PRIMARY RESEARCH PAPER

Abiotic factors driving cyanobacterial biomass and composition under perennial bloom conditions in tropical latitudes

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Abstract While warming and eutrophication have increased the frequency and magnitude of harmful cyanobacterial blooms globally, the scenario for many eutrophic tropical freshwaters is a perennial year-round bloom. Yet, the drivers of persistent blooms are less understood when conditions such as light, temperature, and nutrients favor cyanobacteria growth year-round, and especially in regions facing recurrent periods of drought. In order to understand the drivers of cyanobacteria dominance, we assessed the abiotic conditions related to the abundance and dominance of the two dominant bloom-forming genera *Raphidiopsis* and *Microcystis*, in six shallow, man-made lakes located in the semiarid Northeastern region of Brazil during a prolonged regional drought. Lower water level corresponded to increased phosphorous and nitrogen concentration and, consequently, phytoplankton biomass. Cyanobacterial biomass was also proportional to phosphorus concentrations during year-round blooms. Yet, the two dominant cyanobacterial genera, *Raphidiopsis* and *Microcystis,* seldom co-occurred temporally and the switch between them was driven by water transparency. Our results illustrate the effects of drought induced water level reductions on the biomass and composition of

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cyanobacterial blooms in tropical shallow man-made lakes. Given the ideal year-round conditions (i.e., high light and temperature), droughts may be expected to intensify the risk and multitude of problems associated with eutrophication.

Introduction

The link between harmful cyanobacterial blooms and eutrophication has long been recognized as a critical threat to freshwater ecosystems (Paerl, 1988). Cyanobacteria blooms alter energy flux in aquatic food webs, leading to loss of biodiversity and threatening the sustainability of aquatic ecosystems (Paerl & Otten, 2013). Eutrophication and high cyanobacteria biomass affect many ecosystem services, promoting significant economic losses, including the increase in water treatment cost for drinking supply, decline of commercial and subsistence fishing and aquaculture, and impairment of recreational use of freshwaters (Aylward et al., 2005; EPA, 2015; Le Moal et al., 2019). Furthermore, the increase of organic matter caused via blooms promote trihalomethanes (THM) formation, when chlorination is applied for disinfection purposes of drinking supply, which are environmental pollutants and potentially carcinogenic (Rook, 1974; Gallard & Von Gunten, 2002). Moreover, the production of cyanotoxins poses a potential health hazard for pets, livestock, wildlife, and also humans, especially when drinking water supplies are affected (Carmichael, 1992; Merel et al., 2013; Paerl, 2018).

The observed enhancement of blooms in terms of distribution, frequency, and magnitude is a consequence of the combined and even interactive effects of eutrophication and climate change, including warming (Paerl & Huisman, 2008; Burford et al., 2016; Harke et al., 2016; Paerl & Otten, 2016; Paerl, 2017; Salmaso et al., 2018). High dominance and biomass of cyanobacteria in freshwaters are triggered by combined abiotic and biotic drivers such as anthropogenic nutrient over-enrichment, namely from excessive loads of phosphorus and nitrogen, high temperatures and light intensity, shallow depth, low flushing, high inorganic turbidity, and weak grazing pressure (Soares et al., 2009; Moss, 2011; Rigosi et al., 2014; Costa et al., 2016; Paerl, 2017; Leitão et al., 2018; González-Madina et al., 2019; Havens et al., 2019; Amorim et al., 2020). There also is an effect of temperature and solar irradiance on the susceptibility of shallow lakes to develop blooms for a given nutrient concentration (Kosten et al., 2012).

In tropical latitudes, cyanobacterial blooms in shallow eutrophic waters are more frequent and last longer when compared to their higher latitude counterparts, where key drivers such as light and temperature fluctuate seasonally (Lind et al., 2016). Indeed, in the absence of such seasonality, blooms often persist year-round in eutrophic waters (Figueredo & Giani, 2009; Figueredo et al., 2016; Batista et al., 2018; Giani et al., 2020). Yet, factors regulating cyanobacterial biomass and community composition during persistent blooms are less understood, which is, at least partly, because most information on blooms is from regions where such phenomena are seasonal (McGregor & Fabbro, 2000; Soares et al., 2009; Muir & Perissinotto, 2011; Lind et al., 2016; Ma et al., 2016; Batista et al., 2018).

Seasonal droughts also play a major role in cyanobacteria bloom dynamics (Naselli-Flores, 2003; Medeiros et al., 2015; Brasil et al., 2016; Costa et al., 2019; Tilahun & Kifle, 2019). The lack of precipitation during droughts reduces lake depth and subsequently affects multiple physical, chemical, and biological conditions (Naselli-Flores, 2003; Olds et al., 2011; Mosley, 2015). The abiotic effects resulting from droughts have been reported to favor cyanobacteria dominance (McGregor & Fabbro, 2000; Bouvy et al., 2003; Brasil et al., 2016). Conversely, periods of extreme prolonged drought in shallow lakes may also limit cyanobacteria due to high inorganic turbidity, in favor of mixotrophic organisms or diatoms (Costa et al., 2016, 2019; Crossetti et al., 2019). Hence, while there is little doubt that droughts result in a general decline in water quality, the impacts of drought on bloom dynamics are variable and likely lake-specific. Overall, the role of drought induced water level reduction on the dynamics of persistent year-round blooms is poorly understood.

Successful water quality management depends on identifying the local drivers of the cyanobacterial assemblage for a given lake (Mantzouki et al., 2016; Paerl, 2017; Moura et al., 2018; Le Moal et al., 2019).

Despite several shared traits among genera, cyanobacteria are a heterogeneous group responding differently to environmental conditions and abiotic regulators. Therefore, understanding the link between key traits and environmental regulators is essential to develop specific management actions to improve water quality (Mantzouki et al., 2016). For instance, toxigenic colonial *Microcystis* and filamentous *Raphidiopsis* are the main known genera to form blooms in tropical waters (Soares et al., 2013; Brasil et al., 2016; Tilahun & Kifle, 2019). These genera produce distinct toxins with implications for water quality, *Microcystis* mostly produces the hepatotoxin microcystin, while *Raphidiopsis* may synthesize a diverse array of neurotoxins such as saxitoxin, neosaxitoxin, and gonyautoxins in addition to cytotoxic cylindrospermopsin (Sukenik et al., 2012; Cirés et al., 2017). Higher diversity of potential toxin classes during *Raphidiopsis* blooms may increase management costs (i.e., toxin analysis and water treatment) of this genus compared to *Microcystis* (Paerl & Otten, 2016).

