

Tilapia rendalli increases phytoplankton biomass of a shallow tropical lake

O incremento da biomassa fitoplancônica por *Tilapia rendalli* em um lago raso tropical

Lúcia Helena Sampaio da Silva¹, Marlene Sofia Arcifa², Gian Salazar-Torres¹,
Vera Lúcia de Moraes Huszar¹

¹Departamento de Botânica, Museu Nacional, Universidade Federal do Rio de Janeiro – UFRJ,
Quinta da Boa Vista, CEP 20940-040, Rio de Janeiro, RJ, Brazil
e-mail: luciahssilva@gmail.com; giann.salazar@gmail.com; vhuszar@gbl.com.br

²Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto – FFCLRP,
Universidade de São Paulo, CEP 14040-901, Ribeirão Preto, SP, Brazil
e-mail: marcifa@usp.br

Abstract: Aim: This study aimed to experimentally test the influence of a planktivorous filter-feeding fish (*Tilapia rendalli*) on the phytoplankton dynamics of a small and shallow tropical reservoir (Lake Monte Alegre, Brazil). Adults of *T. rendalli* of this lake feed preferentially on phytoplankton, and we hypothesize that: I) adults of *T. rendalli* will decrease the phytoplankton biomass and composition through direct herbivory, and II) as it is a eutrophic system, fish would not have strong influence on phytoplankton through nutrient cycling. **Methods:** To evaluate these different effects on algae, a field experiment was performed in the summer period for 15 days, in mesocosms isolated from the sediment, using a control group (no fish) and a treatment group (with one fish in each mesocosm). Physical and chemical variables and phyto- and zooplankton were evaluated at the start, middle, and end of the experiment. **Results:** At the end of the experiment, it was observed a significant increase in ammonium concentrations and total phytoplankton biomass, Cyanobacteria and Zygnemaphyceae and all size classes except class II (20-30 µm) in the treatment group (with fish). The biomass increase of the potentially toxic cyanobacterium *Cylindrospermopsis raciborskii* was also observed in the fish treatment at the end of the experimental period. **Conclusion:** This study did not support both initial hypotheses. It supports the assertion that in tropical water bodies, with similar characteristics to the environment studied, planktivorous filter-feeding fish, such as *T. rendalli*, are not effective in reducing phytoplankton biomass through direct grazing, even when phytoplankton is one of their main food items. *T. rendalli* can contribute to the increase of phytoplankton biomass and can promote or increase the eutrophication of aquatic systems.

Keywords: mesocosm experiment, exotic omnivorous fish, direct grazing, nutrient increase.

Resumo: Objetivos: Este estudo visou testar experimentalmente a influência de um peixe planctófago filtrador (*Tilapia rendalli*) sobre a dinâmica fitoplancônica de um reservatório tropical pequeno e raso (Lago Monte Alegre, Brasil). Adultos de *T. rendalli* deste lago alimentam-se preferencialmente de fitoplâncton e nossas hipóteses são: I) adultos de *T. rendalli* reduziriam a biomassa e composição do fitoplâncton através da herbivoria direta, e II) como este é um sistema eutrófico, o peixe poderia não ter grande influência sobre o fitoplâncton através da ciclagem de nutrientes. **Métodos:** para avaliar esses diferentes efeitos sobre as algas, um experimento de campo foi feito no período de verão durante 15 dias em mesocosmos isolados do sedimento, usando um grupo controle (sem peixe) e um grupo tratamento (com um peixe em cada mesocosmo). As variáveis físicas e químicas e o fito- e zooplâncton foram avaliados no início, meio e fim do experimento. **Resultados:** No final do experimento, foi observado um incremento significativo nas concentrações de íon amônio, biomassa fitoplancônica total, de cianobactérias e zignemafíceas e de todas as classes de tamanho, exceto a classe II (20-30 µm) no grupo tratamento (com peixe). Foi observado o incremento da biomassa de uma cianobactéria potencialmente tóxica (*Cylindrospermopsis raciborskii*) no tratamento com peixe, no final do período experimental. **Conclusão:** Este estudo não deu suporte às duas hipóteses iniciais. Ele suporta a afirmação de que em corpos de água tropicais, com características semelhantes ao ambiente estudado, peixes planctófagos filtradores, como *T. rendalli*, não

são efetivos na redução da biomassa fitoplanctônica através da herbivoria direta, mesmo sendo o fitoplâncton um dos seus principais itens alimentares. *T. rendalli* pode contribuir para o incremento da biomassa fitoplanctônica e pode promover ou incrementar a eutrofização de sistemas aquáticos.

Palavras-chave: experimento em mesocosmos, peixe onívoro exótico, herbivoria direta, incremento de nutrientes.

