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ECOLOGY

Sodium and nitrate favor the steady state of cyanobacteria in a semiarid ecosystem

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ABSTRACT. This study characterized steady state events (SS) in a semiarid reservoir (Brazil) dominated by cyanobacteria for 130 weeks, and evaluated the influence of different abiotic variables on their occurrence. It was hypothesized that, in semiarid reservoirs, steady state events are independent from seasonality and influenced by high nutrient concentrations, and steady state periods show low variation of species. Our data revealed the occurrence of SS events in both the dry and wet seasons. Higher concentrations of nitrate and sodium together with higher values of color favored the development of SS. Species composing the SS dominated by *Microcystis aeruginosa* (Kützing) Kützing was correlated with higher sulfate concentrations, while higher values of turbidity and sodium concentrations favored the SS of *Cylindrospermopsis raciborskii* (Woloszynska) Seenaya and Suba Raju and *Planktothrix agardhii* (Gomont) Anagnostidis and Komárek. The results supported the hypothesis and showed the importance of variables rarely evaluated in works of this nature, such as sodium and sulfate in SS establishment of cyanobacteria.

Keywords: Abiotic variables; Driving force; Equilibrium phase; Phytoplankton; Tropical ecosystems

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Introduction

Depending on the abiotic conditions, some dominant species in the environment may not show a significant variation in biomass within a time interval, constituting a steady state event, regulated by the production and loss of biomass in a balanced manner (Rojo & Álvarez-Cobelas, 2003; Teubner et al., 2003; Hui, Xie, Guo, Chu, & Liu, 2014). In accordance with Sommer, Padisák, Reynolds, and Juhász-Nagy (1993), criteria for identification of steady state phases in natural systems are: up to three species contributing with, at least, 80% total biomass for over two weeks without significant variation in total biomass.

In tropical environments, temperatures are high, but with small annual range compared to temperate environments (Komárková & Tavera, 2003). Because of its relative stability, it is assumed that the steady state is more likely to occur at lower latitudes environments (Becker, Huszar, Naselli-Flores, & Padisák, 2008; Baptista & Nixdorf, 2014). Steady state has been reported in tropical ecosystems in drier seasons, when higher thermal stability is observed. During rainy periods, there may be disturbances in the water column and avoid the steady state maintenance (Sutherland, Turnbull, & Craggs, 2017; Havens, Beaver, Fulton III, & Teacher, 2019).

Long steady state events have been reported in studies conducted in tropical ecosystems, which report that the steady state phases are typically dominated by high biomass of a single species, commonly *Microcystis aeruginosa* (Kützing) Kützing and species of the order Nostocales, especially *Cylindrospermopsis raciborskii* (Woloszynska) Seenaya and Suba Raju (Komárková & Tavera, 2003; Rojo & Álvarez-Cobelas, 2003).

In tropical zones, semiarid regions cover a large area and possess a peculiar climate dynamics. The Northeast Brazil, for example, is characterized by a semiarid climate, where it is observed water shortage, high temperatures, high water residence time, and artificial eutrophication, with rainfall concentrated in about three months and the remaining months comprise the dry season (Moura, Tavares, & Amorim, 2018). In this way, in semiarid environments, it would be expected longer steady state events.

Despite these traits, studies in semiarid regions addressing the occurrence of steady state, considering all the pre-requisites established by Sommer et al. (1993), are scarce. Instead, authors have attempted to explain the factors leading to the dominance and persistence of phytoplankton species in these ecosystems, carrying out studies with monthly samplings (Moura, Oliveira, Dantas, & Arruda-Neto, 2007; Dantas, Moura, & Oliveira, 2011; Tavares, Moura, & Dantas, 2017), so it is not possible to apply the concept of steady state in these studies.

Studies focusing on the dominance and persistence of cyanobacteria are common in the Northeastern Brazil. Authors have pointed out the trophic level to explain the persistence of cyanobacteria in these semiarid ecosystems. Bouvy, Falcão, Marinho, Pagano, and Moura (2000) analyzed 39 reservoirs in Brazilian semiarid ecosystems and noted that *C. raciborskii* corresponded to deeper, warmer and hypertrophic reservoirs characterized by the combination of nutrient concentrations, high temperature, thermal stability and pH values. Volume reduction, water column stability and long water retention time in the reservoirs combined with drought would have created excellent conditions of temperature and irradiation for the dominance of *Cylindrospermopsis* sp. Studies carried out by Tavares et al. (2017) also showed that the high nutrient concentrations (nitrate, nitrite and orthophosphate) influenced persistence of *C. raciborskii* throughout the study in semiarid reservoirs in Brazil.

Conversely, *C. raciborskii* persistence has also been reported under P-limited conditions, shallowness and low water column transparency (Henemmann & Petrucio, 2016) as well under N-limited conditions, since this is a species able to fix atmospheric nitrogen (Chellappa, Borba, & Rocha, 2008). Studies have reported that reservoirs located in the Brazilian semiarid region, characterized by high trophic levels, phosphorus and nitrogen concentrations, temperatures and water retention time; low turbulence and pH alkaline did not present dominance or persistence of cyanobacterial species (Barbosa et al., 2012). Persistence of cyanobacterial species in eutrophic, oligotrophic, and mesotrophic reservoirs is often related (Chellappa et al., 2008, Okello, Ostermaier, Portmann, Gademann, & Kurmayer, 2010; Fonseca, Vieira, Kujibida, & Costa, 2015), suggesting that eutrophication level is not the solely responsible for steady state events.