Each cyanobacteria genus shows specific ecophysiological traits that represent adaptations to distinct environmental conditions (Dokulil & Teubner, 2000; Mantzouki et al., 2016). Although both *Microcystis* and *Raphidiopsis* have been associated with eutrophic waterbodies (Soares et al., 2013), they have different environmental preferences. *Raphidiopsis* is a shade-tolerant species that dominates during dry periods and under low light availability in warm, mixed, and shallow environments (Padisák, 1997; Reynolds et al., 2002; Soares et al., 2009, 2013; Costa et al., 2019). In contrast, buoyant *Microcystis* is adapted to higher light intensity (Paerl et al., 1985; Soares et al., 2009; Torres et al., 2016), low turbulence (Huisman et al., 2004), and stratified environments (Soares et al., 2013). Moreover, *Raphidiopsis* (potential N_2 fixer) might be expected to dominate when nitrogen is limiting, while *Microcystis* (non-N_2 fixer) is expected to dominate when nitrogen is not limiting growth (Schindler et al., 2008; Paterson et al., 2011; Mowe et al., 2015). Although eutrophic conditions stimulate both genera, *Raphidiopsis* blooms are more common under higher nutrient concentrations, especially phosphorus (Soares et al., 2013; Bonilla et al., 2016). Yet, few studies have reported on the abiotic regulators of tropical and truly year-round blooms (Mowe et al., 2015).

Here, we aimed at identifying environmental factors related to the temporal variability of phytoplankton abundance, community composition, and cyanobacterial dominance in six shallow man-made multi-use lakes in the Brazilian semiarid tropical region during a prolonged drought. We hypothesized that (i) low water level will correspond to increased nutrient, phytoplankton, and cyanobacterial biomass concentration, and (ii) the composition of year-round cyanobacterial blooms will change with euphotic depth. We discuss the implications of the results for multiple uses of semiarid man-made lakes in tropical climates with perennial blooms.

Material and methods

Study site

We studied six lakes located in the northeast region of Brazil (Fig. 1), where the regional climate is tropical Semiarid (BS'h', Alvares et al. 2013), characterized by low annual rainfall (average rainfall of 550 mm/year), high average annual temperature ($\sim 26.5°C$), and evapotranspiration rates above 1500 mm year^{-1} (Menezes et al., 2012; Braga et al., 2015). Rainfall is concentrated in a few months, usually from February to May (i.e., the rainy season), while the other months are characterized by negative water balance representing the drought season (Marengo et al., 2017). Drought is a natural phenomenon in this region; however, the intensity and duration of dry periods have been increasing (Marengo et al., 2020). The most recent drought lasted from 2012 until mid-2018, and represented one of the longest droughts in the Brazilian semiarid region in the last decades (Marengo et al., 2018). This prolonged drought varied from moderately to extremely dry before our sampling, according to the Standard Precipitation Index (SPI) (Figueiredo & Becker, 2018; Braga & Becker, 2020; Marengo et al., 2020), with rainfall anomalies between 20 and 60% below the 1981–2000 mean. During this period, 2012 and 2016 were the driest years with rainfall 300–400 mm year^{-1} below the expected amount (Marengo et al., 2018). Hence, we sampled lakes with relatively low water volume during this drought period in 2017, i.e., three of them had their volume between 11 and 33% of its maximum capacity (Table 1).
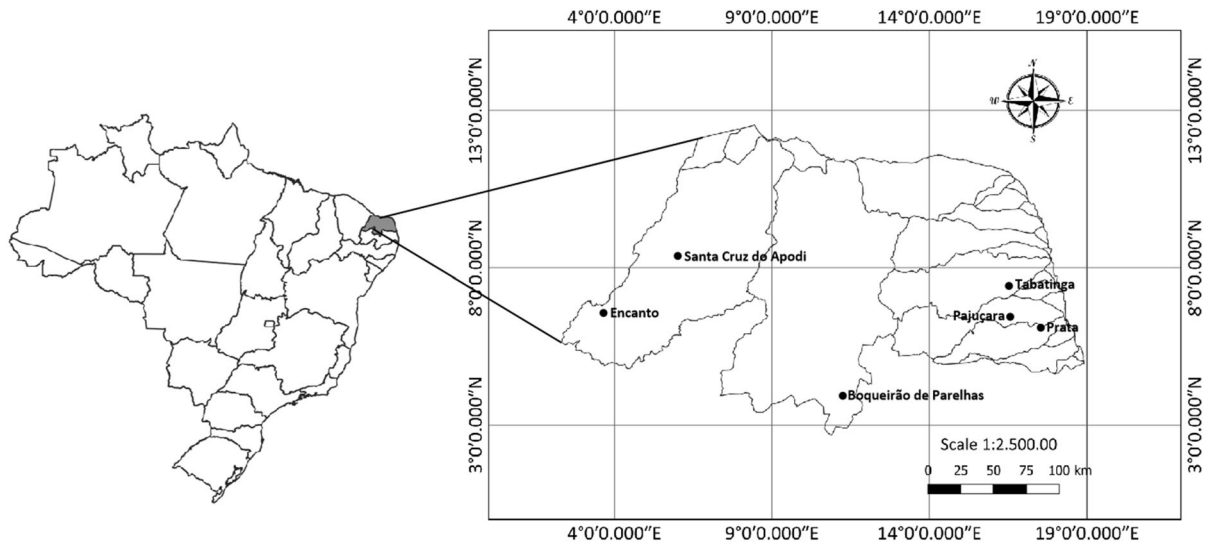
Fig. 1 Study area showing the location of the six studied lakes

Table 1 Morphometric variables of the six lakes included in the study

Man-made lakes	Basin	Area (ha)	Maximum capacity (m³)	Volume (%)
Boq. Parelhas	Piranhas/Assu	1.267	84.792.119	33.22
Encanto	Apodi/Mossoró	124	5.192.538	74.98
Prata	Jacú	151	9.321.149	81.87
Tabatinga	Potengi	1.090	89.835.678	11.76
Sta. Cruz	Apodi/Mossoró	3.413	599.712.000	24.75
Pajuçara	Rio Trairi	NA	NA	NA

Volume (%) means annual average of volume during the year 2017 compare to its maximum capacity near to the dam. Data on the area and maximum capacity for the Pajuçara lake were not available (NA). Data source: State Department of the Environment and Water Resources, (SEMARH)

The morphometric variables, area, and maximum capacity of the lakes were obtained from the State Department of Environment and Water Resources (SEMARH, 2017) (Table 1). The studied lakes have been used for multiple purposes, including irrigation, fishing, leisure activities, livestock maintenance and, two of them, Santa Cruz do Apodi (Sta. Cruz) and Boqueirão de Parelhas (Boq. Parelhas), also for drinking water supply. This study was conducted as part of a monthly monitoring program (12 months) designed to evaluate whether such lakes may be suitably used for fish cage culture. These lakes match the scenario described to favor cyanobacteria populations: warm temperatures, high solar irradiance, and high vulnerability to nutrient input, especially from

diffuse anthropic sources and internal fertilization from sediments (Kosten et al., 2011; Cavalcante et al., 2018).

Sampling and analysis

Water samplings from the six lakes were carried out on two consecutive days at monthly intervals from January to December 2017. The sampling point was set in the deepest part of each lake near the dam. The mean of three depth measurements at the sampling point was used as a proxy for maximum depth (Z_{max}). Water transparency was assessed using a Secchi disk. The euphotic depth (Z_{eu}) was calculated as 2.7 times the Secchi transparency (Cole, 1994). Water

temperature was measured in situ at the bottom and top of the water column. Water samples were collected with a PVC tube in each lake (2 m in length) integrating the first two meters of the water column beneath the surface. This procedure was repeated five times spaced around the collecting point with $\sim$ 2 m horizontal distance between them. Water samples ($\sim$ 30 l/sample) were integrated and stored into pre-washed bottles. Phytoplankton samples were immediately fixed with acetic Lugol solution. Samples for chemical analyses were transported to the laboratory in a refrigerated cooler box.

