41.5 | 43.3 | 34.7 | 58.4 | 34.4 | 30.0 | 7.8 | 16.6 | 24.8 | 543.9 | 675.4 | 619.8 | 150.0 | 130.6 | 111.8 | 15.4 | 14.2 | 19.8 | 0.1 | 2.1 | 4.3 | 0.8 | 1.9 | 1.9 |
| $NO_2^-$ | 0.3 | 2.3 | 1.7 | 2.3 | 2.0 | 1.2 | 4.3 | 3.8 | 4.0 | 210.9 | 223.6 | 206.3 | 7.2 | 8.4 | 8.9 | 4.3 | 7.8 | 1.4 | 1.4 | 1.7 | 1.7 | 1.4 | 1.2 | 1.2 |
| $NH_4^+$ | 41.3 | 13.4 | 54.7 | 250.8 | 239.4 | 279.7 | 273.5 | 163.1 | 83.6 | 2472.7 | 2379.8 | 2569.7 | 162.0 | 160.0 | 186.3 | 19.6 | 16.5 | 221.9 | 23.7 | 67.1 | 28.9 | 18.6 | 132.1 | 55.7 |
| DIN | 83.0 | 59.0 | 91.1 | 311.5 | 275.9 | 310.8 | 285.6 | 183.6 | 112.5 | 3227.4 | 3278.8 | 3395.8 | 319.2 | 298.9 | 307.0 | 39.3 | 38.5 | 243.1 | 25.3 | 70.9 | 35.0 | 20.9 | 135.1 | 58.8 |
| $PO_4^{3-}$ | 6.6 | 14.9 | 10.0 | 26.6 | 38.2 | 14.9 | 8.3 | 31.5 | 46.5 | 6.6 | 14.9 | 8.3 | 664.0 | 670.6 | 1020.9 | 654.0 | 707.2 | 715.5 | 788.5 | 791.8 | 780.2 | 859.9 | 720.4 | 823.4 |
| TP | 136.0 | 111.9 | 154.2 | 114.9 | 42.3 | 102.8 | 193.5 | 172.3 | 269.1 | 347.7 | 450.4 | 399.0 | 885.7 | 879.7 | 1641.5 | 931.1 | 946.2 | 973.4 | 976.4 | 1030.8 | 1046.0 | 1094.3 | 1136.6 | 1121.5 |

chemical water variables were observed between the reservoirs. The first group was the mesotrophic reservoir, characterized by high values of nitrogen (ammoniacal nitrogen (eigenvalue = 7.43), nitrite (eigenvalue = 6.80), nitrate (eigenvalue = 6.89), DIN (eigenvalue = 7.35)), dissolved oxygen (eigenvalue = 1.04), luminous intensity (eigenvalue = 0.0009), and by variation in pH (eigenvalue = 0.42) and $Z_{eu}$:$Z_{max}$ (eigenvalue = 9.16). The second group was the

**Table II. Statistical values of ANOVA *two-way* of limnological variables and zooplankton biomass (µg PS $m^{-3}$) and phytoplanktonic classes (mg $L^{-1}$) between the depths (surface, $Z_{eu}$ and bottom) and the months studied (July, September, January and March) in the mesotrophic (Tabocas) and supereutrophic (Tapacurá) reservoirs. Numbers in bold represent significant values ($p < 0.05$). $Z_{max}$ = Maximum depth (m); Transparency = Water transparency (cm); $Z_{eu}$ = Depth of euphotic zone; $Z_{eu}$:$Z_{max}$ = Ratio between euphotic zone:maximum depth; WT = Water temperature (°C); EC = Electrical conductivity (µS $cm^{-1}$); Luminous intensity (µmol photons $m^{-2}$ $s^{-1}$); TDS = Total dissolved solids (mg $L^{-1}$); DO = Dissolved oxygen (mg $L^{-1}$); $NO_2^-$ = Nitrite (µg $L^{-1}$); $NO_3^-$ = Nitrate (µg $L^{-1}$); $NH_4^+$ = Ammoniacal nitrogen (µg $L^{-1}$); DIN = Dissolved inorganic nitrogen (µg $L^{-1}$); $PO_4^{3-}$ = Orthophosphate (µg $L^{-1}$); TP = Total phosphorus (µg $L^{-1}$).**

