CHARACTERISTICS AND DRIVING FACTORS OF THE PHYTOPLANKTON COMMUNITY IN DANJIANGKOU RESERVOIR, CHINA

SUN, W.[1] – WU, W.[1*] – TIAN, W.[2] – TAN, H.[3] – ZHANG, Y.[1] – ZHOU, H.[1]

[1]*State Key Laboratory of Simulation and Regulation of Water Cycle in River Basin, China Institute of Water Resources and Hydropower Research, Beijing 100038, China*

[2]*China South-to-North Water Diversion Corporation Limited, Beijing 100036, China*

[3]*South to North Water Diversion Middle Route Water Source Corporation Limited, Shiyan 442700, China*

[*]*Corresponding author*
e-mail: wwqemail@126.com

(Received 21st May 2025; accepted 10th Jul 2025)

Abstract. Vertical heterogeneity of phytoplankton communities is crucial in assessing water quality and ecosystem functioning in deep reservoirs. As the primary water source for China's South-to-North Water Diversion Project, the Danjiangkou Reservoir is vital for drinking water security. However, most studies have focused on surface-layer phytoplankton, overlooking vertical patterns. This study investigated thermal stratification and its influence on phytoplankton and phosphorus fractions at six sites in July (stratified period) and November (mixed period) across the Han and Dan sub-reservoirs. Strong thermal stratification was observed in the Han sub-reservoir, whereas stratification was weak in the Dan sub-reservoir. In July, Cyanophyta and Chlorophyta dominated, with decreasing cell abundance with depth and significant vertical gradients in particulate phosphorus. In November, Bacillariophyta dominated, and vertical differences in cell density were minimal. Redundancy analysis identified particulate phosphorus (19.14%) and water temperature (14.3%) as the main environmental drivers of phytoplankton community structure, while total dissolved phosphorus had limited influence (0.15%). These findings revealed strong vertical coupling between phytoplankton and particulate nutrients under stratified conditions and offer important insights for the ecological management of drinking water reservoirs. This study enhanced understanding of phytoplankton community structure in stratified reservoirs, offering a valuable reference for reservoir ecosystem management.
Keywords: *vertical heterogeneity, south-to-north water diversion, thermal stratification, phytoplankton community structure, ecological environmental management*

Introduction

Phytoplankton are the primary producers and foundation of the food web in aquatic ecosystems and play a crucial role in material cycling and energy flow (Falkowski et al., 2003). The species composition, community structure, and cell density of phytoplankton not only reflect the quality of the water environment but also serve as indicators of the ecological health of lake and reservoir ecosystems (Cabecinha et al., 2009). Understanding changes in phytoplankton community structure is critical for monitoring water columns in reservoirs.

Temperature and nutrients are the primary factors driving vertical distribution changes in phytoplankton community structures in deep reservoirs (Fornarelli et al., 2013; Xin et al., 2015). Phosphorus, an essential element for life, is an important nutrient in ecosystems. Changes in phosphorus concentration directly affect phytoplankton growth, thereby influencing the degree of eutrophication in the water column (Hecky et al., 1988).

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

In natural environments, phosphorus exists in both dissolved and particulate forms. The migration and transformation of different forms of phosphorus in aquatic environments are influenced by various biogeochemical processes. Moreover, the impact of changes in phosphorus concentration on the phytoplankton community structure varies across different forms of phosphorus. Fluctuations in phosphorus concentrations can either promote or limit phytoplankton growth and reproduction, thereby altering phytoplankton community structure (Lagus et al., 2004). Temperature directly affects key processes such as phytoplankton photosynthesis and respiration (Yue et al., 2024), whereas thermal stratification leads to an uneven temperature distribution in the vertical water column of reservoirs (Kraemer et al., 2015; Lindholm-Lehto et al., 2019). Thermal stratification also hinders phosphorus exchange between the upper and lower layers of the reservoir water column (Wang et al., 2020; Stockwell et al., 2020), which can directly or indirectly affect the phytoplankton community structure in different water layers. Wu et al. found that thermal stratification is a key factor in determining the vertical distribution of the phytoplankton community structure in front of a dam in the Xinanjiang Reservoir (Wu et al., 2012). Moreover, changes in the vertical distribution pattern of the phytoplankton community structure have significant implications for the structure of such aquatic systems as reservoirs (Padisak et al., 2006). Therefore, studying the distribution characteristics and driving factors of phytoplankton communities during different thermal stratification periods in reservoirs is crucial for improving water ecological environment management in reservoirs.

