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Effects of the Oligochaete *Limnodrilus hoffmeisteri* on Nutrients and Zooplankton in the Presence of the Bivalve *Hyriopsis cumingii*

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Abstract

Deposit-feeding aquatic oligochaete worms are abundant and widely distributed benthic animals in lakes that affect the nutrient cycling between sediments and the water and thus the water quality. This effect can be density-dependent and affected by the presence of filter-feeding bivalves, which can modulate the worms' impact. We conducted a mesocosm experiment with high, medium, and low densities of the tubificid worms *Limnodrilus hoffmeisteri* (*Oligocheata*, *Tubificida*, and *Naididae*) in the presence of the filter-feeding bivalve *Hyriopsis cumingii*. In the low-density treatment, the concentrations of nitrate nitrogen (NO_3^--N), ammonium nitrogen (NH_4^+-N), and organic suspended solids (OSSs) increased moderately compared with the control. In the medium- and high-density treatments, there were also increases in total nitrogen (TN), total phosphorus (TP), soluble reactive phosphorus (SRP), total suspended solid (TSS) and inorganic suspended solid (ISS) concentrations. Moreover, the biomass of phytoplankton (Chl *a*), the light attenuation coefficients, and the abundance of both cladoceran and rotifer zooplankton rose with increasing worm densities. Water quality deteriorated in both the medium and high worm density treatments, likely due to increased nutrient leading to an increase in the biomass of phytoplankton in our mesocosms, even though plankton-consuming bivalves were present. Thus, during the restoration of eutrophic shallow lakes with a high density of worms, more bivalves are needed to compensate for the negative impact of worms on water quality.

Keywords: oligochaete; bioturbation; nutrient; density dependence; eutrophication

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1. Introduction

Benthic animals, especially deposit-feeding worms and filter-feeding bivalves, contribute significantly to ecosystem dynamics in shallow lakes, affecting nutrient cycling and trophic status. As ecosystem engineers, filter-feeding bivalves are common in freshwater

systems and play an important role in decreasing the phytoplankton biomass, increasing water transparency and improving water quality in aquatic ecosystems [1–3]. Their ecological roles in freshwater ecosystems have been extensively studied and they are considered the key benthic animal for use as a biomanipulation tool to help control eutrophication [1,3,4].

Deposit-feeding benthic worms are also widely distributed in freshwater ecosystems, especially in eutrophic lakes, where they can dominate and reach high densities, sometimes exceeding 10,000 ind. m^{-2} [5–7]. These worms serve as indicators of trophic status [6,8–10]; densities between 100 and 999 ind. m^{-2} indicate oligotrophic systems, between 1000 and 5000 ind. m^{-2} indicate mesotrophic systems, 5000–10,000 ind. m^{-2} indicate eutrophic systems, and densities > 10,000 ind. m^{-2} indicate hypereutrophic systems [8,11].

Bioturbation by worms can affect nutrient cycling and water quality, and can alter the dynamics of phytoplankton and zooplankton communities in aquatic ecosystems [12]. Bioturbation is defined as the combined effects of the burrowing, feeding, and defecating activities of animals living at the surface and/or within the superficial layers of the sediment [13,14]. These activities can mix the sediment and transport water and accompanying solutes across the sediment–water interface [15,16].

Some studies have shown that this bioturbation promotes nutrient release from the sediment to overlying water [17–20]. In addition, bioturbation can enhance sediment resuspension [21–23], deteriorating water quality. However, other studies have reported the opposite effect, i.e., improved water quality [18,24–26]. Because worms may increase oxygen levels at the sediment surface, which may lead to oxidation of Fe (II) to Fe (III), which is better at adsorbing phosphorus, resulting in decreased soluble phosphate release to the overlying water [18,27,28]. These ambiguous results may reflect differences in worm density, i.e., high densities not only cause stronger bioturbation and sediment nutrient release, but also higher oxygen consumption through respiration, potentially decreasing oxygen levels and promoting the release of ironbound phosphorus to the overlying water. Thus, bioturbation by worms influences nutrient dynamics and water quality [5,29–31], particularly in shallow systems and the effect is likely density-dependent.

The effects of worms on water quality in shallow systems may depend on their densities. Puigagut et al. (2014) found that worm densities of 550 ind. m^{-2} had no significant influence on nutrient concentrations [32], while Saaltink et al. (2019) reported that densities of 5000 ind. m^{-2} and 15,000 ind. m^{-2} enhanced sediment nutrient release to the overlying water, particularly ammonium (NH_4^+) [33]. Geta et al. (2004) found that worm densities of about 22,000 ind. m^{-2} significantly increased nitrate (NO_3^-) release from sediments [34]. Furthermore, Mermillod-Blondin et al. (2005) showed that worm densities of 20,000 ind. m^{-2} increased the release of NH_4^+ and phosphate (PO_4^{3-}) from sediments by factors of 2 and 4, respectively [29]. Nutrient increases may result in higher biomasses of phytoplankton and zooplankton [35–37]. In addition, the impact of worms on plankton and nutrients may also depend on the presence or absence of filter feeders like bivalves [38–40], which may modulate the negative effects of the worms; bivalves can decrease the phytoplankton biomass, increase water transparency, and improve water quality [1–3]. However, the effect of different densities of deposit-feeding worms on water quality in a shallow system with filter-feeding bivalves has not been evaluated.

