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Intraguild predation dampens trophic cascades in shallow aquatic mesocosms in the subtropics: Implications for lake restoration by biomanipulation

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Abstract

1. Intraguild predation (IGP), defined as killing and eating among potential competitors, is commonly observed in shallow lakes and is predicted to dampen trophic cascades and affect ecosystem properties (e.g. phytoplankton biomass or primary production). We tested this hypothesis by manipulating the density of two common lake predators, the small-sized fish *Pelteobagrus fulvidraco* (the intraguild predator) and the shrimp *Exopalaemon modestus* (the intraguild prey), in outdoor mesocosms containing natural phytoplankton and zooplankton communities.

2. In single predator treatments, both predators induced a strong trophic cascade, as evidenced by extinction of the key herbivore, *Daphnia pulex*, and increasing phytoplankton biomass and chlorophyll *a* concentration.

3. When the two predators were added together, however, the strength of collective predator effects on zooplankton and the cascading effects on phytoplankton growth were weaker than the sum of the individual predator effects. We attributed this antagonism among predators to intraguild predation as demonstrated by the lower shrimp catch per unit effort in the presence of fish.

4. Our study suggests that common predators in subtropical shallow lakes may act antagonistically and thereby dampen trophic cascades in food webs. Thus, when implementing biomanipulation efforts to suppress algal growth via enhancing zooplankton herbivory, both the quantity and diversity of lake predator assemblies should be considered.

KEYWORDS
mesocosm experiment, phytoplankton, predator diversity, predator–prey interaction, zooplankton

1 | INTRODUCTION

Intraguild predation (IGP) is the killing and eating of a potential competitor from a different species that uses similar resources (Polis et al., 1989), and this is a widespread phenomenon in ecosystems (Arim & Marquet, 2004). As a special case of omnivory, IGP increases the dietary breadth of a consumer species and consequently it increases the complexity of the whole food web (Duffy et al., 2007).

Theoretical and empirical studies indicate that IGP among multiple predator species could release prey suppression and dampen trophic cascades (Douglass et al., 2008; Finke & Denno, 2005; O'Gorman et al., 2008; Vance-Chalcraft et al., 2007; Wang et al., 2019; Wootton, 2017). For instance, Finke and Denno (2004) found that adding hunting spiders to a predator community reduced the overall predation on the herbivorous planthopper (*Prokelisia dolus*), which indirectly reduced the aboveground biomass of *Spartina* grass in a coastal salt marsh community. In a marine food web, Bruno and O'Connor (2005) found that contrasting carnivorous predators alone induced a strong trophic cascade by reducing herbivore abundance and increasing algal biomass but that these effects were reversed as predator diversity increased due to the performance of omnivorous fish in diverse predator assemblages.

However, multiple predator effects do not necessarily have to interact antagonistically (Bruno & Cardinale, 2008; Vance-Chalcraft et al., 2007), and examples of additive or synergistic interactions are also found (Losey & Denno, 1998; Moran et al., 1996; Snyder & Wise, 2001). Several parameters could influence the magnitude and direction of IGP in diverse predator assemblages, such as feeding specificity, size, mobility, and predator aggressiveness, as well as bottom-up factors such as primary production and habitat complexity (Diehl & Feissel, 2001; Finke & Denno, 2006; Lucas et al., 1998). For instance, in the above-mentioned case of coastal salt marsh food webs, Finke and Denno (2006) also found that structurally complex habitats diminished IGP by providing a refuge for the intraguild prey, thereby increasing the combined effectiveness of multiple predators in suppressing planthopper populations. Thus, to predict the effects of diverse predator assemblages on a given ecosystem function or property, biological traits (e.g. mobility of predator and prey) and environmental context (e.g. habitat characteristics and seasonality) should be considered (Bruno & Cardinale, 2008; Finke & Denno, 2006; Snyder & Wise, 2001).

Predator omnivory is widespread in shallow lakes (González-Bergonzoni et al., 2012; Jeppesen et al., 2010). However, limnologists and lake managers have so far paid little attention to the ecological theory of intraguild predation (but see Hart, 2002; Wootton, 2017), although IGP has long been studied in terrestrial ecosystems within the context of pest control (Cardinale et al., 2003; Rosenheim et al., 1995; Snyder & Wise, 2001). Lake management and restoration efforts often assume that food chains are linear, as reflected by the desire to manage trophic cascades via straightforward biomanipulation, i.e. introduction of measures reducing the abundance of zooplanktivorous fish or invertebrates with the aim to enhance zooplankton herbivory on phytoplankton and thereby reduce eutrophication (Carpenter et al., 1985; Jeppesen et al., 2012). No study has

assessed the effects of lake biomanipulation from the perspective of predator richness. Indeed, in subtropical or tropical (hereafter *warm*) shallow lakes, changes in predator dominance after biomanipulation are often more obvious than variation in biomass as one or two predators, for instance crucian carp, often recruit quickly and occupy the predator niche (Gao et al., 2014; Jeppesen et al., 2012; Yu et al., 2016). The shift to dominance of a few specie may reduce the occurrence of IGP in predator assemblages, thus buffering the positive effects of the reduced predator biomass on zooplankton suppression (Polis et al., 1989; Wang et al., 2019). This mechanism may partially explain the observation in some studies that the key herbivore, *Daphnia*, did not return after biomanipulation in warm lakes (Liu et al., 2018). Thus, for those engaged in controlling lake eutrophication, a central question is whether current biomanipulation efforts strengthen or weaken zooplankton grazing on phytoplankton in warm lakes?

