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Effects of the Nile tilapia (*Oreochromis niloticus* L.) on the plankton community of a tropical reservoir during and after an algal bloom

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Abstract The invasive species Nile tilapia is a filter-feeding omnivorous fish that can have a negative effect on zooplankton and phytoplankton resources. However, the strength of its effects on plankton communities should decrease with increasing plankton biomass, e.g., during an algal bloom. We tested this hypothesis by performing two experiments in a tropical reservoir, where we randomly allocated two treatments (with and without tilapia) to 20 mesocosms. The first experiment was conducted during an algal bloom (biovolume = 1038.34 mm^3 l^{-1}), while the second experiment was conducted after the bloom (biovolume = 1.05 mm^3 l^{-1}). The negative effects of fish on mesozooplankton (mean size of 480 μm in both experiments) and large algae (GALD $\geq$ 50 μm) were stronger in the second than in the first experiment. On the other hand, the negative effects of fish on microzooplankton (experiment 1: mean size 180 μm; experiment 2: mean size 128 μm) and small algae (GALD < 50 μm) were stronger in the first than in the second experiment. We conclude that the Nile tilapia can suppress phytoplankton and zooplankton biomass in tropical lakes and reservoirs, but the magnitude of this effect depends on plankton biomass and size-structure.

Keywords Invasive species · Nile tilapia · Omnivory · Trophic cascade · Eutrophication · Community size-structure

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Introduction

The Nile tilapia (*Oreochromis niloticus* Linnaeus, 1757) is an invasive fish species native from Africa that has been introduced into many tropical and subtropical lakes and reservoirs around the world for aquaculture and fisheries purposes. The choice of this species to enhance yields of inland fisheries and aquaculture in the tropics is motivated by its high

growth and reproductive rates, its capacity to adapt to a wide range of environmental conditions, and its omnivorous feeding habits (Canonico et al., 2005). These are actually the same features that also make the Nile tilapia a successful invader and there is a concern that this invasive species may have caused negative ecological impacts in the habitats where it has been introduced (Canonico et al., 2005). For instance, the analysis of a 30-year time series of fisheries records from a tropical reservoir shows a significant reduction in the catches per unit of effort of other fish species after the introduction of the Nile tilapia, suggesting that tilapia may have caused the observed changes, possibly through competition for plankton resources with larvae and juveniles of other fish species, although other mechanisms cannot be ruled out (Attayde et al., 2011).

Both visual and pump filter-feeding are utilized by Nile tilapia in the ingestion of larger crustacean zooplankton, while pump filter-feeding alone is employed in the ingestion of phytoplankton and small zooplankton (Beveridge & Baird, 2000). Omnivorous filter-feeding fish like the Nile tilapia can affect phytoplankton communities by grazing on larger phytoplankton species (Lu et al., 2006; Menezes et al., 2010), but also suppressing herbivorous zooplankton, suspending settled phytoplankton, and excreting nutrients in dissolved forms into the water column (Drenner et al., 1996, 1998; Vanni, 2002). Therefore, while filter-feeding fish can reduce the biomass of large phytoplankton, they can also increase the biomass of small phytoplankton due to suppression of their competitors (large phytoplankton) and predators (herbivorous zooplankton) and to nutrient recycling (Radke & Kahl, 2002; Figueredo & Giani, 2005; Okun et al., 2008; Rondel et al., 2008; Zhao et al., 2013). Hence, the overall effect of filter-feeding fish on total phytoplankton biomass and water transparency can be either positive or negative and it is not surprising that stocking filter-feeding fish to control phytoplankton biomass in eutrophic lakes and reservoirs is a highly controversial issue (Zhang et al., 2008; Attayde et al., 2010).

Despite efficient feeding on phytoplankton by some tilapia species, their potential for suppressing algal blooms and improving water transparency has been considered low because estimates of instantaneous plankton mortality caused by fish ingestion is much lower than maximum potential plankton growth rates

during blooms (Hambright et al., 2002). Moreover, the per capita ingestion rates of algal biomass by filter-feeding fish like Nile tilapia increases with algal biomass in a curvilinear way (i.e., type II functional response; Turker et al., 2003). This means that the proportion of algal biomass ingested by filter-feeding fish decreases with increasing algal biomass. Therefore, based on previous work on tilapia's functional response (Turker et al., 2003), we expect that tilapia will have a weaker effect on plankton resources during algal blooms.