1. Introduction

Food web theory states that predators can control species from lower trophic levels and determine changes in the environment productivity. According to this theory, top consumers may indirectly affect the primary producers in food webs due to its effects on intermediate consumers (top-down control; Sarnelle, 1992). The influence of predators on the organisms is not limited to top-down control as they also influence the recycling of nutrients, a bottom-up control (Carpenter et al., 1992; Vanni, 1996; Schindler et al., 1996). Thus, planktivorous fish may have a direct effect on phytoplankton through direct grazing or indirectly through selective predation on zooplankton and nutrient cycling (Carpenter et al., 1992; Starling, 1993a, b; Vanni and Layne, 1997; Attayde and Hansson, 1999, 2001a; Jeppesen et al., 2002; Scheffer, 2004). Under experimental conditions, it was observed that nutrient cycling (phosphorus) by planktivorous (Vanni and Layne, 1997; Attayde and Hansson, 1999) and omnivorous fish (Starling et al., 2002) could affect phytoplankton community structure. However, the relative importance of direct and indirect mechanisms for phytoplankton dynamics remains unclear (Attayde and Hansson, 2001a, b; Figueredo and Giani, 2005; Attayde et al., 2010).

The intensity of the effects of planktivorous fish on trophic cascade also depends on the trophic status of lakes (Brett and Goldman, 1997; Pace et al., 1999). Studies have shown that the importance of nutrient excretion by planktivorous fish is higher in oligotrophic systems, and can be an important mechanism for controlling phytoplankton when herbivorous zooplankton is found in small densities (Vanni and Layne, 1997; Schaus and Vanni, 2000; Jeppesen et al., 2002). In eutrophic lakes, phytoplankton is less limited by nutrients and the top-down control by fish predation on zooplankton may be the major driver for this community, especially when phytoplankton is not dominated by cyanobacteria (Attayde and Hansson, 2001a). However, top-down control is more important when visual predator fish are abundant, and can

consume efficiently large zooplankton, allowing an increase of phytoplankton biomass (Lazzaro et al., 1992; Starling, 1993a, b).

It has been proposed that in tropical lakes and reservoirs, especially in the shallow eutrophic ones, the regulatory effects of interactions fish/zooplankton on phytoplankton would be less important than the observed in the temperate zone (Schiemer, 1996). Zooplanktivorous fish in the tropics can exert a higher predation pressure on *Chaoborus* than on the typical small zooplankton species, with indirect influence on the zooplankton (Lewis, 1996). Furthermore, tropical and subtropical lakes are often dominated by omnivorous species (Jeppesen et al., 2005), not always efficient in controlling phytoplankton.

Temporal variations in the phytoplankton biomass of southeastern Brazilian lakes and reservoirs have been linked mainly to climatic influences (dry and rainy seasons) (Arcifa et al., 1998; Marinho and Huszar, 2002; Soares et al., 2008). Several studies have also investigated the applicability of the top-down control on tropical and subtropical freshwater ecosystems (Arcifa et al., 1986; Northcote et al., 1990; Starling and Rocha, 1990; Starling, 1993b; Figueredo and Giani, 2005; Attayde et al., 2007; Rondel et al., 2008; Menezes et al., 2010), and a recent review compares the differences between (sub)tropical and temperate systems regarding biomanipulation techniques (Jeppesen et al., 2012).

In this study, we assessed the influence of *Tilapia rendalli* on phytoplankton community in a tropical lake. Our main hypotheses are: I) adult *Tilapia rendalli* will decrease the phytoplankton biomass and composition through direct herbivory (top-down control), because phytoplankton is one of its main food items, and II) as the lake is eutrophic, fish would not influence phytoplankton through nutrient recycling (bottom-up control). This study aimed to assess the influence in experiments, of a planktivorous filter-feeding fish (*Tilapia rendalli*) on the phytoplankton dynamics in a small tropical eutrophic lake.

2. Material and methods

2.1. Study area

The Lake Monte Alegre is located in Ribeirão Preto, São Paulo State, Brazil (21° 10' 04"S, 47° 51' 28"W) at 500 m of altitude and resulted from the impoundment of the Laureano Creek, in 1942, which belongs to the Pardo River basin. This lake is located in the tropical region with two defined seasons: cool-dry season (May-September) and warm-wet season (October-April) (Arcifa et al., 1990). It is small, shallow (area 7 ha, Z max. = 5 m, Z mean = 2.9 m), eutrophic (Silva, 1995), and warm discontinuous polymictic lake, with more stable stratification in the warm season. The thermal stratification leads to chemical stratification and dissolved oxygen depletion at the bottom (Arcifa et al., 1990). These features plus a small drainage basin, low runoff inputs and anthropogenic interference, suggest that the ecosystem dynamics is primarily controlled by internal interactions of their biotic and abiotic variables.