We conducted a mesocosm experiment with varying densities of the worm *Limnodrilus hoffmeisteri* in the presence of the bivalve *Hyriopsis cumingii* under eutrophic conditions. *L. hoffmeisteri* is a deposit feeder, primarily feeding on organic detritus in sediments, while *H. cumingii* is filter feeder that efficiently filters phytoplankton, detritus and suspended particles from water using their gill structures. We hypothesized high worm densities would deteriorate water quality, while low densities would not due to the modulating effect of bivalves. Nutrient, total suspended solid (TSS), inorganic suspended solid (ISS),

and organic suspended solid (OSS) concentrations, phytoplankton biomass (Chl *a*), the light attenuation coefficient, and zooplankton were measured. The results of our study provide insights into the negative impacts of aquatic oligochaetes on the water quality in shallow systems, especially at high densities, even in the presence of plankton-consuming bivalves.

2. Materials and Methods

2.1. Experimental Mesocosm Set-Up

The experiment was conducted in 16 mesocosms (upper diameter of 52 cm, bottom diameter of 38 cm, and height of 56 cm) containing sediment and lake water. The sediment was collected from Ming Lake (a shallow lake) in Guangzhou (23°14′10″–23°14′15″ N, 113°36′02″–113°36′14″ E), air dried and sieved to remove coarse particles, debris, and large-bodied macroinvertebrates (mesh size = 0.5 mm). Then, the sediment was homogenized and a 6 cm layer was added to each mesocosm. This sediment contained 4.13 mg g^{-1} total nitrogen (TN) and 2.96 mg g^{-1} total phosphorus (TP). Subsequently, a plastic tank (upper diameter—31 cm; bottom diameter—24 cm; height—28 cm) with a 6 cm layer of the same homogenized sediment was placed in each mesocosm for worms and worm collection at the end of the experiment. The worms were only added in this tank. Thereafter, 85 L of filtered (64 μm) lake water (TN = 0.81 mg L^{-1}, TP = 0.06 mg L^{-1}) was added to all mesocosms to remove large zooplankton. The mesocosms were equilibrated under natural sunlight conditions for two weeks. At the start of the experiment, the nutrient concentrations of the water were 1.2 ± 0.096 mg L^{-1} for TN and 0.062 ± 0.019 mg L^{-1} for TP.

After equilibration, three densities of *Limnodrilus hoffmeisteri* were added to each of the four tanks at densities representing oligotrophic (low-density treatment—57 (0.053 ± 0.001 g) individuals or 500 ind. m^{-2}), mesotrophic (medium-density treatment—113 (0.105 ± 0.002 g) individuals or 1000 ind. m^{-2}), and eutrophic (high-density treatment—571 (0.525 ± 0.003 g) individuals or 5050 ind. m^{-2}) [8,11]. The last four mesocosms without worms acted as controls. Each tank with worms was placed into a mesocosm. Simultaneously, one individual of *Hyriopsis cumingii* (average fresh weight 102.3 ± 6.5 g) was added to each mesocosm, including the controls, and placed outside the tanks. The *H. cumingii* were purchased from a local market and acclimated in tanks with lake water for two weeks prior to introduction to the mesocosms. Both the worm and bivalve densities used in the experiment are within the range found in natural lakes.

Solutions of KNO_3 and NaH_2PO_4 were added to each mesocosm immediately after water sampling at rates of 1.5 mg N L^{-1} and 0.1 mg P L^{-1} per 10 days, respectively, to mimic external nutrient loading [20] because ecosystems are always suffering from large variations in external loading, including precipitation, and point and non-point source pollution. Lake water filtered through a plankton net (64 μm) was added as needed to the mesocosms to maintain water levels. The mesocosm experiment was conducted under natural outdoor conditions from 26 October to 15 December 2023. The 16 mesocosms were arranged randomly. During the experiment, the average water temperature was 24.5 ± 3.0 °C in the control, and 24.0 ± 2.9 °C in the low-density treatment, 23.8 ± 2.8 °C in the medium-density treatment, and 23.8 ± 2.8 °C in the high-density treatment. The average dissolved oxygen (DO) concentrations were 8.18 ± 1.65 mg L^{-1} in the control, 8.38 ± 1.63 mg L^{-1} in the low-density treatment, 8.60 ± 1.44 mg L^{-1} in the medium-density treatment, and 8.81 ± 1.60 mg L^{-1} in the high-density treatment.

2.2. Sampling and Analysis

Every 10 days, 1.5 L of water from each mesocosm was collected from 25 to 30 cm below the water surface to measure nutrients, TSSs, OSSs, and Chl *a*. TN, NO_3^--N, NH_4^+-N, TP, and SRP were determined using APHA (1998) [41]. Water samples (500 mL) were filtered

through a Whatman GF/C fiber membrane (Whatman, Maidstone, UK), dried at 108 °C for 2 h, and weighed to obtain the TSS amount. This material was then ashed at 550 °C for 2 h to obtain the ISS and OSS amounts [42]. Chl *a* was quantified by filtering a 200 mL water sample through a 0.45 µm filter, and subjecting it to acetone extraction and measurement using UV–vis spectrophotometry (Shanghai Youke Instrument & Meter Co., Ltd., Shanghai, China) [43]. Light intensities at the water surface and at a depth of 30 cm underwater were measured between 10:00 am and noon using an underwater irradiance meter (ZDS-10W) (Shanghai Jiading Xuelian Instrument Factory, Shanghai, China) [44] to calculate the light attenuation coefficient [45].

Zooplankton that hatched from the sediments and developed populations were sampled through a plankton net (64 µm mesh) by filtering 10 L of water from each mesocosm on day 0 (at the start), day 20 (during), and day 50 (at the end of the experiment). The samples were fixed and stored in 5% formaldehyde. Cladocerans and copepods were counted and identified at 4× magnification, and rotifers at 10×. At the end of the experiment, the worms were gently collected from each plastic tank with a sieve.

