Succession of phytoplankton in a shallow lake under the alternating influence of runoff and reverse water transfer

Qing Li, Guoqiang Wang, Zhongxin Tan and Hongqi Wang

ABSTRACT

Both runoff and water diversion can interfere with the physical and chemical environment of a lake and affect aquatic organisms. In this study, previously obtained data were used to analyze the phytoplankton community, water quality, water level, and temperature in Dongping Lake (DPH) before, during, and after the water diversion caused by the South-to-North Water Transfer Project. The results showed that the total density and diversity index of phytoplankton decreased in the water transfer period, and was related to low temperature. Temperature also affected the recovery of phytoplankton community structure when the water transfer period ended. In a water transfer cycle, changes in dominant genera were more drastic than that of a whole phytoplankton community, and dominant genera were sensitive to total phosphorus (TP) and total nitrogen (TN) changes. Water transfer alleviated the deterioration of water quality in DPH, but water transfer process increased the risk of water pollution. Runoff from Dawen River carried TN, TP, and chemical oxygen demand (COD) into DPH in the rainy season, which indirectly affected phytoplankton, while it also carried phytoplankton directly into DPH. Overall, these findings provide a clear understanding of the impact of water transfer projects on ecology in shallow lakes.

Key words | Dongping Lake, phytoplankton community, reverse water transfer, runoff, shallow lake, the South-to-North Water Transfer Project

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HIGHLIGHTS

- Dominant genera change greater than genera in a whole phytoplankton community.
- Reverse water transfer and runoff affect phytoplankton community alternately.
- There is a risk of water quality deterioration during the water transfer process.
- Runoff transfers water, pollutants and phytoplankton to the lakes.

INTRODUCTION

The influence of hydrology on the water ecosystem in shallow lakes is obvious. Both natural runoff and water diversion projects affect lakes by changing hydrology and water quality. In particular, the water transfer projects change the original hydrologic conditions in lakes and disrupt natural, stable patterns. This affects the habitats of aquatic organisms and controls their community structure and distribution. When hydrology changes, a series of water physical and chemical properties such as water level, flow velocity, and water quality are changed (Tuttle *et al.* 2008; Liu *et al.* 2017). When hydrology is the driving factor, the specific responses of the aquatic communities in lakes are diverse and complex.

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Most natural runoff is caused by rainfall. In areas significantly affected by the monsoon climate, natural runoff is concentrated in the rainy season. During this period, runoff is characterized by a big flow amount and high flow velocity that results in flooding or seasonal pulses (Rodger *et al.* 2016; Galir Balkić *et al.* 2018; Han *et al.* 2018). However, rainfall-runoff during dry seasons is characterized by low flow velocity and a small water amount. Natural runoff showed the same pattern in every hydrological year in areas controlled by a temperate continental climate. For a long time, runoff has increased the water amount and brought pollution (Wang *et al.* 2019a, 2019b), which constantly affects the water ecosystem in lakes (Silva *et al.* 2019; Sun *et al.* 2019). Runoff affects the phytoplankton succession by changing temperature and nutrients (Cao *et al.* 2018). Increased runoff in the rainy season has also introduced pollutants, which favor the massive development of Cyanobacteria in lakes (Rao *et al.* 2018; Silva *et al.* 2019; Sun *et al.* 2019) and also reduce the abundance of diatoms (Da Silva *et al.* 2019) or phytoplankton biomass (Cobbaert *et al.* 2014). Flood pulses in rainy seasons have also been shown to influence community structure by affecting food and nutrient levels (Galir Balkić *et al.* 2018). In addition to the recognition that rainfall runoff increases nutrients in lakes, runoff also has the potential to dilute pollutants (Cobbaert *et al.* 2014; Ho & Michalak 2019). These factors complicate the effects of runoff in lakes.

Increasingly, water transfer projects are being designed to solve the problem of uneven distribution of water resources. One of the main functions of these projects is to introduce exogenous water to a receiving lake in dry seasons. In areas in which natural precipitation is extremely scarce, water diversion has helped alleviate the decline of water levels and deterioration of water quality, then affecting algal blooms in lakes (Amano *et al.* 2010; Li *et al.* 2013; Huang *et al.* 2015; Yao *et al.* 2018). In the dry season, water diversion increases the water amount, raises the water level, and changes the habitat environment, leading to a chain reaction in the community structure of aquatic organisms (Guo *et al.* 2019). Under the influence of water transfer projects, the dominant species of the phytoplankton community has changed because of the changing water quality (Amano *et al.* 2010) and hydrodynamic conditions in lakes (Li *et al.* 2013). What is more, both exogenous water introduced by water transfer projects and water pollutants in water conveyance channels affect the water quality in receiving lakes (Zhuang 2016; Liu *et al.* 2017; Zhuang *et al.* 2019). Unlike natural runoff, man-made water transfer projects have changed the natural pattern and broken the dynamic and stable influence of natural runoff on lakes. Although the effects of water diversion are complex, the reverse water diversion exacerbates this complexity. Accordingly, it is necessary to study the ecology in shallow lakes under the influence of reverse water transfer projects; however, few studies have investigated reverse water transfer.