Long-term dataset on the phytoplankton seasonal dynamics in the lake showed that the nanoplankton (2-20 µm) was numerically dominant, whereas the microplankton (>20-200 µm) predominated in biomass. Zooplankton was composed of relatively large cladoceran species (*Daphnia gessneri* and *Daphnia ambigua*, max. length 1.17 and 0.90 mm, respectively), intermediate-sized species (*Diaphanosoma birgei* and *Ceriodaphnia richardi*, max. length 0.60 and 0.80 mm, respectively), and small species (*Bosmina tubicen* and *Ceriodaphnia cornuta*, both with max. length of ca. 0.40 mm). Predation by fish on zooplankton is low, since it represents a small proportion (1.8%) of the diet of the fish fauna, which is mostly distributed in the littoral zone (Arcifa and Meschiatti, 1993; Meschiatti and Arcifa, 2002). The only planktivorous fish in the Lake Monte Alegre is the adult *Tilapia rendalli* (Perciformes-Cichlidae), a filter-feeder that consumes more phytoplankton than zooplankton (Arcifa and Meschiatti, 1993, 1996). It was introduced from Africa, where it is, generally, a leaf chopper and a macrophage (Zengeya and Marshall, 2007; Zengeya et al., 2011). However, the scarcity of macrophytes in the lake may have led to change in the diet of this species.

2.2. Experimental design

The experiment was performed during the summer period (11 to 25 January 1999), when the lake presented a higher phytoplankton biomass (Arcifa et al., 1998). Six mesocosms made of

atoxic plastic cylinders (0.3 mm thick) connected to aluminum frames (Arcifa and Guagnoni, 2003) were set in the lake. Each mesocosm was 2.5 m high, with a diameter of 1.3 m, holding a volume of 2.5 m³. Six units (3 replicates per treatment) were distributed in the selected area of the lake, in a systematic way, according to Hurlbert (1984), for avoiding pseudoreplication. They were closed at the bottom and opened to the atmosphere and covered with a 3 mm meshed net in order to prevent the entrance of other organisms (e.g. fish and birds).

The field experiment consisted of two treatments, with three replicates each: 1. **Treatment A (with fish)** contained total phytoplankton, total zooplankton and fish (one adult *Tilapia rendalli* collected in the Lake Monte Alegre, ~ 30-31 cm of standard length); 2. **Treatment B (no fish)** contained phytoplankton + zooplankton < 60 µm, and was filled with the lake water filtered through a 60 µm mesh net (Arcifa and Guagnoni, 2003), which retained 80% of the zooplankton, but did not alter substantially the phytoplankton community. The largest and most efficient zooplankton was removed in treatment B to compare phytoplankton biomass without loss through herbivory. Thus, **Treatment A** contained total phytoplankton, total zooplankton and fish, and **Treatment B** (control group) contained phytoplankton and a few species of rotifers in low abundance (Figure 1).

2.3. Sampling data

For phyto- and zooplankton analyses, samples were taken in the whole water column of the mesocosms with a pump (Jabsco ITT Ind., USA, Model 34600-0000), that delivered 30 L min⁻¹.

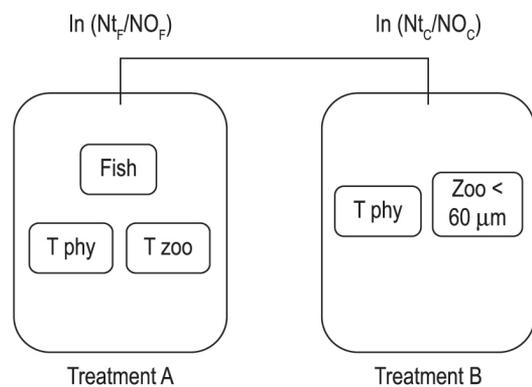


Figure 1. Experimental design. Treatment A (with fish), Treatment B (control, no fish), T phy = total phytoplankton, T zoo = total zooplankton, zoo < 60 µm = zooplankton < 60 µm, N_{t_f} = biovolume in t days in treatment A, N_{0_f} = initial biovolume in treatment A, N_{t_c} = biovolume in t days in treatment B, N_{0_c} = initial biovolume in treatment B.

Physical and chemical variables, such as water transparency (Secchi disc), dissolved oxygen, water temperature (Yellow Springs Inc. 95), pH (YSI 60) and electric conductivity at 25°C (YSI 30), were measured at the start, middle, and end of the experiment (1, 9 and 15 days). To assess the concentrations of dissolved nutrients that could be potentially limiting for phytoplankton, samples were collected on days 1, 9 and 15.

