


Nitrogen loading increases both algal and non-algal turbidity in subtropical shallow mesocosms: Implication for nutrient management

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Abstract – Excess nitrogen (N) loading in summer often boosts phytoplankton growth and increase algal turbidity. In eutrophic shallow lakes, the increased algal production may also augment the abundance of deposit-feeding tubificid worms and thereby sediment resuspension and non-algal turbidity. However, few studies have explored the effects of high N loading on this benthic process in eutrophic shallow lakes. Here, we conducted an outdoor mesocosm experiment in a summer-winter season (177 days) on the shore of subtropical Lake Taihu, China. Each mesocosm contained a 10 cm layer of lake sediment and 450 L of lake water. Nitrate was added weekly to three of the mesocosms, while another three functioned as controls. Our results showed that N addition significantly increased algal particles as water chlorophyll *a* (Chl-*a*) increased significantly following N addition. Moreover, significantly higher levels of inorganic suspended solids (ISS) were observed in the mesocosms with added N, indicating elevation of non-algal turbidity as well by the N addition. We attribute the latter to increased sediment resuspension as the abundance of tubificid worms was significantly higher in the N addition mesocosms. Accordingly, our study indicates that high N loading in subtropical shallow lakes may boost both algal and non-algal turbidity in part via benthic-pelagic coupling processes. Our results suggest that alleviation of eutrophication in shallow eutrophic lakes may require a strategic approach to adequately control both N and phosphorus.

Keywords: Phytoplankton / sediment resuspension / tubificids / suspended solids / internal loading

1 Introduction

Nitrogen (N) and phosphorus (P) are the key limiting factors determining autotroph growth in both terrestrial and aquatic ecosystems (Elser *et al.*, 2007; Conley *et al.*, 2009). In eutrophic shallow lakes, summer phytoplankton growth is often limited by N due to high denitrification rates and strong P release at the higher temperatures in this season (Xu *et al.*, 2010; Xu *et al.*, 2021; Søndergaard *et al.*, 2017; Shatwell and Köhler, 2019). Therefore, excess N loading often boosts

phytoplankton growth in summer (Xu *et al.*, 2010; He *et al.*, 2015; 2021), which may subsequently increase sediment P release by various mechanisms such as increasing diffusion, bacteria activity, high pH, and increased mineralization of organic matter (Gao *et al.*, 2014; Chen *et al.*, 2018). The released P, in turn, creates positive feedback on phytoplankton growth and algal sedimentation (Fig. 1, Gao *et al.*, 2014; He *et al.*, 2021).

Although the effect and potential mechanisms of N loading on algal turbidity have been well elucidated in shallow lakes (Gonzalez Sagrario *et al.*, 2005; Xu *et al.*, 2010; Paerl *et al.*, 2011; He *et al.*, 2015), few studies (but see He *et al.*, 2021) have explored the responses of non-algal turbidity, *e.g.*, due to

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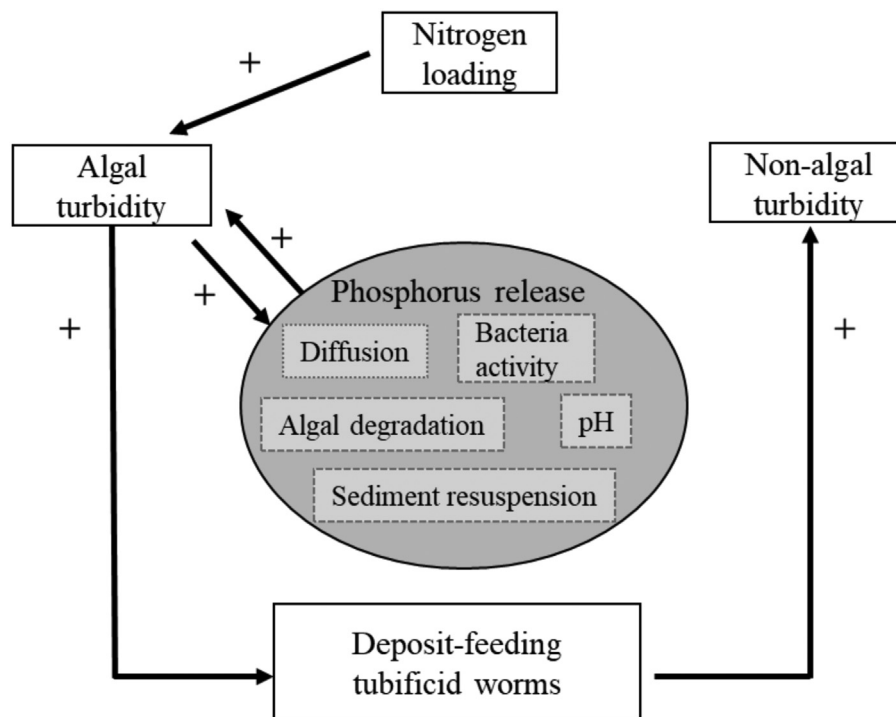