As the obviously seasonal succession, phytoplankton community change rapidly in a short period with changes in habitat environments. Accordingly, phytoplankton community changes are commonly used to reflect the influence of external disturbances (Sharov 2008; Snit'ko & Snit'ko 2014; Toporowska *et al.* 2018; Weng *et al.* 2020). Community structure, diversity, total density, and biomass are all important indicators of habitat environment changes (Deng *et al.* 2016; Özkan *et al.* 2016; Anneville *et al.* 2019). In the shallow lakes, the water depth is small and the water stratification not obvious, characteristics at different depths tend to be consistent, and the exchange of sediments and water is more frequent than in deep lakes (Scheffer 1998; Ongun Sevindik *et al.* 2017). Phytoplankton in shallow lakes is more responsive to outside influences, such as changes in temperature, hydrological conditions, and water quality. The effect of water quality on phytoplankton in lakes is obvious, total nitrogen (TN), total phosphorus (TP), and ammonia nitrogen (NH_4-N) are closely related to the phytoplankton in most lakes (Borics *et al.* 2013; Zhu *et al.* 2018; Tang *et al.* 2019). Temperature also affects the phytoplankton succession, the increase in temperature contributes to the increase in total phytoplankton biomass (Markensten *et al.* 2010). Also, Rao *et al.* (2018) thought that the effect of temperature on phytoplankton was highly species-specific and temperature also modulated the effects of nutrients on phytoplankton. In addition, water level fluctuation also has an obvious influence on phytoplankton succession (Kivrak 2006; Tian *et al.* 2015; Qian *et al.* 2016; Rao *et al.* 2018). However, under the influence of runoff and water transfer, the effect of temperature, hydrological conditions and water quality on phytoplankton should be rethought.

Rainfall in northern China is mostly concentrated in summer and autumn, while the region is cold and dry during spring and winter. Dongping Lake (DPH) is a typical shallow lake located in northern China that mainly receives river runoff from the Dawen River (DWR) in the rainy season. In the dry season before the South-to-North Water Transfer Project (SNWTP), the water level in DPH frequently dropped because of reduced inflow, which seriously threatens the lake ecosystem (He *et al.* 2014). Implementation of the SNWTP alleviated the water loss and eutrophication in DPH (Hu *et al.* 2019). However, the SNWTP also introduced the possibility of adverse impacts on the environment (Liu *et al.* 2020), and even caused biological invasion (Qin *et al.* 2019). To date, the SNWTP has mainly transferred water into DPH in the dry season. Therefore, after implementation of the SNWTP, DPH mainly received runoff in the rainy season and transferred water in the dry season. The alternations of runoff and transferred water have complicated the effects on the ecology in DPH. Accordingly, water transfer projects participate in the effect of runoff on the aquatic organisms in lakes. What is more, it is important to understand how runoff and water transfer under the continuous influence of the SNWTP affect the ecology in DPH within a water transfer cycle, but this has not yet been investigated. Therefore, we (1) investigated and analyzed the phytoplankton and water quality in DPH and the DWR before, during, and after the water transfer period and (2) analyzed the main factors influencing phytoplankton and the impacts of runoff inflow and diversion inflow on the phytoplankton community in DPH. Additionally, (3) the phytoplankton community structural changes and dominant taxa replacement of phytoplankton under the alternating influence of runoff and water diversion were discussed.

MATERIALS AND METHODS

Study area

DPH, located in Shandong Province, China, is a major freshwater lake with diverse aquatic life. This lake has many functions including flood control, storage, irrigation, water supply, and preservation of biodiversity. DPH is not only an important flood detention area in the lower reaches of the Yellow River, but is also the last regulating and storing lake of the eastern route of the SNWTP. Accordingly, the protection of the ecosystem in the DPH is very important.

The surface area of DPH is about 125 km^2 and the lake basin is narrow in the north and wide in the south (Figure 1). DPH is a shallow lake with an annual average water depth of about 2 m. The eastern part of the lake is mainly hilly, while there are dams to the south and west. Few rivers flow into DPH. The DWR flows from east to west into the lake, and then flows into the Yellow River. DPH mainly depends on surface runoff and lake surface precipitation supply. The region in which DPH is located is characterized by a cold and dry winter and hot and rainy summer, with more than 70% of the annual precipitation falling during the flood season. Therefore, the main inflow of the lake is from the DWR in the rainy season. The eastern route of the SNWTP was completed in 2013. Liuchang River serves as the route from south to north to bring water from the Nansihu Lake (NSH) to DPH via Denglou station (DL). The water transfer period of the SNWTP is generally concentrated in winter and spring, when there is less rainfall and low water depth in DPH. The water transfer period in DPH in 2018 was from December 2018 to June 2019, during which the inflow was mainly composed of the inflow of the DWR and the transferred water from the upper lakes of NSH (UNSH) via the Liuchang River. Therefore, the inflow during the water transfer period and non-water transfer period is different.

Data description and sample collection

Water diversion in DPH always occurs in the dry season, so one year is considered as a water transfer cycle, including before the water transfer period (S1) (August 2018), during the water transfer period (S2) (March 2019), and after the water transfer period (S3) (July 2019). Water quality samples and phytoplankton samples were collected at four sites in DPH and one site in the DWR. Water quality samples were collected at one site in the UNSH.

Quantitative phytoplankton samples were collected using a 2.5 L water sampler from a depth of 0.5 m, after which, samples were fixed with Lugol's solution and 40% formalin. Qualitative phytoplankton samples were collected

