

Variability in mean size of phytoplankton in two floodplain lakes of different climatic regions

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Received: 14 May 2017/Revised: 23 June 2018/Accepted: 29 June 2018/Published online: 11 July 2018
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Abstract Phytoplankton size has an important functional role in ecosystem processes, such as nutrient production and cycling. It has been suggested that warmer temperatures may favor the smaller organisms in biological communities. We evaluate the mean size of the phytoplankton organisms and apply a morphology-based functional groups (MBFG) approach. We use time series of two floodplain lakes that present mean annual temperature difference of 10°C and similar hydrodynamic, area, and mean depth. We expected that a smaller mean size of MBFGs would be

associated with higher temperatures. The Akaike Information Criterion was used to investigate environmental factors predicting the mean size of MBFGs within each lake. The mean size was most associated to nutrients and dissolved oxygen in the subtropical lake, and to temperature in the temperate lake. Large filaments with aerotopes and the small flagellated with siliceous exoskeletal structures showed high mean size at higher temperatures, thus contradicting temperature–size rules. Probably the high variability of mean size was provided by the high variability observed around environmental factors. Our findings reveal that other functional traits may be associated with the phytoplankters mean size, which result in adaptation to high variability of various environmental factors.

Handling editor: Mariana Meerhoff

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Keywords Plankton community · Bergmann's rule · Functional traits · Biovolume · Temporal variability

Introduction

The size of organisms provides important ecological information about community functioning (Peters, 1983; White et al., 2007). Size is linked to several processes such as nutrient cycling, trophic interactions, and growth rate (Ohlberger, 2013; Sommer et al., 2016). Also, the size distribution of the organisms in a community may determine the functioning of pelagic food webs (Marañón et al., 2001),

and may affect the resistance and stability of an ecosystem to perturbations (Woodward et al., 2010). The analysis of the sizes variation of sizes and shapes of organisms allows identification of the processes (physical, chemical, and biological) that drive community assemblages (Margalef, 1978; Reynolds, 1988).

The physiological, behavioral, and life-history features of phytoplankton are also related to their size (Litchman et al., 2010; Edwards et al., 2013). A smaller size of a phytoplankton organism implies a more-active metabolism, greater efficiency in nutrient uptake, higher reproductive rate, and lower sedimentation loss (Reynolds, 1984; Litchman & Klausmeier, 2008). Smaller organisms are likely to have more competitors and predators than are larger ones (Sabetta et al., 2005; Sigee, 2005). On the other hand, larger organisms have low metabolic activity, high capacity to store nutrients, and greater resistance to predation, and tend to be more tolerant to environmental stress (Finkel et al., 2010).

The temperature–size relationship has been analyzed traditionally based on classical biogeographic rules. The Bergmann rule, the James rule, and the temperature–size rule (TSR), for example, associate an increase in temperature with a reduction in organism size (Bergmann, 1847; James, 1970; Atkinson, 1994). Reduction of body size associated with global warming has been proposed as the third universal response to global warming (Daufresne et al., 2009).

The smaller body size at higher temperatures has been related mainly to the increase in metabolic rate (Rose & Caron, 2007; Mousing et al., 2014). At high temperatures and in unlimited resource conditions, the phytoplankton would become smaller because growth would be limited to compensate for the high metabolic demand (Brown et al., 2004). In addition, at higher metabolic rates and limiting resource conditions, competition would be intensified, and smaller algae that are more efficient in nutrient uptake would be favored (Winder et al., 2009; Finkel et al., 2010).

Variations in the water-column mixing, oscillations in light and nutrients, as well as biotic relationships (e.g., predation and competition) can also trigger changes in the size structure and in several other functional characteristics of the phytoplankton (Sommer & Lengfellner, 2008; Gardner et al., 2011; Winder & Sommer, 2012; Fu et al., 2016). Phytoplankton

organisms exhibit, besides body size, several other characteristics, that allow their adaptation to most diverse environmental changes; some of these characteristics are the capacity to form colonies and fix atmospheric nitrogen, aerotopes, flagellum, mucilage, and the high ratio surface:volume. Classifications based on morphological traits (morphology-based functional groups) as proposed by Kruk et al. (2010) involve the knowledge of purely morphological traits of taxa and can be used to explain how the phytoplankton community responds to environmental factors (Kruk & Segura, 2012; Segura et al., 2018).

Studies testing the effect of temperature variation on the size distribution of phytoplankton include observational and experimental studies in coastal, oceanic, and lacustrine environments (Marañón et al., 2001; Morabito et al., 2007; Rasconi et al., 2015; Fu et al., 2016). In experimental designs, phytoplankton is usually subjected to temperature gradients in mesocosms, to assess the isolated effect of temperature on the mean size (Yvon-Durocher et al., 2011; Peter & Sommer, 2012, 2015). Although experiments are widely used in temperature–size investigations, they are frequently criticized. For example, experiments in mesocosms do not reflect the complexity of the natural environments. Also, in assays using clonal cultures it is impossible to identify the effect of temperature on the phenotypic plasticity of phytoplankton (Atkinson et al., 2003; Adams et al., 2013).

Several approaches have been used (experiments, long-term studies, species-specific responses) to study the effects of temperature on the functioning of aquatic ecosystems. The space-for-time approach has been an alternative to the obtention of realistic responses of temperature effects in different ecosystems, including lakes (Pickett, 1989; Meerhoff et al., 2007, 2012). Therefore, ecological studies in environments located at different latitudes allow the inclusion of temperature variation and provide an excellent opportunity to investigate the relationship between temperature and phytoplankton size.

Floodplain lakes of temperate and subtropical regions show high phytoplankton diversity (Nabout et al., 2007; Segura et al., 2015). The processes that structure the communities in each of these environments vary, but temperature plays an important role in both these environments (Adrian et al., 2009). Thus, predicting the effects of temperature changes on body

size is critical to designing appropriate conservation policies and strategies (Sheridan & Bickford, 2011).

In this study, we used a space-for-time approach with empirical data from a subtropical and a temperate lake to determine the factors that drive the phytoplankton size variation. We hypothesized that temperature is the main driver of this variation. Additionally, we expected that a smaller mean size would be associated with higher temperatures.

