Vertical and temporal variation in phytoplankton assemblages correlated with environmental conditions in the Mundaú reservoir, semi-arid northeastern Brazil

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Abstract

The goal of this study was to analyse the vertical structure of the phytoplankton community at the Mundaú reservoir, located in the semi-arid region of northeastern Brazil, and to correlate it to environmental conditions over two distinct seasons, dry and rainy. Samples were collected bimonthly at eight depths in the dry and rainy season for analyses of the physical and chemical variables of the water, as well as density, abundance, dominance, species diversity index and equitability of the community. Analysis of variance (ANOVA-two way) was used to analyse the vertical and seasonal differences, and Canonical Correspondence Analysis (CCA) was used to assess associations between phytoplankton and environmental variables Cylindrospermopsis raciborskii (Woloszynska) Seenaya and Subba Raju was the only dominant species and Geitlerinema amphibium (C. Agardh) Anagnostidis, Merismopedia punctata Meyen and Synedra rumpens Kützing. Others six taxa were abundant in at least one of the samples. Distinct vertical distribution patterns were observed for the abundant taxa between depths and seasons. The cyanobacteria, with the exception of C. raciborskii, showed similar seasonal patterns, with higher densities in the dry season. The CCA showed a strong correlation between the density of the phytoplanktonic species and abiotic variables. The vertical changes in abundant taxa revealed distinct patterns regulated by the variation in the environmental factors that were directly linked to seasonality, with the success of one or more species being dependent on their life strategies and ecological needs. The present study restates the importance of environmental and seasonal factors for phytoplankton composition and distribution in a freshwater tropical reservoir through a vertical gradient.

Keywords: freshwater, microalgae, seasonality, spatial dynamics, tropical region

Variações vertical e temporal nas assembleias fitoplanctônicas correlacionadas com condições ambientais no reservatório Mundaú, semiárido do nordeste do Brasil

Resumo

O objetivo deste estudo foi avaliar a estrutura vertical da comunidade fitoplanctônica no reservatório Mundaú localizado na região semiárida do nordeste do Brasil e correlacioná-la com as condições ambientais durante dois períodos sazonais distintos, seca e chuva. Amostras foram coletadas bimensalmente em oito profundidades em duas estações climáticas, seca e chuvosa para análises de variáveis físicas e químicas da água, bem como, da densidade, abundância, dominância, índice de diversidade especifica e equitabilidade da comunidade. Análise de variância (ANOVA - dois critérios) foi usada para avaliar as diferenças vertical e sazonal e Análise de Correspondência Canônica (CCA) as associações entre o fitoplâncton e variáveis ambientais. *Cylindrospermopsis raciborskii* (Woloszynska) Seenaya and Subba Raju foi a única espécie dominante e *Geitlerinema amphibium* (C. Agardh) Anagnostidis, *Merismopedia punctata* Meyen e *Synedra rumpens* Kützing, foram abundantes em ambas as estações. Outros seis táxons foram abundantes em, pelo menos, uma das amostras. Distintos padrões de distribuição vertical foram observados para os táxons abundantes entre as profundidades e estações. As cianobactérias, com exceção de *C. raciborskii*, apresentaram padrão sazonal similar com maiores densidades no período seco. A CCA mostrou uma correlação entre a densidade das espécies fitoplanctônicas e as variáveis ambientais. As mudanças verticais nos táxons abundantes revelaram distintos padrões regulados pela

variação nos fatores ambientais que estiveram diretamente ligados à sazonalidade, sendo assim, o sucesso de uma ou mais espécie está ligado à sazonalidade, às suas estratégias de vida e às suas necessidades ecológicas. O presente estudo corrobora a importância de fatores ambientais e sazonal na composição e distribuição do fitoplâncton ao longo de um gradiente vertical em um reservatório de água doce de região tropical.

Palavras-chave: água doce, microalga, sazonalidade, dinâmica espacial, região tropical.

1. Introduction

The phytoplankton community is an important biological component of water bodies, because it is responsible for a large part of the primary production, constituting a food chain basis. From currently published estimates for land plants and for coastal vegetation, the production of phytoplankton accounts for nearly 50% of the global net primary production (Field et al., 1998; Salmaso et al., 2012).