Fig. 1. Conceptual model showing how nitrogen (N) loading boosts algal and non-algal turbidity in shallow lakes. Firstly, N addition mitigates summer N deficiency, which increases algal biomass and subsequently causes higher P concentrations via feedback mechanisms between algal blooms and sediment P release. Secondly, N addition-triggered high algal biomass increases the abundance of deposit-feeding tubificid worms and therefore enhances non-algal turbidity via sediment resuspension.

sediment resuspension, under different N loading scenarios. In most cases, increased nutrient loading is expected to increase the abundance of some benthic macroinvertebrate and vertebrate taxa, *e.g.*, tubificids, chironomids, and cyprinid fish, due to elevated lake productivity (Köhler *et al.*, 2005; Pan *et al.*, 2015; Wang *et al.*, 2017). The feeding activities of these benthic animals might enhance sediment resuspension by sediment disturbance or indirectly by alteration of sediment properties, *e.g.*, water content or particle size (Dafoe *et al.*, 2011; Zhang *et al.*, 2014; Chakraborty *et al.*, 2022). For instance, Zhang *et al.* (2014) found that tubificid worms (*Limnodrilus hoffmeisteri*) loosened the sediment through their feeding and defecation activities and increased the suspended solids (SS) concentrations. Therefore, in eutrophic shallow lakes, it is possible that excess N inputs may increase water non-algal turbidity by stimulation of benthic animal production due to higher production and sedimentation of algae (Fig. 1). He *et al.* (2021) found significantly higher inorganic SS levels in N addition treatments than in the N-free controls, which they attributed to the increased strength of sediment resuspension caused by crucian carp present in these experiments, but the role of benthic invertebrates, *e.g.*, tubificid worms, in mediating these processes is not well-studied.

To obtain a better mechanistic understanding of the effects of N loading on both algal and non-algal turbidity in shallow eutrophic lakes under fish-free conditions, we conducted a mesocosm experiment involving contrasting N loadings at the shore of Lake Taihu, one of China's best studied lakes, known for its severe cyanobacterial blooms (Guo, 2007; Qin *et al.*, 2019). Previous bioassay experiments and field monitoring

studies have revealed that the phytoplankton in Lake Taihu is generally N limited or N, P co-limited during summer and fall (Xu *et al.*, 2010; 2021; Paerl *et al.*, 2011). Thus, we hypothesized that increasing summer N loading would increase algal turbidity via the feedback loop between phytoplankton blooms and internal P release (Fig. 1). Moreover, we expected that the increased algal biomass would benefit benthic macroinvertebrates, *e.g.*, tubificids or chironomids, and thereby increase non-algal turbidity via the enhanced sediment disturbance (Fig. 1).

2 Methods and materials

2.1 Experimental design

The outdoor experiment was conducted at Taihu Lake Laboratory Ecosystem Research Station (TLLER), located in Meiliang Bay on the northern edge of Lake Taihu, China (31°25'9.93"N, 120°12'56.17"E). The experiment was conducted from June 8 to December 2, 2020 (in total 177 days). On May 30, six cylindrical, high-density polyethylene tanks (95 cm height × 87 cm upper diameter × 77 cm bottom diameter) were filled with a 10 cm layer of lake sediment and 450 L of water collected from Meiliang Bay. The sediment had previously been sieved (mesh size: 1.7 mm) and mixed to ensure uniformity and similar starting conditions. The prepared sediment contained natural quantities of organism resting stages, which allowed zooplankton and benthic macroinvertebrates to hatch and supported community development during the experimental period. We did not