| Variables | Mesotrophic Reservoir | | | | | | Supereutrophic Reservoir | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Depths | | | Months | | | Depths | | | Months | | |
| | Df | F | *p* | Df | F | *p* | Df | F | *p* | Df | F | *p* |
| $Z_{max}$ | | | | 3 | 3.25 | **<0.05** | | | | 3 | 0.13 | 0.93 |
| Transparency | | | | 3 | 6.18 | **<0.05** | | | | 3 | 7.18 | **<0.05** |
| $Z_{eu}$ | 2 | 1.37 | 0.303 | 3 | 9.61 | **<0.05** | 2 | 0.75 | 0.501 | 3 | 1.64 | **<0.05** |
| $Z_{eu}$:$Z_{max}$ | | | | 3 | 2.19 | **<0.05** | | | | 3 | 2.69 | **<0.05** |
| WT | | | | 3 | 5.70 | **<0.05** | | | | 3 | 12.06 | **<0.05** |
| EC | 2 | 0.00 | 0.997 | 3 | 836.2 | **<0.05** | 2 | 0.02 | 0.983 | 3 | 193.9 | <**0.05** |
| Luminous intensity | 2 | 5.6 | 0.06 | 2 | 0.01 | 0.992 | 2 | 134.5 | **<0.05** | 3 | 0.09 | 0.965 |
| TDS | 2 | 0.00 | 0.998 | 3 | 842.9 | **<0.05** | 2 | 0.02 | 0.983 | 3 | 193.1 | <**0.05** |
| pH | 2 | 0.05 | 0.995 | 3 | 169.1 | **<0.05** | 2 | 0.20 | 0.824 | 3 | 43.84 | **<0.05** |
| DO | 2 | 0.28 | 0.763 | 3 | 4.43 | **<0.05** | 2 | 19.8 | **<0.05** | 3 | 0.13 | 0.939 |
| $NO_2^-$ | 2 | 0.00 | 0.998 | 3 | 9.43 | **<0.05** | 2 | 0.01 | 0.987 | 3 | 8.51 | **<0.05** |
| $NO_3^-$ | 2 | 0.01 | 0.99 | 3 | 9.46 | **<0.05** | 2 | 0.19 | 0.829 | 3 | 90.32 | **<0.05** |
| $NH_4^+$ | 2 | 0.00 | 0.997 | 3 | 854.7 | **<0.05** | 2 | 0.75 | 0.501 | 3 | 2.07 | 0.287 |
| DIN | 2 | 0 | 1 | 3 | 185 | **<0.05** | 2 | 0.21 | 0.818 | 3 | 6.69 | 0.08 |
| $PO_4^{3-}$ | 2 | 0.91 | 0.437 | 3 | 2.26 | 0.174 | 2 | 1.46 | 0.283 | 3 | 4.44 | 0.218 |
| TP | 2 | 0.08 | 0.921 | 3 | 31.55 | **<0.05** | 2 | 1.60 | 0.255 | 3 | 4.85 | 0.183 |
| **Phytoplankton** | | | | | | | | | | | | |
| Cyanophyceae | 2 | 0.88 | 0.428 | 3 | 14.26 | **<0.05** | 2 | 4.11 | **<0.05** | 3 | 3.61 | **<0.05** |
| Zygnematophyceae | 2 | 2.18 | 0.135 | 3 | 43.13 | **<0.05** | | | | | | |
| Bacillariophyceae | 2 | 4.10 | 0.08 | 3 | 18.79 | **<0.05** | | | | | | |
| Synurophyceae | 2 | 0.28 | 0.757 | 3 | 1.55 | 0.229 | | | | | | |
| Others | 2 | 1.79 | 0.189 | 3 | 14.83 | **<0.05** | 2 | 0.29 | 0.750 | 3 | 21.72 | **<0.05** |
| **Zooplankton** | | | | | | | | | | | | |
| Rotifera | 2 | 89.06 | **<0.05** | 3 | 1466.19 | **<0.05** | 2 | 0.26 | 0.772 | 3 | 49.04 | **<0.05** |
| Cladocera | 2 | 2.44 | 0.109 | 3 | 537.13 | **<0.05** | 2 | 5.18 | **<0.05** | 3 | 58.22 | **<0.05** |
| Calanoida | 2 | 20.71 | **<0.05** | 3 | 187.14 | **<0.05** | 2 | 9.00 | **<0.05** | 3 | 35.36 | **<0.05** |
| Cyclopoida | 2 | 11.32 | **<0.05** | 3 | 1.96 | 0.580 | 2 | 2.09 | 0.351 | 3 | 20.85 | **<0.05** |
| Nauplii | 2 | 14.67 | **<0.05** | 3 | 24.23 | **<0.05** | 2 | 16.95 | **<0.05** | 3 | 3.25 | 0.354 |

supereutrophic reservoir, characterized by high concentrations of orthophosphate (eigenvalue = 13.98), total phosphorus (eigenvalue = 11.26), total dissolved solids (eigenvalue = 12.38), high electrical conductivity (eigenvalue = 12.38), water temperature (eigenvalue = 6.61), and $Z_{eu}$ (eigenvalue = 4.29) (Figure 2).

The biomass and composition of total phytoplankton (PERMANOVA: F = 34.29 and *p* = 0.001), besides the biomass of the classes (PERMANOVA: F = 25.00 and *p* = 0.001), were significantly different between the reservoirs. Zygnematophyceae represented 92% of the total average biomass in the mesotrophic reservoir (37.35 mg $L^{-1}$) (Figure 3a), with *Staurastrum tetracerum* Ralfs ex Ralfs representing 59% of total average biomass (24.16 mg $L^{-1}$), while Bacillariophyceae represented 3% of total average biomass with *Thalassiosira* sp. the most representative species (0.77 mg $L^{-1}$). In the supereutrophic reservoir, Cyanophyceae was dominant (98%) (Figure 3b), with cyanobacteria *M. panniformis* and *P. agardhii* presenting the highest values of total average biomass of 46% (68.39 mg $L^{-1}$) and 27% (39.65 mg $L^{-1}$), respectively.

