Piscivore stocking significantly suppresses small fish but does not facilitate a clear-water state in subtropical shallow mesocosms: A biomanipulation experiment

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HIGHLIGHTS

- Stocking of piscivorous snakehead suppresses small carp but does not increase zooplankton herbivory.
- Snakehead stocking inversely increases water turbidity by bioturbation in subtropical mesocosms.
- Biomanipulation by stocking of snakehead to improve water quality is not recommendable in warm lakes.

GRAPHICAL ABSTRACT
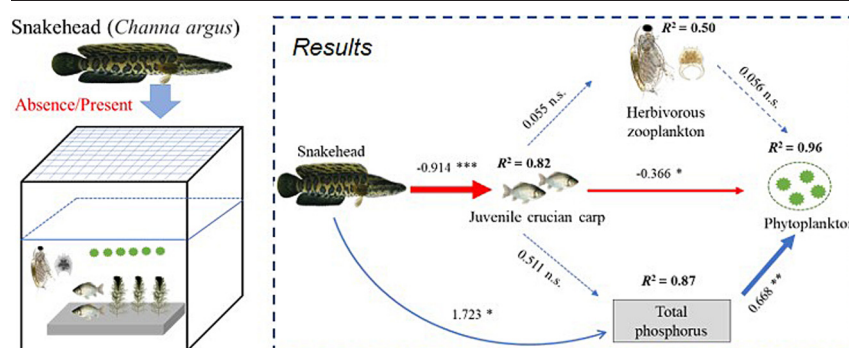
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ABSTRACT

Biomanipulation by piscivore stocking has been widely used to combat eutrophication in north temperate lakes, but its applicability in warm lakes has not yet been well elucidated. Here, we used experimental mesocosms to test the effects of a native benthi-piscivore (snakehead, *Channa argus* Cantor) on water clarity under subtropical conditions where small omni-benthivorous fish like crucian carp (*Carassius carassius* L.) prevail. Our results showed that, despite of a great reduction of crucian carp biomass, snakehead stocking did not create a strong trophic cascade as neither (herbivorous) zooplankton biomass nor their grazing pressure, indicated by biomass ratio of (herbivorous) zooplankton to phytoplankton, changed significantly. Moreover, snakehead stocking significantly increased water non-algal turbidity as well as nutrient and chlorophyll-*a* concentrations, suggesting that these benthi-piscivores also disturbed sediments like crucian carp did. Our study showed that biomanipulation by stocking of snakehead does not facilitate clear-water state in warm shallow lakes, even on the short-term.

1. Introduction

Despite the fact that major efforts have been made worldwide to improve the ecological quality of shallow lakes by reducing the external nutrient loading, many of them have remained eutrophic and turbid (Jeppesen et al., 2007; Gulati et al., 2008; Chen et al., 2013). A method

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to accelerate lake recovery after external loading reduction is biomanipulation, a term coined in 1975 and since embraced as one of the more controversial applications of ecological theory (Shapiro et al., 1975; DeMelo et al., 1992; Hansson et al., 1998; Jeppesen et al., 2012). Generally, the word refers to manipulation of the fish community, e.g., removal of zooplanktivorous fish and stocking of piscivorous fish, to reduce predation on large-sized zooplankton such as *Daphnia* spp.. This, in turn, should lead to higher grazing on phytoplankton and, subsequently, increased water clarity (Carpenter et al., 1985; Hansson et al., 1998; Jeppesen et al., 2012).

Although numerous lab, enclosure and whole-lake studies have found clear cascading effects on lower trophic levels following introduction of a piscivore predator (Jacobsen et al., 1997; Carpenter et al., 2001; Skov et al., 2002; Olin et al., 2006; Potthoff et al., 2008), the effectiveness and the long-term stability of piscivore stocking remain equivocal (DeMelo et al., 1992; Hansson et al., 1998; Søndergaard et al., 2007; Jeppesen et al., 2012). Several fish manipulation experiments have failed to achieve enhanced zooplankton herbivory on phytoplankton (Hansson et al., 1998; Liu et al., 2018; Kokkonen et al., 2019). For instance, a meta-analysis revealed a strong effect of fish manipulation on phytoplankton in only about one-third of 54 separate enclosure and pond experiments (Brett and Goldman, 1996). Theoretically, a trophic cascade, despite widespread, does not necessarily occur in natural ecosystems (Pace et al., 1999; Polis et al., 2000; Su et al., 2021). A variety of factors, such as food web complexity (i.e., omnivory), resource quality and edibility, as well as landscape factors such as spatial subsidies and refugia, may affect the strength and occurrence of community-level trophic cascades (Polis et al., 2000; Pujoni et al., 2016; Wootton, 2017; He et al., 2021; Su et al., 2021). In previous biomanipulation experiments, strong short-term trophic cascades are usually seen in systems when large *Daphnia* are the primary herbivores, but not when smaller-bodied herbivores are dominant (Brett and Goldman, 1996). This may reflect that the food webs in the former ecosystem type had a simple chain–like structure, while being more reticulated in the latter type (McCann et al., 1998; Hart, 2002). Therefore, the effect of stocking piscivorous fish on a natural freshwater lake ecosystem may be context dependent (Lazzaro et al., 2003; Jeppesen et al., 2012).

Besides trophic cascades, underlying mechanisms of stocking of piscivores may also involve reduction of the risk of sediment resuspension by benthivorous fish, leading to increased water clarity (Skov et al., 2002; Bernes et al., 2013). A decrease in fish-induced sediment disturbance may further reduce the nutrient release from sediments and thereby limit eutrophication via bottom-up control (Starling et al., 2002; Han et al., 2020). For instance, Skov et al. (2002) found a major decline in suspended solids, total phosphorus concentrations, and chlorophyll-*a* concentrations after stocking of 0^+ pike (*Esox lucius*) and perch (*Perca fluviatilis*, 20–30 cm length) in a shallow eutrophic lake in Denmark.

In most studies, the effects of stocking of piscivores and potential mechanisms have been well studied in shallow lakes in temperate regions such as North Europe and North America (Jacobsen et al., 1997; Hansson et al., 1998; Carpenter et al., 2001; Skov et al., 2002; Olin et al., 2006; Potthoff et al., 2008). Despite recent advances (Mazzeo et al., 2010; Jeppesen et al., 2012; Ofir et al., 2017; Liu et al., 2018), the applicability of piscivore stocking for restoration of warm (i.e., subtropical, tropical and Mediterranean) shallow eutrophic lakes is not well assessed. Compared to temperate regions, trophic cascades are expected to occur less frequently in warm lakes due to the more complex food webs characterized by factors such as high abundance of invertebrate predators, high dominance of small-sized zooplankton species, and a high degree of fish omnivory (Lazzaro, 1997; Meerhoff et al., 2007; Jeppesen et al., 2012; Su et al., 2021). For instance, restoration attempts involving fish manipulation in subtropical Huizhou West Lake in China and Lake Kinneret in Israel showed no obvious increases of zooplankton herbivory after fish removal and piscivore stocking (Blumenshine and Hambright, 2003; Ofir et al., 2017; Lin et al., 2014). Piscivores may also disturb the sediment, directly or indirectly, by chasing their prey. However, so far, no experimental studies have elucidated the effects of piscivore stocking on bottom-up processes,

i.e., sediment resuspension and nutrient release caused by fish foraging, which is often considered as more important than top-down process in warm lakes (Liu et al., 2018, 2020).