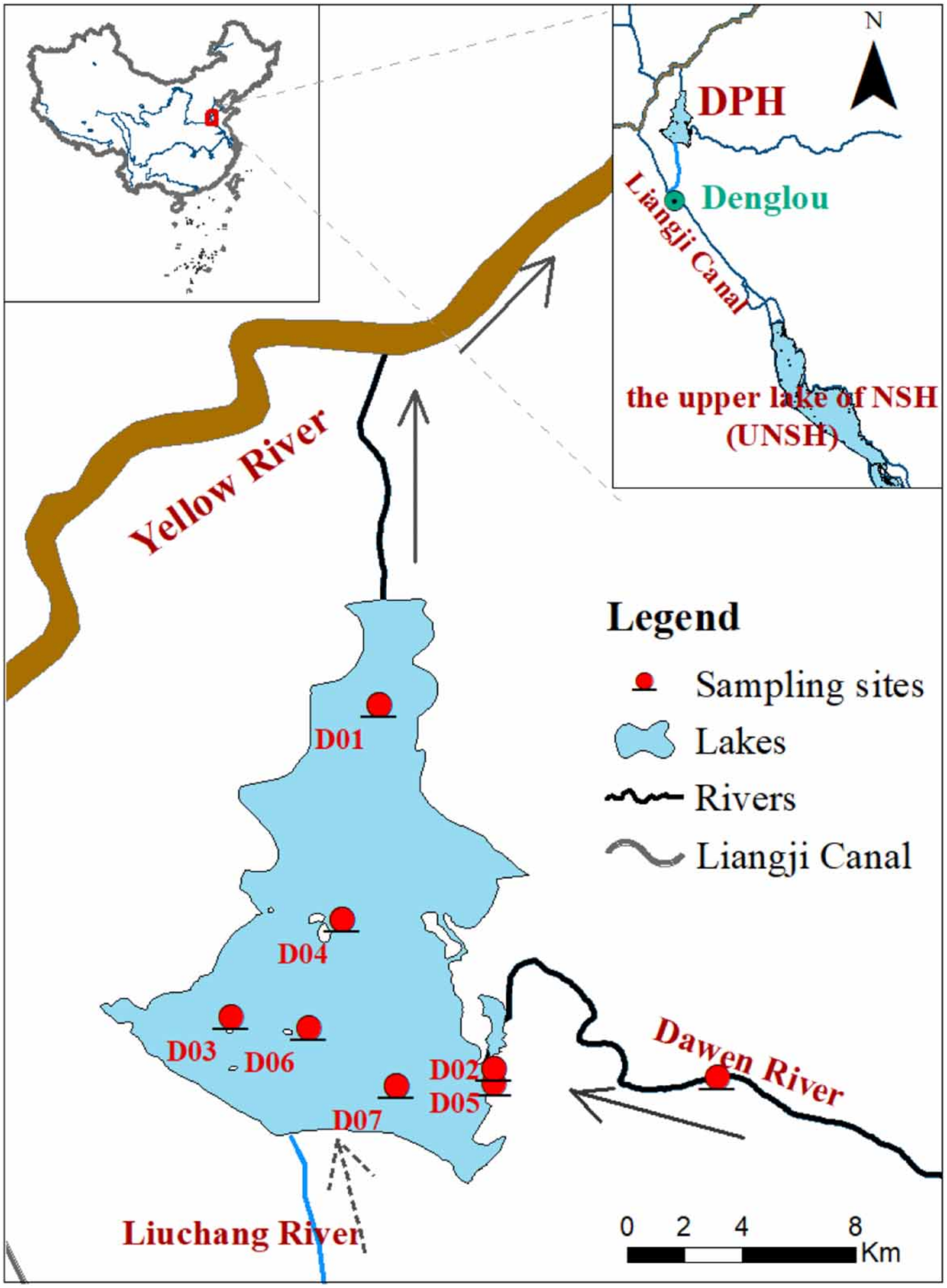

Figure 1 | The location of Dongping Lake (DPH). The arrows indicate the directions of the water flow, and the dotted arrow indicates the direction of the water transfer.

using a 25# floating net and then were kept at 4 °C. All samples were collected twice at each sampling site. After the samples were sent to the laboratory, the phytoplankton was identified and quantified. Upon arrival in the laboratory, total nitrogen (TN), total phosphorus (TP), ammonia nitrogen (NH_4-N), and chemical oxygen demand (COD) were measured. Data describing the transferred water and water level were obtained from the local government, while rainfall and temperature data were downloaded from the China Meteorological Data Service Center.

Materials and methods

Calculation of phytoplankton community diversity

We calculated the diversity to evaluate changes in phytoplankton communities during different periods. Here, we used the Shannon–Wiener index (Equation (1)) (Shannon 1948) to evaluate the diversity of the phytoplankton community:

$$H = -\sum_{i=1}^{N} (P_i \log_2 P_i) \tag{1}$$

where H is the Shannon–Wiener index; P_i is the density ratio of the i-th genus; and N is the total number of the genera.

We used the Jaccard similarity coefficient (Equation (2)) (Jaccard 1900) to obtain the community similarity:

$$C = \frac{j}{a + b - j} \tag{2}$$

where C is the Jaccard similarity coefficient of the community; j is the number of the common genera in different communities; a and b are the number of genera in particular communities.

Analysis of key driving factors

Redundancy analysis (RDA) was selected to evaluate the relationship between environmental factors and phytoplankton communities. RDA is an ordination method that combines regression analysis with principle component analysis, which is widely used to identify influencing factors. Detrended correspondence analysis (DCA) is required before RDA can be applied. If the first axis value of the gradient length is less than 3.0, the RDA method is appropriate. Here, environmental factors include TN, TP, NH_4-N, COD, and temperature in water. The biomes includes phytoplankton phylum. The calculation and visualization of RDA results are based on the R package 'vegan'.

Niche breadth models were used to analyze the change in phytoplankton community with the environment. Shannon–Wiener index (Equation (3)) is often used to calculate niche breadth (Heino & Tolonen 2018; Li *et al.* 2020), and its significance is different to Equation (1):

$$H_i' = -\sum_{j=1}^{R} (P_{ij} \log_2 P_{ij}) \tag{3}$$

where H_i' is the niche breadth index of the i-th genus; R is the total number of sampling sites; P_{ij} is the ratio of the numbers of the i-th species at the j-th sampling site to the total number of the i-th genus.

Identification of dominant taxa

Dominant genera in the phytoplankton were screened to analyze community changes. The dominant genera were determined according to the dominance. The genus in the top 25% of dominance was selected as the dominant genus. The formula used to calculate dominance was as follows:

$$Y_i = \frac{\sum_{j=1}^{M} n_{ij}}{N} \times f_i \tag{4}$$

where Y_i is the dominance of the i-th genus; n_{ij} is the density of the i-th genus at the j-th site; M is the site number; N is the total density of phytoplankton; and f_i is the occurrence frequency of the i-th genus.

