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RESEARCH PAPER OPEN ACCESS

Effects of two subtropical piscivorous fish species on sediment disturbance and water quality: Implication for restoration by stocking piscivores

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Abstract – Subtropical lakes are often dominated by benthi-omnivorous fish (*e.g.*, crucian carp) that may substantially disturb sediments and thereby increase water turbidity and nutrient concentrations. Piscivores stocking is sometimes used to control these benthi-omnivores in the expectation that they will reduce their adverse effects on the water quality. However, in shallow subtropical lakes the benthic foraging activities of piscivorous fish may also disturb sediments, a topic that has not yet been well elucidated. Here, we conducted a 6-day mesocosm experiment to explore the bioturbation effects of two native subtropical piscivorous fish (*i.e.*, snakehead, *Channa argus* and mandarin fish, *Siniperca chuatsi*) in prey fish (crucian carp, *Carassius carassius*) present and absent scenarios. Our results showed that in mesocosms without prey, both snakehead and mandarin fish greatly increased the concentrations of suspended solids. However, the concentrations of total, organic and inorganic suspended solids were significantly higher in the mesocosms with snakehead than in those with mandarin fish, suggesting that snakehead has higher bioturbation effects than mandarin fish. When crucian carp were present, we found that both snakehead and mandarin fish significantly reduced prey abundance, whereas piscivore stocking did not significantly decrease the suspended solids and nutrient concentrations. Our study revealed differential effects of two subtropical piscivorous fish species on sediment disturbance and water quality, and we suggest that for lake restoration with piscivores stocking, mandarin fish are a better option than snakehead fish as their predation effect was equal but the strength of sediment disturbance by mandarin fish was lower than that of snakehead.

Keywords: Biomanipulation / snakehead / mandarin fish / bioturbation / crucian carp

1 Introduction

An alarming escalation of eutrophication poses a serious threat to the health and water quality of lakes around the world (Carpenter, 2005; Howarth *et al.*, 2011; Cabrita *et al.*, 2015). Lake eutrophication reflects excessive loading (external and internal) of nitrogen and phosphorus, which may lead to an imbalance in nutrient cycling and affect stability of the lake ecosystem (Le *et al.*, 2010; Ferreira *et al.*, 2011; Cheng *et al.*, 2023). Fish are a major component of aquatic ecosystems and play a crucial role in nutrient cycling (Vanni, 2002; Weber and Brown, 2009) and ecosystem dynamics (Carpenter *et al.*, 1985). Biomanipulation, a widely used technique in lake management, seeks to improve water transparency and

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*Corresponding author: `hehu@niglas.ac.cn`; `kyli@niglas.ac.cn` ecological state (Shapiro *et al.*, 1975; Benndorf *et al.*, 2000), and is typically used to speed up recovery after nutrient loading reduction (Jeppesen *et al.*, 2012). A classical biomanipulation involves stocking of piscivorous fish to control planktivorous fish with the aim to trigger a cascading top-down control on phytoplankton by predation of zooplanktivorous fish (Horppila *et al.*, 1998; Drenner and Hambright, 1999; Carpenter *et al.*, 2001); this technique has particularly been used in temperate lakes, although with mixed results (Lyche *et al.*, 1990; Søndergaard *et al.*, 1997; Skov *et al.*, 2002).

In many subtropical shallow lakes (*e.g.*, Wuli Lake and Huizhou West Lake in China), the fish community is dominated by benthi-omnivorous fish (*e.g.*, crucian carp and common carp) (Xu *et al.*, 2016; Yu *et al.*, 2021; Guo *et al.*, 2022). Due to the higher temperature, they have higher metabolic and excretion rates, earlier and more frequent reproduction, and smaller sizes than temperate fish species (Teixeira-de Mello *et al.*, 2009; Jeppesen et al., 2010). One of the most detrimental effects of benthi-omnivorous fish is reworking of sediment at the sediment-water interface (bioturbation) (Meysman *et al.*, 2006), which leads to reduced water transparency, enhanced internal nutrient loading (Breukelaar *et al.*, 1994; Scheffer *et al.*, 2003; Volta *et al.*, 2013; Pledger *et al.*, 2017), and consequently increased phytoplankton growth and eutrophication (Zambrano *et al.*, 2001; He *et al.*, 2017; Liu *et al.*, 2020; Chen *et al.*, 2021).