To obtain a better mechanistic understanding of the effects of IGP on cascading top-down effects in warm shallow lakes, we exposed natural spring zooplankton and phytoplankton communities to different predator scenarios using a full-factorial design. We chose two common predators from a subtropical lake in China: the small-sized fish species *Pelteobagrus fulvidraco* (Richardson, 1846) and the shrimp *Exopalaemon modestus* (Heller, 1862). The latter was chosen as invertebrate predators are generally abundant in warm shallow lakes and play an important role as predators on zooplankton (Meerhoff et al., 2007). Gut content analysis (GCA) studies have shown that *P. fulvidraco* preys on *E. modestus* (Yu et al., 1996; Yuan et al., 2011) and that both predators consume zooplankton (Shi et al., 1995; Yu et al., 1996). According to theory, we hypothesised that fish and shrimp would interact antagonistically and dampen trophic cascades when both are present. That means that the combined impact of the two predators on zooplankton suppression and the cascaded phytoplankton promotion would be expected to be lower than the sum of their individual impacts.

2 | METHODS

2.1 | Experimental design

The outdoor mesocosm experiment was conducted from 7 April (Day 0) to 2 June 2020 (Day 56) at Taihu Laboratory for Lake Ecosystem Research (31°30′N, 120°30′E), located in Meiliang Bay on the northern edge of Lake Taihu, China. We chose the spring season as it is the breeding season of the shrimp *E. modestus*, allowing one-generation reproduction (Chen et al., 2015; Shi et al., 1995). Also, it is the annual time window for *Daphnia* spp. (the key herbivore) development in Lake Taihu (Yang et al., 2012). The mesocosm system consisted of 24 500-L plastic tanks (97 cm high; 90 cm inside diameter at the top; 78 cm inside diameter at the base). All tanks were filled with 480 L water from eutrophic Lake Taihu. The water was pre-screened (64 µm mesh size) to remove crustacean zooplankton and large inorganic particles and mixed to ensure homogeneity before addition to the tanks. To simulate submerged macrophytes in shallow lakes,

we placed eight artificial plants (90 cm height) with an architecture resembling that of the common submerged macrophyte species *Cabomba caroliniana* in the centre of each tank. The plants were fixed in a common ceramic base (20 cm length and 6 cm width). In each mesocosm, the volume infested by submerged macrophytes (sensu Canfield et al., 1984) was approximately 35%, which is commonly observed in subtropical shallow lakes (Guan et al., unpublished data). Each mesocosm was covered by a screened lid (mesh size: 0.83 mm; light transmission: 77%) to prevent entry by other predators such as aquatic insects. Two weeks before the experiment, we released 100 *Daphnia pulex* (length: 1.6 mm) acting as the key herbivore into each mesocosm. The daphnids were collected from a nearby pond, having an initial density (0.2 ind/L) corresponding well with the natural concentrations in Lake Taihu (Yang et al., 2012).

A two-way factorial experiment was carried out: two shrimp levels (shrimp present/absent) and two fish levels (fish present/absent). The four treatments were designated as C (control), F (fish addition), S (shrimp addition), and FS (fish addition plus shrimp addition). Each treatment had 6 replicates. Individuals of the species *E. modestus*, an economically important species in Lake Taihu, were caught in shrimp traps in Lake Taihu. According to the natural sex ratio in the breeding season, we added 18 females (fresh weight: 0.5 ± 0.15 g/ind) and 12 males (0.16 ± 0.08 g/ind) to each of the shrimp mesocosms (Chen et al., 2015). The fish, small-sized *P. fulvidraco* individuals, were obtained from a local aquaculture facility and acclimatised in lake water for 1 week before the experiment began. We added two fishes to each mesocosm of the fish treatments, which corresponded to a biomass of 4.5 ± 0.5 g per mesocosm. Total predator (fish + shrimp) biomass in both the fish and shrimp mesocosms was approximated to 81 kg/ha, which is lower than the natural fish biomass in Lake Taihu (Mao et al., 2020). All fish were alive throughout the experiment.

Nutrients (5 μg P L^{-1} day^{-1}; 130 μg N L^{-1} day^{-1}) were supplied daily to each mesocosm throughout the experiment to simulate the external loading in Lake Taihu (Paerl et al., 2011). Phosphorus and nitrogen were added separately as aqueous solutions of potassium dihydrogen phosphate (KH$_2$PO$_4$) and potassium nitrate (KNO$_3$), the dominant inorganic nutrient forms in Lake Taihu.