Phytoplankton biomass varied throughout the months in the mesotrophic reservoir (Table II), with higher biomass recorded in July/2016, September/2016, and January/2017 to Zygnematophyceae, Bacillariophyceae, and Cyanophyceae (Figure 3a). Significant differences in Zygnematophyceae biomass were observed between the depths in January/2017, with higher biomass in the bottom than on the surface (Tukey's HSD, *p* = 0.02) and $Z_{eu}$ (Tukey's HSD, *p* = 0.05). In the supereutrophic reservoir, Cyanophyceae and other phytoplankton classes varied both temporally and vertically (Table II), with higher cyanobacteria biomass (September/2016 and January/2017) (Figure 3b).

In the mesotrophic reservoir, in addition to desmids, significant differences were observed in the biomass of diazotrophic filamentous (Kruskal-Wallis, H = 12.962 e *p* = 0.004) and non-diazotrophic (F = 13.152 and *p* <0.0001) cyanobacteria and colonial cyanobacteria

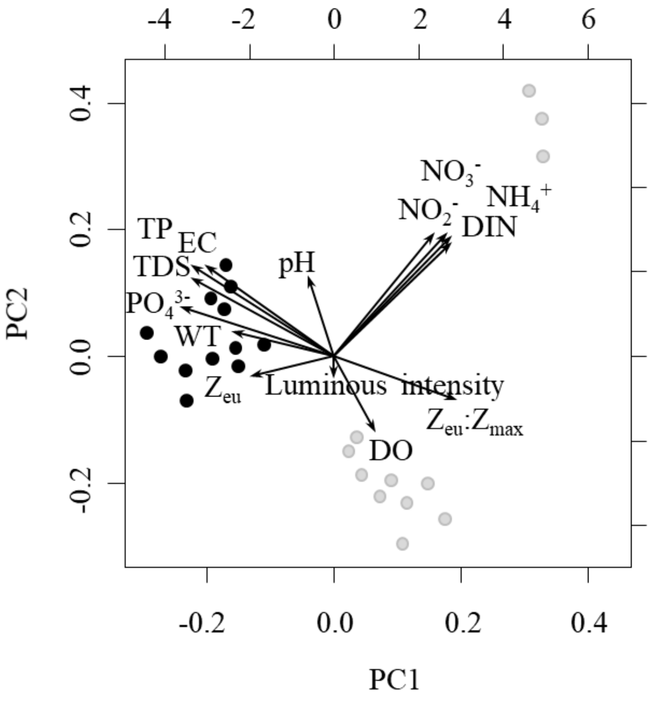

**Figure 2. Principal component analysis (PCA) of environmental variables between mesotrophic (Tabocas, grey) and supereutrophic reservoirs (Tapacurá, black). TDS = Total dissolved solids; EC = Electrical conductivity; WT = Water temperature; $Z_{eu}$ = Euphotic zone; $Z_{eu}$:$Z_{max}$ = Ratio between euphotic zone:maximum depth; DO = Dissolved oxygen; $NO_2^-$ = Nitrite; $NO_3^-$ = Nitrate; $NH_4^+$ = Ammoniacal nitrogen; DIN = Dissolved inorganic nitrogen; $PO_4^{3-}$ = Orthophosphate; TP = Total phosphorus.**

(Kruskal-Wallis, H = 10.482 and $p = 0.01$) between months. Higher biomass was observed in July/2016 and January/2017 for non-diazotrophic filamentous cyanobacteria (Figure 4a), with dominance of the species *Anagnostidinema* (previously *Geitlerinema*) *amphibium* (C.Agardh ex Gomont) Strunecký, Bohunická, J.R.Johansen & J.Komárek (Strunecky et al. 2017). From diazotrophic and colonial cyanobacteria, *R. raciborskii* and *Aphanocapsa elachista* West & G.S.West were dominant, respectively.

In the supereutrophic reservoir, diazotrophic filamentous cyanobacteria differed between months (F = 6.814 and $p = 0.002$), as well as non-diazotrophic cyanobacteria (F = 58.810 and $p < 0.0001$), presenting higher biomass in March/2017 and September/2016, respectively (Figure 4b). Significant variation in the colonial cyanobacteria biomass was observed (F = 18.732 and $p < 0.0001$), with higher biomass recorded in January and March/2017 (Figure 4b). In July/2016, codominance was observed between the non-diazotrophic colonial and filamentous species of cyanobacteria. In September/2016, the filamentous species *P. agardhii* was dominant, and in the other months, the colonial species *M. panniformis* was dominant (Figure 4b). No variation in cyanobacteria biomass was observed between depths.

The RDA explained 78% (F = 2.91 and $p = 0.001$) of the phytoplankton distribution in the mesotrophic and supereutrophic reservoirs, with the axes 1 and 2 representing 46% ($p = 0.002$) and 32% ($p = 0.001$) of the distribution, respectively. The dissolved oxygen ($p = 0.01$), $Z_{eu}$:$Z_{max}$ ($p = 0.002$), DIN ($p = 0.02$), and biomass of nauplii ($p = 0.05$) significantly influenced phytoplankton species in the mesotrophic reservoir, and in the supereutrophic reservoir, the RDA showed that non-diazotrophic filamentous cyanobacteria (*P. agardhii* and *Planktothrix isothrix* (Skuja) Komárek & Komárková), diazotrophic filamentous cyanobacteria (*R. raciborskii*), and colonial cyanobacteria (*M. panniformis* and *M. aeruginosa*) were positively influenced by nitrogen (DIN), luminous intensity ($p = 0.01$), $Z_{eu}$ ($p = 0.03$), pH ($p = 0.005$), water temperature ($p = 0.005$), electrical conductivity ($p = 0.005$), total phosphorus ($p = 0.003$), $PO_4^{3-}$ ($p = 0.005$), total dissolved solids ($p = 0.001$), and biomass of Cyclopoida ($p = 0.01$) (Figure 5a).