Here, we used experimental mesocosms to evaluate whether stocking of a native piscivore could facilitate a clear-water state in warm shallow lakes and reveal the potential mechanisms top-down and bottom-up processes involved. We set an initial clear-water scenario which was achieved by plant transplantation, a common restoration method in warm lakes (Liu et al., 2018). We then stocked high abundance of small omni-benthivorous fish which potentially made the clear-water state unstable (Jeppesen et al., 2012). We hypothesized that measures like piscivore stocking through predation on these omni-benthivorous fish may help maintaining the clear water state by increasing the zooplankton grazing on phytoplankton and reducing bioturbation due to a decline of fish benthivory, at least on the short-term (Fig. 1a; Carpenter et al., 2001; Skov et al., 2002; Potthoff et al., 2008).

2. Materials and methods

2.1. Experimental setup

The outdoor mesocosm experiment was conducted from June 9 to August 9, 2021 at Eastern Lake Taihu Field Station, situated on the southeast shore of Lake Taihu, China (31°02′1.32″N, 120°25′15.71″E). The mesocosms were nine square cement mesocosms with a side length of 3 m and a depth of 2.5 m (Fig. 1b-c). On 7 May, nine plastic frames (2 m long, 1.5 m width and 0.15 m height) filled with a 5 cm layer of sediments were prepared for planting of the submerged macrophyte *Myriophyllum spicatum*. The sediments were collected from a nearby pond and well-mixed to ensure homogeneity before addition. *M. spicatum* is common in freshwater waterbodies and grow well during late spring and summer in the subtropics. We collected top shoots (15 cm long) of the *M. spicatum* from the nearby pond and carefully rinsed them with a soft brush and clean water to remove mud and periphyton. We planted 50 shoots of *M. spicatum* (10 columns and 5 rows) in each plastic frame. Afterwards, we placed the plastic frame in the center of each mesocosm and filled lake water to a water depth of 1 m. The water that we added to mesocosms was all pre-screened (3-mm mesh size) to remove large inorganic particles and organisms such as small fish and amphipods. We
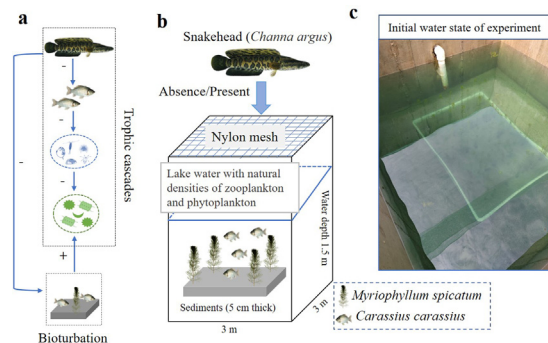

Fig. 1. A conceptual framework (a) illustrating the potential effects of stocking of piscivorous fish on phytoplankton growth in subtropical shallow lakes. Stocking of piscivorous fish may reduce small omnivorous fish and thereby increase zooplankton grazing on phytoplankton through trophic cascades, a top-down route. Stocking of piscivorous fish may simultaneously reduce bioturbation of crucian carp and thereby decrease nutrient availability of phytoplankton, a bottom-up route. (b) Experimental design and (c) a picture of mesocosms: Nine top-open concrete pools of 3 m × 3 m × 1.5 m (depth) filled with unfiltered lake water including natural phytoplankton and zooplankton communities. We transplanted the submerged macrophyte, *Myriophyllum spicatum*, and released juvenile crucian carp, *Carassius carassius*, to each mesocosm with an equal biomass before the experiment began. Subsequently, we stocked snakehead (*Channa argus*) to six assigned mesocosms. For further details see Methods.

used a nylon mesh (3-mm mesh size) to cover each mesocosm to prevent entry by frogs, snakes, and terrestrial insects.

After 15 days (on 22 May), the water was clear and the plants grew well (Fig. 1c), and lake water to a final depth of 1.5 m was then added. On May 29, the juvenile crucian carp, *Carassius carassius*, with an average total length of (2.10 ± 0.19) cm and a wet weight of (0.22 ± 0.07) g, were collected from a local aquaculture company, and 900 individuals were added to each mesocosm, corresponding to 220 kg ha^{-1}, which is comparable to the natural fish biomass observed in Lake Taihu (Mao et al., 2020). Crucian carp (*Carassius carassius* L.) is a widespread omni-benthivorous fish species in subtropical and tropical freshwater waterbodies and constitute a major threat to the water clarity in warm shallow lakes (Gao et al., 2014). Studies have shown that juvenile crucian carp can enhance eutrophication by unrooting submerged macrophytes, disturbing sediments, enhancing internal loading, and preying on herbivorous zooplankton and zoobenthos (Gu et al., 2016, 2018; He et al., 2017; Han et al., 2020). In hypereutrophic lakes, however, gut content analysis showed that crucian carp also ingest bloom-forming and/or filamentous phytoplankton (Kolmakov and Gladyshev, 2003; Liu, 2008).

In our experiment we used snakehead, *Channa argus* Cantor, as it is one of the most common benthic piscivores in warm shallow lakes in China, and therefore occur together with crucian carp in many lakes in eastern China (Yu et al., 2016). Juvenile 0$^+$ snakehead (total length: 17.1 ± 1.5 cm, wet weight: 50.9 ± 14.3 g) were collected from the same local aquaculture company on 29 May and acclimatized in lake water for 10 days. Piscivore density was the single treatment factor in our experiment. According to the range of piscivore dominance in 20 shallow lakes in the middle and lower Yangtze River basin (Yu et al., 2021), we originally set three density levels, each with three replicates. That is, we added two individuals to each of three mesocosms (36 % piscivore dominance in terms of biomass), and three individuals to another three mesocosms (41 % piscivore dominance). The remaining three mesocosms functioned as controls (0 %). The experiment began after the snakehead individuals were stocked in their assigned mesocosm.

2.2. Sampling and processing

2.2.1. Nutrients, chlorophyll-a, and suspended solids

Nutrient samples were collected at 10-day intervals during the experiment. Suspended solids were measured on June 9, June 29, July 19, July 29, and August 9. At each sampling event, we collected 15 L water samples from three different depths (surface, ~60 cm, and ~ 120 cm) and mixed them for each mesocosm. We collected 2 L depth-integrated water samples for laboratory analyses of nutrient, suspended solids, and chlorophyll-*a* (Chl-*a*) concentrations.

In the laboratory, total nitrogen (TN), total phosphorus (TP), total dissolved nitrogen (TDN), and total dissolved phosphorus (TDP) were determined through colorimetry after digestion with $K_2S_2O_8$ and NaOH solution (APHA, 1998). Total suspended solids (TSS) were determined from 100 to 200 mL water samples filtered through pre-combusted (450 °C for 2 h) and pre-weighed GF/C filters, which were then dried to a constant weight at 60 °C for 48 h. After determining TSS, the filters were combusted in a muffle furnace at 550 °C for 2 h, cooled in a desiccator, and finally weighed to determine the level of inorganic suspended solid (ISS). We used ISS concentration as a proxy of bioturbation strength.

