

# Effects of benthivorous and planktivorous fish on phosphorus cycling, phytoplankton biomass and water transparency of a tropical shallow lake

Danyhelton D. F. Dantas · Pablo L. Rubim · Fabiana A. de Oliveira ·  
Mariana R. A. da Costa · Caroline G. B. de Moura · Leonardo H. Teixeira ·  
José L. Attayde

Received: 15 July 2017 / Revised: 7 March 2018 / Accepted: 30 March 2018 / Published online: 13 April 2018  
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**Abstract** We investigated the roles of a benthivorous (*Prochilodus brevis*, Steindachner 1875) and a planktivorous (*Oreochromis niloticus*, Linnaeus, 1758) fish in translocating phosphorus from the benthic to the pelagic habitat of a tropical eutrophic shallow lake and its impact on phytoplankton biomass and water transparency. We performed two field experiments in 20 mesocosms (6 m<sup>3</sup>) with a 2 × 2 factorial design. Fish presence/absence was manipulated in combination with the presence/absence of a fish cage (4 m<sup>3</sup>) that prevented fish accessing the sediment. Benthivorous fish increased total phosphorus and chlorophyll a concentrations and decreased water transparency, but only when they had access to the sediment. Planktivorous fish increased the concentration of chlorophyll a without changing total phosphorus concentrations, whether or not they had access to the sediment. Results suggest that only the benthivorous fish increased phytoplankton biomass by translocating phosphorus from benthic to pelagic habitats. However, the planktivorous fish increased

phytoplankton biomass by removing zooplankton and recycling nutrients within the pelagic zone. We conclude that removal of either fish species can improve the water quality of eutrophic shallow lakes in tropical regions, but only the removal of benthivorous fish will reduce the internal loading of phosphorus.

**Keywords** Habitat coupling · Bioturbation · Nutrient transport · Water quality · Biomanipulation

## Introduction

Fish play a central role in maintaining the turbid state of shallow eutrophic lakes. This is because they increase phytoplankton primary production and biomass by controlling the abundance of herbivorous zooplankton (Carpenter & Kitchell, 1993; Scheffer, 1998), recycling nutrients within the pelagic zone and translocating nutrients from benthic to pelagic habitats (Vanni, 2002). Moreover, they can increase water turbidity by causing sediment re-suspension while searching for benthic food (Zambrano et al., 2001; Scheffer et al., 2003). Fish removal (i.e. biomanipulation) has long been used as a management tool to improve the quality of water in shallow eutrophic lakes in temperate regions (Hansson et al., 1998; Mehner et al., 2002; Cooke et al., 2005; Sondergaard et al., 2008; Jeppesen et al., 2012). However, few studies have investigated the role of fish in (sub)

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Guest editors: S. Nandini, S.S.S. Sarma, Erik Jeppesen & Linda May / Shallow Lakes Research: Advances and Perspectives

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D. D. F. Dantas · P. L. Rubim · F. A. de Oliveira ·  
M. R. A. da Costa · C. G. B. de Moura ·  
L. H. Teixeira · J. L. Attayde (✉)  
Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Natal, RN CEP 59078-970, Brazil  
e-mail: attayde@cb.ufrn.br

tropical shallow lakes and the effects of biomanipulation on the water quality of these systems (Jeppesen et al., 2012; Yu et al., 2016).

It has been suggested that (sub) tropical shallow lakes may not respond to fish manipulation in the way that shallow lake theory predicts, because zooplankton grazing pressure on phytoplankton is likely to be weaker in these systems than in temperate lakes (Jeppesen et al., 2007). This is because, in warm lakes, zooplankton is often dominated by small-sized grazers (Lacerot, 2010; Iglesias et al., 2011), while phytoplankton is often dominated by large colonial or filamentous cyanobacteria (Pearl & Huisman, 2008; Kosten et al., 2012) that cannot be grazed efficiently by such small-sized herbivores (Carpenter & Kitchell, 1993). Aggregation and colony formation may decrease cyanobacterial vulnerability to zooplankton grazing but it also, simultaneously, increases their vulnerability to omnivorous filter-feeding fish (Attayde et al., 2010). Attempts have been made to use filter-feeding fish to reduce phytoplankton biomass and improve water quality in some (sub) tropical shallow lakes (Lazzaro & Starling, 2005; Zhang et al., 2008). However, the effects of such nontraditional biomanipulation on phytoplankton biomass and water transparency have been contradictory (Attayde et al., 2010). A simple model of planktivory by omnivorous filter-feeding fish predicts that they could increase or decrease phytoplankton biomass, depending on the biomass of fish and the relative strengths of the direct grazing and indirect trophic cascade effects of these fish on the phytoplankton (Attayde et al., 2010).