2.2 | Sampling and processing

Sampling for determination of nutrient and chlorophyll *a* (Chl-*a*) levels and analysis of phytoplankton communities was carried out at the end of the experiment (Day 56). We used a tube sampler (8 cm diameter, 64 cm length) to collect 2 L depth-integrated water. A 1-L subsample was taken to the laboratory for water chemical analysis and determination of Chl-*a* concentrations. Total nitrogen (TN) and total phosphorus (TP) were measured according to Chinese standard methods (Jin & Tu, 1990). Chl-*a* concentrations were obtained spectrophotometrically from matter retained on a GF/C filter and extracted in a 90% (v/v) acetone/water solution for 24 hr. No correction was carried out for pheophytin interference (SEPA, 2002). Another 1-L depth-integrated subsample taken from each mesocosm was treated with 10 ml Lugol's iodine solution and

sedimented for 48 hr. The supernatant was removed, and the residue was collected and examined under 100×–400× magnification for enumeration of phytoplankton. Phytoplankton was identified to genus level according to Hu and Wei (2006) and, as far as possible, following recent taxonomic revisions (Guiry & Guiry, 2014). 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 & Huang, 1991). Where possible, at least 1,000 cells of each taxon were counted per sample, but for less common taxa the calculations were based on fewer measurements.

Zooplankton were also sampled at the end of the experiment. Before sampling, we firstly used a long stick to stir the water to avoid temporal heterogeneity of zooplankton. After that, a 10-L depth-integrated water sample was filtered through a 64-μm net and the retained material was preserved in Lugol's solution. Crustacean zooplankton (cladocerans, copepodites, and adult copepods) were counted at magnifications between 10× and 40×, while rotifers were counted at 100× magnification. Species represented by more than 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.

At the end of the experiment (day 54), we placed a small square shrimp trap (length: 31 cm; width: 17 cm; height: 11 cm) in each mesocosm overnight. The mesh size of the traps was 6 mm, with three opening holes (diameter: 10 cm). The shrimps were collected from the shrimp mesocosms (12 tanks) and their numbers recorded.

2.3 | Data analysis

To assess the predation strength of predators on zooplankton, we calculated density-weighted body sizes and biomass ratios of *Daphnia* (sensitive to predation) relative to the total biomass of cladocerans. Zooplankton size (μg dry weight per animal) was calculated as total biomass divided by density. Both proxies are commonly used to indicate the predation pressure on the zooplankton community in aquatic ecosystems (Jackson et al., 2007; Jeppesen et al., 1997, 2012). Similarly, the ratios of zooplankton to phytoplankton biomass and Chl-*a* to TP ratio were calculated to evaluate the grazing pressure on phytoplankton by zooplankton (Jackson et al., 2007; Jeppesen et al., 1997, 2012). We multiplied the phytoplankton biovolume by a factor of 0.29 to convert it to algal dry mass (Reynolds, 1984).

All data processes and statistical analyses were carried out in R (R Core Team, 2019). We studied the influence of fish, shrimp and their interaction (fixed effects) on the nutrient concentration, plankton biomass and top-down metrics (response variables) using generalised linear mixed models with mesocosm identity as a random effect (GLMM; 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).

We added 1 μg to *Daphnia* biomass in each mesocosms to avoid convergence issues in model fitting because of too many zeros (14 zeros in 24 mesocosms). For each response variable, we assessed the relative fit of the five different candidate models (fixed effect: fish × shrimp, fish + shrimp, fish, shrimp, and null) and selected the best model based on the lowest AIC value from the default *ANOVA* function. If the interaction term was significant in the best model, we then performed a post hoc test on the best model to study the potential antagonistic or synergistic effects between both predators using Tukey's post hoc tests (function emmeans from package *emmeans*). Shrimp count data at the end of the experiment were also fitted using GLMM with an assumption of Poisson error distribution. The best models of two candidates (fixed effect: fish and null) were selected from the default ANOVA function, as above.

3 | RESULTS

3.1 | Nutrients

Shrimp and fish were found to significantly reduce TN concentrations (Table 1; Figure 1a). No significant interaction effect was traced for TN as the interaction term was not included in the best GLMM model (Table 1; Figure 1a).

Model selection by GLMMs confirmed a significant interaction effect of fish and shrimp on the TP concentration (Table 1). Shrimp increased TP, but the level of increase was dependent on the presence of fish. In the fish-absent mesocosms (C and S), addition of shrimps caused a 2-fold increase in TP (Figure 1b). However, the shrimp had a slight, but not significant, elevated TP in the presence of fish (F vs. FS; Figure 1b).

3.2 | Phytoplankton

The phytoplankton communities in the C and FS treatments were dominated by chlorophytes (mainly *Scenedesmus* and *Arthrodesmus* genera), comprising >75% of the total biomass. In the single-predator treatments, cryptophytes (*Cryptomonas* sp.) was exclusively dominant (>80%) in treatment F, while cyanophytes (mainly *Pseudoanabaena* and *Microcystis* genera) and chlorophytes dominated in treatment S.