Materials and methods

Study area

Sampling was carried out in two lakes from the temperate and subtropical regions in both natural and shallow lakes. The subtropical Lake (22°43'S, 053°17'W) is located in southern Brazil, on the Paraná River floodplain and the temperate Thompson Lake (40°20'N, 090°01'W) is located in the midwestern United States, on the Illinois River floodplain (Fig. 1). These lakes were chosen because they showed a high percentage of shared phytoplankton species, and also because of their similarities in hydrodynamics (mixing regime) and nutrient concentrations (phosphorus and nitrogen), most of the time (Rodrigues et al., 2002; Lemke et al., 2017). Therefore, these characteristics, together with the temperature disparity, make them suitable for investigations on the relationship between size and temperature using a space-for-time approach.

Patos Lake has an area of ca. 7.46 ha (Souza Filho & Stevaux, 1997), mean depth of 3.97 m, and mean annual temperature of 25°C. In the study period, the temperature ranged from 17 to 31°C. This lake preserves pristine conditions and is permanently connected to Ivinhema River through a sinuous channel of approximately 1,300 m. The Ivinhema River is 245 km long, with a meandering drainage pattern, and is an important tributary of the Paraná River. The Ivinhema watershed occupies an area of 46,000 km² (Pott et al., 2014). The Paraná River is the main controller of the hydrodynamics of the entire floodplain system (Agostinho et al., 2004b).

Thompson Lake is ca. 10 ha in area, with a mean depth of 2.77 m and a mean annual temperature of 15°C (Fig. 1). The temperature ranged from 1.7 to 27°C in the study period. This lake was drained and the lakebed used for agriculture for decades (Sparks et al.,

2017). The process of restoration of the lake had begun in 2007; from then, the lake does not have direct connection with the river (isolated lake). The Illinois River (ca. 439 km long) is one of the main tributaries of the Mississippi River and the most important river in the State of Illinois. The Illinois River watershed covers approximately 75,000 km² (Warner, 1998). Water-level fluctuations in the Illinois River are heavily regulated by dams in its watershed (Sparks et al., 2017).

Sampling strategy and sample analyses

Our sampling was carried out quarterly from 2008 to 2012, in the spring, summer, autumn, and winter. We obtained 20 samples from each lake. Biotic and abiotic samples were collected at the subsurface of the pelagic zone of the lakes. Phytoplankton was sampled directly with bottles and preserved with 1% acetic Lugol solution.

Phytoplankton abundance was estimated according to Utermöhl (1958) and the American Public Health Association (APHA, 2005). Biovolume was estimated by multiplying the density of each taxon by its volume. We estimated the cell volume by calculating the volume of the geometric shape most similar to each cell form (Sun & Liu, 2003). The actual mean size of the phytoplankton community was evaluated through the mean size of the organisms, which was obtained by dividing the biovolume by the total density in each sample (Marañón, 2015; Sommer et al., 2017).

We used the morphology-based functional groups (MBFGs) approach according to Kruk et al. (2010), for a better understanding between the mean size of organisms and their other traits, such as maximum linear dimension, surface area, and the presence of mucilage, flagella, aerotopes, heterocysts, and siliceous exoskeletal structures. All organisms were classified into the MBFG. In this approach, phytoplankton organisms are distinguished in seven MBFGs based on morphological traits identified for each organism at the light microscopy (Kruk et al., 2010): Group I: small organisms with high S/V; Group II: small flagellated organisms with siliceous exoskeletal structures; Group III: large filaments with aerotopes; Group IV: Organisms of medium size lacking specialized traits; Group V: unicellular or colonial flagellates of medium to large size; Group VI: Non-flagellated