Climatic variables are also used to assess the persistence of cyanobacterial species. In semiarid ecosystems, dry climate favors evaporation and decrease the reservoir volume and should lead to dominance of cyanobacteria species (Bowling et al., 2013; Braga et al., 2015), and could contribute to the steady state in dry seasons (Naselli-Flores, Barone, Chorus, & Kurmayer, 2007). Water level rise can lead to a reduction in the biomass of filamentous cyanobacteria and a dilution of *M. aeruginosa* colonies (Li et al., 2018), probably due to disturbance of the water column or changes in the concentration of nutrients dissolved in water, compromising the persistence of cyanobacteria (Bakker & Hilt, 2016). However, several studies have shown that in semiarid ecosystems, it is common to observe persistence of cyanobacteria throughout the year (Moura et al., 2007; Dantas et al., 2011), suggesting that seasonality and stability have less influence than in other ecosystems.

It is noteworthy that the studies that aim to relate climatic variables to cyanobacteria, often consider air temperature and rainfall. Nevertheless, other climatic variables should also exert influence, such as wind, humidity and air speed. According to Bouvy, Molica, Oliveira, Marinho, and Becker (1999), the fluctuating nutrient supply, probably associated with sediment resuspension by wind in shallow waterbodies, is an advantageous factor for cyanobacteria.

The growth and dominance of phytoplankton species in reservoirs are controlled by a complex combination of physical and chemical factors, acting synergistically (Huszar, Kruk, & Caraco, 2003; Çelik & Ongun, 2008). Therefore, it is expected that other abiotic variables, besides rainfall, phosphorus and nitrogen, are involved in establishing the steady state of cyanobacterial species. Considering this scenario, the influence of other variables not included in other studies, such as micronutrients and other macronutrients, besides nitrogen and phosphorus, should be considered. According to Du, Creed, Sorichetti, and Trick (2019), lake managers concerned with the persistence of cyanobacteria should incorporate sampling for trace metals, such as Fe (iron), and other micronutrients into routine sampling campaigns. Studies have shown that micronutrients are required for essential metabolic functions in photosynthetic electron transport, respiratory electron transport, nitrate and nitrite reduction, sulfate reduction, nitrogen fixation, and detoxification of reactive oxygen species (Sorichetti, Creed, & Trick, 2016; Zhang et al., 2019), which could help to understand the growth and persistence of some species of cyanobacteria.

In this way, the present study hypothesized that in semiarid reservoirs steady state events are independent from seasonality and influenced by other nutrients besides nitrogen and phosphorus. Thus, aiming to better understand how cyanobacteria establish steady state in semiarid regions, this study evaluated the influence of rainfall, nitrogen, phosphorous and other thirteen abiotic variables in a semiarid, eutrophic ecosystem from Northeast of Brazil dominated by cyanobacteria.

Material and methods

Study area

Pedro Moura Júnior (8°20'9''S, 36°25'28''W) is a eutrophic reservoir located in the municipality of Belo Jardim (Northeast of Brazil) and is part of the Ipojuca River basin, one of the largest in the region. It is responsible for the supply of approximately 80,000 inhabitants, and has a maximum accumulation volume of 30,740,000 m^3 and an average depth of 14 m. The climate of the region is semiarid (Alvares, Stape, Sentelhas, Gonçalves, & Sparovek, 2013) with rainfall concentrated between March and August. During the study, the average rainfall in the dry and rainy periods was 43.5 mm and 203.4 mm, respectively, and the average monthly air temperature ranged from 23.0°C to 24.2°C.

Sampling procedures and laboratory analysis

Water samples were taken weekly between July 2014 and December 2016 in the limnetic region of the reservoir for 130 monitoring weeks. Phytoplankton samples were collected in duplicate for qualitative and quantitative analysis under the water surface of the reservoir (approximately 30 cm depth), around 11 a.m., due to the higher intensity of sunlight, and then preserved and stored according to American Public Health Association (APHA, 2012). Samples were not taken at other depths, due to the absence of thermal stratification in the reservoir throughout the study period.

Cyanobacteria were identified to the lowest possible taxa, according to the literature (Komárek & Anagnostidis, 1989; 1999; 2005; Komárek & Cronberg, 2001). Other phytoplankton groups did not show significant biomass in this ecosystem, compared to cyanobacteria, and were identified to the genus level, according to Bicudo and Menezes (2006).

Phytoplankton density (cells. mL^{-1}) was determined following the methodology described in APHA (2012), using Sedgewick-Rafter counting chambers and optical microscope (Leica, Germany). Species biomass (mm^3 L^{-1}) was calculated from the cell biovolume values (n = 30), based on Hillebrand, Dürselen, Kirschtel, Pollingher, and Zohary (1999).

All parameters were analyzed in the laboratory. Values of turbidity (NTU), color (UC) and pH were obtained from measurements with turbidimeter (Hach, USA), colorimeter (Hach, USA) and potentiometer (Digimed, Brazil), respectively.

Measurements of conductivity (mS cm^{-1}), alkalinity (mmol L^{-1} $CaCO_3$), calcium (mmol L^{-1}), magnesium (mmol L^{-1}), sodium (mmol L^{-1}), potassium (mmol L^{-1}) chloride (mmol L^{-1}), sulfate (μmol L^{-1}), ammonia (mmol L^{-1}), nitrate (mmol L^{-1}) and phosphate (mmol L^{-1}) were made according to APHA (2012).