Chlorophyll-*a* concentrations were measured spectrophotometrically from matter retained on a GF/C filter and extracted in a 90 % (*v/v*) acetone/water solution for 24 h. No correction was carried out for pheophytin interference (SEPA, 2002).

2.2.2. Zooplankton and phytoplankton

Zooplankton and phytoplankton communities were sampled at 20-day intervals. We filtered 10-L depth-integrated water samples through a 64-μm net and preserved the retained material in Lugol's solution. Crustacean zooplankton (cladocerans and copepod adults and copepodites) were counted at magnifications between 10× and

40×, while rotifers were counted at 100× magnification. Species represented by >100 individuals were considered dominant and identified according to Chiang and Du (1979) and Shen and Du (1979). Copepod nauplii were counted without further taxonomic distinction. Zooplankton biomass (dry weight) was estimated using equations from Dumont et al. (1975) and Huang (1999). Where possible, up to 20 individuals of each taxon were measured.

For phytoplankton, a 1-L depth-integrated water sample was taken from each mesocosm and sedimented for 48 h after being treated with 10 mL Lugol's iodine solution. The supernatant was removed, and the residue was collected and examined at ×100 – ×400 magnification for enumeration of phytoplankton. Phytoplankton was identified to genus level according to Hu and Wei (2006) and following recent taxonomic revisions (Guiry and Guiry, 2021). The biomass of common phytoplankton taxa was calculated based on cell size measurements of at least 30 cells of each taxon and using formulae for geometric shapes approximating cell forms (Zhang and Huang, 1991). Where possible, at least 1000 cells of each taxon were counted per sample, but for less common taxa the calculations were based on fewer measurements.

2.2.3. Fish and sumberged macrophytes

On 14, 21, 29 July and 5, 9 August, we placed a fish trap (length: 3 m; width: 0.25 m; height:0.2 m) in each mesocosm overnight to measure the standing crops of crucian carp. The mesh size of the traps was 4 mm, with 9 opening holes (diameter: 9 cm). After recording the numbers, crucian carp were immediately released to their original mesocosms.

At the end of experiment, we drained the water and collected all fishes in each mesocosm. The numbers and biomass of crucian carp and snakehead were recorded. Samples of *M. spicatum* in each frame were also collected and thoroughly rinsed with running water to estimate total wet biomass in each mesocosm. Before weighing, the washed plants were allowed to drain on the absorbent paper for 10 min. Afterwards, the plant material was gently pressed down on the paper until no water appeared on the paper.

2.3. Data analysis

For unknown reasons, no snakehead survived to the end of the experiment in one of the mesocosms stocked with two individuals. Since the time-series data of crucian carp CPUE (collected by traps) in this mesocosm was similar to the three control mesocosms (Fig. S1), we inferred that the snakehead died at an early stage and therefore included the data from this mesocosm in the "no stocking" treatment. In the other five mesocosms with initial snakehead stocking, survivals were 1/2 in two mesocosms and 2/3 in three mesocosms at the end of experiment; these were combined as "stocking" treatment (Fig. S1). Thus, our analyses were reduced to two treatments, with and without piscivores.

To assess the cascading food-web effects of snakehead stocking, we calculated several metrics indicative of top-down control. Zooplankton and cladoceran body mass (μg dry weight per animal), calculated as total biomass divided by density, was used to indicate the predation pressure on the zooplankton community in aquatic ecosystems (Jeppesen et al., 2012; Jackson et al., 2007). Zooplankton to phytoplankton biomass (dry weight) ratios and Chl-*a* to TP and TN ratios were used to evaluate the grazing pressure of zooplankton on the phytoplankton. The phytoplankton biovolume was multiplied by 0.29 to obtain an approximation of phytoplankton dry weight (Reynolds, 1984). These metrics (when combined) are widely used in long-term monitoring, cross-system lake comparison, and mesocosm studies (Liu et al., 2018; He et al., 2018, 2021).

All data processes and statistical analyses were carried out in R (R Core Team, 2021). We studied the influence of snakehead, time, and their interaction (fixed effects) on the nutrient and suspended solid concentrations and on phytoplankton and zooplankton biomass using generalized linear mixed models (GLMMs) with mesocosm identity as a random effect (Bolker et al., 2009). We assumed Gaussian error distributions for all response variables and fitted modes using the *glmmTMB* function from

the "glmmTMB" package (Brooks et al., 2017). For each response variable, we assessed the relative fit of the five different candidate models (fixed effect: fish * time, fish + time, fish, time, and null) and selected the best model based on the lowest Akaike's Information Criterion corrected for small sample size (AICc) from the "MuMIn" package (*AICc* function, Bartoń, 2022). At the end of experiment, the differences in plant numbers and weight and crucian carp numbers and weight between both treatments were compared by Student's *t*-test (*t. test* function) after data were logarithmic transformed to ensure normality and homoscedasticity.

To quantify the relative importance of cascading effects and bioturbation for phytoplankton growth, we fitted piecewise structural equation models (piecewise SEM) using data at the end of experiment. We assumed that stocking of snakehead could reduce crucian carp density and thereby limit phytoplankton growth through alterations of both increased zooplankton herbivory and reduced sediment disturbance by benthivores. This model included direct paths from snakehead density to carp biomass, from carp biomass to zooplankton body mass, from snakehead density and carp biomass to total phosphorus (TP), and from herbivorous zooplankton biomass and total phosphorus (TP) to phytoplankton biomass. We used linear mixed-effects models to fit our piecewise SEM with treatment as a random intercept. The piecewise SEM analysis was conducted in the R packages 'piecewiseSEM' and 'nlme' (Lefcheck, 2016).

3. Results

3.1. Nutrients and suspended solids

During the experiment, water total nitrogen (TN) and total dissolved nitrogen (TDN) concentrations generally increased with time, while total phosphorus (TP) and total dissolved phosphorus (TDP) showed declining trends (Fig. 2). Model selection by GLMMs confirmed a significant

interaction effect of snakehead stocking and time on the TN and TDN concentrations (Table 1; Table S1), suggesting that the differences between the treatments were time dependent. At the end of experiment, the concentrations of TN and TDN were 1.2 and 0.9 times higher in the treatment with snakehead than in the snakehead absent mesocosms, respectively. Although the TP and TDP concentrations also seemed higher in snakehead treatment than in the mesocosms without snakehead, the differences between the two treatments were not significant (Table 1; Fig. 2).

The concentrations of suspended solids (TSS and ISS) generally increased with time in both treatments (Table 1). The effect of snakehead stocking on TSS concentration was not significant (Table 1), while the ISS concentration was significantly higher in the snakehead treatments (Table 1; Fig. 2).

3.2. Phytoplankton and zooplankton

Snakehead and time synergistically increased Chl-*a* concentrations (Table 1; Table S1). At the end of experiment, the average Chl-*a* concentration was 2 times higher in the mesocosms with snakehead than in the snakehead-free mesocosms (Fig. 3a). At the beginning of experiment (Day 0), phytoplankton communties in both treatments were dominated by genra of *Microcystis* (mean biomass percentage: 26 %), *Synedra* (36 %), *Cryptomonas* (11 %) and *Ankistrodesmus* (6 %). After that, the phytoplankton communities in both treatments were exclusively dominated by *Aphanizomenon* spp., with a biomass percentage > 90 % in both treatments (Fig. 3b-c). Results from GLMMs suggested that effects of snakehead stocking on total phytoplankton and *Aphanizomenon* biomass were not significant (Fig. 3b-c; Table 1; Table S1).