The biomass and composition of total zooplankton (PERMANOVA: F = 11.31 and $p = 0.001$) and the biomass of the groups (PERMANOVA: F = 7.96 and $p = 0.001$) were significantly different between the reservoirs. The zooplankton groups showed variation in biomass between months and depths in both reservoirs (Table II). Copepoda Calanoida was dominant in the mesotrophic and supereutrophic reservoir, contributing to 67% (312.98 µg $DW^{-3}$) and 59% (222.33 µg $DW^{-3}$) of the total average biomass of zooplankton, respectively (Figure 6a, b).

The RDA explained 65.47% (F = 9.45 and $p = 0.007$) of the relationship between zooplankton with abiotic variables and phytoplankton of the mesotrophic and supereutrophic reservoirs. The axis 1 represented 54.11% ($p = 0.001$) of the distribution of variables, while axis 2 represented 11.36% ($p = 0.03$). *Staurastrum tetracerum* ($p = 0.05$), *Staurastrum* sp. ($p = 0.03$), *Euastrum abruptum* Nordstedt ($p = 0.01$), nitrate ($p = 0.04$), nitrite ($p = 0.03$), DIN ($p = 0.02$), and luminous intensity ($p = 0.04$) positively influenced Calanoida biomass in the mesotrophic reservoir, while in the supereutrophic reservoir Cyclopoida biomass was positively related to water temperature ($p = 0.005$), pH ($p = 0.02$), and the biomass of *Pseudanabaena catenata* Lauterborn ($p = 0.02$), *A. amphibium* ($p = 0.02$), and *M. aeruginosa* ($p = 0.05$) (Figure 5b).

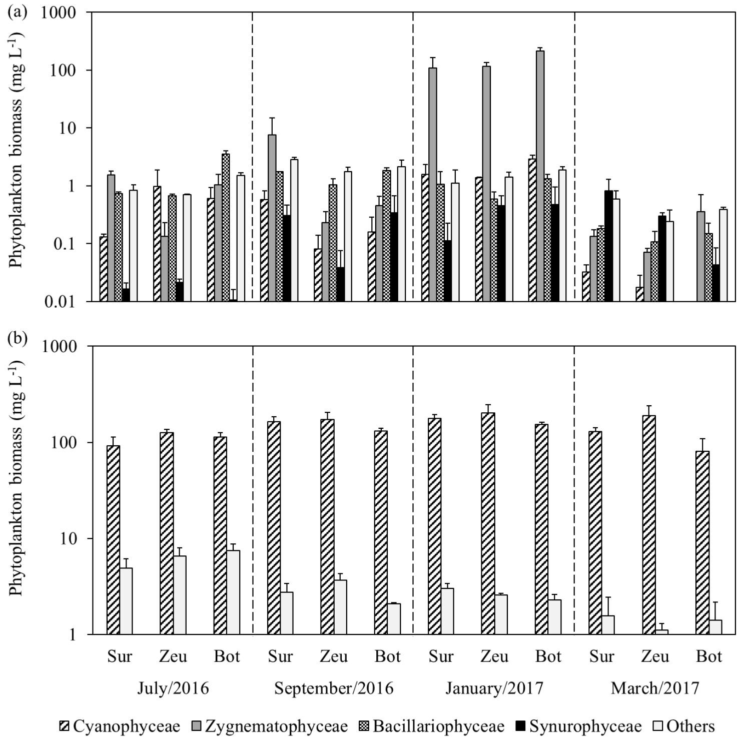

**Figure 3.** Phytoplankton biomass in the mesotrophic (Tabocas, a) and supereutrophic (Tapacurá, b) reservoirs between July/2016 and March/2017 at different depths. Sur = surface; $Z_{eu}$ = euphotic zone limit; Bot = bottom. Vertical lines represent the standard error of the mean (±SEM).

