The spatiotemporal characteristics of water quality and phytoplankton community in a shallow eutrophic lake: Implications for submerged vegetation restoration

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The spatiotemporal characteristics of water quality and phytoplankton community in a shallow eutrophic lake: Implications for submerged vegetation restoration

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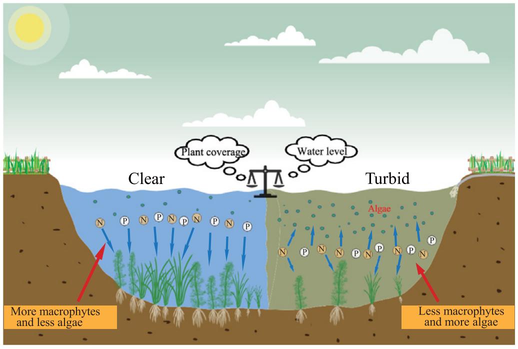
HIGHLIGHTS

- The recovery of macrophytes was achieved on the entire lake scale.
- The recovery of macrophytes can significantly decrease the density of phytoplankton.
- Water level in spring was the main driving force triggering the change of lake state.
- The presence or absence of macrophytes determines the state of lake.

GRAPHICAL ABSTRACT



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ABSTRACT

One of the most serious consequences of eutrophication in shallow lakes is deterioration of water quality, proliferation of phytoplankton and disappearance of submerged macrophytes. After removing herbivorous and plankti-benthivorous fish, submerged macrophyte restoration was utilized at the entire lake (82.7 km^2) to combat eutrophication and improve water quality in the shallow subtropical aquaculture of Lake Datong. We conducted two years of monitoring, from March 2018 to February 2020. During the first year of restoration, 80% of the area of Lake Datong (approximately 60 km^2) was successfully recovered by submerged vegetation, and the water quality was improved. For example, the phosphorous (P) content (including total P (TP), dissolved reactive P (DRP) and total dissolved P (TDP)) and turbidity decreased, and the Secchi depth (SD) increased. However, the submerged vegetation disappeared from autumn 2019 in the intermittent recovery area (MN), while the continuous recovery area (DX) continued to recover with an abundance of submerged vegetation. During the second year, the water quality continued to improve significantly in the DX area, with high biomass and coverage of submerged vegetation. In the MN area, although turbidity and ammonia nitrogen (NH_4^+-N) increased significantly and SD decreased significantly, the P content (TP, TDP, and DRP) still continued to decrease. The restoration of submerged macrophytes could significantly decrease the density of phytoplankton. Over time, there was a regime shift in Lake Datong. The structural equation model (SEM) results illustrated that the water level and submerged plant coverage were the primary drivers that triggered changes in the state of the lake ecosystem. Our results highlight the potential of restoring submerged vegetation to control water eutrophication at the whole-lake scale. However, the water level in spring was the primary driver that triggered changes in the state of the lake ecosystem. Water level management should be emphasized during the early stages of recovery of submerged plants.

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1. Introduction

Currently, eutrophication occurs in lakes worldwide (Smith, 2003; Jeppesen et al., 2017). Phosphorus (P) is considered to be the most important limiting nutrient in freshwater ecosystems and a major driver of eutrophication (Smith, 2003; Conley et al., 2009). Lake eutrophication caused by excessive nutrient inputs usually leads to deterioration of the water quality (Smith et al., 1999) and declines in aquatic vegetation (Phillips et al., 2016), as well as frequent outbreaks of harmful algal blooms (Brookes and Carey, 2011). Due to irrational fishery management and anthropogenic eutrophication, the amount of aquatic vegetation, especially submerged macrophytes, has decreased or even disappeared in many lakes in China (Zhang et al., 2017). In addition, the state of the affected lakes has changed from clear water dominated by submerged macrophytes to turbid water dominated by phytoplankton (Scheffer et al., 1993). Therefore, it is of great significance for the control and management of lake eutrophication to restore lakes to the state dominated by submerged macrophytes.

Numerous studies have demonstrated that the recovery of submerged macrophytes is an important ecological measure for the rehabilitation of degraded lake ecosystems and the improvement of the water quality of shallow eutrophic lakes (Phillips et al., 2016; Hilt et al., 2018). As the main primary producer in shallow lakes, submerged macrophytes perform key ecological functions in lake ecosystems, such as providing shelter and food for organisms (Wood et al., 2017), reducing phytoplankton biomass by allelopathic inhibition (Wang et al., 2013), removing nutrients in water and controlling sediment resuspension (Scheffer et al., 1993; Cao et al., 2018), which are helpful in improving water quality and maintaining a clear water state. However, submerged macrophytes are affected by many complex factors and by their interactions in the process of recovery, such as insufficient external load reduction and water level (WL) fluctuation (Bucak et al., 2012; Hilt et al., 2018). Previous studies have shown that high WLs in spring may be more conducive to the transition to turbid water and low WLs to a return to macrophytes (Blindow et al., 1993). Moreover, fish disturbance is also an important factor affecting the recovery of submerged macrophytes and water quality (Chen et al., 2020), especially in aquaculture lakes. Thus, the removal of plankti-benthivorous fish is a typical measure of recovery (Gulati et al., 2008). Currently, the recovery of submerged macrophytes in an entire lake has been considered an important indicator of the successful recovery of eutrophied lake ecosystems (Jeppesen et al., 2017). However, unstable plant succession or delayed resettlement of macrophytes often occurs during the preliminary stage of lake restoration, which may cause the lake to switch to a state dominated by phytoplankton. Therefore, the frequent dynamic changes in the composition and abundance of submerged macrophytes and phytoplankton during the preliminary stage of shallow lake restoration should receive more attention.

Phytoplankton are the main producers in lake ecosystems and are frequently used as important ecosystem indicators for evaluating water quality (Boyer et al., 2009). Many problems associated with eutrophication are usually caused by the overproduction of phytoplankton, such as cyanobacterial blooms. High bloom densities of cyanobacteria can have many negative effects, such as lower water quality, increased turbidity and disturbed aquatic plant growth, which act antagonistically on the stability of the lake ecosystem (Havens et al., 2019). Previous studies have suggested that nutrient levels, especially the P content, are the main driving factors affecting the growth and succession of phytoplankton (Abell et al., 2010; Jakobsen et al., 2015). Phytoplankton dynamics are also affected by other abiotic variables, such as physical light, temperature, wind speed, and sudden rises in WLs caused by rainfall (Yang et al., 2017; Stockwell et al., 2020; Mao et al., 2021). Additionally, submerged macrophytes and phytoplankton interact in multiple ways to take advantage of alternating phases through shading, nutrient competition and allelopathy (Van Donk et al., 1993; Van Donk and van de Bund, 2002; Terborgh et al., 2018). Recent studies have shown that submerged macrophytes are effective in reducing the phytoplankton biomass after the removal of omnivorous fish from shallow lakes in China, and the bottom-up effect provided by submerged macrophytes becomes more prominent (Yu et al., 2016; Liu et al., 2018). Although numerous studies have explored the response of phytoplankton to the ambient environment, the response of phytoplankton to the entire lake macrophyte recovery in subtropical aquaculture lakes remains largely unclear (Pinto and O'Farrell, 2014; Litchman et al., 2015; Phillips et al., 2016).

