ECOSYSTEMS

Short-term responses of littoral phytoplankton in a large shallow subtropical lake

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Abstract: The littoral zone is an essential compartment for lake biota because of its high productivity and diversity. Moreover, phytoplankton is expected to have non-equilibrium dynamics on it. The study's aimed to explore phytoplankton in the littoral zone of a shallow lake over a short-term scale. Daily sampling was conducted for 25 consecutive summer days in 2016, at two marginal points of a continuously warm, polymictic, and oligo-mesotrophic subtropical lake (Lake Mangueira, Brazil). Cyanobacteria and Chlorophyta contributed 86% of total biomass. We observed high variability in phytoplankton structure, with species turnover over diel cycles. Redundancy analysis indicated spatial differentiation for phytoplankton structure in relation to abiotic conditions. Nutrient dynamics and humic substances were significant drivers for phytoplankton variability. Phytoplankton was positively correlated with SRP and negatively with humic substances. Our results showed a non- equilibrium state for the littoral phytoplankton of Lake Mangueira, given the high variability of abiotic conditions, even at short distances. Due to its high temporal and spatial variability, the littoralzone seems to contribute to the recruitment and maintenance of phytoplankton biodiversity in shallow lakes. Further studies should consider the functional attributes of species and the complex biological interactions of phytoplankton and macrophytes along the littoral zone.

Key words: mixed lake, non-equilibrium theory, phytoplankton diel variation, phyto-plankton littoral zone.

INTRODUCTION

The littoral zone of lakes is generally overlooked in limnological research, with most ecological studies in these ecosystems being in pelagic habitats (Cattaneo et al. 2011, Vadeboncoeur et al. 2011, Jurca et al. 2012). This zone is a lake boundary, as an interface zone acts a buffer between the watershed and landscape of the lake ecosystem (Loeb et al. 1983). The environmental dynamics of the littoral zone experience a high effect of both direct and indirect mechanisms (Carmignani & Roy 2017), such as climatic factors (Vadeboncoeur et al. 2014), water level fluctuations (Hofmann et al. 2008, Cantonati et al. 2014, Evtimova & Donohue 2016), the input of allochthonous nutrients (Janssen et al. 2014, Mäemets et al. 2018) and interactions with the adjacent landscape (Schindler & Scheuerell 2002). These peculiarities make the littoral zone a habitat with variable conditions and resources, which recruits specialized organisms that can live in such circumstances (Faria et al. 2015, Timoshkin 2018). Most of the species in lakes are restricted to this zone or completely depend on it for part of the life cycle, while the proportion of littoral habitats usually represents a small fraction of the total lake area (Strayer & Findlay 2010, Vadeboncoeur et al. 2011). In

addition, several studies point out that littoral bioindicators may serve as a primary sign of degradation of the littoral zone that cannot be efficiently detected within the pelagic portion (Rosenberger et al. 2008, Crossetti et al. 2013, Cantonati & Lowe 2014, Rimet et al. 2016). Thus, there is an increasing demand for monitoring the biological communities of the littoral zones of lakes.

The littoral zones of lakes are considered ecotones (Schiemer et al. 1995) and are recognized as being important for the biota of shallow lakes (Wetzel 2001, Vadeboncoeur et al. 2011, Jurca et al. 2012), providing feeding and breeding habitat for several communities (Rosenberger et al. 2008, Hampton et al. 2011, Kosten & Meerhoff 2014). Many organisms leave the pelagic region for resources or refuge, such as horizontal zooplankton migrations (Burks et al. 2002, Meerhoff et al. 2007a) or fish seeking food (Carmignani & Roy 2017). In addition, intense biological interactions are commonly observed in the littoral zone, such as periphyton-macrophyte connection (Faria et al. 2015), zooplankton-macrophyte relationships (Šorf et al. 2015, Gebrehiwot et al. 2017), and negative interactions between macrophytes and phytoplankton (Švanys et al. 2014, Hilt 2015). Commonly, lake littoral zone is extensively colonized by emergent and submersed macrophytes, which can perform important biogeochemical functions (Strayer & Findlay 2010) and contribute with large amounts of organic carbon and yellow substances to the system (They et al. 2013), altering underwater light incidence (Barrow et al. 2019). Moreover, the competition for nutrients (Van Donk & Van de Bund 2002, Vanderstukken et al. 2014) and the release of allelopathic substances by macrophytes (Gross et al. 2007, Mulderij et al. 2007), can cause significant reductions in phytoplankton biomass (Mulderij et al. 2005)

and specific functional forms (Finkler Ferreira et al. 2018). These complex interactions can drive the biological dynamics of littoral communities (Cardoso et al. 2018).

The phytoplankton community is an essential primary producer in shallow lakes (Wetzel 2001). Phytoplankton can closely track both short- and long-term environmental variation in lakes (Salmaso 2002) and, with their short generations, they are sensitive indicators of environmental change in those ecosystems (Reynolds et al. 2002, Crossetti et al. 2013, Weithoff & Gaedke 2017). Given this fast response time, studies over short-time intervals provide a more accurate assessment of species recruitment due to resources variability (Nixdorf et al. 2003). This approach is critical for recognizing phytoplankton's stable states, which are, in some species, optimize resource consumption when they are constantly available (Sommer et al. 1993). Thus, due to the susceptibility to changes in the abiotic conditions of littoral zones of shallow lakes, non-equilibrium phytoplankton dynamics can be expected, assuming the recurrent disturbances affect this zone (i.e., high variability of nutrients and light), even though there is evidence that permanent circulation can be a low disturbance status (Reynolds et al. 1993), which enables steady states.

Studies on phytoplankton from the littoral zone of lentic ecosystems have been carried out using different approaches. For instance, comparative studies between the pelagic and littoral zones have explored the influence of the temperature and water level regimes on phytoplankton (Sakharova & Korneva 2018), the variability of phytoplankton metabolism in both zones (Dunalska et al. 2013) and the community structure and dynamics regarding the seasonality (Szelag-Wasielewska 1993) or the system trophic state (Lemly & Dimmick 1982). Beyond that, studies focusing on distribution

transects between littoral and pelagic zones, exploring the interchange of phytoplankton community between both zones (Schweizer 1997) and phytoplankton littoral monitoring for comparison purposes with long-term data (Bondarenko & Logacheva 2017) and for ecological state assessment (Crossetti et al. 2013) have also been performed.

Whereas the littoral zone of lakes represents an important transitional area, integrating terrestrial and aquatic conditions, besides being heavily used by humans, and since phytoplankton dynamics should accurately reflect the high environmental variability of this zone, the study aim to assess phytoplankton structure and dynamics over a short term in a highly hydrodynamic system. Then, the following questions were addressed: (i) How do the indicators of phytoplankton structure (biomass, species richness and diversity) and dynamics (descriptor species) vary over a short time scale in the studied zone?, and (ii) What are the environmental drivers of the observed variability? It is expected to observe the non-equilibrium dynamics of phytoplankton and succession rate variability in the littoral zone, due to the fast-changing environmental conditions and resource availability to be seen in this compartment. This work seeks to contribute to a better understanding of the still little-studied littoral phytoplankton communities.

MATERIALS AND METHODS
Study site
Lake Mangueira is a large, shallow lake situated in a protected area (Taim Hydrological System - THS) on a narrow strip of land between the Atlantic Ocean and Mirim Lake (Fig. 1), on the southern coastal plain of the state of Rio Grande do Sul, South Brazil (33º31'22''S; 53º07'48''W). The region has a subtropical climate Cfa (Kottek et

al. 2006). The lake has mean depth of 2.6 m, a maximum depth of 6 m, and is 90 km long and 3–10 km wide with a total surface area of 820 km^2. The main axis of the lake is oriented from north-east to south-west and corresponds to the direction of the prevailing winds (Fragoso et al. 2008). Thus, the hydrodynamics of the lake is determined manly by strong and constant winds that frequently resuspend sediment in the water column (Cardoso et al. 2012), directly affecting the plankton communities. The mixing regime of the lake is continuously warm and polymictic with daily mixing by strong winds, according to Lewis' (1983) system.