2.3. Statistical Analyses

Statistical analyses were conducted using SPSS Statistics 25.0. Repeated measures analysis of variance (RM-ANOVA) was applied to test the effects of the worm treatments on nutrient concentrations; plankton biomass; TSS, OSS, and ISS concentrations; and the light attenuation coefficient, with time as the repeated factor. One-way analysis of variance (ANOVA) was used to compare the zooplankton abundance and the abundance of dominant species of the treatment groups at days 0, 20, and 50. When significant effects were detected, differences among treatments were further examined using Tukey's Honestly Significant Difference (HSD) test. Prior to analysis, the assumptions of normality and homogeneity of variance were assessed using the Shapiro–Wilk test and Levene's test, respectively. Model diagnostics were conducted by examining residual distributions and variance homogeneity to ensure the validity of the statistical analyses. All data are presented as the mean ± 1 standard deviation (SD).

3. Results

3.1. Nitrogen

TN, NO_3^--N, and NH_4^+-N increased monotonically with increasing tubificid worm density (Tukey HSD, each $p < 0.05$; Figure 1a–c), except for TN in the low-density treatment group, compared to the control (Tukey HSD, $p > 0.05$).

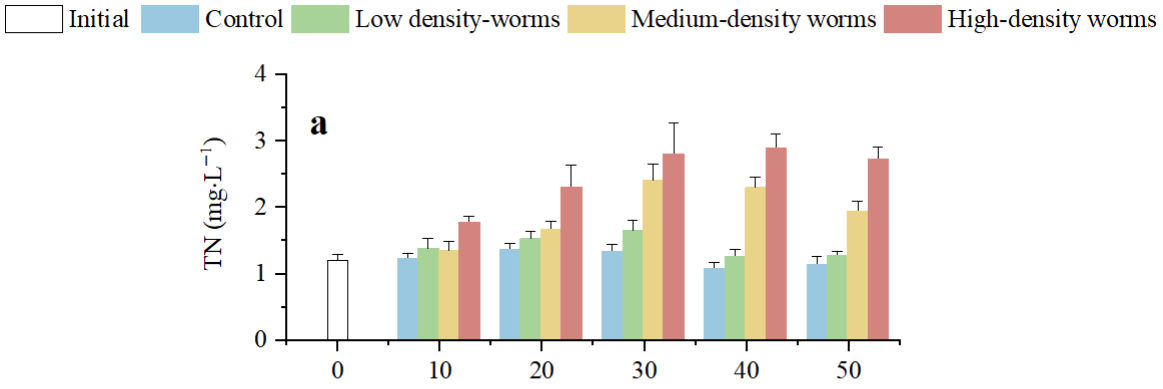


Figure 1. *Cont.*

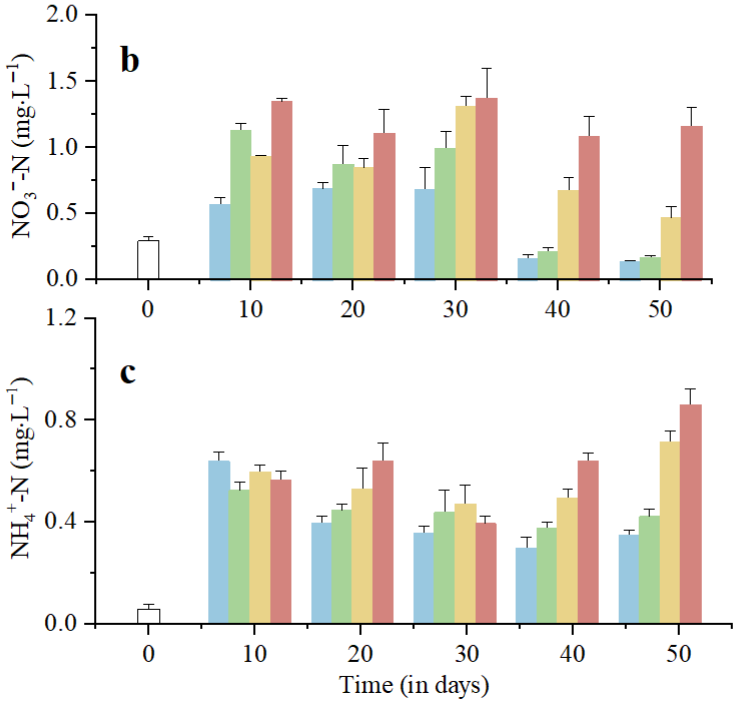


Figure 1. Concentrations of TN (**a**), NO_3^--N (**b**) and NH_4^+-N (**c**) (mean ± 1 SD) in the control and worm treatment groups over time.

All nutrient indices varied significantly over time (RM-ANOVA, time effect, each $p < 0.001$). The interaction effects of time and treatment for these indices were also significant (RM-ANOVA, interaction effect, $p = 0.003$ for TN and $p < 0.001$ for NO_3^--N and $p < 0.001$ for NH_4^+-N).

3.2. Phosphorus

TP and SRP also increased monotonically with increasing tubificid worm density (Tukey HSD, $p < 0.001$ and $p < 0.001$, respectively; Figure 2a, b), except between the low-density treatment group and the control (Tukey HSD, $p = 0.355$ for TP and $p = 0.447$ for SRP).