The interactions among water parameters, phytoplankton communities and submerged macrophytes play a vital role in regulating the ecosystem structure and maintaining ecosystem stability (Scheffer et al., 2001). Therefore, we need to further understand the possible corresponding effects of submerged macrophyte restoration on phytoplankton growth and water quality. In this study, after removing herbivorous and plankti-benthivorous fish, submerged macrophytes were utilized to control eutrophication and improve water quality in a subtropical aquaculture shallow lake. Simultaneously, the seasonal variation and spatial distribution characteristics of the phytoplankton community during the process of submerged macrophyte restoration were analyzed. Our study aims to (1) reveal the influence of submerged macrophyte restoration on water quality, (2) reveal the spatiotemporal dynamics of phytoplankton community composition under the influence of a large-scale submerged macrophyte restoration, and (3) understand lake state changes under the influence of submerged macrophyte restoration.

2. Materials and methods

2.1. Study area

Lake Datong (29°04′-29°22′ N, 112°17′-112°42′ E) is located in the middle reaches of the Yangtze River and faces Lake Dongting to the east. With an average depth of 2 m and a maximum depth of 3 m, it is the largest aquaculture lake in Hunan Province, China. Lake Datong is located in a subtropical continental monsoon humid climate area, with an average annual precipitation, evaporation and temperature of 1240.8 mm, 1129.8 mm and 16.5 °C, respectively. There are four major rivers flowing into Lake Datong, namely, the Daxin River, the Jinpen Canal, the Wuqi Canal and the Su River, each of which has locks to artificially control water storage. Tributary water mainly enters Lake Datong through the sluice at the mouth of the Wuqi Canal and flows to the Jinpen Canal along the south bank. A fresh fish production rate of 12,000 tons per year and fish feed and fertilizer application rates of approximately 14,000 tons and 12,000 tons per year over the past decade were found in Lake Datong, respectively (Yang et al., 2016). Due to the long-term artificial culture fishery, Lake Datong is strongly eutrophic, with the TP in the overlying water exceeding 0.2 mg L^{-1} in recent years (Wu et al., 2018). In addition, the number of diatom and cyanobacterial cells is growing. Additionally, our previous research showed that native submerged macrophytes in Lake Datong almost completely disappeared by 2017 (Li et al., 2021). Sediment samples were collected from areas where submerged macrophytes existed historically, and subsequent germination experiments showed that no submerged macrophytes germinated (data not shown).

In an effort to improve water quality, the local government stopped aquaculture in 2016 and started lake restoration by fish removal in 2017. In January 2018, the submerged macrophyte restoration project was implemented in Lake Datong. Before the implementation of the restoration project, a total of 123.2 tons of fish was removed by seine fishing, of which 99% were bighead carp, silver carp and common carp, and 1% were herbivorous fish (Li et al., 2021). According to the theoretical pristine state of the aquatic macrophyte community and historical data on the original state of the submerged macrophyte community in Lake Datong (Li et al., 2012), the winter buds of *Hydrilla verticillata* (L.f.) Royle and soaked fruits of *Vallisneria denseserrulata* (Makino) Makino were manually sown in the lake from January to March, while mature plants of *Myriophyllum spicatum* L. and

Ceratophyllum demersum L. were transplanted around the lake shore from March to May.

2.2. Field sampling and laboratory analysis

After nearly a year of restoration, the submerged macrophytes covered nearly 80% of the lake by October 2018 (Li et al., 2021). However, since the summer of 2019, the number of submerged macrophytes has gradually decreased and even disappeared in some areas, but submerged macrophytes still exist in some areas. Therefore, based on the restoration status of vegetation in March 2020, Lake Datong was divided into two sampling fields: a continuous recovery area of submerged vegetation, named DX (A1, A2), and an intermittent recovery area, named MN (A3-A8), with a total of eight fixed sampling sites (Fig. 1). Each sampling point was positioned by global positioning system (GPS) data and marked with bamboo poles. Phytoplankton, water and submerged vegetation samples were collected monthly from March 2018 to February 2020. Phytoplankton and water samples were collected 50 cm below the surface water at each sampling site. Unfortunately, the phytoplankton samples collected in December 2019 were damaged. Portable water quality monitors (PROPLUS, YSI, United States) were used to measure water temperature (T), electrical conductivity (EC), dissolved oxygen (DO) and pH in real time at each sampling site. Water turbidity was measured *in situ* with a turbidity meter (2100Q, HACH, United States). The WL and the Secchi depth (SD) were measured using a hand-held depth sounder and a white and black Secchi disk, respectively. The total nitrogen (TN), TP, dissolved reactive P (DRP) and total dissolved P (TDP) contents of the water were measured according to the standard methods published by China's State Environmental Protection Administration (Jin and Tu, 1990). Ammonia N (NH_4^+-N) and chemical oxygen demand (COD) were analyzed with a digestion solution for the corresponding parameters and by using the landscape photometry (DR900, HACH, United States; Lv et al., 2018).