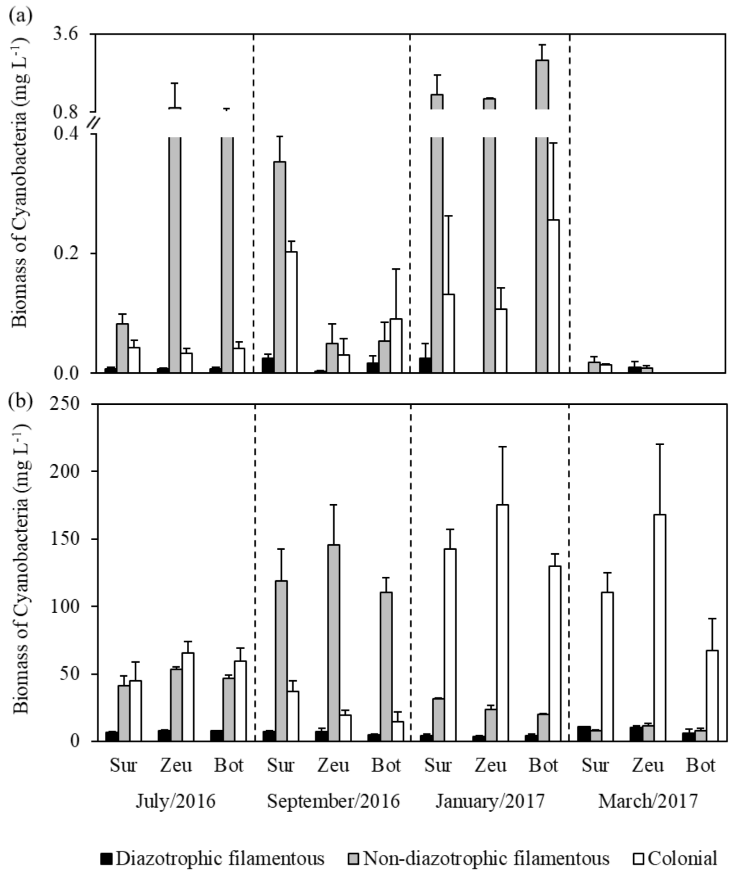

**Figure 4.** Biomass of diazotrophic and non-diazotrophic filamentous and colonial cyanobacteria in the mesotrophic (Tabocas; a) and supereutrophic (Tapacurá; b) reservoirs between July/2016 and March/2017 at different depths. Sur = surface; $Z_{eu}$ = euphotic zone limit; Bot = bottom. Vertical lines represent the standard error of the mean (±SEM).

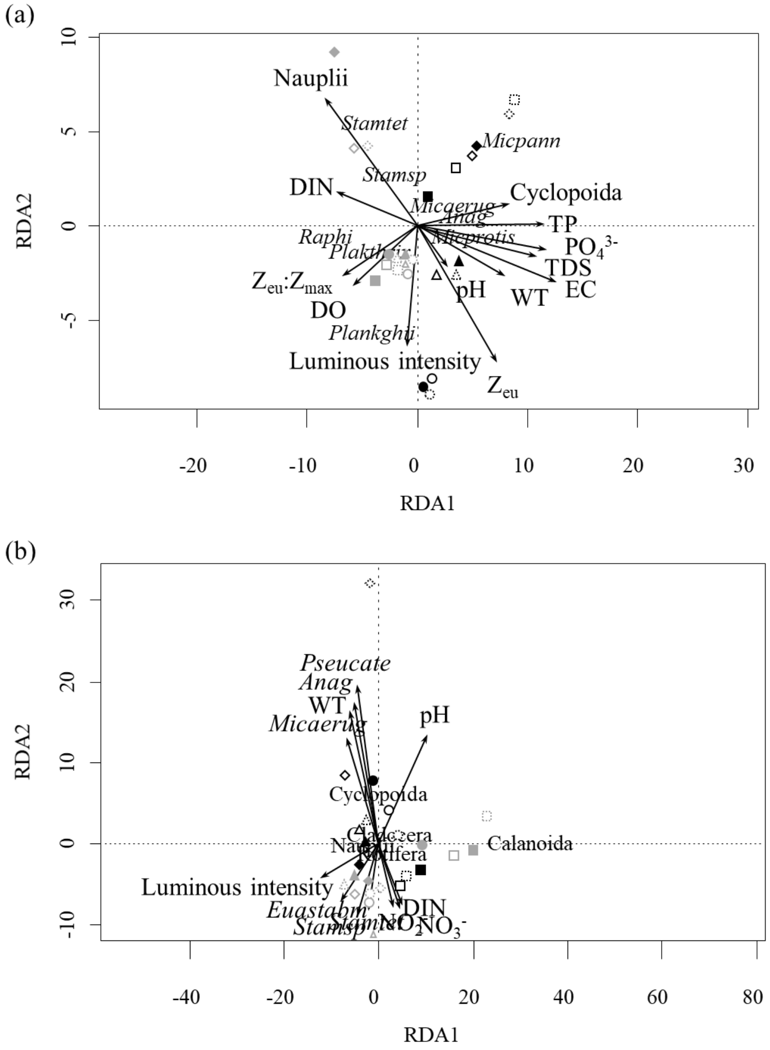

**Figure 5.** **Redundancy Analysis (RDA) of phytoplankton (a) and zooplankton (b) in the mesotrophic (Tabocas, grey) and supereutrophic (Tapacurá, black) reservoirs. Geometric shapes represent months of study: triangles (July), circles (September), rhombuses (January) and squares (March). The filling of the shapes represents the depths: solid line (surface), traced line ($Z_{eu}$) and all black (bottom). TDS = Total dissolved solids; EC = Electrical conductivity; WT = Water temperature; $Z_{eu}$ = Euphotic zone; $Z_{eu}$:$Z_{max}$ = Ratio between euphotic zone:maximum depth; DO = Dissolved oxygen; $NO_2^-$ = Nitrite; $NO_3^-$ = Nitrate; DIN = Dissolved inorganic nitrogen; $PO_4^{3-}$ = Orthophosphate; TP = Total phosphorus; *Plankghii = Planktothrix agardhii*; *Plnkthrix = Planktothrix isothrix*; *Raphi = Raphidiopsis raciborskii*; *Micaerug = Microcystis aeruginosa*; *Micpann = Microcystis panniformis*; *Micprotis = Microcystis protocystis*; *Anag = Anagnostidinema amphibium*; *Stamsp = Sataurastrum* sp.; *Stamtet = Staurastrum tetracerum*; *Pseucate = Pseudanabaena catenata*; *Euastabm = Euastrum abruptum*.**