The phytoplankton distribution and structure are strongly related to the physical and chemical features of water bodies. Variations of abiotic water conditions occur naturally throughout the day and over the seasons of the year. These variations can be either vertical or horizontal and may be closely related to stratification and mixing of the water column, resulting in changes in the availability of light and nutrients for the development of the phytoplankton community (Lopes et al., 2005). Other factors such as herbivory, internal seiches, turbulence and water renewal rate may also influence the vertical distribution of the phytoplankton (Litchman et al., 2010; Mellard et al., 2011). Associated to these conditions, sewage discharge, agricultural and industrial waste, is constantly released into water bodies, leading to eutrophication of the water, changing the phytoplankton structure and enabling an uncontrolled increase in some populations such as cyanobacteria. The excessive development of the biomass of these organisms (blooms), which often produce toxins, results in an unpleasant taste and odor of the water, affecting the availability of drinking waters, and leads to loss of environmental scenic characteristics compromising thereby its quality for the most varied uses (Heo and Kim, 2004; Salmaso et al., 2012).

Reservoirs located in semiarid regions of northeastern Brazil are used for public water supply as well as recreation, irrigation, fishing, farming of aquatic organisms and other uses (Bittencourt-Oliveira et al., 2011, 2012; Moura et al., 2011). The climate of this region has limited rainfall and a high degree of evaporation, which favours considerable variation in the abiotic characteristics of the aquatic ecosystems, thereby influencing the distribution and growth of phytoplankton communities (Chellappa and Costa, 2003). Thus, understanding the dynamics of these organisms is of fundamental importance to optimise the use and management of these aquatic ecosystems.

The tropical Mundaú reservoir is an important public water supply located in the northeastern region of Brazil. This reservoir receives a large amount of polluting material and has frequent blooms of cyanobacteria (Bittencourt-Oliveira et al., 2011). The goal of this study was to analyse the vertical structure of phytoplanktonic communities in

the Mundaú reservoir, northeastern Brazil and correlate it to environmental conditions over two distinct seasons.

2. Material and Methods

2.1. Study area and sampling procedure

The Mundaú reservoir is located in the city of Garanhuns (8°55'40"S to 8°57'04"S and 36°30'40"W to 36°29'02"W), 716 m above sea level, in the state of Pernambuco (northeastern Brazil). The reservoir has an area of 4 km² and accumulation capacity of approximately 1.9x10⁶ m³ with mean depth of 11m. It is used for fishing, irrigation and is the water supply for about 120 thousand inhabitants (Pernambuco, 2000). The geographical region is characterised climatologically by a dry season from August to January and a rainy season from February to July. Over the study period the air temperature ranged from 20.2°C to 22.5°C in the dry season and from 18.9°C to 23.4°C in the rainy season; wind direction and speed were instable in the dry season, alternating between southeasterly, easterly and northeasterly; in the rainy season, the wind direction alternated between southerly and northeasterly. Monthly precipitation ranged from 4.1mm to 62.7mm in the dry season and from 115.8mm to 161.1mm in the rainy season.

Sampling was carried out between January and November 2006, during two seasonal periods: dry (January, September and November) and rainy (March, May and July). The water samples were collected with van Dorn bottles in the limnetic region at eight depths defined on the basis of indirect calculation of the vertical light attenuation coefficient (Poole and Atkins, 1929) (K = $1.7/Z_{ds}$): a) surface (100% available light); b) 0.5m; c) 1.0m; d) 2.0m; e) 4.0m; f) 6.0m (to 1% available light); g) 8.0m; and h) 9.0m (total absence of light).

2.2. Abiotic and biotic variables

Water temperature and dissolved oxygen were determined using an oximeter (Schott Glaswerke Mainz, Handylab OX1), turbidity (NTU) with a turbidimeter (Hanna Instruments, HI 93703), pH, electrical conductivity (μ S.cm⁻¹) and total dissolved solids (mg.L⁻¹) were accessed with a field YSI device (model 556) *in situ*. Samples for biological and nutrient analysis (total nitrogen and total phosphorus) were collected with a van Dorn bottle.