Aliquots of unfiltered lake water were stored in a freezer ($-$ 20°C) for total phosphorus (TP) and total nitrogen analyses (TN). For chlorophyll-a (Chl-a), total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP), total suspended solids (TSS), volatile suspended solids (VSS—Organic), and fixed suspended solids (FSS—Inorganic), aliquots of water (250–500 ml) were filtered onto GF/C glass fiber filters (1.2 μm pore size). TN and TDN were analyzed by standard techniques using SHIMADZU TOC$_{VCPN}$ sampler with the SSM-5000A solid sample combustion unit by chemiluminescence. TP and TDP were determined using the persulfate oxidation method (Valderrama, 1981). Chlorophyll-a (Chl-a) was quantified by spectrophotometry using ethanol 95% as a solvent (Wintermans & De Mots, 1965; Jespersen & Christoffersen, 1987), while TSS, VSS, and FSS were determined using gravimetric analyses (Chanlett, 1947). To assess the trophic states of the lakes, we used the criteria proposed by Thornton & Rast (1993). According to these authors, waters of semiarid lakes with total phosphorus (TP) concentrations lower than 50 μg l^{-1} and total chlorophyll-a (Chl-a) lower than 15 μg l^{-1} may be classified as mesotrophic while those samples with TP and Chl-a higher than 50 μg l^{-1} and 15 μg l^{-1}, respectively, may be considered as eutrophic.

The identification and quantification of phytoplankton community was performed with an optic light and inverted microscope ($\times$ 400 magnification), until species level (or the lowest taxonomic level possible) via morphologic and morphometric characteristics. The individuals (cells, colonies, and filaments) were enumerated in random fields (Uhelinger, 1964), using the sedimentation technique (Utermöhl, 1958). At least 100 specimens of the most frequent species ($P < 0.05$; Lund et al., 1958) were counted. The

volume of the sedimentation chamber was selected depending on the amount of algae and/or detritus in the sample. The biovolume (mm^3 l^{-1}) of phytoplankton was obtained based on approximated geometric forms (Hillebrand, 1999; Fonseca et al., 2014) after counting 40–60 specimens. Phytoplankton biomass (mg l^{-1}) was calculated by assuming that the unit of fresh weight is equivalent to a mass of 1 mm^3 l^{-1} = 1 mg l^{-1} (Wetzel & Likens, 2000). Species representing more than 5% of the total biomass were included in the statistical analyses. The estimation of mean cell size was based on measurements of at least 40 cells or individuals (case of *Raphidiopsis*). In the case of cyanobacteria species with dense colonies such as *Microcystis* (except *M. protocystis*), biovolume was calculated according to Fonseca et al., (2014), which uses a conversion factor to consider the free space between cells as a taxonomic characteristic of each species. In general, geometric shapes such as sphere, spheroid, ellipsoid, or a combination there of were used, while considering three different categories about colony size, small, medium, and large based on their greatest axis linear dimension, as detailed further in Fonseca et al., (2014).

We considered a species or genus dominant if its relative biomass was > 50% of the total phytoplankton biomass. To assess the abiotic drivers regulating *Raphidiopsis* or *Microcystis* dominance during persistent blooms, we used a "*Raphidiopsis* index" (i.e., R-index), which is the ratio between the biomass of *Raphidiopsis* and the sum of the biomass of *Raphidiopsis* plus *Microcystis*. Here, 0.5 means equal biomass of both taxa, 1.0 represents absolute dominance of *Raphidiopsis*, and 0 (zero) indicates absolute dominance of *Microcystis*. The R-index was calculated for the three eutrophic lakes where the bloom consisted mostly of *Raphidiopsis* or *Microcystis* (i.e., 3 out of the 4 bloom dominated lakes). The R-index result was compared to all abiotic variables measured (Zeu, Zmax, TP, TDP, TN, TDN, TSS, VSS, and FSS) to identify the difference in environmental conditions where *Microcystis* or *Raphidiopsis* populations dominate. The Chl-a/TP ratio indicates phytoplankton resource efficiency, values equal to 1:1 indicating maximal resource use efficiency which phytoplankton can make use of the carrying capacity, while the ratio can increase at low values of TP or higher values of Chl-a under light limitation conditions (Reynolds, 1992; Chorus & Spijkerman, 2020).

Statistical analyses

The relationships between Zmax, total and dissolved nutrients, phytoplankton, and cyanobacterial biomass were evaluated with single factor generalized linear models (GLM). The deviance value (%D) provided by the GLM analysis shows the percent of the variability in the dependent variable that is explained by the independent variable(s). The normality of the data was confirmed via Shapiro–Wilk test and when necessary, variables were $\log_{10}(x)$ or $\log_{10}(x + 1)$ transformed to meet the assumptions of linear models: The specific transformations can be seen in the regression equations for each GLM (Table 3). The criterion of $P < 0.05$ was considered as statistically significant. All statistical analyses were performed using R software (R Core Team, 2018).

Results

Based on eutrophication threshold values regarding TP and Chl-a, the lakes ranged from mesotrophic (Sta. Cruz and Prata) to eutrophic (Encanto, Boq. Parelhas and Pajuçara) (Table 2). Tabatinga lake was considered meso-eutrophic, with TP concentrations below the eutrophic threshold and Chl-a concentrations above the eutrophic threshold (Table 2). Euphotic depth (Zeu) was highest for the mesotrophic and lowest for enriched lakes (Table 2). TDP was always above 3 μg l^{-1}, expecting one month in Sta. Cruz, and TDN above 450 μg l^{-1} (Table 2). TP ranged from 12.83 to 231.89 μg l^{-1}, TN from 500.30 to 6864.00 μg l^{-1}, and Chl-a from 0.45 to 193.65 μg l^{-1} among lakes (Table 2). The Chl-a/TP ratio varied from 0.02 to 1.44 during our study and was seldom above the maximal resource use efficiency (1:1), only 6 out of 71 samples, the lowest overall annual mean value in Sta. Cruz (0.07) and highest annual mean in Tabatinga (0.75). Total suspended solids (TSS), volatile suspended solids (VSS) and fixed suspended solids (FSS) were higher in the eutrophic and meso-eutrophic lakes (Table 2). Most of the lakes had a mean temperature of 28°C (Table 2). The lakes were well mixed and the difference between the temperatures of the surface versus deepest layer was less than 1°C save a single exception.

