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PRIMARY RESEARCH PAPER

Freshwater mussels can enhance zooplankton size and their grazing potential on phytoplankton with implications for water clarity in tropical eutrophic shallow lakes

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Abstract Filter-feeding freshwater mussels are ecosystem engineers that significantly modify the structure of biological communities and trophic status, affecting water quality. An 8-week mesocosm-experiment, with and without the freshwater mussel *Sinanodonta woodiana,* tested the hypothesis that this filtering-feeding mussel alters the plankton community by reducing chlorophyll *a* (Chl *a*) of larger phytoplankton (> 2.0 μm), reducing small zooplankton such as rotifers and increasing the biomass of large zooplankton such as cladocerans and copepods. These changes would enhance the ability of zooplankton to control phytoplankton in eutrophic shallow waters. Compared with the mussel-free control, treatment with mussels led to a decrease in the Chl *a* of phytoplankton, particularly microphytoplankton (> 20 μm) and nanophytoplankton (> 2.0 μm), and an increase in the biomass of large zooplankton such as cladocerans and copepods, while the biomass of rotifers did not change. As a result, mussels enhanced

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the biomass ratio of zooplankton to phytoplankton, indicating stronger grazer control of phytoplankton. Total suspended solids were reduced, and light intensity and benthic algal Chl *a* increased in the mussel treatment. Our study shows that this native freshwater mussel may directly and indirectly facilitate a reduction in Chl *a* of phytoplankton thereby improving the water quality in tropical eutrophic shallow lakes.

Keywords Benthic animal · Phytoplankton · Zooplankton · Water quality · Aquatic ecosystem

Introduction

Zooplankton, especially large cladocerans such as *Daphnia*, are important consumers of phytoplankton in lakes (Shapiro, 1995; Moss et al., 1996); the larger the size of the zooplankton, the stronger is their control of the phytoplankton (Brett et al., 1994; Cyr and Curtis, 1999; Cottingham and Schindler, 2000; Cottingham et al., 2004). Most freshwater mussels are also consumers of phytoplankton and, due to their high biomass, their filter-feeding ability is often greater than that of zooplankton (Hwang et al., 2004). Moreover, because of their large body size and benthic distribution, they are less affected by planktivorous fish predation although they may be impacted by molluscivorous fish (e.g., Rudstam and Gandino, 2020).

Freshwater mussels are often the dominant zoobenthos in terms of biomass. They feed on various organic particles in the water column, including phytoplankton, zooplankton, bacteria, and detritus (Vaughn et al., 2008; Tuttle-Raycraft and Ackerman 2018). By filtering, freshwater mussels reduce the concentration of suspended solids and the biomass of phytoplankton in the water column, thus increasing the transparency of the water and the potential for phytobenthos to grow (Zhu et al., 2006; Genkai-Kato et al., 2012). Further, they couple the pelagic and benthic ecosystems through filter-feeding activities, which has an important impact on aquatic ecosystem processes (Vaughn, 2018). Freshwater mussels like dreissenids have large effects on the ecosystem (Higgins and Vander Zanden 2010, Karatayev et al., 2023) and are considered ecosystem engineers (Jones et al., 1997).

Filter-feeding freshwater mussels are selective feeders. Each species has its own specific filtering range (Rosa et al., 2018). For example, *Corbicula fluminea* (Müller, 1774) captures particles in the 0.3–20 µm range, mainly 3–5 µm (Atkinson et al., 2011), zebra mussels *Dreissena polymorpha* (Pallas, 1771) in the 5–45 µm range (Sprung and Rose 1988; Gergs et al., 2009), and *Sinanodonta woodiana* (Lea, 1834) in the 2–30 µm range (Zheng & Wei, 1999), while *Macoma contabulata* (Deshayes, 1855) filter particles ranging from 20 to 40 µm. Thus, all these species feed selectively on phytoplankton yet mainly on species larger than 2.0 µm.

Besides phytoplankton, freshwater mussels consume zooplankton (Hwang et al., 2004), but the consumption is highly size dependent (Pace et al., 1998). Microzooplankton, including rotifers and copepod nauplii, are more likely to be preyed upon, while macrozooplankton, such as cladocerans and copepods, are less vulnerable (Marroni et al., 2017; Pearson & Duggan, 2019; Rong et al., 2021). For example, after a zebra mussel invasion in Hudson River, New York, Wong et al. (2003) found a sharp decrease in the number of small (~140 µm) and medium-sized (~210 µm) zooplankton. Quagga mussels *Dreissena bugensis* (Andrusov, 1897) reduce nauplii and have a great impact on zooplankton < 128 µm (Whitten et al., 2018) but they may also impact larger zooplankton

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like daphnids (Higgins & Vander Zanden, 2010; Karatayev et al., 2023). Freshwater mussels may also indirectly affect zooplankton by competing for food (Jack & Thorp, 2000). Thus, freshwater mussels can alter the structure of zooplankton assemblages both directly and indirectly (Jin, et al., 2025).

The grazing pressure of zooplankton on phytoplankton is commonly expressed by a ratio between zooplankton biomass and phytoplankton biomass; the higher the ratio, the stronger control ability of zooplankton on phytoplankton growth (Søndergaard et al., 2008; Jeppesen et al., 2012). However, zooplankton species composition also affects their ability to control phytoplankton. Furthermore, the ability of zooplankton to control phytoplankton is size dependent. Species with larger body size are better than small species at suppressing phytoplankton; for example, cladocerans are better controllers than rotifers (Jeppesen et al., 2012), and *Daphnia* is more efficient than *Bosmina* (Gliwicz, 1990; Scheffer, 1998).