Lake Mangueira's trophic state varies from oligotrophic to mesotrophic. Mesotrophic conditions occur in spring and summer, when enormous volumes of water are drawn from it to irrigate rice fields (2 L.ha^{-1} s^{-1} for 100 days), decreasing the volume of water at the same time that high nutrient concentrations enter the lake from the watershed (Fragoso et al. 2008). This nutrient input drained from rice fields to the lake temporarily favors the increase in plankton production in the system. After this cultivation period, nutrient concentrations remain low, characterizing the lake as oligotrophic. Submerged, free-floating and emergent macrophytes cover large areas of the southern portion of the lake (Rodrigues et al. 2015). The predominant macrophyte species in this portion of the lake are *Egeria densa* Planchon, *Myriophyllum spicatum* Linnaeus, *Nitella* sp. C.Agardh, *Potamogeton illinoensis* Morong, *Potamogeton pectinatus* (Linnaeus) Börner, *Schoenoplectus californicus* (C.A.Meyer) Palla, *Utricularia* sp. Linnaeus, *Zizaniopsis bonariensis* (Balansa and Poitrasson) Spegazzini, *Cabomba caroliniana* A. Gray, *Myriophyllum spicatumicatum* Linnaeus, and *Ceratophyllum demersum* Linnaeus (Finkler Ferreira et al. 2018).
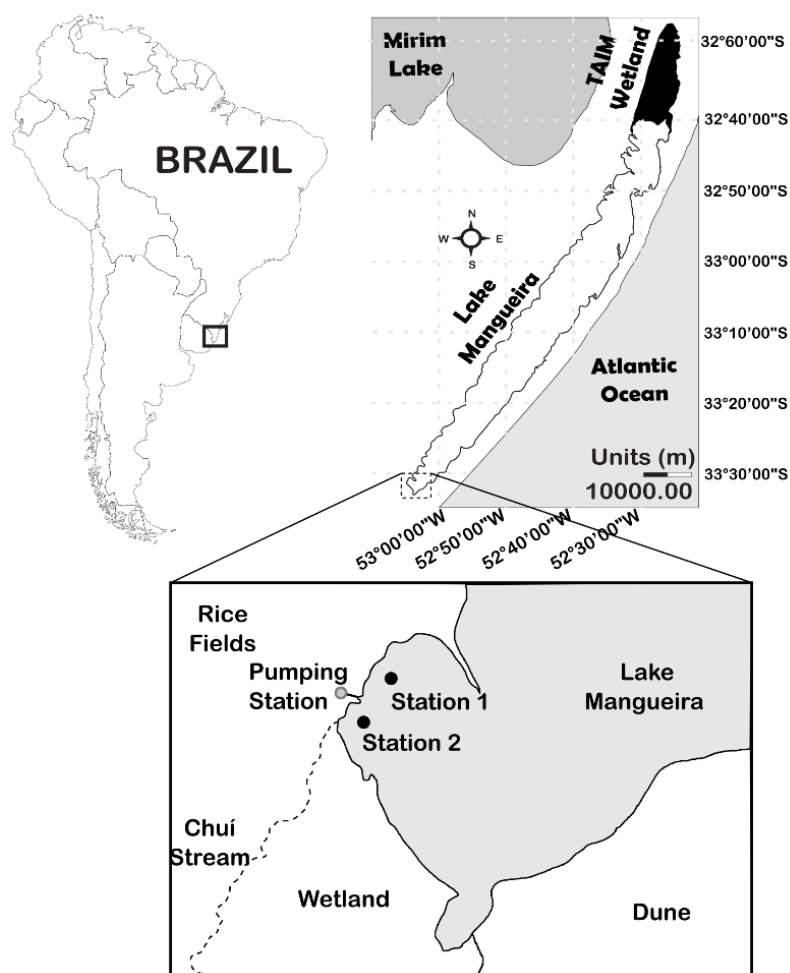
Figure 1. Map of Lake Mangueira showing its location within Brazil and the location of the sampling stations.

Sampling

Water subsurface samples were collected in the morning of 25 consecutive summer days (January 2016) at two sampling sites located in the littoral zone of the southern portion of Lake Mangueira: Station 1 (S1) (33°30'03.6"S 53°08'33.7"W) and Station 2 (S2) (33°30'15.8"S 53°08'41.6"W). The stations presents a mean depth of 1,3 m, are located 500 m from each other and 250 m from the shoreline (Fig. 1). Neither sampling station was situated within macrophyte beds, although macrophytes densely inhabited the area. Physical, chemical, and biological samples were collected from the subsurface with polypropylene bottles. Conductivity (Cond), pH, dissolved oxygen (DO), and water temperature (Temp) were measured in situ with a portable multiparameter probe (YSI 6920). Water transparency was estimated with a Secchi disk (SD). Soluble reactive phosphorus (SRP), total nitrogen (TN), and total dissolved nitrogen (TDN) were analyzed using colorimetric methods according to Rice et al. (2012). Total phosphorus (TP) analysis followed by Mackereth et al. (1989). Dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) were analyzed using specific equipment (Shimadzu VCPH). Soluble reactive silicon (SRSi) analysis followed by Rice et al. (2012). Humic acid absorbance coefficient at 365 nm (Abs365) was measured using a Varian Cary 1 – Spectrophotometer (Strome & Miller 1978). Meteorological data (wind velocity and direction, precipitation) were

collected from the conventional and automatic stations of Santa Vitória do Palmar and Chuí (INMETRO), about 23 km from the study area. Radiation values were derived from CERES data sets and downloaded through the web interface at *https://ceres.larc.nasa.gov/index.php*. CERES products consist of hourly radiation data (UTC time), based on Moderate Resolution Imaging Spectroradiometer (MODIS) (Data Quality Summary 2017). For this study, the average values of the morning period of each sampling day was considered for radiation (Rad) and wind velocity (WV) estimation, as well as the predominant wind direction (WD), was considered.

Data analysis

Samples of the phytoplankton community were fixed with 1% acetic Lugol immediately after collection for later quantitative analysis under an inverted microscope, following the method of Utermöhl (1958), and determination of settling time according to Lund et al. (1958). At least 400 170 individuals were enumerated per sample (95% of confidence limit, Lund et al. 1958). Density was expressed in individuals/mL. The biovolume of each species was determined according to Hillebrand et al. (1999) based on geometric shapes, and converted in biomass following Wetzel & Likens (2000), where mm³/L = mg/L. Biomass (mg/L) was considered the estimate of phytoplankton abundance. Descriptor species were considered as those that contributed a minimum of 1% to total biomass on at least one sampling occasion. The succession rate of phytoplankton was calculated using the sum of differences method (Lewis 1978):

$$\sigma = \frac{\sum^{i} \left| \left[\frac{b_i(t_2)}{B(t_2)}\right] - \left[\frac{b_i(t_1)}{B(t_1)}\right] \right|}{\left(t_2 - t_1\right)}$$

where $b_i(t)$ is the abundance of the nth species; $B(t)$ is the sum of individuals constituting the community sampled; t_1 and t_2 are the

two successive days. Species richness was expressed in terms of the total number of taxa per sample. Ecological diversity was calculated using the Shannon index (Shannon 1948), from phytoplankton biomass (mg/L), using PAST software 182 version 2.13 (Hammer et al. 2001).

Environmental variability of the littoral zone was assessed by multivariate descriptive analysis using Principal Component Analysis (PCA) of covariance matrices. Spatial differences between sampling sites in biological and limnological data were tested using a non-parametric Wilcoxon test and p-values were adjusted using post-hoc Bonferroni correction. A Redundancy Analysis (RDA) (ter Braak & Smilauer 1998) was performed to determine the influence of abiotic variables on the phytoplankton assemblage, with the significance being tested by the Monte Carlo permutation test (999 permutations), after testing the data with Detrended Correspondence Analysis (DCA) (Hill & Gauch 1980), to select the most appropriate method to be applied. The environmental variables for the RDA were selected based on a PCA using a Pearson and Kendall correlation matrix. The environmental dataset was transformed to a 0–1 scale by ranging (Sneath & Sokal 1973): first extracting the minimum observed for each variable and then dividing by the range (Legendre & Legendre 1998). The biological data (phytoplankton biomass) were transformed by *log x + 1*.

Correlation analyses (r - Pearson; *p* < 0.05) were also performed between phytoplankton total biomass, succession rate, diversity index, species richness, and environmental data to identify any relationships. All multivariate analyses were done using PC-ORD version 6.08 software (McCune & Mefford 2011), while Wilcoxon's test was performed using Statistica 7.1 software (StatSoft, Inc. 2005), and correlation analysis using PAST software version 2.13 (Hammer et al. 2001).

RESULTS

Environmental conditions

No rainfall was recorded during the study period and the wind velocity remained between 3 and 7 m/s and the predominant direction swung between Northeast and South-Southwest (Fig. 2a). Radiation reached higher values above 200 W/m2 between days 5 and 19 (except for day 17) and had intermediate values at the beginning and end of the study (Fig. 2b). Wind direction did not present any significant correlation with any of the abiotic or biological variables.

The first three axes of the PCA explained 48% of the variability in the abiotic data ($p < 0.05$; Fig. 3). The positive side of the first axis (20%, $p = 0.001$; Fig. 3a) ordinated most sampling units of the beginning and middle of the time series (days 1 to 15) due to higher concentrations of SRSi ($r = 0.55$) and TN ($r = 0.34$). The negative side of this axis ordinated the final sampling units of the time series of both sampling stations due to higher values for TDN ($r = -0.43$), Cond ($r = -0.40$), DOC ($r = -0.28$), and TP ($r = -0.26$). The positive side of the second axis (17%, $p = 0.001$) grouped most S1 samples due to higher values for SRP ($r = 0.62$) and DO ($r = 0.45$). On the other hand, the negative side of this axis ordinated all the S2 sampling units due to higher values of Abs365 ($r = -0.36$), DOC ($r = -0.28$), DIC ($r = -0.28$), and TDN ($r = 0.27$). The positive side of the third axis (11%, $p = 0.05$; Fig. 3b) ordinated both S1 and S2 sampling units from different periods due to higher values of SRSi ($r = 0.46$), TDN ($r = 0.43$), DIC ($r = 0.32$), WV ($r = 0.31$), TN ($r = 0.26$), DOC ($r = 0.24$), and SRP ($r = 0.21$). The same tendency was observed on the negative side of this axis with sampling units from both stations being grouped especially due to the higher values of SD ($r = -0.36$) and Abs365 ($r = -0.23$). In general, the analysis evidenced a temporal distribution
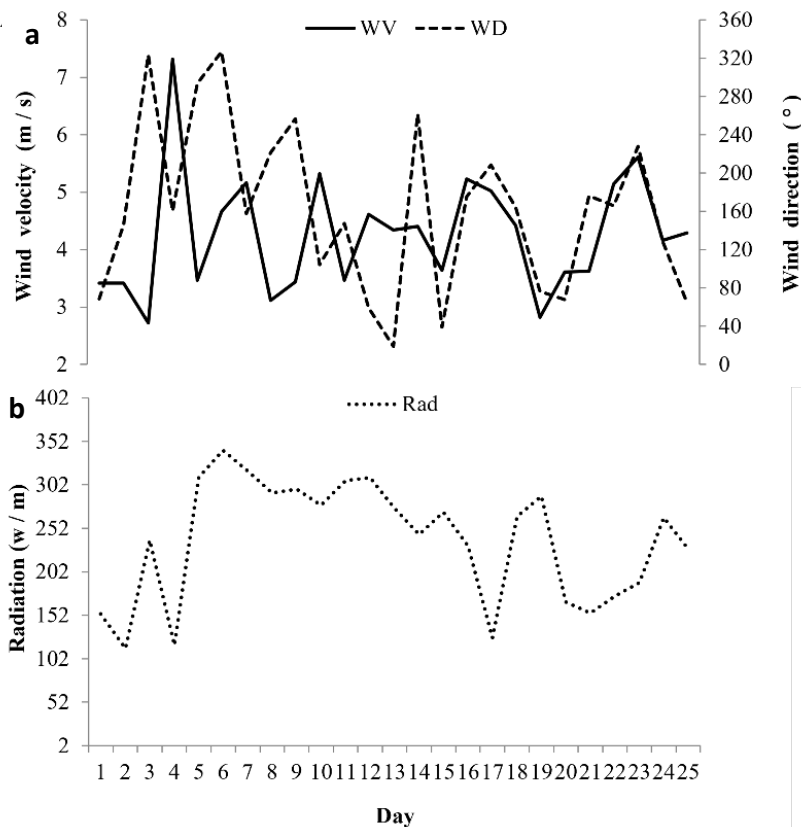

