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Phytoplankton-zooplankton interactions at Duas Bocas Reservoir, Espírito Santo State, Brazil: Growth responses in the absence of grazing

Interação fitoplâncton-zooplâncton no reservatório Duas Bocas, Espírito Santo, Brasil: resposta de crescimento à ausência de herbivoria

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Abstract

The aim of this study was to analyze phytoplankton development in the absence of grazing pressure in the Duas Bocas Reservoir (DBR). The DBR is located in the Duas Bocas Biological Reserve and supplies some of the water demand of Great Vitória, Espírito Santo State. On September 25, 2008, 40 L of water were collected below the water's surface, from the lacustrine region of the reservoir. In the laboratory, six microcosms were established (glass boxes), each with a six-liter volume of water, and were maintained for seven days. Three microcosms served as controls (C). In the other three microcosms, zooplankton was removed by water filtration in a plankton net with a 60-μm mesh size. A positive trend in cyanobacteria and chlorophyte growth was found in the absence of grazing. Cyanobacteria benefited under herbivore feeding pressure (Controls) to the detriment of chlorophytes. However, in the absence of grazing pressure, the competition between these groups was sometimes higher, resulting in an alternative dominance. The chlorophyte *Monoraphidium griffithii* was dominant in both microcosms. *Chlorella vulgaris* was abundant, and the cyanobacteria *Limnothrix bicudoi* and *Synechocystis* sp. were abundant in both microcosms. No significant phytoplankton growth was found in the absence of grazing pressure. Then, other environmental factors might act as important regulators of phytoplankton growth in the DBR.

Key words: herbivory, microcosms, plankton, tropical reservoir.

Resumo

Este estudo teve como objetivo analisar o desenvolvimento do fitoplâncton na ausência de herbivoria pelo zooplâncton no reservatório Duas Bocas, um sistema de abastecimento público inserido na Reserva Biológica de Duas Bocas, ES. Em 25 de setembro de 2008, 40 L de água foram coletados na sub-superfície da região lacustrina do reservatório. Foram montados em laboratório seis microcosmos (aquários de vidro), com 6 litros de água em cada um, mantidos durante sete dias. Três deles serviram como Controle e nos outros três (Tratamento), foi retirado o zooplâncton através de filtração da água em rede de malha de 60 μm. Foi observada uma tendência positiva de crescimento de cianobactérias e clorofíceas na ausência de herbivoria. Na presença dos herbívoros (Controle), as cianobactérias foram beneficiadas em detrimento das clorofíceas. Porém, na ausência, a competição entre esses grupos pode ser maior, resultando em alternância na sua dominância. A clorofícea *Monoraphidium griffithii* foi a espécie dominante em ambos os

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microcosmos. *Chlorella vulgaris* foi considerada abundante. As cianobactérias *Limnothrix bicudoi* e *Synechocystis* sp. foram abundantes tanto no Controle quanto no Tratamento. Não houve crescimento significativo do fitoplâncton na ausência de herbivoria. Isso pode sugerir que outros fatores ambientais atuam como importantes reguladores do crescimento fitoplanctônico no reservatório Duas Bocas.

Palavras-chave: herbivoria, microcosmos, plâncton, reservatório tropical.

Introduction

Plankton diversity and distribution in aquatic systems is dependent on complex biotic and abiotic factors. The factors influencing phytoplankton growth and reproduction include the quantity and quality of light, which varies with the climate, and the nutrient concentrations. Competition, grazing and parasitism are other important factors that control the productivity, biomass and phytoplankton succession (Reynolds, 1987).

Zooplankton grazing is one of the main factors controlling phytoplankton growth. The zooplankton community is characterized by high species richness in freshwater systems because it is constituted by different invertebrate groups of algae predators (protozoans, rotifers, cladocerans and copepods; Tundisi and Matsumura-Tundisi, 2008) that exert a grazing pressure on phytoplankton (Rocha *et al*., 1995). The phytoplanktonic species in aquatic environments are those that developed morphological adaptations to reduce grazing, such as body extensions and cell arms, and produce mucilage and impalatable compounds such as toxins (Happey-Wood, 1988; Paerl, 1988).