Freshwater mussels may also affect the nutrient concentrations in the water by filter feeding, where they filter phytoplankton and organic suspended particles and transfer particles to sediments as feces and pseudofeces, thereby reducing the nutrients concentrations in the water column (McLaughlan & Aldridge, 2013; Coelho et al., 2018). However, physiological activities, such as secretion and excretion, of freshwater mussels can release nutrients to the water (Cyr et al., 2017) and enhance phytoplankton growth. In addition, the biological activities of freshwater mussels disturb the sediments, accelerating the release of nutrients from the sediments into the water column (Zhang et al., 2014), which also promotes phytoplankton growth. The net effect of nutrient reduction and enhancement mechanisms is uncertain and may vary depending on the trophic state and characteristics of the sediments (Zhang et al., 2014; Rong et al., 2021).

There are numerous studies on freshwater mussels, including their feeding habits (Zheng & Wei, 1999; Tuttle-Raycraft & Ackerman, 2018), filtration rates, and their effects on water quality and nutrient concentrations (Zhang et al., 2011; Marescaux et al., 2016; Jin et al., 2025). However, the influence of freshwater mussels, especially large species such as *Sinanodonta woodiana*, on the structure of zooplankton and their ability to control phytoplankton need further studies. This species is native to Yangtze River basin and Taiwan (Lopes-Lima et al., 2020). In addition, *S. woodiana* has been proposed to be used in the restoration of eutrophic waters in China and is therefore a relevant species to focus on (Zhang et al., 2014). In a previous study using this species, Jin et al. (2025) found that the bivalves being positioned in both the benthic and the pelagic habitats, reduced the biomasses of total phytoplankton and nanophytoplankton and decreased total suspended solids concentrations. We hypothesize that in addition to feeding directly on phytoplankton, this native freshwater mussels may indirectly enhance the filtering pressure of large zooplankton such as cladocerans and copepods on phytoplankton and thereby further improve water clarity.

Materials and methods

Experimental mesocosm set-up

The experiments were carried out outdoors in eight circular plastic tanks (upper diameter = 57 cm, bottom diameter = 46 cm, height = 82 cm, i.e., 171 l) containing sediment and water. Sediment (total nitrogen (*TN*) = 3.40 mg g^{-1}, total phosphorus (TP) = 1.52 mg g^{-1}) was collected from a shallow eutrophic lake in Guangzhou, China (Zhang et al., 2014), air-dried, and sieved (mesh size = 0.5 cm) to remove coarse debris. A 10 cm thick layer of sediment was added uniformly to each mesocosm. Then, the mesocosms were filled with lake water (*TN* = 2.63 mg l^{-1}, *TP* = 0.012 mg l^{-1}) that was filtered through a plankton net (mesh size = 64 μm) to remove most zooplankton. The mesocosms were exposed to natural sunlight and allowed to equilibrate for two weeks. At the end of this period, nutrient concentrations in the mesocosms were: TN, 2.87 ± 0.24 mg l^{-1} and TP, 0.07 ± 0.01 mg l^{-1}. A petri dish (diameter 6.0 cm) filled with sieved sediment was placed on the sediment surface of each mesocosm to allow growth of benthic algae.

Sinanodonta woodiana were bought from a clam culture pond in Foshan, China. The mussels were maintained in 200-l tanks for two weeks before introduction to the mesocosms. One mussel with an average wet weight 339.2 (± 15.9 g), which is a common size in nature (Dobler et al., 2022), was added to each of the four mesocosms, termed treatment mesocosms. The remaining four mesocosms with no freshwater mussel acted as control. The mesocosms were checked daily. One dead mussel (July 8, 2022) was replaced by a living one of similar weight.

Nitrogen (N) in the form of KNO_3 and phosphorus (P) as NaH_2PO_4 were added weekly to each mesocosm at 1.5 mg N $l^{-1}wk^{-1}$ and 0.1 mg P $l^{-1}wk^{-1}$ to simulate natural external loading (Zhang et al., 2014). During the experiment, lake water filtered through a plankton net (as described above) was added to the mesocosms to maintain a constant water level. The experiment was conducted from June 7 to August 2, 2022.

Sampling and analysis

Every two weeks, light intensity was measured at 10 a.m. by an underwater irradiance meter (ZDS-10W) at 50 cm depth. Water temperature, pH and dissolved oxygen (DO) were measured using a YSI Model 556 multi-parameter probe. After that, water samples (1L) were taken approximately 20 cm under the water surface in the middle of each mesocosm with a clean polyethylene plastic bottle for analysis of total suspended solids (TSS) and phytoplankton Chl *a*.

A 200 ml water sample was filtered on 20 µm filters for measurements of micro-phytoplankton (> 20 µm), nano-phytoplankton (2.0–20 µm) and pico-phytoplankton (0.2–2.0 µm) and for Chl *a* determination (Rong et al., 2021). Another 200 ml water sample was filtered on 0.45 µm cellulose acetate membrane filters for determining phytoplankton Chl *a*. Different size classes of phytoplankton Chl *a* were extracted using a 90% acetone/water solution for 24 h. After that, the concentration was measured spectrophotometrically (Jespersen and Christoffersen, 1987). TSS was recorded as the residue retained from 400 ml water filtered through a Whatman GF/C fiber membrane and dried at 108 °C for 2 h. A 10 l water sample was taken and filtered through a 64 µm mesh to collect zooplankton from each mesocosm. The sample was fixed and stored in 5% formaldehyde. Species were identified according to Zhao (2016). Their densities (ind. l^{-1}) were measured under a microscope. The wet weight biomass of zooplankton was calculated by the equation $W = q\,L^b$, where W (mg) is zooplankton wet weight biomass, L (mm) is zooplankton length, and q and b are coefficients with specific values detailed in SC/T 9402–2010. The ratio of zooplankton biomass/phytoplankton wet weight biomass was calculated. Wet weight biomass of phytoplankton was estimated from the Chl *a* of phytoplankton by dividing by 0.505% (Kasprzak et al., 2008). The dominant zooplankton species was determined at the beginning and at the end of the experiment according to Yu et al. (2018).