As expected, the mesotrophic lakes (Sta. Cruz and Prata) had the lowest mean biomass of total

phytoplankton (0.60 and 3.90 mg. mg l^{-1}; Table 2) and cyanobacteria (0.05 and 0.70 mg l^{-1}; Table 2). In contrast, the most nutrient-enriched lakes (Boq. Parelhas and Pajuçara) had the highest mean phytoplankton (149.24 and 97.29 mg l^{-1}; Table 2) and cyanobacteria biomass (148.19 and 94.40 mg l^{-1}; Table 2). The mesotrophic lakes were characterized by a more diversified phytoplankton composition. Sta. Cruz was mostly dominated by Bacillariophyceae with cyanobacteria dominance only in January, while Prata was mostly dominated by Chlorophyceae with cyanobacteria dominance from October to December (Fig. 2a, b). Tabatinga had a more pronounced dominance of cyanobacteria (Fig. 2c), and the eutrophic lakes (Encanto, Boq. Parelhas e Pajuçara) had persistent dominance of cyanobacteria virtually during the entire year (Fig. 2d–f). Thus, increased dominance of cyanobacteria corresponded closely to the decline in the relative abundance of eukaryotic phytoplankton in the more eutrophic lakes.

Cyanobacteria dominated the phytoplankton community (i.e., cyanobacteria > 50% of phytoplankton biomass) in the meso-eutrophic (Tabatinga) and the three eutrophic lakes (Boq. Parelhas, Pajuçara, and Encanto) for most months of the year (Fig. 2). Moreover, the three eutrophic lakes had high cyanobacterial dominance throughout the year save one month, and cyanobacteria was > 80% of the total phytoplankton biomass for at least nine months over the year (Fig. 2). In the eutrophic lake Boq. Parelhas, cyanobacteria was always > 80% of total phytoplankton biomass (Fig. 2).

During these persistent blooms of cyanobacteria (i.e., lakes with 11 months of cyanobacterial dominance per year), the dominant cyanobacterial taxa differed among lakes over time. In the eutrophic lakes, the high cyanobacteria dominance was manifested in high biomass throughout the year and total cyanobacteria biomass was nearly equal to phytoplankton biomass. The dominant genera in these eutrophic lakes (Boq. Parelhas, Pajuçara, and Encanto) was either *Raphidiopsis raciborskii* (Woloszynska) Aguilera, Berrendero Gómez, Kastovsky, Echenique & Salerno, or *Microcystis aeruginosa* (Kützing) Kützing, and these two species rarely co-occurred (Fig. 3d–f). Encanto and Pajuçara had a temporal switch of dominance between these species (Fig. 3d, f). *Pseudanabaena catenata* Lauterborn also appeared from January to March in Encanto (Fig. 3d). *Microcystis*

Table 2 Descriptive statistics (average, maximum and minimum values between parentheses) of limnological variables from each lake during the year 2017

| Variables	Sta. Cruz	Prata	Tabatinga	Encanto	Boq. Parelhas	Pajuçara
Zeu (m)	7.5	3.8	2.2	1.9	1.3	1.6
	(3.5–12.1)	(3.2–4.3)	(1.6–2.4)	(0.8–3.5)	(0.3–1.6)	(0.3–2.7)
Zmax (m)	16.6	3.9	5	5.9	5	4.52
	(10.9 -19.3)	(2.1–11)	(3–7)	(3.8–8.3)	(3.4–6.8)	(1.3–7)
Temp (°C)	28	28	28	28	26	28
	(26–30)	(26–31)	(25–30)	(25–31)	(23–28)	(25–30)
TP ($\mu g\ l^{-1}$)	22.7	38.7	45.4	67.6	97.5	107.6
	(12.8–35.8)	(22.9–69.2)	(33.1–56.1)	(16.7–111.9)	(50.24–170.76)	(42.9–231.9)
TDN ($\mu g\ l^{-1}$)	10.7	17	23.25	29.5	38.8	40.7
	(1.7–20.2)	(3.5–60.8)	(12.8–45)	(12.8–52.3)	(16.78–119.75)	(17.8–67.4)
TN ($\mu g\ l^{-1}$)	690.6	652.6	2150.2	1502.3	1824.83	3462.9
	(543.7–802.4)	(500.3–830.3)	(1640–2389)	(707.9–2502)	(1278–2383)	(1328–6864)
TDN ($\mu g\ l^{-1}$)	603.9	573.7	1809.4	1046.9	1530	2736.3
	(510.3–748.2)	(456.1- 742.1)	(1473–2042)	(746.1–1324)	(1212–2070)	(1370- 5574)
TSS ($mg\ l^{-1}$)	3.2	6.8	16.9	10.4	15.9	16
	(1.5–6.3)	(2.8–12.1)	(10.4–32)	(3–34.7)	(8.2–27.7)	(8 –37)
FSS ($mg\ l^{-1}$)	1.6	3.1	5.5	3.2	9.7	5.1
	(0 -3.7)	(0.2–8.4)	(1.6–13.5)	(0.6–12)	(3.4–19.7)	(2.2–10.8)
VSS ($mg\ l^{-1}$)	1.6	3.7	11.4	7.2	6.2	10.8
	(1–2.6)	(2–6.8)	(8.5–18.5)	(2.2–22.6)	(4.5–8)	(3 (83–28.5)
Chl-a ($\mu g\ l^{-1}$)	3	7.6	35	32.6	29.1	70.3
	(0.9–10.8)	(3.7–11.6)	(20.2–53.6)	(9–112.7)	(4.8–51.2)	(10.4–193.6)
Chl-a/TP	0.07	0.2	0.7	0.36	0.4	0.57
	(0.0–0.22)	(0.0–0.4)	(0.4–1.4)	(0.13–1.3)	(0.1–0.7)	(0.23–1)
Phytoplankton ($mg\ l^{-1}$)	0.60	3.9	13.3	48.4	149.2	97.3
	(0.0–2.1)	(0.5–12.7)	(4.7–64.5)	(1.6–175.8)	(4.8–643.1)	(7.8–469.8)
Cyanobacteria ($mg\ l^{-1}$)	0.05	0.7	10	45.8	148.2	94.4
	(0.0–0.11)	(0.0–5.3)	(0.9–63.8)	(0.9–171.7)	(4.1–643)	(0.8–468.4)

Temperature refers to measurements at the surface (with < 1°C difference between surface and deepest point, see results for details)

aeruginosa represented the highest biomass achieved in the meso-eutrophic and all eutrophic lakes (Fig. 3c–f). In the meso-eutrophic lake, Tabatinga, cyanobacteria biomass varied with time, and in most months cyanobacteria biomass dominated the phytoplankton community (Fig. 2); the dominant species was *Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg, though *Microcystis panniformis* Komárek reached the highest biomass in April (55.30 mg l^{-1}) (Fig. 3c). In contrast, cyanobacteria biomass contributed very little to phytoplankton total biomass in the mesotrophic lakes most of the months (i.e., 7 months cyanobacteria < 10% of

phytoplankton biomass in both lakes), where the main species found was *Aphanocapsa* sp. in Sta. Cruz and Prata, though *Planktolyngbya sp.* also appeared in Prata (Fig. 3a, b).