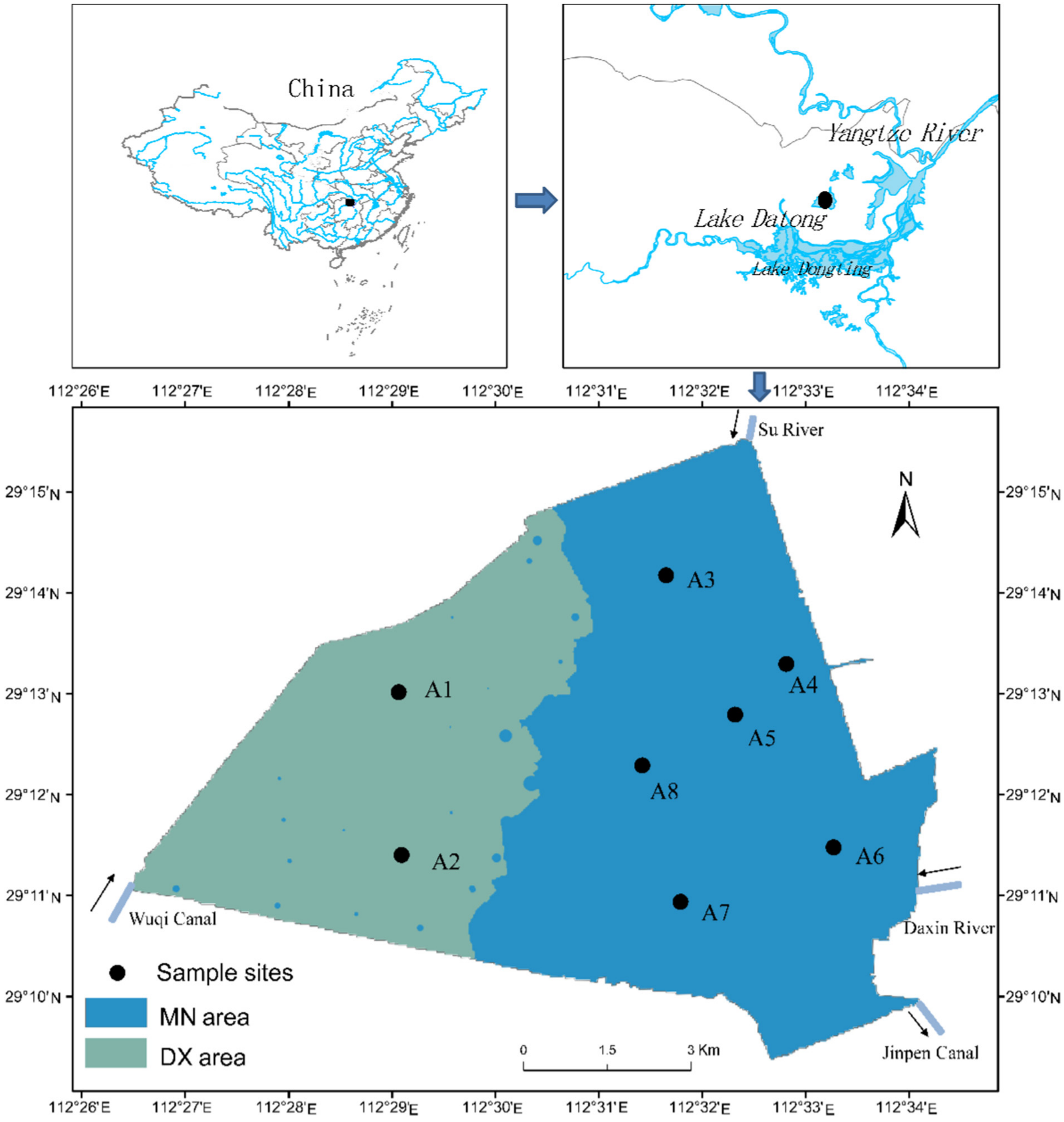
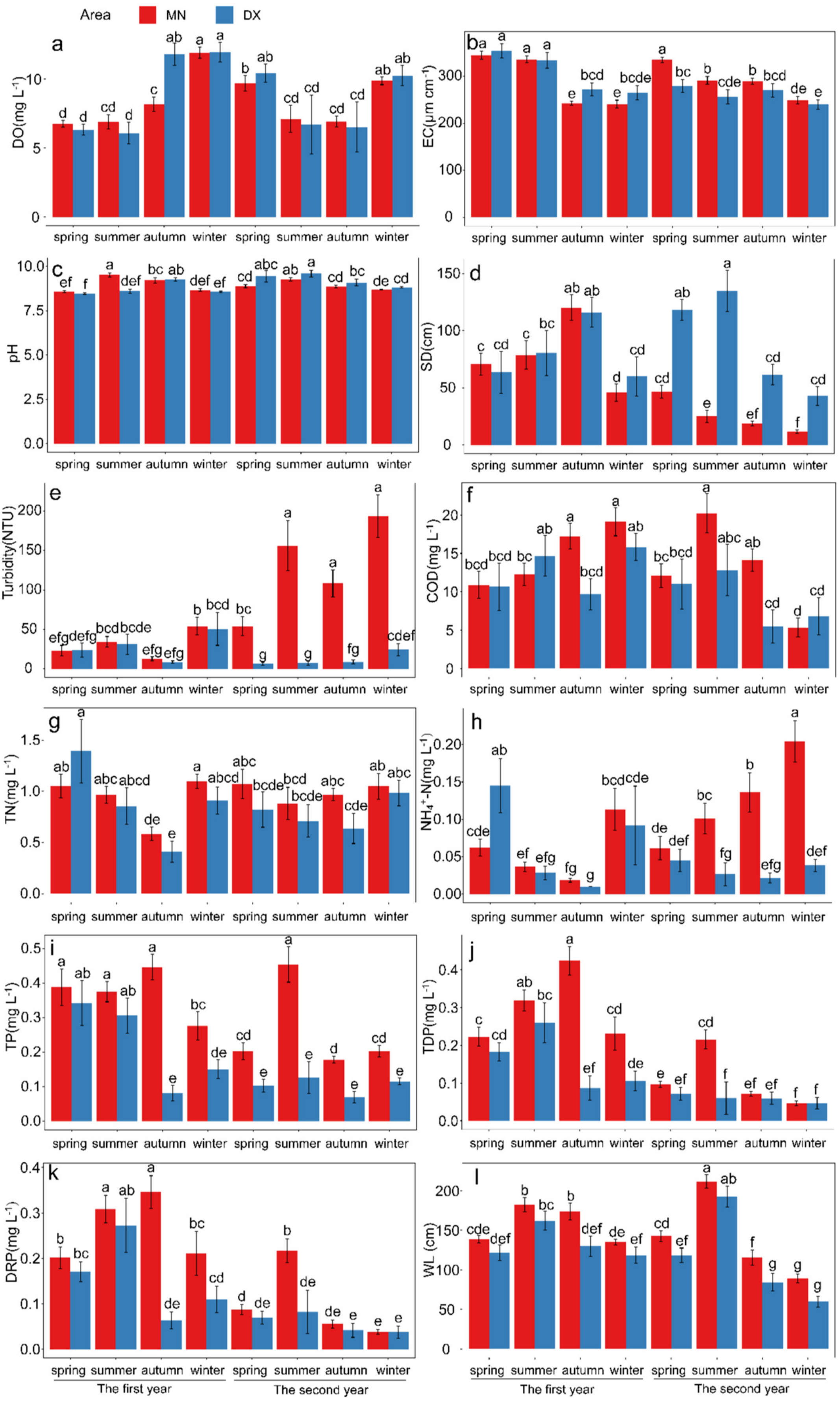


Fig. 1. Locations of the sampling sites in Lake Datong.


Area
🟥 MN
🟦 DX
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DO(mg L^{-1})
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d d cd d c ab a a b ab cd cd cd cd ab ab
b
EC(μm cm^{-1})
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300
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c
pH
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7.5
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ef f a def bc ab def ef cd abc ab a cd bc de cd
d
SD(cm)
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Turbidity(NTU)
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200
efg defg bcd bcde efg efg b bcd bc g a g a fg a cdef
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COD(mg L^{-1})
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5
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20
bcd bcd bc ab a bcd a ab bc bcd a abc ab cd d cd
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TN(mg L^{-1})
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1.5
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NH$_4^+$-N(mg L^{-1})
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0.05
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TP(mg L^{-1})
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DRP(mg L^{-1})
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0.3
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l
WL (cm)
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50
100
150
200
cde def b bc b def de ef cd ef a ab f g g g
spring summer autumn winter spring summer autumn winter
The first year
The second year

The water samples for phytoplankton analysis were preserved with Lugol's iodine solution (final concentration 2%) and kept in the dark in a vacuumed 3 L flasks for 48 h. Then, the settled phytoplankton were transferred to smaller bottles. The sedimentation process was repeated every 48 h until approximately 50 mL of phytoplankton samples were produced. Phytoplankton species were identified and quantified with a microscope (BX53 + DP74, OLYMPUS, Japan) using the blood count plate method (Qian et al., 2015).

To investigate the submerged macrophyte composition and distribution, three repeated submerged macrophyte samples were collected by a pronged grab (25 cm × 35 cm) at each sampling site. An ocular estimation was used to investigate macrophyte coverage by measuring the percentage of vertical projection area of macrophytes in a square metal frame (1 m × 1 m) to the sample area (Fang et al., 2009), and the macrophyte species richness of each site was counted. After drying the submerged macrophyte samples at 80 °C for 48 h to constant mass, the biomass per unit area was measured with an electronic balance.