Among the phytoplanktonic groups that predominate in lakes and reservoirs, chlorophytes, cyanobacteria and diatoms have been cited as the main groups in both temperate (Padisák, 1992; Romo and Miracle, 1995) and tropical systems (Huszar and Reynolds, 1997; Marinho and Huszar, 2002). Rotifers are the main zooplankton groups (*Phylum* Roratoria), and two sub-classes of crustaceans (Cladocera and Copepoda) aside from protists include protozoans and heterotrophic flagellates (Wetzel, 2001). Rotifers are specialized in the filtration of seston particles, mainly detritus and bacterioplankton (Oliveira *et al*., 2003), but they also feed upon phytoplanktonic cells, including cyanobacteria. This group is registered as the main zooplanktonic group in eutrophic reservoirs of the northeastern Brazilian region, which are dominated by cyanobacteria (Eskinazi-Sant'Anna *et al*., 2007).

Cladocerans represent the main group that is characteristic of freshwater environments. Species in this group are essentially herbivores, but they can also use bacteria as a supplementary food source (Melão, 1999). Copepods are the typical group of organisms termed "net plankton", which can develop well in more diverse aquatic systems. Some copepods are herbivores, while others can feed on phytoplankton, microzooplankton, detritus, bacteria, or on copepod eggs and nauplii. Some species can feed on toxic cyanobacteria, such as the hepatotoxic genus *Microcystis* (Melão, 1999).

Microalgae are the main food source for zooplankton; however, the bacterioplankton can represent an important complementary food source (Wetzel, 2001). Among microalgae, chlorophytes are the preferential food source because they posses thin cell walls resulting in a high organic carbon to dry weight ratio (Sipaúba-Tavares and Rocha, 1984). Cyanobacteria are considered to be nutritionally deficient as a food source for zooplankton because of their internal chemical composition. In addition, cyanobacteria can develop big mucilaginous colonies that pose difficulties in the filtration process (Brett and Müller-Navarra, 1997). Rotifers are typically the primary zooplanktonic group in tropical eutrophic reservoirs because of their ability to feed on cyanobacteria (Eskinazi-Sant'Anna *et al*., 2007).

The interactions between planktonic communities can be studied by experimental approaches with small-scale ecosystems called microcosms and mesocosms. These experiments, which can be performed both *in situ* and under controlled conditions, have been carried out in several aquatic systems. Data from such experimental ecosystems can provide specialized information about how the systems are structured and about the functions of the systems at the community level (La Point and Fairchild, 1994). These experiments have a low cost of implementation and provide rapid results and basic data about the ecosystem. On the other hand, data from microcosms can represent some limitations as they may not be accurate representations of processes at the ecosystem level, since natural conditions are sometimes simplified under controlled experimental conditions (Carpenter, 1996).

Experimental studies investigating planktonic communities in Espírito Santo State, southeastern Brazil, are very scarce. A mesocosm experiment on phytoplankton responses to nutrient enrichment was carried out by Delazari-Barroso (2007) at the Duas Bocas Reservoir, which supplies drinking water to Great Vitória, Espírito Santo State. The phytoplanktonic community of this reservoir is dominated by desmids and cyanobacteria. To date, no data have been provided regarding the zooplanktonic community in this system.

In this study, a microcosm approach was adopted to evaluate phytoplankton growth responses in the absence of zooplanktonic grazing at the Duas Bocas Reservoir. As there are no data regarding the zooplankton in this system, it is difficult to predict what algae group would benefit in the absence of grazing pressure. Nevertheless, a positive growth response is expected under experimental laboratory conditions in the absence of zooplankton grazing.

Materials and methods

The Duas Bocas Reservoir – DBR (20°18' S and 40°28' W) – and its entire watershed (Figure 1) are located within the Duas Bocas Biological Reserve (2,910 ha, at an altitude of 200 to 800 m). It is a small and relatively shallow reservoir (z_{max}: 10.0 and z_{mean}: 4.3 m) with an area of 0.51 km^2 and a water volume of 2.0 x 10^6 m^3. The reservoir supplies drinking water to the 100,000 inhabitants of the municipality of Cariacica, Espírito Santo State. The DBR is a warm monomictic reservoir with a winter overturn and is co-limited by nitrogen and phosphorus (Delazari-Barroso *et al.*, 2009).