As a water source for the South-to-North Water Diversion Project, the water quality of the Danjiangkou Reservoir closely reflects the safety of potable water for the large population in the water-receiving areas. Since the completion of the Danjiangkou Reservoir, most studies have focused on the phytoplankton community structure in the surface layer at a spatial scale, with less attention paid to its vertical distribution (Wang et al., 2016; Pan et al., 2018; Jia et al., 2019). To investigate the vertical differentiation characteristics of the phytoplankton community structure in the Danjiangkou Reservoir during different thermal stratification periods, we selected three monitoring sites based on thermal stratification characteristics and systematically investigated phosphorus concentrations in different forms across the water column layers, phytoplankton cell abundance, and the Shannon–Wiener diversity index. This study aimed to explore the vertical distribution characteristics of phytoplankton community structure and its driving factors to provide scientific support for ecological research in deep reservoirs.

Materials and methods

Study area

The Danjiangkou Reservoir (32°36'~33°48'N, 110°59'~111°49'E, *Fig. 1*) consists of the Han and Dan Reservoirs. It is located in the middle and upper reaches of the Han River, situated between Danjiangkou City in Hubei Province and Xichuan County in Nanyang City, Henan Province. It is the largest artificial freshwater lake in Asia and serves as the water source for the central route of the South-to-North Water Diversion Project in China. Since the official commencement of water delivery in December 2014, the central route of the South-to-North Water Diversion Project has experienced a continuous increase in water transfer volume, surpassing 40 billion m^3 by July 2021 (Zhao et al., 2022). The initial dam height of the Danjiangkou Reservoir was 162 m, with a normal water storage level of 127 m and a water surface area of 745 km^2. After the dam

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

height was increased to 176.6 m, the normal water storage level reached 170 m, and the reservoir surface area expanded to 1050 km². The Danjiangkou Reservoir is located in a subtropical monsoon climate zone in China and is characterised by significant transitional climate features. The average annual precipitation is 808 mm, with an average annual temperature ranging from 15 to 16 °C, exhibiting seasonal water temperature stratification characteristics (Cui et al., 2019; Zhang et al., 2024).