A total of 27 zooplankton taxa were recorded in the two treatments across the entire experimental period, including four cladocerans (*Chydorus sphaericus, Bosmina longirostris. Alona* sp., and *Diaphanosoma*
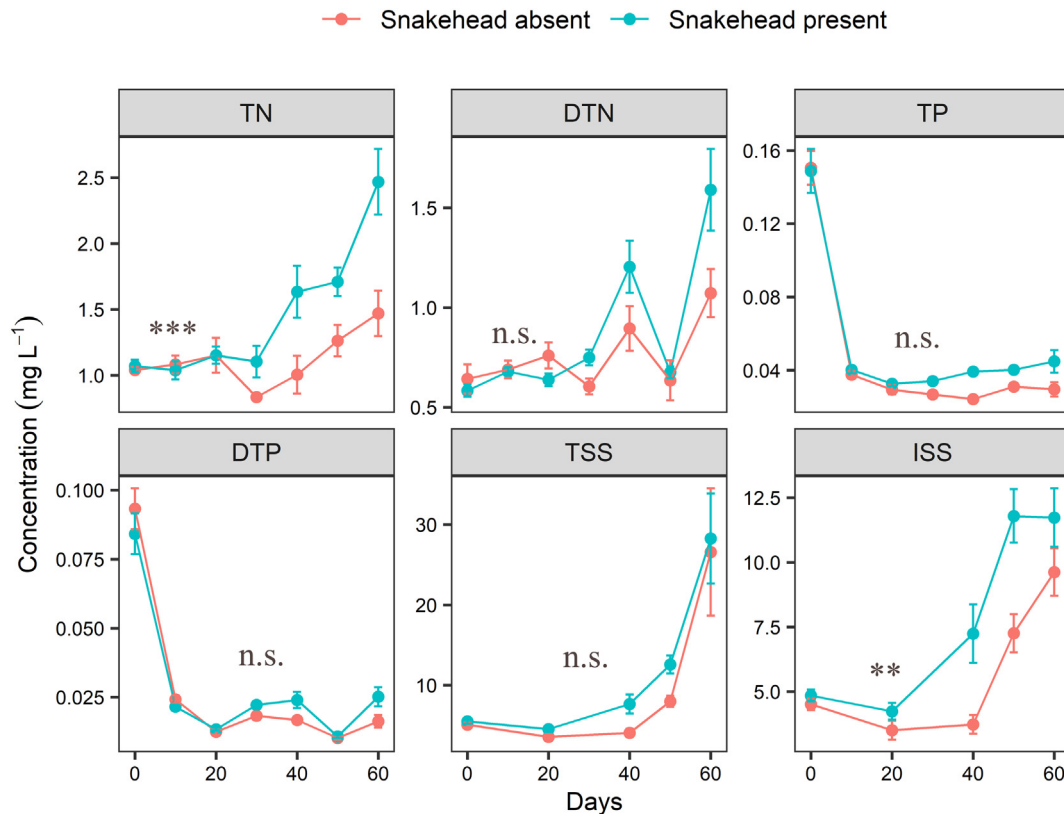

Fig. 2. Time series of total nitrogen (TN), total phosphorus (TP), dissolved total nitrogen (DTN), dissolved total phosphorus (DTP), total suspended solids (TSS), and inorganic suspended solids (ISS) with and without snakeheads. Values are mean ± SE (*n* = 4 for control, *n* = 5 for snakehead treatment). Letters indicate statistical significance of snakehead effects, *** *P* < 0.001, ** *P* < 0.01, * *P* < 0.05, n.s. *P* > 0.05. The color legend is similar in plots (c) and (d).

Table 1
GLMM best model results using the function "*glmmTMB*" from the R package "glmmTMB" v1.0.2.1 (Brooks et al., 2017).

Variables	Coeffecients	Estimates	Std. error	z value	p
TN (mg L^{-1})	Intercept	0.960	0.118	8.171	**<0.001**
	Snakehead	−0.151	0.158	−0.960	0.337
	Time	0.005	0.003	1.958	**0.050**
	Snakehead * Time	0.016	0.004	4.389	**<0.001**
TP (μg L^{-1})	Intercept	87.337	7.690	11.349	**<0.001**
	Time	−1.210	0.210	−5.673	**<0.001**
DTN (mg L^{-1})	Intercept	0.616	0.089	6.916	**<0.001**
	Snakehead	−0.125	0.120	−1.044	0.296
	Time	0.005	0.002	1.900	0.057
	Snakehead * Time	0.008	0.003	2.435	**0.015**
DTP (μg L^{-1})	Intercept	51.460	4.670	11.007	**<0.001**
	Time	−0.780	0.130	−5.995	**<0.001**
TSS (mg L^{-1})	Intercept	0.712	2.319	0.307	0.759
	Time	0.294	0.057	5.103	**<0.001**
ISS (mg L^{-1})	Intercept	1.957	0.722	2.710	**0.007**
	Snakehead	2.246	0.683	3.287	**0.001**
	Time	0.111	0.015	7.346	**<0.001**
Chl *a* (μg L^{-1})	Intercept	6.140	5.086	1.207	0.227
	Snakehead	−4.360	6.824	−0.639	0.523
	Time	0.416	0.119	3.504	**<0.001**
	Snakehead * Time	0.752	0.159	4.720	**<0.001**
Phytoplankton biomass (mg L^{-1})	Intercept	−8.957	6.678	−1.341	**0.180**
	Snakehead	12.436	7.302	1.703	0.087
	Time	1.211	0.129	9.388	**<0.001**
Aphanizomenon biomass (mg L^{-1})	Intercept	−3.035	5.560	−0.546	0.585
	Time	1.141	0.127	9.005	**<0.001**
Zooplankton biomass (μg L^{-1})	Intercept	140.566	24.623	5.709	**<0.001**
	Time	−1.323	0.658	−2.011	**0.044**
Herbivore biomass (μg L^{-1})	Intercept	120.513	21.548	5.593	**<0.001**
	Time	−1.141	0.576	−1.982	**0.048**
Cladoceran biomass (μg L^{-1})	Intercept	3.678	8.658	0.425	0.671
	Snakehead	25.166	11.616	2.167	**0.030**
Nauplii biomass (μg L^{-1})	Intercept	23.387	6.344	3.686	**<0.001**
	Snakehead	24.713	6.344	3.895	**<0.001**
	Time	−0.482	0.141	−3.424	**<0.001**
Mesocyclops biomass (μg L^{-1})	Intercept	14.588	4.109	3.551	**<0.001**
Rotifer biomass (μg L^{-1})	Intercept	22.166	4.287	5.171	**<0.001**
	Snakehead	−9.786	5.752	−1.702	0.088
	Time	−0.373	0.114	−3.255	**0.001**
	Snakehead * Time	0.453	0.154	2.950	**0.003**
Zooplankton body mass (μg DW ind^{-1})	Intercept	0.302	0.098	3.053	**0.002**
Cladoceran body mass (μg DW ind^{-1})	Intercept	0.378	0.127	2.963	**0.003**
	Snakehead	0.263	0.171	1.540	0.124
Zooplankton: Phytoplankton	Intercept	0.154	0.015	9.719	**<0.001**
	days	−0.003	0.000	−6.861	**<0.001**
Herbivore:Phytoplankton	Intercept	0.141	0.014	9.764	**<0.001**
	days	−0.003	0.000	−6.949	**<0.001**
Chl-*a*:TN	Intercept	7.617	2.383	3.196	**0.001**
	Snakehead	1.342	3.198	0.420	0.674
	Time	0.269	0.066	4.083	**<0.001**
	Snakehead * Time	0.184	0.088	2.079	**0.037**
Chl-*a*: TP	Intercept	0.084	0.101	0.837	0.402
	Snakehead	−0.033	0.136	−0.246	0.805
	Time	0.016	0.003	6.340	**<0.001**
	Snakehead * Time	0.011	0.004	3.098	**0.002**