Here we show the results of two mesocosm experiments performed in a tropical reservoir to investigate the effects of the invasive fish species Nile tilapia on the water quality and the plankton communities of tropical lakes and reservoirs. We took advantage of the natural development of an algal bloom and its collapse to test the hypothesis that the effects of Nile tilapia on plankton communities depend on lake primary productivity and decrease in strength during an algal bloom. Our results suggested that Nile tilapia can suppress both zooplankton and phytoplankton, but the magnitude of this effect depends on both plankton biomass and size-structure.

Method

Experimental design

The experiments were performed from September 4th to October 12th (first experiment) and from October 16th to November 17th (second experiment) of 2006 in a small and shallow lake with an accumulation capacity of 433.000 m^3 situated in the Seridó Ecological Station, Rio Grande do Norte, Brazil (06°34′8520″N, 37°15′519″W). The experiments were carried out in cylindrical mesocosms with a diameter of 2.5 m and a height of 2 m (c. 9.8 m^3), which were placed side by side along the lake shore. The walls of the mesocosms were made of transparent plastic (thickness: 0.45 mm) and they were open to the atmosphere and to the sediment, but completely isolated from the surrounding lake water.

In both experiments, treatments with and without the invasive species Nile tilapia (*Oreochromis niloticus*) were replicated ten times and randomly allocated to 20 mesocosms containing lake water and natural plankton community. In the first experiment, nutrients were also added to half of the mesocosms with and

without tilapia but since the effects of nutrients were not significant on all variables except rotifers (Menezes et al., 2010), we reanalyzed the results of this experiment considering only the fish effects regardless of nutrient addition. The first experiment was conducted during an algal bloom and had a high initial phytoplankton biovolume (1038.34 ± 66.16 mm^3 l^{-1}), representing a condition of high primary productivity. The second experiment was conducted just after the collapse of the algal bloom and had a low initial phytoplankton biovolume (1.05 ± 0.1 mm^3 l^{-1}), representing a condition of low primary productivity. After the first experiment, mesocosms were removed from the lake for maintenance and cleaning. Afterwards, they were reintroduced in the lake for the second experiment in the same positions they were during the first experiment.

The fish were collected at a fish hatching station nearby the lake and stocked in the treatments with fish at a density of 1 fish m^{-3}. Fish were measured and weighted at the start and at the end of each experiment. Fish sizes in the beginning of the first and second experiments were, respectively, 16.61 ± 0.67 and 20.03 ± 0.74 cm standard lengths. We assume that fish used in our experiments were filter-feeding because it has been demonstrated that Nile tilapia can shift from visual particle feeding to a mainly filter-feeding behavior when it reaches about 6–7 cm of standard length (Beveridge & Baird, 2000). The same fish individuals were used in both experiments to avoid differences between the fish effects in the two experiments caused by fish identities. Thus, fish were kept inside fish cages placed in the lake when we removed the mesocosms from the lake between the two experiments.

Samples and analysis

In both experiments, sampling was performed once a week, totalizing five sampling events, but for the second experiment phytoplankton samples were collected only at the first, third, and fifth weeks. The water samples were collected through a 2 m long PVC tube at three different points of each mesocosm and integrated in a single representative sample, from which subsamples were taken for total nitrogen (TN), total phosphorus (TP), and phytoplankton analysis. Zooplankton samples were collected through vertical tow at the center of each mesocosm with a plankton net with 20 μm mesh size (volume filtered ∼ 212 l). The phytoplankton samples were fixed with lugol's solution and the zooplankton samples with 4% formaldehyde. The TP analysis was done according to the ascorbic acid method after persulfate digestion (Apha, 1997), while TN was analyzed as nitrate by the sodium salicylate method (Muller & Weidemann, 1955) after persulfate digestion in alkaline medium (Valderrama, 1981). The temperature, pH, electric conductivity, and oxygen concentrations were measured through a multiparameter analyzer U-22 HORIBA (Kyoto, Japan). At the fifth week of the first experiment, we were unable to measure the previous variables with our multiparameter probe. The water transparency was measured with a Secchi disk.