On September 25, 2008, 40 L of water were collected from subsurface of the Duas Bocas Reservoir in the lacustrine region near the water withdrawal tower (Figure 1). In addition, zooplankton samples were collected for qualitative analyses with a 60-μm mesh plankton net.

Six microcosms (transparent glass boxes – 10 L total volume), each with 6 L of reservoir water, were performed and maintained over seven days under the following laboratory conditions: 20-22 ^{o}C air temperature, 380-420 lux PAR (photosynthetic active radiation) or 0.6 a 0.7 cal/cm^2/min, a 12 hour photoperiod and constant water aeration by air pumps to prevent the sedimentation of cells. Three microcosms were used as controls. In the other three microcosms (the treatments), zooplankton were removed by water filtration through a 60-μm mesh plankton net.

Water temperature (^{o}C), pH and electrical conductivity (μS cm^{-1}) were measured daily at both control and treatment microcosms. Water samples (100 mL) for phytoplankton quantitative analysis were collected daily and fixed with Lugol's solution, for a total of 42 samples. Phytoplankton species were identified according to the previous work carried out at the DBR (Delazari-Barroso *et al.*, 2007).

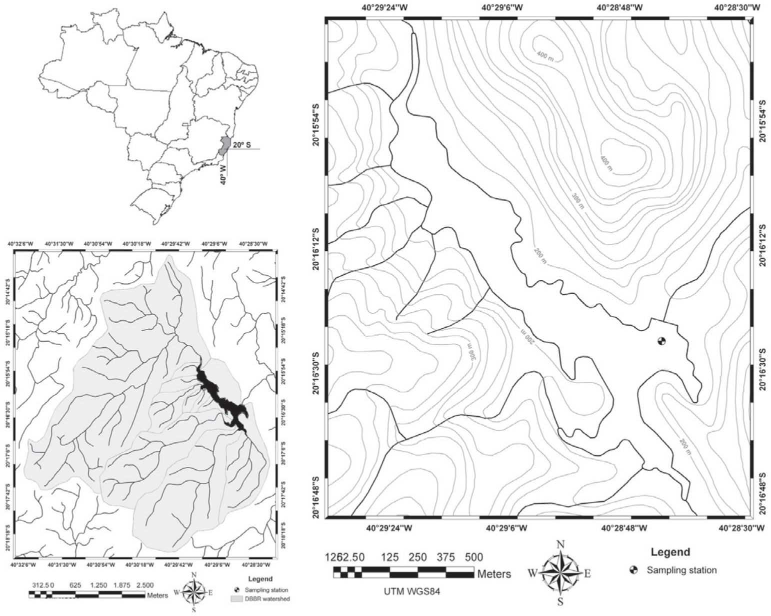

Figure 1. Location and map of the Duas Bocas Reservoir showing the sampling site (Source: LimnoLab/DOC/UFES).

Phytoplankton population densities were estimated using the settling technique (Utermöhl, 1958) under an inverted microscope. Cells, colonies and filaments were enumerated in random fields so that at least 100 specimens of the most frequent species were counted (Lund *et al.*, 1958). Specific biomass (mg fresh-weight L^{-1}) was estimated from the product of the population density (ind mL^{-1}) and the mean unit volume (μm^3) of each species (Edler, 1979), assuming a specific density of phytoplankton cells of 1 g cm^{-3}. In general, the average cell size was based on measurements of at least 20 specimens. Species diversity was estimated according to the Shannon and Wiever Index (Shannon and Weaver, 1949), while dominant and abundant species were determined according to Lobo and Leighton (1986). Zooplankton species were identified to genus level according to Koste (1978) and Rocha and Matsumura-Tundisi (1976). Zooplankton population densities were estimated by filtration of six liters of reservoir water into 100 mL of distilled water and the settling counting technique (Utermöhl, 1958).

Descriptive statistics were also calculated for zooplankton (mean, standard deviation, and coefficient of variation). The non-parametric Mann-Whitney's U-test ($p < 0.05$) was applied to test for significant biological differences between the control and treatment microcosms.

