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Using morphofunctional characteristics as a model of phytoplankton dynamics in a tropical reservoir

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Abstract
The study of phytoplankton morphological characteristics, using the morphology-based functional classification (MBFG), reflects the different abilities for absorption of light and nutrients, growth, mechanisms for preventing sedimentation and predation in the aquatic ecosystem and can be a model in simplification of the phytoplankton community dynamics in the reservoirs. This study that was developed in a tropical reservoir aimed to evaluate which phytoplankton morphofunctional characteristics are selected by the spatial and temporal heterogeneity in the reservoir, and how these characteristics are related to the environmental conditions. For this, phytoplankton and environmental variables were sampled in different sites along the spatial extent of the reservoir during dry and rainy periods. The lotic region showed the greatest environmental dissimilarity in relation to the other regions, both in the dry and rainy periods. Differences in density of all MBFG were verified along the spatial extent of the reservoir, with higher values in the lentic region, while differences between hydrological periods were verified for MBFG I (small organisms with a high surface/volume ratio), MBFG IV (medium-sized organisms without specialized traits) and MBFG VII (large mucilaginous colonies). The conditions of pH, temperature and turbidity were important in the selection of the morphofunctional characteristics and in MBFG dynamics. Therefore, the use of MBFG can be a form of simplification of the relationship between phytoplankton and environmental heterogeneity, reflecting the reservoir functioning.

Keywords Brazil center west · Environmental heterogeneity · Impoundment · Morphology-based functional classification · Planktonic algae

1 Introduction

The biological communities distributed in the different ecosystems are fundamental, since they directly influence ecosystem functions and services (Rudman et al. 2017). However, the balance between economic development and the environmental conservation has been a challenge (Zhang et al. 2017). Freshwater ecosystems, for example, provide services of critical importance to human societies, but they are among the most heavily altered ecosystems, with an excessive loss of biodiversity (Geist 2011). Therefore, understanding the dynamics of aquatic communities is paramount in ecosystems functioning monitoring, assisting in decisions-making preservation and conservation of water resources, their biodiversity and their multiple uses.

In reservoirs, for example, understanding its functioning is essential to establish monitoring strategies and use priorities (Carneiro and Bini 2020), since these ecosystems offer different ecosystem services such as water for public supply, hydroelectric energy production, agricultural irrigation, commercial and recreational fishing, aquaculture, leisure and water sports (Tundisi 2018). In this sense, water quality monitoring strategies are extremely relevant for the management of water resources, and for guaranteeing their multiple uses, since these ecosystems can present spatial patterns (e.g., longitudinal gradients of hydrodynamics,

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light availability and nutrients), and temporal (e.g., precipitation levels) that influence its biodiversity and consequently its functioning (Kimmel et al. 1990; Nogueira et al. 1999; Stanford and Ward 2001; Tundisi and Matsumura-Tundisi 2003; Deus et al. 2013; Bianchini-Junior and Cunha-Santino 2018).

Among these strategies, the use of different taxonomic resolutions of aquatic communities has been applied as a simplification method in monitoring (Carneiro et al. 2010; Vieira et al. 2017). The idea of using higher taxonomic levels and substitute groups for biodiversity has gained prominence in scientific literature (Machado et al. 2015). For phytoplankton, for example, different methods of taxonomic simplification (e.g., functional groups) have been proposed and applied as an attempt to summarize the similar characteristics of a group of species (Salmaso et al. 2015). This community is composed by different organisms with different characteristics (e.g., morphological, physiological, behavioral and life history), forming different patterns of resource allocation, acquisition of resources, ability to inhibit processes of loss and regulation of buoyancy (Litchman and Klausmeier 2008). However, it is important to highlight that the functional groups do not intend to decimate the extent of information that can be collected from the species (Bortolini et al. 2016), but rather, compose a way of summarizing the relationships between the community and the resources available in the aquatic environment.

The phytoplankton morphofunctional characteristics, represented by the morphological based functional groups or MBFG (see Kruk et al. 2010), have been used as one of these forms of taxonomic simplification for phytoplankton and indicated in the understanding of phytoplankton dynamics in reservoirs (Beamud et al. 2015; Câmara et al. 2015; Rangel et al. 2016; Wojciechowski et al. 2017; Santana et al. 2018; Bortolini et al. 2019; Cupertino et al. 2019; Azevedo et al. 2020; Magalhães et al. 2020). MBFGs reflect different morphological descriptors (e.g., size, shape, ability to form colonies, presence of silica, flagellum) and their relationship with particular environmental conditions (Kruk et al. 2011; Kruk and Segura 2012). Thus, the frequency of certain characteristics in a community reflects a specific physiological status of the community that is part of the environmental signal (Litchman et al. 2015).

Here, we use the phytoplankton morphofunctional characteristics, represented by MBFG, as a model of the phytoplankton community dynamics and their relationship with environmental heterogeneity in a tropical reservoir. Considering the existence of different hydrodynamics and environmental conditions along the spatial extent of the reservoir and the influence of the seasonality of dry and rainy periods on these conditions, we were interested in understanding: i) which phytoplankton morphofunctional characteristics and respective MBFG are select by spatial and temporal heterogeneity and ii) how these characteristics and respective MBFG relate to the different environmental filters.