Whether stocking of piscivorous fish can efficiently suppress benthi-omnivorous fish in warm eutrophic lakes is not well elucidated. One uncertainty is that, even if piscivory would lead to reduction of small benthi-omnivorous fish and thereby reduce their bioturbation strength, the predation activities of piscivorous fish on benthi-omnivorous fish occur near the sediment surface in shallow lakes, which may also lead to sediment disturbance and increased turbidity (Sfakiotakis *et al.*, 1999; He *et al.*, 2022). For instance, Li *et al.* (2018) stocked mandarin fish (*Siniperca chuatsi*) in Biandantang Lake in Hubei Province from 2010 to 2014, and they found that the abundance and biomass of prey fish such as crucian carp (*Carassius auratus*) decreased significantly, but the water transparency and chlorophyll *a* concentration did not improve compared with the period before stocking (2006 to 2008). He *et al.* (2022) also found that introducing snakehead (*Channa argus*) significantly reduced the biomass of *C. carassius*, but the concentration of inorganic suspended solids increased. Catfish (*Ictalurus punctatus*), another potential piscivore usually preying on the sediment-water interface, has been shown to increase the concentration of TP and phytoplankton biomass in aquatic mesocosms (Parkos *et al.*, 2003; Schrader *et al.*, 2016). The piscivory-induced bioturbation potentially weakens the success of fish manipulation. So far, few studies have well assessed the bioturbation effects of piscivorous fish in subtropical shallow lakes (Li *et al.*, 2018; He *et al.*, 2022).

Here, we conducted a mesocosm experiment to compare the bioturbation effects of two ‘sit-and-wait’ piscivores (snakehead, *C. argus*, and mandarin fish, *S. chuatsi*) in the presence/absence of benthi-omnivorous fish (crucian carp, *C. carassius*). We hypothesized that under subtropical shallow conditions: (1) snakehead and mandarin fish would cause bioturbation in the absence of predation activity on prey fish and (2) that snakehead and mandarin fish would decrease sediment disturbance of crucian carp by preying on them, resulting in water quality improvement.

2 Materials and methods

2.1 Experimental design

The outdoor mesocosm experiment was conducted at Taihu Laboratory for Lake Ecosystem Research (31°2′1″N, 120°25′16″E) in Jiangsu Province, Eastern China from August 27 to September 1, 2022. The mesocosms consisted of 24 opaque polyethylene buckets each with 100 cm diameter at the top, 85 cm diameter at the bottom, and 83 cm depth. Before the experiment, each mesocosm received 6 cm thick sediment from a nearby pond, after which it was filled with 450 L water for a week to create a clear water state. The sediment was homogenized and sieved through a 0.5 cm sieve to remove large particles of gravel and debris. The water was directly extracted from the surface of Lake Taihu via a pump. We used juvenile crucian carp (*C. carassius*) as the prey of the piscivorous fish. Crucian carp is the dominant fish species in most subtropical freshwaters and poses a major threat to the water quality (Lorenz *et al.*, 2013; Gu *et al.*, 2018). We selected mandarin fish (*S. chuatsi*) and snakehead (*C. argus*) as piscivores as these are widely distributed in subtropical lakes of China and have been commonly used for biomanipulation (Li *et al.*, 2018; Yu *et al.*, 2021). All fish were obtained from a local aquaculture facility and acclimatized in cages in Lake Taihu for one month prior to the commencement of the experiment. During the acclimation period, we fed the *S. chuatsi* and *C. argus* with live crucian carp every two days.

A two-way factorial experiment was carried out with two prey levels (crucian carp absent and present, respectively) and three piscivore levels (no piscivore, mandarin fish, snakehead). Each treatment had four replicates, making up a total of 24 experimental units. After the clearwater state was established (on August 26), crucian carp were randomly stocked into half of the total mesocosms, which were set as prey present treatments (Gao *et al.*, 2018; Gu *et al.*, 2020). Each crucian carp-present mesocosm was stocked with 10 crucian carp corresponding to density of 10 g m^{-2}, which is a commonly observed density in subtropical lakes (Yu *et al.*, 2016). The remaining half of the mesocosms had no crucian carp (prey absent treatments). One day after the stocking of crucian carp, mandarin fish and snakehead (1 ind. per mesocosm) were stocked into assigned mesocosms at a density of 9 g m^{-2}, and then the experiment began. Before introducing fish into the mesocosms, the average total length and wet weight of crucian carp, mandarin fish, and snakehead were 35.8 ± 1.5 mm and 0.56 ± 0.04 g, 78.9 ± 2.3 mm and 5.21 ± 0.17 g, and 94.5 ± 3.2 mm and 5.36 ± 0.27 g, respectively.