Phytoplankton samples were fixed with modified Lugol solution (Vollenweider, 1974). The water collected for zooplankton quantification was filtered through a 60 µm meshed net and fixed according to Haney and Hall (1973).

2.4. Sample analysis

The water samples collected from the enclosures were filtered through a 0.45 µm glass fiber filters and analyzed according to Mackereth et al. (1978) for nitrate, and Golterman et al. (1978) for ammonium and orthophosphate.

Dark enhancement of carbon fixation by ammonium addition, referred as ammonium enhancement response (AER), was used as a physiological indicator of N limitation of phytoplankton in enclosures (Vanni and Layne, 1997), a value > 1 indicating N limitation. AER was evaluated at the start and end of the experiment.

Phytoplankton populations were enumerated in random fields (Uhelinger, 1964), according to the settling method (Utermöhl, 1958), using an inverted microscope Zeiss, model Axiovert 10 at 400x. The units (cells, colonies and filaments) were counted to attain at least 100 specimens of the most frequent species ($p < 0.05$; Lund et al., 1958).

Quantitative analyses of zooplankton were conducted on replicated sub-samples obtained with Stempel pipettes of 1, 2.5 or 5 mL. A minimum of 60 individuals was enumerated in each sub-sample, maintaining the coefficient of variation <20%, as recommended by McCauley (1984). For low population densities, the whole water sample was quantified. The sub-samples were placed on a gridded Petri dish and counted under a stereomicroscope Wild M5.

2.5. Data analysis

The euphotic zone (Z_{eu}) was calculated as 2.7 times the depth of the Secchi disc, according to Cole (1994). Phytoplankton biovolume was calculated as an estimate of phytoplankton biomass based on the volume of each organism, using geometric models (Hillebrand et al., 1999).

Average calculation of different taxa was performed by multiplying the density of each species by the average body volume, considering the average size of about 25 individuals of each species. Specific biomass was expressed in mg (fresh weight) L⁻¹ (Edler, 1979), assuming a specific density of phytoplankton cells of 1 g cm⁻³.

Phytoplankton was grouped into major taxonomic groups: Cyanobacteria, Bacillariophyceae, Zygnemaphyceae, Chlorophyceae and others (Cryptophyceae + Chrysophyceae + Xantophyceae + Euglenophyceae + Dinophyceae), and into size classes (<20, 20-30, 30-60, >60 µm). Zooplankton was grouped into major taxonomic groups (Rotifera, Copepoda and Cladocera). For taxonomic determination of the principal algae groups, Hoeck et al. (1993) and Komárek and Anagnostidis (1996, 2005) were used.

To evaluate the effects of fish on the plankton, net changes were applied:

$\ln(N_{t_F}/N_{0_F})$ = net change in Treatment group (A - with fish)

$\ln(N_{t_C}/N_{0_C})$ = net change in Control group (B - no fish)

Where,

N_{t_F} = biovolume in t days of Treatment group (A - with fish)

N_{0_F} = initial biovolume in Treatment group (A - with fish)

N_{t_C} = biovolume in t days of Control group (B - no fish)

N_{0_C} = initial biovolume in Control group (B - no fish)

t = duration of the experiment (15 days)

The effect of fish on phytoplankton was assessed by the differences between the ratios (net change) in algal biovolume recorded in the middle and the end of the experiment in relation to the initial date, in the enclosures of the control group (B- no fish) [$\ln(N_{t_C}/N_{0_C})$] and the treatment group (A-with fish) [$\ln(N_{t_F}/N_{0_F})$] (Osenberg et al., 1997) (Figure 1). The ratios of abundances (Nt/N0) were log transformed to stabilize variances as well as for providing a symmetrical scale. The Student *t* test was used to test differences between treatment effects on the net changes in algal biovolume (Attayde and Hansson, 2001a), and on zooplankton.

To test differences for each physical, chemical and nutrient variables on different sampling dates between the two treatments, we used the Student *t* test and when significant differences were found, the Tukey test was used or the nonparametric Mann-Whitney test when the Student *t* test assumptions

were violated. All data were log transformed. Statistical analyses were performed in SigmaPlot 11.0, at the significance level of $p < 0.05$.

3. Results

3.1. Physical and chemical variables

Significant differences in water transparency were observed from the middle of the experiment, being lower in the treatment A (with fish) ($p < 0.001$; Table 1). Average electrical conductivity was not significantly different between the treatments. Similar pH values were observed in both treatments, averaging 7.5 and 7.4 in the treatments A and B, respectively, without significant differences between them throughout the study period. There were no significant differences in dissolved oxygen (DO) concentrations between the treatments, values ranging from a minimum of 5.9 to a maximum of 9.5 mg L⁻¹ (Table 1).