2 Material and methods

Study area and sampling sites selection – This study was carried out at the João Leite reservoir, Goiânia, Goiás, Brazil (Fig. 1), which comprises an important water supply source in the Goiás state. The region has a seasonal tropical climate, with a mean temperature for the state of 23.44 °C (Cardoso et al. 2014). The rainy period in this region is concentrated in spring and summer, between October and March, and the mean annual precipitation ranges from 1200 to 1800 mm, while the dry period occurs between May and September, with precipitation values reaching zero (Santos et al. 2010; Costa et al. 2012), draining the reservoir flow in north–south, with a maximum flow in the rainy period of 11.2 m^3 s^1 and a minimum of 4.0 m^3 s^1 in the dry period (Carneiro et al. 2010).

The João Leite reservoir is a water accumulation reservoir, with time retention of approximately 100 days, presented an area of approximately 10.4 km^2, an extension of approximately 15 km, mean width of approximately 800 m and maximum depth in the dam region of approximately 36 m (Santos et al. 2010; Carmo 2014). We established seven sampling sites along the spatial extent of the reservoir, distributed in regions with different hydrodynamics (S1—downstream; S2, S3 and S4—lacustrine; S5 and S6—intermediate; S7—lotic).

Sampling and analysis of phytoplankton samples – Sampling was performed at seven stations along the reservoir in the months of July, August and September 2018 (dry period, n = 21) and December 2018 and January and February 2019 (rainy period, n = 21). Phytoplankton samples were sample directly with bottles at the subsurface in the limnetic region of each site and fixed in situ with 1% acetic lugol (Bicudo and Menezes 2017).

Phytoplankton density was estimated using an inverted microscope (Olympus CKX41 model at 400 × magnification), with a count of 100 random fields, according to the Utermöhl (1958). The standardization of counting of the number of fields took into account that, although it is indicated to concentrate efforts on the identification of dominant species (Lund et al. 1958), the enumeration of rare organisms should not be ruled out, so that information about the specific richness is not lost to the phytoplankton community (Huszar and Giani 2007). Phytoplankton density was expressed in individuals (cells, cenobes, colonies or