Model selection by GLMMs confirmed a significant antagonistic interaction effect of both predators on phytoplankton growth (Figure 2a,b; Table 1). Phytoplankton biomass and the Chl-*a* concentration were both significantly higher in the single predator treatment than in the no-predator control treatment (Figure 2a,b). However, when both predators were present, the magnitude of the algal increase was not greater than in the singer predator treatments (Figure 2a,b).

3.3 | Zooplankton

A total of 20 zooplankton taxa were recorded in the four treatments, including one large-sized cladoceran (*D. pulex*), three small cladocerans (*Bosmina longirostris*, *Chydorus sphaericus*, and *Alona* sp.), two copepods (*Mesocyclops leuckarti* and *Eucyclops serrulatus*), and 16 rotifers (dominated by *Lacane* spp., *Lepadella* sp., *Brachionus angularis*, *Keratella cochlearis*, and *Synchaeta* sp.).

Predation either by fish alone or by shrimp alone had significant negative effects on the population growth of *D. pulex* (Table 1). In fact, *D. pulex* disappeared in the F and S treatments (Figure 3a). However, there was a significant antagonistic effect between fish and shrimp addition on *D. pulex* population growth (Table 1). In the FS treatment, *D. pulex* had survived in four mesocosms (out of six replicates) at the end of experiment, the average biomass being significantly higher than in the F and S treatments (Table 1; Figure 3a). Both fish and shrimp predation significantly increased the biomass of small cladocerans, while no obvious interaction was observed (Figure 3b; Table 1). GLMMs suggested no significant effect of fish and shrimp on copepod and rotifer biomass (Table 1; Figure 3d,e).

GLMMs showed a significant antagonism effect of both predators on total zooplankton biomass (Table 1). Zooplankton biomass was significantly lower in S than in C (Figure 3e). By contrast, when fish were present, zooplankton biomass did not differ significantly between the F and FS treatments (Figure 3e).

3.4 | Shrimp

Shrimps experienced reproduction in our study, as we found second-generation shrimps in routine observations. The presence of fish had a significant negative effect on the shrimp population (Table 1; Figure 4). At the end of the experiment, shrimp catch per unit effort was significantly higher in treatment S (14.67 individuals per trap per night) than in FS (7.33 individuals per trap per night; Figure 4).

3.5 | Top-down metrics

Both predators had an antagonistic interaction effect on the predation pressure on zooplankton (Table 1). In the absence of fish (C and S), shrimp significantly reduced zooplankton size and the *Daphnia* proportion of the total cladoceran biomass (Figure 5a,b; Table 1). However, these effects were mitigated when fish were present (F and FS; Figure 5a,b; Table 1). Similarly, antagonistic effects of predators were observed on the zooplankton to phytoplankton biomass ratios (Table 1; Figure 5c). However, the effect of shrimp was significant only on the Chl-*a* to TP ratios (Table 1), although the average value was higher in F than in C (Figure 5d; Table 1).

4 | DISCUSSION

As expected, fish and shrimp interacted antagonistically and dampened the trophic cascade. When added alone, each predator induced a strong trophic cascade, as reflected by the extinction of the key herbivore *D. pulex* and the increasing phytoplankton biomass, which

TABLE 1 Generalised linear mixed model best model results using function *glmmTMB* from R package *glmmTMB* v1.0.2.1 (Brooks et al., 2017)

Response variable	Unit	Coefficient	Estimates	SE	z Value	p
Total nitrogen	mg/L	I	1.593	0.038	41.40	**<0.001**
		F	−0.094	0.046	−2.04	**0.042**
		S	−0.111	0.047	−2.35	**0.019**
Total phosphorus	mg/L	I	−3.471	0.096	−36.22	**<0.001**
		F	0.432	0.136	3.19	**0.001**
		S	0.917	0.136	6.76	**<0.001**
		F × S	−0.703	0.192	−3.67	**<0.001**
Chlorophyll *a* concentration	mg/L	I	−0.673	0.317	−2.12	**0.034**
		F	2.460	0.416	5.92	**<0.001**
		S	4.145	0.415	9.99	**<0.001**
		F × S	−4.260	0.562	−7.58	**<0.001**
Phytoplankton biomass	mg/L	I	6.113	0.305	20.08	**<0.001**
		F	2.581	0.430	6.00	**<0.001**
		S	4.267	0.430	9.93	**<0.001**
		F × S	−4.381	0.608	−7.21	**<0.001**
Zooplankton biomass	µg/L	I	6.153	0.249	24.67	**<0.001**
		F	0.547	0.352	1.55	0.121
		S	0.837	0.352	2.38	**0.018**
		F × S	−1.866	0.499	−3.74	**<0.001**
Daphnia biomass	µg/L	I	0.000	0.454	0.00	1.000
		F	6.208	0.643	9.66	**<0.001**
		S	2.601	0.642	4.05	**<0.001**
		F × S	−8.809	0.908	−9.70	**<0.001**
Small cladoceran biomass	µg/L	I	4.690	0.695	6.77	**<0.001**
		F	−1.659	0.803	−2.07	**0.039**
		S	1.723	0.803	2.15	**0.032**
Copepod biomass	µg/L	I	4.419	0.159	27.72	**<0.001**
Rotifer biomass	µg/L	I	3.072	0.342	8.99	**<0.001**
Shrimp catch per unit effort	ind trap^{-1} night^{-1}	I	2.649	0.198	13.41	**<0.001**
		F	−0.789	0.309	−2.56	**0.011**
Zooplankton size	µg ind^{-1}	I	0.275	0.055	5.04	**<0.001**
		F	0.359	0.077	4.65	**<0.001**
		S	0.192	0.077	**2.49**	**0.013**
		F × S	−0.584	0.109	−5.36	**<0.001**
Daphnia to cladoceran		I	0.000	0.355	0.00	1.000
Biomass ratio		F	4.268	0.503	8.47	**<0.001**
		S	1.508	0.503	3.00	**0.003**
		F × S	−5.776	0.712	−8.11	**<0.001**
Zooplankton to phytoplankton		I	−1.304	0.422	−3.09	**0.002**
Biomass ratio		F	3.132	0.597	5.25	**<0.001**
		S	0.952	0.597	1.59	0.111
		F × S	−6.254	0.844	−7.41	**<0.001**
Chlorophyll *a* to TP ratio		I	−1.551	0.285	−5.43	**<0.001**
		S	0.996	0.310	3.22	**0.001**