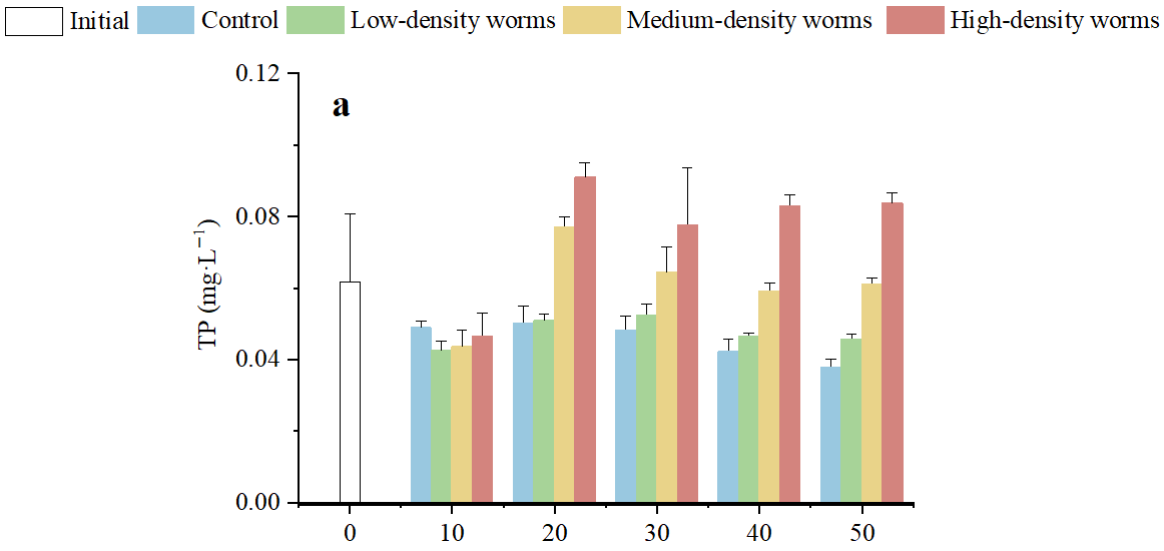


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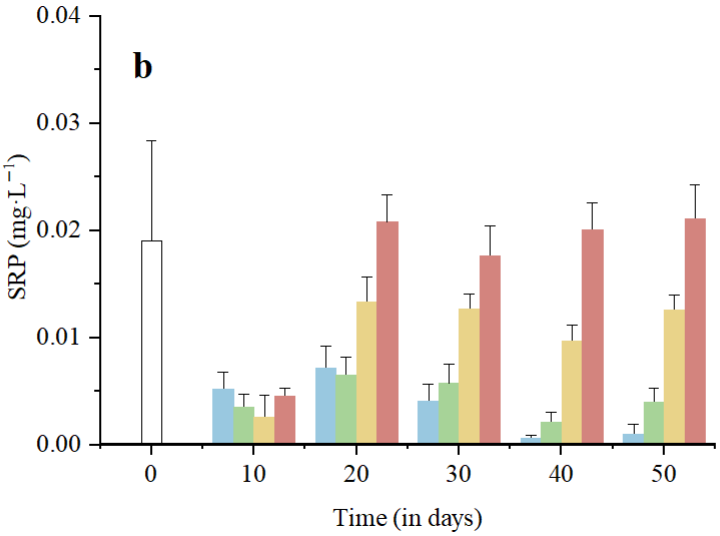


Figure 2. Concentrations of TP (**a**) and SRP (**b**) (mean ± 1 SD) in the control and worm treatment groups over time.

TP and SRP varied significantly over time (RM-ANOVA, time effect, $p < 0.001$ and $p < 0.001$, respectively), and the time x treatment interaction effects were significant (RM-ANOVA, interaction effect $p < 0.001$ and $p < 0.001$ for TP and SRP, respectively).

3.3. Suspended Solids

TSS, OSS, and ISS concentrations increased with increasing worm density (Tukey HSD, each $p < 0.05$; Figure 3a–c), except for TSSs and ISSs in the medium- and in the low-density treatment groups (Tukey HSD, $p = 0.076$ for TSSs and $p = 0.954$ for ISSs).

TSS, OSS, and ISS concentrations varied significantly over time (RM-ANOVA, time effect, each $p < 0.001$), and the interaction effects of time and treatment were significant (RM-ANOVA, interaction effect, $p < 0.001$ for TSSs and $p = 0.008$ for OSSs and $p = 0.013$ for ISSs).