We used a scalpel to scrape off benthic algae on the surface of the petri dish in each mesocosm, and the Chl *a* content was used as a proxy for their biomass. After the collection of water, benthic algae and zooplankton samples, nutrients were added to each mesocosm. A new petri dish was placed in each mesocosm after all sampling events. At the end of the experiment, the wet weight of the mussels (with shells) was recorded.

Statistical analyses

Repeated measures analysis of variance (RM-ANOVAs) was used to determine any significant differences in TN, NO_3^-–N, NH_4^+–N, TP, SRP, TSS, Chl *a*, light intensity, different size classes of phytoplankton Chl *a*, and the abundance and biomass of zooplankton between treatments, with time as repeated factor. Prior to analysis, Mauchly's test of sphericity and test of homogeneity of variances were performed to meet the assumption. All results are presented as mean ± SD. All statistical analyses were carried out using IBM SPSS Statistics 21.

Results

Phytoplankton Chl *a*

Phytoplankton Chl *a* was lower in the mussel treatment than in the control (RM-ANOVAs, treatment effect, $P = 0.024$; Fig. 1a). The phytoplankton Chl *a* changed significantly over time (RM-ANOVAs, time effect, $P = 0.000$). In addition, the interaction effect was significant (RM-ANOVAs, interaction effect, $P = 0.012$).

Microphytoplankton Chl *a* was lower in the mussel treatment than in the control (RM-ANOVAs, treatment effect, $P = 0.026$; Fig. 1b). The Chl *a* of nanophytoplankton was also lower in the mussel treatment than in the control (RM-ANOVAs, treatment effect, $P = 0.016$; Fig. 1c). No significant difference was recorded between treatments for picophytoplankton Chl *a* (RM-ANOVAs, treatment effect, $P = 0.215$; Fig. 1d).