Data of air temperature (°C) and rainfall (mm) were obtained from the *Instituto Nacional de Pesquisas Espaciais* (INPE) and the *Agência Pernambucana de Águas e Clima* (APAC), respectively. Data were obtained from a research station located about 2 km from the sampling sites.

Data analysis

Analytical periods were defined as non-steady state (nSS) and steady state (SS) according to the criteria defined by Sommer et al. (1993). The SS periods were divided based on the cyanobacteria species forming the steady-state. The biotic matrix was only made up by organisms at SS, whose biomass values were transformed into log (x + 1). All values of abiotic parameters were standardized. Species other than cyanobacteria were not included in the analysis because they did not present any steady state events during the study.

In order to test the significance of differences ($p < 0.05$) in biotic and abiotic parameters between nSS and SS periods, t-test was applied. To test the significance of differences ($p < 0.05$) in biotic and abiotic parameters between SS periods, one-way ANOVA followed by Tukey's test was performed. Data sets were tested prior to t-test and ANOVA for compliance with the assumptions of parametric statistics. The Kolmogorov-Smirnov test and the Bartlett test were used to assess normality of the data and the homogeneity of data variance, respectively.

In order to analyze the correlation between rainfall and presence or absence of SS ($p < 0.05$), Spearman test was utilized. The Shapiro-Wilk normality test was used to assess normality of the data.

Detrended Correspondence Analysis (DCA) was run using the biotic matrix to choose the best multivariate analysis to evaluate the influence of abiotic variables on the biotic variables. The length of the first DCA axis < 3 S.D. indicated homogeneous dataset for which linear methods (Redundancy Analysis - RDA) are suitable.

Two RDA, for different purposes, were performed. The first one included all sampling units and categorized them into SS and nSS periods. Conversely, in the second RDA, only the sampling units, in which there has been at least one steady state event, were chosen. These sampling units were categorized according to the SS forming species.

To create an efficient model from the most significant explanatory variables, the ordistep function was applied for selection of variables for both RDA. This procedure led to the exclusion of collinear variables that presented ⩾20% inflation. All the dataset was analyzed using the software R version 3.1.1 (R Core Tean, 2014).

Results

Phytoplankton community and characterization of SS periods

Pedro Moura Júnior Reservoir presented dominance of cyanobacteria throughout the study period, with total biomass values above 1.0 $mm^3 L^{-1}$ (mean: 34.3 ± 69.4 $mm^3 L^{-1}$).

During the study, the phytoplankton community was composed of 17 taxa belonging to the classes Cyanobacteria (35%), Chlorophyceae (35%) and Bacillariophyceae (30%). During monitoring, six species of cyanobacteria were identified: *C. raciborskii*, *Planktothrix agardhii* (Gomont) Anagnostidis and Komárek, *Geitlerinema amphibium* (C. Agardh ex Gomont) Anagnostidis, *M. aeruginosa*, *Aphanizomenon gracile* (Lemmermann) Lemmermann and *Merismopedia tenuissima* Lemmermann.

Eleven events fully met the requirements for maintenance of SS. Out of the 130 studied weeks, steady state events were observed in 47 weeks (36%), alternately. SS events were divided into periods I to XI, wherein: I (weeks 7 to 9), II (weeks 10 to 12), III (weeks 15 to 19), IV (weeks 23 to 33), V (weeks 43 to 47), VI (weeks 83 to 85) and VII (weeks 94 to 96), VIII (weeks 99 to 102), IX (weeks 114 to 116), X (weeks 121 to 124) and XI (weeks 125 to 127) (Figure 1A).