Significantly higher concentrations of ammonium (N-NH₄⁺) were observed from day 9 to the end of the study period, with high concentrations in the treatment A (with fish) (mean values of 659.3 to 929 μg L⁻¹; Table 1).

Orthophosphate (P-PO₄³⁻) and nitrate (N-NO₃⁻) concentrations showed no significant differences between the treatments throughout the experiment (Table 1). Despite high concentrations of dissolved nutrients, ammonium enhancement response (AER), indicated N limitation in both treatments (mean > 1.0), with no significant differences between them (Table 1).

3.2. Phytoplankton

Total phytoplankton biomass was statistically similar between treatments, at the start of the experiment ($p > 0.05$), with mean values varying from 8.1 to 8.9 mg L⁻¹. The phytoplankton was initially composed of chlorophyceans (31%), zygnemaphyceans (23%), cyanobacteria

(11%), diatoms (6%) and others (29%) in both treatments (Figure 2). Until day 15, the total phytoplankton biomass increased during the course of the experiment, reaching a higher value in the

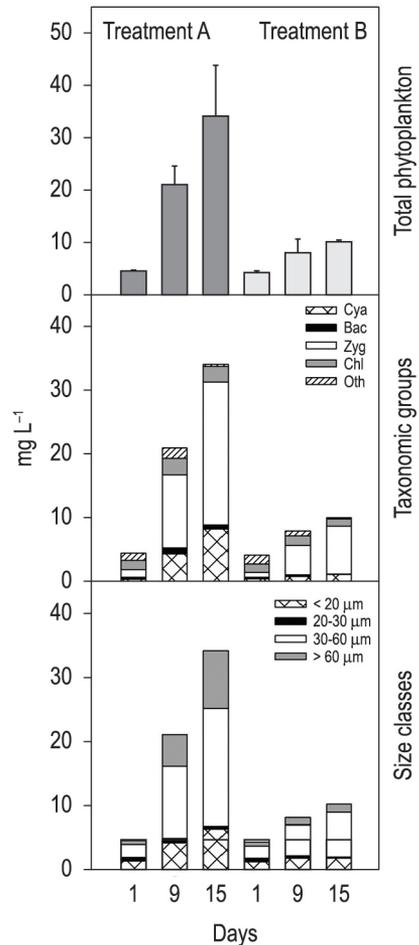


Figure 2. Mean and standard deviation of the total phytoplankton biomass, taxonomic groups and size classes in the mesocosms on day 1 (start), 9 (middle) and 15 (end) of the experiment. Treatment group (A= with fish), Control group (treatment B= no fish), Cya=Cyanobacteria, Bac=Bacillariophyceae (diatoms), Zyg=Zygnemaphyceae, Chl=Chlorophyceae, Oth=Others and size classes <20, 20-30, 30-60, >60 μm.

Table 1. Mean values of the physical and chemical variables in the mesocosms with fish (Treatment A) and fish free (Treatment B).

Days	Treat	Trans (m)	Temp (°C)	pH	DO (mg L ⁻¹)	N-NH ₄ ⁺ (μg L ⁻¹)	N-NO ₃ ⁻ (μg L ⁻¹)	P-PO ₄ ³⁻ (μg L ⁻¹)	NL (AER)
01	A	1.5 (a)	27.9 (a)	7.3 (a)	7.2 (a)	659.3 (a)	103.3 (a)	126.7 (a)	2.8 (a)
	B	1.6 (a)	27.4 (a)	7.3 (a)	6.9 (a)	671.3 (a)	110.0 (a)	126.0 (a)	3.8 (a)
09	A	1.4 (a)	28.2 (a)	7.7 (a)	9.4 (a)	682.0 (a)	105.7 (a)	79.7 (a)	
	B	2.0 (b)	27.9 (a)	7.6 (a)	9.5 (a)	668.3 (b)	103.7 (a)	86.7 (a)	
15	A	1.1 (a)	28.4 (a)	7.7 (a)	5.9 (a)	929.0	96.0 (a)	99.7 (a)	3.8 (a)
	B	1.9 (b)	27.9 (b)	7.3 (a)	6.8 (a)		100.3 (a)	166.7 (a)	5.1 (a)

Different letters (in bold) indicate significant differences ($p < 0.05$). Treat=Treatment; Trans=Transparency; Temp=Temperature; NL=N limitation.

treatment A (with fish), zygnephyceans (66%) and cyanobacteria (24%) contributing a larger proportion (Figure 2). In the treatment B (no fish), the composition of the phytoplankton groups also changed, at the end of the experiment, increasing the contribution of zygnephyceans (74%), and decreasing that of chlorophyceans (12%). Except the fraction 20-30 μm , the proportion of the fractions increased in the treatment A, from the start to the end of the experiment. In the treatment B, only the fraction 30-60 μm increased over time.