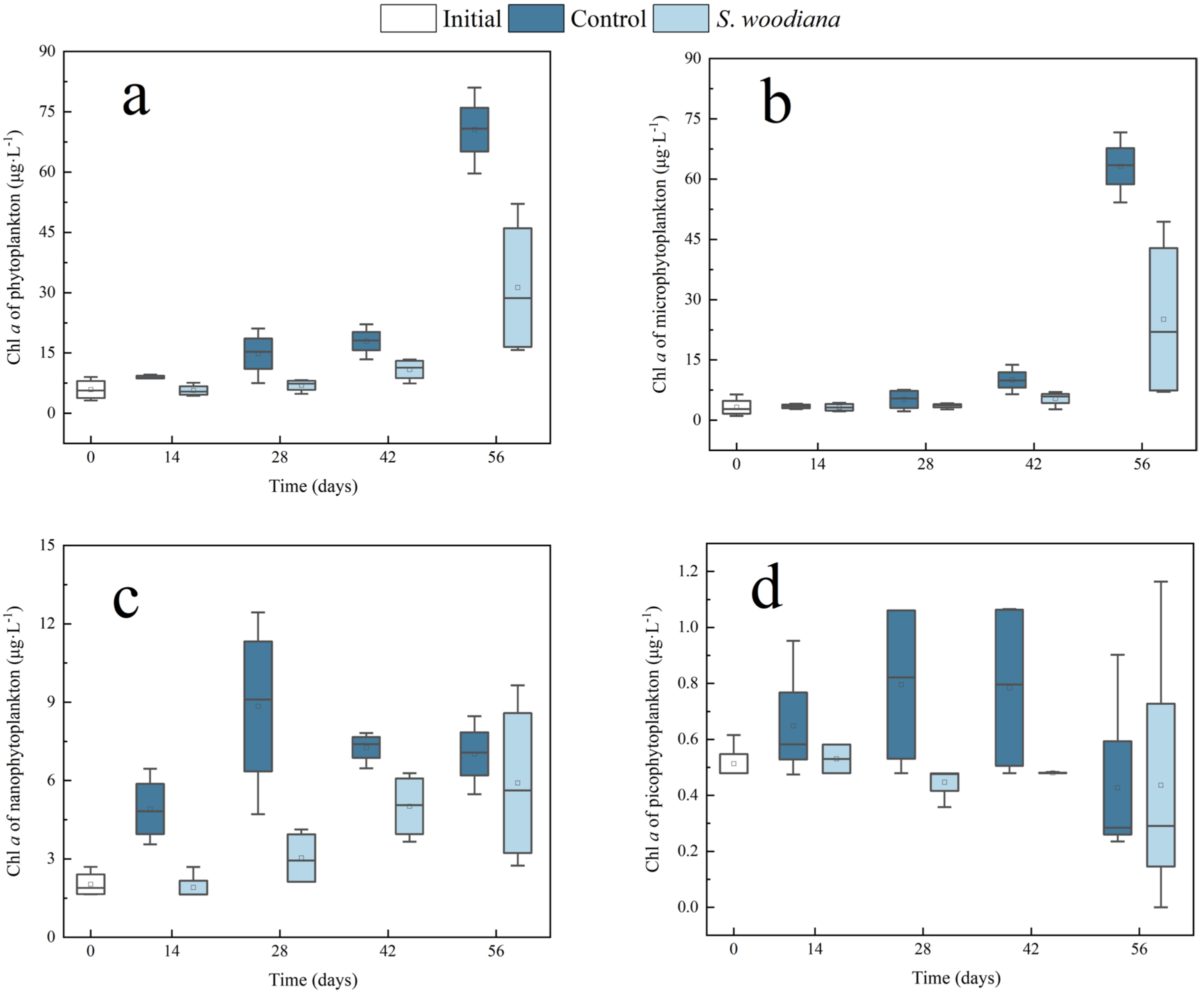

Fig. 1 Chlorophyll *a* (Chl *a*) concentration of phytoplankton (mean ± 1SD; **a**), microphytoplankton (mean ± 1SD; **b**), nanophytoplankton (mean ± 1SD; **c**), and picophytoplankton (mean ± 1SD; **d**) in *S. woodiana* treatments and controls over time

The Chl *a* of microphytoplankton and nanophytoplankton changed significantly over time (RM-ANOVAs, time effect, $P = 0.048$ and 0.045), while the Chl *a* of picophytoplankton remained constant (RM-ANOVAs, time effect, $P = 0.079$). The interaction effects for the Chl *a* of microphytoplankton, nanophytoplankton, and picophytoplankton were not significant (RM-ANOVAs, interaction effect, $P = 0.265$, 0.126 and 0.399, respectively).

Zooplankton

Biomass

Total zooplankton biomass was higher in the mussel treatment than in the control (RM-ANOVAs, treatment effect, $P = 0.027$; Fig. 2a) and changed significantly over time (RM-ANOVAs, time effect, $P = 0.002$). In addition, the interaction effect was

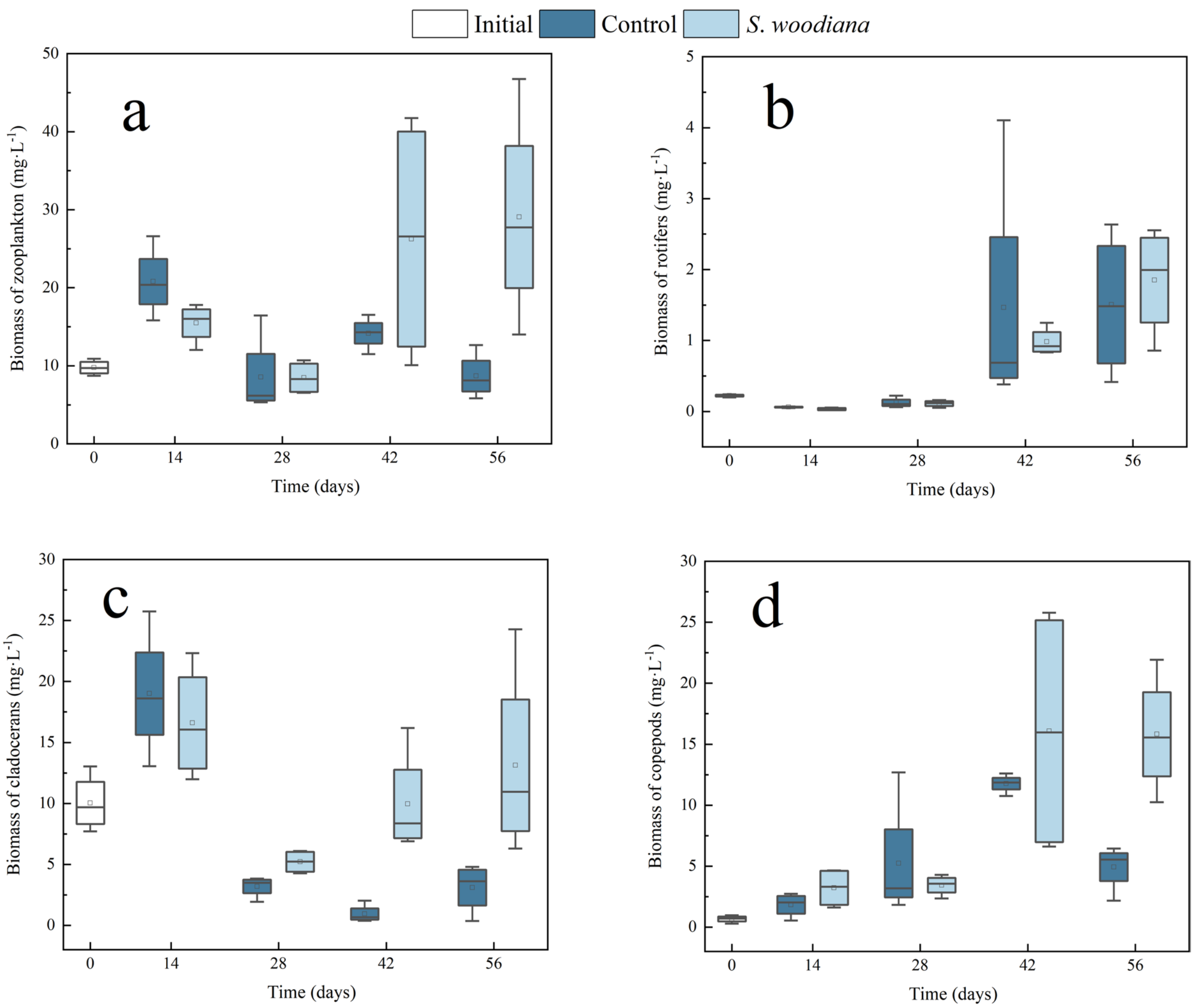

Fig. 2 Biomass (wet mass) of total zooplankton (mean ± 1SD; **a**), rotifers (mean ± 1SD; **b**), cladocerans (mean ± 1SD; **c**) and copepods (mean ± 1SD; **d**) in *S. woodiana* treatments and controls over time

significant (RM-ANOVAs, interaction effect, $P = 0.033$).