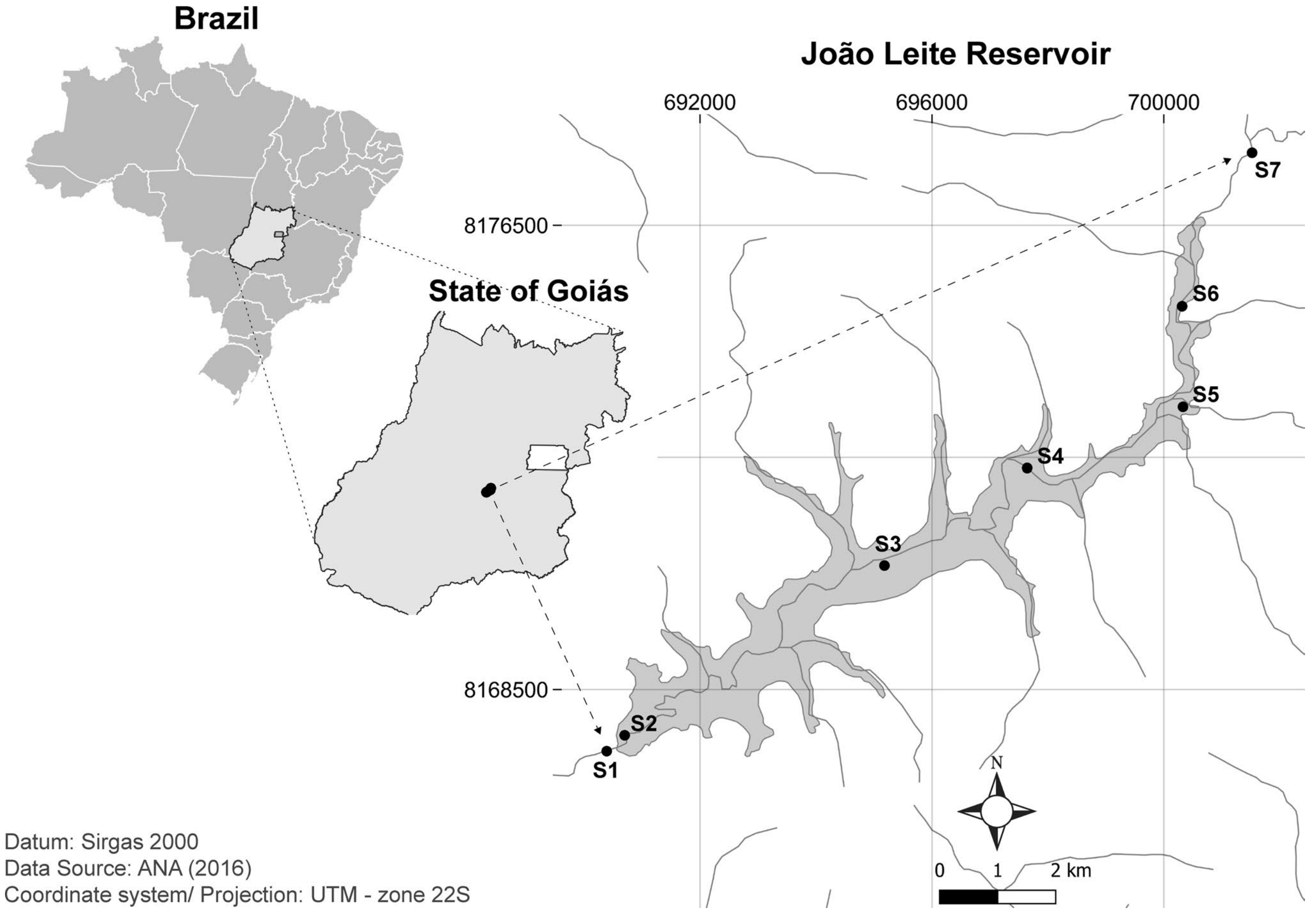


Fig. 1 Map of study area and sampling sites in the João Leite reservoir, Goiânia, Goiás, Brazil (S1—downstream; S2, S3 and S4—lacustrine; S5 and S6—intermediate; S7—lotic)

filaments) per milliliter (ind mL^{-1}), considering the forms in which cyanobacteria and algae occur in nature.

The phytoplankton taxa identified were grouped according to the morphofunctional characteristics of the seven MBFG described in Kruk et al. (2010): MBFG I—small organisms with a high surface-to-volume ratio; MBFG II—small organisms with the presence of flagellum and silica wall; MBFG III—large filamentous organisms with the presence of aerotopes; MBFG IV—medium-sized organisms with no specialized characteristics; MBFG V—single-celled organisms with the presence of flagellum; MBFG VI—organisms with siliceous exoskeleton without flagellum; and MBFG VII—large mucilaginous colonies.

Sampling and analysis of environmental filters – The data for water temperature (ºC), pH, electrical conductivity (µS cm) and turbidity (NTU) were obtained concomitantly with the phytoplankton community and were measured with portable digital potentiometers, while the dissolved oxygen (mg L^{-1}) was measured in laboratory using the titration method according to Apha (2017). Water aliquots were also sampled to perform nutrient analyses, such as nitrogen forms (nitrite, nitrate and ammonia, mg L^{-1}), total phosphorus (mg L^{-1}), total iron and soluble iron (mg L^{-1}) according to the methodology described in Apha (2017). The dissolved inorganic nitrogen (DIN, mg L^{-1}) was determined from the nitrite, nitrate and ammonia concentration (see Soares et al. 2008). Precipitation data (mm) in the reservoir area were provided by Companhia Saneamento de Goiás S/A (Saneago).

Methods of data analysis – To evaluate the influence of environmental filters along the spatial extent in the reservoir as well as between dry and rainy periods, we performed a principal component analysis (PCA). To evaluate and test the existence of significant differences in MBFG over the spatial extent of the reservoir (downstream, lacustrine, intermediate and lotic regions) as well as between hydrological periods (dry and rainy), we performed analysis of variance (*two-way* ANOVA). Finally, to investigate the relationship of MBFG with environmental filters we performed a redundancy analysis (RDA), using the MBFG density as a response variable and the environmental filters (temperature, pH, electrical conductivity, dissolved oxygen, turbidity, total phosphorus, total iron, soluble iron and dissolved inorganic nitrogen) as explanatory variables. The Hellinger transformation was applied to the response matrix, since the RDA is a linear method, in addition to reducing the effect of double zeros as similarities between locations (Boccard et al. 2011). The existence of multicollinearity between the predictor variables was examined using the variance inflation factor (VIF < 10; in this case, no collinear variables were verified, and all environmental filters were used in the RDA), and the selection of the most significant predictor variables was performed using the forward method (p < 0.05; 999 permutations). All analyses were performed using the free program R (R Development Core Team 2017) with a vegan (Oksanen et al. 2019) and ISwR (Dalgaard 2020) packages.

3 Results

Spatial extent and hydrological periods Different levels of precipitation were recorded throughout the study, with the lowest values in dry period and highest in rainy period (Fig. 2). In addition to the temporal heterogeneity of hydrological periods, we also verify an environmental heterogeneity along the spatial extent of the reservoir, according to the PCA, which explained about 57% (Fig. 3).

On axis 1 (42%), the variables of temperature (0.22), pH (0.37), turbidity (– 0.43), soluble iron (– 0.45) and total iron (– 0.47) were the main responsible for ordination. On axis 2 (14%), the variables with the greatest influence on spatial and temporal heterogeneity were temperature (0.65), electrical conductivity (0.65) and total phosphorus (– 0.58).