Figure 2. Values of wind velocity and wind direction (a) and solar radiation (b) at Lake Mangueira, during the studied period. WV = Wind velocity (m/s), WD = Wind direction (°) and Rad = Radiation (W/m2). Wind direction categories tracked the degrees scale, as follows: North (338° to 22°); Northeast (23° to 67°); East (68° to 112°); Southeast (113° to 157°); South (158° to 202°); Southwest (203° to 247°); West (248° to 292°) and Northwest (293° to 337°).

of environmental data, with most of the initial sampling units being separated from the later ones, followed by spatial segregation of S1 and S2. The variables DO, SRP, TN, DIC, and DOC differed significantly between sampling stations (Table I).

Phytoplankton

Phytoplankton total biomass (TB) did not differ significantly between the sampling stations ($p > 0.05$). Besides biomass peaks on days 15 and 22 (10.3 mg/L and 13.4 mg/L), S2 generally had lower TB than S1, which had its peak on day 14 (12.7 mg/L) (Fig. 4a). TB and Abs365 were negatively correlated at both sampling stations ($r = -0.42$ at S1 and $r = -0.47$ at S2, $p < 0.05$). At S1, TB was positively correlated with SRP ($r = 0.60$, $p = 0.001$) and TN ($r = 0.46$, $p = 0.02$), while at S2 TB was negatively correlated with TN ($r = -0.46$, $p = 0.02$), SRSi ($r = -0.42$, $p = 0.04$) and DIC ($r = -0.41$, $p = 0.04$). The succession rate (σ) of phytoplankton at both stations presented similar patterns of continuous variation throughout the studied period (Fig. 4b). Overall, the phytoplankton succession rate was higher at S2, being negatively correlated with SRSi ($r = -0.39$, $p = 0.05$) and Abs365 ($r = -0.41$, $p = 0.04$), and positively correlated with SRP at S1 ($r = 0.67$, $p = 0.002$).

A total of 97 phytoplankton species were found: 85 species at S1 (30 exclusive taxa) and 67 species at S2 (12 exclusive taxa). Phytoplankton species were sorted into eight major groups: Chlorophyceae (39.2% of the identified taxa), followed by Cyanobacteria (36.1%), and less than 10% for the other groups (Zygnemaphyceae, Bacillariophyceae, Euglenophyceae, Chrysophyceae, Dinophyceae, and Cryptophyceae). Chlorophyceae was the most abundant group (43.9% of TB), followed by Cyanobacteria (41.9%), and less than 10% for the other groups. The relative contribution of
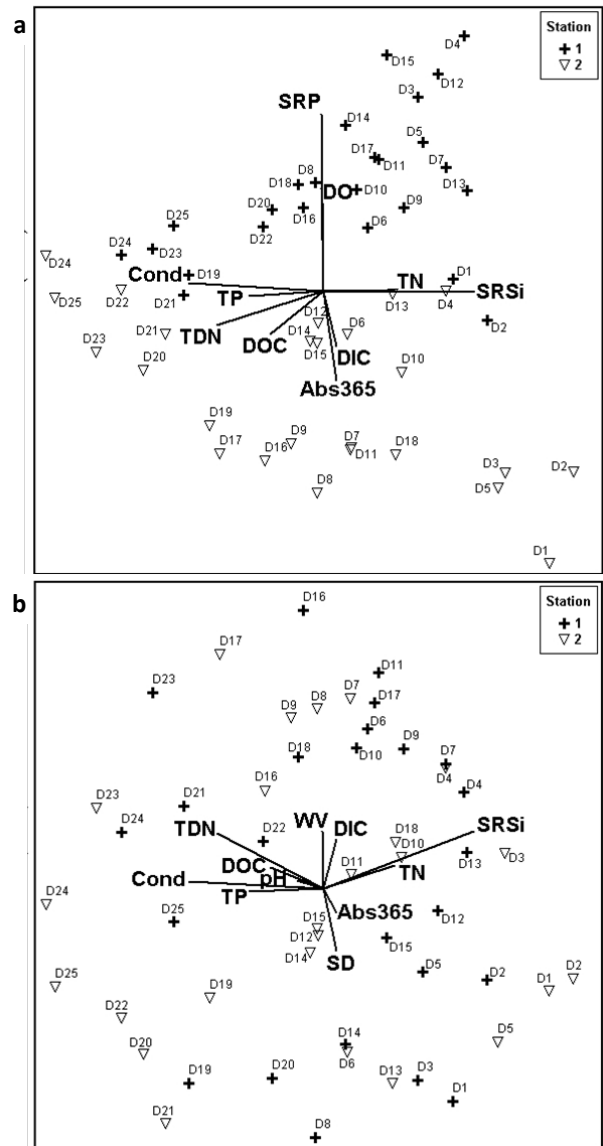
Figure 3. Principal Component Analysis (PCA) biplots of environmental variables of axes 1 and 2 (a) and axes 1 and 3 (b) in the littoral zone of Lake Mangueira during the studied period. Abs365 = humic acid 365 absorbances; Cond = conductivity; DIC = dissolved inorganic carbon; DO = dissolved oxygen; DOC = dissolved organic carbon; SD = Secchi depth; SRP = soluble reactive phosphorus; SRSi = soluble reactive silica; TP = total phosphorus; TN = total nitrogen; TDN = total dissolved nitrogen and WV = wind velocity.

phytoplankton groups at each sampling site was very similar, being dominated most of the time by cyanobacteria (CYA) and chlorophytes (CHL). Lower biomass of those groups coincided with

Table I. Abiotic parameters, phytoplankton biomass, and ecological indices: minimum (min), maximum (max), mean, and standard deviation (sd), during the study at stations S1 and S2 (n = 25 per station). Bold values indicate significant differences (Wilcoxon, p < 0.05).

| Variable	Code	S1				S2			
		Min	max	mean	sd	min	max	mean	sd
Depth (m)	Dep	1.3	1.9	1.6	0.2	0.8	1.2	1.0	0.1
Secchi depth (m)	SD	1.0	1.9	1.4	0.2	0.8	1.2	1.0	0.1
Water temperature (°C)	Temp	22.6	26.9	24.7	1.1	22.7	27.5	24.9	1.2
Conductivity (µS/cm)	Cond	0.4	0.5	0.4	0.0	0.4	0.5	0.4	0.0
Hydrogenionic potential	pH	8.1	9.0	8.6	0.3	8.4	9.0	8.7	0.2
Dissolved Oxygen (mg/L)	DO	7.0	8.4	**7.7**	0.4	7.6	12.4	**8.2**	0.9
Soluble Reactive Silica (mg/L)	SRSi	0.0	10.2	6.4	3.2	3.5	6.8	5.3	1.1
Total Phosphorus (µg/L)	TP	9.7	76.6	17.1	14.5	15.9	43.9	21.4	6.0
Soluble Reactive Phosphorus (µg/L)	SRP	2.6	8.1	**6.5**	1.2	5.6	28.6	**12.0**	4.9
Total Nitrogen (µg/L)	TN	514.7	655.7	600.3	44.9	487.0	586.7	540.8	27.6
Total Dissolved Nitrogen (µg/L)	TDN	421.5	596.5	486.3	53.6	415.7	510.9	466.3	28.3
Dissolved Inorganic Carbon (mg/L)	DIC	9.3	10.8	10.2	0.4	7.4	10.9	9.6	0.9
Dissolved Organic Carbon (mg/L)	DOC	4.2	6.7	4.9	0.7	4.3	7.2	5.6	0.8
Humic Acid 365 absorbance (nm)	Abs365	0.000	0.071	0.016	0.015	0.007	0.027	0.015	0.005
Phytoplankton total biomass (mg/L)	TB	1.8	12.6	5.3	2.3	0.4	13.4	4.5	3.1
Richness (number of taxa)	H	14.0	29.0	20.8	3.8	11.0	28.0	19.3	4.1
Shannon Diversity (bits mg/L)	S	2.1	2.8	**2.5**	0.2	1.7	2.8	**2.3**	0.3

increased biomass of chrysophytes (CHR), which reached 32% of TB on day 23, when CYA and CHL had their lowest recorded relative abundances with 34% and 21%, respectively.