The effects of benthivorous fish on phytoplankton biomass and water transparency in shallow lakes are likely to be more similar in temperate and tropical regions, although the higher proportion of benthivorous fish in tropical lakes may increase their importance (González-Bergonzoni et al., 2012). Benthivorous fish feed on benthic resources and release nutrients into the water column, translocating nutrients from benthic to pelagic habitats and transforming them from particulate to dissolved forms (Vanni, 2002). Nutrient translocation by benthivorous fish differs from nutrient recycling by planktivorous fish, because the latter release nutrients into the pelagic habitat in which food was ingested. Thus, nutrient translocation by benthivorous fish brings “new” nutrients into the euphotic zone, increasing the total mass of nutrients and stimulating “new

primary production” (Vanni, 2002). In contrast, nutrient recycling by planktivorous fish does not increase the mass of nutrients in the pelagic zone. Instead, it sustains “recycled production” (Vanni, 2002). In addition, some fish can also influence nutrient cycling and primary production through bioturbation of the sediment, which is defined as all transport processes carried out by animals that directly or indirectly affect sediment matrices (Kristensen et al., 2012). This process can occur due to feeding, resuspension and/or burrowing activities (e.g. nest building). Through bioturbation, these organisms can increase turbidity and nutrient concentration in the water column (Vanni, 2002; Croel & Kneitel, 2011; Adamek & Marsalek, 2013; Fulton et al., 2015).

In this study, we examined the effects of two omnivorous fish, a native benthivorous species (*Prochilodus brevis*, Steindachner 1875) and an exotic planktivorous species (*Oreochromis niloticus*, Linnaeus, 1758), on the phosphorus (P) cycling, phytoplankton biomass and water transparency of a shallow eutrophic man-made lake in the tropical semi-arid region of Brazil. These two species are the most important fish for inland water fisheries and aquaculture in this region. Because both of them can bioturbate lake sediment, we investigated whether their effects on water quality are mediated by their interactions with the sediment. The benthivorous *P. brevis* bioturbate the sediment by feeding on the sediment surface (Bowen, 1983; Flecker, 1996; Montoya et al., 2006; Taylor et al., 2006), while the planktivorous *O. niloticus* bioturbate the sediment by digging holes for nest building (Jiménez-Montealegre et al., 2002). We hypothesised that omnivorous fish interaction with the sediment is a key mechanism by which they affect the water quality of lakes. If our hypothesis is correct, then we predict that fish will increase total P (TP) and algal biomass and reduce water transparency when they have access to the sediment, but will not affect these variables when they do not.

## Materials and methods

### Experimental design

Two enclosure experiments were carried out in a shallow eutrophic man-made lake located within the

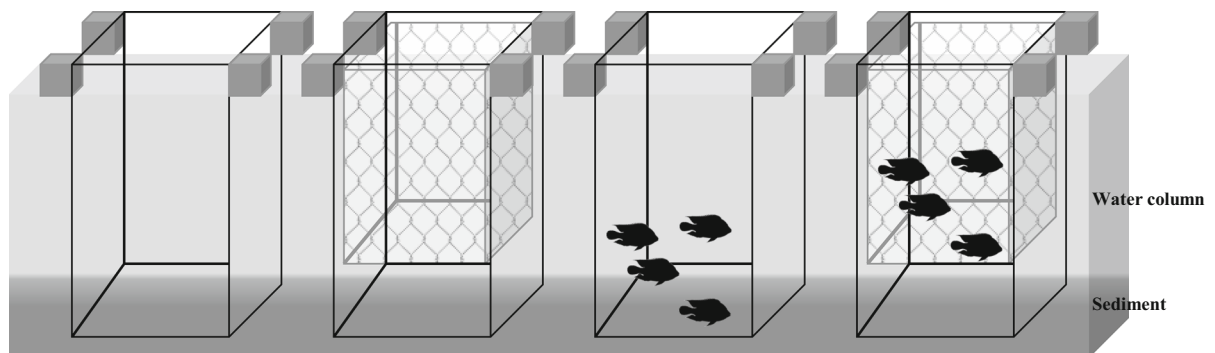
Ecological Station of Seridó, Rio Grande do Norte, Brazil (6°34'49.3"S; 37°15'20"W). The first experiment was conducted with the native benthivorous fish *Prochilodus brevis* (curimatã) between 20 June 2013 and 26 July 2013. The second experiment was conducted with the exotic planktivorous fish *Oreochromis niloticus* (Nile tilapia) between 10 February 2014 and 11 March 2014. Because the experiments were performed at different times, they had different initial conditions (Table 1). As a result of an extreme drought in the region during the period of study, the lake lost volume, and its maximum depth reduced