The determination of total phosphorus and total nitrogen was based on the procedure described by Valderrama (1981). For the study of phytoplankton, 100mL aliquots (n=3) were stored in plastic bottles and preserved with Lugol acetic acid. These were analysed under an optical Zeiss Jenaval microscope coupled with a measuring ocular to analyse the morphological characteristics of the species,

which were used for taxonomic identification using keys available in books and specialised articles. Quantification was performed using Utermöhl methods (Utermöhl, 1958) with an inverted microscope (Zeiss, Axiovert). Abundance and dominance were determined from the density data, following Lobo and Leighton (1986). Species diversity index (bits.cell⁻¹) were accessed using Shannon and Weaver (1948) and equitability were calculated using Pielou (1977). The monthly data were used as repetitions of the climatic seasons and presented as the mean for each period.

Analysis of variance (ANOVA two-way) was used to test differences in abiotic factors (p < 0.05) between depths and for different seasons using the BioEstat 5.0 software (Ayres et al., 2003). Canonical Correspondence Analysis (CCA) was used to assess associations between phytoplankton and environmental variables. The matrix with biotic data was constructed only with species abundant in at least one sample. Significance (p<0.05) was tested with the Monte Carlo test, with 999 unrestricted permutations using the Canoco 4.5 program.

3. Results

Stratification was observed in the Mundaú reservoir over both seasons (Figure 1a, e). Smaller thermal stratification was found in the rainy season (Figure 1). In both seasons, the epilimnion occurred at 2.0m while the hypolimnion started at 6.0m. The reservoir shows stratified dissolved oxygen levels throughout the whole study, with clinograde patterns. The pH ranged from slightly acid to alkaline in the dry season (Figure 1c) and was neutral to alkaline in the rainy season (Figure 1g). There was no significant difference in total nitrogen and phosphorous, both vertically and seasonally, however, in both seasons the highest concentrations were generally recorded at the bottom (Figures 1d, h). Significant differences between the dry and rainy season were observed for temperature (F=11.76, p=0.01), dissolved oxygen (F=12.69, p=0.009), (F=98.66, p=0.0001), pH (F=12.05, p=0.01) and total dissolved solids (F=333.52, p < 0.0001). Significant differences were observed between depths for temperature (F=71.37, p < 0.0001), dissolved oxygen (F=31.46, p = 0.0003) and pH (F=43.74, p=0.0002).

Seventy-one taxa distributed in six classes were identified. The Chlorophyceae Class was the richest species throughout the study and, together with cyanobacteria, accounted for 83.10% of the community (Table 1). Density variations were observed between different sampling depths (vertical variation), with a greater density of organisms down to a depth of 2.0m (Figure 2). The mean density was higher in the rainy season (Figure 2b). Cyanobacteria and Bacillariophyceae showed the greatest densities.

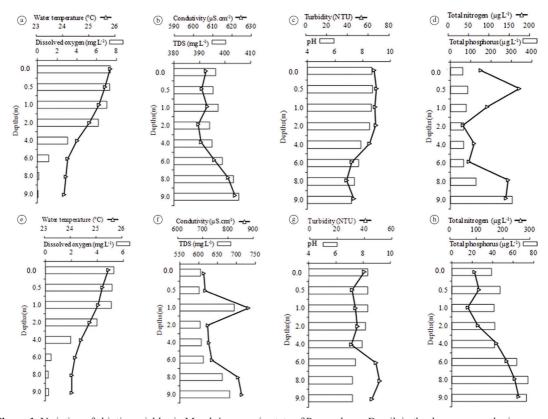


Figure 1. Variation of abiotic variables in Mundaú reservoir, state of Pernambuco, Brazil, in the dry season and rainy season at different depths. (a-d). Dry season; (e-h). Rainy season. (a). Water temperature and dissolved oxygen; (b). Conductivity and Total Dissolved Solids; (c). Turbidity and pH; (d). Total nitrogen and total phosphorus; (e). Water temperature and dissolved oxygen; (f). Conductivity and Total Dissolved Solids; (g). Turbidity and pH; (h). Total nitrogen and total phosphorus.

