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ORIGINAL ARTICLE

Assessing temporal and spatial variability of phytoplankton composition in a large reservoir in the Brazilian northeastern region under intense drought conditions

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ABSTRACT

The present study was carried out in Castanhão Reservoir, a large aquatic system in the Brazilian semi-arid region that serves multiples uses as water drinking supply and intensive fish-cage aquaculture site. In order to understand the effects of environmental conditions on the spatial and temporal variability of the phytoplankton functional groups (FG) and the main 'characterizing taxa', sub-superficial water samples were collected from March 2012 to August 2013, a period distinguished by the continuous drop in reservoir volume due to rainfall shortage. Eighteen functional groups and 102 total phytoplankton taxa were found in the Castanhão reservoir during the study. No significant differences were observed relative to spatial variation of total phytoplankton composition throughout the reservoir (PERMANOVA, $P>0.05$). On the other hand, according to cluster analysis results, three temporal phases have been identified (Similarity Profile, $P<0.05$), based on 102 phytoplankton taxa. The 'characterizing taxa' was found using the Similarity Percentage procedure (cut-off 90%), being thus defined as those taxa that contributed the most to the similarity within each temporal phase. Nineteen 'characterizing taxa' described the Castanhão reservoir, with predominance of those typical of mixing and turbidity conditions. Cyanobacteria dominated through the three temporal phases. According to the redundancy analysis, nutrient availability and water transparency were found to influence the phytoplankton temporal dynamics. The phase I (rainy season) was most represented by *Planktolyngbya minor*/*Pl. limnetica* (FG=S1), which reached best performance under strongly decreased phosphate-P concentrations and low water transparency. In phase II (dry season), *Pseudanabaena* sp.1 (FG=?) outcompeted other cyanobacteria probably due the increase in water transparency and decrease in ammonium-N. Finally, in phase III (rainy season) the decrease of water transparency triggered a recovery of shade-adapted cyanobacteria, but at this time mostly represented by *Pseudanabaena limnetica* (FG=S1). Phase III was also distinctive from the other ones by the highest Nitrate-N and phosphate-P concentrations related to thermocline disruption, which favored an increase in total phytoplankton biomass recorded by the augment of green algae density (FGs=X1, J and F). We concluded that the temporal dynamics of phytoplankton composition was associated to environmental changes in Castanhão Reservoir from 2012 to 2013, which were driven by seasonal climate variation from region (rainy/dry seasons), as well as, by the reduction in reservoir volume that resulted in the disruption of the thermocline, water mixing and an increase in inorganic P and N.

Key words: Functional groups; cyanobacteria; green algae; nutrients; turbidity.

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INTRODUCTION

Phytoplankton is composed of a diverse community responsible for the primary productivity in water supply reservoirs. Due to their role as the basis of the food web as well as because of their short life cycles, the spatial and temporal dynamics of the phytoplankton community can provide important information about other biotic components and on general environmental conditions of an ecosystem (Reynolds, 2006). Additionally, water supply reservoirs are convenient environments to investigate the effects of environmental variables on phytoplankton structure due their highly dynamic conditions (Chellappa *et al.*, 2009; Yang *et al.*, 2017).

Seasonal fluctuations in rainfall alter the water volume stored by reservoirs as well as other environmental variables, such as mixing conditions, turbidity, oxygen and nutrients contents in the water column (Chaves *et al.*, 2013; Mosley *et al.*, 2015; Santos *et al.*, 2017). These changes, in turn, lead to shifts in phytoplankton attributes (Chellappa *et al.*, 2009; Câmara *et al.*, 2015), which reinforce the use of this community to evaluate the environmental status of these aquatic ecosystems. For example, high concentrations of nutrients, high conductivity and increased phytoplankton biomass could be expected in reservoirs and lakes located in semi-arid regions with reduced water volume (Naselli-Flores, 2003; Bouvy *et al.*, 2003; Mosley *et al.*, 2012; Jirsa *et al.*, 2013). On the other hand, since the reduction of water volume occurs along with intensification in sediment resuspension and turbidity, a negative impact on phytoplankton biomass could also be expected (Braga *et al.*, 2015). Additionally, the dominance of few species, with particular concern for the dominance of potentially harmful cyanobacteria, often occurs in semi-arid regions under drought conditions (Bouvy *et al*., 1999; Brasil *et al.*, 2016).

The phytoplankton classification into functional groups rather than only based on taxonomic affiliations has been often used as tool for environmental characterization of reservoirs (Silva *et al*., 2015; Rangel *et al*., 2016; Rodrigues *et al*., 2017). In the present study we have use Reynolds's functional groups (FGs), when the species with similar sensibilities, tolerances and ecologies affinities are placed together, being each FG selected by a set of environmental variables (habitat template) (Reynolds *et al*., 2002 reviewed by Padisák *et al*., 2009). This approach provides some advantages: i) it can be used to a clear characterization of the environment since the habitat template is known to each Reynolds's FG; and ii) it is of easy application because the FGs are already defined for a large amount of species and it does not require biovolume measurements to fitting each species into predetermined FGs, as other functional schemes need, such as that of Kruk *et al.* (2010). In this way, Reynolds *et al*. (2002) FG selection was the better adapted to our goal and the data set (species densities and total phytoplankton biomass), available for our studied reservoir. Other particular characteristic of Reynolds's functional scheme is that it requires the identification at the species level and sometimes genus level, an important information for characterizing water supply in reservoirs where potentially harmful cyanobacteria often occurs (Brasil *et al*., 2016). Additionally, Reynolds's FGs were previously used by Molisani *et al.* (2010) in the same studied reservoir, allowing a comparative approach.

In this sense, the objective of this work was to evaluate the effect of environmental changes on phytoplankton composition using taxonomic affiliations and Reynolds's functional groups in a large semi-arid reservoir during eighteen months of severe drought, when the water volume continually dropped due to rainfall shortage. Since droughts are increasing in frequency and severity in many regions such as in tropical semi-arid areas (Marengo *et al.*, 2013; Marengo and Bernasconi, 2015), this study may give us clues to understanding the effect of climate change on phytoplankton of artificial reservoirs. These systems play fundamental roles in the Brazilian semi-arid due their multiple uses as drinking water supply and intensive fish-cage aquaculture sites (Cirilo, 2008; Molisani *et al*., 2015).

Additionally, the results obtained in the present study were compared with those found by Molisani *et al.* (2010) in the same reservoir, in order to evaluate possible shifts in the phytoplankton composition and biomass from the first years when the Castanhão Reservoir was completely filled (2006/2007) to the period eight years later (2012/2013), when the reservoir suffered nearly 50% of water reduction.

METHODS

Study area

The study was carried out in the Castanhão reservoir (5.50°S 38.47°W) in the Middle Jaguaribe River watershed, which is located entirely within the semi-arid region in the State of Ceará, NE Brazil (Fig. 1). The total storage capacity of the reservoir is 6.7 billion m^3, and the normal operating capacity is 4.45 billion m^3. The reservoir reached its full capacity for the first time only in 2004 and covers an area of 325 km^2 and is 48 km in length, with a depth exceeding 50 m in some areas (DNOCS, 2014). The Castanhão reservoir accounts for 97% of the total storage capacity from the Middle Jaguaribe River basin and is the largest reservoir in Ceará State. It serves multiple uses, including water supply for drinking water, agriculture and aquaculture (COGERH, 2011). The categories of the World Commission on Dams (2000) classify the Castanhão as a large reservoir.

The semi-arid climate of northeastern Brazil is characterized by annual rainfall means commonly ranging from 400 to 1000 mm, with average of 756.5 mm during the past 80 years (FUNCEME, 2014). Rainfall occurs from January to June and is scarce from July to December.

Although the years of 2012 and 2013 have not been under El Niño influence, a phenomenon associated to lower rainfall in northeastern Brazil, these years were characterized as extreme drought due to the Atlantic dipole (Marengo *et al.*, 2016). Some studies have reported that the heating of the North Atlantic waters, combined with a cooling of the South Atlantic waters, characterizing a positive Dipole, leads to a situation of descending movements of air over the Brazilian Northeast region, inhibiting the formation of clouds (Marengo *et al*., 2013; Nóbrega and Santiago 2014; Marengo *et al.*, 2016). In fact, it was observed that in the years of 2012 and 2013, rainfall was only 302.3 mm $year^{-1}$ and 656.5 mm $year^{-1}$, respectively, significantly below the historical annual average (FUNCEME, 2014).

As a consequence of this period of intense drought during 2012/2013, the Castanhão reservoir showed a very distinctive situation from those observed until 2009, when the reservoir almost reached the limit of its total capacity storage, and even from 2011, when the reservoir volume was about 80% of its capacity (DNOCS, 2014). During the study period, the reservoir volume dropped progressively, reaching 72%, 65%, 55% and 50% of its total capacity in March 2012, August 2012, January 2013 and August 2013, respectively (DNOCS, 2014).

Sampling, environmental variables and chlorophyll *a*

Sampling campaigns occurred in March and August 2012 and January and August 2013, covering 8 stations located throughout the reservoir (Fig. 1). The stations P1 and P2 corresponded to the inner zone, P3 and P5 to the middle zone, while P6, P7, P8 and P10 to the dam zone. Due to operational issues data from P1, P2 and P3 in March 2012, P1 in January/13 and P3 in August/13 were not collected.