from 3.8 to 2.2 m for the first and second experiments, respectively (ESEC Lake in Costa et al., 2016).

The experiments had a 2 × 2 factorial design, where fish presence/absence was manipulated in combination with the presence/absence of fish access to the sediment (Fig. 1). The four treatments were randomly allocated across 20 mesocosms (4 m<sup>2</sup> area × 1.5 m depth) placed side by side in the littoral zone of the lake. All mesocosms were fixed to the lake bottom and isolated from the surrounding lake water by a transparent plastic film, but were open to the atmosphere and to the sediment inside the mesocosms. To prevent fish access to the sediment inside the mesocosms, fish were placed inside a cage (4 m<sup>2</sup> area × 1 m depth) with a 2-cm mesh size. Although the cage limited fish interaction with the sediment, it allowed all other chemical and biological interactions between the pelagic and benthic habitats to take place inside the mesocosms. In both experiments, fish were caught in the lake and added to the mesocosms shortly after the initial water samples were taken. Four individuals of the benthivorous fish (335.9 ± 35.9 g mean weight, i.e. ± 1SD) and three individuals of the planktivorous fish (482.5 ± 66.7 g mean weight i.e. ± 1SD) were added to each of the respective fish treatment mesocosms. Fish densities used in the experiments were within the range found in the experimental lake (Costa et al., 2016) and in other man-made lakes within the tropical semi-arid region of Brazil. At the end of the experiments, all fish were recovered from the mesocosms and re-weighed.

**Table 1** Limnological conditions of the experimental lake at the beginning of the first (Jun 2013) and second (Feb 2014) experiments (data from Costa et al., 2016)

Variable	Unit	Jun 2013	Feb 2014
Z maximum	m	3.8	2.2
Secchi disc	m	0.6	0.3
Temperature	°C	28.6	28.5
Conductivity	µS cm <sup>-1</sup>	250	374
pH		7.4	7.0
Dissolved oxygen	mg l <sup>-1</sup>	5.5	5.2
Turbidity	NTU	11.2	102.0
Total suspended solids	mg l <sup>-1</sup>	10.0	28.9
Fixed suspended solids	mg l <sup>-1</sup>	6.3	20.9
Volatile suspended solids	mg l <sup>-1</sup>	3.7	8.0
Total nitrogen	µg l <sup>-1</sup>	5387.0	2678.0
Total phosphorus	µg l <sup>-1</sup>	27.6	269.0
Chlorophyll a	µg l <sup>-1</sup>	41.2	20.1



**Fig. 1** The experimental design used in both experiments; two levels of fish (present/absent) were combined with two levels of cages (with/without). The presence of cages prevented fish access to the sediment within the mesocosms

## Sampling and analyses

Water samples were taken from each mesocosm just before fish additions and after 15 and 30 days. Oxygen concentration and water temperature were measured in situ with an oxygen probe. Water transparency was measured with a Secchi disc. Water samples were collected at different points within each mesocosm with a PVC tube (1.5 m in length) and integrated into a single representative sample for each mesocosm. Subsamples were taken to quantify total nitrogen [TN], TP and chlorophyll *a* [Chl *a*] concentrations and zooplankton densities. TN was analysed using a carbon analyser TOC-V *Shimadzu* with a TN analyser attached; TP was analysed using the ascorbic acid method after persulphate digestion (Valderrama, 1981), following the method of Murphy & Riley (1962). Chlorophyll *a* was determined in a spectrophotometer after filtration onto a 1.2 µm glass fibre filter (VWR 696); the pigment was extracted with ethanol (Jespersen & Christoffersen, 1988).