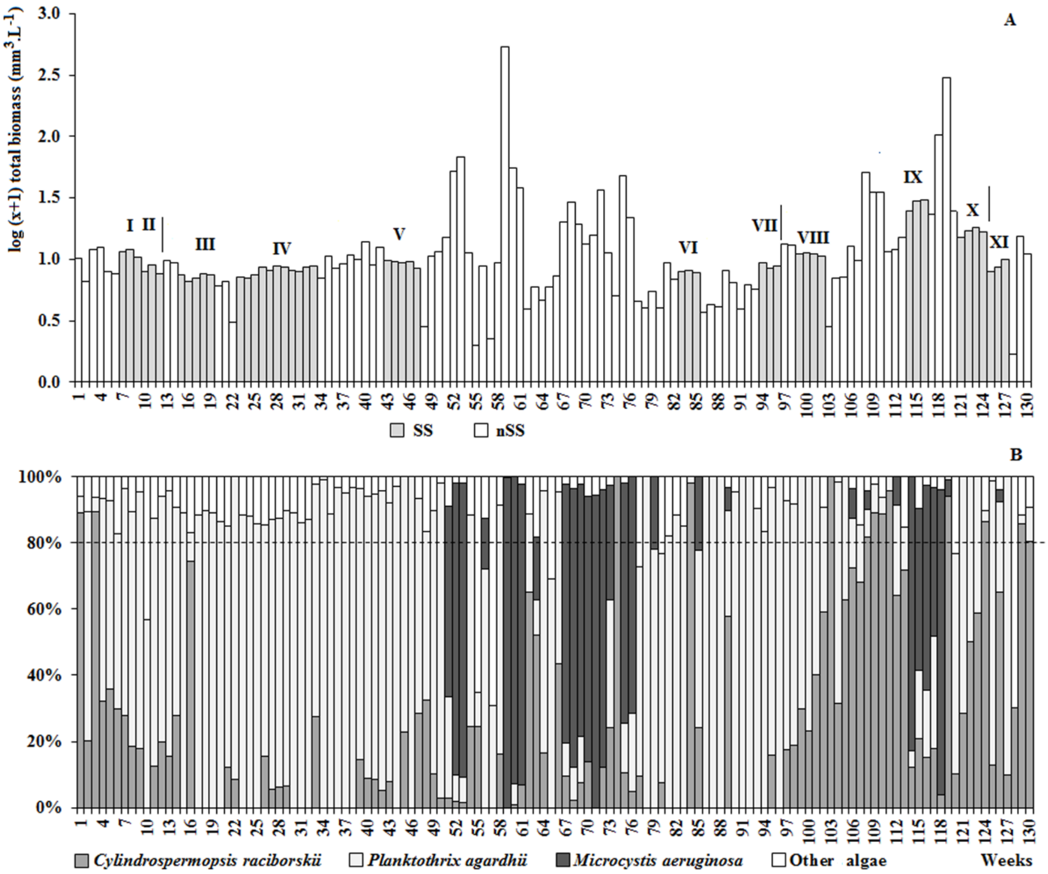

Figure 1. A – Variation in total phytoplankton biomass; B - Contribution to the biomass (%) of taxa forming the steady state in relation to the total phytoplankton biomass in the Pedro Moura Jr. Reservoir, State of Pernambuco, Brazil. SS - steady states; nSS - periods without steady state; I-XI – steady state periods

There was no correlation between rainfall and SS occurrence (*S*=1759, RHO=-0.14, $p > 0.05$). Then, SS events occurred both in drier and rainy periods (Figure 2). The SS length varied between 3 and 11 weeks (mean = 4.3 ± 2.4 weeks), and there was no significant difference in the duration between the drier and rainy periods (T = 1.1, $p > 0.05$). SS events were alternated with nSS periods, that lasted, on average, 8.4 ± 10.2 weeks.

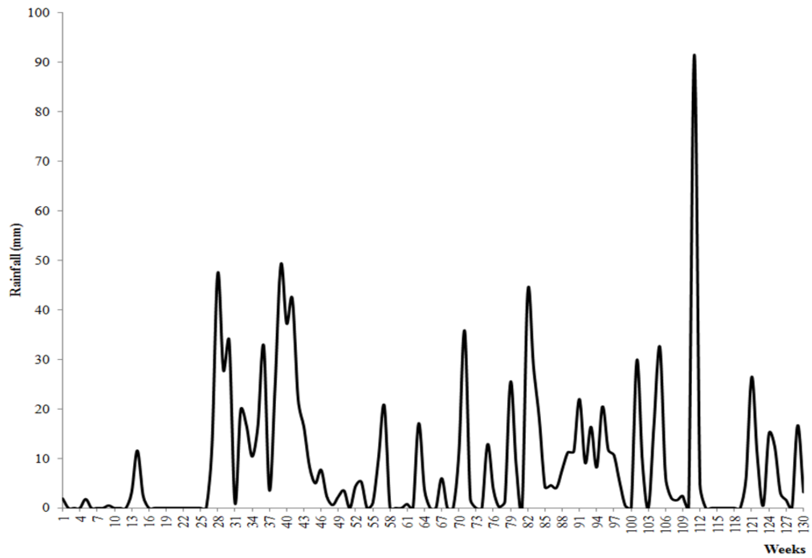

Figure 2. Rainfall variation in the municipality of Belo Jardim (State of Pernambuco, Brazil) between October 2013 and March 2016

Of the SS periods observed, three had *P. agardhii* as the only species with biomass above 80% total biomass (IV, V and VII). In seven periods, two species amounted to 80% total biomass (*P. agardhii* and *C. raciborskii*), showing dominance of *P. agardhii* (I, II, III and VIII), dominance of *C. raciborskii* (X and XI) and co-dominance of these species (VI). In period IX, three species together amounted to 80% total biomass (*P. agardhii, C. raciborskii* and *M. aeruginosa*), with dominance of the colonial species (Figure 1B). Periods of heavy rainfall coincided with steady state of only *P. agardhii*, while, in other periods, the average volume of rainfall were lower (Table 1).

Abiotic characterization

Throughout the study period, the ecosystem showed neutral-alkaline water with high conductivity (> 1.5 mS cm^{-1}), chloride concentrations higher than 1.7 mmol L^{-1} and ammonium around 0.05 mmol L^{-1}.

The SS period, compared to nSS period, showed significantly higher values of color and turbidity, higher concentrations of hardness, magnesium, sodium and nitrate, and lower concentrations of sulfate (Table 1).

Of all the abiotic parameters, color, calcium and ammonia showed no significant difference between the SS periods. The SS periods with co-dominance between *P. agardhii* and *C. raciborskii* exhibited significant difference in pH, conductivity, hardness, magnesium and sulfate, occurring in circumneutral samples, with lower values of conductivity and higher concentrations of hardness, magnesium and sulfate (Table 1).