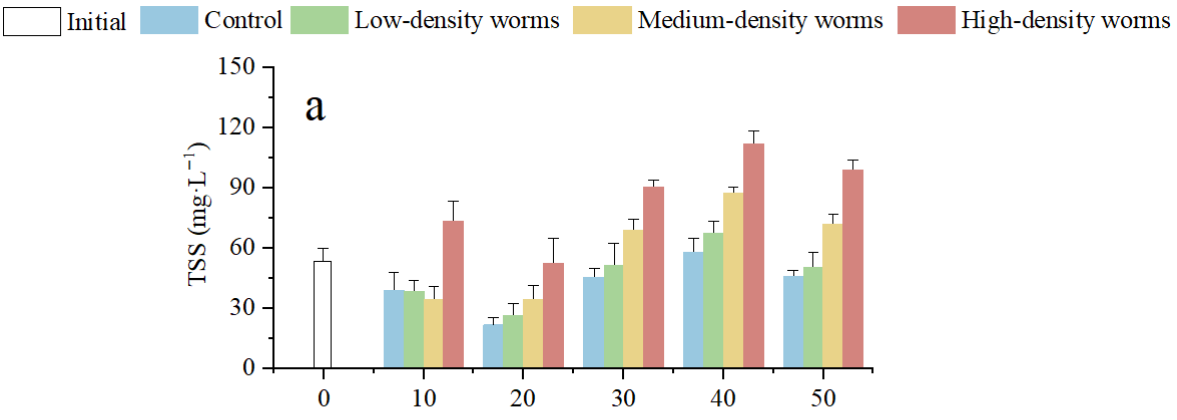


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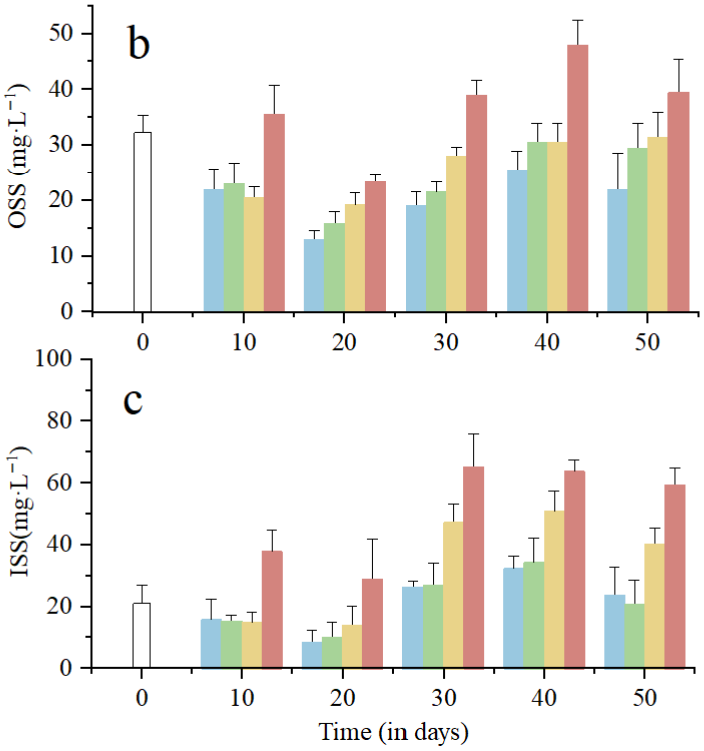


Figure 3. Concentrations of TSSs (**a**), OSSs (**b**) and ISSs (**c**) (mean ± 1 SD) in the control and worm treatment groups over time.

3.4. Light Attenuation Coefficient

The light attenuation coefficient increased with increasing worm density (Tukey HSD, $p \leq 0.001$; Figure 4). It varied significantly over time (RM-ANOVA, time effect, $p < 0.001$), and the interaction effects of time and treatments were significant (RM-ANOVA, interaction effect, $p < 0.001$).

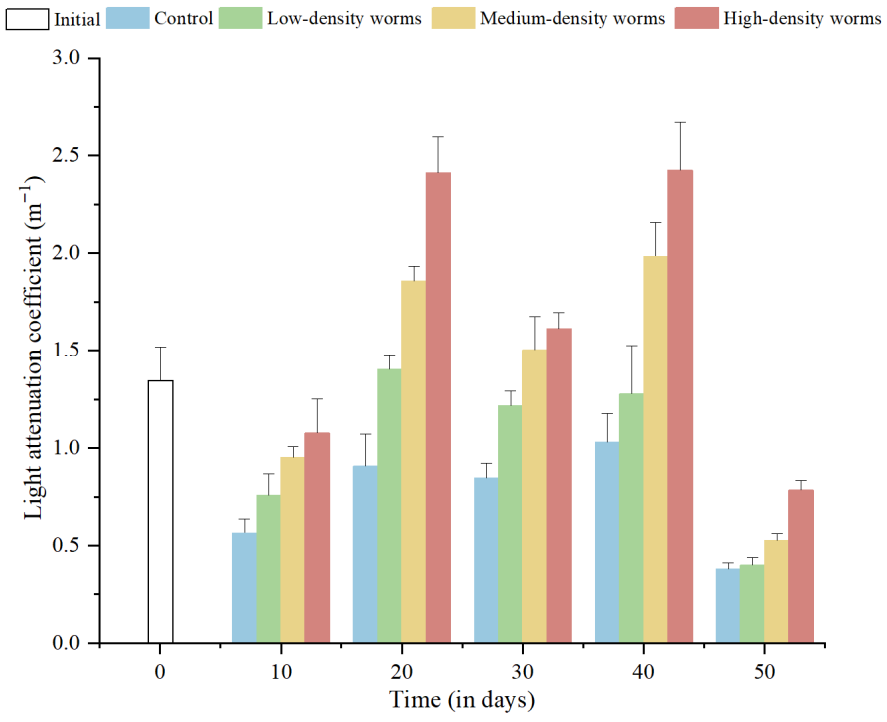


Figure 4. Light attenuation coefficient (mean ± 1 SD) in the control and worm treatment groups over time.

3.5. Phytoplankton Biomass

Chl *a* increased with increasing worm density (Tukey HSD, $p < 0.001$; Figure 5). Chl *a* varied significantly over time (RM-ANOVA, time effect, $p < 0.001$), and the interaction effects of time and treatment were significant (RM-ANOVA, interaction effect, $p < 0.001$).