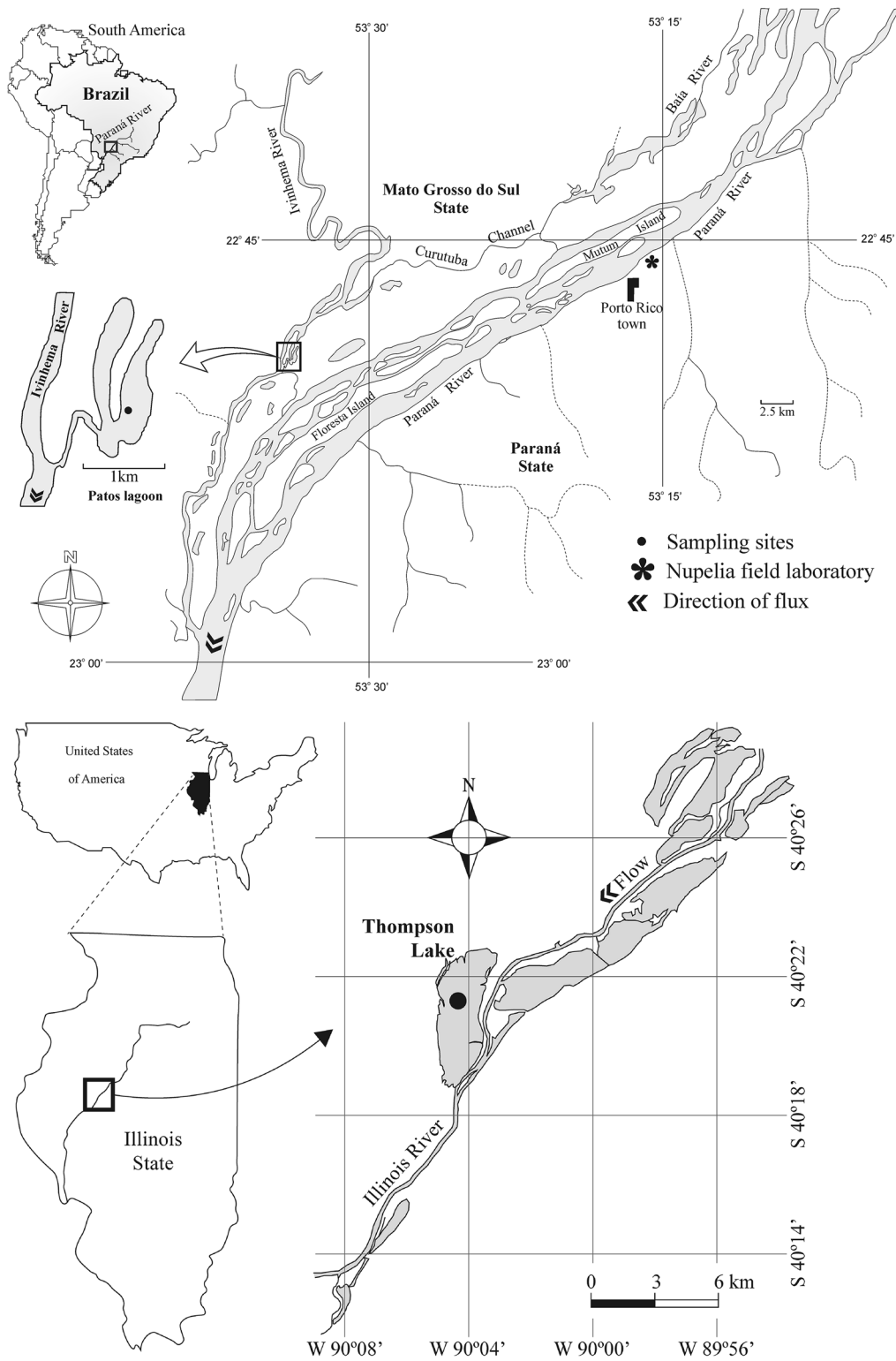


Fig. 1 Map and location of the study area, showing the sampling sites in the temperate lake (Thompson Lake, Illinois River floodplain) and the subtropical lake (Patos Lake, upper Paraná River floodplain)

organisms with siliceous; and Group VII: large mucilaginous colonies.

In the subtropical lake, zooplankton was collected using a motorized pump and filtering 600 l of water per sample through a 68 μm mesh plankton net. The samples were preserved in a 4% formalin solution buffered with calcium carbonate. The collection and conservation of zooplankton, as well as the physical and chemical variables of the temperate lake, were obtained following the methodology described in Lemke et al. (2017). We estimated the abundance of zooplankton (Cladocera, Copepoda, and Rotifers) following recommendations by Lansac-Tôha et al. (2009).

Water temperature (WT), pH, electrical conductivity (EC), dissolved oxygen (DO), and turbidity (Tur) were obtained with portable digital potentiometers. Total suspended material (TSM) was estimated following Wetzel & Likens (2000). Total phosphorus (TP) and soluble reactive phosphorus (SRP) were determined according to Mackereth et al. (1978). Total nitrogen (TN) was estimated according to Bergamin et al. (1978). Dissolved inorganic nitrogen (DIN) was obtained by the sum of nitrate, nitrite (Giné et al., 1980), and ammonium (Koroleff, 1976). The mixing zone (Z_{mix}) was estimated from the thermal profile, and the euphotic zone (Z_{eu}) was calculated as 2.7 times the Secchi depth (Cole, 1994). The $Z_{\text{mix}}:Z_{\text{max}}$ ratio was used to evaluate the physical stability of the water column. The $Z_{\text{eu}}:Z_{\text{mix}}$ ratio was used as a measure of the light availability in the mixing zone, and the $Z_{\text{eu}}:Z_{\text{max}}$ ratio was used as a measure of light availability in the water column (Jensen et al., 1994). The samplings were standardized, and community analyzes were performed by the same team. Data for water level were provided by the Agência Nacional de Águas (ANA), Itaipú Binacional for the Paraná River, and by National Weather Service Products for the Illinois River.

Data analysis

A Principal Components Analysis (PCA) was performed to summarize the environmental variability and to evaluate the existence of spatial and temporal patterns (Legendre & Legendre, 1998). The axes for interpretation were selected according to the broken-stick criterion (Jackson, 1993). The Spearman correlation was used to analyze the relationship between the

water level of each lake and the water level of the associated river.

We used the Kruskal–Wallis test to assess differences ($\alpha = 0.05$) in the mean size of phytoplankton between the lakes (Gotelli & Ellison, 2011), for total phytoplankton and each MBFG. We performed the analysis for each climate season (e.g., temperate lake in spring versus subtropical lake in spring).

Multiple linear regressions were performed to determine the factors influencing the mean phytoplankton size in each lake. In addition to temperature, we used as explanatory variables DIN, SRP, DO, and the $Z_{\text{eu}}:Z_{\text{max}}$ ratio, representing the availability of resources and $Z_{\text{mix}}:Z_{\text{max}}$ ratio representing the hydrodynamics that act in the selection of phytoplankton sizes (Sommer et al., 2017). The abundance of zooplankton (proxy for grazing pressure) was also used as an explanatory variable because it affects the phytoplankton community directly through predation (Naselli-Flores & Barone, 2011). Because the phytoplankton groups have different environmental requirements (Reynolds, 1984), we also performed multiple linear regressions for each MBFG. We used Akaike's Information Criterion (AIC) to select the best approximating model for the data. Models with $\Delta\text{AIC} \leq 2$ were used for inferences (Burnham & Anderson, 2002).

The Kruskal–Wallis analysis and Spearman correlation were performed by using the Statistica program version 7.1 (StatSoft, 2005). PC-ORD[®] v.6 software (McCune & Mefford, 2011) was used to perform the PCA. The program Spatial Analysis in Macroecology (SAM: Rangel et al., 2010) was implemented for model selection.

Results

Water temperature differed by ca. 10°C between the lakes. In both lakes, the temperature varied widely in winter and spring. Both lakes showed low light availability in the mixing zone. The mean values and the coefficients of variation of the environmental variables and zooplankton abundance are listed in Table 1. The temperate lake showed greater abundance of zooplankton, mainly rotifers. The water level of the subtropical lake was strongly correlated with the water level of the Ivinhema (Spearman, $r = 0.76$, $P < 0.05$) and Paraná River (Spearman, $r = 0.50$,

Table 1 Mean values and coefficient of variation (in parentheses) of the maximum depth (Z_{max} , m), euphotic zone (Z_{eu} , m), mixing zone (Z_{mix} , m), euphotic zone (Z_{mix} , m), euphotic zone (Z_{mix} , m), mixing zone (Z_{mix} , m), mixing zone: maximum depth ratio ($Z_{mix}:Z_{max}$), euphotic zone: mixing zone ratio ($Z_{eu}:Z_{mix}$), water temperature (WT, °C), dissolved oxygen (DO, mg l⁻¹), pH, electrical conductivity (EC, μS cm⁻¹), turbidity (Tur, NTU), total nitrogen (TN, μg l⁻¹), dissolved inorganic nitrogen (DIN, μg l⁻¹), total phosphorus (TP, μg l⁻¹), soluble reactive phosphorus (SRP, μg l⁻¹), total suspended material (TSM, mg l⁻¹), total zooplankton abundance (Zoo, ind l⁻¹), cladoceran abundance (Clad, ind l⁻¹), copepod abundance (Cop, ind l⁻¹), and rotifer abundance (Rot, ind l⁻¹) from 2008 to 2012 in the subtropical lake and the temperate lake