The net change of phytoplankton biomass showed significant differences between the two treatments (Table 2). A highest biomass increase occurred on day 9, in the treatment A, for the total phytoplankton ($p = 0.007$), cyanobacteria ($p = <0.015$) and all size classes ($p = 0.006$ to 0.031), except the class II (20-30 μm). On day 15, a similar tendency remained for the same phytoplankton attributes, except a significant increase of zygnephyceans in the fish mesocosm ($p = 0.001$).

3.3. Zooplankton

At the start of the experiment, the zooplankton community in the treatment A (with fish) was mostly composed of rotifers (92.6%), and a smaller proportion of copepods (7.32%) and cladocerans (0.04%; Figure 3). To compare phytoplankton

biomass without loss through herbivory, the largest and most efficient zooplankton in controlling phytoplankton was removed in treatment B (no fish) and rotifers were virtually the only group (99%). As expected, zooplankton densities were always larger in the treatment A, varying from 1851 to 5286 ind L^{-1} . The densities ranged from 366 to 796 ind L^{-1} , in the treatment B. Rotifers were the dominant group throughout the study period in both treatments. The net-change evaluation applied to total zooplankton and rotifers, showed differences only on day 15, when a significant increase of the total zooplankton occurred in the fish mesocosm (Table 3).

4. Discussion

Our experiment showed a greater influence of nutrient excretion by the fish than grazing on the phytoplankton, supporting a phytoplankton biomass significantly higher in the treatment with fish. Thus, our results do not support the first hypothesis of this study, which assumed that the omnivorous - planktivorous fish, *Tilapia rendalli*, would control the phytoplankton through direct herbivory. Likewise, our results do not support the second hypothesis, that there would be no increase in phytoplankton biomass owing to fish excretion in a eutrophic lake.

Table 2. Mean and standard deviation (SD) of the net changes in phytoplankton biomass of the major groups and size classes in the mesocosms, on days 9 and 15 of the experiment, and the t test results for differences of net changes between the treatment A (fish+) and the treatment B (fish-) ($p < 0.05$). Significant values are in bold.

	Mesocosms				
	Mean (no fish)	SD	Mean (with fish)	SD	p
Day 9					
Total phytoplankton	0.61	0.23	1.52	0.20	0.007
Cyanobacteria	0.34	0.84	2.35	0.18	0.015
Zygnemaphyceae	1.73	0.40	0.89	2.43	0.587
Chlorophyceae	0.16	0.49	0.76	0.60	0.251
Bacillariophyceae	0.29	0.29	0.90	0.39	0.096
Size class I (<20 μm)	0.34	0.28	1.17	0.13	0.010
Size class II (<20-30 μm)	-0.34	1.11	0.26	0.06	0.405
Size class III (30-60 μm)	0.92	0.26	1.71	0.33	0.031
Size class IV (>60 μm)	0.49	0.49	1.98	0.06	0.006
Day 15					
Total phytoplankton	0.87	0.09	1.99	0.31	0.004
Cyanobacteria	0.83	0.04	2.93	0.86	0.014
Zygnemaphyceae	2.24	0.10	2.92	0.11	0.001
Chlorophyceae	-0.13	0.61	0.49	0.92	0.390
Bacillariophyceae	-0.66	0.80	0.28	0.70	0.199
Size class I (<20 μm)	0.38	0.28	1.17	0.13	0.012
Size class II (<20-30 μm)	-1.40	1.12	-0.36	0.79	0.259
Size class III (30-60 μm)	1.32	0.17	2.19	0.34	0.016
Size class IV (>60 μm)	0.75	0.15	2.53	0.77	0.017

Table 3. Mean and standard deviation (SD) of the net changes in zooplankton density of the major groups in the mesocosms, on days 9 and 15 of the experiment, and the *t* test results for differences of net changes between the treatment A (fish+) and the treatment B (fish-) ($p < 0.05$); n.a = not assessed.