2.2 Sampling and monitoring

We collected 1-L samples of the water column (30 cm) daily in the morning in the middle of the mesocosm using an acrylic tube water sampler. The samples were analyzed for suspended solids. Total suspended solids (TSS) were determined by passing 500–1000 mL water samples through pre-combusted (450 °C for 2 h) and pre-weighed GF/C filters, which were then oven dried at 105 °C for 4 h and weighed followed by heating in a muffle furnace at 550 °C for 2 h to combust all organic matter and finally cooled in a desiccator to calculate the concentrations of inorganic suspended solids (ISS). Organic suspended solids (OSS) concentrations were calculated by subtracting the concentrations of ISS from TSS. On the last day of the experiment, besides suspended solids sampling, another 1-L water samples was collected for analysis of water chemicals and chlorophyll *a* (Chl *a*) concentrations. Total nitrogen (TN) and total phosphorus (TP) were examined using the unfiltered water samples by the alkaline potassium persulfate digestion-UV spectrophotometric method and the potassium persulfate oxidation-molybdenum blue colorimetric method, respectively (MEEPRC, 2002). Chl *a* was determined from filtered matter retained on a glass microfiber filter (Whatman GF/C International Ltd.) and extracted in a 90% acetone/water solution over 24 h, after which the concentrations were measured by a spectrophotometer (SEPA, 2002). After water sampling, we harvested all fish by emptying the water from mesocosms. The wet weight of each fish was measured. The relative growth rate (RGR) of piscivorous fish was calculated with the following equation:

$$\mathrm{RGR}\ (\%\ \mathrm{d}^{-1}) = 100 \times \mathrm{In}(W_t/W_0)\ /\ \mathrm{days}$$

where W_0 (g) and W_t (g) are wet weight of the piscivore per mesocosm at the beginning and end of the experiment, respectively.

2.3 Statistical analyses

The R software was used for statistical analyses and graph plotting (R Core Team, 2021). We fitted generalized linear mixed models (GLMMs, Bolker *et al.*, 2009) to explore the effects of both piscivores on suspended solids in prey present and absent scenarios. We used the interactive terms of piscivores (no piscivore, mandarin fish and snakehead) and stocking time (fixed effects) as a fixed factor in prey present and absent scenarios and included mesocosm identity as a random factor. We assumed Gaussian error distributions for all response variables and fitted modes using the *glmmTMB* function from the ‘glmmTMB’ package (Brooks *et al.*, 2017). Oneway analysis of variance (one-way ANOVA) was used to analyze the TN, TP, Chl *a*, survival of crucian carp and RGR of piscivorous fish between treatments at the end of the experiment, with Tukey's post-hoc multiple comparisons using the *TukeyHSD* function from the ‘multcomp’ package (Bretz *et al.*, 2002; Hothorn *et al.*, 2008). All data were log-transformed to ensure normality and homoscedasticity prior to fitting to GLMMs.

3 Results

3.1 Suspended solids

At the beginning of the experiment, there were no significant differences in the concentrations of total suspended solids (TSS), inorganic suspended solids (ISS), and organic suspended solids (OSS) between the treatments ($p > 0.05$; Fig. 1), indicating that all experimental groups were uniform before the fish were stocked. In the prey absent mesocosms, GLMMs confirmed significant interaction effects of stocking the two piscivores and time on the TSS and ISS concentrations ($p < 0.05$; Tab. 1). The interaction effect of stocking snakehead and time significantly increased the concentration of OSS ($p < 0.05$), while no effect of stocking mandarin fish and time interaction was observed ($p > 0.05$; Tab. 1). At the end of the experiment, the mean concentrations of TSS, ISS, and OSS were 9.6, 19.9, and 4.4 times higher, respectively, than in those without snakehead. For mandarin fish, TSS and ISS were 3.4 and 7.3 times higher, respectively, than when absent (Fig. 1).