RESULTS

Variations in the phytoplankton community in a water transfer cycle

Changes in phytoplankton community structure during different periods

In the whole water transfer cycle, eight phyla and 59 genera, including Cyanophyta, Bacillariophyta, Chrysophyta,

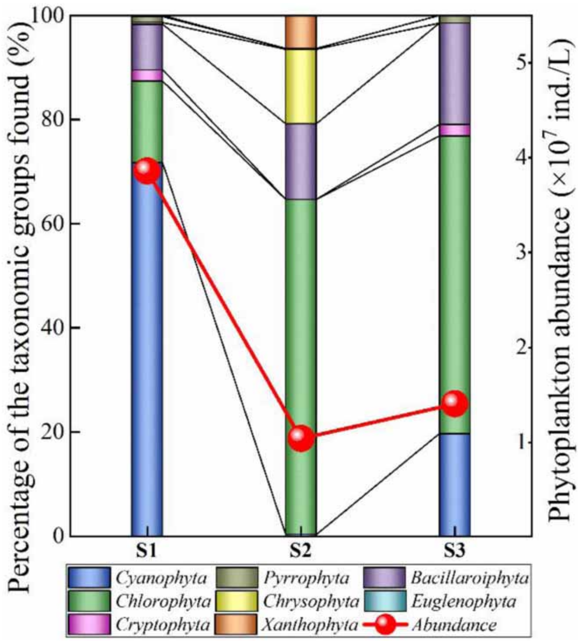

Figure 2 | Variations in phytoplankton community structure in a water transfer cycle. S1, S2, and S3 refer to before, during, and after the water transfer period, respectively.

Pyrrophyta, Cryptophyta, Euglenophyta, Chlorophyta, and Xanthophyta, were identified in DPH (Figure 2). Community structure in S1, S2, and S3 showed that Chlorophyta, Cyanophyta, and Bacillariophyta were the dominant phyla, while Cryptophyta and Euglenophyta were not identified during the water transfer period and Xanthophyta was not identified during two non-water transfer periods (S1 and S3). Total density of phytoplankton decreased rapidly during the water transfer period, and then recovered slowly after the water transfer period. Cyanophyta showed the same pattern as the total density. Cyanophyta dominated the phytoplankton community before the water transfer period, decreased during the water transfer period, and recovered slowly after the water transfer period. The proportion of Chlorophyta increased rapidly during the water transfer period, then decreased after the water transfer period. The proportion of Chrysophyta also increased during the water transfer period, while the proportion of Bacillariophyta was stable in different periods and did not change significantly, indicating that this phylum had good adaptability to changing environments. Additionally, 40, 21, and 32 genera of phytoplankton were identified during the three periods, respectively (Table 1). Analysis of the

Table 1 | The composition difference of the phytoplankton in a water transfer cycle

Scenarios	Genus number	Similarity coefficient	Dominant genus number	Similarity coefficient
S1∩S2∩S3	9	0.11	0	0
S1∩S2	10	0.20	0	0
S2∩S3	13	0.33	1	0.04
S1∩S3	24	0.50	3	0.14
DWR∩S2	9	0.39		
DWR∩S3	18	0.45		

similarities and differences revealed that a total of nine genera appeared in three periods at the same time with a similarity coefficient of 0.11. Moreover, the community similarity coefficient was 0.20 in S1 and S2, 0.33 in S2 and S3, and 0.50 in S1 and S3. Hence, the community similarity between two non-water transfer periods was higher than that between the water transfer period and the non-water transfer period.

Variations in phytoplankton diversity during different periods

To further understand the changes in different phytoplankton taxa in a water transfer cycle, we analyzed the changes in qualitative structure of phytoplankton. As shown in Figure 3, the Shannon–Wiener index of phytoplankton was significantly different between the water transfer period and the non-water transfer period. During

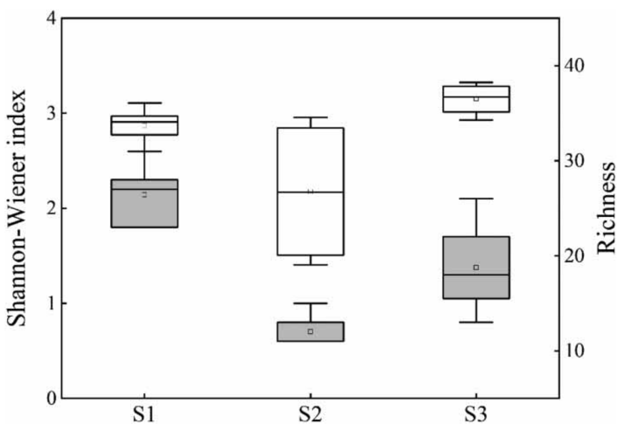

Figure 3 | The diversity index of the phytoplankton in a water transfer cycle. The white boxes are Shannon–Wiener indexes, the grey boxes are richness values.

the water transfer period, the Shannon–Wiener index was relatively low, and the richness value was also low; this indicated that low phytoplankton diversity was probably due to low richness. Moreover, the Shannon–Wiener index differed greatly among sites during the water transfer period. Specifically, the Shannon–Wiener index in the central area (D04) (1.61) and the northern part of DPH (D01) (1.41) was smaller than at other sites, while the Shannon–Wiener index near the entrance of the DWR (D05) (2.74) and at the southern part of DPH (D07) (2.95) was larger than at other sites. During two non-transfer periods, the Shannon–Wiener index of genus was relatively high and consistent at each site. Overall, the density of the phytoplankton community in the study area was relatively uniform before and after the water transfer period. After the water transfer period, phytoplankton diversity gradually recovered, but was not the same as the original state, which might also be related to the insufficient sampling interval between S2 and S3.