2.3. Statistical analysis

Data were analyzed according to seasons: spring (March to May), summer (June to August), autumn (September to November) and winter (December to February). Because the data were not homoscedastic and normal, the nonparametric Kruskal–Wallis test (Breslow, 1970) was used to determine the difference in phytoplankton characteristics, water parameters and submerged macrophyte characteristics for different seasons and areas. Nonmetric multidimensional scaling (NMDS) analysis was used to evaluate changes in phytoplankton composition, and permutational multivariate analysis of variance (PERMANOVA) was used to test the significance of differences between two areas during the two-year restoration period. NMDS and PERMANOVA were carried out using the ‘vegan’ package in R (Oksanen et al., 2016). Spearman correlation analysis was used to evaluate the relationship between the submerged macrophyte characteristics and water quality. Multivariate generalized linear models were used to rank the main environmental factors affecting phytoplankton features. We fitted a piecewise structural equation model (SEM) using the *psem* function in the piecewise SEM package (Lefcheck and Freckleton, 2015) to test the direct and indirect effects of plant coverage, WL, TP, TN and COD as drivers of algal density. All analyses were conducted in R 3.6.2 (R Development Core Team, 2019).

3. Results

3.1. Spatial and seasonal characteristics of water parameters

There was no significant difference in the water SD and turbidity between the two areas in the first year of restoration, but a significantly higher SD and lower turbidity were found in the DX area in all seasons in the second restoration year (Fig. 2d, e). From September 2018 to November 2019, the COD values were lower in the DX area than in the MN area (Fig. 2f). During the first year of restoration, TN and NH_4^+-N in the entire lake showed a downward trend in spring, summer and autumn and then increased in winter. Over time, the TN content remained constant in the entire lake, while the NH_4^+-N content in the MN area continued to increase during the second year of restoration (Fig. 2g, h). In addition, NH_4^+-N in the MN area was significantly higher during the second year of restoration than in the first year and significantly higher than in the DX area (Fig. 2h). In the MN area, the TP decreased significantly in winter of the first year of recovery and maintained similar values in the second year of recovery (except for summer). In the DX area, the TP began to decrease in autumn 2018 and maintained a similar value until February 2020 (Fig. 2i). Excluding spring and summer 2018, TP in the DX area was significantly lower than in the MN area during the two-year restoration period. TDP and DRP in the entire lake showed a general downward trend (Fig. 2j, k). During autumn and spring 2019, the WLs in DX were significantly lower than in the MN area (Fig. 2l). Higher WLs were found in summer, especially the maximal WL that occurred in summer 2019. There was no significant difference in water DO, pH, TN, TDP and DRP between the two areas during most seasons (Fig. 2a, c, g, j, k). After 6 months of recovery, EC in the entire lake decreased significantly and remained relatively stable thereafter (except for the EC value of the MN area in spring 2019; Fig. 2b).

3.2. Spatiotemporal dynamics of phytoplankton

During the two-year study period, 95 species of phytoplankton belonging to 64 genera and 7 phyla were recorded in Lake Datong (Table S1). Fig. 3a, b shows the monthly variations in phytoplankton density. The algae had the highest mean cell density (up to 1.68×10^7 cells·L^{-1}) in August 2019, whereas the algae had the lowest density (only 2.54×10^5 cells·L^{-1}) in October 2018. In terms of the annual mean community composition, Bacillariophyta and Cyanobacteria were the most abundant taxonomic groups in the first and second year after restoration, respectively. Cyanobacteria was the dominant group in summer, and its cell density reached a peak of 1.58×10^7 cells·L^{-1} in August 2019. In addition, their increase was more significant in the second restoration year. Cryptophyta was the dominant group only in early spring (March and April) during the surveyed years (Fig. 3a, b).

The PERMANOVA results showed that the phytoplankton community composition was significantly affected by year, season and area, and the three factors had interactive influences on the composition of the phytoplankton community (Table 1). From the NMDS results, the phytoplankton community composition showed significant annual variations (Fig. 4). The annual variation was also reflected in the spatial distribution. There were significant differences in the phytoplankton community composition between the two areas, and the phytoplankton community composition had significant seasonal differences (Fig. 4; Table 1).

The seasonal pattern of phytoplankton varied in different areas and years (Fig. 3c). There was no significant difference in the phytoplankton density between the two areas during the first year of restoration (Fig. 3c). During the second year of restoration, the phytoplankton density in the MN area was significantly higher than that in the DX area except in winter. Moreover, the phytoplankton density in the MN area during the second year of restoration was significantly higher than during the first year (Fig. 3c).

3.3. Spatial and seasonal variation in submerged macrophytes

In total, five species of submerged macrophytes were observed during the two-year survey, namely, *V. denseserrulata*, *H. verticillata*, *C. demersum*, *M. spicatum*, and *Vallisneria spinulosa* Yan. The maximal richness, coverage and biomass were found in autumn of the first year of restoration (Fig. 5a, b, c). Except for the higher biomass in DX during autumn 2018, no significant differences in richness, coverage or biomass between DX and MN in autumn and winter 2018 were recorded. During the second year of restoration, significantly higher richness, coverage and biomass in the DX area were found in summer and autumn, respectively (Fig. 5a, b, c).

Fig. 2. Spatial and seasonal characteristics of water parameters (mean ± SE) in Lake Datong during the two-year restoration period. (a) DO, (b) EC, (c) water pH, (d) SD, (e) water turbidity, (f) COD, (g) TN, (h) NH_4^+-N, (i) TP, (j) TDP, (k) DRP, and (l) WL. MN and DX are lake areas in Lake Datong. Different letters (a, b, c, d, e, f, g) represent significant differences ($P < 0.05$) in the mean values based on Kruskal tests.