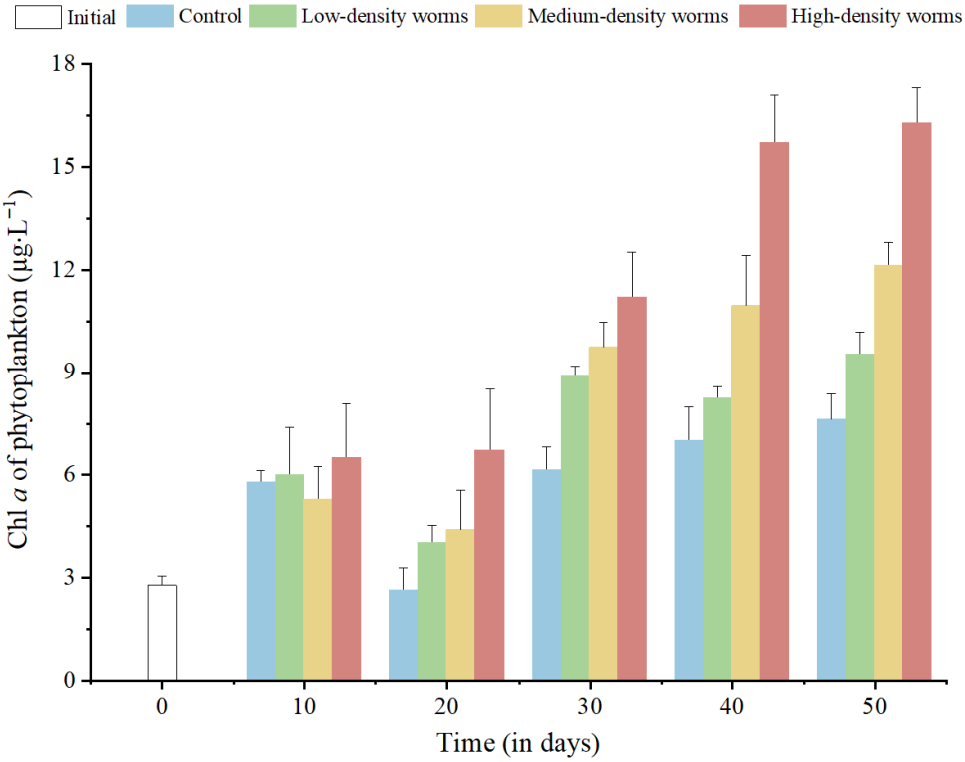


Figure 5. Phytoplankton biomass (Chl *a*, mean ± 1 SD) in the control and worm treatment groups over time.

3.6. Zooplankton

On day 0 of the experiment, only cladocerans were recorded in all mesocosms, with *Daphnia pulex* as the dominant species. Cladoceran abundances did not differ between the worm treatment groups and the control (one-way ANOVA, treatment effect, $p = 0.146$; Figure 6A,B).

On day 20 and at the end of the experiment (day 50), the abundances of zooplankton, especially rotifers, increased with increasing worm density (Tukey HSD, $p < 0.05$; Figure 6C,E). On day 20, both the high- and medium-density treatment groups exhibited significantly higher cladoceran abundances than the control (Tukey HSD, $p = 0.004$ and $p = 0.002$, respectively; Figure 6C), whereas no significant differences were observed among the other groups.

On day 50, cladoceran abundance was higher in the high-density treatment group than in the medium-density treatment group and higher in the medium-density treatment group than in the low-density treatment group (Tukey HSD, $p = 0.005$ and $p < 0.001$, respectively; Figure 6E). No significant difference was detected between the low-density treatment group and the control (Tukey HSD, $p = 0.199$; Figure 6E).

Copepod abundance remained very low throughout the experiment.

In all worm treatment groups and the control, the dominant zooplankton species were *Daphnia pulex* and *Brachionus urceus* throughout the experiment (Figure 6B,D,F). At the end of the experiment, the dominant species were *D. pulex* and *B. urceus* in the control, and *D. pulex*, *B. urceus*, and *B. calyciflorus* in the worm treatment groups (Figure 6F). A list of the

zooplankton species in the different treatment groups at the end of the experiment is given in Table 1.