	Mesocosms				
	Mean (no fish)	SD	Mean (with fish)	SD	P
Day 9					
Total zooplankton	0.31	0.78	-0.24	0.54	0.372
Rotifers	0.27	0.74	-0.26	0.62	0.395
Copepods	n.a	n.a	n.a	n.a	n.a
Cladocerans	n.a	n.a	n.a	n.a	n.a
Day 15					
Total zooplankton	0.41	0.07	0.81	0.24	0.050
Rotifers	0.35	0.02	0.76	0.32	0.096
Copepods	n.a	n.a	n.a	n.a	n.a
Cladocerans	n.a	n.a	n.a	n.a	n.a

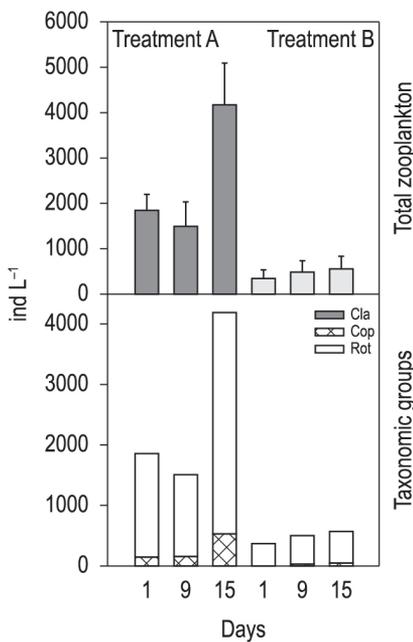


Figure 3. Mean and standard deviation of the total zooplankton density and taxonomic groups in the mesocosms on day 1 (start), 9 (middle) and 15 (end of the experiment). Cla=cladocerans, Cop=copepods, and Rot=rotifers. Treatment A (with fish), treatment B (no fish).

Despite the indication of nutrient limitation through physiological indicator, high concentrations of dissolved nutrients were observed, above the values considered as limiting to phytoplankton growth (DIN $> 100 \mu\text{g L}^{-1}$, Reynolds, 2006; SRP $> 10 \mu\text{g L}^{-1}$, SAS, 1989). The indication of nutrient limitation at the end of the experiment may have occurred by the rapid and high phytoplankton growth, in the treatment with fish, exceeding the nutrient carrying capacities.

The opportunism of the exotic cichlid species *T. rendalli*, used in our experiment, was expressed

by a change from a macrophagous diet in Africa to planktivory in the Lake Monte Alegre, leading adult individuals to inhabit the limnetic zone (Arcifa and Meschiatti, 1993, 1996). This species can filter and ingest algae varying from 2 to 200 μm in length in the lake, apparently without selection, but selects zooplanktonic prey with lower escape ability, which are commonly smaller species (Arcifa and Meschiatti, 1996). These facts indicate that it is a filter-feeder in this lake, since it was able to switch from a particulate to a filter-feeding behavior in other experiments (Lazzaro, 1991).

Filtration rates of *T. rendalli*, from Lake Monte Alegre, measured experimentally in the laboratory, ranged from $0.09 \pm 0.6 \cdot 10^6$ to $1.66 \pm 0.83 \cdot 10^6$ algae/g wet fish/h (A. J. Meschiatti, unpublished data). Based on the experimental data, an approximate estimate of algae consumption by *Tilapia rendalli* in the treatment with fish indicated a loss of about 20% of the total algae at the end of the experiment. However, the direct grazing on phytoplankton and a 20% loss, theoretically imposed by tilapia, was not effective in controlling its biomass as has also been shown for the primary productivity (Feresin et al., 2010).

In addition, zooplankton, represented mainly by small rotifers, was unable to control the phytoplankton biomass, despite the high densities in the treatment with fish (ca. 4000 ind L⁻¹). As the phytoplankton was probably mostly affected by nutrient excretion by fish, it is likely that the algae composition in the presence of fish was related to their ability to use nutrients or to take advantage of other abiotic factors, prevailing in the experiment.

Cylindrospermopsis raciborskii, the main representative of the Cyanobacteria, which increased in the treatment with fish, is a species that can grow in nutrient-limited environments (O'Neil et al.,

2012), and develops blooms in eutrophic systems with high pH. It has also physiological adaptations to grow in low light intensities (Shafik et al., 1997), showing high absorption capacity of phosphate and ammonium (Padisák, 1997). Moreover, it has been observed that in lakes with high fish biomass, Cyanobacteria may be favored by fish excretion (Starling and Lazzaro, 1997; Attayde and Hansson, 2001b). This may be related, among other factors, to the increase in pH, providing competitive advantage for Cyanobacteria (Caraco and Miller, 1998). The increase of Zygnemaphyceae, might be explained by its size and/or inadequate forms for consumption by zooplankton which also showed an increase the treatment with fish. Furthermore, this group consists of species that can tolerate moderate light intensity (Reynolds et al., 2002), characteristic observed primarily in the treatment with fish.