Zooplankton were counted and sorted into rotifers, cladocerans, calanoid and cyclopoid copepods, and copepod nauplii. They were grouped into small (rotifers and copepod nauplii) and large (cladocerans and adult copepods) zooplankton. Five subsamples from each sample were counted under a stereomicroscope. The average number per subsample was recorded for each group of organisms counted. This value was divided by the subsample volume (mL) and multiplied by the sample volume to estimate the density of organisms in the original sample (ind. l<sup>-1</sup>).

## Statistical analyses

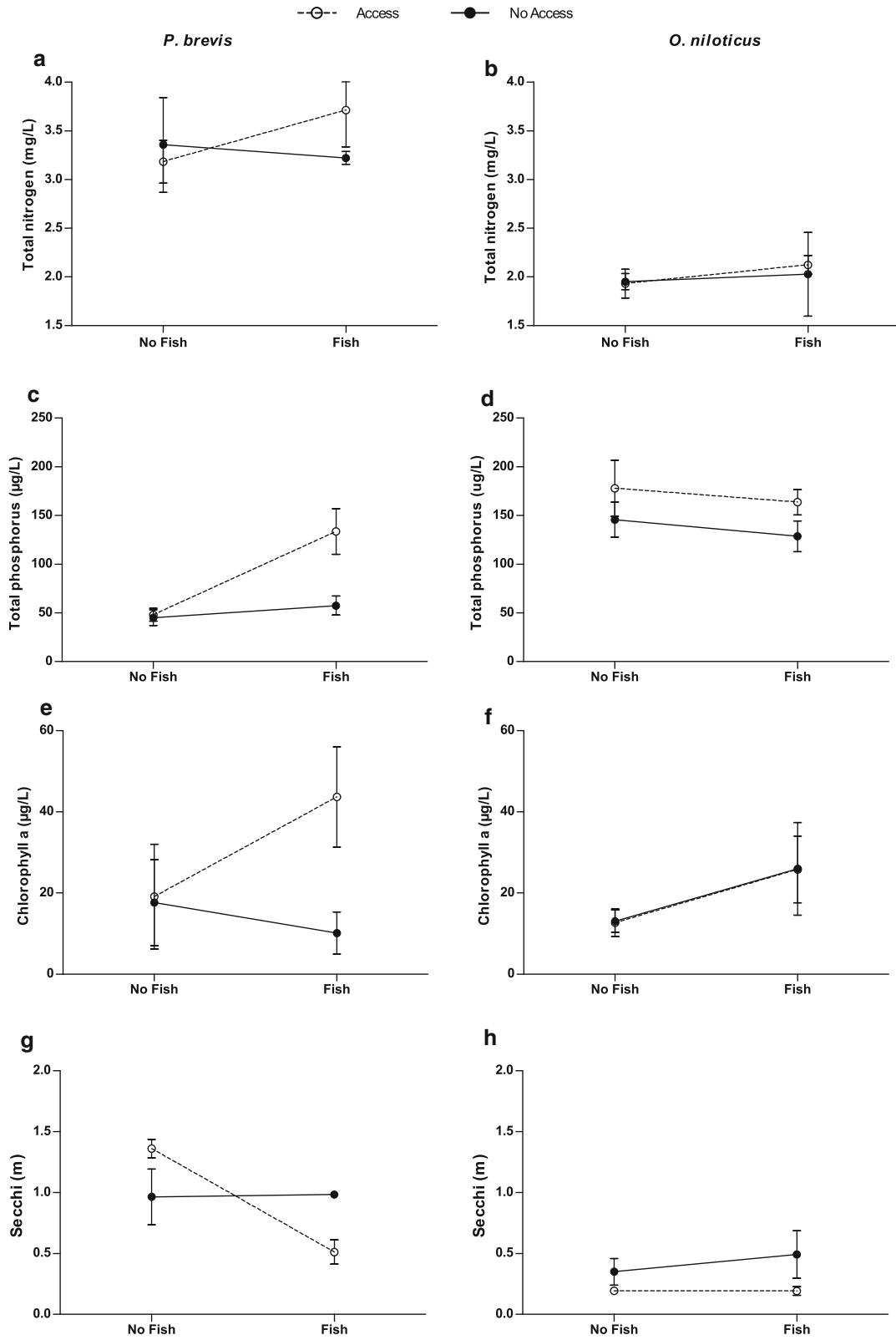
A one-way ANOVA was used to test for differences in the initial conditions between the treatments. A two-way ANOVA was used to test for the effects of fish and of their access to the sediment as well as the interaction between these two factors on the measured variables after 15 and 30 days. Before the statistical analyses, compliance with the ANOVA assumptions was checked with a normal probability plot of the residuals and a Levene's test of homogeneity of variances. When necessary, data were log-transformed to homogenise variances. A paired *t* test was used to test for differences in fish weight between the beginning and end of the experiments. For all analyses, *P* values were considered significant if *P* < 0.05. All