Table 1. Taxonomic summary and occurrence of the phytoplanktonic taxa at the Mundaú reservoir, state of Pernambuco, Brazil in the rainy and dry seasons at different depths (metres). 0.0, 0.5, 1.0, 2.0, 4.0, 6.0, 8.0, 9.0; Ad: all depths; -: absence of taxa

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Coelastrum sphaericum Nägeli 1.0 -	.0, >.0
Crucigenia fenestrata (Schimidle) Schimidle 0.5; 8.0 0.0; 4.0; 9	0
Crucigenia quadrata Morren - 0.5; 1; 2; 4; 6	
Crucigenia tetrapedia (Kirchner) Kuntze 0.0; 0.5; 1.0; 2.0; 4.0	, 0,)
<i>Dictyosphaerium pulchellum</i> Wood 1.0; 4.0; 8.0; 9.0 0.0; 1.0	
Golenkinia radiata Chodat Ad 0.5; 1.0; 2.0	6.0
Kirchneriella lunaris var. irregularis G.M. Smith Ad O.S, 1.0, 2.0	, 0.0
Kirchneriella obesa (West) West and G.S. West Ad Ad Micractinium pusillum Fresenius Ad 0.0; 2.0; 4.0	. 6.0

Table 1. Continued...

Taxa Seasons		ns
laxa	Dry	Rainy
Monoraphidium arcuatum (Korshikov) Hindák	Ad	Ad
Monoraphidium contortum (Thuret) Komárkova- Legnerová	Ad	Ad
Monoraphidium griffithii (Berkeley) Komárková- Legnerová	Ad	Ad
Phythelios viridis Frenzel	0.0	0.0
Planktosphaeria gelatinosa G.M. Smith	Ad	Ad
Scenedesmus acuminatus (Lagerheim) Chodat	Ad	Ad
Scenedesmus arcuatus (Lemmermann) Lemmermann	0.0	-
Scenedesmus bicaudatus Dedusenko	Ad	Ad
Scenedesmus bijugus (Turpin) Lagerheim	0.0; 0.5; 1.0; 2.0; 4.0; 6.0; 9.0	0.5; 1.0
Scenedesmus denticulatus Lagerheim	1.0; 2.0; 4.0; 9.0	0.5; 6.0; 8.0; 9.0
Scenedesmus quadricauda (Tupin) Brébisson	Ad	Ad
Scenedesmus quadricauda var. quadrispina (Chodat) G.M. Smith	-	1.0
Schroederia sp.	0.5; 2.0; 8.0	9.0
Sphaerocystis sp.	Ad	Ad
Staurastrum sp.	-	2.0; 6.0
Tetradesmus wisconsinensis G. M. Smith	6.0	-
Tetraedron minimum (A. Braun) Hansgirg	Ad	Ad
Tetrastrum sp.	-	0.0; 1.0; 4.0; 6.0; 8.0; 9.0
Tetrastrum triangulare (Chodat) Komárek	Ad	2.0; 8.0
DINOPHYCEAE		
Gymnodinium sp.	0.5;1.0; 2.0	0.5; 1.0; 9.0
Peridinium sp.	-	0.5; 1.0; 2.0; 4.0; 6.0; 8.0
CHRYSOPHYCEAE		
Dinobryon sertularia Ehrenberg	1.0	-
EUGLENOPHYCEAE		
Euglena sp.	Ad	Ad
Euglena acus (O.F. Müller) Ehrenberg	-	2.0
Phacus curvicauda Svirenko	0.0; 2.0	Ad
Trachelomonas volvocina (Ehrenberg) Ehrenberh	0.0; 0.5; 1.0; 2.0; 4.0; 6.0; 8.0	Ad

The species *C. raciborskii* (Woloszynska) Seenaya & Subba Raju was the only dominant species and *G. amphibium* (C. Agardh) Anagnostidis, *M. punctata* Meyen and *S. rumpens* Kützing were abundant in both seasons. In addition, another six taxa (*Golenkinia radiata* Chodat, *Merismopedia minima* Beck, *Microcystis aeruginosa* (Kützing) Kützing, *M. wesenbergii* (Komárek) Komárek, *M. robusta* (Clark) Nygaard, *Pseudanabaena* sp.) were abundant in at least one of the samplings.