measure sediment characteristics, but literatures have recorded that for the top 10 cm of sediments in Meiliang Bay, the TN and TP content ranged from 1.4–2.8 and 0.1–0.9 mg/g (dry weight), respectively. The organic matter content was ranged between 2%–4% (Zhao *et al.*, 2007). The water had also been previously screened using a 64 μm mesh filter to remove large organisms and detritus. When the experiment began, nitrate (KNO_3) was supplied weekly to three mesocosms throughout the experiment. The daily N loading was equal to 130 $\mu\text{g N L}^{-1} \text{ day}^{-1}$, which was within the range of external loading in Lake Taihu (Paerl *et al.*, 2011). The remaining three mesocosms functioned as controls.

2.2 Sampling and analytical methods

2.2.1 Water physico-chemical properties and chlorophyll *a*

Water samples were collected biweekly from Day 0 to Day 70 and every four weeks from Day 70 to Day 177. For sampling, we used a tube sampler (8 cm diameter, 64 cm length) to collect 2 L depth-integrated water samples from each mesocosm. These water samples were used for determination of the concentrations of nutrients, chlorophyll *a* (Chl-*a*), and suspended solids 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 $\text{K}_2\text{S}_2\text{O}_8$ and NaOH solution (APHA 1998). Chl-*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). Total suspended solids (TSS) were determined from 200 to 400 mL water samples filtered through pre-combusted (450 °C for 2 h) and pre-weighed GF/C filters, which were then dried and weighted 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). The organic fraction (OSS) was calculated by subtracting ISS from TSS. In our study, we used Chl-*a* to reflect algal turbidity. We used ISS concentrations as a proxy of non-algal turbidity, as it is significantly positive related to the non-algal turbidity (Fig. S1, see Appendix) which was calculated based on the Secchi depth (Ma *et al.*, 2021).

2.2.2 Benthic macroinvertebrates

On Day 70, a sediment core was collected from the middle of each mesocosm using a tube sampler (8 cm diameter), and subsequently the sediment was washed over a 250 μm mesh sieve. The remaining material was fixed with a 7% buffered formaldehyde solution. In the laboratory, the samples were sorted on a white tray, and the numbers of tubificids and chironomids were counted.

2.3 Data analysis

All data processes and statistical analyses were carried out in R (R Core Team, 2021). We used generalized linear mixed models (GLMM, Bolker *et al.*, 2009) to explore the interactive effects of N addition and time on the time series data, *e.g.*, nutrients, suspended solids, and Chl-*a* concentrations. For each

GLMM, we used the interactive term (N addition \times time) as fixed factor and included mesocosm identity as a random intercept. We assumed Gaussian error distributions for all response variables. The GLMMs were fitted via the glmmTMB function from the glmmTMB package (Brooks *et al.*, 2017). On Day 70, the densities of tubificids, chironomids and total macroinvertebrates (tubificids + chironomids) were compared by Student's *t* test (function *t.test*) after normality (function *shapiro.test*) and homoscedasticity (function *bartlett.test*) tests. All figures were plotted by ggplot2 package (Wickham *et al.*, 2011). The values for each variable are presented as mean \pm SE ($n = 3$).

3 Results

3.1 Nutrients, suspended solids, and chlorophyll *a*

GLMMs confirmed significant interactive effects of N addition and time on TN, TDN, TP, and TDP concentrations (Tab. 1). In the N addition treatment, TN and TDN concentrations were significantly higher than in the controls (Fig. 2). Moreover, the increment magnitude tended to increase with time (toward winter) (Fig. 2). The TP and TDP concentrations in the N addition mesocosms showed a unimodal temporal change, with the highest values in September and October, respectively (Fig. 2). The significant interactions indicated that the differences in TP and TDP between the two treatments changed with time (Tab. 1; Fig. 2).

N addition and time had significant interactive effects on suspended solids (Tab. 1), indicating that the temporal trends differed between the two treatments. In the N addition treatments, both TSS and OSS showed a unimodal change, with peak values on 14 September (Day 98), while ISS demonstrated a steady increase during the experiment. In the controls, TSS, OSS and ISS were overall low during the experiment (Fig. 2). Similar to OSS, the Chl-*a* concentration in the N addition treatment also showed a unimodal temporal pattern, which was significantly stronger than in the controls.