**Fig. 2** Mean values (± 1SD) of total nitrogen (a, b), total phosphorus (c, d), and chlorophyll *a* (e, f) concentrations, and Secchi disc transparency (g, h) in the experiments with benthivorous fish (left panels) and those with planktivorous fish (right panels). Open circles represent treatments with free access to the sediment (i.e. without cages); black circles represent treatments with no access to the sediment (i.e. with cages)

statistical tests and graphical outputs were performed using the GraphPad Prism 6.

## Results

In the first experiment, the benthivorous fish increased TP and chlorophyll *a* concentrations, and reduced water transparency, but only when they had access to the sediment as indicated by the significant interaction terms of the two-way ANOVA (Table 2; Fig. 2). In the second experiment, the planktivorous fish also increased chlorophyll *a* concentrations, but without changing the TP concentrations or the water transparency (Table 2; Fig. 2). Moreover, the effects of the planktivorous fish were independent of their access to the sediment, as indicated by the nonsignificant interaction terms of the two-way ANOVA (Table 2). No effect of fish on TN concentration was observed in either experiment (Table 2; Fig. 2). Zooplankton density was not affected by benthivorous fish, but was reduced by planktivorous fish whether or not they had access to the sediment (Table 2; Fig. 3). Zooplankton composition was changed by the planktivorous fish, which favoured small zooplankton over large zooplankton (though marginally significant); it was not affected by benthivorous fish (Table 2; Fig. 3). Finally, the benthivorous fish lost about 15% of their initial weight in both of the 'with fish' treatments during the first experiment (mean of the differences between final and initial weight was of - 53.44 g, with a 95% CI of 38.78–68.10, and - 55.63 g, with a 95% CI of 43.04–68.22, in the treatments with and without access to the sediment, respectively). In contrast, the planktivorous fish did not lose or gain weight in either of the 'with fish' treatments during the second experiment (Fig. 4).



## Discussion

Our results show that the two omnivorous fish species can increase phytoplankton biomass in shallow lakes through different mechanisms. The effects of the tropical benthivorous fish *P. brevis* on phytoplankton biomass and water transparency were clearly mediated through their interaction with the sediment. By feeding on benthic resources, resuspending sediments and releasing P into the water column, these fish increased P concentration in the pelagic zone. This P stimulated phytoplankton growth and reduced water transparency without changing total zooplankton density or community size structure. When placed inside the cages (i.e. fish treatment with no access to the sediment), the benthivorous fish had no effect on the variables measured. This supports our hypothesis that the key mechanism through which they affect phytoplankton biomass and water transparency is translocation of P

