Diverse drivers of phytoplankton dynamics in different phyla across the annual cycle in a freshwater lake

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\textbf{ABSTRACT}

An understanding of the annual variations in the phytoplankton community in freshwater lakes, and of the drivers responsible for these variations, is essential for lake management. In this study we collected and analyzed seasonal samples of phytoplankton and assessed environmental variables in Nansi Lake from 2011 to 2015, in order to identify the seasonal dynamics of the phytoplankton community and the main drivers in each phylum. The results showed that phytoplankton diversity in Nansi Lake followed annual cycles, which were interrupted by a water diversion in 2013. The disruption of equilibrium was clearly demonstrated by the Shannon–Wiener diversity index, Pielou’s evenness index, and Simpson’s dominance index, whereas the species richness and abundance showed resilience, maintaining regular annual cycles. The dominant species were frequently \textit{Syedra acus} Kütz (Bacillariophyta), \textit{Closterium gracile} Bréb (Chlorophyta), and \textit{Scenedesmus quadricauda} Bréb (Chlorophyta) in summer and autumn. Non-metric multidimensional scaling (NMDS) analysis suggested that the phytoplankton was most widely distributed in summer, when conditions were more conducive to phytoplankton growth and reproduction. Redundancy analysis (RDA) indicated that the main drivers for the phytoplankton community varied in different taxonomic units. Specifically, the NP ratio and permanganate index (COD\textsubscript{Mn}) had significant effects on Chlorophyta, whereas pH, dissolved oxygen (DO), and transparency significantly influenced Bacillariophyta. This study highlights the importance of seasonal phytoplankton succession and the need for identification of the main drivers in each phylum in order to achieve more effective control of phytoplankton blooms in freshwater lakes.

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Introduction

In aquatic ecosystems, phytoplankton communities act as important sources of primary productivity and are controlled by both biotic and abiotic factors. However, the mass growth of macrophytoplankton in freshwater ecosystems may lead to eutrophication and algal blooms, which can impair water quality, pose a serious threat to ecosystem structure and function, and contaminate drinking water with toxins (Dodds et al. 2009). Studies of seasonal phytoplankton succession provide critical information about the ecosystem dynamics, such as changes in biomass, cell density, species composition, and spatial distribution (Yu et al. 2012; Cao et al. 2018; Nankabirwa et al. 2019; Zhang et al. 2020). Seasonal fluctuations in the phytoplankton community can be attributed to annual cycles of phytoplankton, which undergo a unidirectional and slow shift (Ignatiades 1969; Salmaso 2010). The annual cycles of phytoplankton have been described in terms of cell concentration, genotypes, abundance, and diversity (Ignatiades 1969; Burch 1988; Mühling et al. 2005). Changes in the annual cycle are mainly due to variations in those species that are most affected by yearly climate fluctuations and nutrient enrichment (Jeppesen et al. 2005; Schindler and Smol 2006; Huber et al. 2008; Winder and Hunter 2008; Salmaso 2010).

As it has been demonstrated that phytoplankton has specific sensitivity to environmental variables in the aquatic ecosystem, it is clearly important to identify the driver factors that affect plankton communities. Changes in biotic and physicochemical factors, also known as bottom-up and top-down effects, may regulate the seasonal phytoplankton succession (Jeppesen et al. 2005; Sinistro 2010; Guo et al. 2019; Li et al. 2020). However, most of these studies revealed the relationship between the phytoplankton community and environmental factors at the phylum level. Silva et al. (2014) suggested that the phytoplankton community in tropical reservoirs was mainly regulated by water temperature, light, dissolved organic carbon concentration, and pH. Davis et al. (2015) evaluated the responses of phytoplankton to increasing nitrogen and phosphorus concentrations in Sandusky Bay, where annual blooms of algae occur. Li et al. (2019) reported that water temperature, 5-day biochemical oxygen demand (BOD$_5$), nitrate (NO$_3^-$), and dissolved total organic carbon had the most significant effects on the phytoplankton community in Taihu Lake. Li et al. (2020) demonstrated the effects of zooplankton on the phytoplankton community through top-down effects, while bottom-up effects were also documented in Nansi Lake. Most of these studies demonstrated a relationship between the phytoplankton community and environmental factors at the phylum level, and any explanation involving a more detailed classification would require a greater understanding of phytoplankton dynamics. The relationship between the phytoplankton community and environmental factors has been investigated at the genus or species level, but only one or two of the dominant phyla were studied, such as Chlorophyta, Cyanophyta, and Bacillariophyta (Goldstein et al. 2012; Rigosi et al. 2014; Filstrup et al. 2014; Xu et al. 2015). Different taxonomic groups of phytoplankton may well respond differently to environmental changes. Therefore, there is an urgent need to determine which factors contribute significantly to seasonal phytoplankton succession at the genus or species level, as this could aid the improved control of phytoplankton blooms in aquatic ecosystems.