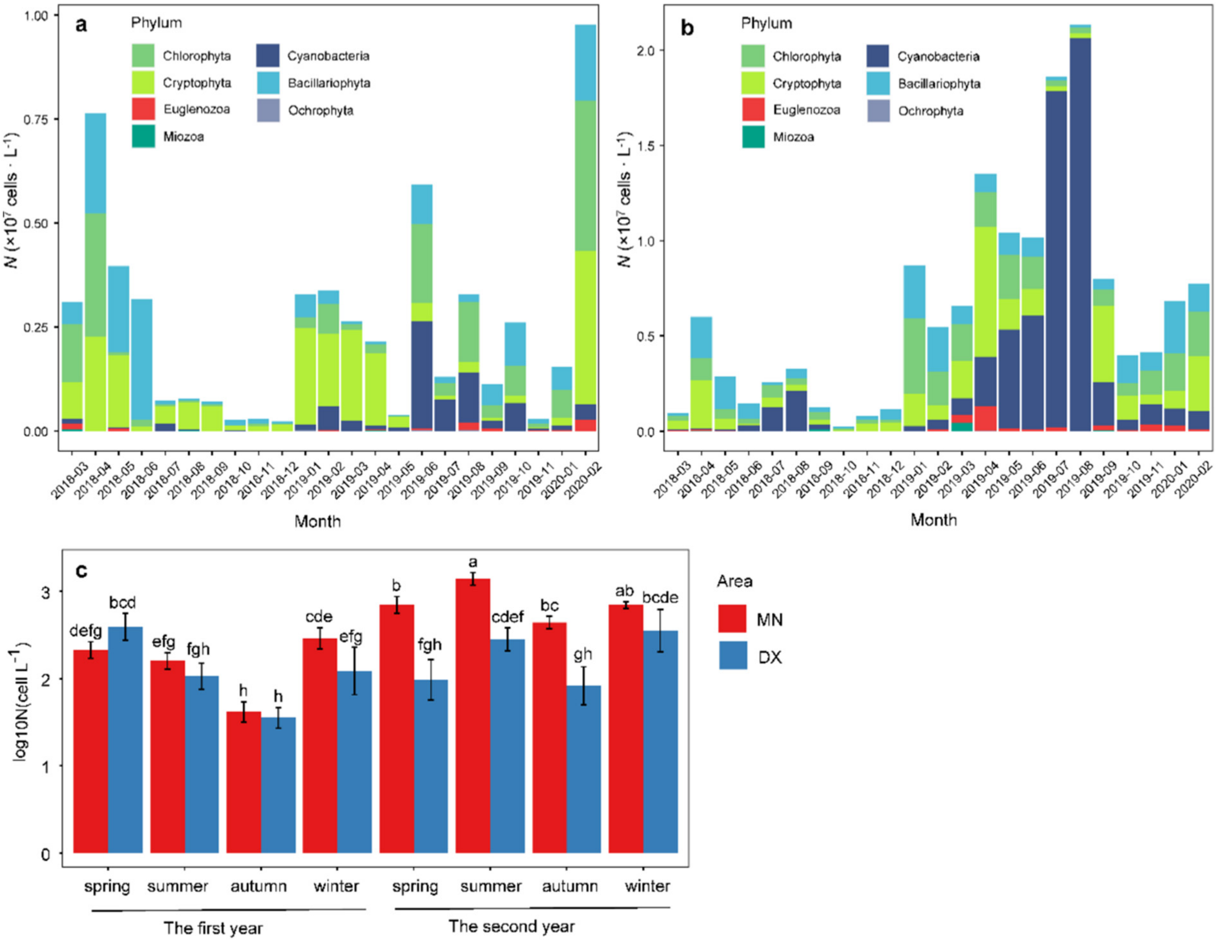

Fig. 3. (a) and (b): Temporal variation in phytoplankton composition and cell density in Lake Datong during the two-year restoration period. (c): Spatial and seasonal characteristics of the phytoplankton cell density (mean ± SD) in Lake Datong. DX and MN are lake areas in Lake Datong. Different letters represent significant differences ($P < 0.05$) in the mean values based on Kruskal tests.

3.4. Relationship among phytoplankton, water quality and submerged macrophytes

Spearman correlation analysis showed that submerged macrophyte richness, coverage and biomass were significantly negatively correlated with EC, NH_4^+-N, COD, TN, TP and turbidity but significantly positively correlated with pH and SD. Additionally, there was a significant positive correlation between richness and DO in the water (Table 2).

Multivariate generalized linear models were used to ordinate the main variable environmental factors on phytoplankton features. For the cell density of the phytoplankton communities, eight environmental factors accounted for 36.5% of the variance (Fig. 6a). For the phytoplankton Shannon–Wiener index, richness and evenness, environmental factors accounted for 24.4%, 20.1% and 26.8% of the variance, respectively (Fig. 6b, c, d).

Table 1
The effects of year, season and area on phytoplankton composition based on PERMANOVA.

	Df	*F*	R^2	*P*
Year	1	28.46	0.11	0.001
Season	3	8.21	0.10	0.001
Area	1	4.44	0.02	0.001
Year × season	3	5.44	0.06	0.001
Year ×area	1	3.80	0.01	0.001
Season × area	3	2.12	0.02	0.001
Year × season ×area	3	2.16	0.03	0.001

SEM analysis was performed to outline the direct or indirect influence of biotic and abiotic factors on a highly variable algal density recorded during the investigated period (Fig. 7). During the first year of restoration in the entire lake and the second year of restoration in the DX area, the density of algae was negatively affected by the coverage of submerged macrophytes and positively affected by the COD, while these models did not show significant indirect effects of coverage and WL on algal density (Fig. 7a, b). In the MN area, TP and COD increased with increasing WL, and TP positively affected the density of algae (standardized $\beta = 0.364$, $P < 0.01$). Therefore, the density of algae was positively affected (indirectly) by the WL through its positive effect on TP (Fig. 7c).

4. Discussion

4.1. Effects of recovering submerged macrophytes on water quality

Many studies have shown that submerged macrophytes can improve the water quality of shallow lakes by reducing nutrient concentrations and increasing water transparency (Bai et al., 2020; Liu et al., 2020). During the first year of restoration, the annual and seasonal TN and NH_4^+-N showed decreasing trends in the entire lake. Meanwhile, TP in the DX area showed a decreasing trend, and TP decreased by 73.5% in autumn compared with summer (Figs. 2g, h, i, S1). These results could be due to the submerged macrophytes in Lake Datong beginning to grow rapidly in summer and

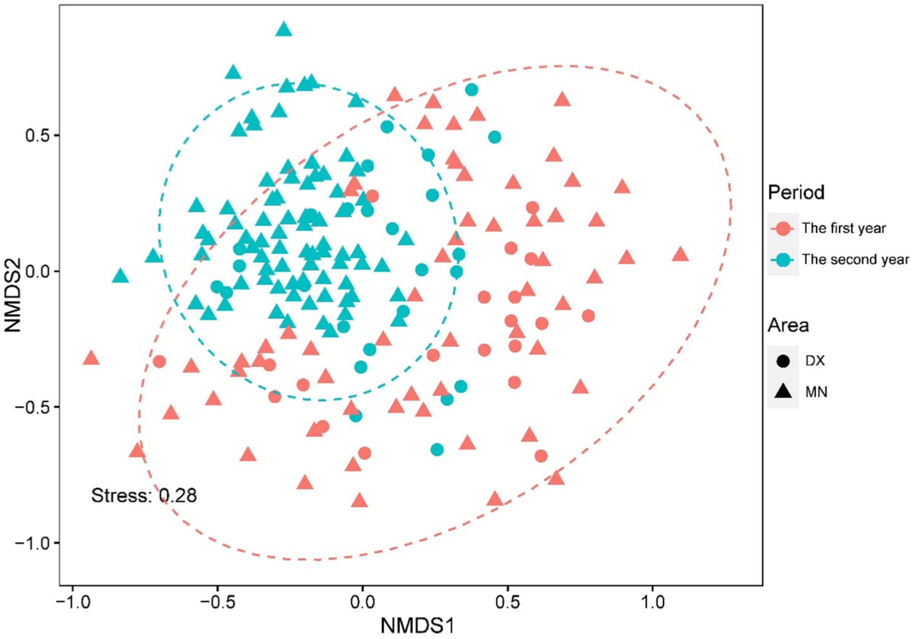

Fig. 4. Nonmetric multidimensional scaling diagram showing phytoplankton community composition differences obtained during the two-year restoration period. Two areas (DX, MN) were analyzed during two restoration periods: 2018.3–2019.2 and 2019.3–2020.2.

reaching their maximum area (almost 80% of the entire lake) in autumn 2018. Lake Datong showed a clear state with high SD and low turbidity in summer and autumn 2018. These results suggest that the distribution of large areas of submerged macrophytes greatly controls the resuspension of sediments and reduces nutrient load in shallow lakes through direct absorption and indirect inhibition of sediment release (Graneli and Solander, 1988; Levi et al., 2015).