Season	Autumn		Winter		Spring		Summer	
	Subtropical	Temperate	Subtropical	Temperate	Subtropical	Temperate	Subtropical	Temperate
Z_{max}	4.69 (39.76)	2.67 (14.49)	3.65 (18.33)	2.71 (18.97)	3.62 (15.92)	2.71 (18.97)	4.00 (18.87)	2.82 (17.36)
Z_{eu}	1.85 (42.65)	1.29 (70.53)	2.28 (24.65)	1.29 (23.91)	1.77 (66.86)	1.23 (29.27)	1.30 (43.21)	1.49 (39.29)
Z_{mix}	4.36 (52.77)	2.35 (29.02)	3.65 (18.33)	2.71 (18.97)	2.78 (50.77)	2.89 (18.38)	3.24 (21.56)	2.16 (25.53)
$Z_{mix}:Z_{max}$	0.90 (26.17)	0.87 (20.54)	1.00 (0.00)	1.00 (0.00)	0.75 (39.52)	1.00(0.00)	0.84 (28.53)	0.78 (26.24)
$Z_{eu}:Z_{mix}$	0.53 (77.30)	0.52 (42.22)	0.65 (35.07)	0.47 (6.14)	0.70 (45.29)	0.43 (28.44)	0.41 (43.51)	0.69 (35.00)
WT	28.74 (2.49)	21.98 (9.56)	22.06 (21.58)	4.30 (60.02)	21.84 (13.36)	10.88 (12.76)	28.36 (8.14)	25.76 (5.89)
DO	3.29 (89.89)	9.50 (38.02)	5.59 (38.97)	12.17 (12.56)	6.66 (54.25)	10.79 (17.59)	2.94 (81.82)	9.61 (25.87)
pH	6.39 (5.38)	8.50 (4.84)	6.45 (5.54)	8.38 (5.01)	7.06 (10.62)	8.13 (2.55)	6.35 (6.79)	8.74 (1.51)
EC	45.46 (17.90)	34.39 (10.29)	39.02 (23.61)	23.81 (16.77)	38.14 (34.38)	24.08 (57.92)	43.18 (20.76)	35.09 (14.22)
Tur	19.02 (122.69)	16.28 (82.40)	10.84 (74.47)	16.52 (39.90)	20.34 (78.45)	30.92 (99.55)	29.99 (113.54)	10.70 (99.03)
TN	728.05 (24.53)	2066.91 (67.33)	859.91 (30.71)	1717.39 (58.21)	1092.28 (64.38)	876.43 (56.95)	1169.46 (29.34)	668.00 (124.28)
DIN	9.21 (52.31)	30.05 (110.46)	15.63 (70.16)	60.10 (114.60)	12.10 (112.02)	46.12 (175.06)	17.03 (59.03)	42.01 (170.35)
TP	44.06 (47.51)	253.61 (83.82)	26.68 (14.53)	248.47 (147.29)	49.28 (68.98)	141.42 (103.96)	62.18 (29.02)	596.85 (124.37)
SRP	0.01 (33.99)	0.08 (215.16)	0.01 (46.68)	0.01 (0.54)	0.01 (45.22)	0.10 (220.12)	0.02 (59.25)	0.06 (223.61)
TSM	0.71 (82.58)	20.18 (65.55)	1.26 (37.82)	18.85 (44.72)	1.56 (51.60)	17.09 (114.91)	2.35 (184.23)	13.28 (68.32)
Zoo	43883.96 (81.19)	64232.00 (29.61)	25731.60 (26.87)	124106.40 (116.73)	103423.70 (79)	333933.20 (60.31)	126326.83 (128.84)	405556.00 (100.27)
Clad	7153.99 (184.94)	10536.5 (115.83)	6228.67 (67.50)	7845.2 (123.65)	44656.10 (159.47)	25373.6 (85.72)	6185.56 (137.77)	130909.2 (93.43)
Cop	14103.92 (135.18)	23640 (44.32)	10230.84 (64.59)	18432.8 (159.40)	27633.33 (61.41)	19720.8 (108.52)	32329.34 (157.78)	69640 (76.09)
Rot	22626.04 (62.90)	23613.5 (106.04)	9272.09 (58.97)	97828.4 (120.40)	31134.27 (103.57)	288838.8 (61.36)	87811.91 (198.67)	205006.8 (120.34)

$P < 0.05$), whereas the water level of the temperate lake was only weakly correlated with the water level of the Illinois River (Spearman; $r = 0.28$, $P < 0.05$).

The PCA explained 58% of the variability of the data (axis 1 = 38%, axis 2 = 20%) and highlighted environmental differences between the lakes (Fig. 2). The first axis showed a separation between the lakes that was mainly related to temperature. The subtropical lake was associated with greater depth (-0.79), temperature (-0.71), and EC (-0.77). The temperate lake was associated with higher dissolved oxygen (0.89) and pH (0.86). The second axis was influenced by higher $Z_{eu}:Z_{max}$ (0.92) and Z_{eu} (0.61) in winter and spring for the subtropical lake, and higher DIN availability for the temperate lake (-0.40).