Prior to water collection, major physical and chemical variables were measured *in situ* in sub-superficial waters (0.5 to 1.0 m depth): dissolved oxygen (YSI 556 probe, YSI Inc., Yellow Springs); water temperature, turbidity, electrical conductivity (Compact-CTD model AST D687; JFE Advantech Co., Ltd., Nishinomiya); pH (Portable 826 pH-meter; Metrohm AG, Herisau); and water transparency with a Secchi disk. Oxygen, water temperature, turbidity, electrical conductivity and pH were measured with an accuracy of 0.1 mg L^{-1}, 0.1°C, 0.1 NTU, 1.0 µS cm^{-1} and 0.1, respectively.

Water samples collected from the subsurface (1.0 m) layer with a Van Dorn bottles were filtered in 47-mm-diameter AP40 glass fiber filters and analyzed for inorganic nutrients: nitrate-N (Braga *et al*., 2015), nitrite-N (Bendschneider and Robinson, 1952), ammonium-N (Koroleff, 1970) and phosphate-P (Murphy and Rilley, 1962). Unfiltered samples were used to determine total phosphorus (TP) and total nitrogen (TN) (Valderrama, 1981). All nutrients were quantified in triplicate by visible spectrum spectrophotometry reaching detection limits of 1.0 µg L^{-1}, 10 µg L^{-1}, 0.1 µg L^{-1}, 1.4 µg L^{-1}, 0.1 mg L^{-1} and 5.0 µg L^{-1} for phosphate-P, nitrate-N, nitrite-N, ammonium-N, TN and TP, respectively. The chlorophyll *a* concentrations were used as an estimative of total phytoplankton biomass in each sample and were obtained in a spectrophotometer according to the ISO 10260 (1992) protocol. For chlorophyll *a* analysis the samples were filtered immediately after sampling in a field lab through 47-mm-diameter AP40 glass fiber filters. More detailed field procedures and analytical methods were described previously by Santos *et al.* (2017).

Phytoplankton analysis

Phytoplankton samples were taken from the subsurface layer with a Van Dorn bottle concomitantly with those for nutrients and were immediately fixed with Transeau solution (ratio 1:1). The quantification and identification of phytoplankton organisms were performed ac-

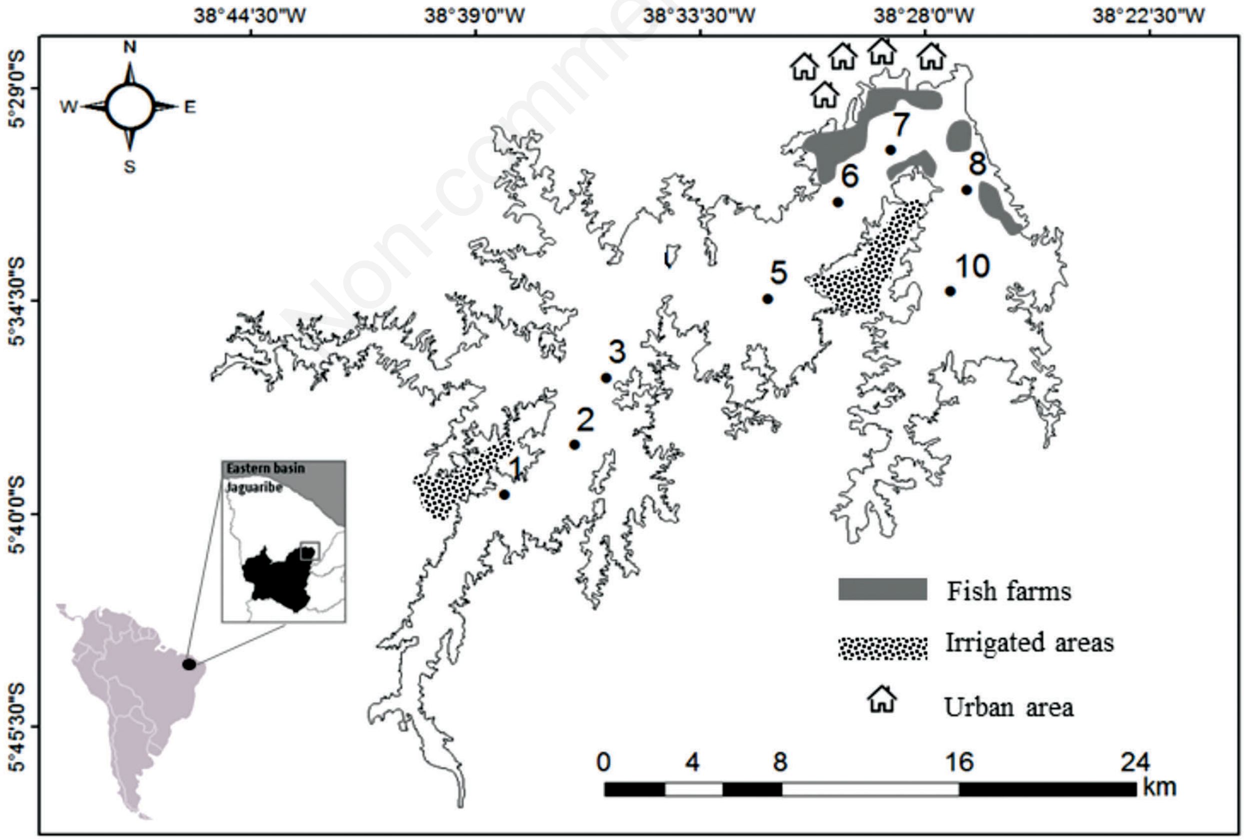

Fig. 1. Study area and location of sampling stations in the Castanhão reservoir, NE Brazil.

cording to the Utermöhl (1958) method in an inverted microscope equipped with phase-contrast (Olympus CK2) (Edler and Elbrächter, 2010). The phase-contrast was used to improve the quantification and identification of slender cyanobacteria. The volume of sedimentation chambers was of 2 or 5 mL, depending on the organisms' concentration and sedimentation time ranged from 24 to 48 hours. The counting was standardized to obtain at least 100 organisms (cells, colonies, filaments and trichomes) of the dominant taxa, with the standard error estimated to be 20% and the confidence limit of 95% (Edler and Elbrächter, 2010).

During the counting procedure the organisms were quantified and identified concomitantly at 400x magnification. However, to help in qualitative analysis, at the time of counting, the organisms were photographed and subsequently measured and analyzed according their morphology for identification at the lowest possible taxonomic level using the bibliography cited thereafter. The images were processed using Axio Vision Rel. 4.7 software which allowed the accurate measurement of the organisms, even those slender cyanobacteria with a diameter of about 1.0 μm. When necessary, organisms were also observed under 1000x magnification. In this step, it was possible to identify four pairs of species that were not separated during the counting procedure, due their large morphology similarity. They were i) *Planktolyngbya minor* and *Pl. limnetica*; ii) *Pseudanabaena catenata* and *Ps. papillaterminata*; iii) *Cylindrospermopsis* sp. and *C. raciborskii* (on coiled morphotypes); iv) *Synedra acus* and *Fragilaria delicatissima*. Therefore, though in qualitative analysis these species have been discriminated, in statistical analysis these four pairs of species were considered as four taxa because they were previously counted together. It is important to emphasize that, as each pair of species was classified in the same Reynolds's FG, no bias was introduced in data interpretation.

The identification was based on specific bibliography (books and articles) for each phytoplankton group (Komárek and Anagnostidis, 2000; Komárek, 2001; Brassac and Ludwig, 2003; Cronberg and Komárek, 2004; Komárek and Anagnostidis, 2005; Bicudo and Menezes, 2006; Komárek, 2013; McGregor, 2013; and references therein). The identified taxa were assembled into functional groups, using the criteria established in Reynolds *et al.* (2002) and reviewed by Padisák *et al.* (2009).

Data analysis

Relative abundance and frequency of occurrence

In order to evaluate the structure of the phytoplankton community, the following indicators were used: density expressed in organisms L^{-1} (org L^{-1}), relative abundance (RA) and frequency of occurrence (F) expressed as a percentage. The relative abundances (RA) (%) of each taxonomic class, taxa or functional group were calculated based on the density of each one in relation to total density of organisms in the sample. In turn, the frequencies of occurrence of each taxon were calculated based on the numbers of samples where each taxon occurred divided by the total number of total samples. Regarding the frequency of occurrence, each taxon could be classified as: Rare ($F \leq 10\%$); Common ($10\% < F \leq 50\%$) or Constant ($F > 50\%$).

Statistical analysis

Contents of chlorophyll *a* and other environmental variables (except pH) were transformed by log (x+1) before all multivariate analysis. For phytoplankton densities (total and of each taxon), data were transformed by fourth root prior to statistical analysis.

The differences among the reservoir zones (inner, middle and dam) relative to environmental variables, total phytoplankton density and chlorophyll *a* were analyzed using one-way analysis of variance (ANOVA) followed by Tukey's honestly significant different test (T-HSD) at $P<0.05$ level of probability. In turn, to test the hypothesis of significant differences among the reservoir zones relative to total phytoplankton composition, we used a Permutational Multivariate Analysis of Variance based on Bray-Curtis similarity (PERMANOVA, $P<0.05$).

Bray-Curtis similarity based on densities of all phytoplankton taxa was also used to access the degree of similarity of phytoplankton community among samples. Cluster analysis based on the Bray-Curtis similarity was performed using UPGMA, and the significance of groups was tested with the Similarity Profile test (SIMPROF). A similarity percentage analysis (SIMPER) was applied to obtain the contribution of each taxa in percent terms to the similarity within each group. The 'characterizing taxa' was defined as those taxa that most contributed to the similarity within each group using a cut-off of 90%. The significance level for SIMPROF and SIMPER was $P<0.05$.