The biomass of rotifers did not differ between the mussel treatment and the control (RM-ANOVAs, treatment effect, $P = 0.561$; Fig. 2b) and did not change over time (RM-ANOVAs, time effect, $P = 0.065$), while the biomasses of cladocerans and copepods were higher in the mussel treatment than in the control (RM-ANOVAs, treatment effect, $P = 0.035$ and 0.020; Fig. 2c and d). The biomass of cladocerans and copepods changed significantly over time (RM-ANOVAs, time effect, $P = 0.011$ and 0.000, respectively). The interaction effect of time and treatment was significant for the biomass of copepods (RM-ANOVAs, interaction effect, $P = 0.007$), but not for the biomasses of rotifers and cladocerans (RM-ANOVAs, interaction effect, $P = 0.712$ and 0.073, respectively).

Zooplankton grazing potential on phytoplankton

Zooplankton/phytoplankton ratio

The ratio of zooplankton biomass/phytoplankton wet weight biomass was higher in the mussel treatment than in the control (RM-ANOVAs, treatment effect, $P = 0.008$; Fig. 3a). The interaction effect for the ratio

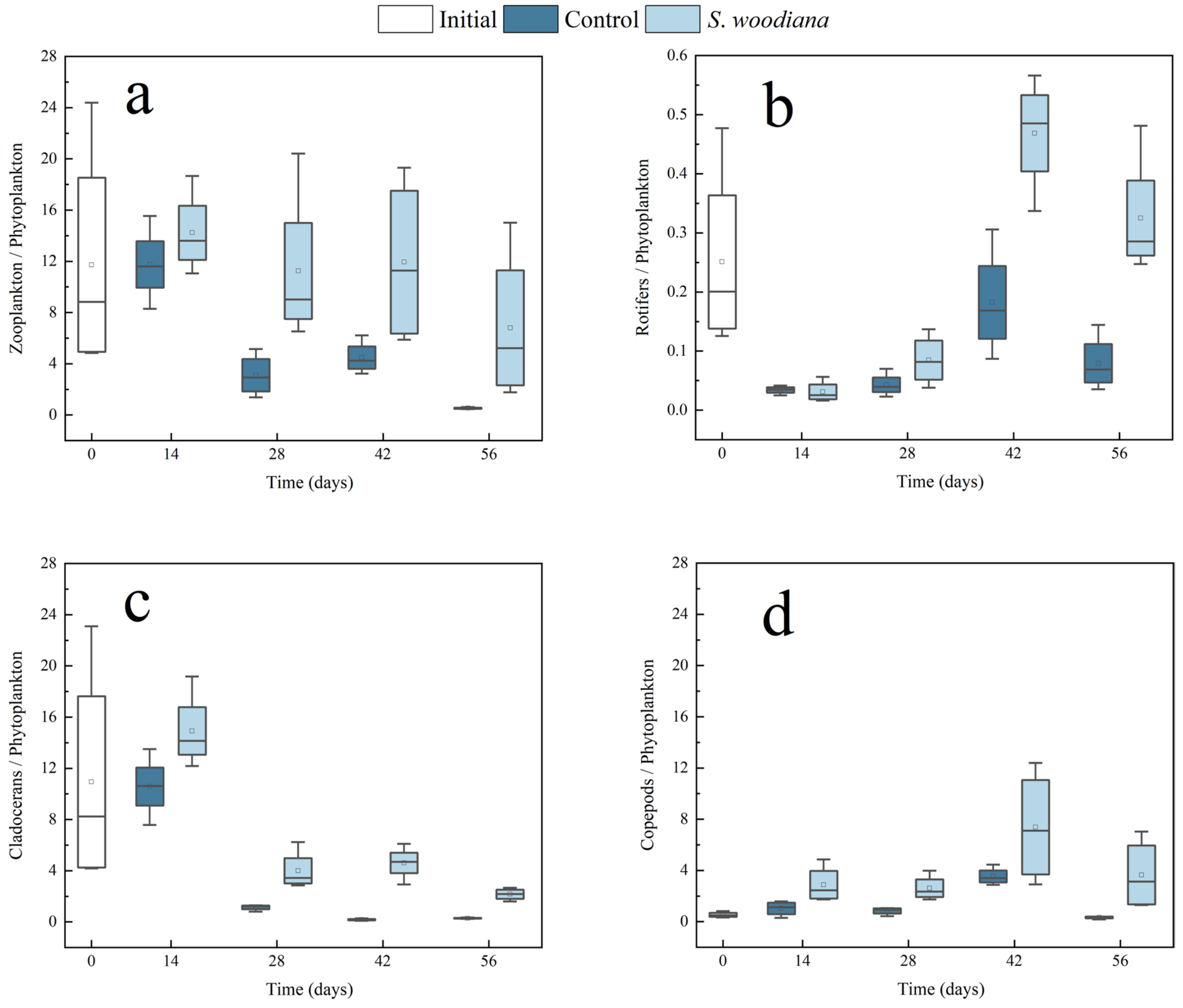

Fig. 3 Ratio of zooplankton (**a**), rotifer (**b**), cladoceran (**c**) and copepod (**d**) wet biomass to phytoplankton wet biomass (mean ± 1SD) in *S. woodiana* treatments and controls over time

was not significant (RM-ANOVAs, interaction effect, $P = 0.969$).