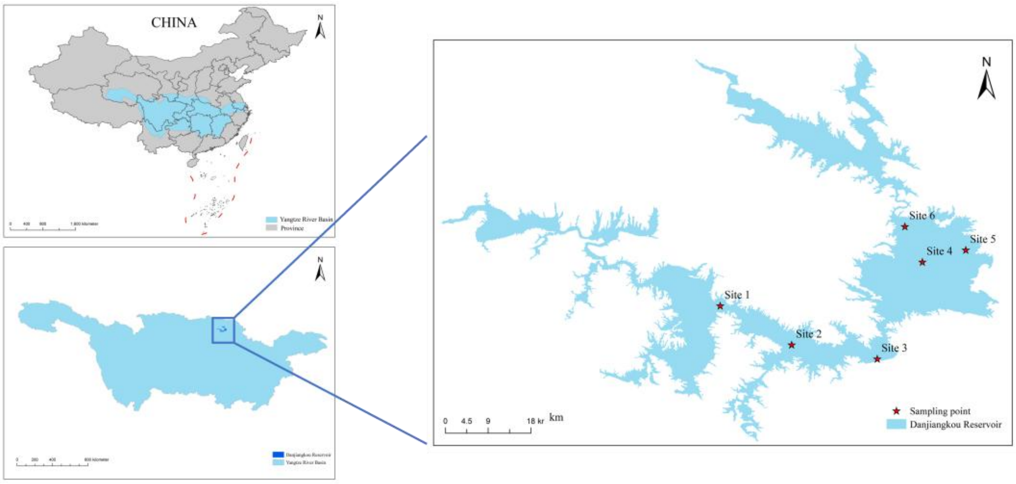

Figure 1. *Study area*

Sample collection and processing

Six sampling sites were selected between the Han River Reservoir (HR) area (Site 1 (Longkou), Site 2 (Langhekou), and Site 3 (Baqian)) and the Danjiang Reservoir (DJR) area (Site 4 (Dankuxin), Site 5 (Songgang), Site 6 (Heijiju)) for vertically stratified sampling in July and November, 2023, within the Danjiangkou Reservoir. On-site measurements of water temperature (WT) were conducted using an EXO-YSI multiparameter water quality analyser, with data transmitted in real time. Based on the vertical temperature variation characteristics, the water column was divided into five layers (A-E) for sampling purposes. The surface layer (A) was defined as the area 0-0.5 m below the water surface, layer B represented the surface thermocline at a depth of 3–10 m, layer C was the mixed layer at a depth of 15–30 m, layer D was the second thermocline at a depth of 30–37 m, and layer E was the hypolimnion at a depth of 40–45 m. However, the depths at different sampling sites in the Danjiangkou Reservoir varied. Therefore, in July, seven samples were collected at each vertical stratification layer (A, B, C, D, and E) of the water column at the sampling points in the Hanjiang reservoir. Moreover, seven, five, and five samples were collected in the vertical direction of the Danjiang reservoir according to the different water depths. In November, eight samples were collected from the vertical water column at each point of the Danjiangkou Reservoir. The sampling points and water depths are shown in *Table 1*.

Water samples were collected using a 5 L capacity water sampler to analyse physicochemical indicators. Water chemistry samples for laboratory analysis were aliquoted into 1 L brown glass bottles and transported to the laboratory within 4 h for filtration, refrigeration, and pretreatment. Total phosphorus (TP) and total dissolved phosphorus (TDP) were completed within two days, and the detection methods for these

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

indicators followed the "Water and Wastewater Monitoring and Analysis Methods" (4th edition) (State Environmental Protection Administration., 2002). The concentration of particulate phosphorus (PP) was calculated by subtracting TDP concentration from TP concentration.

Table 1. *Sampling points and water depth*

Point	Depth/m (July)	Depth/m (November)
Site 1	0.5, 5, 10, 20, 30, 35, 40	0.5, 5, 10, 20, 30, 35, 40,43
Site 2	0.5, 5, 10, 20, 30, 35, 40	0.5, 5, 10, 20, 30, 35, 40,43
Site 3	0.5, 5, 10, 20, 30, 35, 40	0.5, 5, 10, 20, 30, 35, 40,43
Site 4	0.5, 5, 10, 20, 30, 35, 40	0.5, 5, 10, 20, 30, 35, 40,43
Site 5	0.5, 5, 10, 20, 30	0.5, 5, 10, 20, 30, 35, 40,41
Site 6	0.5, 5, 10, 20, 30	0.5, 5, 10, 20, 30, 35, 40,43