The SIMPROF results showed that samples could be divided in three significant groups relative to total phytoplankton composition ($P<0.05$). In order to test the hypothesis of differences among these three sample groups for environmental variables, chlorophyll *a* and total phytoplankton density, ANOVA was used followed by Tukey's honestly significant different test ($P<0.05$).

Redundancy analysis (RDA), a constrained ordination method, was used to examine the relationships between the environmental variables and phytoplankton community and to select the variables that best described the temporal variability of phytoplankton structure. Firstly, two RDA models were performed in order to test the efficiency of the top 'characterizing taxa' to summarize the overall temporal variability of phytoplankton structure and their correlations with environmental variables: one using biotic data of all 102 taxa (response matrix 1) found along the survey; and another using only the top nineteen ‘characterizing taxa’ (response matrix 2) defined by the SIMPER (cut-off 90%). The length of the first axis (<3.0) of Detrended Correspondence Analysis (DCA) of response matrices data supported the use of RDA.

For both response matrices 1 and 2, the same procedures were adopted to reach the final RDA and to access the relationships between environmental variables (predictor matrix) and phytoplankton structure (response matrix). Firstly, a preliminary RDA was performed with all available environmental variables: Secchi depth (Secchi), turbidity, pH, Temperature, Conductivity, Dissolved Oxygen, Total Phosphorous, Total Nitrogen, phosphate-P, nitrate-N, nitrite-N and ammonium-N. Only the significant variables ($P<0.05$) were retained in the second RDA. In order to know the collinearity among the explanatory variables, we calculated the variation inflation factor (VIF) of each one. The VIF >10 indicates that a variable is strongly dependent on others and therefore does not have independent information (Oksanen *et al*., 2015). Only variables with VIF <10 were used in the second RDA model. We tested the marginal significance of the remaining variables by 999 permutations, and only those with significance were used in final RDA. The significance of the first two axis and of the final RDA models were tested by 999 permutations. The adjusted R^2 values were computed to obtain the explanatory power of the final RDAs.

As the same results were found for RDAs using the response matrix 1, based on biotic data of all 102 taxa (data not shown), and the response matrix 2, based on the top nineteen ‘characterizing taxa’, only the last one is shown due its higher power to summarize the variability of phytoplankton composition in the Castanhão reservoir throughout the survey.

The ANOVA and T-HSD tests were performed using the software Statistica® 7.0 (Statsoft Inc., Tulsa, OK, USA). The Bray–Curtis similarity followed by cluster analysis, the SIMPROF test and SIMPER procedure were carried out using the software PRIMER 6.0 (Plymouth Marine Laboratory). PERMANOVA, DCA and RDA analyses were done using the vegan package in R software (Oksanen *et al*., 2015).

RESULTS

A total of 102 taxa were identified, distributed among the classes Cyanophyceae (cyanobacteria) (34), Chlorophyceae (green algae) (42), Bacillariophyceae (diatoms) (18), Zygnemaphyceae (4) and Euglenophyceae (4), besides one unidentified phytoflagellate taxon. Within this total set of 102 taxa, we discriminated 18 functional groups, being Cyanophyceae in seven codons; MP, S1, L, LM, Lo, S_N and H1, Bacillariophyceae in six; P, B, D, MP, C and B, Chlorophyceae in four; P, X1, F and J, Zygnemaphyceae in two; N e NA and Euglenophyceae in one codon; W2. Furthermore, 26 taxa from the total data set were not classified to any functional group described by Reynolds *et al.* (2002) and Padisák *et al.* (2009) either because their identification did not occur at the taxonomic level of species or genera or because they have not yet been included within the associations described by those authors. Among the most representative taxa not assigned to any functional group, we highlight *Pseudanabaena papillaterminata, Pseudanabaena* cf. *biceps*, *Pseudanabaena* sp.1 and *Myxobaktron* sp. This reinforces the fact that the categorization of phytoplankton into Reynolds’s functional groups, especially taking into account tropical ecosystems, needs to be revised aiming the inclusion of new species within the previously described groups as well as with the proposition of new functional groups. For this, the ecology of each species still needs to be better understood.

Therefore, taking into consideration the recommendations provided by Padisák et al. (2009) we classified *Ps.* cf. *biceps* and *Ps. papillaterminata* on functional group MP, which included periphytic or epilithic species occasionally found in plankton samples. Komárek and Anagnostidis (2005) described *Ps. papillaterminata* as a benthonic species. In turn, *Ps.* cf. *biceps* is found mainly attached to substrate (Komárek and Anagnostidis, 2005; Douma *et al.*, 2009; Klemenčič *et al.*, 2010).

For *Myxobaktron* sp. we propose its classification as X1 codon, because it reached the better performance along with small green algae of similar morphology belonging to X1 codon (see Discussion section). However, as *Myxobaktron* is a genus poorly cited in limnological studies and information about its autoecology is scarce, we prefer to assign it as FG=X1 (?). In the case of *Pseudanabaena* sp.1, a slender genus of cyanobacteria, which the classification on Reynolds’s FG depends on species, it was not proper to assign it to any functional group because it reached maximum density in a distinct moment from the other ‘characterizing taxa’ of similar morphology. Additionally, due to their close association with Secchi depth, we have avoided its classification in MP or S1, typical codons from turbid environments (Padisák *et al*., 2009). Therefore, from the list of 102 taxa, where 26 of them were not previously classified to any Reynolds’s FGs, 23 taxa remained as unsigned.

Spatial variability

The results from abiotic variables characterizing the inner, middle and dam zones during the sampling period are summarized in Supplementary Tab. 1. Except for turbidity, no significant differences were found between the zones (ANOVA, $P>0.05$). The turbidity values in the inner zone were significantly higher than those found in middle and dam zones (ANOVA, T-HSD, $P<0.05$). In the inner zone, the lowest Secchi-disk transparency values were also observed. In all three zones, alkaline pH and high-water temperature (>27.0°C) were observed, as well as, high levels of oxygen (> 6.0 mg L^{-1}) and conductivity (>300 µS cm^{-1}). On the other hand, the levels of inorganic nutrients were generally low, ranging from non-detectable to maximum concentrations of 11.2 µg L^{-1}, 44.6 µg L^{-1}, 2.5 µg L^{-1} and 132.4 µg L^{-1} for phosphate-P, nitrate-N, nitrite-N and ammonium-N, respectively. The TN and TP concentrations ranged from low to intermediated values in each zone, with average values of these nutrients below 30 µg L^{-1} (TP) and 620 µg L^{-1} (TN).

Average phytoplankton densities were 4.0 (±3.0) 10^{6} organisms L^{-1}, 6.0 (±4.0)×10^{6} organisms L^{-1} and 10 (±8.0)×10^{6} organisms L^{-1} at inner, middle and dam zones, respectively. Although the phytoplankton densities have increased toward the dam zone, no significant differences were found between the three reservoir zones (ANOVA, $P>0.05$). Similarly, the total phytoplankton biomass (chlorophyll *a*) increased from the inner to the dam zone, with average values of 2.9±0.5 µg L^{-1}, 4.5±0.7 µg L^{-1} and 5.0±2.1 µg L^{-1} at the inner, middle and dam zones, respectively. A significant difference was found between the inner and dam zone (ANOVA, T-HSD, $P<0.05$), but not between the middle and dam zone (ANOVA, T-HSD, $P>0.05$).

In all three zones of the reservoir the cyanobacteria were dominant with a relative abundance above 80%, followed by green algae and diatoms with relative abundances ranging from 5 to 10% in each zone. The most abundant functional group in all three zones was S1 (Fig. 2), represented mainly by the cyanobacteria *Pseudanabaena limnetica* and *Planktolyngbya limnetica/Pl. minor*. The third more abundant taxon was the cyanobacteria *Pseudanabaena* sp. 1 (FG=?), not assigned to any functional group (Fig. 2). Thus, the phytoplankton composition throughout the reservoir was very constant and no significant differences were found among the zones by PERMANOVA test (F model=1.4061; $r^2=0.05325$; $P=0.234$; 999 permutations).

Temporal variability

The cluster analysis based on the densities of the 102 phytoplankton taxa is presented in Fig. 3. In this Figure, the formation of three significant groups can observed (SIMPROF, $P<0.05$), showing a clear tendency to temporal clustering of samples in three phases/groups: phase I including all samples from March/12; phase II formed by samples from August/2012 and January/2013, plus one sample from August/2013 (P1); and phase III including all samples from August/2013 (except for P1).