The zooplankton organisms were counted under a microscope in a 1 ml Sedgwick-Rafter chamber until a minimum of 100 individuals of each taxonomic group had been counted. The microcrustacean biomass (copepods and cladocerans) was estimated using regression equations relating dry weight and body length according to Bottrell et al. (1976). For estimating zooplankton biomass at least 30, randomly chosen individual were measured, from the most abundant species. For rotifers, geometrical formulae were used to estimate biovolume (Ruttner-Kolisko, 1977). Wet weight was estimated from the biovolume of each individual, assuming that 10^6 μm^3 corresponds to 1 μg of wet weight. Dry weight was estimated as 10% of wet weight (Pace & Orcutt, 1981). We grouped zooplankton in two major groups according to zooplankton's size: microzooplankton (nauplii + rotifers, experiment 1: mean size 180 μm; experiment 2: mean size 128 μm) and mesozooplankton (copepods + cladocerans, mean size of 480 μm in both experiments). The phytoplankton was quantified according to Utermöhl (1958) under an inverted microscope. Before counting, the samples were allowed to sediment for 3 h for each centimeter height of the chamber (Margalef, 1983). The individuals (cells, colonies, and filaments) were enumerated in random fields (Uhelinger, 1964), with an error smaller than 20% and a confidence interval of 95% (Lund et al., 1958). To estimate the phytoplankton biovolume, at least 25 individuals from each species were measured by applying approximations to similar geometric solids (Hillebrand et al., 1999). Phytoplankton was grouped into two groups according to the greatest axial linear dimension (GALD): large algae

(GALD ≥ 50 μm) and small algae (GALD < 50 μm).

Statistical analysis

A one-way ANOVA was undertaken to analyze data from each experiment and test the fish effects (F) on the dependent variables: total phosphorus and total nitrogen concentrations; Secchi depth; total phytoplankton biovolume; GALD ≥ 50 μm and GALD < 50 μm algal biovolume; total zooplankton, microzooplankton, and mesozooplankton biomass. Our focus is on the direction and magnitude of the average fish effects on the dependent variables during and after the algal bloom. Therefore, we used the average values of the dependent variables over the course of each experiment to perform our statistical analysis. However, the effects of fish are consistent when we include time as a factor in a repeated measures ANOVA. We also performed a paired t test to compare the fish biomass at the beginning and at the end of each experiment. Prior to analyses, all data were square root transformed when needed to fulfill ANOVA's assumption. ANOVA tells us about the direction of the fish effect, but not the strength of this effect. As our hypothesis concerns the strength of fish effect during and after algal bloom, it was necessary to calculate the effect sizes to quantify the magnitude (i.e., strength) of the fish effects on the dependent variables in each experiment (Hedges et al., 1999). Then we compared the strength of fish effects between the experiments. We used the following formula to obtain the effect sizes:

$$\theta = \ln\left(\frac{\mu_1}{\mu_2}\right),$$

where θ is the effect size, μ_1 is the mean for a dependent variable group in the treatment with fish (fish), and μ_2 is the mean for the same variable in the treatment without fish (control). To compare the effect sizes for a given variable between the two experiments, we calculated the pooled standard error, and then calculated the z-scores that were used for determining the P value. The significance level assumed was $\alpha = 0.05$. All statistical analyses were performed with STATISTICA 7.0 (Statsoft, Inc., Tulsa, OK, USA).

Results

During the first and second experiments, water temperature, pH, electric conductivity, and dissolved oxygen were not affected by fish and are described here by their average and standard error ($\pm$ 1 SE) across the experimental period and all 20 replicates to characterize the experimental conditions: experiment 1: 29.7 ($\pm$ 0.12°C), 6.9 ($\pm$ 0.08), 0.085 ($\pm$ 0.0003 μS cm^{-1}), and 5.8 ($\pm$ 0.08 mg l^{-1}), respectively, while for the second experiment the average values of the above variables were 31.7 ($\pm$ 0.1°C), 7.4 ($\pm$ 0.05), 0.095 ($\pm$ 0.0003 μS cm^{-1}), and 4.6 ($\pm$ 0.06 mg l^{-1}), respectively. Results of all variables at the beginning and at the end of each experiment show that the first experiment finished before and the second experiment started just after the collapse of the algal bloom (Table 1).