Note: Significant terms in bold. All variables were modeled as Gaussian distribution.

sp.), two copepods (mainly *Mesocyclops leuckarti*), and 21 rotifers (mainly *Brachionus forficula* and genera of *Keratella*). No large-sized cladocerans, e.g., *Daphnia,* were detected in our study. Though somewhat omnivorous, we considered all stages of copepodites and adult of *M. leuckarti* as predatory (Gophen, 1977). We therefore separately calculated total (all species included) and herbivorous zooplankton (with elimination of *M. leuckarti* copepodites and adults) biomass in our study.

Model selection by GLMMs revealed that snakehead stocking significantly increased cladoceran and nauplii biomasses (Table 1; Table S1; Fig. 4), while the differences in adult *M. leuckarti* and rotifer biomasses between treatments were not significant (Table 1; Fig. 4). Overall, no significant effects of snakehead stocking on herbivorous and total zooplankton biomass were detected (Table 1; Fig. 4).

3.3. Crucian carp and submerged macrophytes

Stocking of snakehead significantly suppressed the standing crops of crucian carp whose density and biomass were significantly lower in the mesocosms with snakehead than in ones without (*t*-test, $P < 0.001$ for both parameters; Fig. 5a-b). In three mesocosms with two surviving snakehead individuals, we only caught two crucian carp in one mesocosm at the end of experiment.

In our study, *M. spicatum* stretched towards and concentrated their shoot biomass near the water surface in each mesocosm. Our study did not detect significant effects of snakehead stocking on *M. spicatum* density and biomass (*t*-test, $P > 0.05$ for both parameters; Fig. 5c-d).

No significant effects were observed of snakehead stocking on the zooplankton and cladoceran body mass, the zooplankton to phytoplankton biomass ratios, or the herbivorous zooplankton to phytoplankton biomass ratios (Table 1; Fig. 6a-d). However, snakehead stocking significantly increased the chlorophyll-*a* to TP and TN ratios (Table 1; Fig. 6e-f).

Similar to the results above, piecewise SEMs based on the final sampling data also revealed a strong negative relation between snakehead stocking and crucian carp biomass (Fig. 7). Snakehead stocking was positively related to TP concentrations, which was the main contributor to the increased phytoplankton biomass (represented by chlorophyll-*a* concentrations) (Fig. 7). In our study, the herbivorous zooplankton biomass was not related to either crucian carp or phytoplankton biomass. It is important to note that piecewise SEMs detected a direct negative relation between crucian carp biomass and phytoplankton biomass (Fig. 7).

4. Discussion

In our mesocosm experiment, we tested the effectiveness of the biomanipulation by piscivore stocking in subtropical shallow lakes with prevalence of omni-benthivorous fish. Our results confirmed that snakehead stocking significantly suppressed the crucian carp population. In most mesocosms with snakehead (3 of 5), crucian carp nearly went extinct, which resulted in an average piscivore dominance >85 % (Fig. S2); this is far higher than the values observed in most temperate (<60 %) and subtropical (<40 %) clear shallow lakes (Jeppesen et al., 2000; Yu et al., 2021). Despite that, stocking of snakehead did not reinforce a clear water state but increased water turbidity (Fig. S3).

4.1. Cascading food-web effects

Although snakehead predation greatly reduced the biomass of crucian carp, this top-down effect did not cascade down to zooplankton as otherwise found in most north temperate shallow lake studies (Lathrop et al., 2002; Skov et al., 2002; Potthoff et al., 2008). In our study, both zooplankton biomass and body mass were unchanged (Fig. 4; Fig. 6a). Consistent with some theoretical studies (McCann et al., 1998; Hart, 2002), this nonoccurrence of trophic cascades might, in part, be explained by the reticulate food webs in systems dominated by small-sized zooplankton. This means that, although juvenile crucian carp was significantly reduced by snakehead predation, adult *M. leuckarti* and copepodites, which were less affected by fish predation, may suppress the herbivorous zooplankton (Fig. 6). The intratrophic interference resulting from cyclopoid predation may, consequently, have dampened the response of the herbivorous zooplankton to changes in fish predation, at least in a short term after fish removal (McCann et al., 1998; Hart, 2002). Our results concur with studies
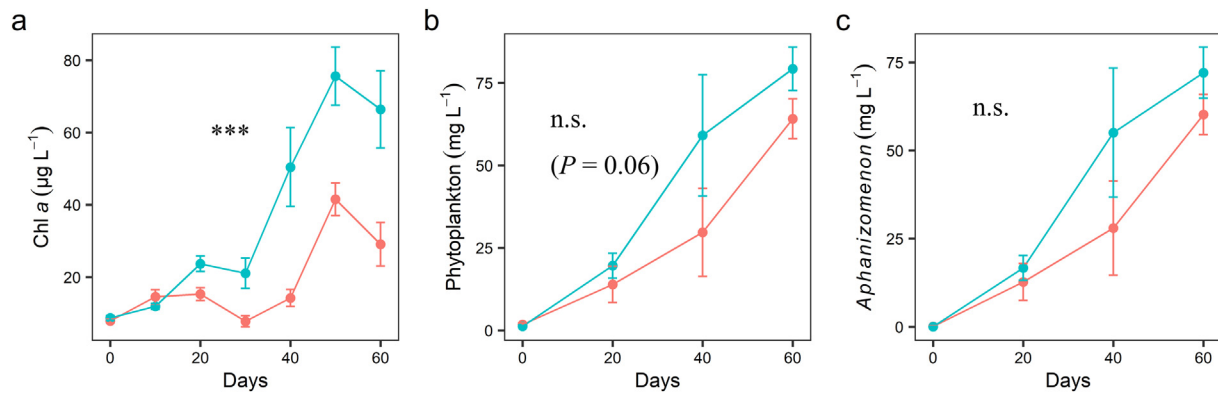
Fig. 3. Time series of (a) chlorophyll-*a* (Chl *a*) concentration, (b) total phytoplankton biomass, and (c) biomass of the dominant genus *Aphanizomenon* in both snakehead scenarios. Values are mean ± SE (n = 4 for control, n = 5 for snakehead treatment). The color legend and meaning of letters are similar to those of Fig. 2.

in subtropical Lake Kinneret where cyclopoids, despite a much lower biomass (<20 μg L^{-1}), accounted for a greater proportion of predation pressure on herbivorous zooplankton than fish (Blumenshine and Hambright, 2003). The intratrophic interference may also partially explained why repeatedly fish removal failed to increase herbivorous zooplankton in Lake Huizhou West Lake (dominated by predatory *Mesocyclops*), although the quickly recruitment of small fish also played a key role in this lake (Liu et al., 2018). Studies have also shown that when the keystone herbivore, *Daphnia,* dominated the zooplankton community at low or absent fish predation, predatory cyclopoids can be outcompeted (Zeng et al., 2016; He et al., 2018). Once *Daphnia* prevail, previous reticulate food webs might thus become simpler and chain-like, which, in turn, facilitate stronger community-level trophic cascades. However, whether single in-lake measure like stocking of piscivore will achieve

this positive feedback in natural warm lakes needs to be tested in long-term experiments.