Results

Physical-chemical variables showed a low variation during the experiment, as demonstrated by the coefficients of variation (Table 1). No significant differences ($p < 0.05$) were detected between the control and treatment

Table 1. Descriptive statistical analyses of the physical-chemical and biological variables studied in the controls and treatments microcosms.

CONTROL	Mean	Stand. Dev.	CV (%)	N
Temperature (ºC)	21.4	0.1	0.5	21
pH	7.4	0.2	2.7	21
Electrical conductivity (mS/cm)	38.4	0.4	1.1	21
Phytoplankton biomass (mg/L)	1.4	0.5	35.7	21
Diversity (bits/mg)	2.7	0.2	7.4	21
Species richness	17	1.3	7.7	21
TREATMENT				
Temperature (ºC)	21.3	0.1	0.5	21
pH	7.5	0.2	2.1	21
Electrical conductivity (mS/cm)	37.5	0.4	1.1	21
Phytoplankton biomass (mg/L)	1.5	0.5	33.4	21
Diversity (bits/mg)	2.8	0.1	3.6	21
Species richness	17	0.9	5.2	21

CV: Coeficient of variation.

microcosms for pH, temperature and electrical conductivity.

The average water temperature presented a lower variation (Table 1), with values declining until the 3rd day (Figure 2). There was an increase in temperature again after the 4th day, coinciding with cyanobacteria growth, primarily in the treatment microcosms.

On the first day of the experiment, the pH was neutral, but alkaline water conditions were recorded after the 4th day of the experiment (Figure 3). Slightly higher values were observed in the treatment microcosms, reaching 8.0 on the 5th day and then decreasing on the last day. The same trend of increased values was observed for electrical conductivity. Higher conductivity values were recorded in the treatment microcosms and reaching 42 µS.cm^{-1} (Figure 4).

The results of the zooplankton community analysis revealed five genera that were classified into groups of rotifers, copepods and protozoans as follows: *Keratella* and *Testunidella* (Rotifera); *Mesocyclops* and nauplii (Copepoda); and the protozoans *Centrotropyxis* and *Arcella* (Rhizopoda). The quantitative analysis of the reservoir water showed that rotifers were the dominant zooplankton group (Figure 5).

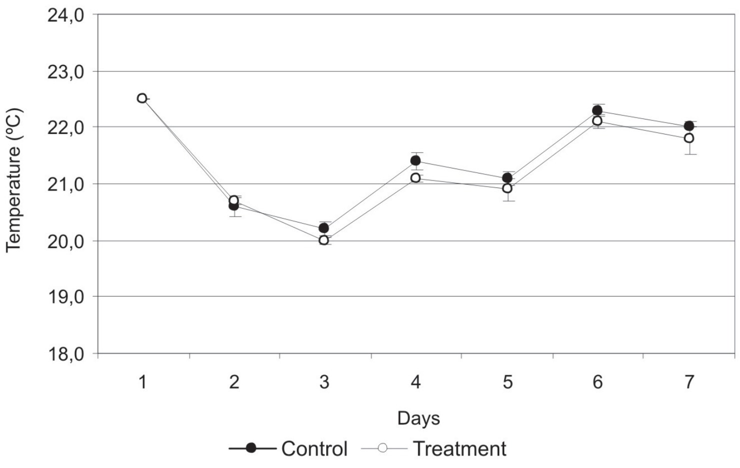

Figure 2. Variation of the average water temperature in microcosms during the experimental period.

The phytoplankton community comprised five classes: Cyanophyceae (cyanobacteria); Chlorophyceae (chlorophytes); Zygnemaphyceae (desmids); Bacillariophyceae (diatoms); and Euglenophyceae (euglenophytes), as well as some small phytoflagellates that were not identified (Table 2).

No significant differences ($p < 0.05$) were detected between the control and treatment microcosms for the phytoplankton density and species diversity. The total phytoplankton biomass varied from 5.0 to 10.5 mg.L^{-1} in the control and from 6.0 a 10.9 mg.L^{-1} in the treatment microcosms. Species diversity varied from 2.3 to 3.2 in the control and from 2.6 to 3.2 in the treatment microcosms.