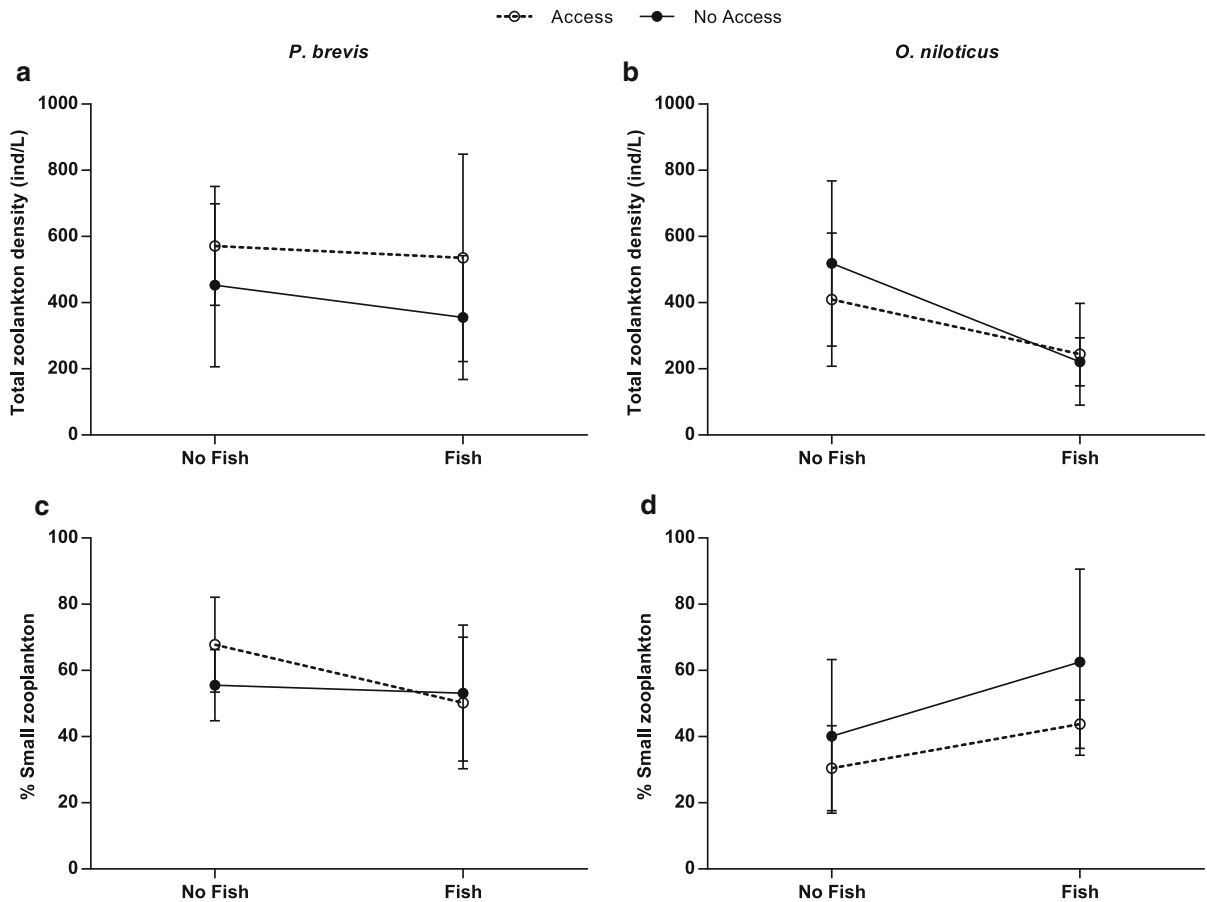
from the benthic to the pelagic habitat, as has been demonstrated for other benthivorous fish (Schaus & Vanni, 2000; Adamek & Marsalek, 2013). Although it is not possible to separate the effects of nutrient excretion from the resuspension of materials (i.e. sediment and detritus) when fish that have access to the sediment are feeding, our results suggest that resuspension of materials is the most likely mechanism involved. This is because the fish lost biomass during the experiment, and because TN concentration was not affected by the presence of fish as would have been expected if nutrient excretion was the dominant mechanism.

The effects of benthivorous fish on the water quality of tropical shallow lakes should be rather similar to those observed in temperate lakes. Some studies of temperate shallow lakes have shown that benthivorous fish enhance phytoplankton biomass (Meijer et al., 1990; Breukelaar et al., 1994; Zambrano & Hinojosa,

**Table 2** Results of the two-way ANOVA for the benthivorous (*P. brevis*) and planktivorous (*O. niloticus*) fish experiments

Variable	Effect	DF	<i>P. brevis</i>		<i>O. niloticus</i>	
			<i>F</i>	<i>P</i> value	<i>F</i>	<i>P</i> value
Total <i>N</i>	Fish	1	1.82	0.196	1.31	0.269
	Access to sediment	1	1.18	0.294	0.25	0.624
	Interaction	1	5.12	<b>0.038</b>	0.54	0.474
	Residual	16				
Total <i>P</i>	Fish	1	63.12	< <b>0.001</b>	3.10	0.098
	Access to sediment	1	41.21	< <b>0.001</b>	14.40	<b>0.002</b>
	Interaction	1	35.00	< <b>0.001</b>	0.02	0.877
	Residual	16				
Chlorophyll <i>a</i>	Fish	1	3.15	0.095	15.60	<b>0.001</b>
	Access to sediment	1	13.30	<b>0.002</b>	0.01	0.928
	Interaction	1	11.10	<b>0.004</b>	0.00	0.967
	Residual	16				
Secchi disc	Fish	1	42.44	< <b>0.001</b>	0.91	0.353
	Access to sediment	1	4.26	0.055	24.60	< <b>0.001</b>
	Interaction	1	50.45	< <b>0.001</b>	1.13	0.304
	Residual	16				
Total zooplankton	Fish	1	0.70	0.415	9.47	<b>0.008</b>
	Access to sediment	1	2.06	0.171	0.24	0.628
	Interaction	1	<b>0.014</b>	0.906	0.32	0.581
	Residual	16				
Microzooplankton	Fish	1	1.63	0.221	3.68	0.074
	Access to sediment	1	0.35	0.562	2.32	0.148
	Interaction	1	0.95	0.347	0.24	0.632
	Residual	16				