Total fish biomass doubled during the first experiment but did not change during the second one ($t_1 = -11.9331$, $P < 0.001$; and $t_2 = 0.3152$, $P = 0.759$, respectively, Fig. 1). All fishes survived during the experiments. TN was affected positively by fish only in the second experiment, whereas TP increased significantly in the presence of fish in the first but not in the second experiment (Fig. 2). Water transparency was negatively affected by fish in both experiments (Fig. 2). We observed a significant negative effect of fish on total phytoplankton (marginally significant in the second experiment, see Fig. 2) and large algae (GALD ≥ 50 μm), but no effect of fish on small algae (GALD < 50 μm) in both experiments (Fig. 2). Total zooplankton and mesozooplankton were also negatively affected by fish in both experiments (Fig. 2). On the other hand, microzooplankton was negatively affected by fish only in the first experiment (Fig. 2).

The negative effects of fish on mesozooplankton and large algae were stronger in the second than in the first experiment as predicted, while the reverse pattern was observed for the negative effects of fish on microzooplankton and small algae (GALD < 50 μm) (Fig. 3). The magnitude of the fish effects on total phytoplankton biovolume was similar in both experiments (Fig. 3).

**Table 1** Means (± SE) of all variables measured at the beginning and at the end of each experiment

Variables	Treatments	Experiment 1		Experiment 2	
		Beginning	End	Beginning	End
Temperature (°C)	Control	29.2 ± 0.07	–	31 ± 0.4	31.8 ± 0.2
	Fish	29.4 ± 0.09	–	31 ± 0.3	31.3 ± 0.2
pH	Control	5.9 ± 0.03	–	7.2 ± 0.2	8.2 ± 0.05
	Fish	5.9 ± 0.03	–	6.8 ± 0.1	7.9 ± 0.08
Conductivity ($\mu S\ cm^{-1}$)	Control	0.08 ± 0.00	–	0.09 ± 0.00	0.1 ± 0.00
	Fish	0.08 ± 0.00	–	0.09 ± 0.00	0.1 ± 0.00
DO ($mg\ l^{-1}$)	Control	5.8 ± 0.14	–	4.1 ± 0.2	5.2 ± 0.06
	Fish	5.5 ± 0.12	–	4.1 ± 0.1	5.3 ± 0.08
Secchi (m)	Control	0.93 ± 0.04	0.88 ± 0.06	0.64 ± 0.02	0.85 ± 0.05
	Fish	0.72 ± 0.02	0.7 ± 0.02	0.77 ± 0.02	0.71 ± 0.03
TN (μM N)	Control	173.5 ± 4.5	172.8 ± 3.5	27.8 ± 6.2	47.3 ± 4.9
	Fish	179.9 ± 4.6	171.3 ± 4.3	39.1 ± 2.4	52.3 ± 5.9
TP (μM P)	Control	2 ± 0.1	1.7 ± 0.06	1.7 ± 0.3	4.4 ± 0.4
	Fish	2.2 ± 0.07	2 ± 0.08	2.2 ± 0.3	4.9 ± 0.7
GALD < 50 μm ($mm^3\ l^{-1}$)	Control	495.8 ± 69.9	239 ± 57.8	0.76 ± 0.08	0.7 ± 0.2
	Fish	382 ± 26.9	221.1 ± 21.1	0.76 ± 0.1	0.69 ± 0.07
GALD ≥ 50 μm ($mm^3\ l^{-1}$)	Control	636.1 ± 57	1576.9 ± 496.7	0.48 ± 0.07	0.88 ± 0.5
	Fish	562.8 ± 65.8	580.3 ± 93.1	0.09 ± 0.02	0.21 ± 0.04
Total phytoplankton ($mm^3\ l^{-1}$)	Control	1131.9 ± 107.5	1815.9 ± 537.4	1.2 ± 0.1	1.6 ± 0.7
	Fish	944.8 ± 70.5	801.4 ± 99.8	0.9 ± 0.1	0.9 ± 0.1
Microzooplankton (μg DW l^{-1})	Control	17.8 ± 1.5	32.4 ± 5.5	40.2 ± 4	119.6 ± 24.7
	Fish	19.4 ± 2.3	24.1 ± 2.7	46.9 ± 4.6	111.6 ± 20.4
Mesozooplankton (μg DW l^{-1})	Control	164.1 ± 19.8	259.6 ± 67.3	49.3 ± 8.4	38.3 ± 6.1
	Fish	127.5 ± 11.8	116.9 ± 16.7	63.6 ± 12	12.2 ± 2
Total zooplankton (μg DW l^{-1})	Control	181.9 ± 20.8	291.9 ± 68.9	89.5 ± 9.8	157.8 ± 25.2
	Fish	146.9 ± 10.6	141.1 ± 18.4	110.4 ± 15.4	123.8 ± 20.3