Species richness (S) did not differ significantly ($p > 0.05$) between the sampling stations (Fig. 4c) and varied from 14 to 29 (days 25 and 16, respectively) at S1, and from 11 to 28 (days 11 and 15, respectively) at S2. Phytoplankton richness was correlated with SRP ($r = 0.61$, $p = 0.001$), DOC ($r = -0.45$, $p = 0.02$) and DIC ($r = -0.39$, $p = 0.05$) at S1, while negatively correlated with Abs365 ($r = -0.41$, $p = 0.02$) at S2. Shannon diversity differed significantly between the sampling stations ($p < 0.05$), with higher values at S1 (Fig. 4d). Phytoplankton diversity

was positively correlated with SRP ($r = 0.39$, $p = 0.05$) and negatively with DIC ($r = -0.39$, $p = 0.05$) at S1.

Thirty-two descriptive species were registered at the sampling stations throughout the time series, with 26 being shared between the stations (Table II). The descriptive species accounted for 85% of phytoplankton TB. The major contributors to TB were the cyanobacteria *Aphanocapsa* spp. and *Planktolyngbya* spp., as well as the chlorophytes *Scenedesmus* spp., *Oocystis lacustris*, *Golenkinia radiata*, *Lagerheimia ciliata* and *Monoraphidium irregulare* and the chrysophycean *Dinobryon sertularia* (Fig. 5).
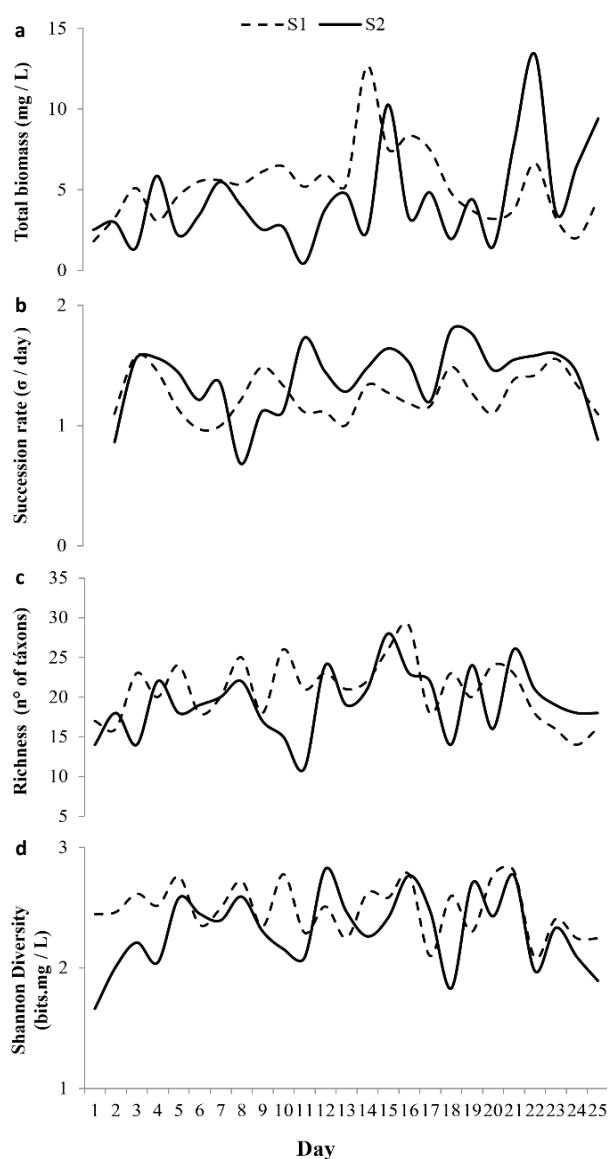
Figure 4. Phytoplankton total biomass (a), succession rate (b), species richness (c), and Shannon diversity (d) in the littoral zone of Lake Mangueira during the studied period at stations S1 and S2.

Integrated analysis of biological and abiotic data

The RDA resulted in high Pearson's correlation between limnological and species data for the first two axes (0.784 and 0.782, respectively), indicating strong relationships among abiotic and phytoplankton variables of the sampling stations. The Monte Carlo test indicated that the

orderings of the first two axes were significant ($p = 0.04$), confirming that the analysis was not randomly generated. The biplot (Fig. 6) demonstrated a slight spatial differentiation of the phytoplankton community in relation to abiotic variables without clear temporal gradients. Most of S2 and some S1 sampling units were ordinated on the positive side of the first axis due to the higher values of Abs365 ($r = 0.68$), DOC ($r = 0.47$), TP ($r = 0.35$), TDN ($r = 0.25$) and DIC ($r = 0.24$), where the species *Chroococcus minor* and *Aphanocapsa koordersii*, also *Peridiniopsis* sp. and *Oocystis borgeii* were ordinated. The negative side of the first axis concentrated S1 and S2 sampling units with the higher values of SRP ($r = -0.68$), TN ($r = -0.31$) and WV ($r = -0.16$), with the species guild ordinated to that side being composed of several chlorophytes and desmids, and the cyanobacteria *Aphanocapsa* spp., *Aphanothece* spp. and *Planktolyngbya* spp. The positive side of the second axis sorted most of S2 due to higher WV values ($r = 0.24$), where *Scenedesmus obtusus* and *Dinobryon sertularia* were ordinated, as well some cyanobacteria species (*Chroococcus* spp., *Merismopedia tenuissima*, *Radiocystis fernandoi* and *Eucapsis* sp.). Greater values of SRSi ($r = -0.62$), SRP ($r = -0.43$) and DIC ($r = -0.35$) grouped most S1 sample units to the negative side of the second axis with the species guild composed of *Dolichospermum circinale*, *Willea crucifera* and *Mucidosphaerium pulchellum*, among others.

DISCUSSION

Our results demonstrated high variability of littoral phytoplankton structure over short-time intervals during the evaluated summer period. No steady state of phytoplankton was recorded at either sampling station. Instead, we observed high variability of biomass and the relative contribution of species throughout the studied

Table II. Descriptive species of the phytoplankton community in the littoral zone of Lake Mangueira during the studied period: values of relative contribution (%) of each taxon at sampling stations S1and S2. Bold values specify the descriptive species of each sampling station.

Class.	Abbrev.	Species	S1	S2
CYA	*Akoor*	*Aphanocapsa* cf. *koordersii* Ström 1923	**3.8**	**7.0**
CYA	*Adeli*	*Aphanocapsa delicatissima* West & West 1912	**3.4**	**3.0**
CYA	*Aelac*	*Aphanocapsa elachista* West & West 1894	**6.9**	**4.6**
CYA	*Ainc*	*Aphanocapsa incerta* (Lemmermann) Cronberg & Komárek 1994	**7.3**	**4.2**
CYA	*Asmit*	*Anathece smithii* (Komárková-Legnerová & Cronberg) Komárek, Kastovsky & Jezberová 2011	**0.8**	**1.0**
CYA	*Anasp*	*Aphanothece* sp. Nägeli 1849	**1.4**	**0.9**
CYA	*Astag*	*Aphanothece stagnina* (Sprengel) Braun in Rabenhorst 1863	**0.5**	**2.1**
CYA	*Cdis*	*Chroococcus dispersus* (Keissler) Lemmermann 1904	**0.4**	**1.1**
CYA	*Cmin*	*Chroococcus minor* (Kützing) Nägeli 1849	**1.6**	**1.1**
CYA	*Dcir*	*Dolichospermum circinale* (Rabenhorst ex Bornet & Flahault) Wacklin, Hoffmann & Komárek 2009	**1.1**	0.0
CYA	*Euca*	*Eucapsis* sp. Clements & Shantz, 1909	**1.1**	**1.6**
CYA	*Llim*	*Limnococcus limneticus* (Lemmermann) Komárková, Jezberová, Komárek & Zapomelová 2010	**1.4**	**2.3**
CYA	*Mten*	*Merismopedia tenuissima* Lemmermann 1898	**1.8**	**2.4**
CYA	*Pcon*	*Planktolyngbya contorta* (Lemmermann) Anagnostidis & Komárek 1988	**4.6**	**2.4**
CYA	*Plim*	*Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg 1992	**1.1**	**0.4**
CYA	*Rfer*	*Radiocystis fernandoi* Komárek & Komárková-Legnerová 1993	0.0	**5.2**
CHL	*Chlvu*	*Chlorella* cf. *vulgaris* Beyerinck [Beijerinck] 1890	**1.6**	**1.1**
CHL	*Hret*	*Hariotina reticulata* (Dangeard) Senn 1899	**0.7**	**1.4**
CHL	*Mpul*	*Mucidosphaerium pulchellum* (Wood) Bock, Proschold & Krienitz 2011	**1.2**	0.0
CHL	*Grad*	*Golenkinia radiata* Chodat 1894	**3.6**	**2.3**
CHL	*Lcili*	*Lagerheimia ciliata* (Lagerheim) Chodat 1895	**4.0**	**2.1**
CHL	*Mirr*	*Monoraphidium irregulare* (Smith) Komárková-Legnerová 1969	**4.4**	**2.0**
CHL	*Oborg*	*Oocystis borgei* Snow 1903	**0.5**	**1.2**
CHL	*Olac*	*Oocystis lacustris* Chodat 1897	**8.8**	**6.5**
CHL	*Secor*	*Scenedesmus ecornis* (Ehrenberg) Chodat 1926	**3.3**	**2.4**
CHL	*Sobtu*	*Scenedesmus obtusus* Meyen 1829	**10.4**	**13.9**
CHL	*Tmin*	*Tetraedron minimum* (Braun) Hansgirg 1888	**1.2**	**1.8**
CHL	*Wruc*	*Willea* cf. *crucifera* (Wolle) John, Wynne & Tsarenko 1974	**1.0**	**0.8**
ZYG	*Ckue*	*Closterium* cf. *kuetzingii* Brébisson 1856	**1.6**	0.0
ZYG	*Cosm*	*Cosmarium* sp. Corda ex Ralfs 1848	**2.7**	0.0
CHR	*Dser*	*Dinobryon sertularia* Ehrenberg 1834	**5.7**	**11.1**
DIN	*Perid*	*Peridiniopsis* sp. Lemmermann 1904	0.0	**2.0**
		Total Biomass	**85%**	**88%**

period related to constant environmental shifts, which lead to continuous species turnover, sometimes during a single diel cycle. Besides, oscillations in the phytoplankton succession rates were registered during all the studied period. Usually, equilibrium is not expected in aquatic ecosystems under very rapidly fluctuating conditions (O'Farrell et al. 2003) or with intermittent mixing (Allende & Izaguirre 2003, Naselli-Flores et al. 2003). Non-equilibrium theories attribute a basic role to environmental disturbances occurring with sufficient frequency to disrupt the course of competitive exclusion (Harris 1986, Wilson 1990, Sommer et al. 1993, Padisák 1994, Krebs 2001, Lengyel et al. 2015). These recurrent perturbations in the littoral zone of shallow lakes are generally related to climatic variation (Cantonati & Lowe 2014), or processes resulting from terrestrial-aquatic interaction (Meerhoff & Jeppensen 2009). These may be one of the explanations to the species

turnover verified in the present study (Fig. 5). For instance, *D. sertularia* and *S. obtusus* were benefited by wind action as evidenced by the RDA, in the same way that SRP drove the *O. lacustris* development. Furthermore, the fast environmental dynamics of the littoral zone added to the fast response time of phytoplankton and the biotic interactions not considered in the present study may also have contributed to that.