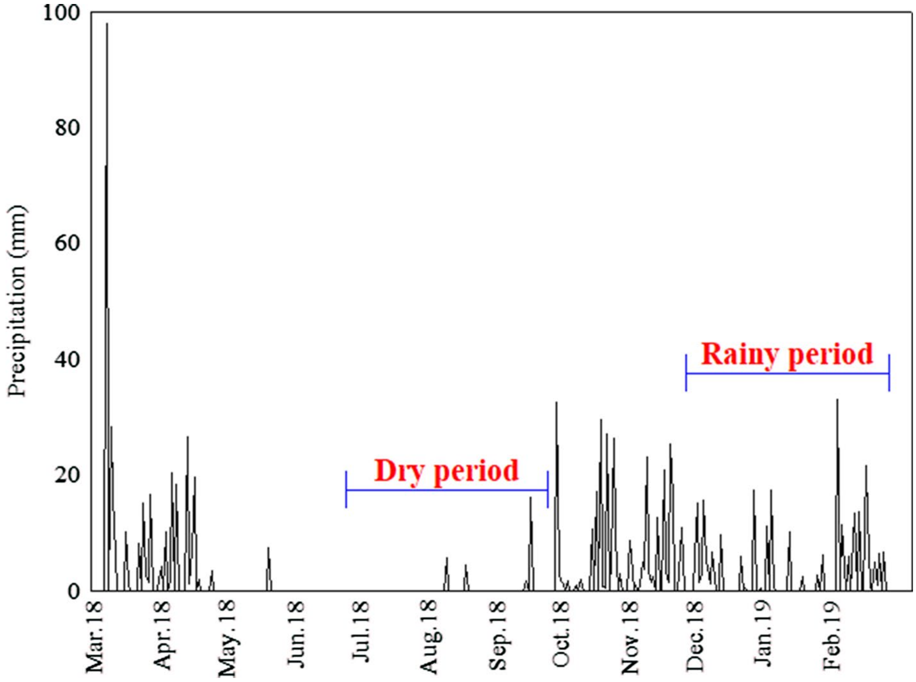
Thus, a clear separation between dry and rainy months seems to occur for the lotic and downstream sites, while for the sites in the lacustrine and intermediate regions, these differences, although exist, seem to be less pronounced.

Spatial and temporal dynamics of MBFG – All seven MBFGs were registered in our study. The spatial and temporal occurrence of each MBFG and main taxa are shown in Fig. 4. According to the space-temporal variation of the MBFG density (Fig. 5), it was possible to verify that both, dry and rainy periods, registered the higher density values in the lentic regions of the reservoir (lacustrine and intermediate), especially due to the contribution of MBFG I, IV and VII. The lowest density values were observed in the lotic region, especially in dry period, with the contribution of MBFG I and VI.

The ANOVA (Table 1) identified significant differences for the density of all MBFGs along the spatial extent of the reservoir, while differences between hydrological periods were identified only for MBFG I, IV and VI.

MBFG and the relationship with environmental filters – According to the RDA analysis (Fig. 6), the conditions of pH ($p = 0.001$), temperature ($p = 0.001$) and turbidity ($p = 0.003$) were significant filters in the MBFG dynamics in the reservoir. Thus, it was possible to verify a clear separation between dry and rainy periods, with the greater association of MBFG IV in rainy period, MBFG VII associated with

Fig. 2 Variation in precipitation levels during the hydrological cycle recorded in the study area in the João Leite reservoir, Goiás, Brazil



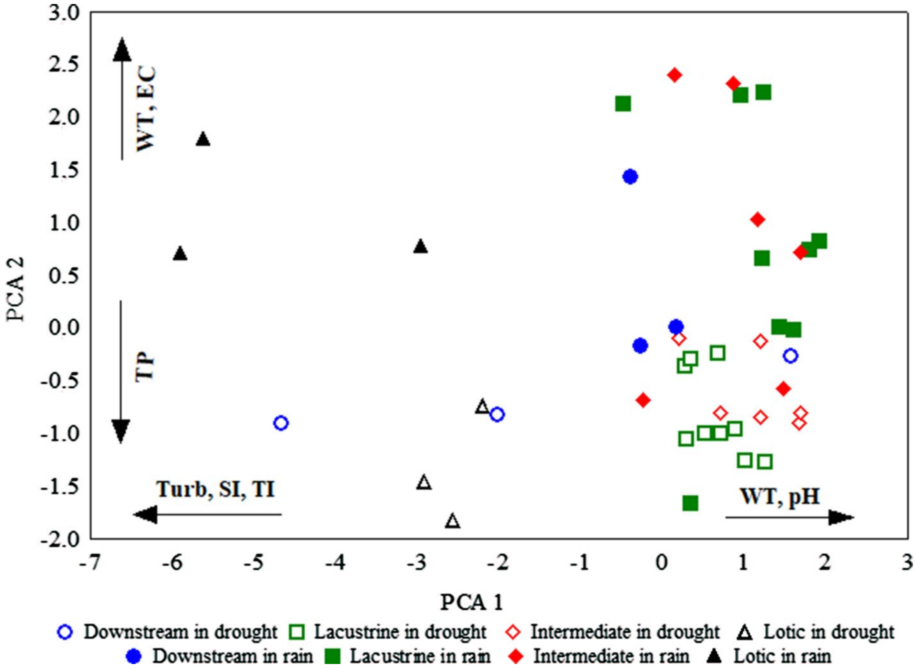


Fig. 3 Dispersion of the scores of the first two axes of the principal component analysis performed with the environmental filters measured in the João Leite reservoir, Goiás, Brazil, during dry and rainy period (WT—water temperature; pH; Turb—turbidity; SI—soluble iron; TI—total iron; EC—electrical conductivity; TP—total phosphorus)