In the crucian carp present mesocosms, stocking of the two piscivores and time had no significant interaction effects on TSS and ISS concentrations ($p > 0.05$; Tab. 1). The concentrations of TSS and ISS generally increased with time in all treatments, but particularly during the first day (Fig. 1). Stocking of snakehead and time increased the OSS concentration, and their interaction was significant ($p < 0.05$; Tab. 1). In the mandarin fish treatment, the OSS concentration did not alter significantly with time ($p > 0.05$; Tab. 1).

3.2 Nutrients and chlorophyll *a*

At the end of the experiment, in the crucian carp absent scenarios, the differences between all treatments were not significant for the mean TN and Chl *a* concentrations ($p > 0.05$; Fig. 2). The mean concentration of TP in the snakehead treatment was significantly and 62.5% higher than in the treatment with mandarin fish ($p < 0.05$; Fig. 2). For the scenarios of crucian carp presence, there were no significant differences in the concentrations of TN, TP, and Chl *a* between the three treatments ($p > 0.05$; Fig. 2).

3.3 Fish

At the end of the experiment, densities of crucian carp were significantly lower in the mesocosms with mandarin fish and snakehead than that in those without piscivores ($p < 0.001$; Fig. 3). All crucian carp survived in the non-stocked piscivore treatment, while two crucian carp evaded predation in each piscivore present mesocosm (Fig. 3). The RGRs of both piscivorous fish species were significantly lower in the treatments without crucian carp than in those with prey fish ($p < 0.001$; Fig. 4).

4 Discussion

We conducted a mesocosm experiment to compare the bioturbation effects of two native subtropical piscivores in the presence/absence of prey fish. Our results showed that when prey fish were absent, snakehead and mandarin fish disturbed the sediments and increased turbidity, but the bioturbation intensity of mandarin fish was significantly weaker than that of snakehead. When prey fish were present, both piscivores significantly reduced crucian carp density, but did not improve the water quality.

We found that when crucian carp were absent, snakehead and mandarin fish themselves caused significant sediment resuspension. Moreover, the concentration of ISS with snakehead stocking was significantly higher than in the mandarin fish treatment. This difference may be attributed to