Studies on the phytoplankton of Lake Mangueira have been carried out using different approaches. Most of these studies were performed in the pelagic zone and showed that changes in both monthly (Crossetti et al. 2007) and seasonal (Crossetti et al. 2013, 2018, Freitas-Teixeira et al. 2016) temporal scales were strongly associated with environmental variation influenced by the lake's hydrodynamics. Similarly, another study demonstrated a significant correlation between environmental dissimilarity and phytoplankton dissimilarity based on long-term monitoring
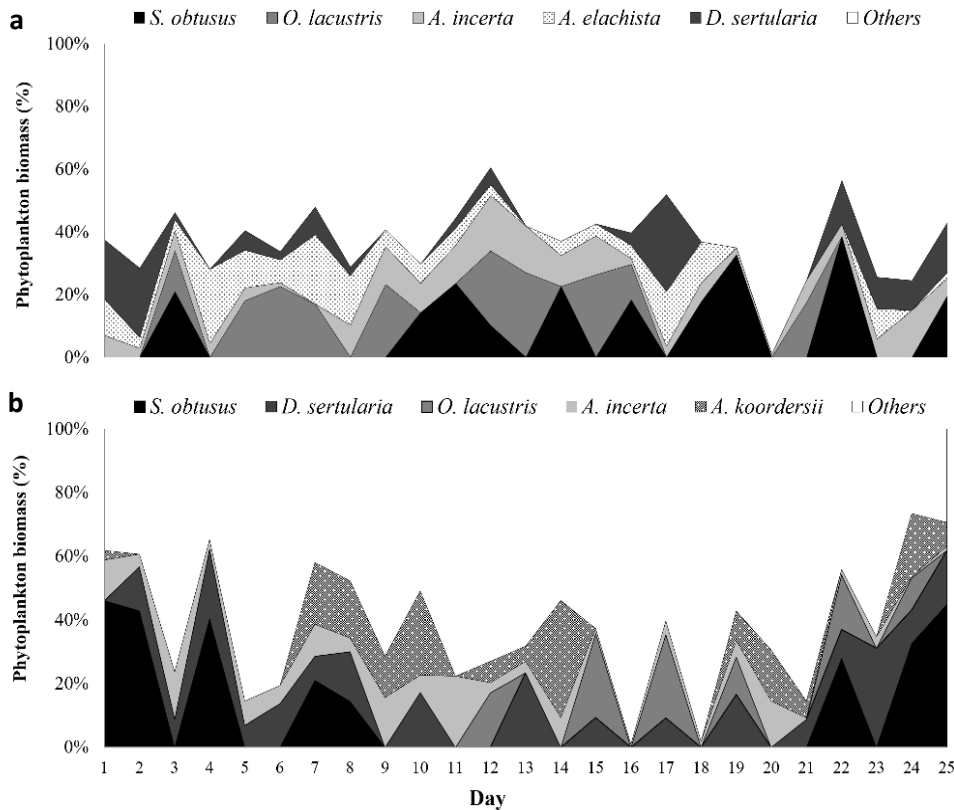
Figure 5. Relative biomass contribution of the five most abundant phytoplankton species at sampling stations S1 (a) and S2 (b) in the littoral zone of Lake Mangueira during the studied period.

data (12 years) (Bohnenberger et al. 2017). Then, even though short-term sampling has not been deeply explored, our experience led us to suppose that in the pelagic habitat of this lake phytoplankton steady states may be less frequent, but are not impossible to occur. An unpublished study carried out with samplings on every three days (for 60 days, in the summer of 2012) in Lake Mangueira showed phytoplankton steady states occurring both in the pelagic and littoral zones, but the equilibrium period had a shorter duration in the littoral. There is evidence that in shallow lakes the conditions for the establishment of phytoplankton steady states are more predictable than in deep lakes (Naselli-Flores et al. 2003, Nixdorf et al. 2003). Besides, in a system adapted to perturbation, as in the case of continuously mixed systems (shallow lakes), this represents a sufficiently stable condition to allow phytoplankton steady state, while the calm phases would be the disturbance (Chorus & Schlag 1993).

The hydrodynamics of the littoral zone of shallow lakes can be complex due to a series of factors that influence the movement of the water mass in this zone. For instance, studies have already shown that wind-driven circulation or ship waves can lead to sediment resuspension in the littoral zone of large lakes (Hofmann et al. 2008, 2011). Likewise, wind direction might be an important factor for horizontal transport, influencing the patchiness of phytoplankton in lakes (Verhagen 1994). Besides, horizontal convective exchanges flow between the littoral zone and open waters of shallow lakes may occur (Stefan et al. 1989), influencing, for example, the nutrient exchange (James & Barco 1991). Not to mention the presence of macrophytes, which may attenuate surface-generated turbulence from penetrating the water column (Coates & Folkard 2009). In the present study, although we have not observed the direct influence of wind (speed and direction) on the abiotic and biological variables, it may have influenced the
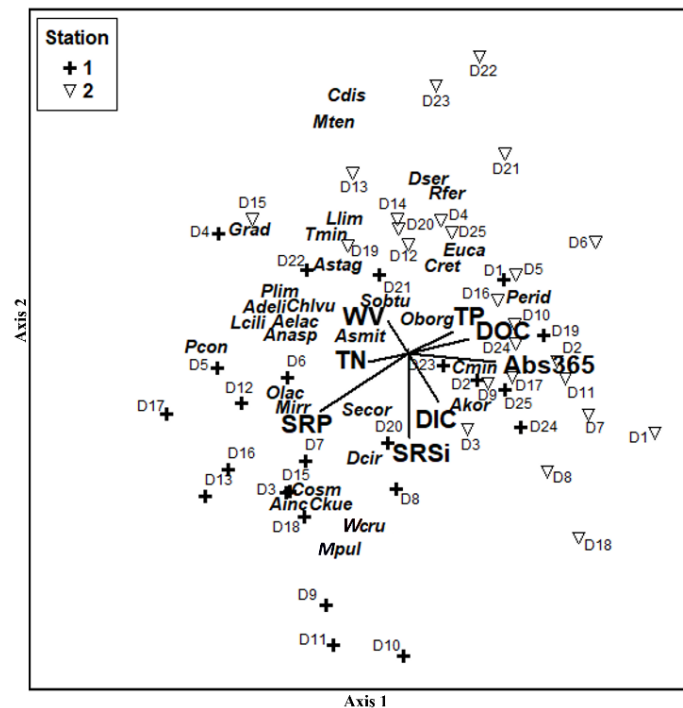
Figure 6. Redundancy analysis (RDA) biplot of environmental variables and descriptive species in the littoral zone of Lake Mangueira during the studied period at Stations 1 and 2. Abs365 = humic acid 365 absorbances; DIC = dissolved inorganic carbon; DOC = dissolved organic carbon; SRP = soluble reactive phosphorus; SRSi = soluble reactive silica; TP = total phosphorus; TN = total nitrogen and WV = wind velocity. For the species legend, see Table II.

dynamics of water masses, not only intensifying the effect of macrophytes on limnological features through transport processes but also justifying the wide environmental variability and the differences observed between the sampling stations. Then, for a better understanding of the environmental and biological dynamics in the littoral region of systems such as Lake Mangueira, the incorporation of variables related to the flow of water masses in this zone is recommended.

Although the extension or the effects of the macrophyte beds near the sampling sites was not quantified, other studies conducted in the southern region of Lake Mangueira have already reported the strong influence that the plants have on limnological processes (They et al. 2013, Rodrigues et al. 2014, 2015, Faria et al. 2016, Finkler Ferreira et al. 2018). Macrophytes can affect both the dynamics of biological communities (Howard-Williams & Lenton 1975, Muylaert et al. 2010, Thomaz & Cunha 2010, Teixeira de Mello et al. 2015, Iacarella et al. 2018) and nutrient cycling (Havens et al. 2004, They et al. 2013) in shallow lakes, by acting as nutrient sinks in several ways (Carpenter 1981, Kufel & Kufel 2002). In this sense, the analyses performed in this study indicated that the occurrence of macrophytes may have played an effective role for littoral phytoplankton structure of Lake Mangueira. Humic substances, which are released by macrophytes, proved to be one of the main drivers of phytoplankton dynamics.

As estimated by Abs365, these substances exhibited a negative correlation with phytoplankton biomass at both stations and were also related to succession rate and richness at S2. A negative interaction between macrophytes and phytoplankton had already been registered for the littoral zone of Lake Mangueira (Finkler Ferreira et al. 2018), when phytoplankton biomass was negatively influenced by humic substances and the presence of the plants.