Discussion

Previous studies have shown that the Nile tilapia effects on plankton communities of tropical lakes and reservoirs can be highly variable and context dependent (Attayde & Menezes, 2008; Lu et al., 2006; Menezes et al., 2010; Okun et al., 2008; Starling et al., 2002; Salazar-Torres et al., 2016; Zhao et al., 2013). Indeed, the effects of press perturbation experiments such as fish addition or removal can be highly unpredictable in both strength and direction due to the prevalence of indirect effects of such perturbations (Attayde & Hansson, 2001; Schmitz, 1997; Yodzis, 1988). In our experiments, the responses of all variables were equally predictable in direction, being

all negative regardless of the initial phytoplankton biomass. However, the response of plankton size-structure was more unpredictable in strength than the response of total phyto- and zooplankton biomass.

As expected, our results suggest that larger zooplankton (i.e., mesozooplankton) and larger algae (i.e., GALD ≥ 50 μm) were more strongly suppressed by fish after the bloom than during the bloom. Filter-feeding fish have non-linear functional responses (Turker et al., 2003) and should consume a smaller proportion of planktonic resources with increasing plankton biomass. Therefore, the strength of the negative effects of filter-feeding fish on their major (larger) planktonic resources was reduced when phytoplankton biomass was high during the algal
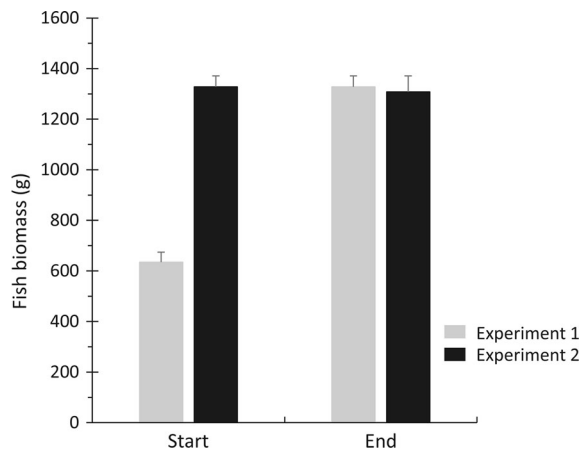
Fig. 1 Average fish biomass ($\pm$ SE) in the beginning and in the end of each experiment

bloom. This result supports the conjecture that filter-feeding fish such as adults of Nile tilapia may have less influence on zooplankton and phytoplankton dynamics in eutrophic than mesotrophic lakes and may not be able to control algal blooms (e.g., Hambright et al., 2002; Rondel et al., 2008). However, this pattern was not observed for the total zooplankton and phytoplankton biomass in our experiments, because smaller zooplankton (i.e., microzooplankton) and smaller algae (i.e., GALD < 50 μm) were more strongly suppressed by fish during than after the algal bloom, counteracting the strength of the response of the larger zooplankton and algae.

Putting in other words, the negative effects of tilapia on microzooplankton were stronger during the algal bloom (experiment 1) than after its collapse (experiment 2), whereas the reverse pattern was observed for mesozooplankton. To explain this result we must recognize that tilapias can have two feeding modes: filter (suction) feeding and visual particulate feeding (Beveridge & Baird, 2000). During the first experiment, when high algal biomass was available for tilapia, they may have affected plankton mainly through filter-feeding. Indeed, filter-feeding is energetically more advantageous than visual particulate feeding when the biomass of large phytoplankton is high (Yowell & Vinyard, 1993). Because microzooplankton (rotifers and nauplii) are less evasive prey than mesozooplankton (mainly copepods), they are more susceptible to predation by filter-feeding tilapia

(Ibrahim et al., 2015). On the other hand, during the second experiment when algal biomass was very low, tilapia may have affected plankton through both filter-feeding and visual particulate feeding. Because visual particulate feeding is highly size-selective, mesozooplankton are then more susceptible to predation by these feeding modes of tilapia. This may explain why the suppression of microzooplankton was stronger in the first experiment, while the suppression of the mesozooplankton was stronger in the second experiment.