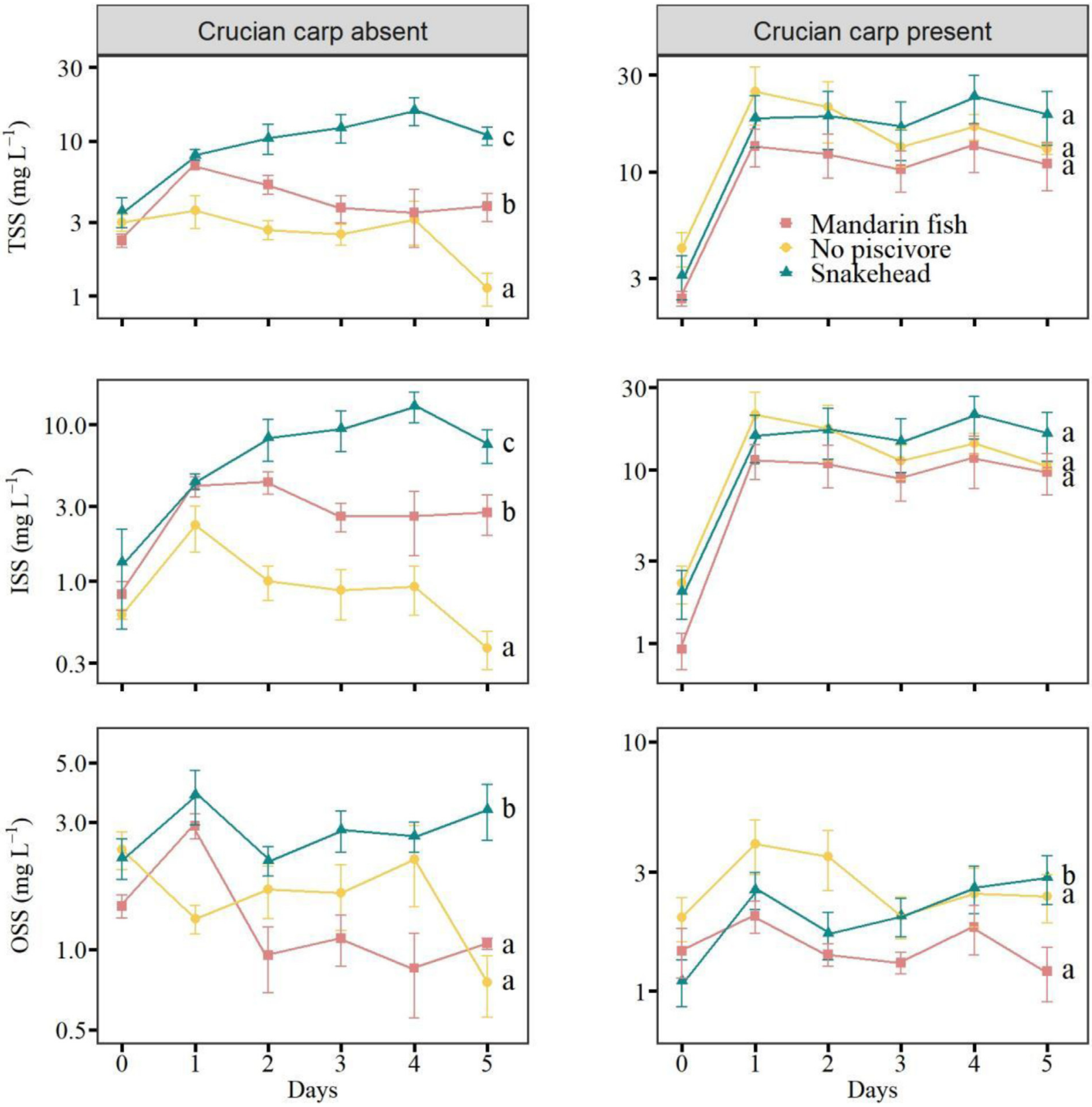

Fig. 1. Time series of total suspended solids (TSS), inorganic suspended solids (ISS), and organic suspended solids (OSS) in different treatments during the experiment. Values are means of the four replicates, and error bars represent standard error. Different letters indicate a significant difference in suspended solids concentrations at the end of the experiment, and the same letters mean not significant. Significance was set to $p < 0.05$.

different living habits and foraging strategies of the two fish species. The mandarin fish, an ambush predator, feed exclusively on live prey (*e.g.*, fish and shrimps) (Ding *et al.*, 2021; Li *et al.*, 2023) and refuse dead prey (Yi *et al.*, 2013; Liu *et al.*, 2015; Dou *et al.*, 2018). When there is no live prey, the mandarin fish generally stay at the bottom and only move occasionally (Liang, 1995), implying minor bioturbation effects. The northern snakehead, another 'sit-and-wait' foraging fish species (Liu *et al.*, 2000) also feed on live prey (Wang *et al.*, 1997), but also feed on dead prey and artificial diets (Liang *et al.*, 2001). Although we did not confirm that snakehead stirs the sediment when searching for prey, Love and Newhard (2021) observed that the northern snakehead (*C. argus*) preferred to burrow into the sediment, possibly as a means for escaping the heat during the summer months. On the other hand, snakehead often sticks its head out of the water surface for breathing via an accessory respiratory organ called a 'fold gill' (Hu and Yi, 1960) and immediately dives into the sediment if frightened (Miu, 1957). Stronger bioturbation may be caused when snakehead shuttle between the water surface and sediment compared with the less active mandarin fish. Pandian and Vivekanandan (1976) reported that starving snakehead (*Ophiocephalus striatus*, 750 ± 70 mg, 4.5 ± 0.5 cm) exposed to 31 cm depth of water swam more than 300 m per day during the first five days of their experiment. Thus, although both snakehead and mandarin fish may disturb the

Table 1. Summary of generalized linear mixed models results on the effect of piscivorous fish on suspended solids in prey present (PP) and absent (PA) scenarios.