both periods and the others MBFG associated with the dry period. Regarding the spatial extension, it was possible to detect the separation of the lotic region in rainy period, while the others regions seem to be more homogeneous in relation to the MBFG density. The RDA was significant ($R^2 = 0.33$; $p = 0.001$), as well as axis 1 (explained 21%; $p = 0.001$) and axis 2 (explained 10%; $p = 0.007$).

4 Discussion

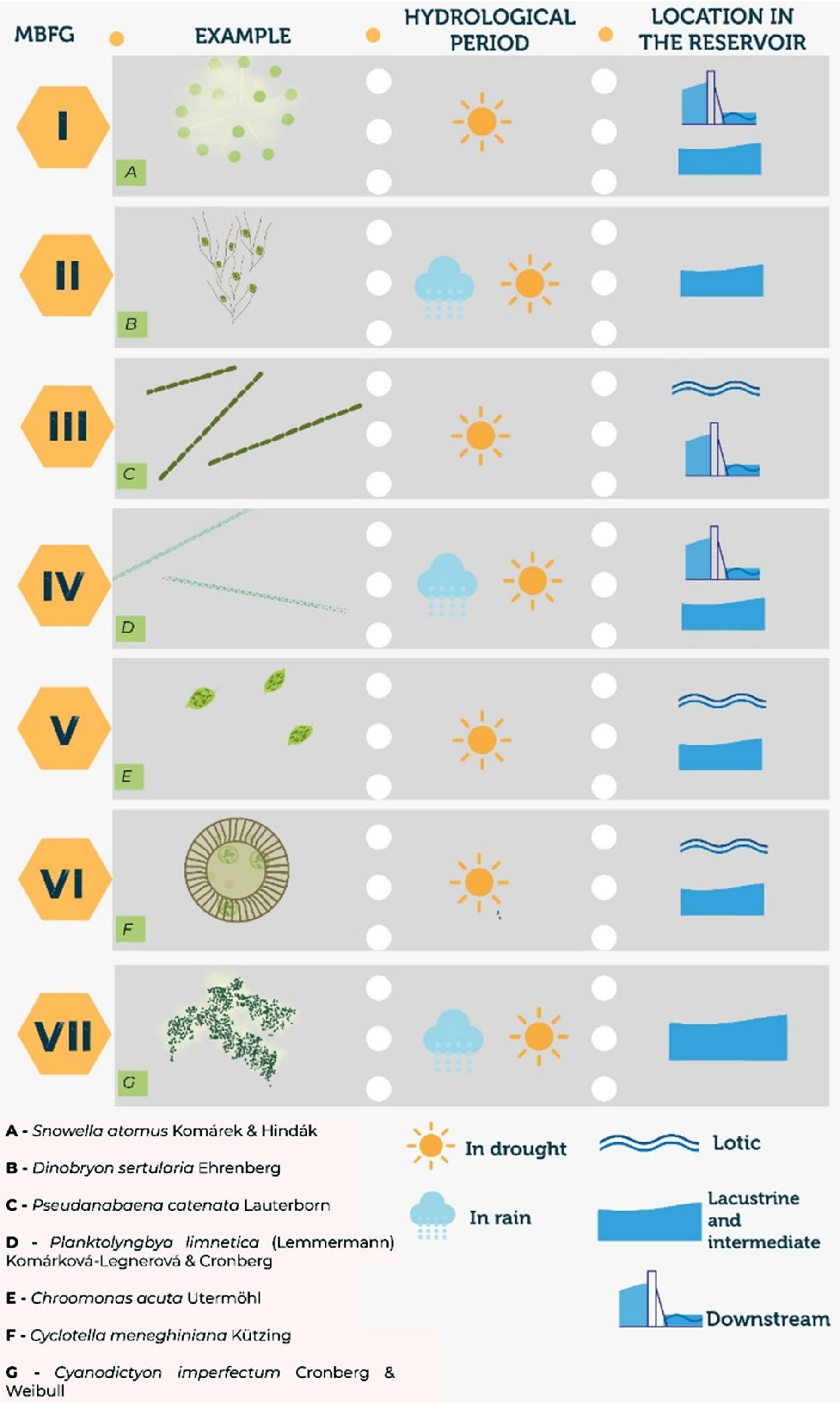
In our study, we search to understand which phytoplankton morphofunctional characteristics, represented by MBFG, are selected for spatial and temporal heterogeneity in a tropical reservoir, as well as to understand the relationship of MBFG with the environmental filters. Our results allowed, therefore, to identify the relationship between MBFG and environmental heterogeneity in the studied ecosystem. In fact, environmental conditions are crucial to the establishment of MBFG, which respond in different ways to the availability of resources according to their habitat template (Kruk and Segura 2012).