3.2 Benthic macroinvertebrates

Addition of N led to significantly higher densities of tubificids on Day 70 ($t = -8.892$, $P = 0.002$; Fig. 3), while no significant difference was detected in the densities of chironomids ($t = 0.477$, $P = 0.665$; Fig. 3). Total densities of benthic macroinvertebrates were also higher in N addition mesocosms than in control, while the difference was marginally significant ($t = -2.721$, $P = 0.076$; Fig. 3).

4 Discussion

We found that persistent N addition greatly increased phytoplankton biomass and algal turbidity (expressed as Chl-*a* and OSS concentrations). Moreover, we found that N addition increased non-algal turbidity as the ISS concentrations increased significantly. The results therefore suggest that summer N loading may increase both algal and non-algal turbidity in subtropical shallow eutrophic lakes.

The increased algal turbidity caused by N loading is not surprising as the phytoplankton in Lake Taihu was N limited or

Table 1. Results of the generalized linear mixed model using the function `glmmTMB` from the R package `glmmTMB` v1.0.2.1. Units are mg L^{-1} .

Variable	Effect	Estimate	Standard error	Z value	P
TN	Intercept	-0.365	0.085	-4.278	<0.001
	Nitrogen	0.800	0.120	6.642	<0.001
	Time	-0.001	0.001	-1.638	0.101
	Nitrogen \times Time	0.007	0.001	6.172	<0.001
TDN	Intercept	-0.922	0.119	-7.756	<0.001
	Nitrogen	0.673	0.168	4.002	<0.001
	Time	0.000	0.001	0.430	0.667
	Nitrogen \times Time	0.005	0.002	3.593	<0.001
TP	Intercept	-3.239	0.140	-23.096	<0.001
	Nitrogen	0.434	0.198	2.191	0.029
	Time	-0.003	0.001	-2.506	0.012
	Nitrogen \times Time	0.007	0.002	4.008	<0.001
TDP	Intercept	-4.142	0.124	-33.450	<0.001
	Nitrogen	-0.152	0.175	-0.870	0.386
	Time	-0.001	0.001	-0.950	0.340
	Nitrogen \times Time	0.007	0.001	4.910	<0.001
Chl- <i>a</i>	Intercept	-4.893	0.316	-15.470	<0.001
	Nitrogen	1.356	0.447	3.032	0.002
	Time	-0.008	0.003	-3.109	0.002
	Nitrogen \times Time	0.014	0.004	3.976	<0.001
TSS	Intercept	1.827	0.196	9.314	<0.001
	Nitrogen	0.072	0.277	2.598	0.009
	Time	-0.004	0.002	-2.236	0.018
	Nitrogen \times Time	0.011	0.002	4.959	<0.001
OSS	Intercept	1.393	0.219	6.348	<0.001
	Nitrogen	0.857	0.310	2.761	0.006
	Time	-0.007	0.002	-3.070	0.002
	Nitrogen \times Time	0.011	0.003	3.607	<0.001
ISS	Intercept	0.724	0.206	3.508	<0.001
	Nitrogen	0.452	0.291	1.553	0.121
	Time	-0.001	0.002	-0.485	0.628
	Nitrogen \times Time	0.011	0.003	3.879	<0.001

Note: All data were modelled as Gaussian distribution. Significant terms in bold.

N, P co-limited in summer and fall (Xu *et al.*, 2010). In our study, N addition alleviated the N deficiency in summer and thereby increased the phytoplankton growth, which is consistent with numerous bioassays and mesocosm experiments conducted in summer (Xu *et al.*, 2010; Kolzau *et al.*, 2018; He *et al.*, 2021). The effects of N addition on phytoplankton biomass tended to decrease toward winter, which can be attributed the lower growth rate of phytoplankton and lower internal phosphorus loading in the cold seasons. The unimodal changes of Chl-*a* concentrations in early summer to late fall period are in line with the seasonal pattern of phytoplankton growth in Lake Taihu (Zhang *et al.*, 2018). Previous studies have suggested that P deficiency limits the growth of winter phytoplankton in Lake Taihu (Xu *et al.*, 2010). However, this was not the case in our study as the dissolved P concentrations in the mesocosms remained high in winter, indicating sufficient P availability for phytoplankton growth. Our study confirmed the proposed feedback loop between phytoplankton blooms and sediment P release (Gao *et al.*, 2014; Chen *et al.*, 2018; He *et al.*, 2021) as both TP and TDP concentrations were significantly higher in