Nansi Lake, which is the largest freshwater lake in northern China, is located in Shandong Province. The basin of the lake has an area of 31,700 km$^2$, which covers Shandong, Jiangsu, Henan, and Anhui Province. Nansi Lake, with a total area of 1,266 km$^2$, consists of Nanyang, Dushan, Zhaoyang, and Weishan lakes. The South-to-North Water Diversion Project (SNWDP) is an infrastructure project designed to relieve the water shortage in northern China (Li et al. 2016). Nansi Lake is located on the east
route of SNWDP, which serves as a vital water-storing lake. Since the east route of SNWDP has been operated from November 2013, the aquatic ecosystem has been affected in Nansi Lake (Dai et al. 2020; Yu et al. 2020). The water diversion since 2013 provides an opportunity to determine the differences in the phytoplankton community before and after water diversion in Nansi Lake. In view of the huge importance of SNWDP to China’s water safety and the key links between phytoplankton and water quality, it is critically important to identify the responses of the phytoplankton community to water diversion in the aquatic ecosystem in Nansi Lake.

Although variations in some phytoplankton communities have been reported, there have been no detailed studies of the driving factors in relation to phytoplankton for each phylum at the genus or species level in Nansi Lake. In the present study, the phytoplankton community and environmental factors were sampled seasonally, with the aim of clarifying the relationship between environmental factors and the phytoplankton community during water diversion. It was hoped that this would demonstrate (1) the seasonal variations in the phytoplankton community before and after water diversion, and (2) the main factors that influence the variation in each phylum of the phytoplankton community.

**Materials and methods**

**Ethics statement**

No specific permissions were required to collect the samples in our study. We confirm that the field studies did not involve endangered or protected species.

**Study area and sampling methods**

Nansi Lake (116°34’E–117°21’E, 34°27’N–35°20’N) has a total volume of 6.37 × 109 m³, an annual average temperature of 13.7 °C, and annual average rainfall of 870 mm with a warm-temperate monsoon climate. It has 53 in-flowing rivers and three outflowing rivers. A total of 12 sampling sites were set up in Nansi Lake, and samples were collected seasonally from spring 2011 to summer 2015. In this study, the seasonal division was followed by annual temperature variation in Shandong Province, which defined spring (March to May), summer (June to August), autumn (September to November), and winter (December to February in next year) in Nansi Lake.

Water samples were collected along with phytoplankton samples in situ at a depth of 0.5 m using a 1 L Ruttner water sampler. Water samples were stored under low-temperature conditions prior to laboratory analysis, with three replicates for each sample. Water temperature (WT), dissolved oxygen (DO), pH, water transparency, total nitrogen (TN), total phosphorus (TP), permanganate index (CODMn), and ammonia nitrogen (NH₄⁺–N) were measured by means of portable meters and analyzers, as described in detail by Li et al. (2020). Some water quality data were obtained from other studies of Nansi Lake (Wei et al. 2015; Xu et al. 2019), as the missing sampling of water in 2011 and 2014.