In the control microcosms, a rise in algae biomass, excluding euglenophytes, was recorded at the beginning of the experiment. After the 3rd day of the experiment, growth was reduced (Figure 6). However, cyanobacteria showed a higher growth rate at this stage than at the beginning of the experiment.

In the treatment microcosms, an increase in the biomass of chlorophytes and cyanobacteria was detected after the 4th day (Figure 7). These groups shared an alternative dominance when the pH was alkaline and when the water conductivity values were high. The biomass of euglenophytes and desmids alternated between periods of growth and decline, with 3.0 mg/L in the experiment. However, a decrease in these groups began on the 6th day of the experiment. In these microcosms, only a few diatom specimens and low biomass were observed. This group was not detected in the control microcosms.

The chlorophyte *Monoraphidium griffithii* was the dominant species in both control and treatment microcosms. *Chlorella vulgaris* was considered to be an abundant species (Table 2). The cyanobacteria *Limnothrix bicudoi* and *Synechocystis* sp.

Table 2. Phytoplankton classes and species registered in the control and treatment microcosms.

SPECIES	CONTROL	TREATMENT
Bacillariophyceae	-	-
Brachysira brebissoni Ross	P	P
Chlorophyceae	-	-
Ankistrodesmus bernadii Komárek	P	P
A. bibraianus (Reinsch) Koršikov	P	P
A. fusiformis Corda	P	P
A. gracilis (Reinsch) Koršikov	P	P
Ankistrodesmus sp.	P	P
Chlorella vulgaris Beijerinck	A	A
Coelastrum pulchrum Schmidt	P	P
Desmodesmus spinosus (Chodat) Hegewald		P
Golenkinia radiata Chodat	P	P
Monoraphidium arcuatum (Koršikov) Hindák	P	P
M. contortum (Thuret) Komárková-Legnerová	P	P
M. griffithii (Berkeley) Komárková-Legnerová	D	D
M. minutum (Nägeli) Komárková-Legnerová	P	P
Scenedesmus acuminatus (Lagerheim) Chodat	P	P
S. ecornis (Ehrenberg) Chodat	P	P
S. quadricauda (Turpin) Brébrisson	P	P
Cyanophyceae	-	-
Chroococcus minimus (Keissl.) Lemmerman	P	P
Cyanodictyon tropicalis Senna et al.	P	P
Geitlerinema unigranulatum (Singh) Komárek & Azevedo	P	P
Limnothrix bicudoi Azevedo et al.	A	A
L. redekei (van Goor) Meffert		P
Planktolyngbya minor (Geitler & Rutner) Komárek & Cronberg		P
Pseudanabaena sp.	P	P
Synechococcus capitatus Bailey-Watts & J. Komárek	P	P
Synechococcus sp.	P	P
Synechocystis sp.	A	A
Euglenophyceae	-	-
Trachelomonas sp.	P	P
Trachelomonas armata (Ehrenberg) Stein	P	
Zygnemaphyceae	-	-
Actinotaenium perminutum (West) Teiling	P	
Staurastrum controversus (West & West) Teiling	P	P
S. escavatum West & West		P
S. identatus (West) Teiling	P	
S. margaritaceum (Ehrenberg) Ralfs	P	
S. micron West & West		P
S. quadrangulare var. *armatum* West & West		P
S. smithii (Smith) Teiling	P	P
S. tetracerum (Kützing) Ralfs	P	
Fitoflagelados	P	P

A=Abundant; D=Dominant; P=Present.

were abundant species in both control and treatment microcosms.

Linear regressions revealed a positive, though not representative, correlation between cyanobacteria growth and electrical conductivity ($R^2 = 0.38$) and pH ($R^2 = 0.21$). No correlation was observed between cyanobacteria growth and water temperature ($R^2 = 0.0008$).