The authors concluded that the effects of the macrophytes on the phytoplankton structure and water quality could be seen beyond the boundaries of the vegetated area. In our survey, few species had high positive associations with humic substances: only *C. minor*, *A. koordersii* and *Peridiniopsis* sp. According to Wetzel (2001), higher concentrations of humic substances can select only those species that are adapted to those conditions. These substances can make nutrients unavailable for primary producers (Lenard & Ejankowski 2017), and affect not only underwater light intensity but also the penetration of photosynthetically active radiation into the water (Wetzel 2001, Ejankowski & Lenard 2015). More specifically, they inhibit the development of cyanobacteria, which seem unable to use their accessory pigments in the reddish light caused by the higher concentration of yellow humic substances (Steinberg et al. 2006). Therefore, most of the species of cyanobacteria listed in the present study were negatively related to Abs365, demonstrating the negative interaction between this group and macrophytes, as widely reported in others studies (Gross et al. 2007, Mulderij et al. 2007, Vanderstukken et al. 2014, They et al. 2015, Mohamed 2017). Besides, species of blue green algae and diatoms are often significantly inhibited by allelochemicals (Hilt & Gross 2008, Reitsema et al. 2018), and some macrophytes species occur in Lake Mangueira possess such inhibitory capacities (They & Motta-Marques, 2019).

Another particularity registered in the littoral zone of Lake Mangueira was the marked oscillation of nutritional conditions. Nutrient availability in the littoral zone can be strongly influenced by sediment destabilization (Kosten & Meerhoff 2014), the action of fish (Meerhoff & Jeppensen 2009), high assimilation by macrophytes (They et al. 2014) and bacterial

activity (Wetzel 1983). Although these factors were not evaluated here, we recognized that their action could explain the rapid variation in nutrients during the studied period. Slight variation in nutrient levels within short sampling intervals result in a rapid change in the structure of an algae community (Dantas et al. 2008), as we found in the littoral zone of Lake Mangueira. In addition, more oligotrophic conditions stimulate greater competition among phytoplankton and bacteria for nutrients (They et al. 2014). The positive correlations between SRP and phytoplankton total biomass, succession rate, species richness, and Shannon diversity at S1, and the biplot arrangement of the RDA, demonstrate that this resource was an important driver of species performance at this site, which was not recorded at S2, where humic substances were found at higher concentrations. The fact that S1 had substantially lower values of SRP, remaining below the overall limiting concentrations for phytoplankton growth during several periods (Reynolds 2006), may represent a competitive advantage for the small cyanobacteria and chlorophytes present. Most species of these groups benefited from this nutrient, as demonstrated by the integrated analysis (RDA). These organisms possess high surface-volume ratios, which increases the capacity of nutrient absorption (Foy 1980, Negro et al. 2000, Passarge et al. 2006, Reynolds 2006, Brasil & Huszar 2011), and promote faster replication rates than those of larger algae (Raven 1998). This property is important in highly dynamic ecosystems where environmental variables are constantly changing (Palijan 2017), such as the littoral zone of Lake Mangueira.

Our results showed that the littoral phytoplankton of Lake Mangueira is inserted in a highly stochastic and dynamic compartment with high environmental variability. Furthermore, mixing shallow lakes are traditionally considered fast-changing and fluctuating ecosystems featuring quick and unpredictable phytoplankton changes (Naselli-Flores et al. 2003). The non-steady state found for the littoral phytoplankton of the present study was influenced by the nutritional availability in Lake Mangueira. The nearby presence of macrophytes seemed to have influenced the environmental conditions by contributing to species turnover on a short-time scale, demonstrating that the littoral phytoplankton assemblage in Lake Mangueira experiences a constant redefinition of community structure. Further studies of littoral phytoplankton regarding a functional approach, and broader efforts to explore the complex dynamics of biological interactions found in this compartment, should be considered. Finally, the littoral zone of shallow lakes should be included in ecological studies in order to provide enhanced scientific support about the importance of this compartment for overall lake dynamics and lake conservation and management programs.

REFERENCES

ALLENDE L & IZAGUIRRE I. 2003. The role of physical stability on the establishment of steady state in the phytoplankton community of two Maritime Antarctic lakes. Hydrobiologia 502: 211-224.

BARROW JL, BEISNER BE, GILES R, GIANI A, DOMAIZON I & GREGORY EAVES I. 2019. Macrophytes moderate the taxonomic & functional composition of phytoplankton assemblages during a nutrient loading experiment. Freshw Biol 64: 1369-1381.

BOHNENBERGER JE, RODRIGUES LR, MOTTA-MARQUES D & CROSSETTI LO. 2017 Environmental dissimilarity over time in a large subtropical shallow lake is differently represented

by phytoplankton functional approaches. Mar Freshw Res 69: 95-104.

BONDARENKO NA & LOGACHEVA NF. 2017. Structural Changes in Phytoplankton of the Littoral Zone of Lake Baikal. Hydrobiol J 53: 16-24.

BRASIL J & HUSZAR VLM. 2011. O papel dos traços funcionais na ecologia do fitoplâncton continental. Oecol Aust 15(4): 799-834.

BURKS RL, LODGE DM, JEPPESEN E & LAURIDSEN TL. 2002. Diel horizontal migration of zooplankton: costs and benefits of inhabiting littoral zones. Fresh Biol 47: 343-365.

CANTONATI M, GUELLA G, KOMAREK J & SPITALE D. 2014. Depth distribution of epilithic cyanobacteria and pigments in a mountain lake characterized by marked water-level fluctuations. Freshw Sci 33(2): 537-547.

CANTONATI M & LOWE RL. 2014. Lake benthic algae: toward an understanding of their ecology. Freshw Sci 33(2): 475-486.

CARDOSO LS, FARIA DM, CROSSETTI LO & MOTTA-MARQUES D. 2018. Phytoplankton, periphyton, and zooplankton patterns in the pelagic and littoral regions of a large subtropical shallow lake. Hydrobiologia 831: 119-132.

CARDOSO LS, FRAGOSO CR JR, SOUZA RS & MOTTA-MARQUES D. 2012. Hydrodynamic control of plankton spatial and temporal heterogeneity in subtropical shallow lakes. Chapter 2. In: SCHULZ H (Ed). Hydrodynamics - Natural Water Bodies, p. 27-48.

CARMIGNANI JR & ROY AH. 2017. Ecological impacts of winter water level drawdowns on lake littoral zones: a review. Aquat Sci 79: 803-824.

CARPENTER SR. 1981. Submersed vegetation: an internal factor in lake ecosystem succession. Am Nat 118: 372-383.

CATTANEO A, DE SÈVE M, MORABITO G, MOSELLO R & TARTARI G. 2011. Periphyton changes over 20 years of chemical recovery of Lake Orta, Italy: differential response to perturbation of littoral and pelagic communities. J Limnol 70(2): 177-185.

CHORUS I & SCHLAG G. 1993. Importance of intermediate disturbances for the species composition and diversity of phytoplankton in two very different Berlin lakes. Hydrobiologia 249: 435: 67-92.

COATES MJ & FOLKARD AM. 2009. The effects of littoral zone vegetation on turbulent mixing in lakes. Ecol Modell 220: 2714-2726.

CROSSETTI LO, CARDOSO LS, CALLEGARO VLM, SILVA SA, WERNER V, ROSA Z & MOTTA-MARQUES D. 2007. Influence of the hydrological changes on the phytoplankton structure

and dynamics in a subtropical wetland-lake system. Acta Limnol Bras 19: 315-329.

CROSSETTI LO, FREITAS-TEIXEIRA LM, BOHNENBERGER JE, SCHULZ UH, RODRIGUES LR & MOTTA-MARQUES D. 2018. Responses of the phytoplankton functional structure to the spatial and temporal heterogeneity in a large subtropical shallow lake. Acta Limnol Bras 30: e214.

CROSSETTI LO, STENGER-KOVÁCS C & PADISÁK J. 2013. Coherence of phytoplankton and attached diatom-based ecological status assessment in Lake Balaton. Hydrobiologia 716: 87-101.

DANTAS EW, MOURA AN, BITTENCOURT OLIVEIRA MC, ARRUDA NETO JDT & CAVALCANTI ADC. 2008. Temporal variation of the phytoplankton community at short sampling intervals in the Mundaú reservoir, Northeastern Brazil. Acta Bot Bras 22(4): 970-982.

DUNALSKA JA, ZIELIŃSKI RA, BIGAJ I & SZYMAŃSKI D. 2013. Indicators of changes in the phytoplankton metabolism in the littoral and pelagial zones of a eutrophic lake. Rocz Ochr Sr 15(1): 621-636.

EJANKOWSKI W & LENARD T. 2015. Climate driven changes in the submerged macrophyte and phytoplankton community in a hard water lake. Limnologica 52: 59-66.

EVTIMOVA VV & DONOHUE I. 2016. Water-level fluctuations regulate the structure and functioning of natural lakes. Fresh Biol 61: 251-264.

FARIA DM, CARDOSO LS & MOTTA-MARQUES D. 2015. Periphytic diatoms show a longitudinal gradient in a large subtropical shallow lake. Inland Waters 5: 117-124.

FARIA DM, CARDOSO LS & MOTTA-MARQUES D. 2016. Epiphyton dynamics during an induced succession in a large shallow lake: wind disturbance and zooplankton grazing act as main structuring forces. Hydrobiologia 788: 267-280.

FINKLER FERREIRA T, CROSSETTI LO, MOTTA-MARQUES D, CARDOSO LS, FRAGOSO CR JR & VAN NES EH. 2018. The structuring role of submerged macrophytes in a large subtropical shallow lake: clear effects on water chemistry and phytoplankton structure community along a vegetated pelagic gradient. Limnologica 69: 142-154.