Distinct vertical distribution patterns were observed for the abundant taxa between depths and for different seasons (Figure 3). Cyanobacteria (Figures 3a-e, g-h), with the exception of *C. raciborskii* (Figure 3f), showed similar seasonal patterns, with larger densities in the dry season. The species diversity index was low for both seasons and the different sampling depths (varying from 1.79-1.97 bits. cell⁻¹ in the dry season and from 1.52-1.76 bits.cell⁻¹ in the rainy season) and the equitability values were below 0.5

in both seasons (0.47-0.49 in the dry season and 0.39-0.45 in the rainy season), thereby indicating the dominance of populations of one or more species.

In the Canonical Correspondence Analysis, axes 1 and 2 explained 97.4% of the variability of the biotic data (Table 2, Figure 4). Environmental variables explained 99.9% of the total variability of the biotic data, 98.4% of those explained by the first two axes. There is a strong correlation between the density of phytoplankton species and abiotic variables (*p* <0.05) (Table 2, Figure 4). Axis 1 showed the vertical variation of the sampling units in the dry season, separating the samples in the superficial layers from the samples at the bottom, as a function of temperature (T°C), dissolved oxygen (O₂) and pH (Table 2, Figure 4). *M. aeruginosa*, *M. robusta*, *C. raciborskii* e *G. radiata* displayed higher biomasses in the dry season. Axis 2 revealed the establishment of two groups, classified according to the dynamics of the abiotic variables in both seasons studied (Table 2, Figure 4). The

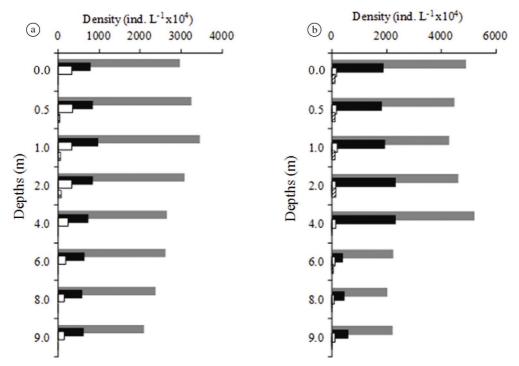


Figure 2. Vertical variation of phytoplankton classes in the Mundaú reservoir, state of Pernambuco, Brazil, in the (a) dry and (b) rainy season. Cyanobacteria (); Bacillariophyceae (); Chlorophyceae (); Dinophyceae (); Euglenoplyceae ().

first group was formed by the cyanobacteria *Merismopedia* punctata, *C. raciborskii* and *G. amphibium* and by the diatom *S. rumpens*, abundant in the rainy season under conditions of high values of electrical conductivity and total dissolved solids and high concentrations of nitrogen and phosphorus. Characteristics contrary to these revealed the establishment of the second group, formed by the cyanobacteria *Merismopedia minima*, *M. aeruginosa*, *M. wesenbergii*, *M. robusta*, and *Pseudanabaena* sp. and the green microalgae *G. radiata* in the dry season.

4. Discussion

For eutrophic tropical reservoirs, water temperature variations, precipitation, wind direction and speed, environment morphometry, and N:P ratios are reported to be the main factors of an aquatic ecosystem, capable of promoting changes in phytoplankton composition and dynamics and the occurrence of cyanobacterial blooms (Chellappa and Costa, 2003; Jöhnk et al., 2008; Delpla et al., 2009).

In the Mundaú reservoir, abiotic variables and seasonality were observed to change the dynamics of phytoplankton and were responsible for the variation in the vertical distribution of the species. Cyanobacteria was the group with the highest density in both seasons studied, showing that the climatological characteristics of the region, as well as the environmental and morphometric characteristics of the ecosystem favour the development of cyanobacteria throughout the year.

Bittencourt-Oliveira et al. (2011) reported that thermal de-stratification in the rainy season favoured the increase in the populations of *C. raciborskii* morphotypes (coiled and straight) by providing more adequate conditions for their growth, namely, lesser light intensity and milder temperatures, which are characteristics of the winter months in the hinterland region of the state of Pernambuco in northeastern Brazil. In the present study, the dominance of this cyanobacterium persisted in the superficial layers of the water column, especially during the rainy season, with consequent low values of species diversity and equitability.