Phytoplankton samples were collected at each site using plankton nets with two different mesh sizes, and there were three replicates for each site. The qualitative samples and quantitative samples were collected and treated respectively (Li et al. 2020). Macroplankton samples were collected using plankton nets with a mesh size of 112 μm, and microplankton samples were collected using plankton nets with a mesh size of 64 μm. Phytoplankton samples and their constituents were identified under a light microscope (Arhonditsis et al. 2004; Lansac-Töha et al. 2009) and by using different approaches (Li
et al. 2020). Plankton density was calculated as described in the *Handbook of Fishery Natural Resource Investigation in The Inside Water Area* (Zhang and He 1991). The phytoplankton community in 2015 was identified down to genus level, whereas prior to that year the samples were identified down to species level. Therefore, all analyses at species level excluded the phytoplankton data for 2015.

**Diversity indices and statistical analysis**

Phytoplankton community composition was assessed by a range of methods, including species abundance (N) (ind./L), species richness (S), the Shannon–Wiener diversity index (Shannon and Weaver 1949) ($H'$), Pielou’s evenness index (Pielou 1966) (E), Simpson’s dominance index (Simpson 1949) (C), and Margalef’s richness index (Margalef 1958) ($D_{MG}$), calculated by the following equations:

$$H' = - \sum_{i=1}^{S} P_i \ln P_i$$

$$E = \frac{H'}{\ln S}$$

$$C = \sum_{i=1}^{S} \frac{N_i(N_i-1)}{N(N-1)}$$

$$D_{MG} = \frac{S-1}{\ln N}$$

where $P_i$ is the abundance proportion of species $i$, $S$ is species richness, and $N$ is the species abundance.

Phytoplankton species with a dominance factor of more than 0.02 were considered to be dominant species, and the dominance factor was measured by dominant degree (Y) in order to determine the dominant species in each phylum by using the following equation:

$$Y = \frac{N_i}{N} \cdot f$$

where $N$ is the species abundance and $f$ is the frequency of occurrence at sampling sites (Xu 2006).

To assess the similarity of phytoplankton species composition between seasons, the Jaccard similarity index ($J$) was calculated by using the following equations:

$$J = \frac{c}{a + b - c}$$

where $a$ is the species number for sample A, $b$ is the species number for sample B, and $c$ is the mutual species number for samples A and B. Jaccard similarity was categorized as extremely dissimilar ($0 < J < 0.25$), dissimilar ($0.25 \leq J < 0.50$), similar ($0.50 \leq J < 0.75$), or extremely similar ($0.75 \leq J < 1.00$). The similarities between phytoplankton communities in Nansi Lake across different seasons from 2011 to 2014 were also plotted using the non-metric multidimensional scaling (NMDS) method with PAST software. For NMDS analysis, the matrix data constructed using the individual numbers of selected genera were normalized by fourth-root conversion and then reassembled using Euclidean distance (Taguchi and Oono 2005).

The detrended correspondence analysis (DCA) was performed using Canoco 5 software, and revealed that the gradient length of the response data was less than 3.0 (the
longest value was 0.75). Therefore, redundancy analysis (RDA) was used to test the relationship between environmental variables and the phytoplankton community in Nansi Lake. Simple effects represent the variability explained by single environmental factors without taking other environmental variables into account. In contrast, conditional effects are obtained by stepwise selection and indicate the variability explained by the target environmental factor after removal of the confounding effects of other environmental variables (covariables) (Smilauer and Leps 2014). Simple effects and conditional effects were both tested by Monte Carlo unrestricted permutation tests. For detailed analysis, phytoplankton data were ranked at the genus level and selected. Only the taxa that were present with a frequency of over 80% in each seasonal sampling from 2011 to 2015 were included in the data analyses. All data except pH values were log ($x + 1$) transformed before analysis (Flores and Barone 1998; Muylaert et al. 2000).