Phytoplankton

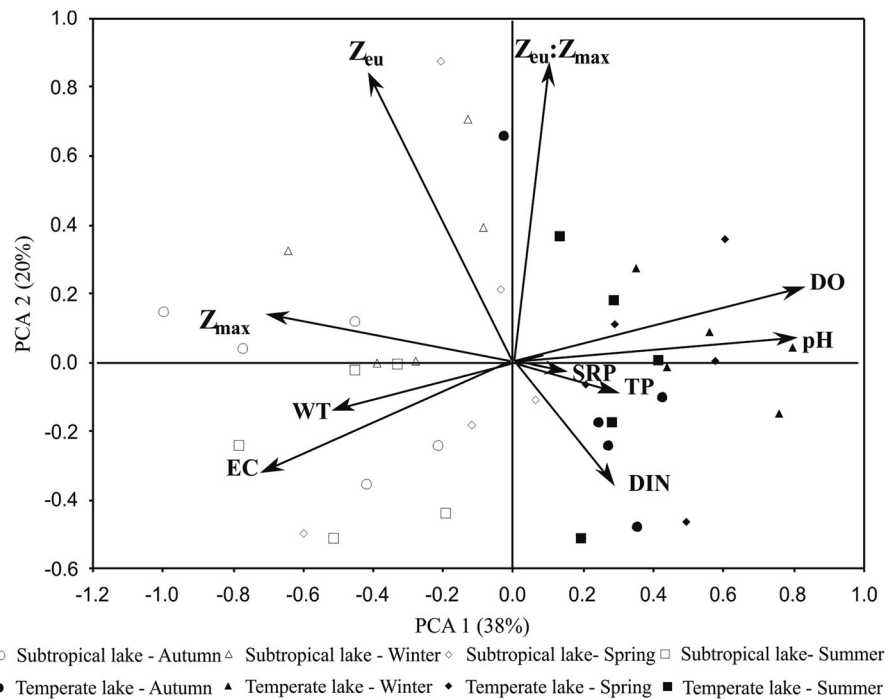
We recorded 236 taxa in the subtropical lake and 179 in the temperate lake; 79 taxa were common to both lakes. Green algae (chlorophyceans and zygnetophyceans), blue-green (cyanobacteria), diatoms, xanthophyceans, and mixotrophic flagellates (Chlamydomphyceans, euglenophyceans, dinoflagellates, chrysophyceans, and cryptophyceans) occurred in both lakes. Raphidophyceans occurred only in the

subtropical lake. All MBFGs were present in both lakes, except for the temperate lake, that the MBFG III (filaments with aerotopes and high ratio surface:volume including potentially toxic species) and MBFG I (small, high surface-to-volume ratio (S/V) organisms) were not recorded in the spring and MBFG II (small flagellated organisms with siliceous exoskeletal structures) was not recorded in the summer.

The subtropical lake showed a higher mean size of total phytoplankton and higher temporal variability (Fig. 3). MBFGs II, III, VI, and VII showed higher mean size variability when compared to the others groups. MBFGs II, III, and VI (Non-flagellated organisms with siliceous) showed higher mean sizes in most study periods. For the temperate lake, MBFG III and MBFG VII (large mucilaginous colonies) showed higher mean sizes in most study periods. Summer and autumn were similar and showed the highest total phytoplankton mean size.

Significant differences for the mean size among the lakes were obtained for MBFG I (KW = 4.60; $P < 0.05$), II (KW = 4.19; $P < 0.05$), IV (KW = 4.81; $P < 0.05$), and total phytoplankton mean size in winter (KW = 3.93; $P < 0.05$). Significant differences among seasons (within each lake) only occurred for MBFG II and III in the temperate lake. For the

Fig. 2 Dispersion of scores along the first two axes of the Principal Components Analysis (explicability of axis shown in brackets), performed for the abiotic variables in the subtropical lake and the temperate lake. (Z_{max} , maximum depth; Z_{eu} , euphotic zone; Z_{mix} , mixing zone; $Z_{eu}:Z_{mix}$, euphotic zone: mixing zone ratio; WT water temperature, DO dissolved oxygen, EC electrical conductivity, DIN dissolved inorganic nitrogen, PT total phosphorus, SRP soluble reactive phosphorus)