Generalized linear regressions with single factor predictors indicated that Zmax was significantly and negatively correlated to TP (Fig. 4a; Table 3), and also TDP, TN, and TDN ($P < 0.001$ see Table 1 in Online Resource), and total phytoplankton biomass (Fig. 4b; Table 3). In general, lower lake depth corresponded to an order of magnitude increase in phytoplankton biomass (Fig. 4b). In turn, TP was significantly and positively correlated to cyanobacteria biomass

Fig. 2 Phytoplankton taxonomic composition shown as relative biomass of each phytoplankton class during the year 2017 for each studied lake
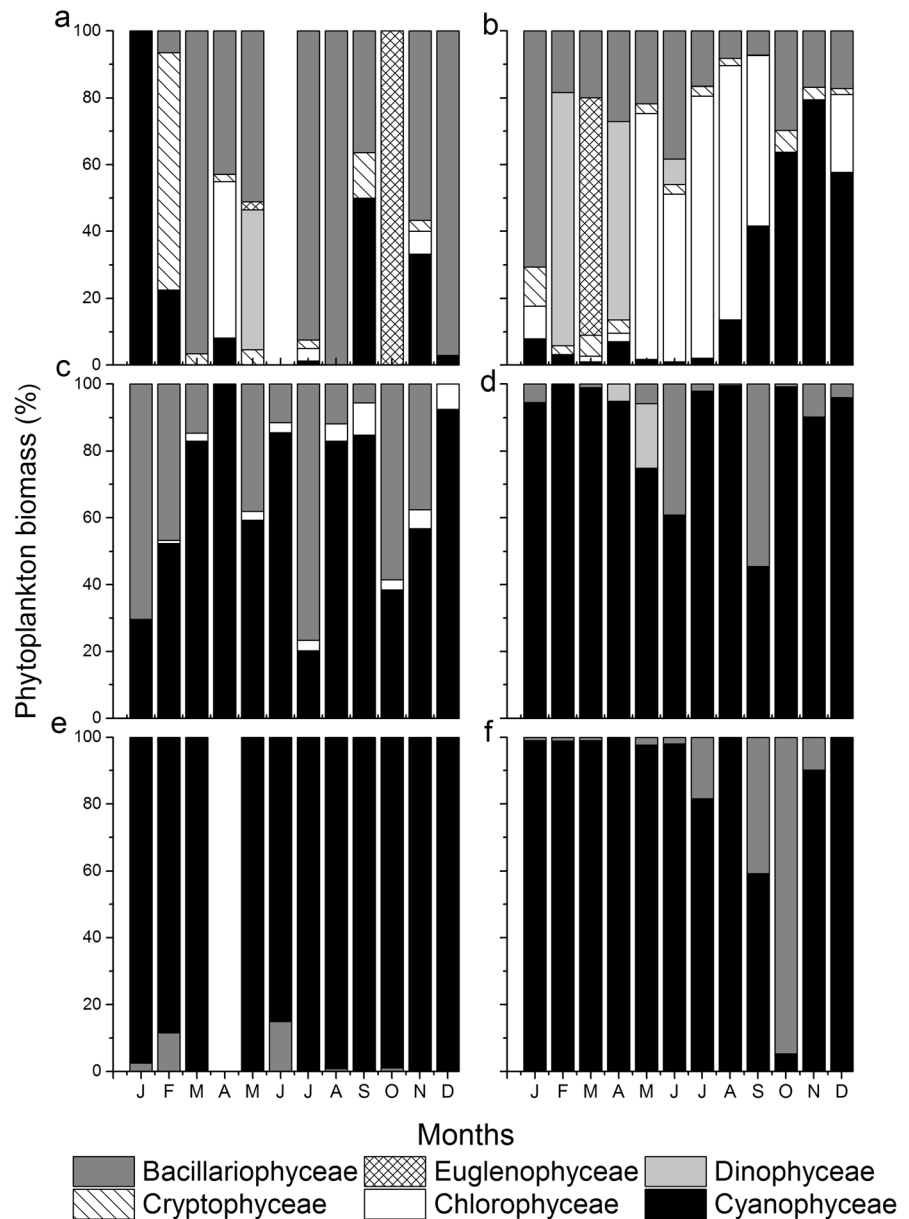
(Fig. 4c; Table 3), Chl-a (Fig. 4d; Table 3), and total phytoplankton (Fig. 4e, Table 3). Based on the deviance value, TP explained 37% of the variability in cyanobacteria biomass, 61% of Chl-a, and 38% of phytoplankton biomass (Table 3). Besides, total phytoplankton was significantly and negatively correlated to Zeu (Fig. 4f; Table 3), while Chl-a was significantly positively correlated to TSS (Fig. 4g; Table 3) and negatively to Zeu (Fig. 4h; Table 3).

Given that *Raphidiopsis* and *Microcystis* were the most representative genera of cyanobacteria in the lakes with persistent dominance of cyanobacteria (Fig. 3), the "*R*-index" was applied to explore the range of environmental conditions that corresponded to the dominance of these genera in the three eutrophic lakes (see methods for details). *Microcystis* dominated when TP was < 123 μg l^{-1} (Fig. 5a); when TDN was < 2260 μg l^{-1} (Fig. 5b); and when TSS was < 16.5 mg l^{-1} (Fig. 5c). In contrast,

Fig. 3 Total phytoplankton and cyanobacteria biomass for each lake from January to December of 2017. Bars indicate biomass of each cyanobacteria genus and the black line total phytoplankton biomass
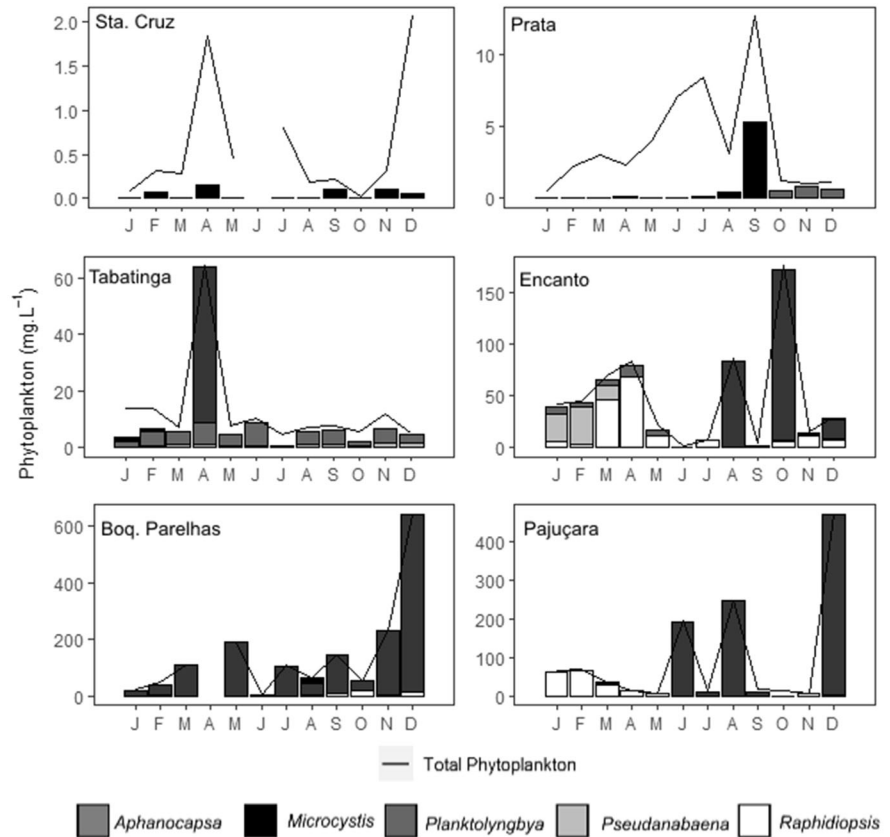