**Results**

**Phytoplankton community composition and diversity**

Across the sampling sites, a total of 153 algal species belonging to 78 genera and 8 phyla were identified (Supplemental Appendix A). From 2011 to 2014, phytoplankton species abundance, species richness, the Shannon–Wiener diversity index, Pielou’s evenness index, and Margalef’s richness index varied across the seasons (Figures 1 and 2). The abundance of phytoplankton and species richness in Nansi Lake increased from spring onward, reaching a peak in summer, followed by a decrease in autumn and winter and a slight rise in spring of the following year. The Shannon–Wiener diversity index and Pielou’s evenness index showed different degrees of increase from spring to summer, and decreased in autumn in the same year. Simpson’s dominance index decreased from spring to summer and increased in autumn, whereas the changes in winter and spring were different from 2011 to 2014. The changes in Margalef’s richness index were in direct...
contrast to the variations in Simpson’s dominance index. For the Shannon–Wiener diversity index, Pielou’s evenness index, Simpson’s dominance index, and Margalef’s richness index, the changes in autumn and winter of 2011 and 2012 differed from those during autumn and winter of 2013 and 2014. This finding might be linked to changes in water quality affecting seasonal changes in the phytoplankton community. The Shannon–Wiener diversity index, Pielou’s evenness index, and Simpson’s dominance index had decreased overall since autumn 2013, whereas there were no notable differences in abundance and species richness before and after the water diversion. From autumn 2013 onward, the Shannon–Wiener diversity index and Pielou’s evenness index fluctuated more irregularly than previously.

The dominant degree ($Y$) of phytoplankton was in the range 0.020–0.059 in summer and autumn in Nansi Lake, whereas $Y$ in spring and winter was less than 0.02 and was not included in the data (Table 1). The dominant species in Nansi Lake did not exhibit a high relative dominance during the study period. The majority of the dominant species belonged to the Bacillariophyta and Chlorophyta, including *Synedra acus* Kütz, *Closterium gracile* Bréb., and *Scenedesmus quadricauda* (Turp.) Bréb.

In order to explore more detail in the seasonal variation in the phytoplankton community in Nansi Lake, Jaccard similarity and NMDS analysis for phytoplankton community were performed at the species level (Figure 3; Supplemental Appendix B). Jaccard similarity between the next seasons was in the range 0.64–0.85, representing a similar or extremely similar level, which indicates that the phytoplankton community in Nansi Lake had undergone little change between successive seasons. On the other hand, NMDS
Table 1. Dominant species and their dominance degree in Nansi Lake from summer 2011 to autumn 2014.

| Phylum         | Dominant species                  | Summer 2011 | Autumn 2011 | Summer 2012 | Autumn 2013 | Summer 2013 | Autumn 2013 | Summer 2014 | Autumn 2014 |
|----------------|-----------------------------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| Bacillariophyta| *Nitzschia lineris* W. Smith      | 0.020       |             |             | 0.024       | 0.026       |             |             |
| Bacillariophyta| *Synedra acus* Kütz.              | 0.029       |             | 0.024       | 0.037       | 0.042       |             |             |
| Bacillariophyta| *Cyclotella bodanica* Eul.        |             |             |             |             |             |             |             |
| Chlorophyta    | *Schroederia setigera* Lemm.      |             |             | 0.038       | 0.038       | 0.020       |             |             |
| Chlorophyta    | *Osteria gracile* Bréb.           | 0.036       | 0.034       |             |             |             |             | 0.039       | 0.026       |
| Chlorophyta    | *Dysmorphococcus variabilis* Tak. |             |             |             |             |             |             | 0.043       |             |
| Chlorophyta    | *Gonium fumosum* Pasch.           |             |             |             |             |             |             | 0.054       |             |
| Chlorophyta    | *Scenedesmus quadricauda* (Turp.) Bréb. | 0.032 | 0.030       | 0.059       | 0.053       | 0.026       | 0.022       |             | 0.025       |
| Chlorophyta    | *Scenedesmus dimorphus* (Turp.) Kütz. | 0.048 | 0.045       |             |             |             |             |             | 0.022       |
analysis showed that the phytoplankton community within each season had relatively independent regions and overlapping positions in two-dimensional space. The most widely dispersed distribution region was that of summer samples, and the smallest distribution region was that of winter samples. The distribution of samples was similar in autumn and spring, indicating that the composition of the phytoplankton community was relatively similar in spring and autumn. Furthermore, it can be clearly seen from the convex hull that the composition of the phytoplankton community in Nansi Lake was richer and more complex in summer than in the other seasons. There was overlap of components of the phytoplankton community across seasons, and the transitional seasons for the community were in spring and autumn.