FOY RH. 1980. The influence of surface to volume ratio on the growth rates of planktonic blue- green algae. Br Phycol J 15(3): 279-289.

FRAGOSO CR JR, MOTTA-MARQUES D, COLLISCHONN W, TUCCI C & VAN NES EH. 2008. Modelling spatial heterogeneity of phytoplankton in Lake Mangueira, a large shallow subtropical lake in South Brazil. Ecol Modell 219: 125-137.

FREITAS-TEIXEIRA LM, BOHNENBERGER JE, RODRIGUES LR, SCHULZ UH, MOTTA-MARQUES D & CROSSETTI LO. 2016. Temporal variability determines phytoplankton structure over spatial organization in a large shallow heterogeneous subtropical lake. Inland Waters 6: 325-335.

GEBREHIWOT M, KIFLE D & TRIEST L. 2017. Emergent macrophytes support zooplankton in a shallow tropical lake: a basis for wetland conservation. Environ Manage 60: 1127-1138.

GROSS EM, HILT S, LOMBARDO P & MULDERIJ G. 2007. Searching for allelopathic effects of submerged macrophytes on phytoplankton-state of the art and open questions. Hydrobiologia 584: 77-88.

HAMMER O, HARPER DAT & RAYAN PD. 2001. PAST. Palentological Statistics Software Package for Education and Data Analysis. Palaeontol Electron 4(1): 9.

HAMPTON SE, FRADKIN SC, LEAVITT PR & ROSENBERGER EE. 2011. Disproportionate importance of nearshore habitat for the food web of a deep oligotrophic lake. Mar Freshw Res 62: 350-358.

HARRIS GP. 1986. Phytoplankton ecology: structure, function and fluctuation. Chapman and Hall, London, UK, 384 p.

HAVENS KE, SHARFSTEIN B, RODUSKY AJ & EAST TL. 2004. Phosphorus accumulation in the littoral zone of a subtropical lake. Hydrobiologia 517: 15-24.

HILL MO & GAUCH HG. 1980. Detrended Correspondence Analysis: An Improved Ordination Technique. Vegetatio 42: 47-58.

HILLEBRAND H, DÜRSEKEN D, KIRSCHIEL D, POLLINGHER U & ZOHARY T. 1999. Biovolume calculation for pelagic and benthic microalgae. J Phycol 35: 403-424.

HILT S. 2015. Regime shifts between macrophytes and phytoplankton – concepts beyond shallow lakes, unravelling stabilizing mechanisms and practical consequences. Limnetica 34(2): 467-480.

HILT S & GROSS EM. 2008. Can allelopathically active submerged macrophytes stabilize clear-water states in shallow lakes? Basic Appl Ecol 9(4): 422-432.

HOFMANN H, LORKE A & PEETERS F. 2008. Temporal scales of water-level fluctuations in lakes and their ecological implications. Hydrobiologia 613: 85-96.

HOFMANN H, LORKE A & PEETERS F. 2011. Wind and ship wave-induced resuspension in the littoral zone of a large lake. Water Resour Res 47(9): 1-12.

HOWARD-WILLIAMS C & LENTON G. 1975. The role of the littoral zone in the functioning of a shallow tropical lake ecosystem. Fresh Biol 5(5): 445-459.

IACARELLA JC, BARROW JL, GIANI A, BEISNER BE & GREGORY-EAVES I. 2018. Shifts in algal dominance in freshwater experimental ponds across differing levels of macrophytes and nutrients. Ecosphere 9(1): e02086.

JAMES WF & BARKO JW. 1991. Estimation of phosphorus exchange between littoral and pelagic zones during nighttime convection circulation. Limnol Oceanogr 36(1): 179-187.

JANSSEN ABG, TEURLINCX S, AN S, JANSE JH, PAERL HW & MOOIJ WM. 2014. Alternative stable states in large shallow lakes? J Great Lakes Res 40: 813-826.

JURCA T, DONOHUE L, LAKETIĆ D, RADULOVIĆ S & IRVINE K. 2012. Importance of the shoreline diversity features for littoral macroinvertebrate assemblages. Fundam Appl Limnol 180(2): 175-184.

KOSTEN S & MEERHOFF M. 2014. Lake Communities. Encyclopedia of Life Sciences (ELS) 15: 1-11.

KOTTEK M, GRIESER J, BECK C, RUDOLF B & RUBEL F. 2006. World Map of the Köppen-Geiger climate classification updated. Meteorol Z 15: 259-263.

KREBS CH. 2001. Ecology: Experimental Analysis of Distribution and Abundance. Addison Wesley, San Francisco, 695 p.

KUFEL L & KUFEL I. 2002. Chara beds acting as nutrient sinks in shallow lakes - a review. Aquat Bot 72: 249-260.

LEGENDRE P & LEGENDRE L. 1998. Numerical ecology. Elsevier, Amsterdam, 852 p.

LEMLY AD & DIMMICK JF. 1982. Phytoplankton communities in the littoral zone of lakes: observations on structure and dynamics in oligotrophic and eutrophic systems. Oecologia 54: 359-369.

LENARD T & EJANKOWSKI W. 2017. Natural water brownification as a shift in the phytoplankton community in a deep hard water lake. Hydrobiologia 787: 153-166.

LENGYEL E, PADISÁK J & STENGER-KOVÁCS C. 2015. Establishment of equilibrium states and effect of disturbances on benthic diatom assemblages of the Torna-stream, Hungary. Hydrobiologia 750: 43-56.

LEWIS WM JR. 1978. Analysis of succession in a tropical phytoplankton community and a new measure of succession rate. Am Nat 112: 401-414.

LEWIS WM JR. 1983. A revised classification of lakes based on mixing. Can J Fish Aquat Sci 40: 1779-1787.

LOEB SL, REUTER JE & GOLDMAN CR. 1983. Littoral zone production of oligotrophic lakes. In: WETZEL R (Ed).

Periphyton of freshwater ecosystems. Dr. W. Junk Publishers, The Hague, p. 161-167.

LUND JWG, KIPLING C & LECREN ED. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11: 143-170.

MACKERETH FJH, HERON J & TALLING JF. 1989. Water analysis: some revised methods for limnologists. Freshwater Biological Association, 120 p.

MÄEMETS H, LAUGASTE R, PALMIK K & HALDNA M. 2018. Response of primary producers to water level fluctuations of Lake Peipsi. Proc Estonian Acad Sci Biol Ecol 67(3): 231-245.

MCCUNE B & MEFFORD MJ. 2011. PC-ORD. Multivariate analysis of ecological data – Version 6.08. MJM Software Design, Gleneden Beach.

MEERHOFF M, CLEMENTE JM, TEIXEIRA DE MELLO F, IGLESIAS C, PEDERSEN AR & JEPPESEN E. 2007a. Can warm climate-related structure of littoral predator assemblies weaken the clear water state in shallow lakes? Glob Chang Biol 13: 1888-1897.

MEERHOFF M, IGLESIAS C, TEIXEIRA DE MELLO F, CLEMENTE JM, JENSEN E, LAURIDSEN TL & JEPPESEN E. 2007b. Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. Fresh Biol 52: 1009-1021.

MEERHOFF M & JEPPESEN E. 2009. Shallow lakes and ponds. In: LIKENS G (Ed). Encyclopedia of inland waters. Oxford, Elsevier, p. 343-353.

MOHAMED ZA. 2017. Macrophytes-Cyanobacteria allelopathic interactions and their implications for water resources management – a review. Limnologica 63: 122-132.

MULDERIJ G, MOOIJ WM & VAN DONK E. 2005. Allelopathic growth inhibition and colony formation of the green alga Scenedesmus obliquus by the aquatic macrophytes Stratiotes aloides. Aquatic Ecol 39: 11-21.

MULDERIJ G, VAN NES EH & DONK EV. 2007. Macrophyte-phytoplankton interactions: the relative importance of allelopathy versus other factors. Ecol Modell 204: 85-92.

MUYLAERT K ET AL. 2010. Influence of nutrients: submerged macrophytes and zoop lanktongrazing on phytoplankton biomass and diversity along a latitudinal gradient in Europe. Hydrobiology 653: 79-90.

NASELLI-FLORES L, PADISÁK J & DOKULIL M. 2003. Phytoplankton and the equilibrium concept: the ecology of steady state assemblages. Developments in Hydrobiology 172: 1-416. (Reprinted from Hydrobiologia, 502).

NEGRO AI, DE HOYOS C & VEJA JC. 2000. Phytoplankton structure and dynamics in Lake Sanabria and Valparaíso reservoir (NW Spain). Hydrobiologia 424: 25-37.

NIXDORF B, MISCHKE U & RÜCKER J. 2003. Phytoplankton assemblages and steady state in deep and shallow eutrophic lakes – an approach to differentiate the habitat properties of Oscillatoriales. Hydrobiologia 502: 111-121.

O'FARRELL I, SINISTRO R, IZAGUIRRE I & UNREIN F. 2003. Do steady state assemblages occur in shallow lentic environments from wetlands? Hydrobiologia 502: 197-209.

PADISÁK J. 1994. Identification of relevant time-scales in nonequilibrium community dynamics: conclusions from phytoplankton surveys. N Z J Ecol 18(2): 169-176.

PALIJAN G. 2017. Short-term response of the phytoplankton size structure to flooding. Inland Waters 7(2): 192-199.

PASSARGE J, HOL S, ESCHER M & HUISMAN J. 2006. Competition for nutrients and light: stable coexistence, alternative stable states, or competitive exclusion? Ecol Monogr 76(1): 57-72.

RAVEN JA. 1998. Small is beautiful: the picophytoplankton. Funct Ecol 12(4): 503-513.