Note: I, model intercept; F, fish effect; S, shrimp effect; F × S, interactive effect. Significant terms in bold. Shrimp count data was modelled as Poisson distribution, while others were modelled as Gaussian distribution.
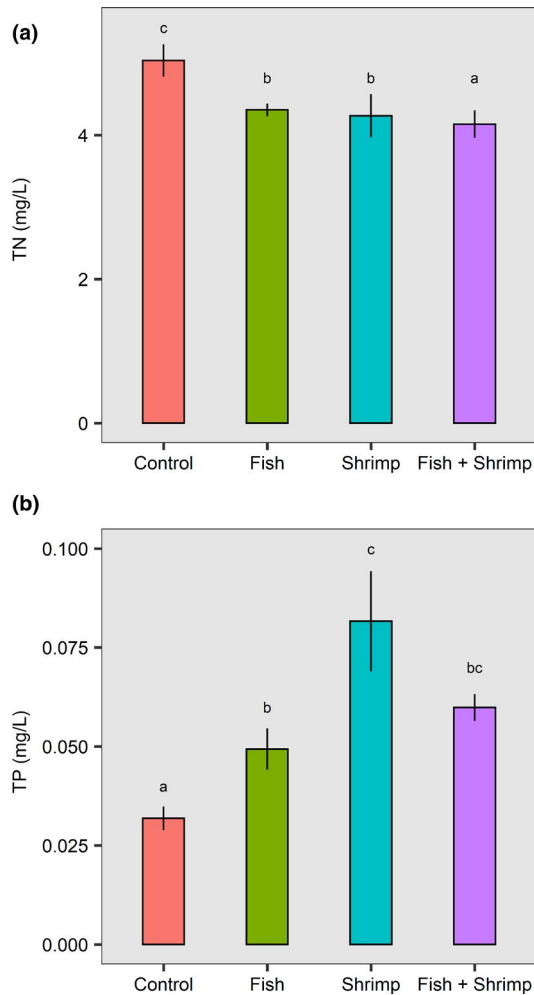
FIGURE 1   Effect of predator treatment on the concentrations of (a) total nitrogen (TN) and (b) total phosphorous (TP). Control: no predators added; Shrimp: shrimp added, Fish: fish added; Fish + Shrimp: both shrimp and fish added. Values represent mean ± SE (n = 6). Means with different letters are significantly different (p < 0.05)

FIGURE 2   Effect of predator treatment on (a) phytoplankton biomass and (b) chlorophyll a (Chl-a) concentration. Control: no predators added; Shrimp: shrimp added, Fish: fish added; Fish + Shrimp: both shrimp and fish added. Values represent mean ± SE (n = 6). Means with different letters are significantly different (p < 0.05)

is in line with the theoretical and empirical studies of linear food chains (Carpenter et al., 1985; Jeppesen et al., 2012). When both predators were added, the strength of collective predator effects on zooplankton and the cascading effects on phytoplankton growth were weaker than the sum of the individual predator effects. Our study supports the view that changes in predator diversity affect ecosystem function (e.g. eutrophication) via predator interference (Douglass et al., 2008; Finke & Denno, 2005; O'Gorman et al., 2008; Wang et al., 2019; Wootton, 2017).