Significant values ( $P < 0.05$ ) are shown in bold



**Fig. 3** Mean values ( $\pm$  1SD) of total zooplankton density (a, b) and percentage of small-sized zooplankton (c, d) in the experiments with benthivorous fish (left panels) and in those with planktivorous fish (right panels). Open circles represent

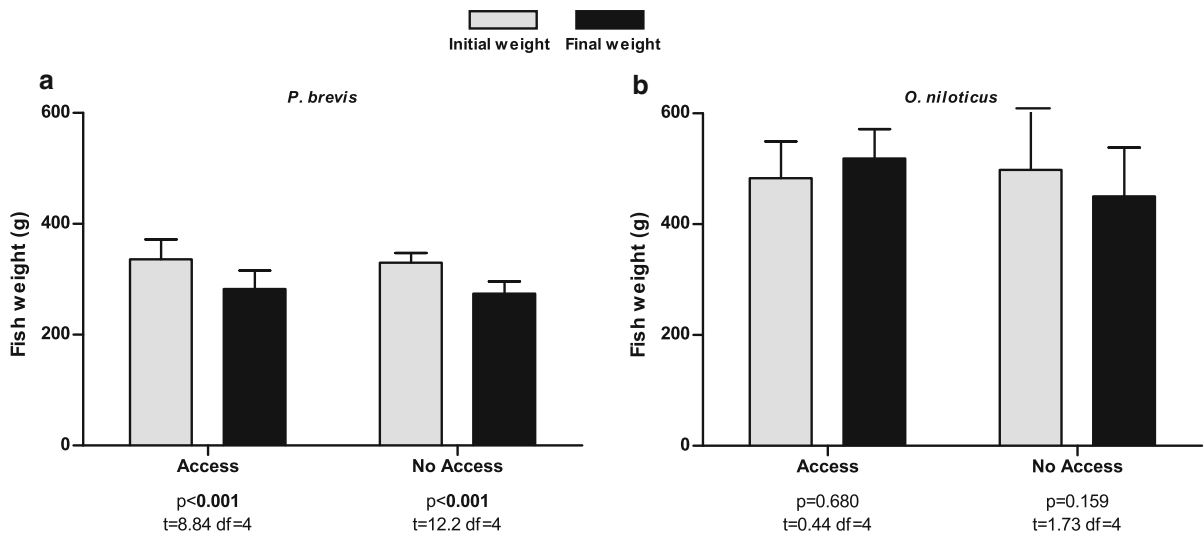
treatments with free access to the sediment (i.e. without cages); black circles represent treatments with no access to the sediment (i.e. with cages)

1999; Roozen et al., 2007; Adamek & Marsalek, 2013). This positive effect occurs through nutrient cycling that results from two functionally distinct processes: i) nutrient release by excretion and egestion, and ii) bioturbation of the sediment during foraging activities (Vanni, 2002). In addition, benthivorous fish can also affect the biomass and community structure of phytoplankton due to mechanical resuspension of settled algal cells (Misson et al., 2011). This could represent another positive impact of benthivorous fish on phytoplankton biomass, since sedimentation of viable phytoplankton cells appear to be one of the most significant processes whereby biomass is reduced in shallow lakes (Roozen et al., 2007).

Although the planktivorous Nile tilapia can also interact with the sediment, causing its resuspension

especially during nest building (Joyni et al., 2011), our results suggest that their effects on phytoplankton biomass had no relationship to their interaction with the sediment. The Nile tilapia increased phytoplankton biomass by reducing total zooplankton density and possibly by recycling nutrients within the pelagic zone. However, in contrast to the benthivorous fish, it did not increase the TP concentration in the water by bringing “new” P into the pelagic habitat from the benthic.