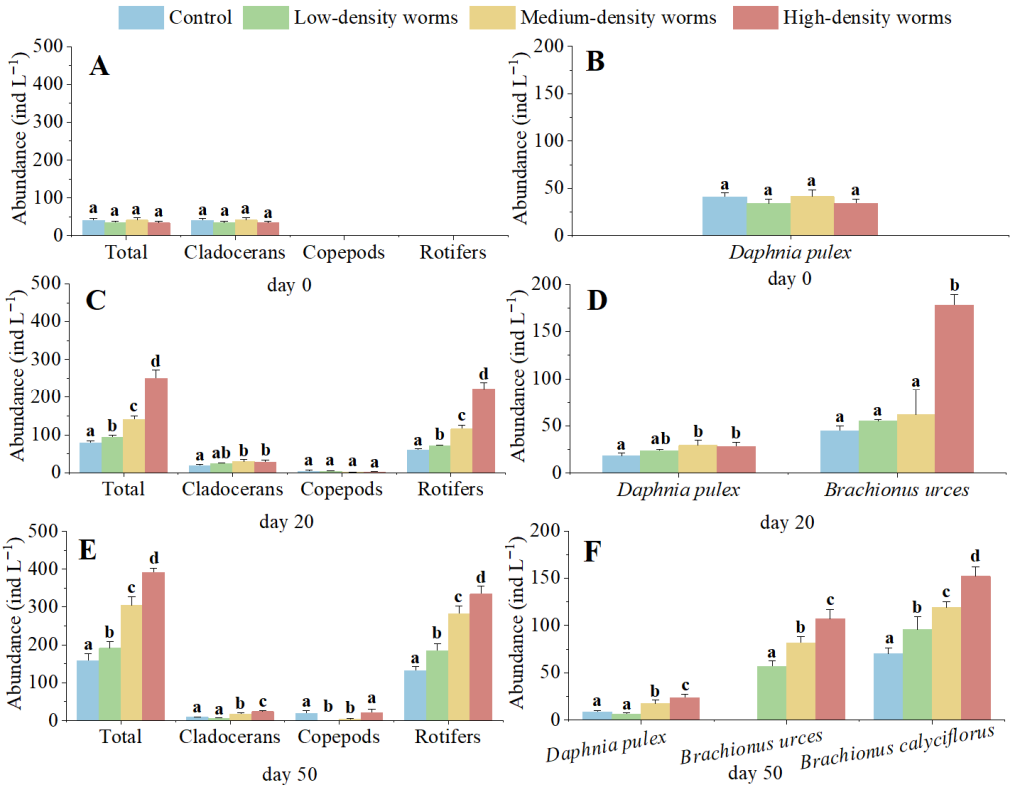


Figure 6. Abundance of zooplankton groups and dominant species (mean ± 1 SD) on days 0 (**A**,**B**), 20 (**C**,**D**), and 50 (**E**,**F**) in the control and worm treatment groups. Different lowercase letters represent significant differences at $p < 0.05$ between groups.

Table 1. List of zooplankton species identified in the experiment.

Treatment	Group	Species
Control	Rotifera	*Brachionus calyciflorus* Pallas, 1766 *Brachionus urceus* (Linnaeus, 1758) *Brachionus budapestiensis* Daday, 1885 *Keratella valga* (Ehrenberg, 1834)
	Cladocera	*Daphnia pulex* Leydig, 1860
	Copepoda	*Neodiaptomus* sp. *Mesocyclops* sp.
Low-density	Rotifera	*Brachionus calyciflorus* Pallas, 1766 *Brachionus urceus* (Linnaeus, 1758) *Brachionus budapestiensis* Daday, 1885 *Keratella valga* (Ehrenberg, 1834)
	Cladocera	*Daphnia pulex* Leydig, 1860
	Copepoda	*Neodiaptomus* sp.
Medium-density	Rotifera	*Brachionus calyciflorus* Pallas, 1766 *Brachionus urceus* (Linnaeus, 1758) *Brachionus budapestiensis* Daday, 1885 *Keratella valga* (Ehrenberg, 1834)
	Cladocera	*Daphnia pulex* Leydig, 1860
	Copepoda	*Neodiaptomus* sp.

Table 1. *Cont.*

Treatment	Group	Species
High-density	Rotifera	*Brachionus calyciflorus* Pallas, 1766 *Brachionus urceus* (Linnaeus, 1758) *Brachionus budapestiensis* Daday, 1885 *Keratella valga* (Ehrenberg, 1834)
	Cladocera	*Daphnia pulex* Leydig, 1860
	Copepoda	*Neodiaptomus* sp. *Thermocyclops* sp.

4. Discussion

As hypothesized, we found that the concentrations of TN, NO_3^--N, NH_4^+-N, TP and SRP, as well as TSSs, OSSs and ISSs were significantly higher in the medium- and high-density treatment groups (Table 2). Contrary to our hypothesis, the concentrations of NO_3^--N, NH_4^+-N, and OSSs also increased in the low-density worm treatment group compared to the control. Phytoplankton biomass (Chl *a*), the light attenuation coefficient, and the abundance of zooplankton increased with increasing worm density. The high- and medium-density treatments, but not the low-density treatment, also resulted in a higher abundance of cladocerans than in the control. The worms also affected the species dominance of zooplankton. The results of our study shed light on the negative impact worms have on water quality in shallow systems, especially at high densities, even in the presence of plankton-consuming bivalves.

Table 2. Effects of worm density on water quality parameters. Values are mean ± SD. Different lowercase letters indicate significant differences among treatments (Tukey HSD, $p < 0.05$).

Parameter	Control	Low-Density	Medium-Density	High-Density
TN (mg L^{-1})	1.57 ± 0.18 ^{a}	1.79 ± 0.23 ^{a}	2.43 ± 0.54 ^{b}	3.14 ± 0.62 ^{c}
NO_3^--N (mg L^{-1})	0.45 ± 0.26 ^{a}	0.67 ± 0.42 ^{b}	0.89 ± 0.30 ^{c}	1.23 ± 0.18 ^{d}
NH_4^+-N (mg L^{-1})	0.47 ± 0.16 ^{a}	0.51 ± 0.07 ^{b}	0.65 ± 0.12 ^{c}	0.72 ± 0.18 ^{d}
TP (mg L^{-1})	0.046 ± 0.006 ^{a}	0.048 ± 0.004 ^{a}	0.061 ± 0.012 ^{b}	0.077 ± 0.017 ^{c}
SRP (mg L^{-1})	0.004 ± 0.003 ^{a}	0.004 ± 0.002 ^{a}	0.010 ± 0.004 ^{b}	0.017 ± 0.007 ^{c}
TSSs (mg L^{-1})	42.03 ± 13.20 ^{a}	46.85 ± 15.66 ^{a}	59.52 ± 22.45 ^{b}	85.50 ± 22.46 ^{c}
OSSs (mg L^{-1})	20.28 ± 5.56 ^{a}	24.07 ± 6.28 ^{b}	27.13 ± 7.32 ^{c}	37.07 ± 9.04 ^{d}
ISSs (mg L^{-1})	21.55 ± 9.91 ^{a}	21.68 ± 10.37 ^{a}	33.63 ± 17.08 ^{b}	51.23 ± 17.02 ^{c}
Light attenuation coefficient (m^{-1})	0.84 ± 0.33 ^{a}	1.07 ± 0.40 ^{b}	1.41 ± 0.56 ^{c}	1.59 ± 0.66 ^{d}
Chl *a* (μg L^{-1})	5.85 ± 1.87 ^{a}	7.34 ± 2.20 ^{b}	8.50 ± 3.31 ^{c}	11.29 ± 4.50 ^{d}