## DISCUSSION

Our study showed that nutrients play an important role in structuring phytoplankton and zooplankton communities since nitrogen forms created two distinct scenarios in reservoirs: one with high phosphorus concentrations (supereutrophic) and another with high nitrogen concentrations (mesotrophic). Our first hypothesis was partially accepted since the phytoplankton biomass differed temporally and vertically only in the supereutrophic reservoir, while in the mesotrophic reservoir only the temporal variation caused significant changes in phytoplankton. Also, the dominance of non-diazotrophic filamentous cyanobacteria was observed under high concentrations of nitrogen in mesotrophic (throughout the study period) and supereutrophic (July/2016 and September/2016) reservoir. Moreover, the zooplankton biomass differed between the reservoirs, which confirms our second hypothesis that cyanobacteria biomass negatively influence the Calanoida copepods, while the chlorophytes positively influence their biomass.

In the supereutrophic reservoir, cyanobacteria blooms were observed throughout the study period. In the past few decades, studies

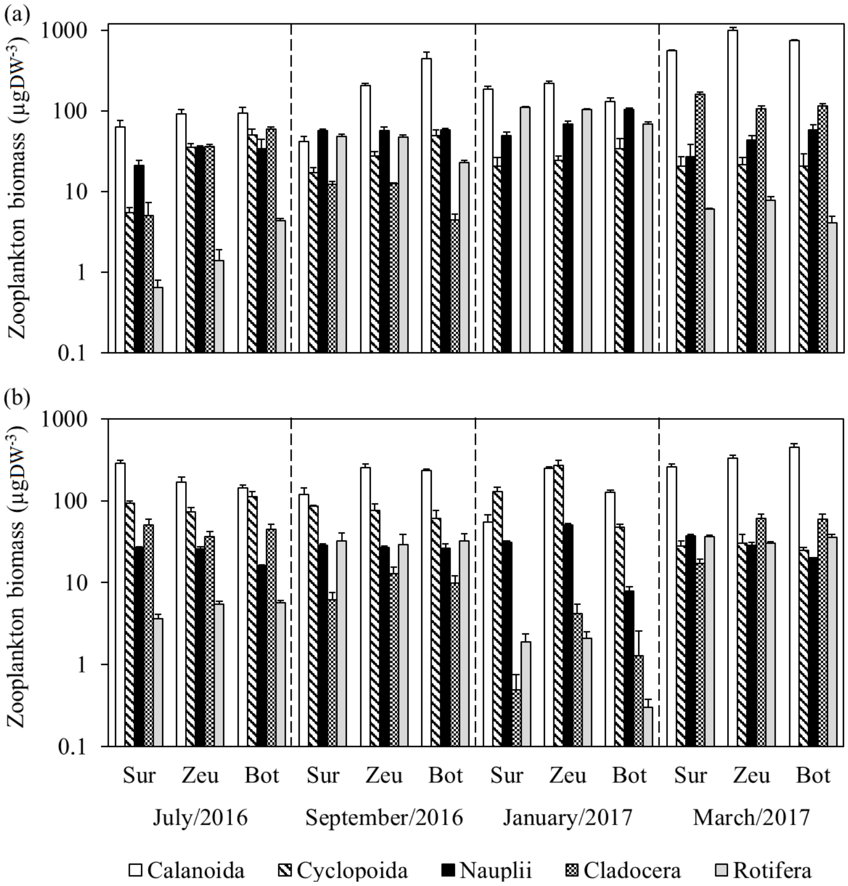

**Figure 6.** **Zooplankton biomass in the mesotrophic (Tabocas, a) and supereutrophic (Tapacurá, b) reservoirs between July/2016 and March/2017 at different depths. Sur = surface; $Z_{eu}$ = euphotic zone limit; Bot = bottom. Vertical lines represent the standard error of the mean (±SEM).**

conducted in reservoirs from Pernambuco, Northeastern Brazil, have detected perennial cyanobacteria blooms with monospecific dominance (Moura et al. 2018). Most studies indicate the dominance of *Cylindrospermopsis*, *Microcystis*, and *Planktothrix* in the blooms (Bouvy et al. 2000, Moura et al. 2018). There is strong evidence that temperature and nutrients are the main factors contributing to the frequent occurrences of cyanobacteria blooms in tropical reservoirs (Rigosi et al. 2014).