The ratio of rotifers, cladocerans, and copepods to phytoplankton

The ratios of rotifer, cladoceran, and copepod biomass to phytoplankton wet biomass were higher in the mussel treatment than in the control (RM-ANOVAs, treatment effect, $P < 0.01$ for all treatments; Fig. 3b–d) and changed significantly over time (RM-ANOVAs, time effect, $P = 0.000$, 0.000 and 0.041, respectively). The interaction effect of time and treatment was significant for the ratio of rotifer biomass/phytoplankton wet biomass (RM-ANOVAs, interaction effect, $P = 0.006$) but not for the cladoceran and copepod biomass/phytoplankton wet biomass (RM-ANOVAs, interaction effect, $P = 0.535$ and 0.262, respectively).

The dominant species

In the control, the dominant species were *Daphnia pulex* Leydig, 1860, *D. hyalina* Leydig, 1860, and *Brachionus urceus* (Linnaeus, 1758) at the beginning of the experiment while *B. urceus*, *Diaphanosoma* sp., *Neodiaptomus schmackeri* (Poppe & Richard, 1892), and *Thermocyclops taihokuensis* Harada, 1931 were dominant at the end. In the mussel treatment, the dominant species were *T. taihokuensis, Ceriodaphnia cornuta* Sars, 1885, *N. schmackeri*, and *Brachionus falcatus* Zacharias, 1898.

TSS and light intensity

TSS concentrations increased significantly over time (RM-ANOVAs, time effect, *P* = 0.000) both in the control and in the mussel treatment, but were lower in the mussel treatment than in the control (RM-ANOVAs, treatment effect, *P* = 0.039; Fig. 4a). The interaction effect of time and treatment for TSS was not significant (RM-ANOVAs, interaction effect, *P* = 0.291).

Light intensity on the sediment surface was higher in the mussel treatment than in the control (RM-ANOVAs, treatment effect, *P* = 0.002; Fig. 4b) and changed significantly over time (RM-ANOVAs, time effect, *P* = 0.000). In addition, the interaction effect of time and treatment was significant (RM-ANOVAs, interaction effect, *P* = 0.023).

Benthic algal biomass

The Chl *a* of benthic algae was higher in the mussel treatment than in the control (RM-ANOVAs, treatment effect, *P* = 0.042; Fig. 5) and changed significantly over time (RM-ANOVAs, time effect, *P* = 0.000). In contrast, the interaction effect was insignificant (RM-ANOVAs, interaction effect, *P* = 0.078).

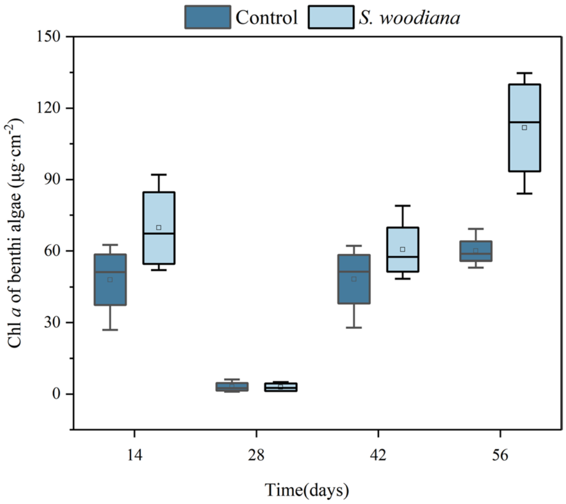

Fig. 5 Chl *a* of benthic algae (mean ± 1SD) in *S. woodiana* treatments and controls over time

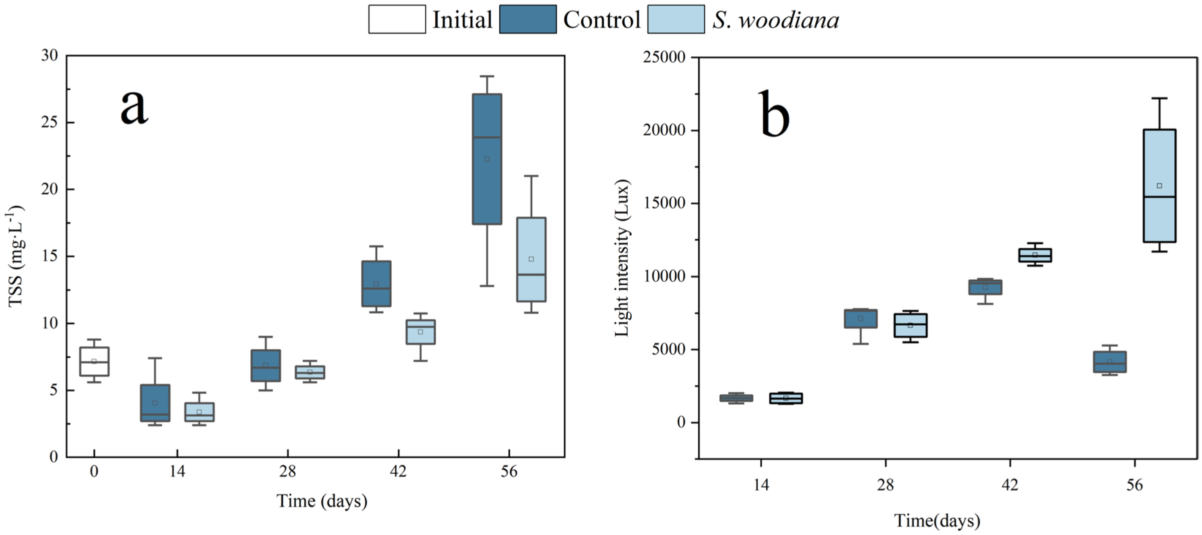

Fig. 4 Total suspended solids (TSS, mean ± 1SD; Fig. 4a) concentrations and light intensity (mean ± SD; Fig. 4b) in *S. woodiana* treatments and controls over time

Discussion

Sinanodonta woodiana decreased the phytoplankton, microphytoplankton and nanophytoplankton Chl *a*, increased the biomass of large zooplankton (cladocerans and copepods, but not the smaller rotifers), altering the zooplankton community structure. In addition, the mussels increased the biomass ratios of total zooplankton, rotifers, cladocerans, and copepods to phytoplankton. The mussels also decreased TSS concentrations, enhancing light intensity on the sediment surface with a subsequent in benthic algae Chl *a*, while the nutrient concentrations remained unchanged (Table 1).