The antagonism can mainly be attributed to IGP, as indicated by the low catch per unit effort of shrimp in the fish-present mesocosms. Although fish gut data were not available in our study, evidence of shrimp consumption by *P. fulvidraco* in the field is given in the literature (Yu et al., 1996; Yuan et al., 2011); for instance, gut content analysis showed that shrimps were the most important diet of *P. fulvidraco* in Lake Gehu, with a frequency of occurrence >83% (Yu et al., 1996). The shrimp losses in fish-present mesocosms could

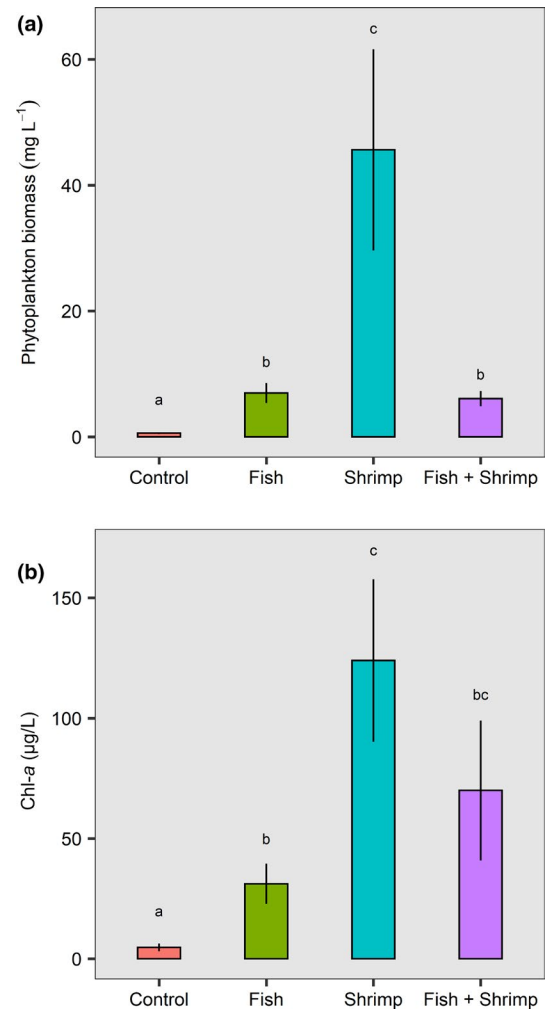not be attributed to food competition from fish, as the *Daphnia* and total zooplankton biomass in the FS treatments was slightly higher than in the S treatments, suggesting that food were actually more abundant when fish were present. Previous studies have suggested that architecturally complex vegetation can dampen antagonistic interactions among predators in salt marsh ecosystems (Finke & Denno, 2006). Intraguild predation, however, did occur in our mesocosms with a submerged macrophyte infestation volume of 35%, suggesting that in warm lakes submerged macrophytes alone do not provide sufficient refuge for shrimps from fish predation, as also evidenced from other studies in subtropical lakes (Meerhoff et al., 2007; Yu et al., 2016).

Our study demonstrated that IGP relaxed zooplankton suppression at the community level (Figure 3e), which is in line with results from food-web models that as the strength of IGP within a trophic level increases, the biomass of its resource level increases (Wang et al., 2019). Compared with the presence of a single predator,