Despite its omnivory, the planktivorous Nile tilapia affected phytoplankton biomass in our study mainly through a trophic cascade, supporting results from a previous experiment (Okun et al., 2008) but contradicting those from another (Menezes et al., 2010); both of these experiments were performed in the same lake. The effects of Nile tilapia and other omnivorous filter-



**Fig. 4** Mean weight ( $\pm$  1SD) of the benthivorous (left panel) and planktivorous fish (right panel) at the beginning (grey bars) and end (black bars) of the experiments in the two fish treatments, with and without access to the sediment. The

*P* values of the *t* test for differences between the initial and final fish weights are shown below each treatment. Significant *P* values ( $< 0.05$ ) are shown in bold

feeding fish, like silver carp (*Hypophthalmichthys molitrix*), on total phytoplankton biomass can be either positive or negative (Starling et al., 1998; Figueredo & Giani, 2005; Attayde & Menezes, 2008; Okun et al., 2008; Rondel et al., 2008; Menezes et al., 2010). It is, therefore, not surprising that stocking with filter-feeding fish to improve the water quality of shallow eutrophic lakes in the tropics is a controversial issue (Zhang et al., 2008; Attayde et al., 2010). Some authors have suggested the removal of tilapias as an approach to improve the water quality of tropical lakes and reservoirs (Starling et al., 2002). Our results support this view.

Moreover, it has been suggested that (sub) tropical lakes may not respond to planktivorous fish manipulation, because zooplankton grazing pressure on phytoplankton is likely to be weak in these systems (Fernando, 1994; Jeppesen et al., 2007, 2017). Therefore, it is assumed that top-down control of phytoplankton is weaker in tropical lakes than temperate lakes and that removing planktivorous fish would have no, or only weak effects, on the water quality of tropical lakes (Lazzaro, 1997). Our results suggest the opposite. However, we recognise that the effects of omnivorous filter-feeding fish on water quality are uncertain, context dependent, vary with the species present and depend on the relative strengths of their

direct and indirect effects on phytoplankton (Attayde et al., 2010; Rao et al., 2015).

The two experiments in this study were performed at different times and under different initial lake depths and TP concentrations in the water. However, we believe that our results were not affected by those differences. The planktivorous fish experiment was performed in the drier year, when lake depth was lower. As no effect of sediment was observed under those conditions, it can be assumed that there would have been no effect if the water had been deeper. It would have been much more problematic if the benthivorous fish experiment had been performed in the drier year, because it could have been argued that the sediment effect was simply due to the shallower water. However, the lower lake depth during the planktivorous fish experiment did introduce a cage effect that was not present in the benthivorous fish experiment. During the planktivorous fish experiment, the fish cages touched the sediment once the depth of the mesocosms had fallen from 1.5 m to about 1.0 m. The disturbance created by the fish cages making contact with the surface of the sediment, whether they contained tilapia or not, may have increased sediment resuspension within the mesocosms and caused the observed ‘with cage’ effect (i.e. access effect) on TP concentrations and Secchi depth.



In conclusion, and contrary to the widely held belief that biomanipulation strategies are likely to be less effective in tropical than temperate lakes (Jeppesen et al., 2007, 2012, 2017), our results demonstrate that they have potential to improve water quality in shallow tropical lakes. Results from our experiments suggest that removing benthivorous and planktivorous fish may help to reduce phytoplankton biomass in eutrophic shallow lakes in both tropical and temperate regions. However, only the removal of benthivorous fish is likely to help to reduce the internal loading of P that tends to increase the resilience of the turbid state and delay restoration in shallow lakes once external P loads have reduced. In the tropical semi-arid region of Brazil, external loading of nutrients is naturally reduced, or almost absent, during a typical long dry season, but most shallow lakes in this area are highly eutrophic all year round (Brasil et al., 2016). Lake water management in the region could benefit from more biomanipulation programs, but whole lake experiments are needed to provide firm evidence for decision-makers of their potential to improve water quality.

**Acknowledgements** The authors thank Vanessa Becker and Andre Amado for their logistic support to the laboratory analyses. The authors greatly appreciate all insights and contributions from the two anonymous reviewers. They also thank the Brazilian Science Foundation (CNPq – [www.cnpq.gov.br](http://www.cnpq.gov.br)) for their financial support to JLA (CNPq/ICMBio number 13/2011) and the Coordination for the Improvement of Higher Education Personnel (CAPES-[www.capes.gov.br](http://www.capes.gov.br)) for the Ph.D. grants given to DDFD and PLR.

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