C. raciborskii produces harmful toxins to humans and other animals, also has invasive behaviour and opportunistic characteristics. The success of this cyanobacteria is attributed to its having the ability to fix atmospheric nitrogen, to use internal sources of phosphorus, and high affinity to phosphorus and ammonium and resistance to herbivory by zooplankton, the high capacity for dispersal and low tolerance to low brightness and variations in water temperature (Padisák, 1997; Briand et al., 2002; Berger et al., 2006). Moreover, it has the ability to move in the water column due to the presence of vesicles which give it buoyancy (Reynolds, 1997). According to Walsby (2005), aerotopes allow filaments to remain in the layer with adequate amount of light and nutrients suitable for growth. The greater availability of nutrients and low light in the Mundaú reservoir, as a result of higher rainfall in the rainy season, were important factors that contributed to the increased density of C. raciborskii.

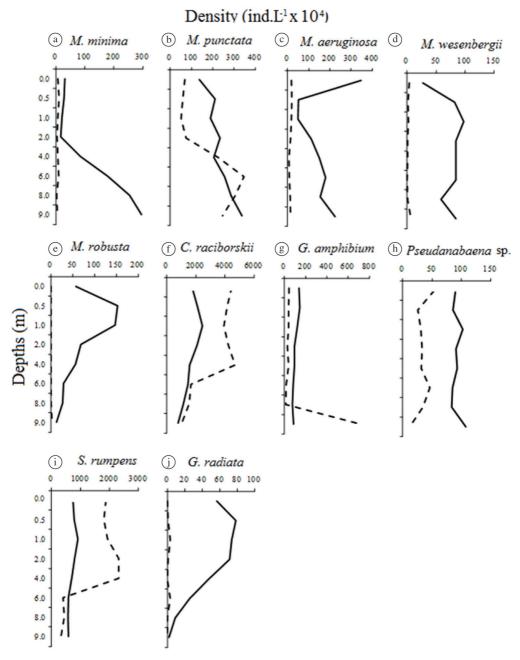


Figure 3. Variation in vertical and seasonal density of abundant species in the Mundaú reservoir, state of Pernambuco, Brazil. . (): Dry season; (): Rainy season.

Padisák (1997) reported that the highest density of *C. raciborskii* occurs in environments with temperatures above 25°C, especially in the epilimnion. At Mundaú reservoir, higher densities of this species occurred up to a depth of 2.0m, limit of the epilimnion in this environment, where higher temperature (between 25°C-26°C), pH and dissolved oxygen values were observed. Other studies developed both in the natural environment and in the laboratory, show the importance of these variables for the

growth of *C. raciborskii* (Bouvy et al., 2006; Costa et al., 2006; Chellappa et al., 2008).

In tropical reservoirs, differences in temperature of 0.5°C between the sub-surface and the bottom promote the formation of stable thermal stratification, with direct influence on the distribution of phytoplankton (Payne, 1986). According to Padisák et al. (1988), sudden variations in temperature, between certain depths, act as a barrier to many phytoplankton species, since they cause changes

Table 2. Statistical summary and correlation coefficients for phytoplankton and abiotic variables on the first two CCA axes for the Mundaú reservoir, state of Pernambuco, Brazil

	Axis 1	Axis 2	
Eigenvalues	0.253	0.014	
Accumulated variance in biotic data (%)	92.2	97.4	
Accumulated variance in species-environment relation (%)	93.1	98.4	
Species-environment correlation	0.999	0.993	
Monte Carlo test			
Significance of first canonical axis $-p$	0.0010		
Significance of all canonical axes $-p$	0.0010		
	Intra-set correlation		
	Axis 1	Axis 2	
Temperature (T°C)	-0.7652	-0.4370	
Dissolved oxygen (O ₂)	-0.8454	-0.3897	
Electrical condutivity (Cond)	0.0564	0.0950	
pH	-0.8552	-0.4339	
Total dissolved solids (TDS)	0.0145	0.0446	
Total nitrogen (TN)	0.0929	0.5879	
Total phosphorus total (TP)	0.6957	0.2643	