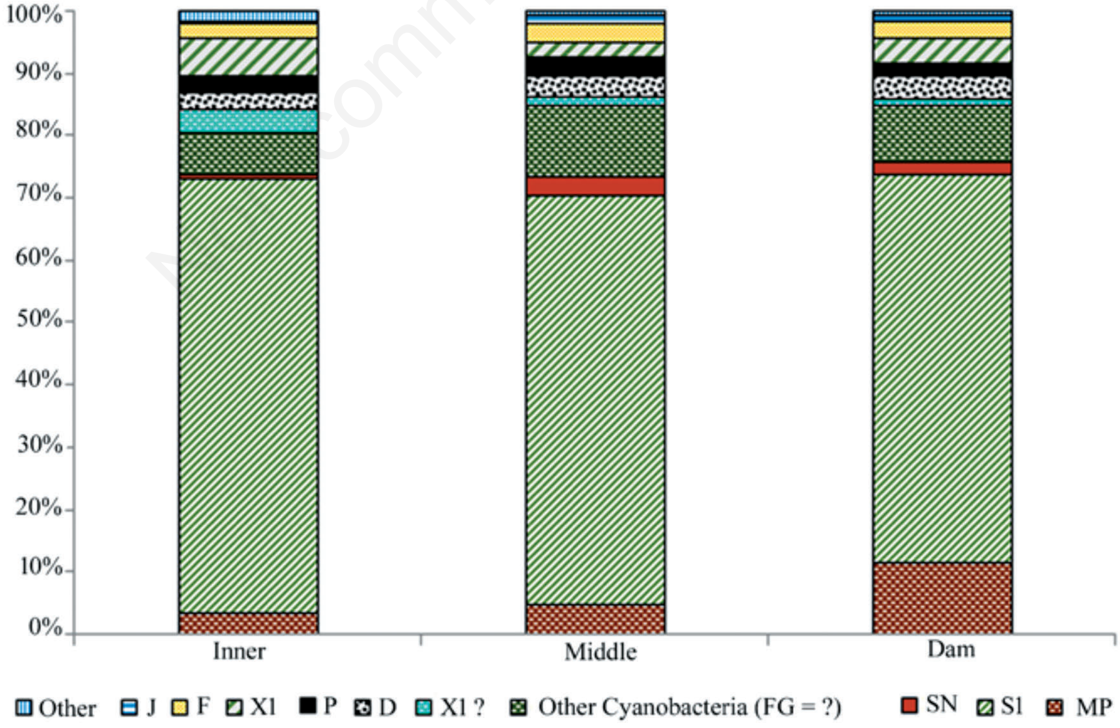

Fig. 2. Mean relative abundance (%) of the main phytoplankton functional groups for the three spatial zones from Castanhão Reservoir during the sampling period. Codon X1? only included *Myxobaktron* sp., while Other Cyanobacteria (FG =?) refers only to *Pseudanabaena* sp. 1.

Supplementary Tab. 2 summarizes the results of abiotic variables of the three temporal phases suggested by cluster analysis. No significant differences were found for turbidity, dissolved oxygen, pH, nitrite-N, TP and TN among the phases (ANOVA, P>0.05). In turn, the water temperature was significantly different among the phases, reaching higher values in temporal phases I and III, corresponding to the rainy period (ANOVA, T-HSD, P<0.05). The higher Secchi-disk depth was found in phase II (ANOVA, T-HSD, P<0.05), while the higher conductivity and nitrate-N were observed in phase III (ANOVA, T-HSD, P<0.05). Phase I was distinctive from the others by the lowest phosphate-P concentrations (ANOVA, T-HSD, P<0.05). Phase II was also distinctive from phase I by the lowest ammonium-N concentrations (ANOVA, T-HSD, P<0.05).

A list of the major contributors ('characterizing taxa') to similarity within each group/phase according to the SIMPER procedure (cut-off 90%) and their frequency of occurrence during the survey are presented in Tab. 1. Tab. 2 summarizes the percentage contribution of the major contributors, but with a cut-off of 70%, to the average similarity within each group/phase. In all phases the cyanobacteria were the dominant class, followed by diatoms in phase II and green algae in phase III (Tab. 2).

The mean relative abundance (%) of the main phytoplankton functional groups for the phases/groups during the sampling period are presented in Fig. 4. Phase I is clearly distinct from phase II by the dominance of the functional group S1, represented mainly by cyanobacteria *Planktolyngbya limnetica/Pl. minor* with relative abundance of 62.3% along with *Pseudanabaena limnetica* (RA=25%). Other important functional groups in phase I were MP represented mainly by cyanobacteria *Ps. catenata/Ps. papillaterminata* (RA=7.5%) and S_N represented by *Cylindrospermopsis* sp./*C. raciborskii* (RA=1.7%).

In phase II the taxa present in phase I decreased in density and were outcompeted mainly by cyanobacteria *Pseudanabaena* sp.1 (FG=?) (RA=36.2%). *Pl. limnetica/Pl. minor* (S1) continued to be an important cyanobacteria in phase II with relative abundance of 21.3%, followed by *Ps.* cf. *biceps* (MP) (RA=8.4%), *Cylindrospermopsis* sp./*C. raciborskii* (S_N) (RA=3.9%) and *Myxobaktron* sp. (X1?) (RA=2.6%). Despite in phase II the Cyanophyceae have also been the dominant class, an increase in Bacillariophyceae was observed, mainly due to *Nitzschia* sp. (D) (RA=5.6%) and *Aulacoseira granulata* var. *granulata* (P) (RA=3.5%) (Fig. 4).

Finally, in phase III the functional group S1 increased again in density and relative abundance, mainly due to the

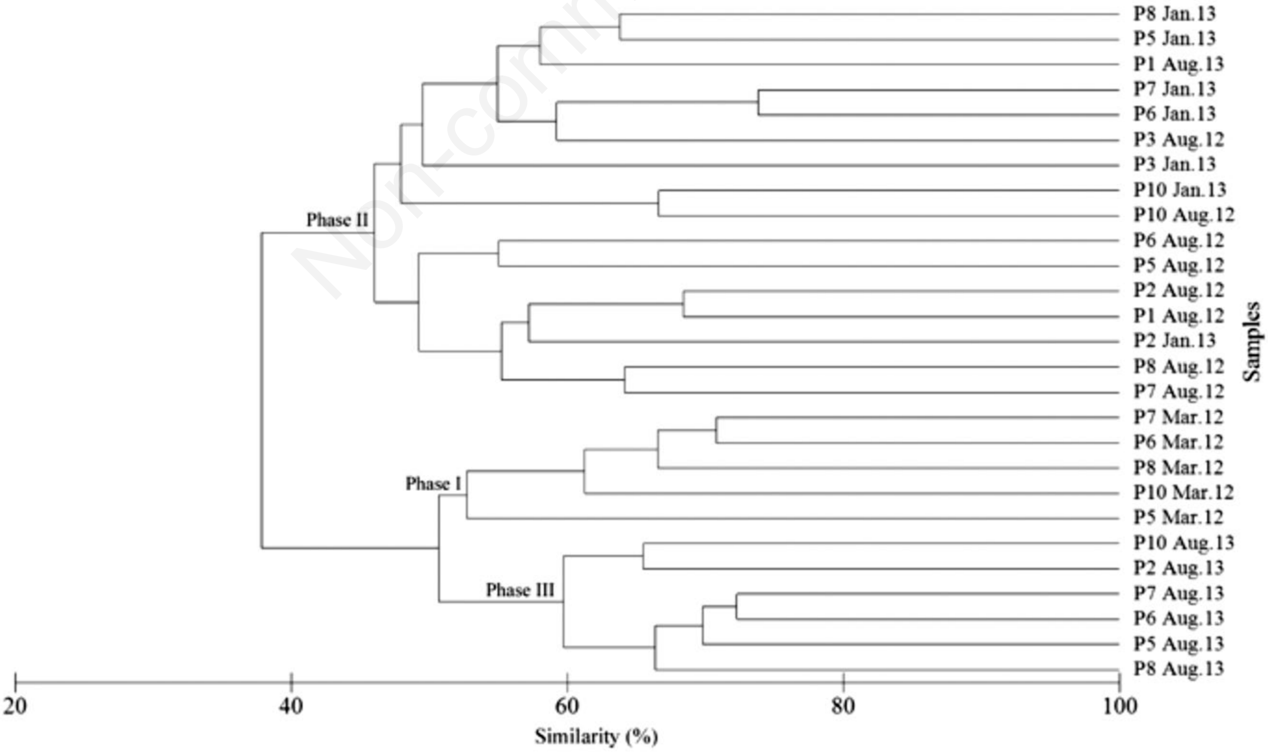

Fig. 3. Cluster analysis based on the density of the 102 phytoplankton *taxa*. Temporal Groups/Phases I, II and III were significant according to the SIMPROF test (P<0.05).

Tab. 1. Major contributors ('characterizing taxa') to similarity within each group in the clustering analysis according to the SIMPER procedure (cut-off 90%), functional group, life form and frequency of occurrence. *Pl. minor* and *Pl. limnetica*; *Ps. catenata* and *Ps. papillaterminata*; *Cylindrospermopsis* sp. and *C. raciborskii*; *S. acus* and *F. delicatissima* weren't identified individually during counting due to strong similarity, therefore counts refer to each pair of species.

Characterizing taxa	Functional group[1]	Life form[2]	Frequence of occurence[3]
Cyanophyceae			
Planktolyngbya minor (Geitler & Ruttner) Komárek & Cronberg / *Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg	S1	Fi	Constant
Pseudanabaena limnetica (Lemmermann) Komárek	S1	Fi	Constant
Pseudanabaena catenata Lauterborn / *Pseudanabaena papillaterminata* (Kiselev) Kukk	MP	Fi	Common
Cylindrospermopsis sp. / *Cylindrospermopsis raciborskii (Woloszynska)* Seenayya & Subba Raju	S_N	Fi	Common
Pseudanabaena sp. 1	?	Fi	Constant
Pseudanabaena cf. *biceps* Böcher	MP	Fi	Constant
Myxobaktron sp.	X1 ?	UNF	Constant
Chlorophyceae			
Schroederia setigera (Schröder) Lemmermann	X1	UNF	Common
Monoraphidium circinale (Nygaard) Nygaard	X1	UNF	Common
Ankyra judayi (G.M.Smith) Fott	X1	UNF	Common
Monoraphidium minutum (Nägeli) Komárková-Legnerová	X1	UNF	Constant
Oocystis lacustris Chodat	F	CNF	Constant
Elakatothrix sp.	F	CNF	Common
Micractinium pusillum Fresenius	F	CNF	Constant
Golenkinia sp.	J	UNF	Constant
Bacillariophyceae			
Nitzschia sp. (12-25 µm)	D	UNF	Constant
Synedra acus Kützing / *Fragilaria delicatissima* (W. Smith) Lange-Bertalot	D	UNF	Common
Aulacoseira granulata (Ehrenberg) Simonsen var. *granulata*	P	CNF	Constant
Aulacoseira granulata (Ehrenberg) Simonsen var. *angustissima*	P	CNF	Constant

[1] *Functional group: defined according to Reynolds* et al. *(2002) and Padisák* et al. *(2009). (? - unidentified functional group).* [2] *Life form: unicellular non-flagellated (UNF), colonial non-flagellated (including coenobia) (CNF) and filaments (Fi).* [3] *Frequency of occurrence (%): rare ($F \leq 10\%$), common ($10\% < F \leq 50\%$) and constant ($F > 50\%$) based on the occurrence related to the total number of samples (? - unidentified functional group).*

Tab. 2. Total phytoplankton biomass (mean ± standard deviation), Total phytoplankton density (mean standard ± deviation), Relative abundance of main taxonomic classes, and major phytoplankton taxa to the average similarity within each group/phase (cut-off 70%). Percentage contribution of each taxa to the similarity within each group are presented in parenthesis.