Dominant taxa during different periods

Ten, five, and nine dominant genera were screened in S1, S2, and S3, respectively. Based on the distribution of the dominant genera in the three different periods, the dominance of each genus was not significantly different, but none of the dominant genera were the same (Figure 4). There was only one genus that was dominant in both S2 and S3, namely, *Chlorella*, which was the dominant genus with the highest dominance value in S2 and S3. The genus

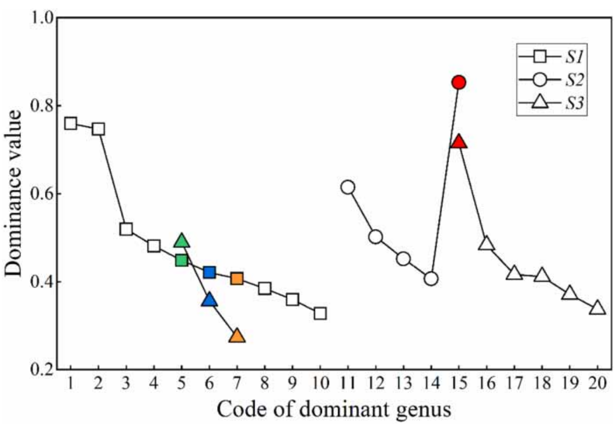

Figure 4 | The dominant genera in different periods. The codes are the same as Table 2.

with the highest dominance in S1 was *Phormidium*. Three dominant genus in S1 and S2 were the same, *Cyclotella*, *Dactylococcopsis*, and *Oscillatoria*. Additionally, the dominance value of *Oscillatoria* in S1 and S3 was different, and it presented the smallest dominance value in S3. No repeat dominant genus was found in S1 and S2.

Environmental factors affecting phytoplankton communities

Variations in environmental and hydrological factors

The water level in DPH fluctuated throughout the water transfer cycle (Figure 5), being generally low in S1 and increasing in S2. In 2018, Shandong Province experienced the heaviest rainfall in years. During that year, rainfall in the rainy season was much heavier than that in the historical period (570 mm), and the water storage volume in DPH was 63% higher than usual. Therefore, the rainfall runoff replenishment of DPH resulted in the overall elevation of the water level in the rainy season. The highest water level in S2 came as a result of the heavy rainfall. DPH was dry in the dry season. The rainfall in post-flood season of 2018 and pre-flood season of 2019 was lower than the post-flood (110 mm) and pre-flood (257 mm) seasons in the same historical period, and the water level dropped accordingly (Figure 6). At this time, the transferred water flowed into DPH, which alleviated the water level decline. Water demand around DPH changes with the seasons. The drop of water level after March was due to an increase in agricultural activities; accordingly, the transferred water amount is adjusted to keep the water level in DPH stable.

Water quality is one of the major factors affecting aquatic communities. In a whole water transfer cycle, water quality differed in different periods, and different water quality indicators also showed different changes. After a water transfer cycle, TP and NH_4-N in DPH decreased, while COD and TN increased. Additionally, TN rose rapidly in S2 and fell in S3, which returned to close to the original level. COD decreased slightly in S2, but showed a higher value in S3. These changes indicated that the water quality fluctuated within a water transfer cycle, but that it returned to close to its original level when the water transfer was completed. However, the water quality

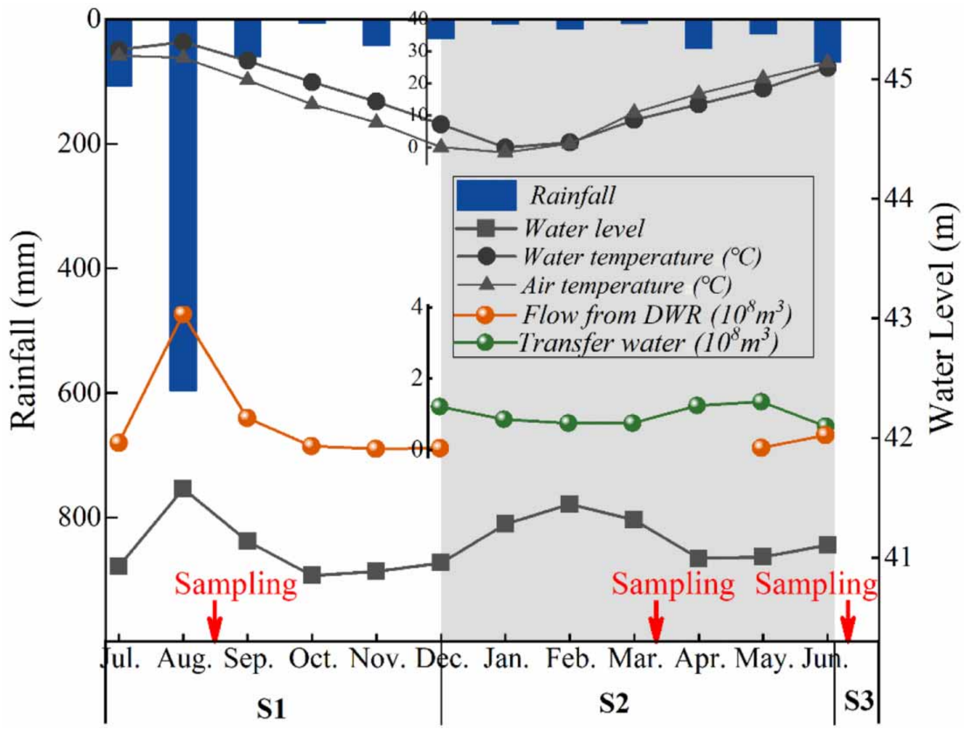

Figure 5 | The dynamics of water level and temperature in DPH during a water transfer cycle.

did not return to the original level after water diversion when it was not in the rainy season. It is possible that the effects of precipitation on the improvement of water quality in the lake were not reflected yet in the collected samples during the third sampling.