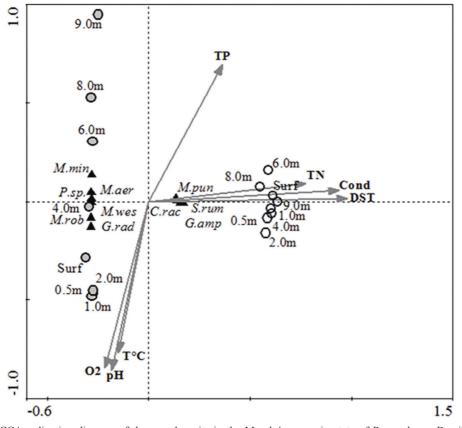


Figure 4. CCA ordination diagram of the sample units in the Mundaú reservoir, state of Pernambuco, Brazil, showing the correlation between phytoplanktonic species and abiotic variables. T°C: Temperature; O₂: Dissolved Oxygen; Cond: Electrical conductivity; DST: Total dissolved solids; TN: Total nitrogen; TP: Total phosphorous; Surf: Surface; M.pun: Merismopedia punctata; M.min: Merismopedia minima; M.aer: Microcystis aeruginosa; M.wes: Microcystis wesenbergii; M.rob: Microcystis robusta; C.rac: Cylindrospermopsis raciborskii; G.amp: Geitlerinema amphibium; P.sp: Pseudanabaena sp.; S.rum: Synedra rumpens; G.rad: Golenkinia radiata. (): Dry season; (): Rainy season; (): Species.

in density, viscosity, pressure, oxygen concentration and solubility, and oxygen concentration in the water. Thus, for cyanobacteria such as *C. raciborskii*, buoyancy mechanisms that regulate the position in the water column act as a competitive advantage over other algal groups.

The colonial forms of cyanobacteria of the genus *Microcystis* also have aerotopes, which would explain the higher density of *M. aeruginosa* and *M. robusta* in the superficial layers of the water column. *Microcystis* spp. commonly form blooms in rivers, lakes and reservoirs in tropical and temperate regions, which can proliferate to the point that surface waters are covered with thick green scum (Otten et al., 2012). Studies have shown that blooms of *Microcystis* spp. are often replaced by *C. raciborskii* (Marinho and Huszar, 2002) and alternation of dominance between these species has been observed, often linked to seasonality (Moschini-Carlos et al., 2009), indicating that there is an overlap of niches which does not permit the occurrence of high densities of both species in the same environment.

Other abundant species in the Mundaú reservoir also showed a preference for specific layers of the water column for growth, such as the preference of species of *Merismopedia* for regions with low luminosity and temperature, or of *Golenkinia radiata* for layers closest to the surface.

According to Lindenschmidt and Chorus (1998) and Wolin and Duthie (1999), due to the high rate of sedimentation of diatoms relative to other algal groups, it is necessary for climatological and hydrological events to occur, thus promoting turbulence in the water column, to keep them in suspension. In the Mundaú reservoir isothermy was not observed during the study period, but the lowest stratification recorded in the period of increased rainfall may have contributed to the increased density of *S. rumpens*. These results show the importance of stratification in the establishment of high densities and dominance of a few phytoplankton species throughout the study.

Overall, seasonal variation has a marked influence on many abiotic parameters in aquatic environments and, as a consequence, the phytoplankton community. In tropical regions, where seasonality is basically defined by a rainy and a dry period, climate change alters precipitation and, as a consequence, the hydrological regime in the neighbouring scenario, inducing deep changes in the input of nutrients. In Mundaú, data on the composition, abundance, dominance, density, diversity index and equitability demonstrate the hypertrophy of the system, with a dominance of Cyanobacteria, especially C. raciborskii. The vertical changes in abundant taxa reveal distinct patterns regulated by the variation of environmental factors that were directly linked to seasonality, with the success of one or more species depending directly on their life strategies and ecological needs.

The present study restates the importance of environmental and seasonality factors in the composition and distribution of phytoplankton in an ecosystem of a tropical region through a vertical gradient.

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