We identify a clear heterogeneity along the spatial extent of the reservoir, as well as between hydrological periods, mainly associated with turbidity, temperature, nutrient concentrations, pH and electrical conductivity. The lotic region showed the greatest environmental dissimilarity in relation to the other regions, both in the dry and rainy periods, showing the longitudinal zoning in the reservoir. Normally, these regions have a narrowed and long shape, sedimentation processes, mixing of the water column, short retention time and less light availability, hindering the development of planktonic organisms, unlike the lentic regions of the reservoir, which are wider, with less mixture, greater light availability and nutrients, as well as lentic hydrodynamics (Thornton 1990; Kimmel et al. 1990).

The distribution of the morphofunctional characteristics and the dynamics of MBFG in the reservoir was mainly related to the conditions of pH, temperature and turbidity, with a clear separation of the dry and rainy periods, as well as the lentic region (lacustrine and intermediate), which presented the greatest abundance of MBFG. In fact, the dynamic of the hydrological cycle and changes in the water level directly influence the longitudinal zoning in the reservoirs and in your phytoplankton communities (Pivato et al. 2006; Li et al. 2018; Rodrigues et al. 2018). Therefore, longitudinal processes can be a combination of different spatial and temporal factors that cause heterogeneity in physical (e.g., light available, water flow) and chemical (e.g., nutrients concentrations) processes, which in turn is reflected in biota and ecosystem functions (Nogueira et al. 1999; Tundisi 2018). In addition, the type of reservoir, in our case of accumulation, that directly influences downstream and upstream flows, as well as the high water retention time (approximately 100 days; see Straskraba (1999)), may also have contributed to the local dynamics and the development of phytoplankton organisms and MBFG selection.

MBFG I (small organisms with a high surface-to-volume ratio), MBFG IV (medium-sized organisms without specialized traits) and MBFG VII (large mucilaginous colonies) were the most representative in our study. However, MBFG I presented a decrease in its abundance in the rainy period,

Fig. 4 Relation between the MBFG, the main representative and occurrence in the hydrological period and reservoir region



unlike MBFG IV, which presented an increase in abundance, confirming the differences evidenced by the analysis of variance. It was also possible to verify temporal differences for the abundance of MBFG I, MBFG IV and MBFG VI (organisms with siliceous exoskeleton without flagellum).

In addition to temporal variability, we also found a clear spatial variability for all MBFG, with the lowest density recorded in the lotic region, and the highest in the lentic region (lacustrine and intermediate), in both hydrological periods. This variability is possibly associated with the

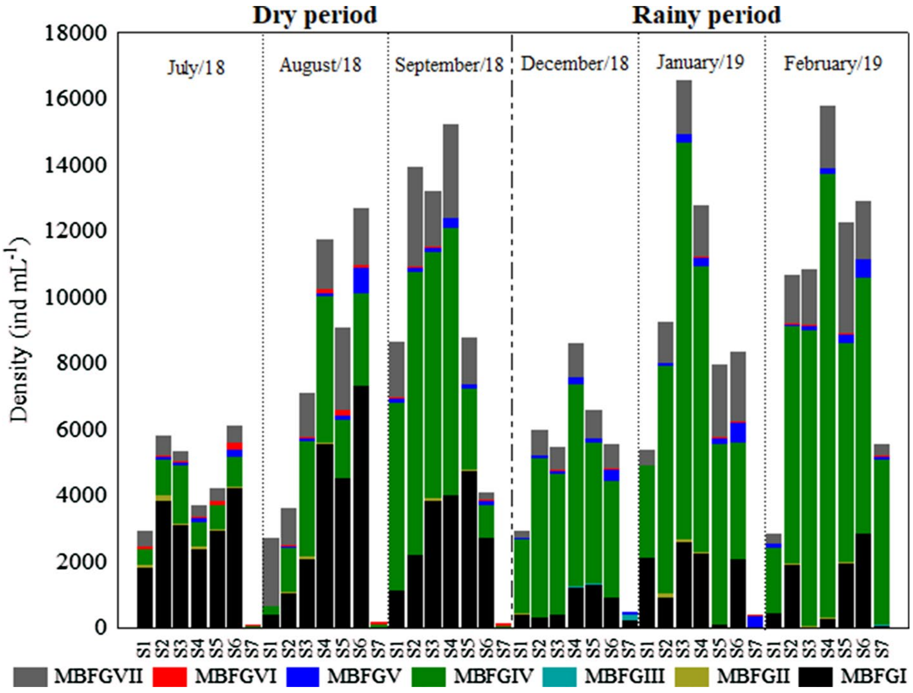


Fig. 5 Spatial and temporal occurrence of MBFG in the João Leite reservoir, Goiás, Brazil

distinct morphofunctional characteristics of the taxa and the type of dynamics (lotic and lentic), which can select organisms with the ideal traits to support the specific conditions of each site.