Another explanation of the lack of a trophic cascade may be poor edibility of phytoplankton (Polis et al., 2000) as filamentous cyanobacteria exclusively dominated in our mesocosms. The increased dominance of *Aphanizomenon* in phytoplankton community during the experiment could be explained by the increased competition advantage of thermophilic cyanobacteria in warm and nutrient-rich waters (Paerl and Huisman, 2008; Kosten et al., 2012). That inedible filamentous cyanobacteria (*Anabaena*) dampened the community-level trophic cascades induced by fish was also shown in enclosure experiment in the tropical Dakar Bango reservoir, Senegal (Rondel et al., 2008). Overall, as invertebrate predators and large inedible cyanobacteria generally prevail in warm lakes, our results suggested that the applicability of the classical biomanipulation tool to
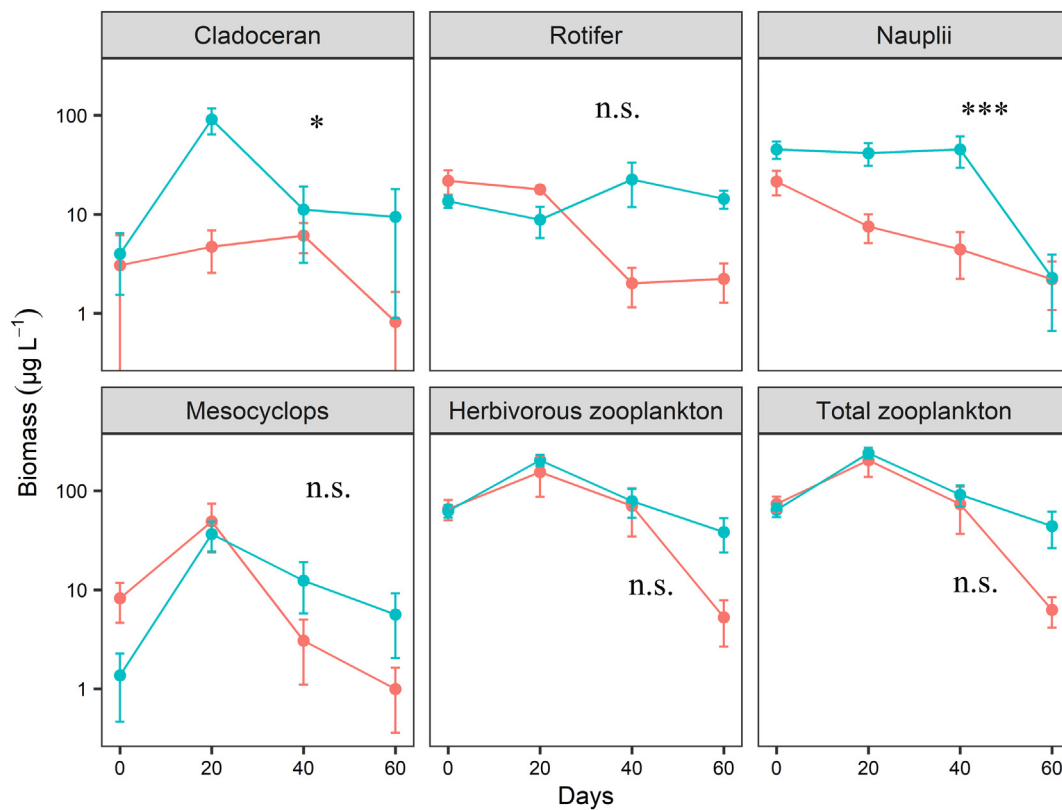

Fig. 4. Biomasses (dry weight) of (a) cladocerans, (b) rotifers, (c) nauplii, (d) *Mesocyclops* adults and copepodites, (e) herbivorous zooplankton (cladocerans + rotifers + nauplii), and (f) total zooplankton with and without snakeheads. Values are mean ± SE (n = 4 for control, n = 5 for snakehead treatment). The color legend and meaning of letters are similar to those of Fig. 2.
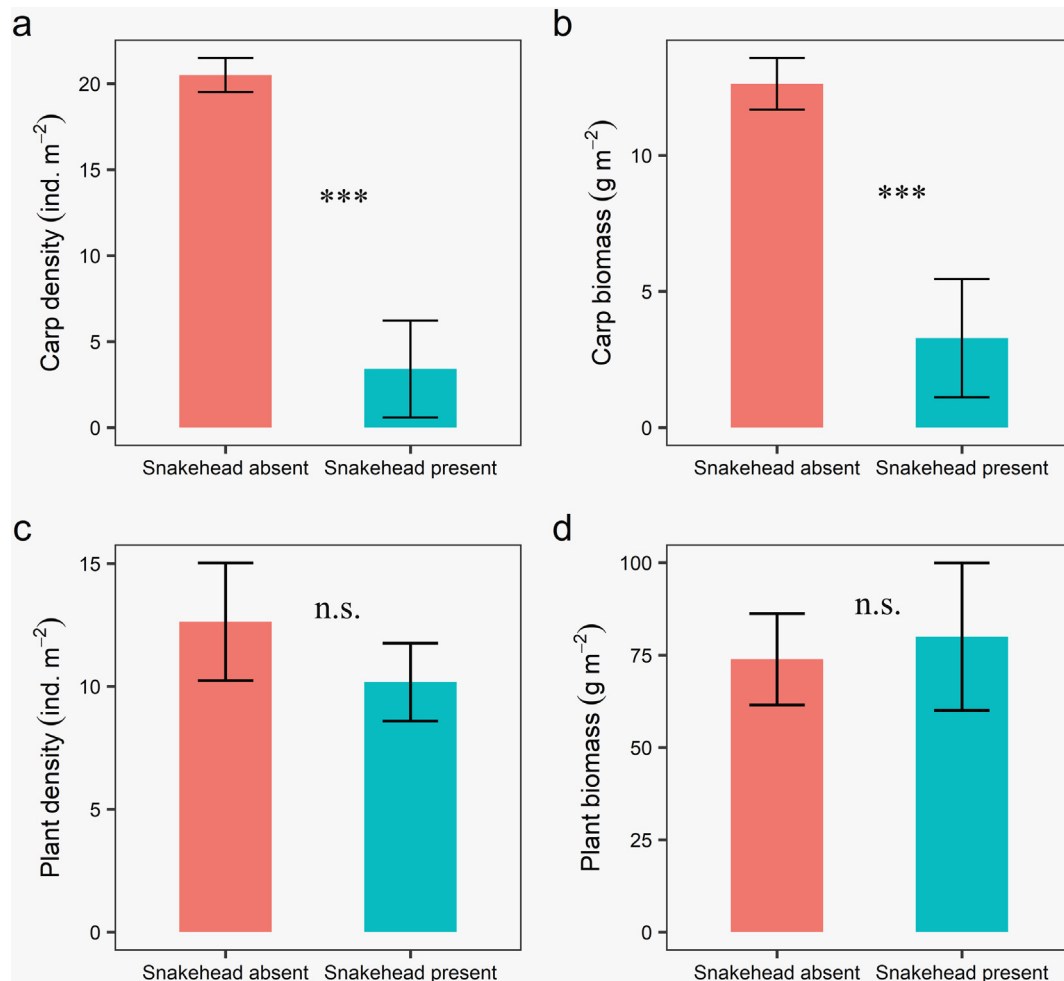
Fig. 5. Comparisons of (a) crucian carp density and (b) biomass and (c) *Myriophyllum spicatum* density and (d) biomass at the end of experiment snakehead treatments. Values are mean ± SE (n = 4 for control, n = 5 for snakehead treatment).