Raphidiopsis dominated in environments with a higher range of nutrient concentrations from 39 to 231 µg l^{-1} TP (Fig. 5a); 953–4910 µg l^{-1} TDN (Fig. 5b); and 3–47 mg l^{-1} TSS (Fig. 5c). Moreover, *Microcystis* dominated in environments with a relatively deeper euphotic depth and was never dominant when the euphotic depth was < 1.1 m (Fig. 5d). Conversely, *Raphidiopsis* dominated at a wider range of euphotic depth, including those < 1.1 m (Fig. 5d). Temporal co-occurrence between *Raphidiopsis* and *Microcystis* was seldom observed. Specifically, out of a total 36 samples, only one (∼ 3%) had a R-index between 0.4 and 0.6 (i.e., temporal co-occurrence of the cyanobacterial taxa). Moreover, only 4 out of 36 samples had an R-index between 0.1 and 0.9, indicating that in 86% of the samples either *Microcystis* or *Raphidiopsis* dominated the cyanobacterial bloom biomass (i.e., > 90% of total).

Discussion

As expected, the biomass of phytoplankton and bloom-forming cyanobacteria increased along the lake´s trophic state gradient. The frequency of cyanobacterial dominance also increased from episodic to perennial year-round blooms from mesotrophic lakes to eutrophic lakes, corresponding to a parallel decline in the relative contribution of eukaryotic phytoplankton. Moreover, the negative relationship between lake depth and nutrient concentration or phytoplankton biomass emphasizes the role of drought associated water level reduction in intensifying the effects of eutrophication (Naselli-Flores, 2003; Aldridge, 2014; Bakker & Hilt, 2016; Brasil et al., 2016; Costa et al., 2016; Havens et al., 2019). Despite the variety of physical, chemical, and biological factors shown to control cyanobacterial blooms, the concentration of nutrients (P and N) is often the key driver of cyanobacteria biomass even in tropical regions with year-round availability of light and high

Fig. 4 GLM regressions showing the relationship between maximum depth (Zmax) and **a** total phosphorous (µg l⁻¹) and **b** phytoplankton biomass (mg l⁻¹). Also between total phosphorus (µg l⁻¹) and **c** cyanobacteria biomass (mg l⁻¹); **d** Chl-a (µg l⁻¹); and **e** total phytoplankton biomass (mg l⁻¹). Also between euphotic zone depth (Zeu) and **f** phytoplankton biomass (mg l⁻¹); **g** Chl-a (µg l⁻¹); and between **h** total suspended solids (TSS) (mg l⁻¹) and Chl-a (µg l⁻¹). Dots represent all samples from the six study lakes from January to December of 2017. The line shows the fit while the shaded area shows the 95% confidence interval for each regression
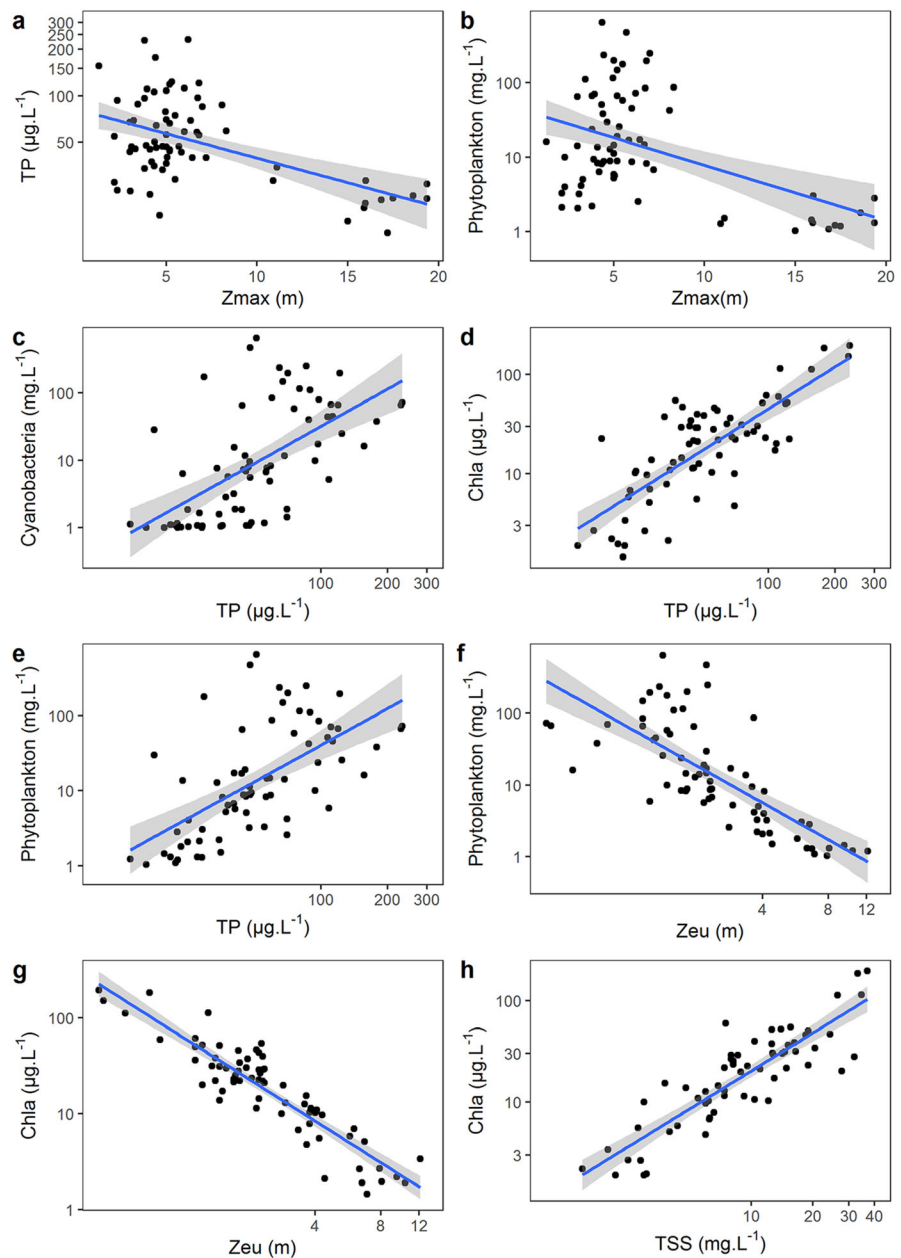
temperatures (Paerl, 2017; Amorim et al., 2020). Indeed, all eutrophic lakes in this study displayed perennial year-round blooms and highlights the potential for constant optimal conditions for cyanobacterial dominance in shallow tropical reservoirs (Figueiredo & Giani, 2009; Soares et al., 2009; Figueredo et al., 2016; Lind et al., 2016; Batista et al., 2018).