However, the water quality of Datong Lake showed obvious spatial heterogeneity during the second year of restoration. In our study, significantly lower turbidity and higher SD in the DX area were found compared with those in the MN area, and water nutrients, such as NH_4^+-N and TP, were significantly lower than those in the MN area, implying a better water quality in the DX area. These results could be related to the opposite distribution trend of submerged macrophytes in the two areas. In autumn 2019, the submerged vegetation in the MN area disappeared, while the vegetation coverage and biomass in the DX area continued to increase. Thus, the coverage, richness and biomass of submerged macrophytes in the DX area were significantly greater than those in the MN area (Fig. 5), suggesting that there were more submerged macrophytes involved in nutrient absorption in the DX area. Moreover, our results showed that submerged macrophyte richness, coverage and biomass were significantly negatively correlated with NH_4^+-N, TN, TP and turbidity but significantly positively correlated with SD (Table 2). These results confirmed the effect of submerged macrophytes on water quality improvement, suggesting that the more abundant submerged macrophytes are, the better the water quality improvement. Compared to the first year of restoration, the MN area was distinguished by a decrease in SD and an increase in NH_4^+-N concentration during the second year of restoration, no significant change in the annual average N content, and a significant decrease in the annual average P content (TP, TDP, and DRP). Although the coverage and biomass of submerged vegetation in the MN area decreased gradually and even disappeared in autumn 2019, the results indicate that the effect of submerged vegetation on reducing the P content did not disappear immediately. Specifically, we found that the P content of the lake water showed an increasing trend from spring to summer 2019 within the MN area, particularly that of TDP and DRP (Fig. 2j, k). These results may have been related to the combined effects of the high external nutrient input due to the increasing WL (Fig. 2l) and disappearance of submerged vegetation during this period. Previous studies have shown that rising WLs usually lead to a decline in water quality (Bucak et al., 2012; Magbanua et al., 2015). The SEM results also showed that the WL had a significant positive effect on TP (standardized $\beta = 0.301$, $P < 0.01$) (Fig. 7a, c). In addition, rising WLs can also lead to the death of aquatic plants, thus affecting water quality (Lu et al., 2018).

4.2. Response of phytoplankton community to submerged macrophyte restoration

Previous studies have shown that an increase in submerged macrophyte coverage leads to a simultaneous decline in phytoplankton density (Jones, 1990; Moss, 1990). Our study showed that the density of phytoplankton remained at a relatively low level during the first year of restoration (Fig. 3), which demonstrates that the recovery of submerged macrophytes can significantly inhibit the growth of phytoplankton. These results could be related to allelopathy (Felpeto et al., 2018), nutrient competition (Ozimek et al., 1990), and shading of submerged macrophytes (Brammer, 1979). In this study, a multivariate generalized linear model also showed a significant negative correlation between submerged macrophyte coverage and phytoplankton density (Fig. 5a). Moreover, the lowest phytoplankton density (only 2.54×10^5 cells·L^{-1}) was observed in October 2018 along with the highest aquatic vegetation coverage, although the nutrient level in the entire lake was still high (average TP 0.33 mg L^{-1}, average TN 0.92 mg L^{-1}). Additionally, the SEM results also confirmed the direct effect of submerged macrophytes on algal density (Fig. 7a). Therefore, we inferred that allelopathy and spatial inhibition of high-coverage submerged macrophytes had stronger effects on phytoplankton density than nutrient competition in Lake Datong during the first year of restoration.

There was a discernible annual variation in the phytoplankton community composition between the first and second year of restoration (Fig. 4; Table 1). This variation was mainly reflected in the significant increase in the abundance of Cyanobacteria during the second year of restoration. Previous studies have shown that the occurrence of meteorological and hydrological disturbances can lead to a sudden and significant increase in cyanobacterial biomass, which is closely related to nutrient concentrations and WL fluctuations, water temperature and rainfall (Ko et al., 2017; Yang

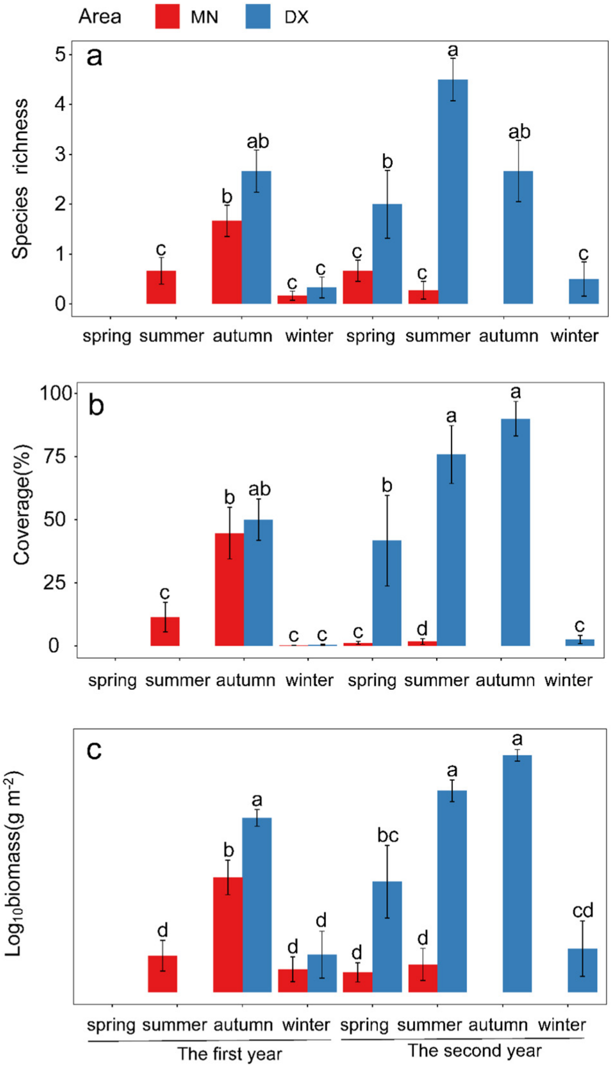

Fig. 5. Spatial and seasonal characteristics of submerged macrophytes (mean ± SE) in Lake Datong. MN and DX are lake areas in Lake Datong. Different letters (a, b, c, d) represent significant differences ($P < 0.05$) in the mean values based on Kruskal tests.

et al., 2017). Dramatic fluctuations in the WL were found in the MN area from spring to summer during the second year of restoration (Fig. 2l). Simultaneously, TP and phytoplankton density showed an increasing trend (Figs. 2i and 3), which was consistent with previous research showing that the variation in the phytoplankton community was closely related to the variation in TP (Jochimsen et al., 2013). In addition, the annual variation of the phytoplankton community density and composition in Lake Datong was significantly different due to the influence of submerged macrophytes. Changes in the phytoplankton community structure induced by aquatic vegetation have also been reported in other lakes (Chia et al., 2011; Wang et al., 2021). In our study, the recovery of submerged macrophytes was found to be capable of reducing phytoplankton density during the first year of restoration. However, the total area of the lake dominated by submerged macrophytes during the second year of restoration was much smaller, thus indicating the weaker effect of submerged macrophytes on phytoplankton.

Table 2

Spearman correlation coefficients between submerged macrophytes and water characteristics (N = 184). TN: total nitrogen; TP: total phosphorus; TDP: total dissolved phosphorus; DRP: dissolved reactive phosphorus; NH_4^+-N: ammonia nitrogen; COD: chemical oxygen demand; DO: dissolved oxygen; EC: electrical conductivity; pH: water pH; SD: Secchi depth; Turbidity: water turbidity.