**Physicochemical variables and their relationship with the phytoplankton community**

The long-term fluctuations in physicochemical variables from spring 2011 to summer 2015 in Nansi Lake are shown in Figure 4. Transparency fluctuated within the range 0.39–0.58 m except for the lowest value (0.20 m) in summer 2015, which might have been caused by rainfall and water disturbance. Ammonia nitrogen levels fluctuated within the range 0.14–0.72 mg/L, and pH values were in the range 7.52–8.36. The NH$_4^+$–N concentration decreased by comparison with the same season before water diversion. The pH fluctuated to a greater extent and the water in Nansi Lake became weakly alkaline after SNWDP performed in 2013. COD$_{Mn}$ showed an overall increase from 2011 to 2015, and
was within the range 4.44–6.11 mg/L. WT had changed with the seasons, consistent with the rapid response of lake water temperature to air temperature changes. The average DO concentration was 7.04 mg/L. The CODMn and WT had changed with the seasons and were not obviously affected by the water diversion, whereas the changes in DO showed no clear pattern. The TN range and TP range were 0.71–2.81 mg/L and 0.04–0.16 mg/L, respectively, and showed a different pattern of change due to the water quality improvement before the water diversion was implemented. Significant differences in WT and TP were found between seasons (one-way ANOVA, \( p < 0.05 \); Supplemental Appendix C).

The relationship between the phytoplankton community at the genus level and the physical and chemical variables showed that the controlling factors varied in different operational taxonomic units (OTUs) (Supplemental Appendix D). The first two RDA axes accounted for 80.17% of the variation, with eigenvalues of 0.73 and 0.07, respectively. The results for the conditional effects showed that NP ratio, CODMn, and TP had a significant influence on the phytoplankton community \( (p < 0.05; \text{ Table 2}) \). Phytoplankton density was positively correlated with TP and negatively correlated with DO. Most phytoplankton, except for the genus Cocconeis, showed negative associations with NP ratio and in general a negative correlation with transparency, pH, TN, NH4\(^+\)-N, and CODMn.

In order to examine more detail in the relationship between the phytoplankton community and environmental factors, RDA analysis was performed for different genera of the phytoplankton community and environmental factors (Figure 5). In the RDA analysis of Bacillariophyta and environmental factors in each genus (Figure 5a), the first two axes accounted for 75.05% of the variation (eigenvalues of 0.59 and 0.16, respectively). The results for the conditional effects indicated that pH, DO, and transparency all had a significant influence on changes in the phytoplankton community of Bacillariophyta.
(p < 0.05; Table 2), accounting for 32.3%, 15.7%, and 13.4%, of the variation, respectively, which suggests that these were the main driving factors in the community of Bacillariophyta. For the RDA analysis of Chlorophyta (Figure 5b), the first two axes accounted for 78.94% of the variation (eigenvalues of 0.70 and 0.09, respectively). The NP
ratio and COD\textsubscript{Mn} were significantly associated with the Chlorophyta community at the genus level ($p < 0.05$; Table 2), accounting for 40.7% and 17.5%, respectively, of the variation as the key influencing factors. For the Cyanophyta community (Figure 5c), the first two axes accounted for 93.0% of the variation (eigenvalues of 0.86 and 0.07, respectively) in the RDA analysis, while the NP ratio, COD\textsubscript{Mn}, and TN were the main factors affecting the Cyanophyta community at the genus level ($p < 0.05$; Table 2). RDA analysis of the Euglenophyta and Xanthophyta indicated that pH was significantly correlated with these communities ($p < 0.05$; Table 2), and the first two axes accounted for 88.64% of the variation (eigenvalues of 0.74 and 0.15, respectively; Figure 5d).