Variables	Prey treatment	Coefficients	Estimate	Std. error	z value	*p*
TSS	PA	I	0.552	0.084	6.544	**<0.001**
		T	−0.075	0.021	−3.539	**<0.001**
		M	0.045	0.119	0.373	0.709
		S	0.147	0.119	1.234	0.217
		T * M	0.066	0.030	2.207	**0.027**
		T * S	0.171	0.030	5.730	**<0.001**
	PP	I	0.951	0.116	8.209	**<0.001**
		T	0.059	0.032	1.853	0.064
		M	−0.240	0.164	−1.467	0.142
		S	−0.149	0.164	−0.908	0.364
		T * M	0.028	0.045	0.619	0.536
		T * S	0.056	0.045	1.241	0.215
ISS	PA	I	0.050	0.127	0.394	0.693
		T	−0.074	0.038	−1.978	**0.047**
		M	0.212	0.180	1.174	0.241
		S	0.224	0.180	1.244	0.214
		T * M	0.115	0.053	2.160	**0.031**
		T * S	0.240	0.053	4.523	**<0.001**
	PP	I	0.762	0.140	5.463	**<0.001**
		T	0.089	0.040	2.229	**0.026**
		M	−0.324	0.197	−1.643	0.100
		S	−0.107	0.197	−0.543	0.587
		T * M	0.055	0.056	0.971	0.332
		T * S	0.047	0.056	0.838	0.402
OSS	PA	I	0.310	0.097	3.178	**0.001**
		T	−0.068	0.025	−2.738	**0.006**
		M	−0.078	0.138	−0.567	0.571
		S	0.068	0.138	0.491	0.624
		T * M	−0.002	0.035	−0.043	0.966
		T * S	0.083	0.035	2.338	**0.019**
	PP	I	0.408	0.081	5.039	**<0.001**
		T	−0.012	0.020	−0.618	0.537
		M	−0.215	0.114	−1.877	0.061
		S	−0.283	0.114	−2.474	**0.013**
		T * M	−0.005	0.028	−0.172	0.863
		T * S	0.073	0.028	2.562	**0.010**

Note: I, model intercept; T, time; M, mandarin fish; S, snakehead.

sediment, our results suggest that snakehead has a greater impact on sediment resuspension than mandarin fish when prey fish are scarce.

In the crucian carp present treatments, snakehead and mandarin fish significantly reduced crucian carp abundance. At the end of the experiment, standing crops of crucian carp in the mandarin fish and snakehead treatments were reduced by 80% to 2 g m^{-2}. A successful biomanipulation case using piscivores stocking (*i.e.*, pike and perch) in Lake Udbyover indicated that the final biomass of benthivorous fish (*i.e.*, crucian carp and roach) exceeded 4 g m^{-2} (Skov *et al.*, 2002), which was higher than in of our experiment (approximately 2 g m^{-2}; Fig. 3). However, although crucian carp thus were reduced in our experiment, the water clarity and nutrient concentrations did not improve, indicating that snakehead and mandarin fish stocking were not efficient in improving water clarity on the short term, in part due to predator-induced sediment disturbance. Another mesocosm experiment with snakehead stocking (He *et al.*, 2022) and a whole-lake biomanipulation experiment with mandarin fish (Li *et al.*, 2018) concur with our results of poor effect on water clarity.

In both the prey-absent and the prey-present scenarios, snakehead stocking resulted in significantly higher concentrations of OSS than mandarin fish stocking, which may also be attributed to the living habits of the piscivores. Compared to the inactive mandarin fish, snakehead travelled back and forth between the sediment and water surface in our mesocosms, causing stronger sediment disturbance and thereby translocation of more nutrients from the benthic to the pelagic zones (Shormann and Cotner, 1997; Dantas *et al.*, 2018), although TN and TP at the end of experiment were not statistically significant. The phenomenon that fish-induced sediment resuspension increases algal concentrations has been well elucidated in many benthi-omnivorous fish (*e.g.*, common carp