In summary, our experimental study showed that nutrient excretion by the exotic cichlid species, *T. rendalli*, surpassed herbivory, indicating that the use of this omnivorous-planktivorous species for biomanipulation purposes is inappropriate. Biomanipulation in this tropical lake, hypothetically adopting it as an example for phytoplankton control, could be hampered by several features: I) the fish species in the lake consume a low amount of plankton (Arcifa and Meschiatti, 1993), and II) their predominant littoral distribution (Arcifa and Meschiatti, 1993; Meschiatti and Arcifa, 2002), segregate them from the pelagic plankton. These two aspects indicate that the fish fauna of this lake would be not only unable to control the phyto- and zooplankton, but also contribute with nutrients to enhance phytoplankton productivity.

5. Final remarks

The possibility of direct control of phytoplankton by omnivorous filter-feeders through grazing is not always supported by data. Some studies actually showed a decrease in total phytoplankton biomass (Zhang et al., 2006; Menezes et al., 2010), whereas others report enhanced biomass (Figueredo and Giani, 2005; this study) or no influence (Attayde et al., 2007; Okun et al., 2008; Rondel et al., 2008). Unlike *T. rendalli*, the exotic *Oreochromis niloticus*, the Nile tilapia, is a planktivore or herbivore/detritivore in African water bodies (Zengeya et al., 2011). Despite its planktivorous habit and ingestion of Cyanobacteria (Turker et al., 2003; Zengeya et al., 2011; Salazar-Torres, 2012), the control of phytoplankton by this species may be null to effective (Figueredo and

Giani, 2005; Rondel et al., 2008; Menezes et al., 2010; Salazar-Torres, 2012).

A question remains, therefore, on the applicability of biomanipulation techniques developed in higher latitudes to (sub)tropical water bodies. Numerous studies in temperate lakes where a more linear trophic chain prevails - piscivorous fish - planktivorous fish - zooplankton - phytoplankton - revealed the possibility of controlling phytoplankton through the trophic cascade effect (reviews by Lazzaro, 1997 and Jeppesen et al., 2007). However, a recent revision (Jeppesen et al., 2012) showed not so promising results of the biomanipulation technique in some temperate lakes, in the long term.

In tropical and subtropical water bodies it is advisable to deepen the knowledge on the food web and overall interactions before any mitigation policy is implemented. For instance, stocking tropical lakes with native piscivorous fish for biomanipulation purposes, would be adequate only in some of the water bodies. As an example, the use of the widespread South American piscivorous fish, *Hoplias malabaricus*, to reduce planktivorous fish was effective in experiments in a subtropical Uruguayan lake (Mazzeo et al., 2010), and probably may work in this lake owing to the fact that both piscivorous and omnivorous-planktivorous fish are littoral dwellers. However, it would be unsuitable for most low latitude lakes, where juveniles and small fish species, living in the littoral, are usually omnivores. Piscivory enhancement in tropical water bodies, besides being a useless technique due to the lack of a linear food chain, can be harmful if misapplied. For instance, cichlid species of the genus *Cichla*, from the Amazonian region, are able to extinguish native fish populations (Arcifa and Meschiatti, 1993; Pinto-Coelho et al., 2008; Menezes et al., 2012), having only a weak cascade control on plankton (Menezes et al., 2012).

The occurrence of native particulate planktivorous fish, such as the predominantly neotropical characids *Astyanax bimaculatus* (current name *A. altiparanae*) and *A. fasciatus* in a tropical water body, affected the phytoplankton in mesocosms, through the trophic cascade effect (Arcifa et al., 1986). However, that was an exceptional situation as both species are omnivores and not planktivores in most water bodies. Furthermore, the predominance of omnivorous fish in tropical and subtropical lakes (Lazzaro, 1997; Jeppesen et al., 2007; González-Bergonzoni et al., 2012) might lead to the direct exploitation of phytoplankton by fish (Starling, 1993a, b; Arcifa

and Meschiatti, 1996; Komárková, 1998; Salazar-Torres, 2012), undoing the cascade effect. Several exotic and native omnivorous-planktivorous fish are filter-feeders, whose selectivity on zooplankton is driven toward prey with lower escape ability and not necessarily on larger prey (Arcifa and Meschiatti, 1996), despite some exceptions (Okun et al., 2008). In addition, young stages or small fish species, which could potentially feed on zooplankton, are often distributed in the littoral zone in tropical and subtropical systems (Arcifa and Northcote, 1997; Meschiatti and Arcifa, 2002; Agostinho et al., 2003; Teixeira-de Mello et al., 2009), and, therefore, spatially segregated from the pelagic zooplankton.

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