**Discussion**

**Seasonal responses of the phytoplankton community: community structure variations**

The trends in diversity indices showed seasonal changes in Nansi Lake, indicating that the phytoplankton community showed changes in diversity over time, in the form of annual cycles. These annual changes exhibited a seasonal oscillation, whereby diversity increased during the warm period and decreased during the cold period (Longhurst 1995; Richardson et al. 2010; Nunes et al. 2018; Mestre et al. 2020). The annual cycles were manifested in relation to phytoplankton abundance, species number, and Margalef’s richness index from 2011 to 2014, whereas yearly equilibrium was only observed during the first two years of the study in relation to the Shannon–Wiener diversity index, Pielou’s evenness index, and Simpson’s dominance index in Nansi Lake. The differences between cycles might be affected by the water diversion in 2013, which caused significant changes in the environmental variables (Tonkin et al. 2017). The annual cycles of the Shannon–Wiener diversity index, Pielou’s evenness index, and Simpson’s dominance index would be particularly sensitive to the effects of changing external factors after 2013. Long-term changes related to environmental factors have been shown to influence shifts in the taxonomic community of phytoplankton (Richardson and Schoeman 2004; Edwards and Richardson 2004; Leterme et al. 2005), which were first demonstrated in relation to the Shannon–Wiener diversity index, Pielou’s evenness index, and Simpson’s dominance index in Nansi Lake. Responses of phytoplankton diversity to water diversion in aquatic ecosystems have been reported in previous studies, the majority of which found an increase in phytoplankton diversity (Fornarelli et al. 2013; Dai et al. 2020). In contrast, our study revealed that the diversity in 2014 was lower than that before the water diversion. This might be a result of (1) improved water quality from the source of water diversion and (2) the effect of water quality management in Nansi Lake on its phytoplankton diversity. By taking into account the annual succession of phytoplankton, predictions and regulations relating to phytoplankton, such as water quality, could be better facilitated in aquatic ecosystems (Bunse and Pinhassi 2017).

Although the diversity of phytoplankton shaped some cycles, the equilibrium of these cycles showed differences in phytoplankton composition depending on the intensity and frequency of biotic and abiotic processes (Chalar 2009). The dominant species are more effective in obtaining resources and deterring competitors or predators than other species (Covich 1976; Stachowicz 2001). Dominant species as defined in our study only appeared in summer and autumn, as the dominance degree was less than 0.02 in spring and winter. During winter and spring, species were generally selected by their tolerance of environmental changes (e.g. low temperature, low light levels), whereas in summer and autumn the environment was much more conducive to the development of phytoplankton
communities, and to the stabilization of the associations of those communities (Padisák et al. 2003). Therefore, phytoplankton communities might more easily establish dominant species in summer and autumn.

The results of Jaccard similarity and NMDS analysis indicated that the phytoplankton community composition did include similar and relatively independent elements. Seasonal changes in external hydraulic and nutrient stress, temperature, and sunlight have been shown to influence the seasonal dynamics in phytoplankton assemblages (Reynolds 1980; Chalar 2009; Arthington and Balcombe 2011). Depending on these environmental fluctuations and disturbances, the equilibrium dynamic might be affected and species diversity might be enhanced (Connell 1978; Tilman et al. 2006). According to the plankton ecology group (PEG) model, phytoplankton has minimum biomass of species in winter, and its diversity varies in populations in summer after the spring blooms (Sommer et al. 2012). The summer composition of phytoplankton was more evident in the distribution in NMDS in a more favourable habitat conducive to growth and reproduction.

Responses of the phytoplankton community to physicochemical variables: controlling factors in different phyla

Long-term phytoplankton succession is a well-studied area of aquatic ecology (Burch 1988; Cabrini et al. 2012; Wei et al. 2015; Nunes et al. 2018; Zhang et al. 2020). This annual succession of phytoplankton is regulated by strong annual variation in biotic and abiotic characteristics in the aquatic ecosystem. Furthermore, the annual changes in concentration of nutrients are important contributing factors with regard to yearly phytoplankton variability (Baines et al. 2000). During the construction of the water diversion project, the water quality in Nansi Lake has been significantly improved (Meng et al. 2017). Moreover, the implementation of water transfer in 2013 further disrupted the yearly equilibrium pattern of water, especially variation in nutrients (Figure 4). We set RDA to demonstrate the relationship between the phytoplankton community and environmental variables during the construction and implementation of the water diversion project. The correlations between environmental variables and the phytoplankton community varied in different operational taxonomic units (OTUs) of phytoplankton. TP, NP ratio, and CODMn were significantly related to the variability of phytoplankton community composition (Supplemental Appendix D; Table 2). In different OTUs at the genus level, physicochemical factors were found to have specific effects on phytoplankton community composition.