We recorded an important contribution of MBFG I, especially due to the high density of *Snowella atomus* Komárek & Hindák, in all regions of the reservoir, which can be explained by the low specificity of traits (Reynolds et al. 2002), and therefore the group's greater adaptability to different conditions. The organisms that make up the MBFG I are *r*-strategists (Pianka 1970; Reynolds 1988), presented high surface-to-volume ratio, high flotation capacity and high growth rate (Kruk et al. 2010). In addition, these organisms have great competitive capacity at the beginning of the temporal succession, which causes them to prevail in various trophic conditions, being phosphorus and nitrogen concentrations the most important variables explaining the distribution of group (Kruk and Segura 2012). The decrease in abundance of the group in the rainy period possibly may also be associated with the size of the organisms, which, with the greater water flow during the rain, favors the dilution of the environment and facilitates the dispersion, interfering negatively in the abundance of these organisms in the water column.

MBFG IV, represented mainly by *Planktolynbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg, presented a greater association with the rainy period, which may indicate the greater success of this group on these conditions, taking into account that this group has a positive response to changes moderate nutrients concentrations and turbidity (Kruk and Segura 2012). In addition, it was possible to verify the relationship of the group with the highest temperatures according to the RDA. In fact, the growth rate of MBFG IV organisms has been identifying as a positive response to higher temperatures (Segura et al. 2018). Despite the high contribution of *P. limnetica*, others organisms that represent the MBFG IV, such as green algae and desmids, may possibly be associated with the greater stochastic dispersion of these organisms to plankton during the rainy period, since these algae often are common components of the periphyton. Thus, green algae and desmids contributed to the abundance of MBFG in the rainy period.

MBFG VII, which had *Cyanodictyon imperfectum* Cronberg & Weibull as the main contributor in density, maintained a high density in both hydrological periods as well as along the spatial extent of the reservoir. This fact is in line with what was expected, given the larger cell size and volume of the colonies, and the low surface/volume ratio, there is the potential increase of organisms in this group in lakes with greater nutrient availability (Kruk et al. 2010; Kruk and Segura 2012). In addition, this group was associated with higher temperatures, which is consistent with the requirements for group growth rates (Segura et al. 2018).

MBFG II (small organisms with the presence of flagella and silica wall), MBFG III (large filamentous organisms with the presence of aerotopes), MBFG V (single-celled flagellate organisms) and MBFG VI (organisms with siliceous exoskeleton and without flagellum) showed lower density values in both hydrological periods and along the spatial extent of the reservoir. MBFG II is composed

Table 1 The results of ANOVA performed for MBFG in the João Leite reservoir with two levels of observation (reservoir region and hydrological periods)

	Hydrological Period			Reservoir Region			Period * Region		
	df	$F_{statistic}$	p	df	$F_{statistic}$	p	df	$F_{statistic}$	p
MBFG I	3	23.9040	**0.0000**	1	10.3670	**0.0000**	3	3.5206	**0.0252**
MBFG II	3	0.7788	0.3837	1	4.5928	**0.0083**	3	0.4102	0.7467
MBFG III	3	2.3086	0.1379	1	4.279	**0.0118**	3	4.271	**0.0113**
MBFG IV	3	14.8772	**0.0004**	1	8.5134	**0.0002**	3	1.0407	0.3870
MBFG V	3	2.44844	0.1242	1	5.2924	**0.0042**	3	0.4537	0.7164
MBFG VI	3	19.5742	**0.0000**	1	3.7086	**0.0207**	3	1.2735	0.2990
MBFG VII	3	0.0067	0.9353	1	5.7672	**0.0026**	3	1.9136	0.1459

Significant values are highlighted in bold ($p < 0.05$)

of chrysophytes, mixotrophic organisms and *r*-strategists (Pianka 1970; Reynolds 1988), and their maintenance in the water column can be favored by the relatively small size and the presence of flagella (Reynolds 1997; Kruk et al. 2010). The smallest group density can be explained by the better relationship of organisms with lower temperatures and oligotrophic environments (Kruk et al. 2010), unlike the recorded conditions in our study.

The MBFG III, composed of filamentous cyanobacteria with aerotopes, has greater resistance to sinking and has a low density both spatially and temporally, being associated with turbidity according to RDA. Studies in reservoirs have associated with the presence of the group, among other factors, to the negative relationship with turbidity (Rangel et al. 2016; Magalhães et al. 2020). The organisms of MBFG V, represented by flagellated algae, show greater motility, which together with the formation of cysts increases tolerance to conditions of lesser nutrient availability (Kruk et al. 2010). Thus, these organisms can tolerate large mixing zones with low light due to the presence of flagella, due to their moderate size and surface/volume ratio; however, they have low tolerance in warmer environments (Kruk and Segura 2012), such as in our study.