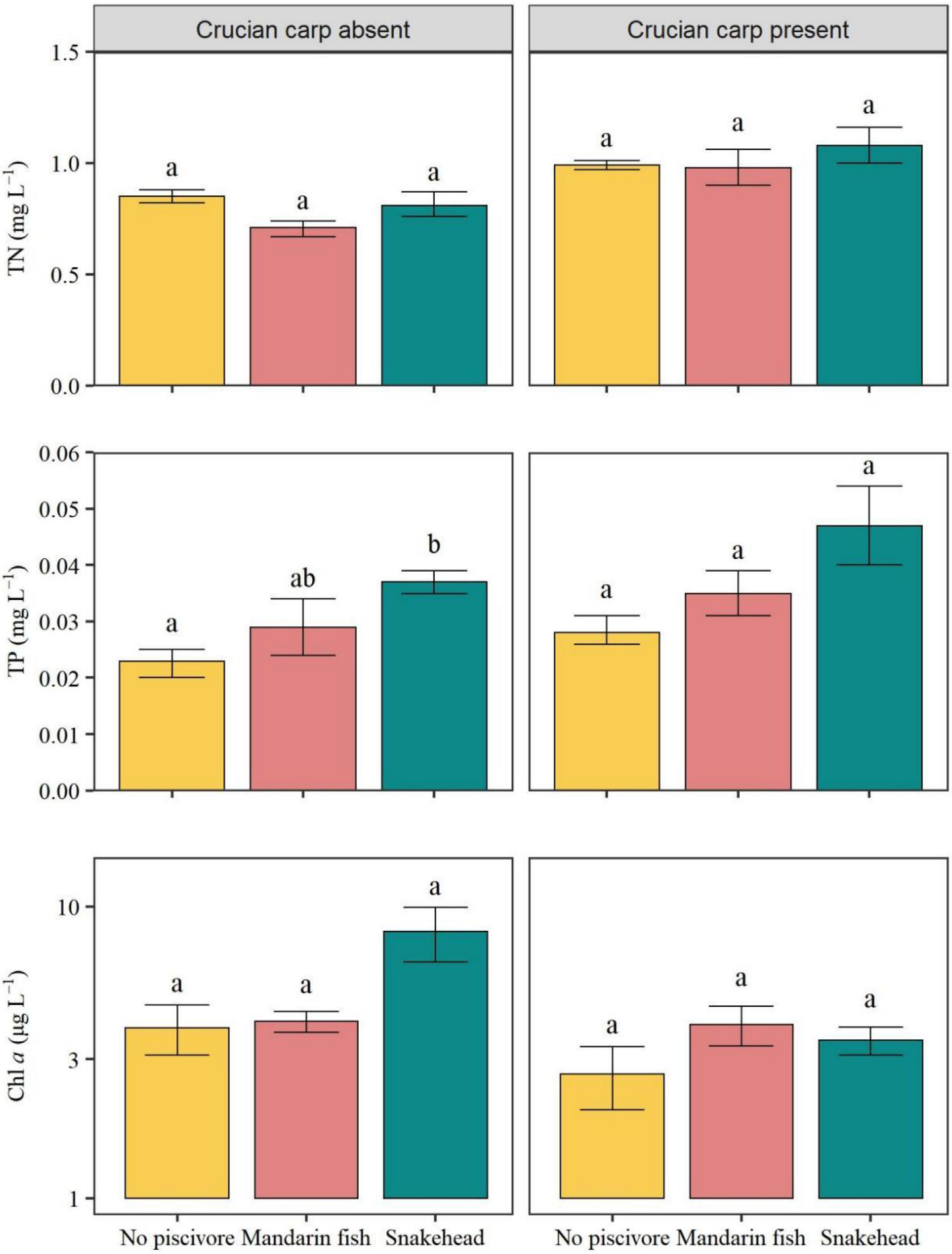

Fig. 2. TN, TP, and Chl *a* concentrations in the different treatments at the end of the experiment. Values are means of the four replicates, and error bars represent standard error. Different letters indicate a significant difference in TN, TP, and Chl *a* concentrations, and the same letters mean not significant. Significance was set to $p < 0.05$.

and crucian carp) studies (Roozen *et al.*, 2007; Badiou and Goldsborough, 2015; He *et al.*, 2017; Han *et al.*, 2022). Our study showed that the non-algal turbidity was augmented by benthi-piscivorous fish in the absence of predation. It is worth noting that regardless of whether prey fish were present or not, snakehead increased algal turbidity.