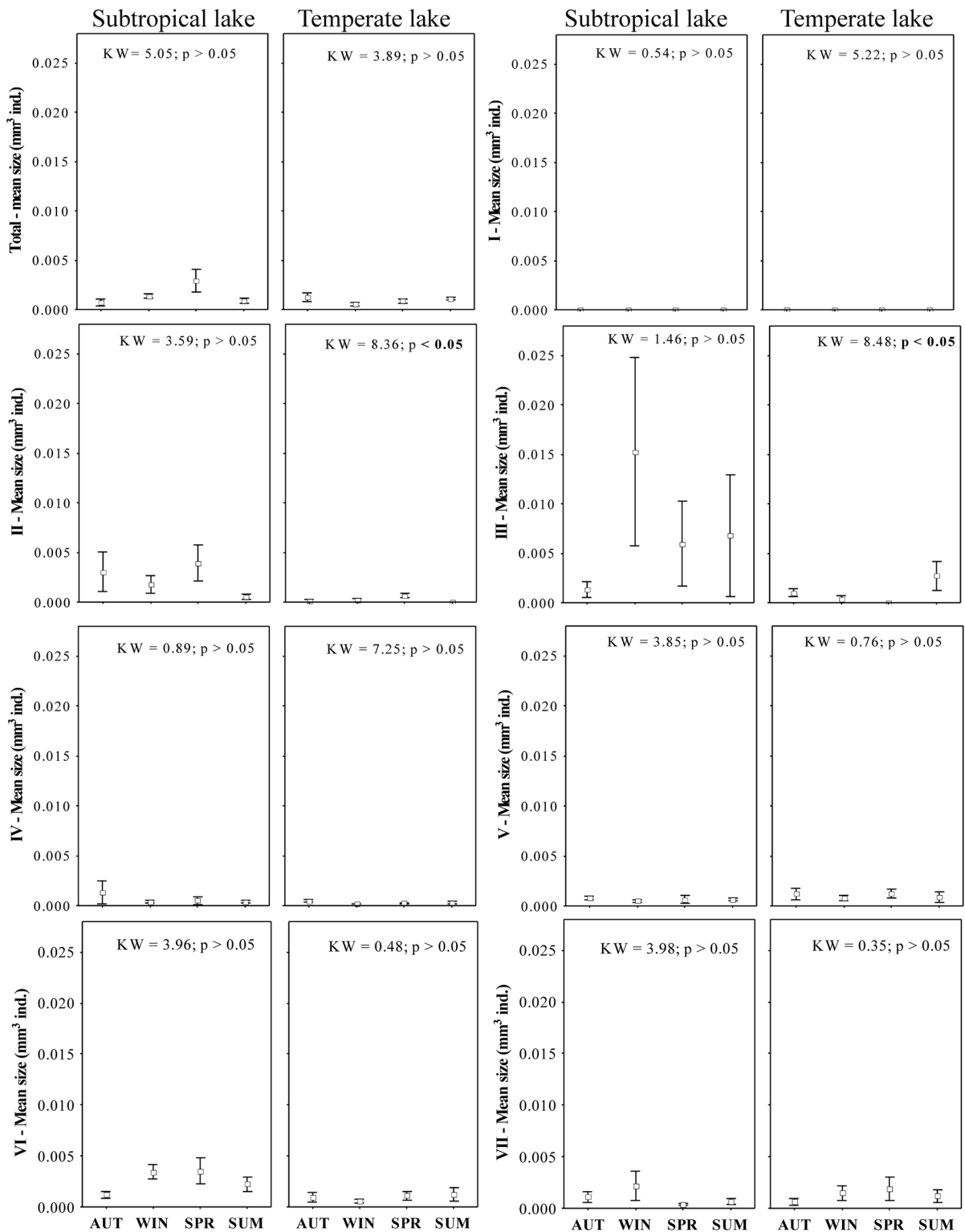


Fig. 3 Mean values (symbols) and standard error (bars) of the mean size of the total phytoplankton and the MBFGs in the subtropical and temperate lakes, from 2008 to 2012

subtropical lake, the best model predicting mean size of total phytoplankton included the DO (positively related) and DIN (negatively related) (Table 2). Other model included also temperature (negatively related), zooplankton abundance, and DO (positively related). For the temperate lake (Table 3), the best model predicting mean size of total phytoplankton included the temperature and SRP (both positively related). Other models included the DO (negatively related). For MBFGs, most of the models included DO and the nutrients (SRP and DIN) for both lakes, and temperature for the temperate lake (Tables 2, 3).

Discussion

The availability of data for phytoplankton composition in natural environments, located in different temperature regimes, allowed us to investigate the behavior of the phytoplankters mean size, not only in relation to temperature, but also to other environmental variables that are considered important drivers for the mean size of these organisms. Contrary to our expectations, there were few significant differences in mean size among different temperatures and the smaller mean sizes were associated with cooler temperatures. The wide variability of size found in our results is likely attributed to response of the phytoplankton community of natural lakes to high environmental variability.

The influence of temperature on body size of phytoplankton has been investigated at various levels of organization of biological systems, from individuals to communities and with the presence or absence of trophic interactions (Peter & Sommer, 2012; Ohlberger, 2013; Sommer et al., 2016). When we study the temperature–size relationships for phytoplankton at the community level we are covering a wide range of sizes from the different life stages of organisms, their natural phenotypic plasticity, trophic interactions, and the turnover caused by environmental filters (Naselli-Flores & Barone, 2011).

The higher variability in mean size in the subtropical lake was probably influenced by the hydrological connectivity to the main river. Although the extent and sinuosity of the connection channel minimizes the influence of the river on this lake, the continuous flow of water facilitates the arrival of new phytoplankters through passive dispersal (Incagnone et al., 2015), and

may favor a greater species richness (Borges & Train, 2009; Pineda et al., 2017), and mean size variability. The importance of hydrological connectivity in structuring communities of microorganisms has been demonstrated in several studies (Agostinho et al., 2004a; Padial et al., 2014; Lansac-Tôha et al., 2016; Naselli-Flores et al., 2016). High connectivity might transport and homogenize active phytoplankters (Rodrigues et al., 2002; Bovo-Scomparin & Train, 2008; Borges & Train, 2009; Descy et al., 2012; Bortolini et al., 2016), and also the resting stages deposited in sediments (Chaparro et al., 2018). Thus can also affect other communities that interact directly with phytoplankton, such as the primary consumers (zooplankton) and its predators (fish) (Beisner et al., 2006; Lansac-Tôha et al., 2016), which could also influence the variability in phytoplankton mean size.

The morphology-based functional groups approach have been frequently addressed in ecological studies (Bortolini & Bueno, 2017; Pineda et al., 2017) and can be considered a tool to explain the relation of other phytoplankton traits to temperature, beyond size (Segura et al., 2018). Significant differences in mean size among the lakes were observed for small organisms with high S/V (MBFG I), small flagellates with siliceous exoskeletal structures (MBFG II), and organisms of medium size lacking specialized traits (MBFG IV). These MBFGs showed larger mean sizes in the subtropical lake, related to nutrients, mixing zone, and OD. Probably the combination of these variables and low temperature variation (mean annual 25°C) favored the development of the species of these MBFGs compared to the temperate lake.

The well-marked seasonality of temperate environments strongly influences the succession of plankton communities, as demonstrated by the PEG-model (Sommer et al., 1986, 2011). The seasonal significant differences between the mean size found in the temperate lake for the MBFGs II and III showed that the mean size of these MBFGs is a sensitive attribute to seasonal dynamics in temperate lakes.

In our study, the diatoms did not present significant differences of mean sizes. These organisms require special attention when we investigate their size in relation to temperature or any other environmental variable, since they present a peculiar process of formation of new frustule, known as the MacDonald–Pfizer rule that can influence the mean size of the population (Nagai & Imai, 1999; Graham & Wilcox,

Table 2 Models selected for the mean size of the phytoplankton, for each morphology-based functional group and the total phytoplankton of the subtropical lake