One problem with comparing two experiments at different times of the year (even back to back) is that differences in total phytoplankton and zooplankton biomass may be confounded by community succession (see Online Resource for a summary of the main phyto- and zooplankton groups). In our study, the size-structure of both zoo- and phytoplankton communities changed from a dominance by mesozooplankton and larger algae (> 50 μm GALD) during the algal bloom (experiment 1) to a dominance by microzooplankton and smaller algae (< 50 μm GALD) after the bloom collapse (experiment 2). However, this change in the size-structure of the plankton did not affect the strength of the tilapia effects on the total biovolume of phytoplankton and total biomass of zooplankton. The strength of the negative effects of tilapia on these variables was similar in both experiments. Finally, the observed changes in fish size between the experiments would have been a problem if there was an ontogenetic change in feeding behavior within the range of fish size used in our experiments (from 16.61 $\pm$ 0.67 to 20.03 $\pm$ 0.74 cm in the first and second experiments, respectively). However, over this size range, the Nile tilapia has a fully developed filtration apparatus and can be considered omnivorous (Beveridge & Baird, 2000).

Finally, the Nile tilapia had positive growth rates in our first experiment but did not grow in our second experiment, indicating that fish growth was supported during but not after the algal bloom. Results from a bioenergetic model suggest that filter-feeding in tilapias of *Oreochromis* genus can support fish growth and results in a positive energy balance only when fish is given access to high abundance of large algae (Dempster et al., 1995). Although *Oreochromis* are capable of entrapping and ingesting particles as small as unattached bacteria (< 1 μm diameter) from the water column (Beveridge et al., 1989), they are
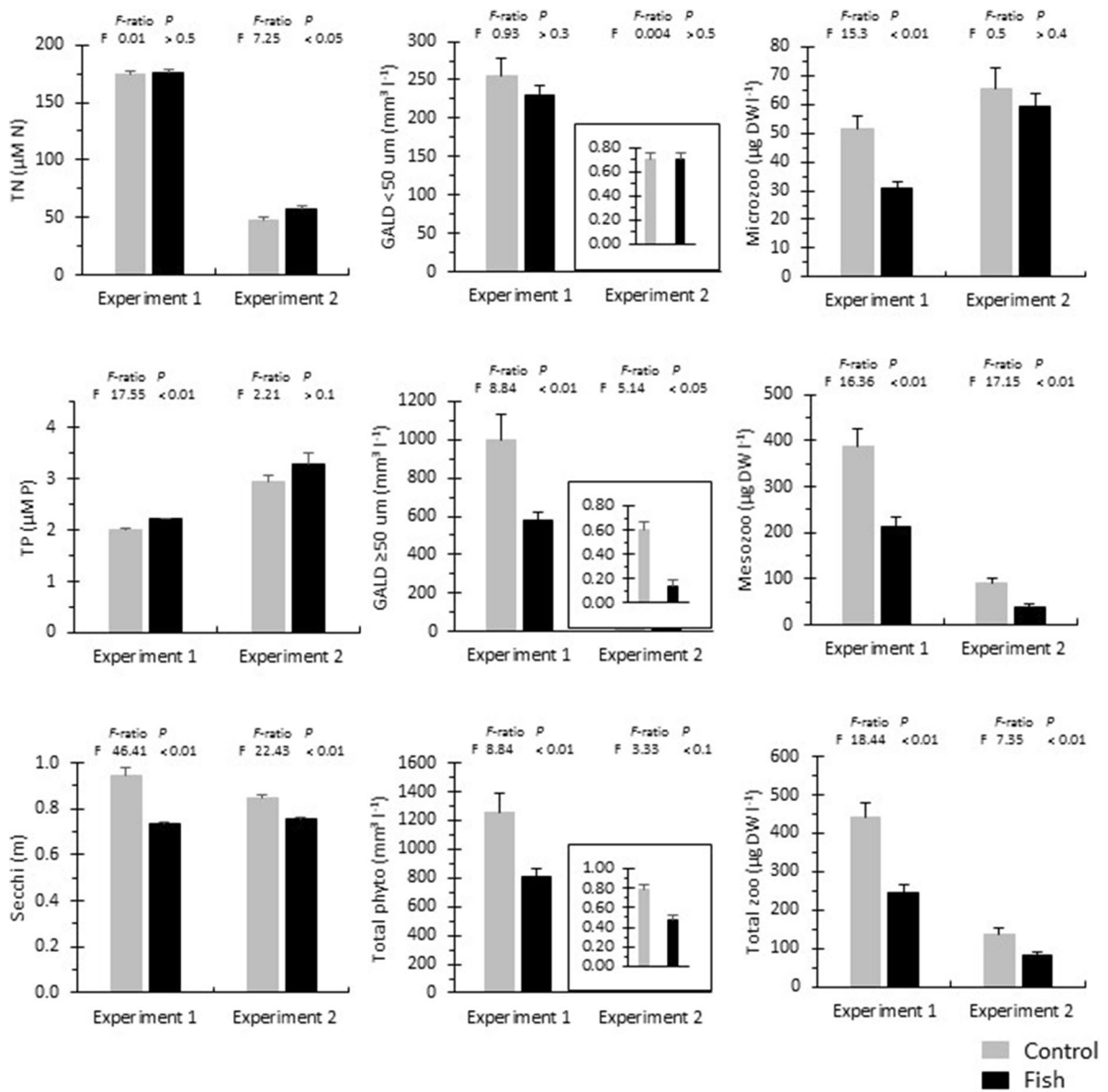
Fig. 2 Results of one-way ANOVA of the effects of fish (F) on total nitrogen (TN), total phosphorus (TP), Secchi depth, biovolume of total phytoplankton (Total phyto), small and large algae (with GALD < and ≥ 50 μm, respectively), microzooplankton (Microzoo), mesozooplankton (Mesozoo), and total zooplankton (Total zoo) biomass in the experiments 1 and 2. The bars over the bar graphs represent the standard errors of the treatments (Control and Fish, gray and black bars, respectively). Results shown over each graph in the panel are the F-ratios of the ANOVA. Values were considered significant assuming α = 0.05. Note that figure regarding phytoplankton biovolume from the experiment 2 is represented by a panel inside the larger figure