Key factors driving phytoplankton distribution

To better understand the environmental impact on phytoplankton, it is necessary to identify the main impact factors. According to the RDA results (Figure 7), water quality had great influence on phytoplankton community in phylum level. Especially, the COD and water temperature (T water) in DPH greatly affected the phytoplankton. COD was related to the Bacillaroiphyta. T water was positively correlated with both Cryptophyta and Pyrrophyta, but negatively correlated with Xanthophyta. TN was positively correlated with Xanthophyta, but negatively correlated with Cyanophyta, while NH_4-N was closely correlated with Cyanophyta. To further analyze the dominant genera changes along environmental gradient, niche breadth values were calculated. As shown in Table 2, the mean niche breadth index was largest on the COD gradient and smallest on the TP gradient, indicating that the change of COD in DPH had no significant impact on the dominant genera, while the change in TP had a greater impact on the dominant genera. *Phormidium*, *Merismopedia*, *Chlorella*, and *Cyclotella* ranked high on each environmental gradient, indicating that they were well adapted to the changing environment. *Merismopedia* and *Cyclotella* were present throughout the water transfer cycle, even though they were not dominant genera in every period. *Chlorella* appeared in S2 and S3, while *Phormidium* appeared in S1 and S3.

DISCUSSION

Water transfer and river inflow jointly affect water quality and water level during the water transfer period

Water transfer is always implemented in the dry season, when there is little rainfall and limited runoff flow into DPH. DPH mainly accepts transferred water and little

Table 2 | Niche breadth index of the dominant genera along environmental gradients

Code	Dominant genera	TP	COD	TN	NH_4-N	R_{NP}	Mean	Rank
1	*Phormidium*	1.4	1.05	1.05	1.87	1.04	**1.282**	**1**
2	*Merismopedia*	1.22	0.97	1.05	1.58	0.87	**1.138**	**3**
3	*Scenedesmus*	0.86	0.54	0.55	1	0.53	**0.696**	**5**
4	*Westella*	0.41	0.44	0.42	0.77	0.46	**0.5**	**8**
5	*Cyclotella*	0.6	1.24	0.8	0.83	0.69	**0.832**	**4**
6	*Dactylococcopsis*	0.51	0.73	0.43	0.61	0.48	**0.552**	**6**
7	*Oscillatoria*	0.49	0.79	0.45	0.51	0.39	**0.526**	**7**
8	*Cryptomonas*	0.38	0.24	0.18	0.45	0.07	**0.264**	**14**
9	*Melosira*	0.2	0.17	0.16	0.15	0.1	**0.156**	**20**
10	*Fragilaria*	0.3	0.15	0.22	0.27	0.07	**0.202**	**18**
11	*Dinobryon*	0.35	0.31	0.98	0.3	0.33	**0.454**	**9**
12	*Tribonema*	0.15	0.19	0.94	0.17	0.3	**0.35**	**11**
13	*Ankistrodesmus*	0.08	0.14	0.7	0.13	0.21	**0.252**	**15**
14	*Synedra*	0.06	0.1	0.43	0.09	0.51	**0.238**	**17**
15	*Chlorella*	0.45	1.63	1.48	0.7	1.62	**1.176**	**2**
16	*Micryocystis*	0.09	0.91	0.03	0.23	0.47	**0.346**	**12**
17	*Chroococcus*	0.06	0.65	0.03	0.14	0.34	**0.244**	**16**
18	*Eudorina*	0.06	0.52	0.01	0.13	0.26	**0.196**	**19**
19	*Nitzschia*	0.1	0.89	0.07	0.21	0.5	**0.354**	**10**
20	*Pandorina*	0.03	0.77	0.05	0.18	0.48	**0.302**	**13**
Mean	**0.39**	**0.621**	**0.501**	**0.516**	**0.486**			
Rank	**5**	**1**	**3**	**2**	**4**			

The table shows the sensitivity of each dominant genus to environmental indicators, and the bold values represent the average value. The larger the value was (Mean), the higher the ranking was (Rank), indicating that the species was less sensitive to the corresponding environmental indicators. This provided important support for the discussion of the relationship between phytoplankton and water quality indicators in this paper. Bold is for better presentation of important data.

inflows in the dry season. According to the section 'Environmental factors affecting phytoplankton communities', the phytoplankton community structure was closely related to water quality factors, and the influence of water diversion on water quality in DPH was obvious. Compared with the results before the water transfer period, TN increased, NH_4-N decreased during the water transfer period. Based on the water quality changes in DPH (Figure 6), TN content in the transferred water from UNSH was about 0.5 times that of DPH and in the inflow from DWR was almost three times that of DPH. Even if the inflow from DWR was too small to be measured during the water transfer period (Figure 5), it was still inevitable that a quite high TN concentration entered the DPH through DWR inflow. Thus, the increase in TN in DPH was mainly due to high TN content in DWR. Although NH_4-N content in DWR was higher than in DPH, it was not high enough to affect the NH_4-N in DPH considering the DWR inflow amount. More importantly, a large amount of transferred water with low NH_4-N content also reduced the influence of NH_4-N in DWR inflow on DPH. COD and TP showed little change during the water transfer period, because the differences in COD and TP content between transferred water and DPH, DWR and DPH were small. It is worth noting that, as the source of transferred water for DPH, the content of each water quality indicator in UNSH was less than that in DPH. However, water quality had already deteriorated at Denglou station. Increase in TN content was evident in Denglou station, and the content of other indicators, such as COD, NH_4-N, TP, were also higher