Relationship between abiotic and biotic factors

Figure 3 illustrates the RDA with all 130 samples analyzed, where it is possible to observe the relationship between environment variables and the species with at least one steady state event during the study (*P. agardhii, C. raciborskii* and *M. aeruginosa*). Eigenvalues of axes 1 and 2 explained 26.4% variation of biological data, of which 80% on the axis 1 and 17% on the axis 2. Both axes were significant to explain the relationship between abiotic and biotic variables ($p = 0.005$). The sampling units that showed SS were negatively correlated with the axis 1. The nSS samples showed heterogeneous distribution with respect to this axis. The variables sodium (-0.38), nitrate (-0.62) and color (-0.77) were negatively correlated with axis 1, while sulfate (0.44) showed a direct correlation. Greater concentrations of nitrate and sodium and higher values of color and turbidity favored the development of SS periods dominated by *P. agardhii. M. aeruginosa* was correlated to the nSS periods and was favored by higher sulfate concentrations. Finally, *C. raciborskii* species showed no correlation with nSS or SS periods, maintaining high biomasses throughout the study period, but not necessarily reaching a steady state.

Table 1. Mean values of abiotic variables in periods of steady state (SS) and non-steady state. (nSS) in Pedro Moura Jr. reservoir between October 2013 and March 2016. PA – *Planktothrix agardhii*; CR – *Cylindrospermopsis raciborskii*; MA – *Microcystis aeruginosa*. Underlined abbreviation indicates the dominant species.

Variables	Periods					
	SS					nSS
	<u>PA</u>+CR	PA	PA+CR	<u>MA</u>+PA+CR	<u>CR</u>+PA	
pH	7.75±0.08^{bc}	7.69±0.08^{b}	7.00±0.00^{a}	7.87±0.15^{c}	7.70±0.05^{b}	7.80±0.30
Conductivity (mS cm^{-1})	1.89±0.18^{b}	1.91±0.29^{bc}	1.39±0.07^{a}	2.07±0.02^{c}	2.07±0.065^{c}	1.66±0.34
Turbidity (uT)[§]	7.3±2.4^{b}	6.7±2.7^{b}	7.4±0.5^{b}	2.7±0.2^{a}	1.6±0.3^{a}	12.1±3.3
Colour (uH)[§]	91±7^{a}	96±10^{a}	99±5^{a}	89±1^{a}	95±3^{a}	110±16
Alkalinity (mmol L^{-1})	0.11±0.1^{bc}	0.10±0.20^{ab}	0.10±0.03^{a}	0.12±0.01^{c}	0.10±0.05^{ab}	0.13±0.07
Calcium (mmol L^{-1})	0.13±0.02^{a}	0.14±0.02^{a}	0.16±0.4^{a}	1.43±0.7^{a}	0.15±0.9^{a}	0.17±0.04
Magnesium (mmol L^{-1}) [§]	0.32±0.01^{a}	0.33±0.03^{ab}	0.05±0.01^{c}	0.35±0.17^{b}	0.35±0.09^{ab}	0.37±0.15
Sodium (mmol L^{-1}) [§]	1.00±0.05^{a}	1.06±0.03^{ab}	1.08±0.01^{b}	1.08±0.04^{b}	1.06±0.03^{ab}	1.55±0.82
Potassium (mmol L^{-1})	0.08±0.03^{b}	0.04±0.03^{ab}	0.06±0.01^{ab}	0.02±0.02^{a}	0.02±0.01^{a}	0.08±0.05
Chlorides (mmol L^{-1})	1.78±0.37^{a}	2.16±0.49^{ab}	2.62±0.05^{b}	2.46±0.93^{b}	2.47±0.01^{b}	1.88±0.44
Sulfate (µmol L^{-1}) [§]	4.1±5.3^{a}	6.1±8.4^{a}	37.7±3.7^{b}	3.1±0.1^{a}	2.7±0.3^{a}	30.2±18.3
Ammonia (mmol L^{-1})	0.07±0.03^{a}	0.06±0.04^{a}	0.06±0.02^{a}	0.11±0.02^{a}	0.04±0.01^{a}	0.04±0.03
Nitrate (mmol L^{-1}) [§]	0.05±0.03^{ab}	0.08±0.04^{b}	0.07±0.00^{b}	0.00±0.00^{a}	0.06±0.06^{ab}	0.03±0.02
Phosphate (mmol L^{-1}) [§]	0.25±0.07^{b}	0.17±0.06^{ab}	0.11±0.01^{a}	0.14±0.03^{a}	0.18±0.02^{ab}	0.13±0.09
Rainfall (mm)	4±8^{ab}	17±21^{ab}	32±24^{b}	0±0^{a}	17±15^{ab}	13±20

Means followed by different letters in the same row are significantly different ($p > 0.05$; Tukey test); [†]T-test comparing means between nSS and SS periods; [‡]Analysis of variance (one way ANOVA) followed by Tukey's test between SS periods; [§]Significant difference between nSS and SS periods ($p < 0.05$, t-test)