The codominance and substitution of non-diazotrophic filamentous cyanobacteria, mainly *P. agardhii*, by colonial cyanobacteria of the *Microcystis* genus was observed in the supereutrophic reservoir, showing a direct relationship with nitrogen availability and increased electrical conductivity and water temperature over the months. In colder conditions, *P. agardhii* can grow and remain in the environment for long periods (Mantzouki et al. 2016), besides growing under high phosphorus concentrations (Aguilera et al. 2019). In the supereutrophic reservoir, we observed the growth of *P. agardhii* when DIN, nitrate, and nitrite presented high availability, however, in low availability, the biomass of *P. agardhii* reduced. Other studies conducted in the Tapacurá reservoir have shown that, in addition to nitrogen and phosphorus concentrations, the mixing zone ($Z_{mix}$), turbidity and $Z_{max}$ contributed to the success and variation of cyanobacteria composition during seasonal changes (Dantas et al. 2012, Diniz et al. 2019).

The $Z_{eu}$ and $Z_{eu}$:$Z_{max}$ showed a positive relationship between diazotrophic and non-diazotrophic filamentous cyanobacteria, and an inverse relationship with colonial cyanobacteria in the supereutrophic reservoir, similar to that observed in other studies conducted in Southeastern and Northeastern Brazil (Bortolini et al. 2016, Costa et al. 2016). Dantas et al. (2012) showed that colonial cyanobacteria were favored by high phosphorus concentrations during the rainy season, coinciding with smaller $Z_{eu}$ and lower biomass of filamentous cyanobacteria, which were favored by greater light penetration in the water column ($Z_{eu}$:$Z_{max}$) in the Jucazinho hypereutrophic reservoir, located in Pernambuco State, Brazil.

The increase in temperature and nutrients favored cyanobacteria blooms by *M. aeruginosa* and *M. panniformis*. Paerl & Otten (2013) and Shan et al. (2019) report the dominance of *Microcystis* in shallow lakes with high temperatures since the temperature can interact synergistically with the high phosphorus values and favor *Microcystis* spp. blooms. The formation of large *Microcystis* colonies, associated with turbid waters, is a factor that inhibits the growth of filamentous cyanobacteria, as it limits light and competition for nutrients (Paerl et al. 2016, Shan et al. 2019). These factors explain why the *Microcystis* biomass was higher in months with higher temperatures and phosphorus availability, followed by lower nitrogen concentrations. Studies point out that phytoplankton growth is only limited by phosphorus (Schindler et al. 2008, Spears et al. 2012). However, our results showed that nitrogen availability is an important factor in the competitive relationship between filamentous and colonial non-diazotrophic cyanobacteria species and plays an important role in cyanobacteria blooms under limited conditions.

The second scenario observed, with high nitrogen values (mainly ammoniacal nitrogen and DIN), pH variation, and dense banks of *E. densa* verified in the mesotrophic reservoir, favored the dominance of desmids. In freshwater environments with low nutrient values and the presence of macrophytes, desmids have high diversity and biomass (Borics et al. 2003, Ngearnpat & Peerapornpisal 2007). The temporal variation, and possibly death and decomposition of macrophytes, were responsible for the variation in the physical and chemical water characteristics throughout the study, which changed the phytoplankton community.

Macrophytes are responsible for the maintenance and functioning of lakes and reservoirs since they accumulate various forms of nutrients available in the environment throughout their lifecycles (Kissoon et al. 2013). However, the death and decomposition of macrophytes release high loads of ammoniacal nitrogen back into the environment, which may favor specific phytoplankton groups (Bellisario et al. 2012). High concentrations of ammoniacal nitrogen in the environment through macrophyte senescence, especially in very shallow lakes, can be toxic to aquatic organisms (Farnsworth-Lee & Baker 2000). The results of the present study showed that typically planktonic desmids, such as *S. tetracerum* and *Staurastrum* sp., were dominant with high concentrations of ammoniacal nitrogen caused by the death of the dense *E. densa* banks.

Although desmid contributed to more than 90% of total average biomass in the mesotrophic reservoir, non-diazotrophic cyanobacteria and other algae such as diatoms and synurophytes were important in the phytoplankton biomass throughout the study period. Phytoplankton composition in mesotrophic reservoirs is usually made up of green algae, diatoms, and flagellates, which are sensitive to changes in nutrient concentrations and physical variables caused by seasonal variations (Oliveira et al. 2020). In the present study, diatoms presented higher biomass under conditions of high water transparency and $Z_{eu}$, and low nutrient concentrations, similar to what Hu et al. (2016) observed in a tropical reservoir, where diatoms were influenced by improved water quality.

In addition to nitrogen, the pH variation (from acid to alkaline) caused changes in the structure of the phytoplankton community in the mesotrophic reservoir. Desmids are commonly found in several environments with low pH (Lenzenweger 2000), however, more recent studies have detected these algae in waters with pH ranging from neutral to alkaline (Ngearnpat & Peerapornpisal 2007, Mataloni et al. 2015). This allows us to infer that desmids have a wide range of adaptations to trophic conditions in an environment. Therefore, the presence of *E. densa* and high pH may explain the dominance of desmids in the mesotrophic reservoir.

In the supereutrophic reservoir, the high pH (8-12) was positively related to cyanobacteria. Such relationship was also observed by Fernandes et al. (2009), who emphasized the advantage of cyanobacteria in assimilating bicarbonate within the medium, making them more competitive than other algae. The conversion of bicarbonate into carbon dioxide by the carbonic anhydrase enzyme occurs within the cell through carbon concentration mechanisms, and the release of OH - into the medium, which results in increased pH (Ataeian et al. 2019). Furthermore, even under ideal nutrient conditions, high pH is an indispensable requirement for cyanobacterial growth (Unrein et al. 2010, Visser et al. 2016).