	Group/Phase I	Group/Phase II	Group/Phase III
Average similarity according cluster analysis	59.9%	50.1%	61.6%
Total phytoplankton biomass (Chlorophyll a) (μg L^{-1})	3.97±1.1^{a}	4.05±1.21^{a}	6±3^{a}
Total phytoplankton density (10^6 organisms L^{-1})	20±5^{a}	4±3^{b}	10±3^{a}
Relative abundance of main taxonomic classes	Cyanophyceae (96.4%), Chlorophyceae (2%), Bacillariophyceae (1.6%)	Cyanophyceae (80.3%), Bacillariophyceae (12%), Chlorophyceae (7.5%)	Cyanophyceae (75%), Chlorophyceae (17.6%), Bacillariophyceae (6.8%)
Major contributors to similarity within each assemblage (by SIMPER procedure, cut-off 70%)	*Planktolyngbya minor* and *Pl. limnetica* (S1) (28.7%); *Pseudanabaena limnetica* (S1) (21.7%); *Ps. catenata* and *Ps. papillaterminata* (MP) (14.4%); *Cylindrospermopsis* sp. and *C. raciborskii* (S_N) (5.8%)	*Pseudanabaena* sp.1 (FG ?) (18.9%); *Aulacoseira granulata* var. *granulata* (P) (11.6%); *Pl. minor* and *Pl. limnetica* (S1) (10.5%); *Ps.* cf. *biceps* (MP) (10.1%); A. *granulata* var. *angustissima* (P) (8.5%); *Nitzschia* sp. (12-25 µm) (D) (6.9%); *Myxobaktron* sp. (X1 ?) (6.5%).	*Ps. limnetica* (S1) (16.53%); *Pl. minor* and *Pl. limnetica* (S1) (9.8%); *Nitzschia sp.* (12-25 µm) (D) (9.3%); *Micractinium pusillum* (F) (8.1%); *Ps. catenata* and *Ps. papillaterminata* (MP) (7.7%); *Monoraphidium minutum* (X1) (7.7%); *Myxobaktron* sp. (X1 ?) (5.7%); *Ankyra judayi* (X1) (4.7%); *A. granulata* var. *granulata* (P) (4.7%).

Different letters are significant different mean values (ANOVA, T-HSD, P<0.05).

cyanobacteria *Ps. limnetica* (RA=40.3%) and *Pl. limnetica/Pl. minor* (RA=14.4%). These taxa were followed by cyanobacteria *Ps. catenata/Ps. papillaterminata* (MP) (RA=7.4%) and *Ps.* cf. *biceps* (MP) (RA=4.6 %). Notwithstanding, different from phase I, other functional groups, such as F (mainly due the green algae *Micractinium pusillum*, RA=5.9%), D (mainly due the diatom *Nitzschia* sp. RA=4.9%) and X1 (mainly due the green algae *Ankyra judayi*, RA=2.5%; and *Monoraphidium minutum*, RA=2.4%) were also well represented in phase III (Fig. 4).

Phase II was distinct from phases I and III by lower total phytoplankton density (ANOVA, T-HSD, $P<0.05$), but no significant difference was observed between phases I and III (ANOVA, T-HSD, $P>0.05$, Tab. 2). In relation to the total phytoplankton biomass (chlorophyll *a*), no significant differences were found among the phases (ANOVA, $P>0.05$, Tab. 2), though the average have increased progressively from phase I to III.

Redundancy analysis

The RDA performed with nineteen top 'characterizing taxa' defined by the SIMPER procedure (cut-off 90%), as presented in Supplementary Tab. 3, included Secchi depth ($P=0.015$), ammonium-N ($P=0.010$), nitrate-N ($P=0.010$) and phosphate-P ($P=0.005$), which showed significant marginal effects and VIF <10 (Fig. 5).

The RDA model selected for these four variables was significant ($F=6.6$, df=4, $P=0.001$) with an explanatory power of 46.3 % ($R^2=0.545$; adjusted $R^2=0.463$). The first RDA axis was significant ($P=0.001$) and mainly positively correlated to ammonium-N (0.5961) and negatively to Secchi depth (-0.7733). Axis 2 was also significant ($P=0.001$) and negatively correlated with nitrate-N (-0.4310) and phosphate-P (-0.8657).

The first axis (RDA1) separated in the positive side the sampling units from phases I and III, characterized by the highest concentration of ammonium-N and nitrate-N, respectively (Fig. 5). The sampling units from phase I were also distinctive from the others by the lowest phosphate-P concentrations, which were below the detection limits of the analytical method (see Supplementary Tab. 2). Thus, the lowest phosphate-P in phase I contributed to the best performance of *Pl. limnetica/Pl. minor* (S1) while the highest ammonium-N favored *Ps. catenata/Ps. papillaterminata* (MP).

On the other hand, in the negative side of axis 1, the sampling units from phase II were separated and characterized by the highest Secchi depth, lowest inorganic nitrogen and an increase in phosphate-P concentrations.

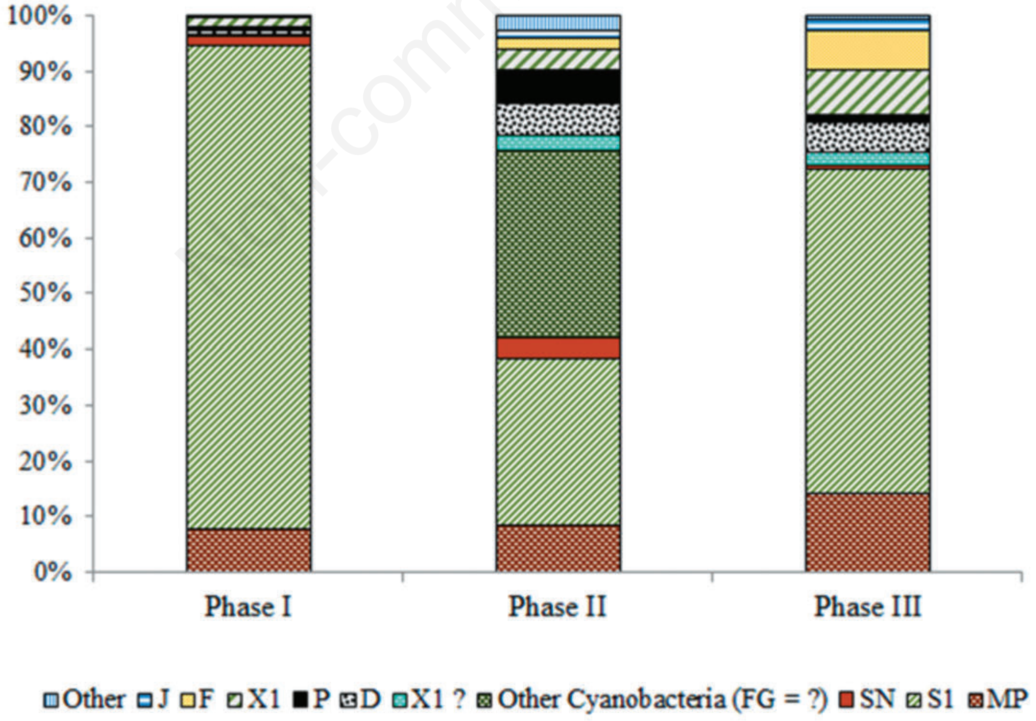

Fig. 4. Mean relative abundance (%) of the main phytoplankton functional groups for the temporal phases/groups defined by cluster analysis during the sampling period. In codon X1? was only included *Myxobaktron* sp., while Other Cyanobacteria (FG =?) refers only to *Pseudanabaena* sp. 1.

This decline in inorganic nitrogen from phase I to phase II, plus an increase in phosphate-P, could be associated to the best performance of *Pseudanabaena* sp.1 (FG ?) over other cyanobacteria, though a decrease in the total phytoplankton density have occurred, which also leaded to high Secchi depth.

Finally, in phase III an increase in inorganic nitrogen, mainly nitrate-N, was observed. This condition can have triggered a recovery of cyanobacteria from functional group S1, but at this time mostly represented by *Ps. limnetica* (S1), which was also associated to low Secchi depth. In phase III, various green algae from functional groups X1, J and F were also favored by increased nitrate-N, but also phosphate-P.

Other important information shown by the RDA model for some species with little known autoecology were the close association of *Pseudanabaena* cf. *biceps* (MP) with the highest concentrations of phosphate-P; and *Myxobaktron* sp. (X1 ?) with highest nitrate-N and phosphate-P concentrations.