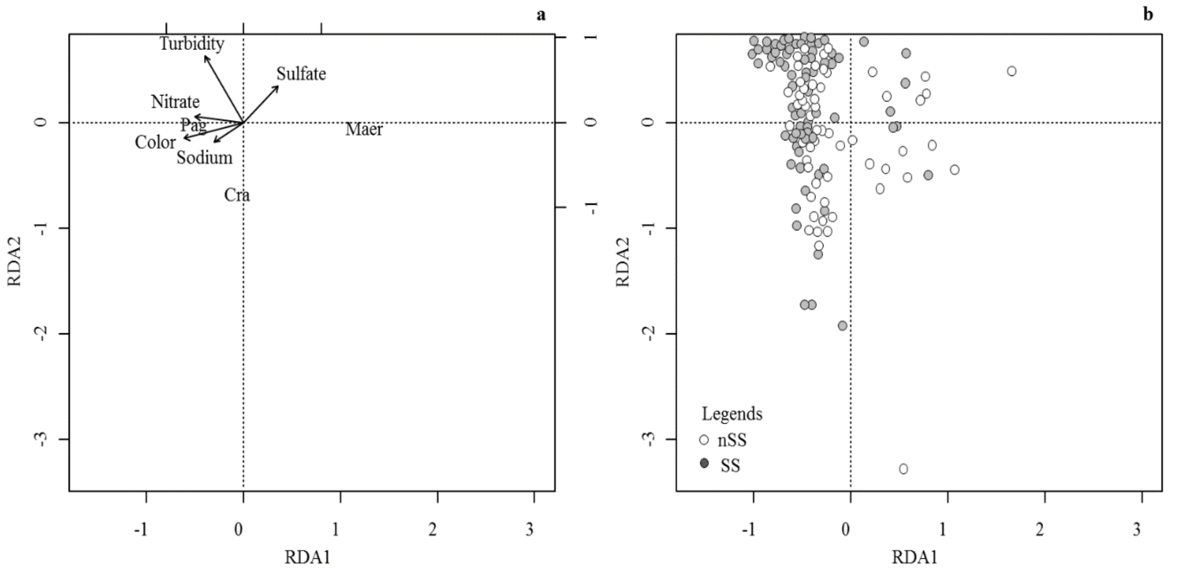

Figure 3. RDA analysis for biotic and abiotic components throughout the study period in the Pedro Moura Jr. Reservoir, State of Pernambuco, Brazil. Cra: *Cylindrospermopsis raciborskii*; Pag: *Planktothrix agardhii*; Maer: *Microcystis aeruginosa;* nSS: periods without steady state; SS: steady state periods

Figure 4 shows the relationship between environmental and biological variables only during SS periods. Eigenvalues of axes 1 and 2 explained 33.6% variation of biological data, of which 77.5% on the axis 1 and 22.0% on the axis 2. Both axes were significant to explain the relationship between abiotic and biotic variables ($p = 0.005$). Sampling units showing steady state of *M. aeruginosa* were negatively correlated with axis 1, whereas those presenting steady state of *P. agardhii* and/or *C. raciborskii* were positively correlated. The variables sodium (0.94) and turbidity (0.38) were positively correlated with axis 1, while sulfate (-0.85) showed an inverse relationship. Steady state of *M. aeruginosa* was correlated with waters with higher sulfate concentrations. Higher turbidity values and sodium concentrations favored steady state of filamentous species.

The second axis was divided according to the species of filamentous cyanobacteria with the highest contribution in biomass to the steady state. The samples, in which *P. agardhii* showed over 80% total biomass, and samples in which the sum of biomass of *P. agardhii* and *C. raciborskii* reached 80% total biomass, but there was dominance of *P. agardhii*, were positively correlated. In turn, the samples in which *C. raciborskii* was the only species at steady state and the sample in which the sum of biomass of *P. agardhii* and *C. raciborskii* reached 80% total biomass, but showed dominance of *C. raciborskii,* presented an inverse relationship with axis 2. Turbidity (0.94) was positively associated with axis 2 and contributed to the steady state phases with the highest percentage in biomass of *P. agardhii*.

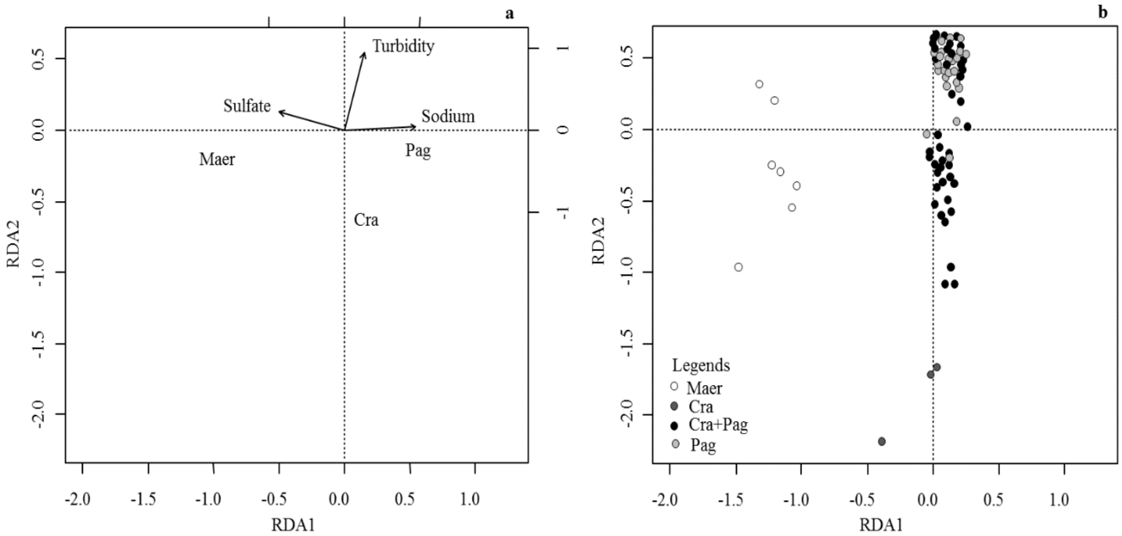

Figure 4. RDA analysis for biotic and abiotic components during the steady state phases in the Pedro Moura Jr. Reservoir, state of Pernambuco, Brazil. Cra: *Cylindrospermopsis raciborskii;* Pag: *Planktothrix agardhii;* Maer: *Microcystis aeruginosa*

Discussion

Throughout the study period, dominance of cyanobacteria was observed, especially *P. agardhii* and *C. racibrorskii*; however, in only 36% of the weeks, the steady state assumptions, according to Sommer et al. (1993), were completely met. The results also showed short SS periods, lasting, on average, four weeks and occurred in both drier and rainy periods with no difference over time.