control phytoplankton via enhancing zooplankton grazing is challenged (Jeppesen, 2005; Meerhoff et al., 2007; Ofir et al., 2017; Liu et al., 2018).

In our study, snakehead stocking disproportionately increased chlorophyll-*a* to nutrient ratios (Fig. 6), indicating a reduction of the top-down pressure on phytoplankton caused by snakehead stocking. As zooplankton herbivory was generally weak and only increased slightly after the piscivore stocking, a direct consumption of phytoplankton by the juvenile crucian carp may be an alternative explanation of the reduced herbivory in enclosures with piscivorous fish. A direct carp-phytoplankton interaction link is also supported by the piecewise SEMs (Fig. 7). Gut content analysis and cultivation experiments have revealed that crucian carp can ingest and digest large-sized filamentous cyanobacteria, e.g., *Aphanizomenon* (Kamjunke et al., 2002; Kolmakov and Gladyshev, 2003; Liu, 2008). Thus, our results indicate that stocking of snakehead to suppress juvenile omnivorous fish may, in the short-term, release the grazing on phytoplankton in subtropical shallow lakes due to the complex food-web interactions.

4.2. Bioturbation effects

Sediment disturbance did not decline but rather increased with the reduction of crucian carp. The high non-algal turbidity (ISS) in snakehead mesocosms can be exclusively attributed to sediment resuspension caused by snakehead as crucian carp occurred in low abundance (0 in 2/5 mesocosms) in the piscivore treatment. Being a benthi-piscivorous fish, it is reasonable to assume that snakehead could cause sediment resuspension, although no studies have previously recorded this. Our results differ from

those obtained from temperate studies showing that stocking of pike and perch caused a significant decline in suspended solids (Skov et al., 2002). Our study indicated that to reduce fish-induced resuspension in warm lakes, direct fish removal may be more appropriate than piscivore stocking; as the applicability success of the former has been confirmed in the restoration of e.g., Huizhou West Lake in China and a tropical reservoir (Lago Paranoa) in Brazil (Starling et al., 2002; Jensen et al., 2017). In our study, snakehead predation and/or cannibalism led to sediment resuspension similar to that caused by crucian carp, promoting nutrient levels supporting phytoplankton growth and thereby maintaining the turbid-water state (Fig. 7). The growth of the submerged macrophyte *M. spicatum* was not noticeably affected by the high turbidity in the snakehead mesocosms; this is, however, likely due to its high turbidity tolerance. Teng et al. (2007) found that *M. spicatum* was not significantly affected by turbidity within 0–60 NTU. In our study, the TSS concentrations were < 30 mg L^{-1}, indicating that turbidity was <33 NTU according to Rügner et al. (2013), who found that the ratios of TSS:NTU were 0.9–2.4. Therefore, the high non-algal turbidities in the snakehead-present mesocosms likely did not inhibit the growth of *M. spicatum*.