The response of phytoplankton to environmental factors is dependent on the taxonomic composition of the community (Salmaso 2010; Rigosi et al. 2014), and our study identified the main drivers of composition change in each phylum of phytoplankton in Nansi Lake. NP ratio and CODMn were negatively related to the density of Chlorophyta and Cyanophyta at the genus level, and TN also showed a significant negative effect on Cyanophyta in Nansi Lake from 2011 to 2015 (Figure 5; Table 2). The nutrient concentration changes in TN and TP were the primary drivers for variation in phytoplankton community composition (Jiang et al. 2014; Wang et al. 2015; Zhang et al. 2020). Human activities, such as fertilization and aquaculture, have increased the nutrient concentration in freshwater lakes and near-shore regions through surface water or groundwater (Conley 1999; Sylvan et al. 2006; Paerl 2009). Low NP ratios contribute to the dominance of cyanobacteria, of which non-nitrogen-fixing species, such as Microcystis, could be preferentially favoured by low NP ratios (Hassell and Tilman 1984; Zhang et al. 2018a). The increased nutrient levels caused an increase in the number of phytoplankton particles,
which in turn further reduced the available underwater light (Zhang et al. 2018b). Previous studies have demonstrated that Chlorophyta were mainly affected by temperature and available underwater light (Zhang et al. 2018a), while Chlorophyta was also significantly affected by COD$_{Mn}$ in Nansi Lake. The relationship between COD$_{Mn}$ and phytoplankton (Chlorophyta and Cyanophyta; Figure 5; Table 2) was primarily the result of physiological activity and decomposition of phytoplankton (Yin et al. 2011). Variation in pH was negatively related to Bacillariophyta, Euglenophyta, and Xanthophyta (Figure 5; Table 2). Changes in pH mainly affect the bioavailability of nutrients and trace metals, and have a direct and serious impact on the physiological activity of phytoplankton in extreme conditions (Chakraborty 2010; Chakraborty et al. 2011). Experimental studies have shown that phytoplankton is resistant to environmental acidification and does not exhibit increased or decreased growth rates within ecologically relevant pH ranges (Iglesias-Rodriguez et al. 2008; Berge et al. 2010). This is in direct contrast to our findings for Bacillariophyta, Euglenophyta, and Xanthophyta. Identification of the main drivers in different OTUs would theoretically aid the regulation of algal blooms and improve the implementation of SNWDP.

**Conclusion**

This study has highlighted the seasonal dynamics of the phytoplankton community in Nansi Lake, in which we found annual cycles of changes in diversity. Furthermore, the annual cycles of phytoplankton diversity were disturbed by water diversion in 2013, as was clearly indicated by the Shannon–Wiener diversity index, Pielou’s evenness index, and Simpson’s dominance index. Our results showed that in summer and autumn in Nansi Lake the dominant species frequently consisted of *Synedra acus* Kütz (Bacillariophyta), *Closterium gracile* Bréb (Chlorophyta), and *Scenedesmus quadricauda* Bréb (Chlorophyta). Assembly of dominant species might occur more readily in summer and autumn, and this theory was supported by the lower degree of dominance in winter and spring. Furthermore, the summer composition of phytoplankton showed a wider distribution according to the NMDS results, which indicated more favourable conditions for phytoplankton growth and reproduction during summer. The RDA demonstrated that the main drivers for phytoplankton changes varied in different OTUs, in which the key impact factors were TP, NP ratio, and COD$_{Mn}$ with regard to the total phytoplankton community. NP ratio and COD$_{Mn}$ showed significant negative correlations with Chlorophyta and Cyanophyta, and TN also had a significant negative effect on Cyanophyta. DO, pH, and transparency mainly affected Bacillariophyta, and pH showed a negative correlation with Xanthophyta and Euglenophyta. Identification of the driving factors for different phytoplankton taxonomic groups will help to clarify the response mechanism of each phylum, and has implications for the management of algal blooms.

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Data availability statement

The data that support the findings of this study are openly available in figshare at http://doi.org/10.6084/m9.figshare.12981458.

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