Worms promote nutrient release from sediments to the overlying water, enhance sediment resuspension and deteriorate water quality [24–26]. However, bivalves can filter phytoplankton and other particles in overlying water, thereby improving water quality. The increase in dissolved nutrients (NO_3^--N and NH_4^+-N) concentrations in the low-density treatment group indicated enhanced nutrient release from the sediment to the overlying water due to bioturbation, and possibly excretion by worms [46,47]. No increase in TP and TN in the low-density treatment group was observed, supporting our hypothesis that a low density of worms would not deteriorate water quality due to the counteracting effect of bivalve particle filtration. However, at higher worm densities (1000 ind. m^{-2} and 5050 ind. m^{-2}), TP and TN increased, suggesting that bivalves' modulating effects were insufficient and bioturbation effects stronger. Higher worm densities intensify sediment reworking and porewater movement, likely accelerating the diffusion of soluble

nutrients across the sediment–water interface [14]. Additionally, burrowing reduces sediment cohesion, facilitating the resuspension of fine inorganic particles, amplifying nutrient efflux [48–50].

The increased nutrients can enhance phytoplankton growth [51–53]. We found that all worm densities increased the biomass of phytoplankton (Chl *a*). Phytoplankton accumulation was clearly observed in the high-density worm treatment group, especially late in the experiment. Increased phytoplankton biomass led to higher OSS levels, even in the low-density treatment group. In addition, higher worm densities resulted in increased ISS concentrations, indicating more bioturbation. The higher OSS and ISS concentrations at higher worm densities led to higher TSS concentrations.

Suspended solids, including OSSs, ISSs, and TSSs, significantly affect light attenuation. Increases in these solids reduce light penetration, leading to higher light attenuation in the water column. In this study, the light attenuation coefficient increased with increasing worm density. It is worth noting that OSSs increased even in the low-density worm treatment group, negatively impacting the light intensity at the sediment surface. Light is crucial for submerged macrophytes in lakes [54,55]; thus, worms can negatively affect the growth of submerged macrophytes by decreasing light penetration to the sediment.

Bivalves can directly filter phytoplankton, decreasing their biomass. In this study, however, the biomass of phytoplankton (Chl *a*) increased with increasing worm density even in the presence of plankton-consuming bivalves, leading us to conclude that increased nutrients were likely responsible for the increased phytoplankton Chl *a*. We observed that total zooplankton abundances, especially rotifers, increased with higher phytoplankton levels associated with greater worm densities. In addition, cladocerans increased in the medium- and high-density worm treatment groups. The increased density of both rotifers and cladocerans is likely due to the higher phytoplankton biomass although we cannot exclude increased hatching of zooplankton eggs in the higher worm density groups due to sediment disturbance. Cladocerans are effective grazers of phytoplankton and can avoid bivalve predation more effectively than smaller rotifers [56,57]. However, we observe an increase in rotifer abundance with the increase in worm densities in this study, likely because a higher phytoplankton biomass (Chl *a*) in the worm treatments compensated for the consumption loss by bivalves due to the better growth conditions for rotifers [39,58].

We attempted to mimic worm and bivalve densities present in different trophic level lakes. The bivalve density/biomass (9 ind. m^{-2} or 900 g m^{-2}) used in this study is within the range found in natural lakes. For instance, the density of *Sinanodonta woodiana* in Konin Lakes is 7–20 ind. m^{-2} or 550–1100 g m^{-2} biomass [59], with the biomass reaching up to 2353 g m^{-2} in some regions [60]. Similarly, the tubificid worm densities used in our experiment (500, 1000, and 5050 ind. m^{-2}) are also within their natural range. For example, worm densities in Lake Taihu vary spatially from 0 to 30,865 ind. m^{-2}. Both the bivalves and worms survived to the end of the experiment and the wet mass of all worms at that time was 0.142 ± 0.009 g in the low-density worm treatment, 0.262 ± 0.014 g in the medium-density treatment, and 1.039 ± 0.021 g in the high-density worm treatment. The biomass of the bivalves from the control to the high-density treatment were 104.7 ± 4.8 g, 105.6 ± 4.4 g, 105.0 ± 7.0 g and 103.0 ± 3.2 g. However, by necessity, the conditions in our mesocosms are different from natural lakes as fish and macrophytes were absent and the mesocosms were small. Hence, our results must be interpreted with caution. Even so, we believe our findings that deposit-feeding worms deteriorated the water quality, especially at high densities, and that the increased nutrient levels due to the worms was likely the key reason for the increased biomass of phytoplankton even in the presence of plankton-consuming bivalves have relevance for the restoration of eutrophic shallow lakes using bivalves as a biomanipulation tool.

5. Conclusions

In summary, increasing the worm density led to higher concentrations of nutrients and suspended solids, biomass of phytoplankton, light attenuation coefficient, and zooplankton abundance, especially rotifer abundance. Unlike low densities, high and medium worm densities also increased the abundance of cladocerans. The increased nutrient levels associated with worm activity was likely the reason for the increased biomass of phytoplankton and abundance of zooplankton. Therefore, even in the presence of plankton-consuming bivalves, deposit-feeding worms negatively impacted water quality. Thus, when restoring eutrophic shallow lakes using bivalves as a biomanipulation tool, the density of bivalves should be increased if the worm density is high to compensate for the negative effect of worms.

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