Models	R^2	AIC	$\Delta AICc$	AICc wi	Beta	\pm SE
Total phytoplankton						
DO and DIN	0.35	– 200.46	0	0.12	0.44	0.001
					– 0.44	0.001
DO	0.2	– 199.27	1.18	0.07	0.44	0.001
DIN	0.19	– 199.21	1.24	0.06	– 0.44	0.001
DO, DIN and Zoo	0.42	– 199	1.45	0.06	0.44	0.001
					– 0.44	0.001
					0.16	0.001
WT	0.18	– 198.97	1.48	0.06	– 0.43	0.004
WT and DIN	0.3	– 198.86	1.6	0.05	– 0.43	0.004
					– 0.44	0.001
Models—group I						
DO	0.25	– 370	0	0.2	0.5	0.001
DO and $Z_{eu}:Z_{max}$	0.3	– 368.37	1.63	0.08	0.5	0.001
					0.37	< .001
Models—group II						
DIN	0.51	– 181.41	0	0.23	– 0.71	0.002
DIN and $Z_{eu}:Z_{max}$	0.57	– 180.66	0.74	0.16	– 0.71	0.002
					0.38	0.011
WT and DIN	0.55	– 179.7	1.7	0.1	– 0.37	0.009
					– 0.71	0.002
Models—group III						
DO	0.17	– 112.72	0	0.19	0.41	0.009
WT	0.08	– 110.81	1.91	0.07	– 0.29	0.039
Models—group IV						
SRP	0.07	– 202.47	0	0.1	0.26	0.109
$Z_{eu}:Z_{max}$	0.05	– 202.16	0.3	0.08	– 0.23	0.005
OD	0.04	– 201.89	0.57	0.07	0.2	< .001
WT	0.04	– 201.88	0.58	0.07	0.2	0.004
Zoo	0.02	– 201.56	0.9	0.06	0.16	< .001
DO and SRP	0.15	– 201.07	1.39	0.05	0.2	< .001
					0.26	0.109
DIN	< .001	– 200.99	1.47	0.05	0.1	< .001
DO and $Z_{eu}:Z_{max}$	0.14	– 200.95	1.51	0.04	0.2	< .001
					– 0.23	0.005
WT and DO	0.13	– 200.83	1.64	0.04	0.2	0.004
					0.26	0.109
Models—group V						
DO	0.56	– 257.87	0	0.29	– 0.75	< .001
DO and DIN	0.59	– 256.34	1.53	0.13	0.27	< .001
Models—group VI						
DO	0.35	– 195.09	0	0.14	0.59	0.001
DO and SRP	0.44	– 194.86	0.22	0.12	0.59	0.001
					– 0.43	0.148

Table 2 continued

Models	R^2	AIC	$\Delta AICc$	AICc wi	Beta	\pm SE
WT and DO	0.43	– 194.32	0.77	0.09	– 0.47 0.59	0.005 0.001
DO and DIN	0.41	– 193.74	1.34	0.07	0.59 0.27	0.001 < .001
DO, Zoo, and NID	0.5	– 193.67	1.42	0.07	0.59 0.17	0.001 < .001
DO and Zoo	0.4	– 193.52	1.57	0.06	– 0.3 0.59 0.17	0.001 0.001 < .001
Models—group VII						
$Z_{eu} \cdot Z_{max}$	0.12	– 193.97	0	0.14	0.35	0.006
$Z_{eu} \cdot Z_{max}$ and DIN	0.2	– 192.71	1.25	0.07	0.35 0.19	0.006 0.001
DO	0.05	– 192.54	1.42	0.07	0.24	0.001
SRP	0.05	– 192.36	1.6	0.06	– 0.22	0.14
DIN	0.04	– 192.15	1.81	0.05	0.19	0.001

The coefficient of determination (R^2), Akaike information criterion (AIC), differences between the AIC of the best model (with the lowest AIC) and the second- or third-best model ($\Delta AICc$), Akaike weights (wi for the best-supported models), standard error (SE), and Beta. The best models are indicated in the text in bold letters

2000). Furthermore, it has been proposed that diatoms may be an exception to temperature–size rules, being interspecific effects were larger contributor to whole-community size differences (Adams et al., 2013).

Plankton communities are strongly influenced by the physical properties of water. For example, higher temperatures imply lower water viscosity that enhances the sinking velocity of the phytoplankters (Zohary et al., 2017). Flat shapes and flagella are favored in environments with low mixing or viscosity, providing a certain independence in relation to body size, because they facilitate the buoyance and thus decrease the sinking rates. Flat shapes and flagella probably favored the wide variation in mean size observed for MBFG II. Considering a future scenario with warmer climates, the large-sized phytoplankton non-motile, with weak buoyancy regulation mechanisms (e.g., MBFG VI) may face competitive disadvantages (Paerl & Huisman, 2008; O’Neil et al., 2012).

The cyanobacteria present a great morphological plasticity expressed mainly in the ability to form colonies and filaments of different sizes and shapes. Large filaments hinder grazing by zooplankton and can be advantageous under conditions of low mixing

or low viscosity, reducing sedimentation rates (Kruk et al., 2010). Given the wide environmental variability of the lakes, together with the availability of nutrients and the high density of zooplankton, such characteristics probably explain the variability and the larger mean size observed for groups III (large filaments with aerobes) and VII (large mucilaginous colonies) in comparison to the other morphological groups.

The phytoplankton community probably was not limited by nutrients in either lake; however, this variable was the main driver for phytoplankton mean size in the subtropical lake. The mechanism of nutrient incorporation in phytoplankton biomass (luxury uptake) (Reynolds, 1984; Powell et al., 2008) is probably responsible for the negative relationships found with phytoplankton mean size (i.e., larger size at lower concentrations of SRP and DIN). Although there is evidence of nutrient influence on mean size selection, the mechanisms that this selection occurs in natural environments are still not completely understood and doubtless depend on the physiological requirements of each MBFG (Litchman & Klausmeier, 2008; Kruk et al., 2010). Smaller mean sizes are expected in environments with high resource availability; however, small-sized organisms are also

Table 3 Models selected for the mean size of the phytoplankton, for each morphology-based functional group and the total phytoplankton of the temperate lake