Arid and semiarid regions face drastic changes in water levels as a consequence of recurrent drought and short rainy periods that modify physical and chemical water characteristics affecting phytoplankton biomass and community structure (Naselli-Flores, 2003; Medeiros et al., 2015). Several studies demonstrated that water depth changes induced by drought can cause an increase in nutrient concentration, favor cyanobacteria dominance, and result in profound impacts on

Table 3 Summary results of the generalized linear models (GLM) analyzing the relationship between depth (Zmax) and total phosphorous (TP) and total phytoplankton biomass

Response variable	Explanatory variable	Equation	D^2
TP	Zmax	$\log_{10}(y) = -0.03x + 1.91$	27.91
Phytoplankton	Zmax	$\log_{10}(y + 1) = -0.07x + 1.63$	22.38
Cyanobacteria	TP	$\log_{10}(y + 1) = 1.84\log_{10}(x + 1) - 2.18$	36.98
Phytoplankton	TP	$\log_{10}(y + 1) = 1.62\log_{10}(x + 1) - 1.64$	37.73
Chl-a	TP	$\log_{10}(y + 1) = 1.40\log_{10}(x + 1) - 1.15$	60.64
Phytoplankton	Zeu	$\log_{10}(y + 1) = -2.53\log_{10}(x + 1) + 2.57$	57.33
Chl-a	Zeu	$\log_{10}(y) = -2.40\log_{10}(x + 1) + 2.51$	82.07
Chl-a	TSS	$\log_{10}(y) = 1.61\log_{10}(x + 1) - 0.43$	74.18

Also, the relationship between TP, euphotic zone (Zeu), and total suspended solids (TSS) and total phytoplankton biomass, cyanobacteria biomass, and chlorophyll-a (Chl-a). The explanatory and response variable for each GLM is shown together with the regression equation and % deviance. All regressions were significant at $P < 0.001$

Fig. 5 *Raphidiopsis* Index in relation to **a** dissolved nitrogen (µg l^{-1}), **b** total phosphorous (µg l^{-1}), **c** total suspended solids (mg l^{-1}), and **d** euphotic zone (m). Horizontal black dash lines represent equal biomass for both genera, 0 means 100% dominance of *Microcystis*, and 1 means 100% dominance of *Raphidiopsis*
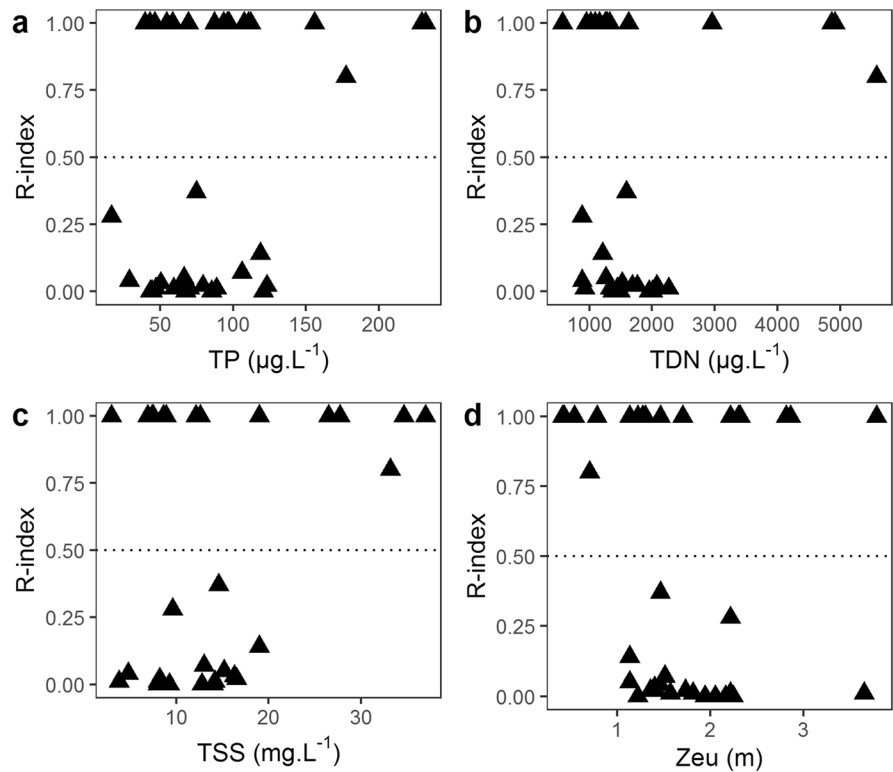
water quality (Naselli-Flores, 2003; Aldridge, 2014; Mosley, 2015; Brasil et al., 2016; Rocha Junior et al., 2018; Havens et al., 2019; Amorim et al., 2020). We found similar results as shallower lakes had higher concentrations of total and dissolved nutrient concentrations and the phytoplankton community was composed mainly of cyanobacteria. In many cases, droughts lead to reduced water level, increased residence time, and reduced dilution capacity in freshwater systems (Mosley, 2015). Besides the increase in nutrient concentration, drought reduces hydrologic flushing events, so that once a bloom is

established it persists until the next flushing (Medeiros et al., 2015; Paerl, 2018). Besides, the reduction of depth may enhance sediment resuspension to the water column, allowing for internal P loading. This may be have been an important source of phosphorus to the studied lakes, since shallow semiarid lakes are susceptible to the internal release of P under certain environmental conditions such as low depths and resuspension of sediment due to the wind drive mixing (Cavalcante et al., 2018). Overall, our findings corroborate previous results highlighting the vulnerability of shallow eutrophic tropical lakes to the role of nutrients for drought-triggered cyanobacteria blooms (Bouvy et al., 2000; Bittencourt-Oliveira et al., 2012; Braga et al., 2015; Medeiros et al., 2015; Costa et al., 2016; Walter et al., 2018).

Our results also highlight factors regulating the composition of perennial year-round tropical cyanobacterial blooms. A key result was that the two main bloom-forming genera (i.e., *Raphidiopsis* and *Microcystis*) almost never co-occurred in time, as shown by the R-index. We show that TP correlated positively with phytoplankton and cyanobacteria biomass; meanwhile, light availability (as indicated by euphotic depth in this study) may be an important regulator of cyanobacterial species composition in tropical eutrophic lakes. Specifically, the filamentous cyanobacterium *Raphidiopsis* dominated in more turbid (i.e., euphotic depths < 1.1 m) and nutrient-enriched waters. Also, Raphidiopsis generally occurred in a wider range of abiotic conditions compared to the colonial *Microcystis*. Similarly, while *Microcystis* did not occur at TP higher than 170 µg l^{-1}, *Raphidiopsis* was present up to the maximum TP concentration observed in our study ($\sim$ 230 µg l^{-1}). In contrast, both cyanobacterial species occurred similarly across a gradient of TDP, which suggests that turbidity—not TP—was the main driver of cyanobacterial species composition. Hence, our results build on previous reports linking higher water transparency with *Microcystis* dominance during perennial blooms (Soares et al., 2009; Batista et al., 2018).