Discussion

The feeding process of herbivorous zooplankton is a selective process that involves both body structures and behavior. The alternative cycling in this predator-prey relation can control primary productivity in aquatic ecosystems (Tundisi and Matsumura-Tundisi, 2008). The scale of these variations is considered to be small, because several aquatic microorganisms are opportunistic species (r-strategists) and present a certain level of resilience in the face of environmental physical disturbances or changes in biological food chains (Shaw *et al*., 1994).

The quality (size, shape and nutritional state) and the quantity of available food changes the succession of zooplankton species, and grazing pressure can substantially modify the composition and succession of phytoplankton species. Seasonal variation in herbivore communities in Lake Lanao was attributed to the variation of food quality and quantity, such as the availability, size and digestibility of phytoplankton species (Tundisi and Matsumura-Tundisi, 2008).

In fact, zooplankton grazing can result in an increase in some groups of microalgae such as euglenophytes, represented by *Trachelomonas* with indigestible cellulose lorica, and desmids, which present long cell processes, spines and mucilage. Herbivore zooplankton prefers small and simple cells that are easy to graze on and to digest.

The dominance of chlorophytes and colonial cyanobacteria in the control microcosms indicates that grazing was selective for small and simple phytoplankton species. In the controls, in the presence of herbivores, cyanobacteria benefited from the loss of chlorophytes because of filamentous and colonial species that are difficult to ingest. Thus, a substantial portion of the available biomass was composed of cells that were inaccessible to zooplankton grazing. The resulting community was dominated by assemblages of colonial and filamentous species (Arfi *et al*., 2003). In the absence of herbivores, competition between chlorophytes and cyanobacteria was higher, resulting in an alternative dominance similar to that observed under natural conditions (Delazari-Barroso, 2007).

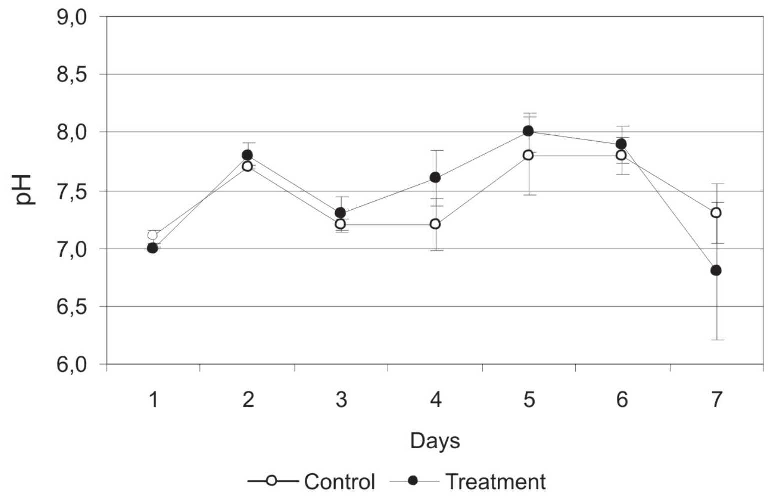

Figure 3. Variation of the average pH values in microcosms during the experimental period.

Selective predation favoring some species might influence species diversity in the microcosms. The relatively high species richness observed in the treatment microcosms had no influence on diversity because many species had low individual numbers and hence a low contribution to the total biomass.

Phytoplankton showed a positive growth trend in the absence of grazing pressure (treatment microcosms), particularly for cyanobacteria and chlorophytes, but this relationship was not statistically significant. Algae were not the only food source because the protozoans observed in the zooplankton community served as a supplementary food source for cladocerans and copepods.

Rotifers dominated the zooplankton community, contributing up to 62% of the total zooplankton density in the reservoir water. Rotifers can select small algae and can thus increase the density of common indigestible algae species, resulting in a decrease in the biomass of small algae, as observed in the control microcosms.