undoubtedly more efficient at feeding on larger algal and cyanobacterial species than on small organisms (Robinson et al., 1990; Northcott et al., 1991).

Conclusion

The above results advance the field of plankton ecology and have implications for the management of tropical lakes and reservoirs through the stocking or
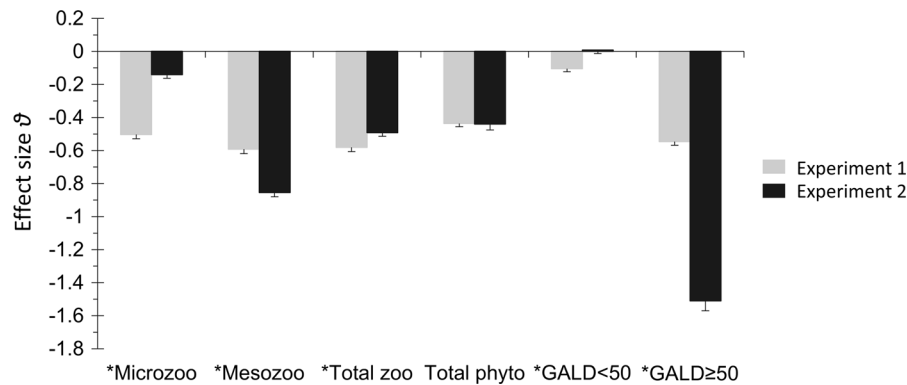
Fig. 3 Fish effect size (θ) on microzooplankton (Microzoo), mesozooplankton (Mesozoo), total zooplankton (Total zoo), total phytoplankton (Total phyto), small algae (GALD < 50 μm), and large algae (GALD ≥ 50 μm) in the experiments 1 and 2 (gray and black bars, respectively). The asterisks (*) denote *P* values < 0.01

fisheries of filter-feeding fishes like the Nile tilapia. Yet, we contribute to the understanding of how invasive species such as Nile tilapia may affect the recipient ecosystem. We show that the Nile tilapia can suppress both phytoplankton and zooplankton biomass in tropical lakes and reservoirs, but the magnitude of this effect depends on phytoplankton biomass and size-structure. Naturally developed algal blooms can support positive growth of filter-feeding fish, but may reduce the strength of their negative effects on total phytoplankton biomass.

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