REITSEMA RE, MEIRE P & SCHOELYNCK J. 2018. The future of freshwater macrophytes in a changing world: dissolved organic carbon quantity and quality and its interactions with macrophytes. Front Plant Sci 9: 629.

REYNOLDS CS. 2006. The ecology of phytoplankton: Ecology, Biodiversity and Conservation. Cambridge University Press, Cambridge, 564 p.

REYNOLDS CS, HUSZAR VLM, KRUK C, NASELLI FLORES L & MELO S. 2002. Towards a functional classification of the freshwater phytoplankton. J Plankton Res 24(5): 417-428.

REYNOLDS CS, PADISÁK J & SOMMER U. 1993. Intermediate disturbance in the ecology of phytoplankton and the maintenance of species diversity: a synthesis. Hydrobiologia 249: 183-188.

RICE EW, BAIRD RB, EATON AD & CLESCERI LS. 2012. Standard Methods for Examination of Water and Wastewater. 22nd ed. American Public Health Association, American Water Works, Water Environment Federation, Washington DC, USA, 1360 p.

RIMET F, BOUCHEZ A & MONTUELLE B. 2016. Benthic diatoms and phytoplankton to assess nutrients in a large lake: complementary of their use in Lake Geneva (France-Switzerland). Ecol Indic 53: 231-239.

RODRIGUES LR, FONTOURA NF & MOTTA-MARQUES D. 2014. Food-web structure in a subtropical coastal lake: how

phylogenetic constraints may affect species linkages. Mar Freshw Res 65: 453-465.

RODRIGUES LR, MOTTA-MARQUES D & FONTOURA NF. 2015. Fish community in a large coastal subtropical lake: how an environmental gradient may affect the structure of trophic guilds. Limnetica 34: 495-506.

ROSENBERGER EE, HAMPTON SE, FRADKIN SC & KENNEDY B. 2008. Effects of shoreline development on the nearshore environment in large deep oligotrophic lakes. Fresh Biol 53: 1673-1691.

SAKHAROVA EG & KORNEVA LG. 2018. Phytoplankton in the littoral and pelagial zones of the Rybinsk Reservoir in years with different temperature and water-level regimes. Inland Water Biol 11: 6-12.

SALMASO N. 2002. Ecological patterns of phytoplankton assemblages in Lake Garda: seasonal, spatial and historical features. J Limnol 61: 95-115.

SCHIEMER F, ZALEWSKI M & THORPE JE. 1995. Land/Inland water ecotones: Intermediate habitats critical for conservation and management. Hydrobiologia 303: 259-264.

SCHINDLER DE & SCHEUERELL MD. 2002. Habitat coupling in lake ecosystems. Oikos 98: 177-189.

SCHWEIZER A. 1997. From littoral to pelagial: comparing the distribution of phytoplankton and ciliated protozoa along a transect. J Plankton Res 19(7): 829-848.

SHANNON CE. 1948. A mathematical theory of communication. Bell Syst Tech J 27(3): 379-423.

SNEATH PHA & SOKAL RR. 1973. Numerical Taxonomy: The Principles and Practice of Numerical Classification. Freeman, San Francisco, 573 p.

SOMMER U, PADISÁK J, REYNOLDS CS & JUHÁSZ-NAGY P. 1993. Hutchinson's heritage: the diversity-disturbance relationship in phytoplankton. Hydrobiologia 249: 1-8.

ŠORF M, DAVIDSON TA, BRUCET S, MENEZES RF, SØNDERGAARD M, LAURIDSEN TL, LANDKILDEHUS F, LIBORIUSSEN L & JEPPESEN E. 2015. Zooplankton response to climate warming: a mesocosm experiment at contrasting temperatures and nutrient levels. Hydrobiologia 742: 185-203.

STEFAN HG, HORSCH GM & BARKO JW. 1989. A model for the estimation of convective exchange in the littoral region of a shallow lake during cooling. Hydrobiologia 174: 225-234.

STEINBERG CEW ET AL. 2006. Dissolved humic substances - Ecological driving forces from the individual to the ecosystem level? Fresh Biol 51(7): 1189-1210.

STRAYER DL & FINDLAY SEG. 2010. Ecology of freshwater shore zones. Aquat Sci 72: 127-163.

STROME DJ & MILLER MC. 1978. Photolytic changes in dissolved humic substances. Verh Internat Verein Limnol 20: 1248-1254.

ŠVANYS A, PAŠKAUSKAS R & HILT S. 2014. Effects of the allelopathically active macrophytes myriophyllum spicatum Linn. on a natural phytoplankton community: a mesocosm study. Hydrobiologia 737: 57-66.

SZELAG-WASIELEWSKA E. 1993. Phytoplankton in the littoral and pelagial of the Lake Miedwie. Verh Int Ver Theor Angew Limnol 25(1): 662-665.

TEIXEIRA DE MELLO F, OLIVEIRA VA DE, LOVERDE OLIVEIRA SM, HUSZAR VLM, BARQUÍN J, IGLESIAS C, SILVA TSF, DUQUE-ESTRADA CHE, SILIÓ-CALZADA A & MAZZEO N. 2015. The structuring role of free-floating plants on the fish community in a tropical shallow lake: an experimental approach with natural and artificial plants. Hydrobiologia 778: 167-178.

TER BRAAK CJF & SMILAUER P. 1998. CANOCO: Reference Manual and User's Guide to CANOCO for Windows (Version 4). Centre for Biometry, Wageningen, 351 p.

THEY NH, FINKLER FERREIRA T, MOTTA-MARQUES D, RODRIGUES LR, SILVEIRA SB, ARRIADA AA, CROSSETTI LO, CARDOSO LS, FRAGOSO CR JR. 2015. Allelopathic effects of macrophytes in subtropical shallow lakes. In: PRICE JE (Ed). New Developments in Allelopathy Research, Nova Publishers, New York, p. 89-134.

THEY NH & MOTTA-MARQUES D. 2019. The structuring role of macrophytes on plankton community composition and bacterial metabolism in a large subtropical shallow lake. Acta Limnol Bras 31: 1-20.

THEY NH, MOTTA-MARQUES D, CROSSETTI LO, BECKER V, CANTERLE E, RODRIGUES LR, CARDOSO LS & FRAGOSO CR JR. 2014. Phytoplankton ecological interactions in freshwater ecosystems - integrating relationships in subtropical shallow lakes. In: SEBASTIÁ MT (Ed). Phytoplankton. Nova Science Publishers, New Work, p. 73-129.

THEY NH, MOTTA-MARQUES D, SOUZA RS & RODRIGUES LR. 2013. Short-Term Photochemical and Biological Unreactivity of Macrophyte-Derived Dissolved Organic Matter in a Subtropical Shallow Lake. J Ecosyst 316709: 1-9.

THOMAZ SM & CUNHA ER DA. 2010. The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurement, causes and consequences on animal assemblages' composition and biodiversity. Acta Limnol Bras 22 (2): 218-236.

TIMOSHKIN OA. 2018. Coastal zone of the world's great lakes as a target field for interdisciplinary research and ecosystem monitoring: Lake Baikal (East Siberia). Limnol Freshw Biol 1: 81-97.

UTERMÖHL H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton: Methodik. Mitteilungen der Internationale Vereinigung für theoretische und angewandte Verh Int Ver Theor Angew Limnol 9: 1-38.

VADEBONCOEUR Y, DEVLIN SP, MCINTYRE PB & VANDER ZANDEN MJ. 2014. Is there light after depth? Distribution of periphyton chlorophyll and productivity in lake littoral zones. Freshw Sci 33(2): 524-536.

VADEBONCOEUR Y, MCINTYRE PB & VANDER ZANDEN MJ. 2011. Borders of Biodiversity: Life at the Edge of the World's Large Lakes. BioScience 61(7): 526-537.

VANDERSTUKKEN M, DECLERCK SAJ, DECAESTECKER E & MUYLAERT K. 2014. Long-term allelopathic control of phytoplankton by the submerged macrophyte Elodea nuttallii Planch. Fresh Biol 59: 930-941.

VAN DONK E & VAN DE BUND WJ. 2002. Impact of submerged macrophytes including charophytes on phyto- and zooplankton communities: allelopathy versus other mechanisms. Aquat Bot 72(3-4): 261-274.

VERHAGEN JHG. 1994. Modeling phytoplankton patchiness under the influence of wind-driven currents inlakes, Limnol Oceanogr 39: 1551-1565.

WEITHOFF G & GAEDKE U. 2017. Mean functional traits of lake phytoplankton reflect seasonal and inter-annual changes in nutrients, climate and herbivory. J Plankton Res 39(3): 509-517.

WETZEL RG. 1983. Attached algal-substrata interactions: fact or myth, and when and how? In: WETZEL R (Ed). Periphyton of freshwater ecosystems. Springer, Netherlands, p. 207-215.

WETZEL RG. 2001. Limnology. Lake and River Ecosystems, Elsevier Academic Press, San Diego, 1006 p.

WETZEL RG & LIKENS GE. 2000. Limnological Analysis. Springer, Berlin, 429 p.

WILSON JB. 1990. Mechanisms of species coexistence: twelve explanations for Hutchinson's 'paradox of the plankton': evidence from New Zealand plant communities. N Z J Ecol 13: 17-42.

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All the authors contributed to the design of the study. Mônica H. Silveira and Luana M. da Rosa performed material preparation, data collection and analysis. Data analysis was performed by José Rafael Cavalcanti, Luciana S. Cardoso, David da Motta-Marques, Lucia R. Rodrigues and Luciane O. Crossetti. The study was oriented by Lucia R. Rodrigues and Luciane O. Crossetti. Mônica H. Silveira wrote the first draft of the manuscript, and all authors commented on previous versions. All authors read and approved the final manuscript.