FIGURE 3 Effect of predator treatment on the biomasses of (a) *Daphnia*, (b) small cladocerans, (c) copepods, (d) rotifers and (e) the total zooplankton community. Control: no predators added; Shrimp: shrimp added, Fish: fish added; Fish + Shrimp: both shrimp and fish added. Values represent mean ± *SE* (*n* = 6). Means with different letters are significantly different (*p* < 0.05)
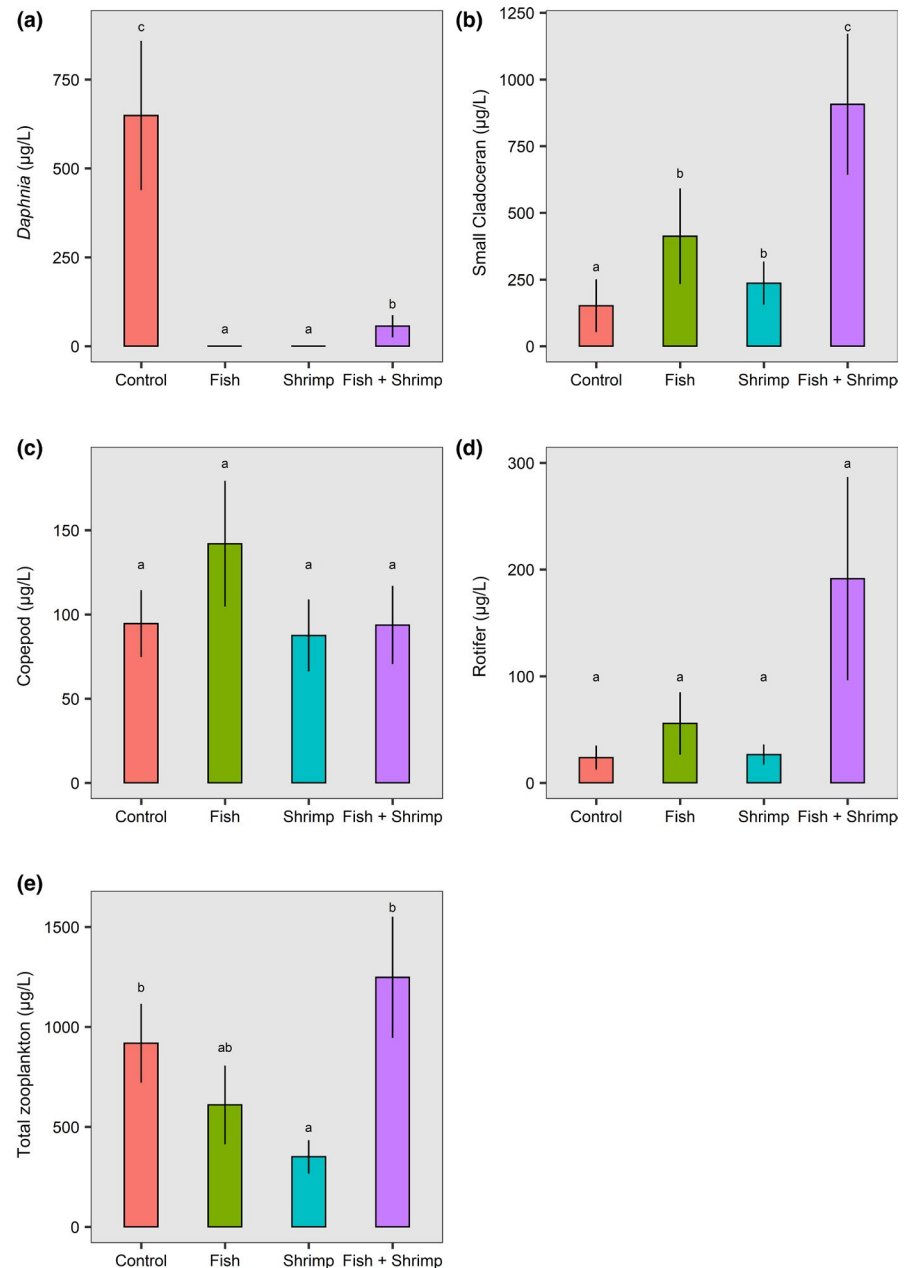
presence of both fish and shrimp elevated not only the survival rates of the key herbivore *D. pulex* but also the total zooplankton biomass. This could be attributed to the overall decline in the predation pressure on zooplankton in the presence of both predators, as evidenced by high proportion of *Daphnia* (sensitive to predation) of the total cladoceran biomass and the high average zooplankton size. In our study, fish and shrimp negatively affected large-sized *Daphnia* but had positive effects on their competitors, the small-sized cladocerans. This probably reflects size-selective predation by small-sized predators. GCA results in the field have also shown that the fish *P. fulvidraco* generally prefer large-sized diets, i.e., small fish, shrimp, and other macroinvertebrates (Yu et al., 1996), which would result in dominance of small-sized zooplankton. Previous GCA studies in Lake Taihu have shown that the shrimp *E. modestus* had no obvious selection effect on the zooplankton community (Shi et al., 1995; Wen &

Xie, 2013), which, however, may be attributed to the low *Daphnia* abundance in the lake (Zhou et al., 2020), due to high fish predation (Mao et al., 2020).

It could be argued that the antagonistic effects of predators on phytoplankton growth were not related to changes in herbivory due to the IGP effect on zooplankton, but instead were a result of predator modification of nutrient availability (Vanni & Layne, 1997), i.e., as in our dual treatment, the fish predation on shrimps resulted in overall lower nutrient excretion, leading to low phytoplankton biomass. Supporting this view, antagonistic interaction effects of predators were also observed for the TP concentration. However, excretion cannot explain the predator-induced changes observed in the Chl-*a* to TP ratio, as we found a high phytoplankton yield per TP concentration and a low zooplankton to phytoplankton biomass ratio in shrimp mesocosms, indicating

that shrimps influenced phytoplankton growth mainly through top-down (predation) and not bottom-up (nutrient excretion) factors (Jeppesen et al., 1997). Accordingly, the antagonistic effects of fish and shrimp on phytoplankton growth could largely be attributed to changes in top-down forces induced by IGP between the two predators.
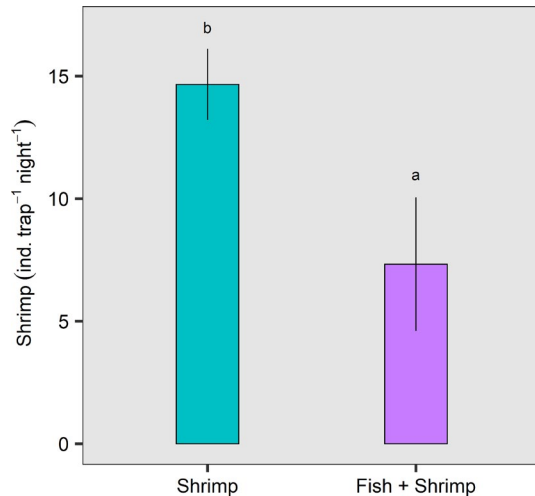