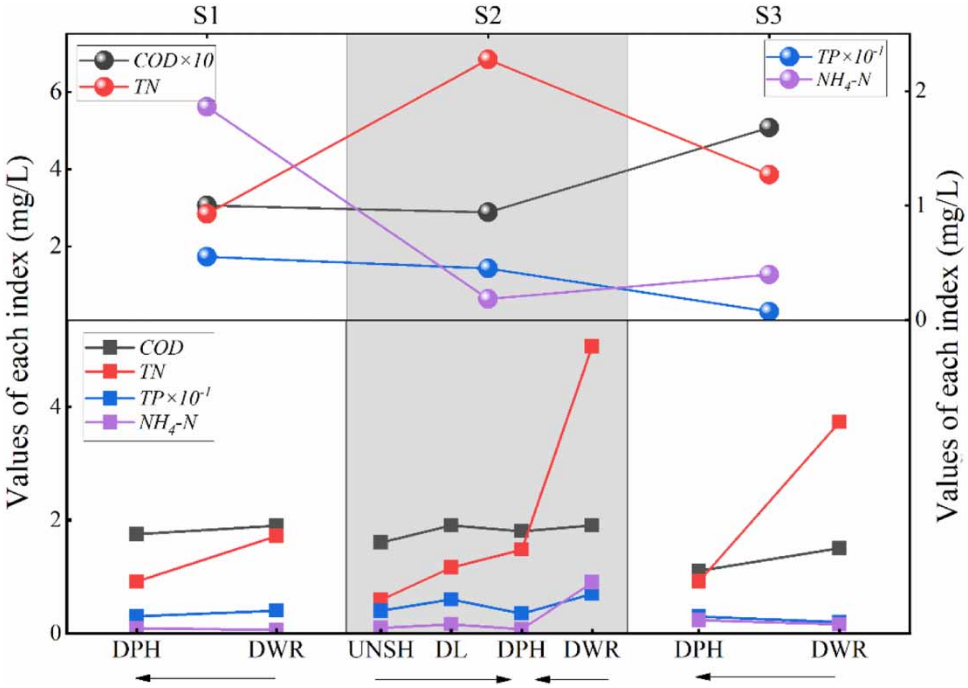

Figure 6 | Variations in water quality factors in different periods. The black arrows refer to the flow direction. (a) The water quality in DPH and (b) the water quality of inflows of DPH.

than that in DPH. Liangji Canal and the Liuchang River serve as water conveyance channels, but are surrounded by residential communities and farmland. Moreover, spring is the primary season for wheat growth in northern China, so fertilization, fishing, and other agricultural activities likely influence the TN content in DPH. Thus, human activities along the diversion route might have polluted the transferred water, thus affecting the phytoplankton in DPH. Therefore, the water diversion and DWR jointly affect the water quality in DPH. Water diversion not only affected water quality, but also maintained the water level in DPH directly. To ensure sufficient water volume in the next stage, the transferred water in DPH must be large enough to raise the water level (Figure 5). Agricultural activities in the spring also greatly increase the water demand during the water transfer period, and this reduces the amount of water in the lake. These frequent water level fluctuations promote material circulation in the lake and are detrimental to the growth of phytoplankton (Kivrak 2006); therefore, they likely also affected the community structure in DPH to some extent. Therefore, these water quality and water level changes caused by water diversion and DWR inflow drove the phytoplankton succession in DPH.

Changes in phytoplankton community structure and replacement of dominant taxa

Changes in habitat will lead to changes in community structure, such as the replacement of dominant taxa. Cyanophyta played a dominant role in the community before and after water diversion. As the dominant phylum, Cyanophyta occupied a large percentage in the whole water transfer cycle, and their distribution was closely related to NH_4-N and TN (Figure 7). Cyanophyta decreased rapidly during the water transfer period, but gradually recovered after water diversion, which was related to the decrease of NH_4-N during the water transfer period (Figure 6). In addition to water quality change, temperature differences caused by seasonal changes also influenced the dramatic changes in Cyanophyta. Increases in temperature have previously been shown to be conducive to the dominance of Cyanophyta (Markensten *et al.* 2010; Gray *et al.* 2019). Hence, Cyanophyta dominated the phytoplankton in the warm non-transfer periods, especially in S1, which had the highest temperature among three samplings. The diversity and the total density of phytoplankton also decreased in S2. Dai *et al.* (2018) also believed that the diversity of

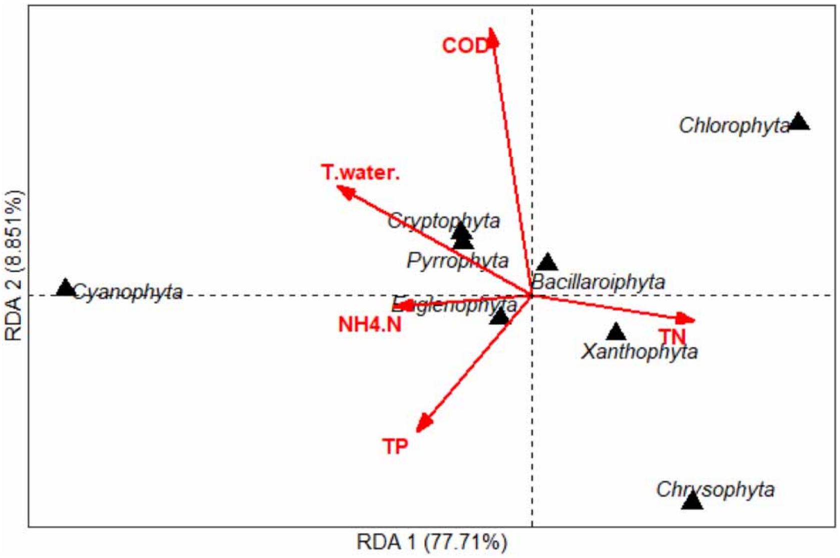

Figure 7 | RDA of environmental factors and phytoplankton community during the whole water transfer cycle.