Zooplankton varied temporally and vertically in the supereutrophic and mesotrophic reservoirs. The temporal and vertical variation in the zooplankton composition and biomass was influenced by temperature, dissolved oxygen concentrations and food availability (Domis et al. 2013, Silva et al. 2018), with zooplankton being more abundant in the water column with a higher concentration of algae (Keppeler & Hardy 2004). In the present study, higher zooplankton biomass was observed in $Z_{eu}$, where higher phytoplankton biomass was recorded. Besides, the vertical migration of zooplankton is different for each group, which is related to the mechanisms of feeding, physiology, and adaptation to the variation of abiotic factors, such as temperature (Ermolaeva et al. 2019) and defense mechanisms against predation (Picapedra et al. 2015).

Calanoida was predominant during the study and at different depths and showed a direct relationship with the phytoplankton composition in both reservoirs. The predominance of Calanoida in tropical eutrophic reservoirs with perennial cyanobacteria blooms has recently been recorded (De-Carli et al. 2018, Diniz et al. 2019). Although cyanobacteria are considered nutritionally poor and difficult for zooplankton to ingest due to their large size and toxin production (Kruk et al. 2016), Calanoida copepods can consume these organisms (Colina et al. 2016, Diniz et al. 2019). In an experiment, Leitão et al. (2018) observed that the calanoid copepod *Notodiaptomus iheringi* (Wright S., 1935) reduced the biomass of *Cryptomonas* sp. and did not affect *Microcystis* sp., because calanoids select eukaryotic algae, which reduces competition with cyanobacteria and facilitates flowering, especially for *Microcystis*. The selective capacity of calanoids is based on mechanical and chemical perception, as they can detect, ingest or reject prey based on size, motility, and nutritional value (Henriksen et al. 2007, Tiselius et al. 2013).

In the mesotrophic reservoir, desmids positively influenced calanoids. Green algae contain a high level of alpha-linolenic fatty acids (ALA) (Taipale et al. 2013), and, therefore, are a nutritious food source for zooplankton. Moreover, a positive relationship was observed between Cyclopoida and cyanobacteria in the supereutrophic reservoir, which can be explained by food selectivity. Gebrehiwot et al. (2019) observed that the cyclopoid copepod *Thermocyclops decipiens* (Kiefer, 1929) preferred to consume diatoms rather than the cyanobacteria *R. raciborskii*. Such food selectivity for smaller sized prey with greater nutritional value favors the coexistence and dominance of cyanobacteria (Hong et al. 2013, Rangel et al. 2016).

Unlike Calanoida, rotifers showed low biomass in the supereutrophic reservoir when compared to the mesotrophic reservoir. Rotifers can directly ingest small-sized cyanobacteria in low biomass (Geng & Xie 2008). However, cyanobacteria blooms dominated by *Microcystis* result in reduced rotifer biomass, as seen in other studies (Soares et al. 2010, Ji et al. 2017). Decreased rotifer biomass can be explained by the predominance of *Microcystis* in the supereutrophic reservoir, while increased rotifers in the mesotrophic reservoir was influenced by the greater availability of palatable algae, such as desmids and euglenophytes. In general, green algae are considered food sources with high nutritional value and are easily ingested by zooplankton (Fragoso et al. 2009), providing a greater diversity of zooplankton species (Colina et al. 2016).

Our study showed that the effects of temporal variation on the composition and structure of phytoplankton and zooplankton communities in the mesotrophic and eutrophic reservoirs were associated with environmental factors, mainly ammoniacal nitrogen, DIN and water temperature. The vertical variation only changed the zooplankton community, since they respond ecologically to abiotic and biotic factors, in this case, phytoplankton. *Planktothrix agardhii*, *M. panniformis*, and *M. aeruginosa* showed different strategic behaviors in response to environmental variations and nutrient availability, mainly from available nitrogen forms. Under mesotrophic conditions, excessive availability of ammoniacal nitrogen in the water, possibly resulting from the death and decomposition of the submerged macrophyte *E. densa*, favored the dominance of desmids (especially *S. tetracerum*) in an environment considered toxic to most aquatic organisms.

Copepoda Calanoida showed a direct relationship with greater availability of palatable algae (Zygnematophyceae) in the mesotrophic reservoir, contrary to what was observed in the supereutrophic reservoir, where phytoplankton algae did not influence the zooplankton groups. Finally, this study supports the need to better understand trophic relationships on a temporal scale through variation in nitrogen forms that act directly on the phytoplankton community in tropical reservoirs, regardless of the trophic state. We emphasize the importance of nitrogen in management strategies for tropical reservoirs, as well as the adaptability of Copepoda Calanoida to different trophic conditions and phytoplankton compositions.

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All authors contributed significantly to the development of the study. ASD and ANM participated in work planning. ASD contributed to sample preparation and quantification of phytoplankton and zooplankton. ASD and SLNF performed the statistical analysis. All author wrote the manuscript. All authors edited and approved the final version of the manuscript.