MBFG VI, represented by diatoms, also had a low contribution in density, being associated with greater turbidity, in addition to depending on re-suspension to the water column, especially in more turbulent water, due to the lack of motility and high cell density (Kruk et al. 2010). Thus, although the group had a lower density compared to the other groups, its greatest contributions occurred mainly in the lotic region, mainly by centric diatoms (e.g., *Cyclotella meneghiniana*), which explains the association of the group with the greater turbidity verified in this site. However, some registered taxa (e.g., *Achnanthidium*, *Navicula*, *Cymbella*, *Gomphonema*) can be meroplankton, since the higher flow velocity in this region of the reservoir can influence the transfer to the plankton of originally periphytic individuals. Therefore, the presence of a siliceous wall makes these organisms more resistant to water column mixing and less light availability (Reynolds 1994).

Tropical and subtropical reservoirs are subject to anthropic interference, influencing the characteristics of environment and the phytoplankton community organization (Rangel et al. 2016). In our case, although the studied reservoir comprises an important water supply source, the region suffers an intense anthropic impact, mainly due to agricultural activity, threatening the quality of the rivers that supply the reservoir (Carneiro et al. 2010), which may suggest a possible explanation for the greater contribution of some groups, such as MBFG I, III and VII, represented mainly by cyanobacteria.

Thus, it is important to consider the influence of tributaries on the formation of reservoirs, since they influence

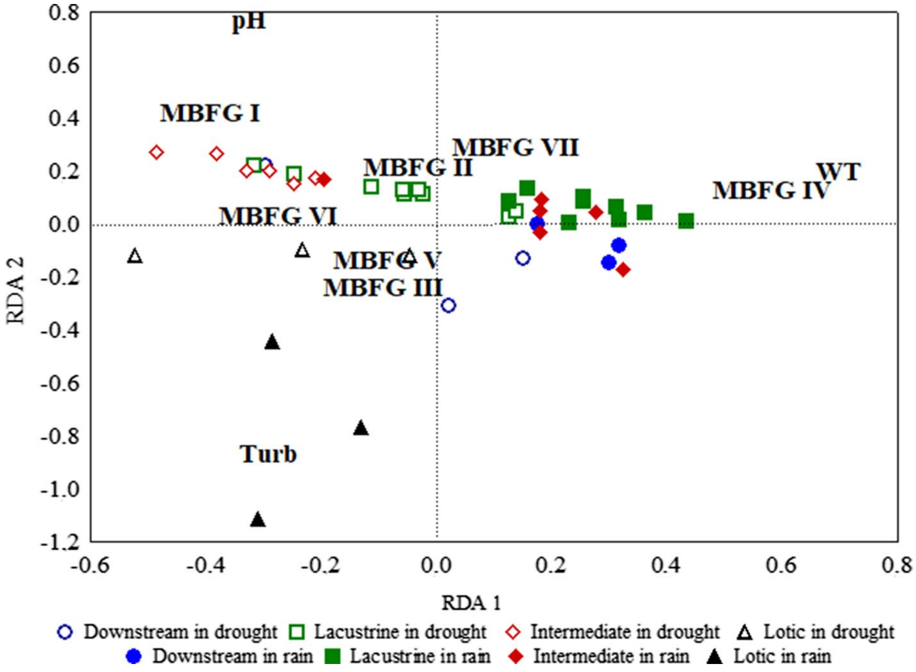


Fig. 6 Diagram of the first and second RDA axes based on the density of MBFG, and environmental filters sampled in the João Leite reservoir, Goiás, Brazil, during dry and rainy period (Turb = turbidity; WT = water temperature; pH)

the geographic, climatic and water quality characteristics (Kennedy et al. 1985). Therefore, we suggest future studies that include the assessment of tributaries that influence the studied reservoir, in order to assess the influence on the central body of the reservoir and its trophic conditions, since the degradation of the rivers that form the reservoir can influence the management of the multiple uses, mainly due to its use for public supply.

The conservation of aquatic ecosystems and the possibility of their multiple uses, such as supply, are dependent on the maintenance of environmental quality. In such a way, the understanding of the organisms' response to environmental variability helps in the understanding of the ecosystem services offered by the reservoirs and in the proposal of a sustainable exploration (Tundisi and Matsumura-Tundisi 2003). Thus, the morphofunctional characteristics grouping organisms in different MBFG have been used by several researchers, making responses to environmental conditions simpler and more objective (Bortolini et al. 2016; Lobo et al. 2018). Then, understanding the MBFG dynamics can be a form of simplification in determining the relationship between phytoplankton and environmental heterogeneity, as well as in the water quality investigation of the reservoirs.

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Author contributions RMLT and JCB contributed to conceptualization and design of study, formal analysis, visualization and writing—review and editing; CRAS was provided funding acquisition; RMLT, SMS, CAS, CRAS and JCB contributed to methodology; and RMLT was provided writing—original draft. All authors approved the final version of the manuscript.

Compliance with ethical standards

Conflict of interest Authors declare that they have no conflict of interest.

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