phytoplankton in the receiving water was lower during the water transfer period than the non-water transfer period, which was consistent with our results. The decrease in the diversity and the total density might be related to low temperature (Ho & Michalak 2019). Low temperature narrows the niche breadth of genus with different niche requirements, leading to a decrease in the genera number in S2 and thus a decrease in the diversity index and richness (Yang *et al.* 2016). Even though the phytoplankton community structure and total density showed a recovery trend after the water transfer period, there were still some differences. Temperature differences caused by seasonal changes might be one of the main reasons for the total phytoplankton density difference between S1 and S2. Water temperature is known to be closely related to the growth of phytoplankton (Markensten *et al.* 2010; Bergstrom *et al.* 2013), and the growth of some algae is known to have an obvious circadian rhythm (Straub *et al.* 2011). Before and after water diversion, the air temperature in DPH was similar, while the water temperature in S1 was higher than in S3 (Figure 5). Thus, the total phytoplankton density remained at a low value after the water diversion.

Compared with the results before the water transfer period (S1), the phytoplankton genus number decreased (Table 1) and phytoplankton diversity increased at the genus level (Figure 3) after the water transfer period (S3). These findings indicated that some sensitive taxa disappeared as the environment changed, but the taxa with better adaptability to the environment were still at a relatively stable level. When compared with the research results before the SNWTP, the phytoplankton community structure and Shannon–Wiener index in DPH changed greatly during the same periods (Tian *et al.* 2013). Further analysis results of quantitative structure showed that the genera among three periods had a similarity coefficient of 0.10, while no dominant genus was the same (Table 1). Additionally, as shown in Figure 4 and Table 1, the three same dominant genera appeared before and after the water transfer period, while only one dominant genus was the same during and after the water transfer period. Moreover, the similarity coefficients of genera (0.33 and 0.50) were larger than that of dominant genera (0.04 and 0.14) during the same periods. Four in nine genera that recurred during these three periods belonged to Bacillariophyta, which maintained a stable percentage throughout the whole water transfer cycle (Figure 2). Therefore, in a water transfer cycle, the change in dominant genus was more drastic than that of a whole phytoplankton community. The sensitivity of each dominant genus to the environment was further analyzed by the niche breadth model. In general, the species with narrower niche breadth are more environmentally sensitive. Results in Table 2 showed that the dominant genera were sensitive to TP and the N/P ratio. Most of the screened dominant genera belonged to the

Cyanophyta and Chlorophyta, which were closely related to the TN and TP. Thus, the TN and TP changes affected the dominant genera of phytoplankton.

Runoff affects phytoplankton by affecting water quality during non-transfer periods

Water quality in DPH gradually recovered after the fluctuation during the water transfer period (Figure 6). Similar water quality conditions led to similar phytoplankton structures before and after water diversion, as well as high genera repetition rates. The water quality in DPH during the non-water transfer periods was mainly influenced by runoff inflow. In the rainy season in northern China, DPH mainly received the runoff supply from DWR. After the water transfer period, the COD in DPH rose rapidly, which was mainly caused by the high COD in the DWR, because of the higher COD content in DWR than in DPH (Figure 6). Even though samples collected after the water transfer were not obtained in the rainy season, the rainfall that occurred carried enough COD into DPH to increase the COD content. TN gradually decreased after the water transfer period, which might also be related to the runoff from the DWR. When compared with the water transfer period, TN content in DWR after the water diversion decreased greatly, but it was still higher than that in DPH. Rainfall-runoff caused the DWR to carry TN into DPH continuously, thus affecting water quality. NH_4-N changed a little after the water transfer period because of the similar content in DPH and DWR. TP concentration in DPH was already very low and could be easily affected. Thus, the slight decrease in TP might be caused by the low TP content in DWR after the water transfer period (S3). The third sampling (S3) occurred soon after the water transfer period, so the dilution effect of the rainfall on pollutants was not reflected. This explained why the water quality indicators did not return to the level before the water transfer period. Moreover, similarity coefficient of the phytoplankton community in DWR and DPH after the water transfer period (S3) (0.45) was bigger than that during the water transfer period (S2) (0.39), and the total number of phytoplankton genera in DPH and DWR in the non-transfer period were much higher than that in the water transfer period (Table 2). This indicated that DWR brought a large amount of phytoplankton into DPH along with runoff in the rainy season, directly affecting the phytoplankton in DPH. These findings confirmed previous findings that hydrological connectivity increased community similarity (Yuan *et al.* 2018).

CONCLUSIONS

Implementation of the SNWTP led to alternations between water diversion inflow and runoff in DPH, but phytoplankton succession was still not clear. In this study, phytoplankton community before, during, and after the water transfer period in a water transfer cycle were analyzed, and various effects of water transfer and runoff on phytoplankton were discussed in combination with the corresponding changes in water quality, temperature, and water level. Low temperature caused Chlorophyta to replace Cyanophyta as the main dominant phylum, and low temperature was also related to the decrease in the total density and diversity index of phytoplankton during the water transfer period. Water temperature affected the recovery of total phytoplankton density after the water transfer period. In a water transfer cycle, changes in dominant genus were more drastic than that of a whole phytoplankton community, and dominant genera were sensitive to TP and TN changes. Transferred water and DWR inflow jointly affected the water quality in DPH during the water transfer period and water quality in DPH was improved. DWR was responsible for the increase in TN content. At the same time, the water transfer process increased the risk of water pollution. Runoff from DWR affected the water quality in DPH during the non-transfer periods. In addition, phytoplankton in DWR entered DPH through runoff, which affected the phytoplankton community directly.

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DATA AVAILABILITY STATEMENT

All relevant data are included in the paper or its Supplementary Information.

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