	Biomass (g m^{-2})	Richness	Coverage (%)
TN (mg L^{-1})	−0.385**	−0.377**	−0.383**
TP (mg L^{-1})	−0.234**	−0.227**	−0.215**
TDP (mg L^{-1})	−0.069	−0.07	−0.049
DRP (mg L^{-1})	−0.061	−0.064	−0.051
NH_4^+-N (mg L^{-1})	−0.448**	−0.44**	−0.444**
COD (mg L^{-1})	−0.164*	−0.161*	−0.148*
DO (mg L^{-1})	0.136	0.145*	0.128
EC (μm cm^{-1})	−0.258**	−0.24**	−0.251**
pH	0.388**	0.428**	0.396**
SD (cm)	0.42**	0.435**	0.43**
Turbidity (NTU)	−0.458**	−0.452**	−0.452**

* $P < 0.05$.

** $P < 0.01$.

With the restoration of submerged macrophytes, the phytoplankton communities of the two areas showed significant spatial differences. Extensive studies have shown that phytoplankton can be used as an ecological indicator to understand water quality and can quickly reflect the ecological and nutritional status of water bodies (Celekli and Kulkoyluoglu, 2007; Jiang et al., 2014). Moreover, different coverages of submerged macrophytes may lead to different densities and diversities of phytoplankton (Dembowska, 2015). Our results showed that the cell density of phytoplankton in the MN area during the two-year recovery period was generally higher than in the DX area. This spatial distribution was also similar to the spatial distribution of nutrients and submerged macrophytes, suggesting that the variation in nutrients and submerged macrophytes in the region might be the main driving force for the formation of phytoplankton spatial patterns (Ho et al., 2019; Liu et al., 2021). In general, the successful recovery of submerged macrophytes can have a strong impact on phytoplankton communities, either directly or indirectly, which depends on the macrophyte coverage.

4.3. Drivers of state shifts in Lake Datong

Understanding the driving mechanisms of regime shifts is critical in guiding the practice of lake restoration. The regime shift theory suggests that only when the driving factors exceed a threshold will a lake switch from a clear state dominated by macrophytes to a turbid state dominated by phytoplankton (Scheffer and Carpenter, 2003). Generally, climate change, nutrient enrichment or WL fluctuation caused by human activities will directly or indirectly lead to a shift in the state of shallow lakes (Scheffer and van Nes, 2007). In the present study, during the first year of restoration, the large area (60 km^2) of the lake was successfully recovered with submerged macrophytes and switched to the clear state. However, the structure of phytoplankton changed greatly during the second restoration year, leaving most of the water (MN area) in the turbid state dominated by Cyanobacteria. During the transition between these two states, we observed dramatic WL fluctuations (Fig. 2l). Many studies have highlighted the importance of the WL on the variation between the macrophyte-dominated clear state and phytoplankton-dominated turbid state in shallow lakes (Coops et al., 2003; Van Geest et al., 2003). In our study, the rise in the WL directly increased the nutrient content (especially TP and COD) in the local waters and indirectly increased the density of phytoplankton in the MN area (Fig. 7c). In addition to nutrients, WL fluctuations can also induce critical transitions by altering the macrophyte cover in lake ecosystems (Bertani et al., 2016). An earlier study showed that WL fluctuation is one of the important physical processes leading to the death of macrophytes, thus affecting the nutrient cycle of macrophytes (Lu et al., 2018). When comparing both lake areas, we observed a significant decline in the submerged macrophytes in the MN area during a dramatic fluctuation of the WL (Fig. 5), indicating that this event may have led to a decrease in submerged macrophytes and indirectly promoted the change of state. Therefore, the subsequent dominance of phytoplankton in eutrophic lakes is more likely to be the result of vegetation loss than the cause (Phillips et al., 2016). In this study, the WL acted as the primary driver that triggered changes in the state of the lake ecosystem. Additionally, more attention

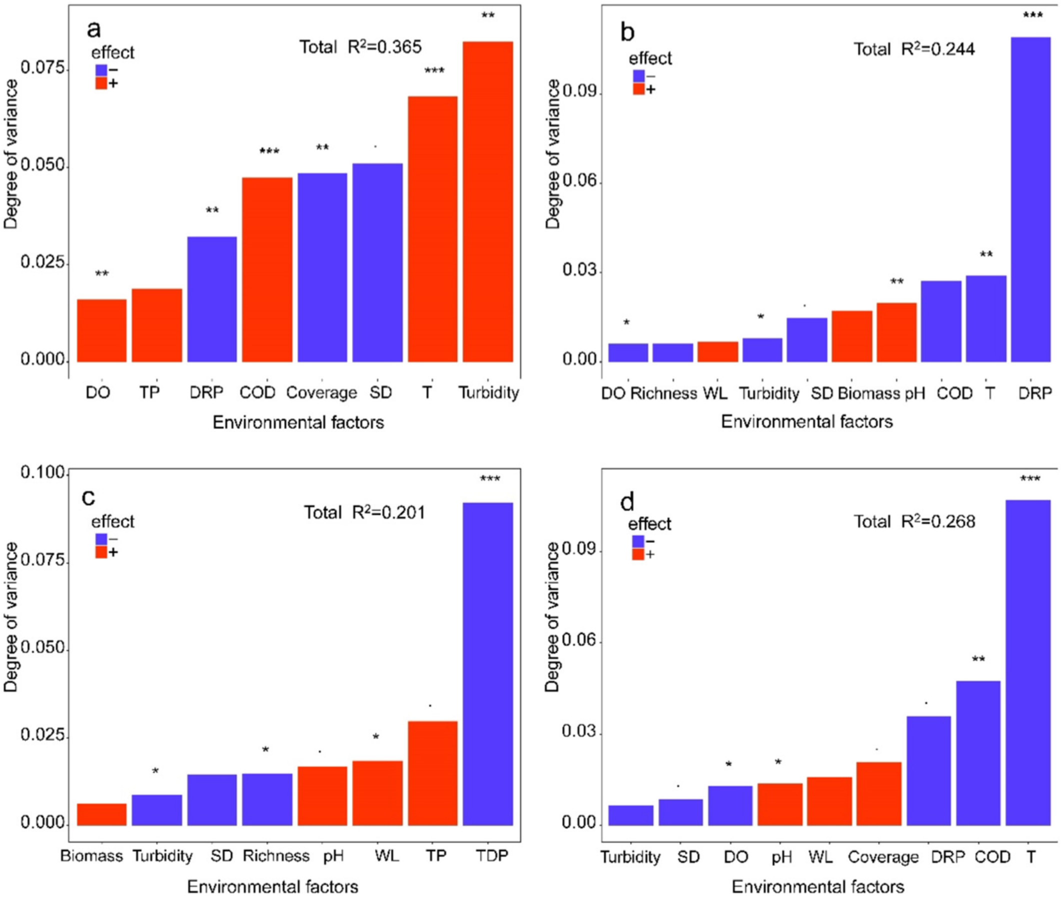

Fig. 6. Multivariate generalized linear model results to determine the effects of environmental factors on phytoplankton: (a) cell density, (b) Shannon–Wiener index, (c) richness and (d) evenness. Turbidity: water turbidity; Coverage: plant coverage; Biomass: plant biomass; Richness: plant richness; all other variables are defined in the main text. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, and $P < 0.1$.

should be given to the management of WLs during the restoration of submerged macrophytes.