FIGURE 4 Comparisons of shrimp catch per unit effort between single shrimp added treatment (Shrimp) and shrimp and fish added treatment (Fish + Shrimp) at the end of the experiment. Means $\pm$ *SE* ($n = 6$) are shown. Means with different letters are significantly different ($p < 0.05$)

Understanding the interaction among aquatic predators is of high importance for lake management and restoration. Biomanipulation, based on the theory of the occurrence of trophic cascades in linear food chains, has long been used to combat eutrophication in temperate and warm shallow lakes, with the purpose of reducing the abundance of predators to increase that of herbivores and thereby suppress phytoplankton growth (Carpenter et al., 1985; Jeppesen et al., 2012). However, changes in predator richness after biomanipulation and their consequences for the occurrence of trophic cascades are often ignored (Wootton, 2017). Our study suggests that intraguild predation between two common predators on lake zooplankton diminished zooplankton suppression and mitigated eutrophication. Thus, when implementing biomanipulation efforts aiming to combat eutrophication via enhancing the herbivory on phytoplankton, lake managers must consider both the quantity and diversity of predator assemblies.
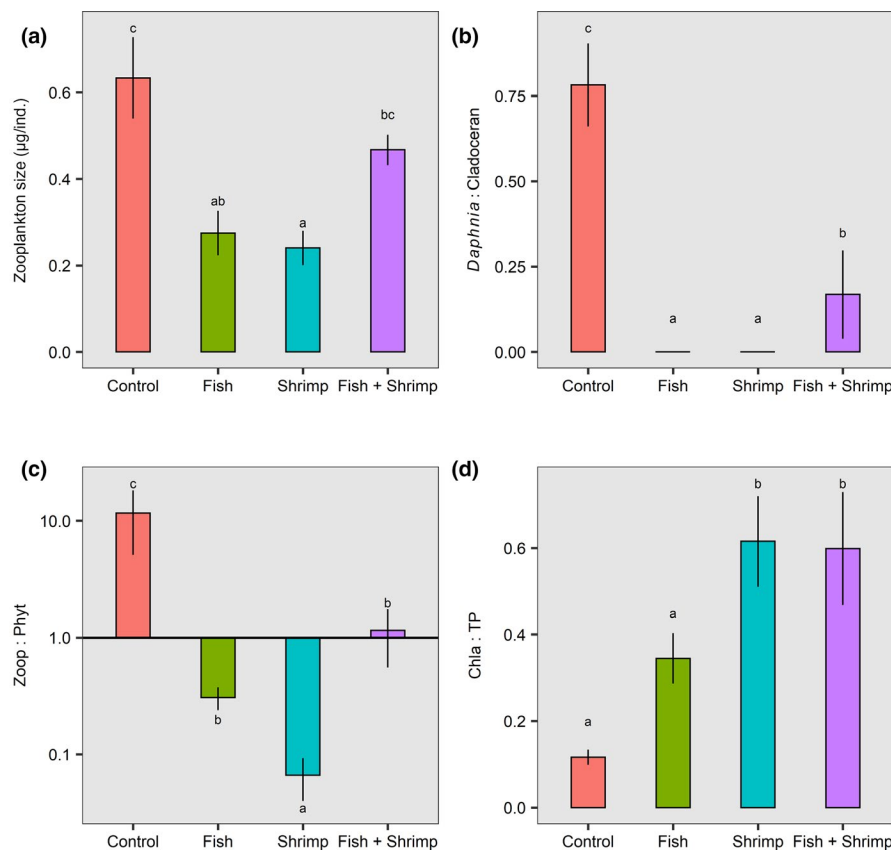
FIGURE 5 Effect of predator treatment on (a) zooplankton size, (b) *Daphnia* to cladocerans biomass ratio (*Daphnia*:Cladoceran), (c) zooplankton to phytoplankton biomass ratio (Zoop:Phyt) and (d) chlorophyll *a* to total phosphorus ratio (Chl *a*:TP). Control: no predators added; Shrimp: shrimp added, Fish: fish added; Fish + Shrimp: both shrimp and fish added. Values represent mean $\pm$ *SE* ($n = 6$). Means with different letters are significantly different ($p < 0.05$)

118C250). All experimental procedures involving fish were approved by the Institutional Animal Care and Use Committee of the Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences.

AUTHOR CONTRIBUTION

Hu He: conceptualisation, methodology, investigation, data curation, writing—original draft. Xiaoyu Ning: investigation, data curation, formal analysis. Kunquan Chen: investigation, data curation, formal analysis. Qisheng Li: investigation, data curation, formal analysis. Kuanyi Li: conceptualisation, methodology, writing—review and editing, funding acquisition. Zhengwen Liu: conceptualisation, methodology, writing—review and editing, funding acquisition. Erik Jeppesen: conceptualisation, methodology, writing—review and 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.

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