the N addition treatments than in the controls. Similar to Chl-*a*, both TP and TDP concentrations also changed unimodally, with a peak in early autumn, reflecting that sediment P release is stronger in warm months (reviewed in Søndergaard *et al.*, 2003). Promotion by N addition of P concentrations is widely observed in eutrophic shallow waterbodies where sediments serve as an important P source (Xie *et al.*, 2003; Gonzalez Sagrario *et al.*, 2005; He *et al.*, 2015; Ma *et al.*, 2018; Ma *et al.*, 2021). The potential mechanisms, *e.g.*, increases in diffusion, bacteria activity, high pH, low oxygen and degradation of settled algae, have been well elucidated in previous studies (Gao *et al.*, 2014; Chen *et al.*, 2018; Ma *et al.*, 2018; 2021). Here we propose an additional mechanism behind the high P concentrations in the N addition mesocosms, *i.e.*, sediment resuspension by benthic macroinvertebrates, as discussed in the following.

We found clear promotion of non-algal turbidity by N loading, which has not been well elucidated in previous studies (but see He *et al.*, 2021). The enhanced ISS concentration we attribute to bioturbation of tubificids, which was significantly higher in the N addition mesocosms. However, we did not

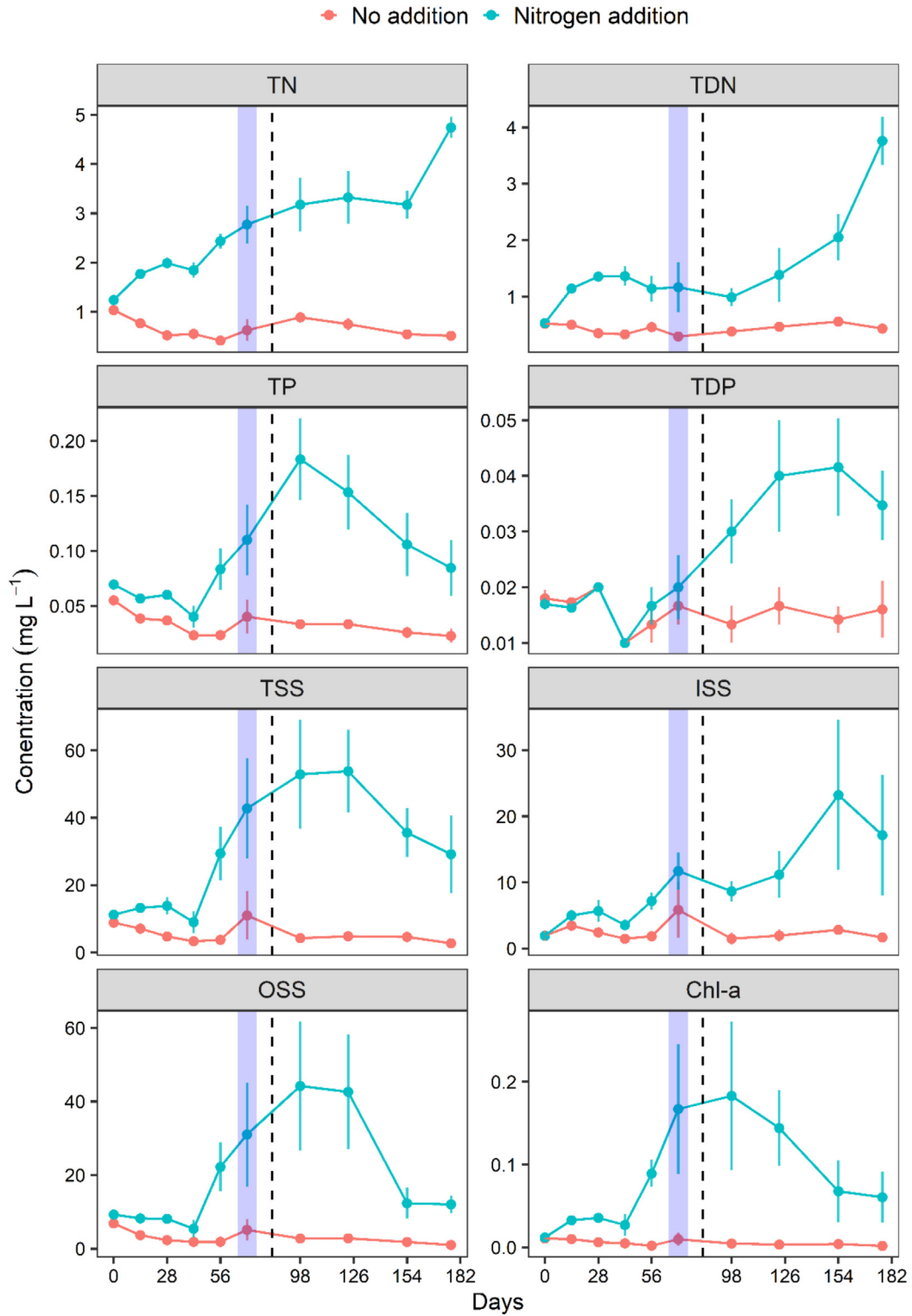


Fig. 2. Temporal dynamics of total nitrogen (TN), total phosphorus (TP), dissolved total nitrogen (TDN), dissolved total phosphorus (TDP), total suspended solids (TSS), organic suspended solids (OSS), inorganic suspended solids (ISS) and chlorophyll *a* (Chl-*a*) in the two nitrogen treatments. The shaded area indicates Day 70 when benthic macroinvertebrates were sampled. The dashed line indicates the boundary of summer and autumn.

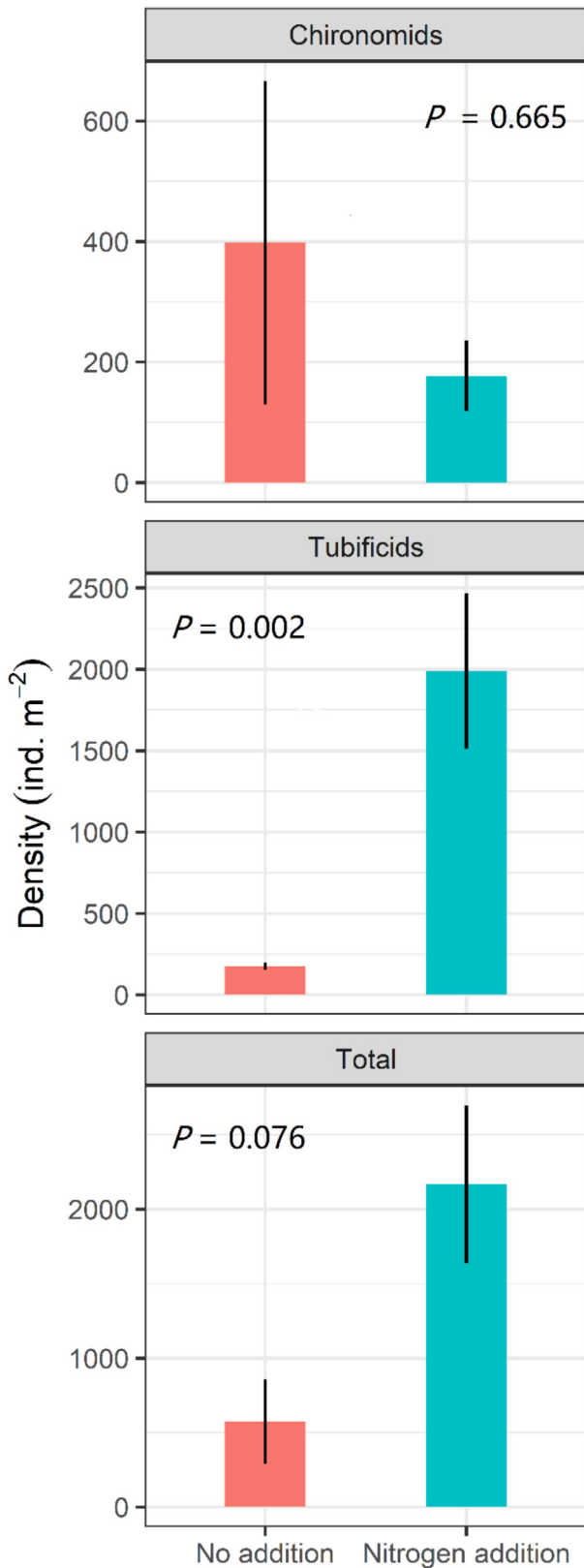


Fig. 3. Comparison of chironomids, tubificids and total macroinvertebrate densities (ind. m⁻²) between the two nitrogen treatments. The *P* value of Student's *t* test was shown on each panel.