In our earlier study (Jin et al., 2025), we found that *S. woodiana* positioned in both the benthic and the pelagic habitat reduced the total phytoplankton and nanophytoplankton Chl *a*—the main component of the total phytoplankton throughout the experiments, but not the microphytoplankton and picophytoplankton Chl *a*. Similarly, in this study we found that mussels decreased the Chl *a* of phytoplankton and nanophytoplankton, whereas picophytoplankton Chl *a* remained unchanged. However, here we also found a negative effect on microphytoplankton—the main component of the phytoplankton throughout the experiments. The difference between the two studies of the microphytoplankton might be due to nutrients and weather conditions. Both studies show that this mussel species alters the structure of the phytoplankton assemblage. The decrease in phytoplankton in the mussel treatment likely reflects the mussels' filter feeding, but it may also be related to changes in zooplankton as the biomasses of cladocerans and copepods were higher in the mussel treatments than in the controls. Consequently, the biomass ratios of total zooplankton and that of all major groups, cladocerans, copepods, and even the smaller rotifers to phytoplankton were higher in the mussel treatment than in the control, indicating that the mussels enhanced the overall ability of zooplankton to control the remaining phytoplankton, as seen also in lakes with reduced fish predation (Jeppesen et al., 2011).

We expected mussels to contribute to changes in zooplankton community structure (Table 2). Many studies have demonstrated that mussels can consume microzooplankton, especially rotifers (Marroni et al., 2017; Rong et al., 2021), while large-sized zooplankton, such as cladocerans and copepods, are less

Table 1 Summary of repeated measures analysis of variance results on the effects of treatment (Control and Bivalve) and time on the concentrations (mg/L) of TN, NO_3^--N, NH_4^+-N, TP, SRP, TSS, OSS, light intensity, and biomass (chlorophyll *a* (μg/cm^{-2})) of benthic algae as well as the biomasses of phytoplankton (Phyto-), microphytoplankton (Micro-), nanophytoplankton (Nano-) and picophytoplankton (Pico-)

Effects	TN	NO_3^--N	NH_4^+-N	TP	SRP	TSS	Light	benthic algae	Phyto-	Micro-	Nano-	Pico-
Treatment	0.709	0.406	0.056	0.339	0.602	0.039	0.002	0.042	0.024	0.026	0.016	0.215
Time	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.048	0.045	0.079
Time × Treatment	0.052	0.342	0.335	0.341	0.086	0.291	0.023	0.078	0.012	0.265	0.126	0.339

Numbers in the table are *P* values. The significance level was set at $P < 0.05$

Table 2 Summary of repeated measures analysis of variance results on the effects of treatment (Control and Bivalve) and time on the biomasses (mg/L) of zooplankton, rotifers, cladocerans, and copepods, as well as the ratio of zooplankton, rotifer, cladoceran and copepod biomass to phytoplankton biomass

Effects	Zooplankton Biomass	Rotifers Biomass	Cladocerans Biomass	Copepods Biomass	Zooplankton/phytoplankton	Rotifers/phytoplankton	Cladocerans/phytoplankton	Copepods/phytoplankton
Treatment	0.027	0.561	0.035	0.020	0.008	0.001	< 0.001	0.008
Time	0.002	0.065	0.011	< 0.001	0.008	< 0.001	< 0.001	0.041
Time × Treatment	0.033	0.712	0.073	0.007	0.969	0.006	0.535	0.262

Numbers in the table are *p* values. The significance level was set at $p < 0.05$

vulnerable to predation because their higher mobility allows them to evade sessile mussels (Marroni et al., 2017). However, we found that the mussels did not change the biomass of rotifers. The overall increase in total zooplankton biomass, including cladocerans and copepods, indicates a positive effect of the mussels on zooplankton biomass under our simulated eutrophic conditions. The increased in zooplankton biomass might be related to changes in food quality induced by the mussel-related shift in phytoplankton size structure and composition, but this remains speculative as we did not assess food quality.

The mussels also changed the species dominance within the zooplankton. At the end of the experiment, the dominant zooplankton species in the controls were the rotifer *Brachionus urceus*, the cladoceran *Diaphanosoma* sp., and the copepods *Neodiaptomus schmackeri* and *Thermocyclops taihokuensis*. In the mussel treatment, the dominant zooplankton species were the same two copepods (*T. taihokuensis* and *N. schmackeri)*, the clacoderan *Ceriodaphnia cornuta*, and the rotifer *B. falcatus*. The decreased dominance of *B. urceus* in the mussel treatment may have been caused by mussels filtration due to their small size and slow movements (Marroni et al., 2017; Rong et al., 2021). The increased dominance of copepods (*T. taihokuensis*) and cladocerans (*C. cornuta*) in the mussel treatment likely reflects their ability to avoid mussel filtration due to their fast movement (Marroni et al., 2017). Meanwhile, *N. schmackeri* remained dominant in both the control and mussel treatments, possibly indicating the resistance to mussel filtration.