Nitrate, color, turbidity and sodium were related to SS periods, while sulfate was related to nSS periods. Our results showed that *P. agardhii* (Oscillatoriales) was related to the SS periods and its biomass was directly related to darker water color and more turbid samples.

Nitrogen is a macronutrient that participates in the formation of various organic molecules, such as proteins and nucleic acids. This nutrient can be absorbed in various chemical forms, including nitrate. In non-nitrogen fixing cyanobacteria, such as *P. agardhii*, nitrate is required for activation of nitrate reductase that catalyzes the conversion of nitrate to ammonium and glutamine, which participates in the construction of amino acids and proteins (Jha, Ali, & Raghuram, 2007). As reported by Von Rückert and Giani (2004), nitrate serves as a long-term nitrogen storage reservoir and this may explain its relationship with the persistence of the high biomass of *P. agardhii* during SS periods.

Studies carried out by Kim, Jo, and Kim (2017) on *M. aeruginosa* show that its growth is affected by nitrate, mainly if a certain minimum PO_4^{3-} concentration is present. Besides, as this species grows in less turbid waters, it moves towards the high-intensity light at the surface, using its gas vacuole, and thereby generates blooms. *M. aeruginosa* recovers its buoyancy more quickly when the nitrate concentration is higher. However, our results detected a negative relationship between this species and nitrate concentrations, corroborating Von Rückert and Giani (2004). According to these authors, under low nitrate concentrations, there is dominance of non nitrogen-fixing species, like *Microcystis* species. They observed *Microcystis* blooms when ammonium concentrations are very high and nitrate not detectable.

Color and turbidity may influence the growth of phytoplankton species, regulating, mainly, the light input and the extension of the euphotic zone, necessary for photosynthetic reactions. Studies suggest that increases in water color favor low-light-adapted phytoplankton species, such as *Nostocales* and *Oscillatoriales*, because of efficient light harvesting systems and buoyancy regulation (Lebret, Langenheder, Colinas, Östman, & Lindström, 2018). According to Reynolds, Huszar, Kruk, Naselli-Flores, and Melo (2002), *C. raciborskii* belongs to the codon Sn and tolerates light deficiency, while *P. agardhii* is a species belonging to the codon S1, whose growth is favored in turbid mixed layers, with highly light deficient conditions. Thus, the SS of *P. agardhii* may have occurred due to the self-shading effect caused by its biomass, inhibiting the development of other phytoplankton species. On the other hand, Reynolds et al. (2002) framed *M. aeruginosa* within the codon M, adapted to high insolation. Thus, it is expected that this species will grow in an environment with lower values of color and turbidity, corroborating the results observed herein, which show turbidity and color on the negative side of axis 1, while *M. aeruginosa* is plotted on the positive side of this axis.

Nitrate and color were variables related to SS periods, however oscillations in their values were not significant to distinguish these periods as the SS dominant species. For this, turbidity, as well as the concentrations of sulfate and sodium, were suitable.

Our study showed high biomasses of *C. raciborskii* throughout the study period, with significant correlation with both the nSS and SS sampling units. Steady states with dominance of *C. raciborskii* and/or *P. agardhii* occurred in the periods X and XI and were concomitant with turbid waters and higher sodium concentrations.

Ruiz, Sampaio, Oliveira, and Venegas (2004) report that the soils from semiarid regions, due to the intense evaporation and low rainfall, generally contain high soluble salt concentrations and elevated sodium concentrations are often. This ion can migrate from soil to the water column and influence the dynamics of phytoplankton communities. However, studies on the influence of sodium on the growth and dominance of these organisms in freshwater ecosystems are scarce. Hence, our knowledge comes from several laboratory studies that highlight the importance of these elements in the physiology of phytoplankton species.

Increased sodium concentrations appear to be correlated with filamentous cyanobacteria (Seale, Boraas, & Warren, 1987). For nitrogen-fixing cyanobacteria species, such as *C. raciborskii*, this nutrient is required for the nitrogenase activity, responsible for the fixation of atmospheric nitrogen, which occurs in differentiated cells, called heterocytes (Apte & Thomas, 1980). Studies conducted by Valiente and Avendaño (1993) show that when sodium is present, *Anabaena* has higher nutrient uptake efficiencies and lower rates of organic matter loss. For non-nitrogen fixing cyanobacteria species, such as *P. agardhii,* sodium also could enhance phosphorus uptake (Seale et al., 1987). Thus, phosphorus input together with sodium could lead to proliferation of both nitrogen-fixing and non-nitrogen fixing cyanobacteria, particularly in warmer conditions. Semiarid ecosystems are characterized by high temperatures throughout the year. The mean values of phosphate ranged from 0.11 to 0.25 mm L^{-1}. These variables, combined with higher sodium concentrations, could have favored the steady state of both *C. raciborskii* and *P. agardhii.*

Different water bodies are characterized by dominance of cyanobacteria, which can be explained by the resistance to zooplankton predation (Dai et al., 2016), through cyanotoxin production. Synthesis of saxitoxin was observed in *M. aeruginosa* (Martínez-Ruiz & Martínez-Jerónimo, 2016), *P. agardhii* and *C. raciborskii* (Sato-Liebe et al., 2012) exposed to high sodium concentrations. Studies have shown that saxitoxin release to the extracellular medium is dependent on the concentration of monovalent cations due to the increase in intracellular osmotic pressure generated by higher sodium concentrations (Sato-Liebe et al., 2012).