DISCUSSION

The analysis of the results of spatial and temporal dynamics of the phytoplankton community in the Castanhão reservoir along the years of 2012 and 2013, when the volume of the reservoir progressively decreased from 70% to 50% (Santos *et al.*, 2017), showed a tendency of temporal rather than spatial variation across the zones. In general, the study period could be divided in three phases based on the phytoplankton structure. Phase I included all samples

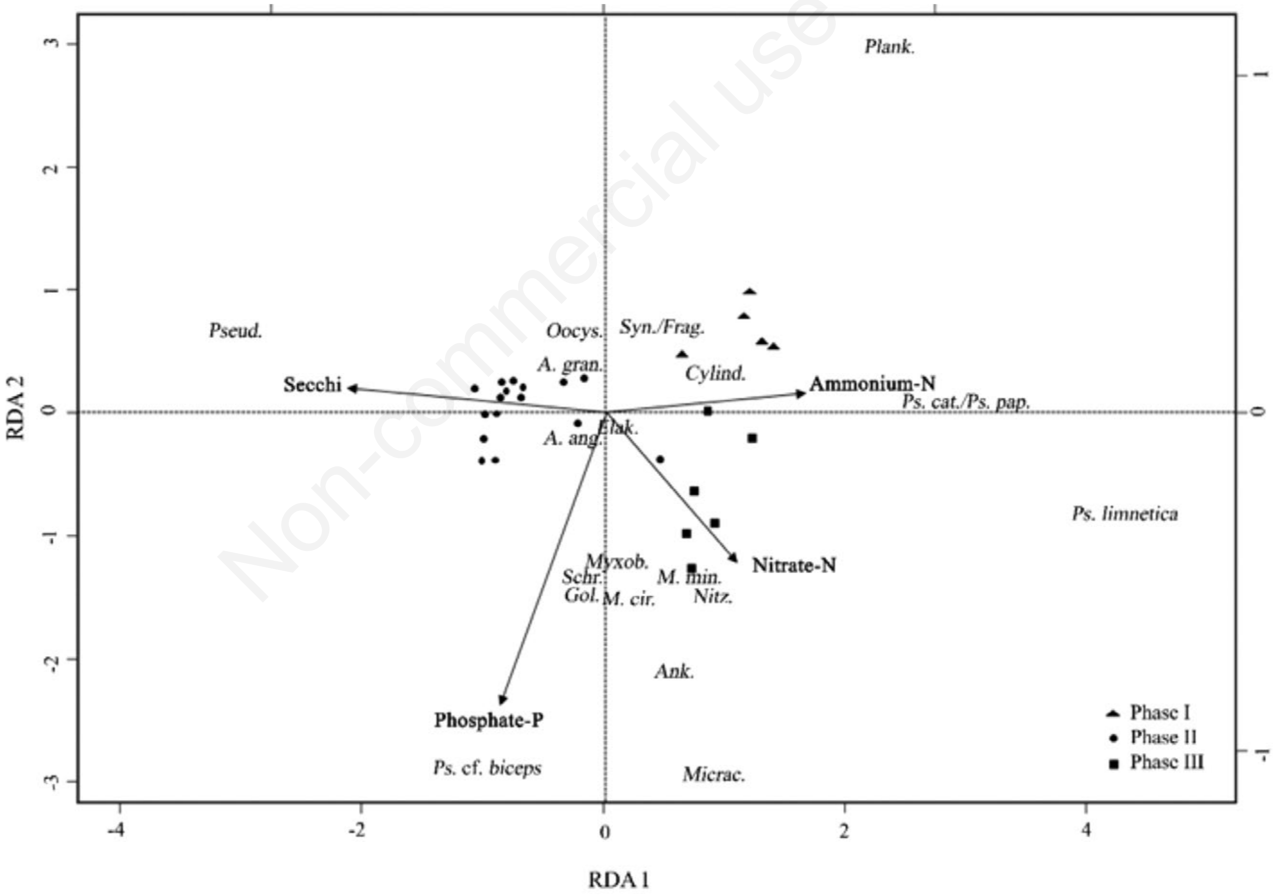

Fig. 5. Triplot diagram for RDA of Castanhão Reservoir data, including only significant ($P<0.05$) environmental variables (explanatory variables), phytoplankton 'characterizing *taxa*' (dependent variables), and samples from respective three temporal phases (I, II and III). RDA 1 and RDA 2 were significant ($P<0.05$). Total RDA model was significant ($P<0.05$) with an explanatory power of 46.3 % ($R^2=0.545$; adjusted $R^2=0.463$). *Plank.* (*Pl. minor* and *Pl. limnetica*); *Ps. cat./Ps. pap.* (*Ps. catenata* and *Ps. papillaterminata*); *Cylind.* (*C. raciborskii* and *Cylindrospermopsis* sp.); *Pseud.* (*Pseudanabaena* sp. 1.); *Myxob.* (*Myxobaktron* sp.); *Schr.* (*S. setigera*); *M. cir.* (*M. circinale*); *Ank.* (*A. judayi*); *M. min.* (*M. minutum*); *Oocys*. (*O. lacustris*); *Elak.* (*Elakatothrix* sp.); *Micrac.* (*M. pusillum*); *Gol.* (*Golenkinia* sp.); *Nitz.* (*Nitzschia* sp.); *Syn./Frag.* (*S. acus* and *F. delicatissima*); *A. gran*. (*A. granulata* var. *granulata*); *A. ang.* (*A. granulata* var. *angustissima*).

from March/12, corresponding to the rainy season, while phase II included all samples from August/12 and January/13, both representing the dry season. In turn, phase III included samples from August/2013, which corresponded to the end of the rainy season, since the rainfall in this year lasted until this month (*data not shown*). The cluster analysis also revealed a high similarity between the phytoplankton composition in phases I and III, which reinforces the influence of climatic seasonality to drive the temporal dynamic of this community. In fact, the development of phytoplankton community in Northeast of Brazil is strongly structured by the seasonal climate (rainy/dry periods) (Chellappa *et al.*, 2009; Brasil *et al.*, 2016).

The highest values of phytoplankton density were found in phase I, being *Pl. limnetica / Pl. minor* (S1) the most successful taxa. Other important taxa were *Ps. limnetica* (S1) and *Ps. catenata / Ps. papillaterminata* (MP). In this phase, the reservoir was classified as oligotrophic based on the total phosphorous and chlorophyll *a* concentrations (Santos *et al.*, 2017). It is important to note that the highest phytoplankton density observed in phase I was not associated to a high phytoplankton biomass (chlorophyll *a*), precisely due to the dominance of these slender filamentous cyanobacteria, especially *Pl. limnetica/ Pl. minor*. All these three taxa of cyanobacteria belong to the functional groups S1 and MP and are well adapted to high turbidity conditions (Padisák *et al.*, 2009), what was confirmed by their inverse association with Secchi depth in Castanhão reservoir in RDA.

Although *Pl. limnetica/Pl. minor* (Delazari-Barroso *et al.*, 2007; Silva and Costa 2015) along with *Ps. limnetica* (Mohebbi *et al.*, 2015) and *Ps. catenata / Ps. papillaterminata* (Moura *et al.*, 2007; Silva and Costa, 2015) have been commonly found in mesotrophic to hypertrophic reservoirs, these slender cyanobacteria frequently outcompeted other phytoplankton species under conditions of reduced P supply (Villena and Romo, 2003). In this sense, in the present study, their highest densities, especially of *Pl. limnetica/Pl. minor*, were mainly associated with reduced phosphate-P supply in phase I, which could be due to the strong thermocline in this period (see Santos *et al.*, 2017). Corroborating this condition, *Pl. limnetica* was previously shown as a strong indicator of a stratified water column with phosphate-P depletion, probably due to its high-affinity phosphate uptake system (Prentice *et al.*, 2015). In the same way, another study performed in a tropical water supply reservoir (Extremoz Lake, NE Brazil) also showed the dominance of *Pl. limnetica* under low values of phosphate-P (Pinto and Becker, 2014), in accordance with our results.

It is important to highlight that although we have associated the successful of *Pl. limnetica*/*Pl. minor* with a condition of stratified water column, the water samples in this study were restrictive to subsurface (1.0 m), and therefore *Pl. limnetica*/*Ps. minor* was recorded in the mixed and turbid surface layer of Castanhão reservoir. This is in agreement with the habitat template (turbid mixed layers) described for codon S1, which this species belongs.

In phase II, the cyanobacteria previously dominant in phase I were partly replaced by other cyanobacteria, mainly *Pseudanabaena* sp.1 (FG=?) and *Ps.*cf. *biceps* (MP). The phytoplankton biomass in phase II was similar to the observed in phase I since the dominance was also of slender filamentous cyanobacteria. Nevertheless, in phase II the reservoir was classified as mesotrophic due to the increase in TP concentration probably driven by the thermocline disruption (Santos *et al.*, 2017).

Pseudanabaena is a genus with tropical planktonic species recorded in lakes and large reservoirs, while *Ps.* cf. *biceps* is a species that lives primarily attached to substrate (Komárek and Anagnostidis, 2005; Douma *et al.*, 2009; Klemenčič *et al.*, 2010) and therefore belonging to MP codon. In the Castanhão reservoir, the most remarkable environmental change associated to the emergence of *Pseudanabaena* sp.1 in phase II (absent in phase I) was the increase in Secchi depth and the decrease in ammonium-N.