We found that the concentrations of total suspended particles (TSS) increased significantly over time both in the control and in the mussel treatment, coinciding with the increase of phytoplankton Chl *a*. In natural systems, TSS may also increase due to resuspension by fish or wind, but the experiment did not involve fish and the mesocosms were wind protected. This means that the enhanced phytoplankton growth is the key reason for the TSS increase over time. We found that TSS was lower in the mussel treatment than in the control, leading to higher light intensity at the sediment surface, which may explain the higher Chl *a* of benthic algae. Thus, mussels promoted benthic algae growth. However, in our earlier, shorter study (35 days), we found a TSS decreased with time (Jin et al., 2025). In that study, we also found that mussels in both the benthic and the pelagic habitat decreased TSS and increased light intensity and benthic algae growth (Jin et al., 2025). Benthic algae may diminish nutrient release from sediment to water (Genkai-Kato et al., 2012; Zhang et al., 2013), and filter-feeding mussels may, by converting undigested food into feces or pseudo-feces, have a similar effect (Vaughn, 2018; Zieritz et al., 2019). The excretion and biological disturbance by freshwater mussels may also increase water column nutrient concentrations (Atkinson et al., 2013; Zhang et al., 2014; Coelho et al., 2018; Parr et al., 2020). The combined effect of nutrient release and retention may have counteracted each other in our experiment, as seen in some other studies (Vaughn, 2018; Rong et al., 2021).

Our study did not involve fish. However, in tropical and subtropical eutrophic lakes, omnivorous fish, such as tilapia, crucian carp, and carp (Jeppesen et al., 2007) exert a high predation pressure on zooplankton (Meerhoff et al., 2007; Chen et al., 2013; Liu et al., 2018). Accordingly, fish presence may partly or totally counteract the positive effects on water quality by freshwater mussels. Further studies at varying densities of fish and freshwater mussels are needed to

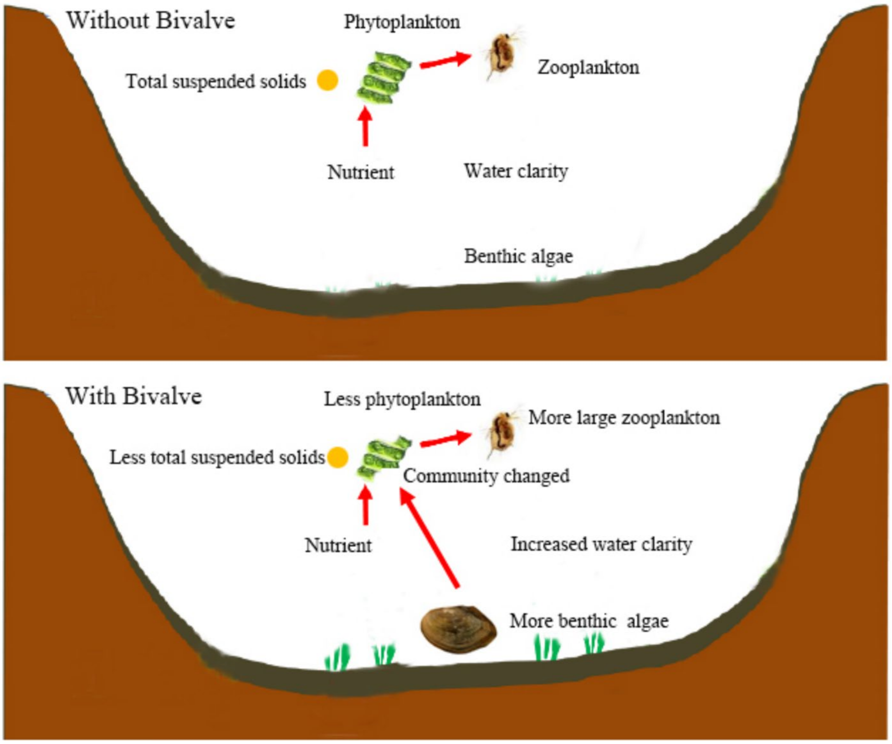

Fig. 6 Conceptual model of freshwater mussels enhancing zooplankton size and their grazing potential on phytoplankton, with implications for water clarity in tropical eutrophic shallow lakes

elucidate the interactive effects of fish and mussels on the zooplankton and, consequently, zooplankton control of phytoplankton. Since our study was conducted at a mesocosm scale, follow-up studies at larger spatial scales are recommended.

Freshwater mussels are of key importance for maintaining ecosystem health and provide valuable ecosystem services (Vaughn, 2018). However, the populations and distribution ranges of many native species have declined worldwide, including North and South America, Europe, and China (Lopes-Lima et al., 2023; Torres, et al., 2024). This decline has led to significant losses in ecosystem functions and services provided by these mussels (Vaughn, 2018). These studies, as well as ours, show the value and need for conserving/restoring native mussels.

In conclusion, we found that freshwater mussels decreased the Chl *a* of phytoplankton, particularly microphytoplankton and nanophytoplankton, and increased the biomass of large zooplankton such as cladocerans and copepods, altering the structure of plankton assemblages. The mussels also increased the biomass ratio of zooplankton (total, rotifers, cladocerans, and copepods) to phytoplankton relative to the control, enhancing the ability of zooplankton to control phytoplankton and providing an additional indirect pathway to improved water clarity in shallow mesocosms representing tropical eutrophic conditions (Fig. 6).

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Data availability All data supporting the findings of this study are included in the manuscript.

Declarations

Conflict of interest The author has no competing interests to declare that are relevant to the content of this article.

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