By comparing the two states of water over a two-year restoration period, it can be speculated that the growth advantage of submerged macrophytes in spring determines the state of the water body in a later period. Our results showed that water quality and phytoplankton began to behave significantly different in the two areas during the springtime of the second year of restoration. Previous studies have shown that the emergence of the spring clear water phase in eutrophic lakes may be the key window for the establishment of submerged macrophytes (Lampert et al., 1986; Phillips et al., 2016), thus emphasizing the importance of light during initial growth. However, the light availability of aquatic plants is also affected by the WL, with some studies reporting that aquatic plants grow more vigorously when the WL is low (Bucak et al., 2012; Ejankowski, 2015). This also explains that the successful recovery of submerged macrophytes during the first year of restoration may be related to the optimum WL and light conditions. Although the WL fluctuated during this period, the persistence of water clarity indicated that submerged plants were always dominant.

5. Conclusion

In this study, submerged macrophytes were applied on a large scale to mitigate eutrophication and to improve water quality parameters. Our study demonstrates that it is feasible to restore submerged vegetation to control water eutrophication at the whole-lake scale. Along with the growth of submerged macrophytes, a clear water state with high SD and low turbidity was observed, suggesting the improved effects caused by the recovery of submerged macrophytes. Moreover, the decrease in water nutrients in the DX area was much greater than that in the MN area, which was related to a more stable plant community. In addition, our study demonstrates that the recovery of submerged macrophytes can significantly inhibit the growth of phytoplankton. Over time, there was a discernible annual variation in the phytoplankton community composition from the first year to the second year of restoration. In particular, the abundance of Cyanobacteria increased significantly, implying a regime shift in Lake Datong. The SEMs results illustrated that the WL was the primary driver that triggered changes in the state of the lake ecosystem. Finally, through the comparison of two states, we speculated that the growth advantage of submerged macrophytes in spring determines the state of water body in a later period.

CRediT authorship contribution statement

Chuanxin Chao and Tian Lv: collected and analyzed the data and wrote the manuscript. Yang Li, Chen Han, Weicheng Yu, Zhiwei Yan, Xiaowen Ma, Haocun Zhao, Zhenjun Zuo, Chang Zhang and Min Tao: collected the samples. Dan Yu, Ligong Wang and Chunhua Liu: designed the experiment, revised this manuscript and provided fund support. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

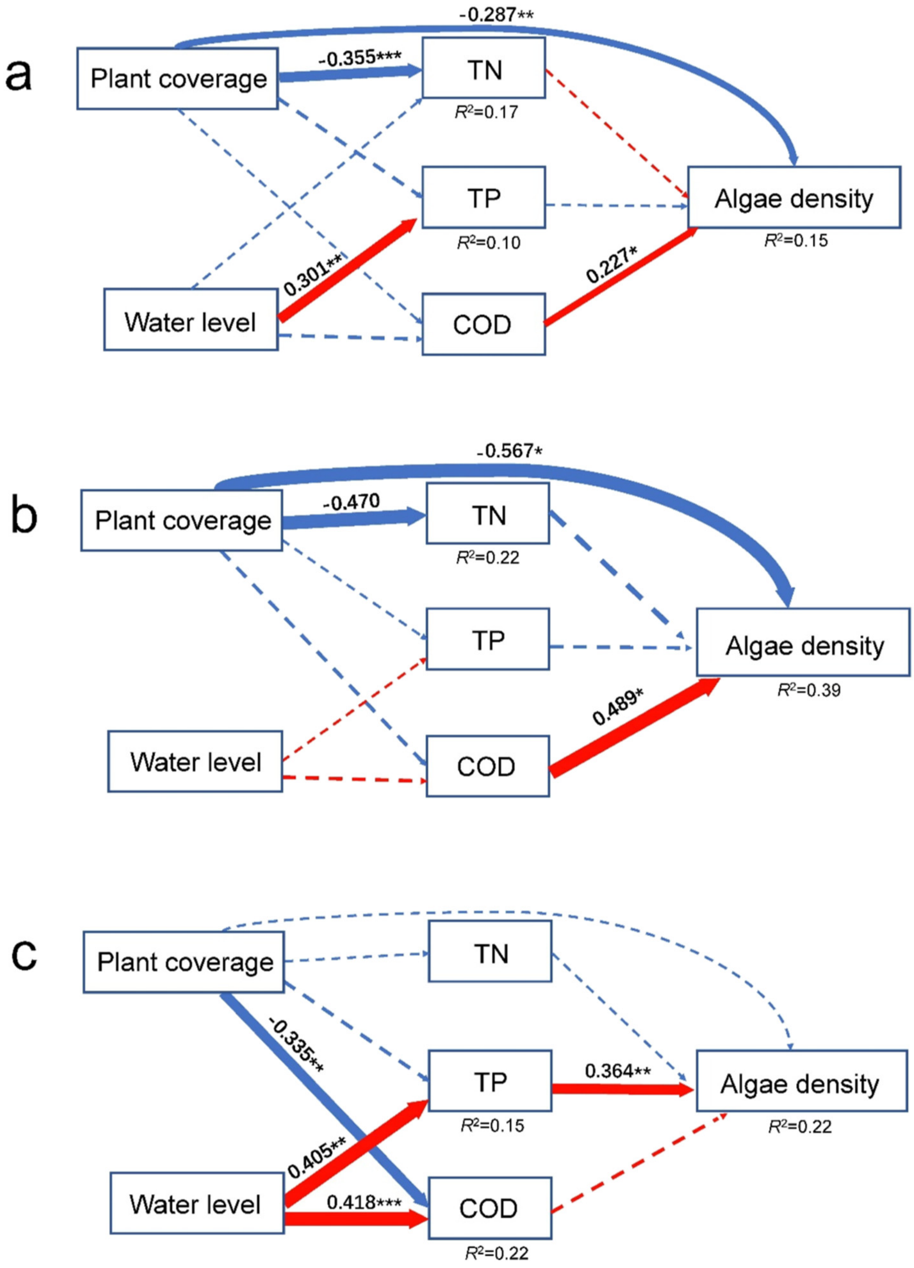

Fig. 7. Piecewise structural equation model exploring the relationships among plant coverage, WL, TN, TP, COD and algal density. (a) The relationship between the variables during the first year of restoration in the entire lake. Model fit statistics: Fisher's C = 9.262, statistical significance (P) = 0.137, degrees of freedom (d.f.) = 12, and Akaike information criterion (AIC) = 45.262. (b) The relationship between the variables in the DX area during the second year of restoration. Model fit statistics: Fisher's C = 7.788, P = 0.650, d.f. = 10, and AIC = 41.788. (c) The relationship between the variables in the MN area during the second year of restoration. Model fit statistics: Fisher's C = 16.121, P = 0.096, d.f. = 10, and AIC = 50.121. Solid and dashed arrows indicate significant ($P < 0.05$) and nonsignificant ($P > 0.05$) relationships, respectively. The red and blue lines represent negative and positive pathways, respectively. The arrow thickness is proportional to the strength of the relationship. The number above each arrow is the normalized path coefficient (significance: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.153460.

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