observe similar promotion on chironomids by N addition. We cannot explain why these two macroinvertebrate taxa responded different to N addition. Physicochemical parameters, *e.g.*, dissolved oxygen, pH and redox potential, in the sediment-water interface that perhaps could have given an answer are unfortunately lacking in this study. The tubificids are known as “conveyor-belt feeders” that ingest particles in deep sediments and egest them on the surface in the form of pseudofeces (Dafoe *et al.*, 2011). They could also directly feed organic matter in the sediment surface (Yu *et al.*, 2013). The activities of these worms also increase sediment water content and porosity and reduce sediment particle size, making the sediment liable to sediment resuspension (Dafoe *et al.*, 2011; Zhang *et al.*, 2014a). Accordingly, experimental studies have shown stronger sediment resuspension in tubificid-abundant than tubificid-absent microcosms (Zhang *et al.*, 2014a; Zhang *et al.*, 2014b). Our results echo this and emphasize the indirect effects of N addition. It can be argued that the effects of N addition on sediment resuspension in our mesocosms is overestimated due to the absence of fish which would reduce tubificid abundance by predation. However, in this case, fish may also gain weight in high N systems via bottom-up process (Wang *et al.*, 2017), and therefore cause higher sediment resuspension as the tubificid did. This process has been confirmed by the promotion of non-algal turbidity by N addition in previous mesocosm experiment with crucian carp (He *et al.*, 2021). It is important to note that sediment resuspension often causes sediment P release in shallow eutrophic lakes (Schellenberg *et al.*, 2014; He *et al.*, 2017). Our study has shown another feedback loop between phytoplankton growth and sediment P release triggered by N addition, *i.e.*, high phytoplankton biomass causes high abundance of tubificids, which, in turn, enhances sediment resuspension and thereby increases the P concentrations, again supporting phytoplankton growth.

The need for controlling N inputs remains a subject of debate in the nutrient management of freshwater shallow lakes (Schindler *et al.*, 2008; Shatwell and Köhler, 2019). Our results showed that N inputs increased both algal and non-algal turbidity due to pelagic and benthic processes. Thus, alleviation of eutrophication in shallow eutrophic lakes requires a balanced and strategic approach to adequately control both nutrients (N & P).

Data availability statement

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

Declaration of competing interest

We declare that we have no conflict of interest.

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Author contribution statement

Hu He: Conceptualization, methodology, investigation, data curation, writing – original draft. **Lei Zhang:** Investigation, data curation, formal analysis, writing – review & editing. **Xiaoyu Ning:** data curation, writing – review & editing. **Zhigang Mao:** Conceptualization, methodology, writing – review & editing, funding acquisition. **Erik Jeppesen:** writing – review & editing. All authors contributed to the interpretation of the analysis and its implications and to the revision of intellectually important content, and all the authors approved of the manuscript's final publication and agree to be accountable for the work.

Supplementary Material

Fig. S1. Temporal dynamics of (a) inorganic suspended solids (ISS) and (b) light attenuation coefficient (K_d). The days were ranged from Day 0 – Day 70. (c) Significant positive relationship between ISS concentration and non-algal turbidity. We calculated the non-algal turbidity using the empirical formula in Lake Taihu ($\text{TurbNonAlgal} = 1/\text{ZSD} - 0.011 \times \text{Chl. a} - 0.18$) (Ma *et al.* 2021), Where ZSD is the Secchi depth which were calculated by the formula: $\text{ZSD} = 1.852/(\text{Kd} - 0.096)$ (Zhang *et al.*, 2004).

The Supplementary Material is available at <https://www.kmae-journal.org/10.1051/kmae/2023019/olm>.

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