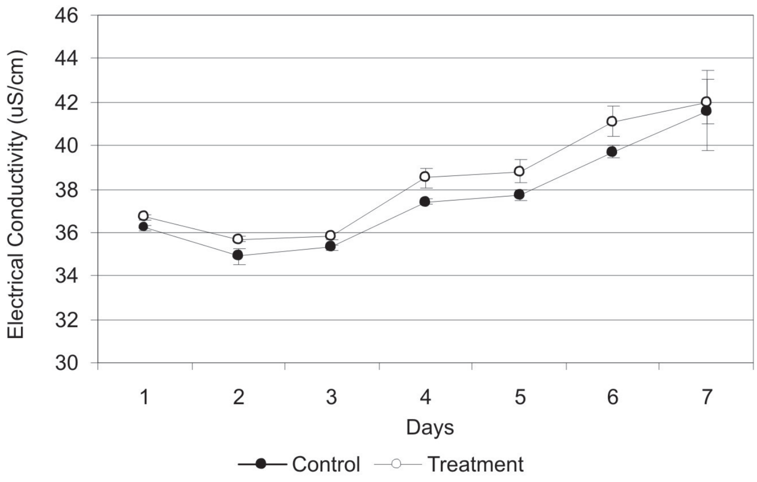

Figure 4. Variation of the average electrical conductivity values in microcosms during the experimental period.

The dominance of r-strategist species groups such as rotifers in the microzooplankton community of reservoirs appears to be associated with the progressive eutrophication of water bodies and with the absence of other zooplankton groups due to its food plasticity (Oliveira *et al*., 2003). The predominance of colonial and filamentous phytoplankton species in eutrophic systems impedes filter feeding by zooplankton (Krienitz *et al*., 1996). In some northeastern eutrophic reservoirs in Brazil that are dominated by colonial and filamentous inedible cyanobacteria, rotifers are favored by high densities of bacteria (Oliveira *et al*., 2003). The eutrophic reservoirs dominated by cyanobacteria in Rio Grande do Norte, Northeast region, Brazil, were typically dominated by cosmopolitan rotifers such as *Keratella tropica*, *K. americana* and *Brachionus havanensis* that are associated with eutrophic environments (Eskinazi-Sant'Anna *et al*., 2007). Our data showed that in the absence of grazing pressure, particularly in the absence of grazing pressure by rotifers (treatment microcosms), cyanobacteria growth was favored after the 5th day of the experiment.

The higher pH in the treatment microcosms indicated a higher rate of photosynthesis (due to the removal of CO_2 in the water, which caused a decline in the pH), as shown by the higher microalgae density in the absence of grazing pressure. The cyanobacterial growth after the 4th day of the experiment coincided with the presence of an alkaline pH (of approximately 8, which favors the growth of cyanobacteria) and a higher electrical conductivity.

At the end of the experiment, cyanobacteria were replaced by chlorophytes when the pH decreased. Linear regressions showed positive correlations but lower significance values between the biomass of cyanobacteria and the electrical conductivity and pH of the water, as expected. The success of cyanobacteria in lakes and reservoirs is related to the high temperatures (above 25º C) and pH values

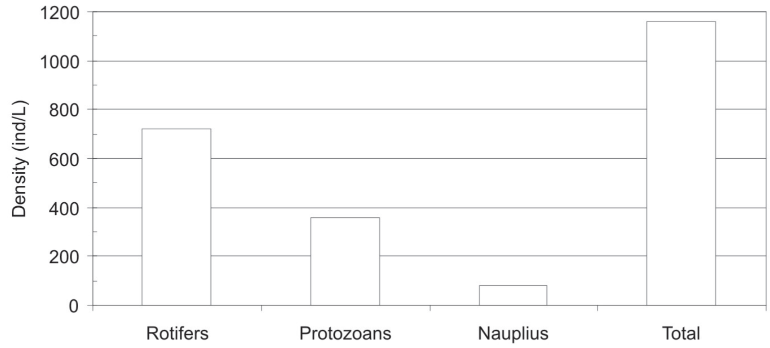

Figure 5. Zooplankton density (ind.L^{-1}) in the lacustrine zone of the Duas Bocas reservoir, Espírito Santo State, in September 2008.