In addition to sodium, sulfate anions may also influence the physiology of cyanobacteria, aiding in the production of cyanotoxins. Sulfate is a common ion in eutrophic freshwater systems, mainly from the discharge of domestic and industrial effluents. It is an essential nutrient and plays a pivotal role in biosynthesis of sulfate-containing metabolites in organisms (Chen, Gin, & He, 2016), such as the amino acids cysteine and methionine and biosynthesis of toxins and proteins that act as electron donors in reductive steps in photosynthesis reactions (Dai et al., 2016; Hughes, Sulesky, Andersson, & Peers, 2018; Zalutskaya, Minaeva, Filina, Ostroukhova, & Ermilova, 2018).

Sulfate starvation has induced a characteristic reduction of cylindrospermopsin, a sulfur-containing cyanotoxin known to be produced by *C. raciborskii* (Bácsi et al., 2006). For another group of cyanotoxins, microcystins, studies developed by Long (2010) have suggested an important role for sulfur-containing metabolites in microcystin biosynthesis by *M. aeruginosa*. According to this author, sulfur is required to support N-methylation and thiolation reactions and to provide sulfur-containing cofactors for microcystin synthesis.

Since SS periods have been related to sodium and sulfate and, according to the literature, they stimulate the synthesis of toxins, it can be assumed that the problem associated with water pollution by these elements may be more damaging than has been discussed in the literature, favoring the stabilization of blooms of toxic species of cyanobacteria in freshwater reservoirs.

In the present study, higher sulfate concentrations were related to nSS periods, although participating in sporadic episodes of SS with dominance of *M. aeruginosa*. Despite its importance for the establishment of SS of *M. aeruginosa,* it is reported that the increase in sulfate in freshwater systems may inhibit photosynthesis, cause oxidative stress and inhibited the growth of *M. aeruginosa* (Chen et al., 2016). High sulfate concentrations can also reduce nitrogen fixation by cyanobacteria, due to the inhibition of nitrogenase activity (Marino, Howarth, Chan, Cole, & Likens, 2003). Nevertheless, low sulfate concentrations can limit the growth of *C. raciborskii*, *G. amphibium* and *P. agardhii* in freshwater ecosystems (Bácsi et al., 2006; Oliveira et al., 2015; Hughes et al., 2018). High sulfate concentrations have been found to cause higher phosphate and ammonium concentrations, which often results in eutrophication and subsequently can causes algal blooms (Chen et al., 2016).

Studies have shown that the disruption of SS can occur after heavy rainfall events (Naselli-Flores & Barone, 2003; Stoyneva, 2003), due to the water column instability (Havens et al., 2019). According to Mowe, Mitrovic, Lim, Furey, and Yeo (2015), the rainy period should break the dominance of *M. aeruginosa*, favoring the development of species more adapted to high turbidity, as *P. agardhii*. However, in our study, no climatic variable presented significant influence on SS events, either in the occurrence, or in the duration or even in the species composition.

Many studies on phytoplankton communities highlight a correlation between SS of cyanobacteria species and nitrogen and/or phosphorous concentrations. Baptista and Nixdorf (2014) reported that low availability of nitrate and phosphorus favored the exclusive SS of *C. raciborskii*. On the other hand, Nasselli-Flores & Barone (2003) showed SS of cyanobacteria species related to high concentrations of total phosphorus and low N: P ratio. Nevertheless, this is the first study that shows the influence of sodium, sulfur and other nutrients on SS of phytoplankton communities.

Semiarid ecosystems have peculiar climatic conditions characterized by high evaporation, scarce and unevenly distributed rainfall. These conditions favor the growth and dominance of cyanobacteria, which is reported in several studies carried out in the region (Bowling et al., 2013; Fonseca et al., 2015; Silva & Costa, 2015). Therefore, it is expected that these climatic conditions, together with other abiotic variables, should contribute to the establishment of SS in these regions. However, there are no studies on the occurrence of SS in semiarid ecosystems. Further, studies explaining the occurrence of SS in ecosystems located in regions with other types of climate test the influence of nitrogen, phosphorus or reservoir stability, not evaluating other abiotic variables that direct phytoplankton growth.

Conclusion

This study shows the robustness of a 130 week-monitoring and presents an important contribution to the understanding of steady state events, highlighting the participation of other abiotic variables besides nitrogen, phosphorus and reservoir stability. In addition, it explains the dynamics of steady state in semiarid ecosystems, whose abiotic characteristics are peculiar to other tropical and temperate ecosystems.

Our findings confirm the hypothesis that SS events occur in semiarid reservoirs, independent of seasonality, but influenced by the concentrations of nutrients.

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