On the other hand, *Ps.* cf. *biceps* seemed to be mostly favored by high phosphate-P concentrations, since its average density increased progressively from phase I to phases II and III (Supplementary Tab. 3), following the rise of this nutrient's concentrations. Since *Ps.* cf. *biceps* belongs to MP, a codon typical of frequently stirred, inorganically turbid shallow lakes (Padisák *et al.*, 2009), it may also have been favored by decreasing in water volume and thermocline disruption.

Other cyanobacteria with close correlation not only with phosphate increase, but also with nitrate-N increase was *Myxobaktron* sp. (X1 ?) that increased in density from phase I to phases II and III (Supplementary Tab. 3). This genus generally forms a minor component of the planktic cyanobacterial biocenosis, but persisted year-round in the tropical regions of northeastern Australia (McGregor, 2013), such as observed in the Castanhão reservoir.

We raised the hypothesis that *Myxobaktron* sp. would be classified in codon X1 because it reached the better performance along with small green algae (*Monoraphidium circinale*, *Monoraphidium minutum*) with fast growth and similar size (length of 5-10 µm), belonging to X1. Both *Myxobaktron* sp. and these green algae increased in density in phase III, following the raise in nitrate-N concentrations and the reduction of the reservoir volume. The habitats templates of X1 codon are shallow and hypertrophic/eutrophic environments (Padisák *et al.*, 2009).

In addition to the dominant cyanobacteria in phase II, we highlight the rise in relative abundance of diatoms represented mainly by *Aulacoseira granulata* var. *granulata* (P) and *A. granulata* var. *angustissima* (P). The functional group P is associated with higher trophic states and mixing conditions (Padisák *et al.*, 2009), in accordance with phosphate-P increase and thermocline disruption observed during this phase (Santos *et al.*, 2017).

In phase III, the shade-adapted cyanobacteria that dominated in phase I, which were *Pl.limnetica / Pl.minor* (S1), *Ps. catenata*/*Ps. papillaterminata* (MP) and *Ps. limnetica* (S1), increased again in density, but at this time with dominance of the last one. *Ps. limnetica* (S1) is a common species in eutrophic reservoirs (Mohebbi *et al.*, 2015), and in the Castanhão reservoir it seemed to have been more favored mainly by the increase in nitrate-N concentration in phase III. Messyasz *et al.* (2015) also indicated the dependence of *Ps. limnetica* to high nitrate-N concentrations.

Another similarity between phases I and III was the absence of *Pseudanabaena* sp.1, suggesting its sensibility to decreasing water transparency (estimated by Secchi depth). *Pseudanabaena* sp.1 was also associated with decreasing in ammonium-N concentrations in phase II. It was not possible to assign *Pseudanabaena* sp.1 to any Reynolds FG, both because the identification did not occur at species level and because it reached the maximum density in a distinct moment (phase II) from the other ‘characterizing taxa’ of similar morphology (other slender cyanobacteria).

Also in phase III, we highlight among the diatoms *Nitzschia* sp., belonging to the functional group D, which is indicative of turbid, eutrophic and shallow waters (Reynolds *et al.*, 2002; Padisák *et al.*, 2009; Silva and Costa, 2015). The decrease in water depth, along with the increase in the trophic conditions of the reservoir in phase III, was also suggested by the rise of green algae belonging to the functional group X1, such as *A. judayi*, *M. minutum, M. circinale* and *S. setigera,* and belonging to J functional group, represented by *Golenkinia* sp. According to Padisák *et al.* (2009), both functional groups, X1 and J, are indicative of shallow and nutrient-enriched systems.

Another functional group within green algae was group F, represented mainly by *M. pusillum*. F group is typical of mesotrophic/eutrophic waters with clear epilimnion (Padisák *et al.*, 2009), which contrasted with the turbidity condition indicated by the other species, mainly the filamentous cyanobacteria from functional group S1.

In this context, the success of *M. pusillum* (F) in phase III, along with the other green algae belonging to the functional groups X1 and J and the cyanobacteria from S1, could be due to its ability to growth rapidly under favorable conditions, such as increasing in nutrients, in addition to a possible tolerance to high turbidity conditions. This tolerance is indicated by the fact that the functional group F is also found in estuaries, which are naturally turbid environments (Costa *et al.*, 2009). Additionally, *M. pusillum* could have an adaptive advantage over other species due to its ability to use organic compounds (mixotrophy) (Bouarab *et al.*, 2004).

Similarly, Dias (2009) studying the Arcoverde reservoir (also located in the northeastern Brazil semi-arid zone as well) observed the success of species belonging to functional group F, more specifically *M. pusillum*, along with others from the functional groups X1 and S1 in the same period (rainy season). In the Arcoverde reservoir, the rainy period in which these functional groups predominated was characterized by high values of turbidity and dissolved oxygen, as well as elevated concentrations of total dissolved phosphorus, nitrite and nitrate (Dias, 2009). Similarly, in the Castanhão reservoir the key-factors to the rise of *M. pusillum* in phase III were the increase in nitrate-N and phosphate-P concentrations, as shown by the RDA.

Finally, in phase III we call attention to the highest phytoplankton biomass, precisely due to the increase of unicellular and mainly colonial green algae, which were mostly induced by the increase in nutrient concentrations, namely nitrate-N and phosphate-P. In fact, the increase in green algae and diatoms in conditions of high nitrate-N and phosphate-P concentrations could be explained by their reduced uptake rates and thus larger requirements when compared to slender filamentous cyanobacteria. For example, Prentice *et al.* (2015) showed that the seasonal phytoplankton succession in a large lake was driven by the capacity of phosphate uptake, which resulted into the cyanobacteria dominance under decreased phosphate concentrations during the summer-stratification period and in a diatom/cryptophyte/chlorophyte dominance in surface water with elevated phosphate concentrations. Despite the change in the phytoplankton structure from phase II to III, in this last phase the Castanhão reservoir was also characterized as mesotrophic based on the total phosphorous and chlorophyll *a* concentrations (Santos *et al.*, 2017).

Overall, our results suggest that in accordance with other studies, shifts in phytoplankton community were associated to changes in nutrient concentrations and water transparency (Medeiros *et al.*, 2015; Costa *et al.*, 2016). Changes in these environmental conditions were closely associated with hydrological changes in the reservoir, namely the reduction in water level due to years of severe drought. However, taking account only the eighteen months of severe drought addressed in this work, the phytoplankton composition seems to have been structured by the climatic rainy / dry regime instead of just by the ongoing decrease in water level.

On the other hand, at least concerning the relative abundance based on density data, this study shows that the dominance of cyanobacteria displayed a decrease from nearly 100% in phase I to 75% in phase III, following the ongoing reduction of water level. This finding agrees with other studies performed in semi-arid reservoirs (Medeiros *et al.*, 2015; Costa *et al.*, 2016), that have shown, in contrast with the expectations, that a reduction in water level would led to an increase in cyanobacterial dominance (Naselli-Flores *et al.,* 2007; Yang *et al*., 2016), other phytoplankton groups (such as cryptomonads and diatoms) could also improve their performance under scenarios of extreme drought.

In our study, although the cyanobacteria have dominated throughout the eighteen months of drought, the relative abundance of slender shade-adapted cyanobacteria in codon S1 decreased in phase II and III relative to phase I, due the rise of diatoms in codon P and D, beyond green-algae in codons X1, F and J, most associated to nutrients enrichment environment (Padisák *et al*., 2009). In this way, the trajectory of phytoplankton succession in water supply reservoirs is not easy to predict, and other particular characteristics such as regional climate (rainy / dry seasons), reservoir type (size and depth), reservoir aging, watershed size and their multiple uses should be considered (Holz, 1997; Medeiros *et al*., 2015).

In addition to the species already mentioned in the diagnosis of temporal variability of phytoplankton community in Castanhão reservoir, we highlight the common frequency of *C. raciborskii* (S_N) and *Cylindrospermopsis* sp. (S_N) across the study, especially in middle and dam zones during phase I.

Cylindrospermopsis, a taxon belonging to functional group Sn, is associated to mixed environments with high temperatures (Padisák *et al*., 2009; Bonilla *et al*., 2012; Soares *et al*., 2013). Additionally, *Cylindrospermopsis* is a cyanobacteria with ability to fix nitrogen (Padisák, 1997; Molot, 2017), although this mechanism does not always seem to explain its success in water systems. In fact, *C. raciborskii* can tolerate variations in nutrient availability, being dominant under a large spectrum of trophic conditions raging from low (Moura *et al*., 2007) to high nitrogen (Chislock *et al.*, 2014; Silva and Costa, 2015) as well as from low (Bonilla *et al*., 2012; Prentice *et al*., 2015) to high phosphorous (Soares *et al*., 2013). Some studies related this large plasticity of *C. raciborskii* to the existence of ecotypes with different environmental preferences (Piccini *et al*., 2011; Bonilla *et al*., 2012). Although in the Castanhão reservoir, *C. raciborskii* and *Cylindrospermopsis* sp. were not dominant species, the highest mean density of these two species together in phase I (Supplementary Tab. 3) was mainly associated to high ammonium-N, low soluble reactive phosphorus and low Secchi depth.

Taking into account the predicted expansion of *C. raciborskii* in water systems around the world under climate-change scenarios (Bonilla *et al*., 2012), the knowledge of the temporal dynamic of this species in years of extreme drought conditions brought by the present study is a result of great relevance. Particularly to *C. raciborskii*, it is very important to know the particular conditions that lead to its high abundance in water supply reservoirs due to its potential for producing cyanotoxins (Sant'Anna *et al.*, 2008). *C. raciborskii* have been recorded as common and, in fact, dominant in many eutrophic to hypertrophic reservoirs in the Northeast of Brazil (Bouvy *et al.*, 2000; Moura *et al.*, 2007; Silva and Costa, 2015).