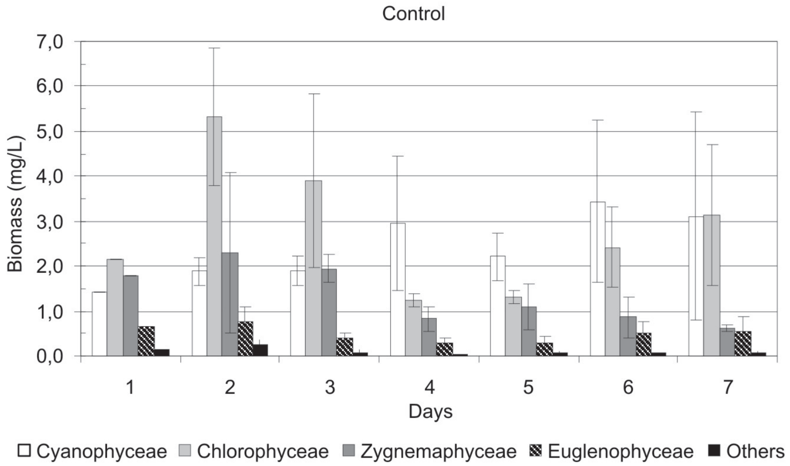

Figure 6. Phytoplankton biomass variation in controls microcosms (Others: phytoflagellates).

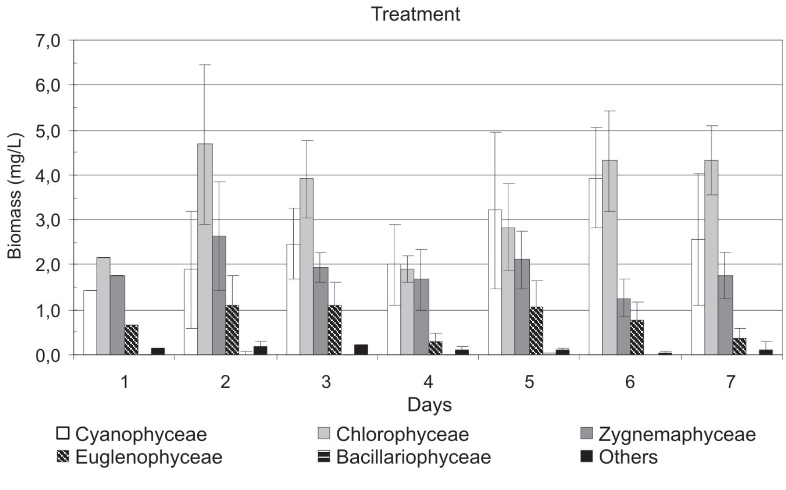

Figure 7. Phytoplankton biomass variation in treatment microcosms (Others: phytoflagellates).

associated with conductivity, among other factors (Shapiro, 1990; Dokulil and Teubner, 2000). In the present study, no positive correlation was observed between cyanobacteria and water temperature, probably because of the low variation in water temperature under controlled laboratory conditions. The classical trophic interaction between phytoplankton and zooplankton in reservoirs can decrease the magnitude of the energy flux of these ecosystems. Data from an eutrophic reservoir in Rio Grande do Norte, Brazil (Eskinazi-Sant'Anna *et al*., 2007) showed that the zooplankton density has a negative correlation with phytoplankton biomass. This phenomenon might reflect the diverse feeding habits of some zooplankton groups that exploit food sources other than microalgae. Aside from this characteristic, the importance of physical and chemical environmental factors and competition can lead to a selective pressure on phytoplankton that is higher than that caused by grazing pressure. Data from Eskinazi-Sant'Anna *et al*. (2007) showed that the copepod density is not related to the phytoplankton density but is related to the water retention time, total phosphorus and electrical conductivity of the water. Melão (1999) found an inverse correlation between water temperature and development time/longevity of the zooplankton under experimental conditions.

The present study found no significant phytoplankton growth in the absence of grazing pressure. This suggests that other environmental factors operate as important regulators of phytoplankton growth in the Duas Bocas Reservoir. Data from Delazari-Barroso *et al*. (2009) showed that the dynamics of the alternating dominance of cyanobacteria and chlorophytes is directly related to the thermal regime of the water (thermal stratification and turnover), which is a consequence of regional climatic patterns and influencing the light and nutrient availability in the water column. Research on zooplankton and bacterioplankton communities in the Duas Bocas Reservoir, which were unknown until now, can elucidate the importance of grazing pressure in controlling phytoplankton growth in this system.

Acknowledgements

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