4.3. Implications for lake restoration by biomanipulation in the subtropics

Biomanipulation, based on the trophic cascade theory, has been widely used as a restoration tool to combat eutrophication in temperate shallow lakes following an external nutrient loading reduction (Jeppesen et al., 2012). However, to our knowledge, there are, so far, no published
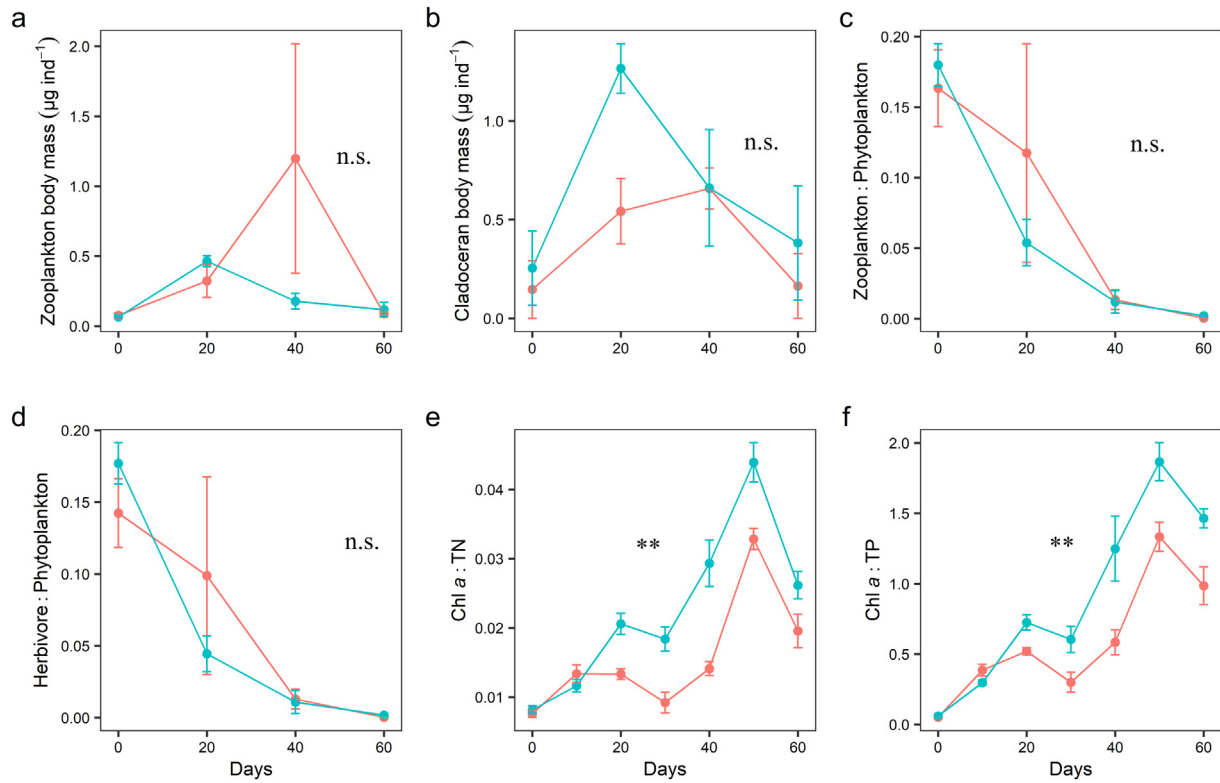
Fig. 6. Comparison of (a) zooplankton body mass (μg dry weight per individual), (b) cladoceran body mass, (c) zooplankton to phytoplankton biomass ratio, (d) herbivorous zooplankton to phytoplankton biomass ratio, (e) Chl-*a* to TN, and (f) Chl-*a* to TP ratios with and without snakeheads. Values are mean ± SE (n = 4 for control, n = 5 for snakehead treatment). The meaning of letters are similar to that of Fig. 2.
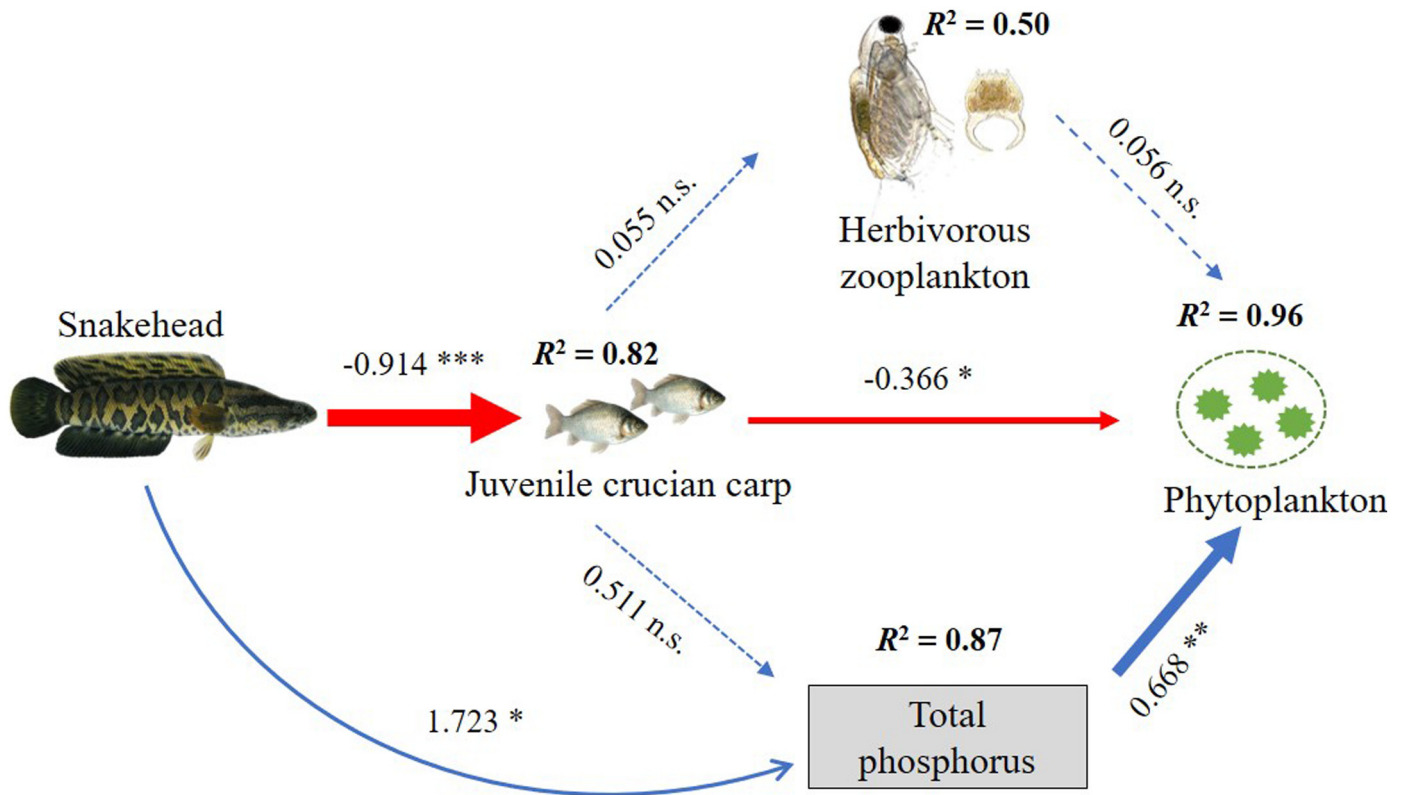

Fig. 7. Piecewise structural equation model (piecewise SEM) based on the final sampling data depicting the direct and indirect effects of stocking of snakehead on phytoplankton growth in subtropical shallow mesocosms. Fisher's C = 9.403; df = 6; P = 0.152; AIC = 47.403. Red, green, and dashed arrows represent negative, positive, and non-significant paths, respectively. The thickness of the significant paths represents the magnitude of the standardized regression coefficient or effect sizes, given on the arrows. R^2s for component models are given on the endogenous variables.

experimental studies revealing the effects of piscivore stocking in warm shallow lakes involving both food web interactions and bioturbation effects. We chose a common native benthi-piscivorous fish (snakehead) in warm lakes to test whether piscivore stocking would suppress a small omni-benthivorous fish species (crucian carp) and thereby diminish its negative effects on water quality. However, we did not find a positive effect of snakehead stocking on the clear-water state, suggest that stocking of snakehead in warm lakes to improve water quality is questionable. In restoration of subtropical eutrophic lakes, the existing information suggested that direct fish removal by extensive fishing is more practicable and have larger effects (Starling et al., 2002; Liu et al., 2018). However, to draw firm conclusions, future long-term studies in warm lakes with large scales, e.g., whole-lake experiment, and other native piscivore species remains need to be conducted.

5. Conclusion

We used experimental mesocosms to test the effects of stocking of benthi-piscivorous fish snakehead on water clarity in subtropical shallow lakes. Our results clearly showed that snakehead stocking, despite of a great suppression of omni-benthivorous fish crucian carp, did not increase zooplankton herbivory via cascading top-down effects. In contrast, snakehead activities significantly increased non-algal turbidity via sediment disturbance. Our results suggest that stocking of snakehead in warm lakes to improve water quality may be not applicable, even on the short term.

CRediT authorship contribution statement

Hu He: Conceptualization, Methodology, Investigation, Data curation, Writing - original draft. **Tian Qian**: Investigation, Data curation, Formal analysis. **Ruijie Shen**: Investigation, Data curation, Formal analysis. **Jinlei Yu**: Methodology, Data curation, Formal analysis, Writing - review & editing. **Kuanyi Li:** Conceptualization, Methodology, Writing - review & editing, Funding acquisition. **Zhengwen Liu:** Conceptualization, Methodology, Writing - review & editing, Funding acquisition. **Erik Jeppesen:** Conceptualization, Methodology, Writing - review & editing. All authors contributed to interpretation of the analysis and implications, revision of intellectually important content, and approved of its final publication and have agreed to be accountable for the work.

Data availability statement

Raw data of nutrient concentrations, phytoplankton and zooplankton biomass were updated as supplementary materials.

Declaration of competing interest

None declared.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.156967.

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