Last but not least in importance, we emphasize that, although the shifts in phytoplankton composition seem to be related to extrinsic effects (environmental variables) discussed here, further studies are needed to evaluate to what extent the intrinsic effects (*e.g.* predation and interspecific competition), could have also influenced the phytoplankton temporal dynamic. Indeed, both intrinsic and extrinsic effects can play a large role in phytoplankton dynamic in reservoirs (Yang *et al*., 2018).

Comparative analysis: Phytoplankton structure in 2006/2007 *versus* 2012/2013

In the first years after the complete flooding of the Castanhão reservoir (2006/2007), a previous study was performed by Molisani *et al.* (2010). Molisani *et al.* (2010) classified the system as a whole as mesotrophic based on chlorophyll *a*, Secchi depth and the total phosphorus concentrations, although the inner reservoir zone has been classified as eutrophic. The phytoplankton composition found in this previous period (2006/2007) reflected these mesotrophic/eutrophic conditions.

In turn, in the present survey, according results from Santos *et al*. (2017), the state index of the reservoir was oligotrophic in phase I and mesotrophic in the others phases. The phytoplankton composition has still indicated mesotrophic/eutrophic conditions, similar to the previous (2006/2007) study, although in phase I the reservoir was dominated by a slender cyanobacteria (*Pl. limnetica/Pl. minor*) very adapted to face phosphate-P deprivation. Both Molisani *et al.* (2010) and Santos *et al*. (2017) adopted the Trophic State Index developed by Lamparelli (2004), thereafter published by Cunha *et al.* (2013).

In both surveys, the phytoplankton biomass in the inner zone was lower than in the middle and dam zones, which is a common behavior in dam reservoirs (Kimmel *et al*., 1990). In 2006/2007, chlorophyll *a* ranged from 3.3±1.4 to 7.5±4.5 $\mu g\ L^{-1}$ (Molisani *et al.*, 2010), while in the present study from 2.9±0.5 to 5±2.1 $\mu g\ L^{-1}$. The lower values of phytoplankton biomass observed recently (2012/2013) may be related to the increase in dominance of slender cyanobacteria over other larger groups that were well represented previously (2006/2007), such as diatoms, cryptomonads and green algae. Additionally, these results agree with Kimmel and Groeger (1986) model that predict a tendency of reduction in phytoplankton production in years after the initial phase of high productivity ('trophic upsurge'), which occurs soon after reservoir filling.

Also, similar to Molisani *et al.* (2010), we used the functional group approach from Reynolds *et al*. (2002)

reviewed by Padisák *et al.* (2009) to study the phytoplankton dynamic. However, while in Molisani *et al.* (2010) the main taxa were defined as 'descriptive taxa', which are those with >5% of the total phytoplankton density (organisms L^{-1}) in at least one sample, in this present work the main taxa have been defined as 'characterizing taxa', and they were obtained by the SIMPER procedure. Despite this, adopting the same criterion, when the list of the 'descriptive taxa' of that previous study (Supplementary Tab. 4) is crossed against the list of 'characterizing taxa' used here (Tab. 1), they match well. Therefore, since similar methodologies were adopted to study the phytoplankton community, which were the Reynolds's functional group approach and a close cut-off value to define the main phytoplankton taxa that were used as indicative of environmental conditions in Castanhão reservoir, the data of both studies could be compared.

In 2006/2007 the main taxa in the inner zone were some diatoms in codons C and MP, cryptomonads in Y, and green algae in J and X1. In turn, in the present work, the same zone was dominated by slender shade-adapted cyanobacteria from the functional group S1, probably related to turbid conditions and the decrease in the availability of inorganic nutrients. Indeed, slender cyanobacteria could be more suitable than green algae, diatoms and cryptomonads to face the reduction of nutrient concentrations, especially phosphate-P (Villena and Romo, 2003; Prentice *et al.*, 2015). This drop in nutrient concentrations in years after the initial phase of reservoir filling agree with the model from Kimmel and Groeger (1986) to describe water quality changes in response to reservoir aging. As consequence of changes in nutrients and light conditions, shifts in phytoplankton composition are expected as well (Holz *et al.*, 1997).

Although water transparency (estimated by Secchi depth) have increased from 2006/2007 to 2012/2013 (in all reservoir zones), the dominance of shade-adapted cyanobacteria (S1) was an indicative that the turbidity could be still considered high for phytoplankton. This increase in water transparency could be, at least in part, also related to a decrease in the relative abundance of large phytoplankton and an increase in dominance of slender cyanobacteria. In addition, S1 is typical of mixing layers and the lower water volume in 2012/2013 may have favored this FG. It is important to note that lower depth of the reservoir could have favored short-term events of higher turbidity due to the effect of strong winds upon a dropping water column depth, which may have not be detected by Secchi data (an instantaneous measurement), but are reflected by phytoplankton community (an integrative proxy). Additionally, the role of other factors, such as changes in zooplankton structure, that direct impact on the phytoplankton size and composition (Yang *et al.*, 2018), cannot be ruled out as drivers of phytoplankton shifts in the Castanhão reservoir and should be investigated as well.

In the middle and dam zones, during 2006 / 2007 the dominance was already of cyanobacteria (Molisani *et al.*, 2010), similar to the present study. The dominance of cyanobacteria belonging to the functional groups S1 and MP, typical of mixing and turbid systems (Padisák *et al.*, 2009), persisted during 2012/2013, while the functional group Lo decreased in abundance. In fact, it is important to note the absence of *Synechocystis aquatilis* in 2012/2013, since it was an abundant species across the zones from Castanhão reservoir in 2006/2007 (Molisani *et al.*, 2010). *Synechocystis aquatilis* belongs to functional group Lo, which is adapted to both low and high nutrients (Padisák *et al.*, 2009), but is sensitive to prolonged and deep mixing (Reynolds *et al.*, 2002). In this sense, the absence of the functional group Lo between the 'characterizing taxa' in 2012/2013, along with a reduction in the reservoir water volume, is indicative of best mixing conditions in 2012/2013 than in 2006/2007, associated with reduced volume and shallower waters as suggested by Santos *et al*. (2017).

From 2006/2007 to 2012/2013 the middle and dam zones also experienced a drop in nutrient concentrations, just as happened in the inner zone. Regardless of this, it is important to take into mind that even with a decrease in nutrient concentrations and phytoplankton biomass, the system remained still mostly dominated by mesotrophic/eutrophic taxa, especially in phase III. In 2012/2013, along the drought months, the system experienced an ongoing increase in trophic state from oligotrophic to mesotrophic, resulting in the rising of the phytoplankton species more associated to a nutrient enrichment environment.

Cylindrospermopsis raciborskii (S_N), a potentially toxic cyanobacterium, was found in 2006/2007 and persisted as a frequent species in 2012/2013 in the middle and dam zones. In addition, other species have appeared, such as *Cylindrospermopsis* sp., which were absent in 2006/2007 (Molisani *et al.*, 2010). Other cyanobacteria observed in the present study and absent in 2006/2007 were *Pseudanabaena* cf. *biceps* (MP) and *Myxobaktron* sp. (X1 ?).

Finally, we highlight the replacement of the dominant diatom *Achnanthidium minutissimum* (MP) in the middle and dam zones in 2006/2007 (Molisani *et al.*, 2010) by other diatoms represented mainly by *Nitzschia* sp. (12-25 µm) (D), followed by *Aulacoseira granulata* (P) in 2012/2013. *A. minutissimum* is a species of smaller size than *A. granulata* and *Nitzschia* sp., which could indicate the more favorable mixing conditions to the diatoms of larger sizes in the middle and dam zones in 2012/2013. Indeed, according to Padisák *et al.* (2009), *A. granulata* (P) is associated to mixing layers, while *Nitzschia* sp. to shallow turbid waters.

CONCLUSIONS

Our study demonstrates that the temporal shifts in phytoplankton community in eighteen months of severe drought in a large reservoir from the Brazilian semi-arid region was associated with sub-surface phosphate-P, ammonium-N and nitrate-N concentrations, along with water transparency changes. We demonstrated a shift in phytoplankton composition, from slender cyanobacteria (S1 and MP) favored by turbid and poor phosphate-P conditions in Phase I to other slender cyanobacteria (FG ?) probably favored by increase in Secchi depth and decrease in ammonium-N in phase II. In turn, in phase III the ascension of opportunistic and fast-growing green algae (X1, F and J) were driven by the increase of phosphate-P and nitrate-N in the reservoir.

In general, although some species substitutions have occurred, especially in the inlet zone, when comparing the first years after the completing flooding of the Castanhão reservoir (2006-2007) with eight years later (2012-2013), the phytoplankton composition, with emphasis on the dominance of slender filamentous cyanobacteria, continued to indicate mesotrophic/eutrophic and turbid conditions of the system, though they have been facing the decrease in inorganic nutrients. The large dominance of functional group S1 (typical of turbid and mixing layers) in the last years was an indicative that the turbidity could still be considered high to phytoplankton, favoring the slender shade-adapted cyanobacteria, especially *Planktolyngbya limnetica*/*Pl. minor* and *Pseudanabaena limnetica*.

The dominance of cyanobacteria from the functional group S1 during most of the time in 2012/2013 was also an indicative of increase in mixing conditions in comparison to 2006/2007. On the same way, the best mixing conditions during drought years related to lower reservoir volume, was indicated by the lack of the functional group Lo between the 'characterizing taxa' in 2012/2013, along with the replacement of small diatoms (MP and C) by large diatoms belonging to functional groups D and P.

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