Our study showed clear bioturbation effects of subtropical piscivorous fishes. Therefore, cautions should be taken in lake restoration when using piscivore stocking. Our results also showed that the strength of sediment disturbance caused by mandarin fish was lower than that of snakehead fish. However, being a mesocosm study, our experiment has clear weaknesses concerning both scale and duration. The small size of the mesocosm (about 0.5 m^3) may have exaggerated the extent of sediment disturbance and the short duration of the experiment may have increased the predation loss of prey. Follow-up

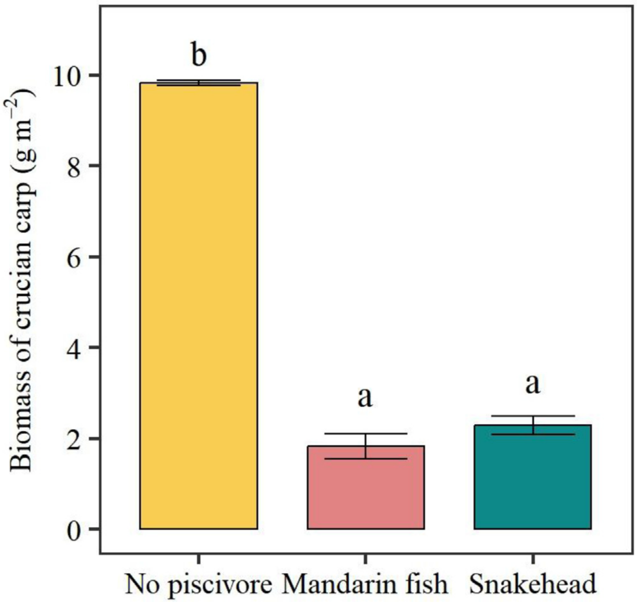

Fig. 3. The biomass of crucian carp in different treatments at the end of the experiment. Values are means of the four replicates, and error bars represent standard error. Different letters indicate a significant difference, and the same letters mean not significant. Significance was set to $p < 0.001$.

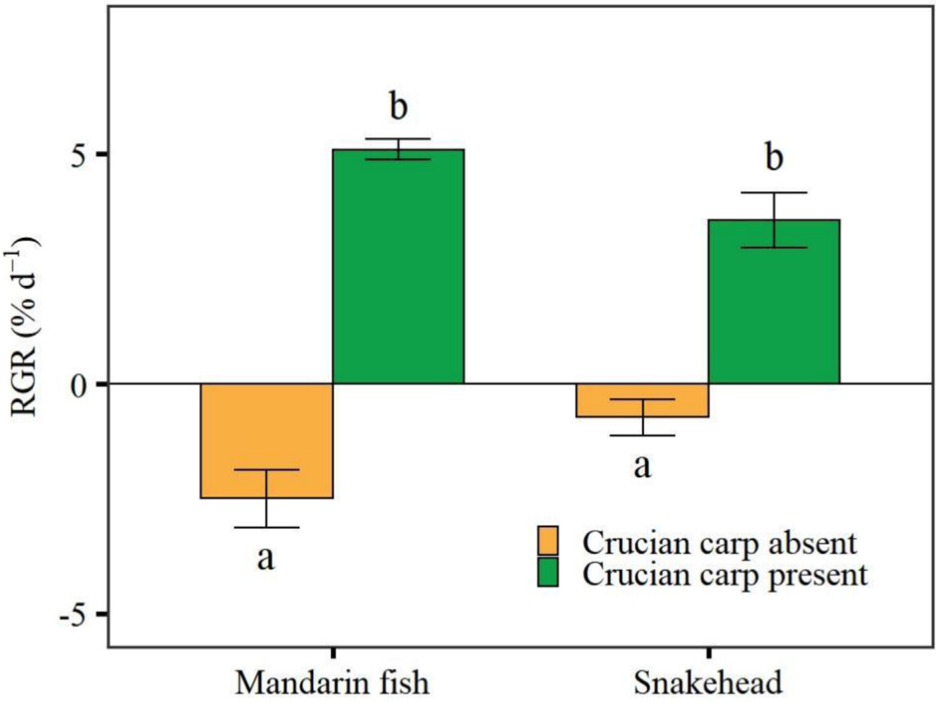

Fig. 4. RGRs of mandarin fish and snakehead in the crucian carp present and absent treatments. Values are means of the four replicates, and error bars represent standard error. Different letters indicate a significant difference, and the same letters mean not significant. Significance was set to $p < 0.001$.

large-scale experiments should be conducted to fully elucidate the role of the subtropical freshwater piscivores.

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Declaration of competing interest

None declared.

Data availability statement

All data were present in the paper.

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