Raphidiopsis is a shade-tolerant species that can form persistent blooms despite self-shading (Padisák, 1997). In contrast, *Microcystis* forms surface blooms and tolerates high levels of UV radiation due to the enhancement of photoprotective pigments and carotenoid (Paerl et al., 1985). Hence, *Microcystis* thrives

in environments with high insolation and it is sensitive to low total light availability (Reynolds et al., 2002; Batista et al., 2018). Our results support the conclusion of these studies, and further indicate that *Microcystis* can be expected to be replaced by *Raphidiopsis* after reductions in euphotic depth due to increased phytoplankton biomass, Chl-a, and turbidity (TSS) during perennial cyanobacterial blooms. In general, the flexibility of *Raphidiopsis* adaptations to a wide range of environmental conditions (e.g., light, nutrients, TSS) via strain-specific responses has been linked to its expanding global success as bloom-forming cyanobacteria (Briand et al., 2004; Bonilla et al., 2012; Burford et al., 2016). Thus, while our results suggest that reduced water transparency may be expected to shift the dominance from *Microcystis* to *Raphidiopsis* during perennial tropical cyanobacterial blooms, the eco-physiology of cyanobacterial species including *Raphidiopsis* and *Microcystis* can have significant strain-specific variability in their responses to light and nutrients (Guedes et al., 2019).

The biomass of *Planktolyngbya*, a shade-adapted filamentous cyanobacterium (Fabbro & Duivenvoorden, 2000), was related to higher concentrations of suspended solids (VSS and TSS) and shallower depth, dominating year-round in the meso-eutrophic Tabatinga lake. In agreement with previous reports, *Planktolyngbya* has been associated with turbid environments, with mixed layers and relatively lower values of phosphate in Brazilian semiarid lakes (Pinto and Becker 2015; Barroso et al. 2018). Meanwhile, *Aphanocapsa*, a coccoid cyanobacterium typically found in eutrophic environments (Padisák et al., 2009), was detected under mesotrophic conditions and associated to lower suspended solids and deeper water depth (Zmax). Although the dominance of *Aphanocapsa* was rare in the studied lakes, microcystin-producing variants of this genus have been frequently found in other semiarid man-made lakes (Domingos et al., 1999; Marcon et al., 2017), making it a potential threat to water quality.

The connection between warmer temperatures and cyanobacteria dominance is well established (Paerl & Huisman, 2008; Paerl & Otten, 2013; Visser et al., 2016; Paerl, 2017; Paerl et al., 2020), even in the tropics (Bouvy et al., 2000; Huszar et al., 2000; Soares et al., 2009). In our study, water temperature did not relate to the biomass or composition of cyanobacteria. During the sampling period, water temperatures often

exceeded 25°C, which is the expected threshold for optimal growth (Paerl, 2018). In a previous microcosm experiment with samples from one of the eutrophic lakes in this study (Boq. Parelhas), bloom-forming cyanobacterial abundance was not favored in the warmer and nutrient-enriched treatment (de Souza et al., 2018). This may indicate that temperature is not a main driver of phytoplankton assemblage in tropical semiarid lakes, likely because temperatures are already optimal and, thus, non-limiting.

Results also indicate that nutrients were not limiting phytoplankton biomass based on nutrient concentrations as well as the Chl-a/TP ratio. Specifically, nutrients were always above concentrations considered limiting for phytoplankton uptake (3–10 µg l^{-1} SRP or 100–130 µg l^{-1} DIN) (Reynolds, 2006; Chorus & Spijkerman, 2020) with TDN more than tenfold higher than TDP. Yet, considering that nitrogen was always above the saturation threshold for phytoplankton nutrient uptake rate, TP was likely determining the carrying capacity of the system. Indeed, TP represents the total pool of phosphorous in the water, and the greater is the pool, the greater is the phytoplankton biomass sustained. High TP values here, however, do not exclude the possibility that other factors such as light or grazers might be limiting the carrying capacity (Reynolds, 1992, 2006; Chorus & Spijkerman, 2020). Indeed, that Chl-a/TP values were mostly < 1 in this study indicates that factors other than TP were likely limiting phytoplankton biomass (Reynolds, 1992; Chorus & Spijkerman, 2020). That said, some of the lakes here, including eutrophic ones, occasionally had Chl-a/TP values close to 1, suggesting that maximal resource use efficiency (i.e., all available TP converted to Chl-a biomass) was at least sometimes attained.

Future climate scenarios emphasize, besides warming, that land affected by drought will expand in North and South America, Africa, southern Europe, and Australia (Feng & Fu, 2013; Huang et al., 2016). The combination of warming, dryland expansion, and increased sediment loading due to land use change (Donohue & Garcia Molinos, 2009; Moss, 2011) may increase cyanobacterial bloom duration and favor *Raphidiopsis*, at least in shallow lakes. *Raphidiopsis* has been long recognized as an invader species (Padisák, 1997; Antunes et al., 2015) and a further increase in the expansion of the species populations dominance is worrisome due to the suite of toxins they can produce (neurotoxins and cytotoxins).

Finally, our results raise a public health concern regarding the use of the studied lakes for fish cage production as intended. The introduction of fish food in the systems increases nutrient input, which will likely increase the risk of eutrophication in the lower trophic state lakes (Gorlach-Lira et al., 2013; Henry-Silva et al., 2019). While we did not measure cyanobacterial toxicity here, microcystins from *Microcystis* and saxitoxins from *Raphidiopsis* are widely reported from other lakes within the same semiarid region of the state of Rio Grande do Norte where the study lakes are, and also from Brazilian Semiarid lakes in general (Molica et al., 2005; Bittencourt-Oliveira et al., 2014; Fonseca et al., 2015; Lorenzi et al., 2018; Moura et al., 2018). Hence, it is likely that cyanotoxins were prevalent in our study lakes as well. Given that fish may accumulate cyanotoxins (Lee et al., 2017), the consumption of fish from these lakes raises additional public health concerns. Furthermore, the economic sustainability of fish cage production in such lakes may be questionable since sub-lethal effects of cyanotoxins even at low concentrations (Calado et al., 2019) may decrease fish health and growth (Drobac et al., 2016).

Conclusion

Overall, our results indicate that in shallow tropical semiarid man-made lakes (i) low water level caused by prolonged drought, and higher concentrations of TP, is a key factor leading to perennial cyanobacteria dominance and (ii) reduced light availability (via reduced water transparency) is a key factor regulating the dominance of *Microcystis* or *Raphidiopsis* in year-round perennial blooms in shallow tropical lakes. *Raphidiopsis* thrives under higher nutrients and suspended solids (lower light) in lakes where the temperature is not a constraint. Equally important, since reports on the dynamics of truly perennial cyanobacterial blooms are scarce, the present study provides useful information for developing strategies for bloom control and management in tropical shallow lakes under dry climates. We encourage future studies to use abundance indices similar to the "R-index" here when evaluating factors associated with shifts in cyanobacterial dominance during longer duration blooms.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest: The authors declare that there is no conflict of interest.

Informed consent The author's consent for the publication.

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