Models	R^2	AIC	ΔAIC_c	AICc wi	Beta	\pm SE
Total phytoplankton						
WT and SRP	0.34	– 235.67	0	0.13	0.44	< .001
					0.43	0.003
SRP and DO	0.33	– 235.38	0.291	0.11	0.43	0.003
					– 0.36	0.001
WT	0.19	– 234.82	0.85	0.08	0.44	< .001
SRP	0.19	– 234.7	0.97	0.08	0.43	0.003
Models—group I						
WT and $Z_{eu}:Z_{max}$	0.5	– 372.47	0	0.3	0.41	< .001
					– 0.54	< .001
WT, SRP and $Z_{eu}:Z_{max}$	0.56	– 371.65	0.82	0.2	0.41	< .001
					– 0.25	< .001
					– 0.54	< .001
Models—group II						
DIN	0.08	– 251.63	0	0.1	– 0.28	< .001
SRP	0.06	– 251.36	0.27	0.09	0.26	0.002
DO	0.03	– 250.74	0.89	0.06	0.19	< .001
WT	0.03	– 250.67	0.96	0.06	– 0.18	< .001
$Z_{eu}:Z_{max}$	0.009	– 250.12	1.51	0.05	– 0.09	0.002
SRP and DIN	0.15	– 250.03	1.6	0.04	0.26	0.002
					– 0.28	< .001
Zoo	< .001	– 249.95	1.68	0.04	0.01	< .001
DIN and $Z_{eu}:Z_{max}$	0.14	– 249.79	1.84	0.04	– 0.28	< .001
					– 0.09	0.002
WT and DIN	0.13	– 249.63	1.99	0.03	– 0.18	< .001
					– 0.28	< .001
Models—group III						
DO	0.22	– 191.48	0	0.22	– 0.47	0.004
WT	0.17	– 190.17	1.3	0.11	0.41	0.001
WT and DO	0.26	– 189.51	1.96	0.08	0.41	0.001
					– 0.47	0.004
Models—group IV						
DO	0.32	– 282.26	0	0.22	– 0.56	< .001
DO and $Z_{eu}:Z_{max}$	0.39	– 281.42	0.84	0.14	– 0.56	< .001
					0.23	0.001
Models—group V						
$Z_{eu}:Z_{max}$	0.1	– 216.39	0	0.11	– 0.32	0.005
Zoo	0.08	– 215.86	0.52	0.08	0.28	< .001
SRP	0.07	– 215.74	0.65	0.08	0.27	0.004
SRP and $Z_{eu}:Z_{max}$	0.2	– 215.6	0.79	0.07	0.27	0.004
					– 0.32	0.005
Zoo and $Z_{eu}:Z_{max}$	0.17	– 214.86	1.53	0.05	0.28	< .001
					– 0.32	0.005
DO	0.01	– 214.5	1.88	0.04	– 0.13	0.002

Table 3 continued

Models	R^2	AIC	ΔAIC_c	AICc wi	Beta	\pm SE
Models—group VI						
WT	0.06	– 213.43	0	0.13	0.26	< .001
DIN	0.04	– 212.92	0.51	0.1	0.20	< .001
DO	0.01	– 212.34	1.09	0.07	– 0.12	0.002
Zoo	0.01	– 212.25	1.18	0.07	0.10	< .001
$Z_{eu}:Z_{max}$	0.004	– 212.11	1.33	0.07	– 0.06	0.006
SRP	< .001	– 212.03	1.4	0.06	0.02	0.005
WT and DIN	0.12	– 211.61	1.82	0.05	0.26	< .001
					0.20	< .001
Models—group VII						
SRP	0.1	– 195.3	0	0.12	– 0.33	0.007
Zoo	0.09	– 194.95	0.35	0.1	– 0.30	< .001
WT	0.05	– 194.09	1.2	0.07	– 0.23	0.001
DIN	0.04	– 193.85	1.44	0.06	– 0.20	< .001
SRP and Zoo	0.04	– 193.62	1.68	0.05	– 0.33	0.007
					– 0.30	< .001

The coefficient of determination (R^2), Akaike information criterion (AIC), differences between the AIC of the best model (with the lowest AIC) and the second- or third-best model (ΔAIC_c), Akaike weights (wi for the best-supported models), standard error (SE), and Beta. The best models are indicated in the text in bold letters

expected in nutrient-limited environments, mainly because of their greater uptake efficiency (Chen et al., 2010; Sommer et al., 2017).

Dissolved oxygen has been evidenced as an important factor in the temperature–size relations (Verberk et al., 2011; Forster et al., 2012). According to Walczyńska & Sobczyk (2017), the diatom size response was strongly evidenced when investigated considering the temperature–oxygen association. In our study, OD was an important driver for the mean size of the phytoplankton; however, most of the time, the relationships with the mean size were opposite between the lakes for the same MBFG. The solubility of oxygen in aquatic environments depends on the processes of salinity, atmospheric pressure, decomposition, and temperature, therefore, in view of the many factors and since the MBFGs of each lake are not necessarily composed of the same species, the opposite relations not only with DO, but also with the other variables, are plausible, considering that each species responds differently to environmental changes.

Grazing may also influence the mean size of phytoplankton, because zooplankton have different grazing preferences (Naselli-Flores et al., 2007; Klauschies et al., 2012). Copepods, for example,

generally feed on larger organisms; rotifers prefer small phytoplankton; and cladocerans have a wider range of prey sizes (Hansen et al., 1994; Colina et al., 2016). Although zooplankton abundance was not the main variable appearing in the models, grazing pressure probably affected the phytoplankton mean size, mainly in the temperate lake, which showed a high abundance of zooplankters, mainly rotifers (Table 1). We believe that the use of zooplankton abundance instead of biomass may be one of the explanations for the slight evidence of zooplankton grazing in the models. The use of biomass is likely a more appropriate proxy to evaluate the grazing pressure, considering that zooplankton also show a great size variation, even within the taxonomic groups, which reflects on their feeding habits. Unfortunately, the lack of data on zooplankton biomass prevents an analysis of this relationship.

Global warming has revitalized interest in the body size–temperature relationship (Daufresne et al., 2009; Sommer et al., 2017). Some scenarios on climate change predict that aquatic environments will be impacted by changes in the rainfall regime, higher rates of evapotranspiration, and changes in the mixing regime (Sarmiento et al., 2013), and these factors also

can select sizes and others functional phytoplankton traits. Thus, although we have not found a strong relationship between temperature and body size, it is likely that environmental changes related to global warming may cause changes in the size structure of phytoplankton.

We conclude that changes in body size were mediated by several factors, such as biotic relationships, nutrient availability and dissolved oxygen, mixing zone, and hydrological connectivity. Most of these factors can be strongly affected by temperature; therefore understanding the causes and intensity of observed changes in the size of organisms is essential to improve our predictions and management of aquatic ecosystems in the face of global warming.

Acknowledgements We are grateful to The Nature Conservancy, Illinois Natural History Survey, Illinois Water Survey, Illinois Department of Natural Resources, and the U.S. Fish and Wildlife Service, for samples and funding. We are grateful to the Center for Research in Limnology, Ichthyology and Aquaculture (Nupélia) at the State University of Maringá for logistical support, and the Coordination for the Improvement of Higher Education Personnel (CAPES) for a scholarship granted to the first author. We thank the Postgraduate Program in Ecology of Continental Aquatic Environments (PEA) of the State University of Maringá (UEM). We also appreciate and thank anonymous referees and the editor for their valuable comments and Hugo Sarmento for the discussions on phytoplankton size.

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