The investigation methods for plankton followed the procedures outlined in the "Methods for Research on Freshwater Phytoplankton". Phytoplankton identification was conducted based on morphological characteristics, including cell shape, size, and arrangement, under a light microscope. For qualitative sampling of phytoplankton, a 25-mesh plankton net was manoeuvred in a repetitive "∞" shape at 0.5 m below the water surface. The collected samples were transferred into 50 mL sample bottles and fixed with 4% formaldehyde. For quantitative sampling, 1 L water samples were collected in brown PET bottles, and Lugol's solution was added on-site for fixation. Samples were then stored at low temperatures until transportation to the laboratory. After allowing the water samples to stand for 48 h, the phytoplankton was concentrated to 50 mL using the siphoning method and preserved in formalin. Phytoplankton identification and counting were performed according to the guidelines of the "Phytoplankton Handbook" and "Chinese Freshwater Algae: Systematics, Classification, and Ecology." A microscope grid method was used for counting, where 0.1 mL of the concentrated sample was placed in a plankton-counting chamber and the count was performed under an optical microscope (10×40 magnification). The concentrated sample was mixed thoroughly, and 0.1 mL was placed in the counting chamber for a full slide count. A minimum of 300 cells were counted and at least two slides per sample were counted, with the average taken as the result. Based on the concentration factor of the sample, the cell count was converted to cells per litre (cells/L), which represented phytoplankton cell abundance.

Data processing and analysis

Thermal stratification stability

The relative stability of water bodies (RWCS) is a parameter to evaluate the degree of water mixing and stratification. The RWCS index and RWCS/H can be used to assess the thermal stratification stability of a reservoir effectively and quickly. However, the RWCS index only considers the density differences between the surface and bottom water columns (Becker et al., 2008; Paerl et al., 2016). Therefore, the RWCS/H was selected to represent the thermal stratification stability level and was calculated according to *Eq. (1)*. The formula was as follows:

$$RWCS / H = \frac{D_b - D_S}{(D_4 - D_5)H} \qquad \text{(Eq.1)}$$

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

where RWCS/H is the thermal stratification stability index (m^{-1}). When RWCS/H > 2 m^{-1}, the water column is in a stable stratification period. The higher the value, the more stable is the stratification. D_b represents the water column density 0.5 m above the bottom of the thermal stasis layer ($kg \cdot m^{-3}$). D_s is the water column density 0.2 m below the surface layer ($kg \cdot m^{-3}$). D_4 is the density of pure water at 4 °C ($kg \cdot m^{-3}$). D_5 is the density of pure water at 5 °C ($kg \cdot m^{-3}$). H is the depth of the water at the end of the second thermal stasis layer (m). In this study, D_b and D_S were not separately collected water samples, but represent the water density values at specific depths—0.5 m above the bottom and 0.2 m below the surface, respectively—used in the calculation of the Relative Water Column Stability (RWCS). These density values were derived from the vertical water temperature profiles measured during field monitoring and calculated using standard density formulas. Therefore, it was not necessary to collect separate samples at these specific depths.

Given the relatively low turbidity of the Danjiangkou Reservoir, the water density was calculated from temperature using *Eq. (2)* (Shi et al., 2022):

$$\rho = [1 - \frac{(T + 288.9414) \cdot (T - 3.9863)^2}{508929.2 \times (T + 68.12936)}] \times 1000 \quad \text{(Eq.2)}$$

where ρ is the water column density (kg/m³), and T is the water column temperature (°C).

Calculation of TP flux

The TP flux was calculated as shown in *Eq. (3)*.

$$F = C \cdot Q \cdot 10^{-9} \quad \text{(Eq.3)}$$

where F is the TP inflow flux (Tg), C is the water column TP concentration (mg/L), and Q is the runoff volume (m^3).

Algal diversity index and dominance

(1) In this study, the Shannon-Wiener diversity index was used to assess the diversity of phytoplankton communities. This index is based on species composition and relative abundance, and has been widely applied in ecological studies for measuring community diversity, particularly in aquatic ecosystems (Shannon et al., 1948; O'Keeffe, 2004). The Shannon-Wiener diversity index, as a community parameter (Xu et al., 2017), was calculated using *Eq. (4)*.

$$H' = -\sum (n_i / N) \ln(n_i / N) \quad \text{(Eq.4)}$$

(2) The dominance of the species was determined based on the McNaughton dominance index (McNaughton et al., 1967; Habib et al., 1997) using *Eq. (5)*.

$$Y = \frac{n_i}{N} \cdot f_i \quad \text{(Eq.5)}$$

where n_i represents the abundance of the i-th species of phytoplankton, N is the total number of phytoplankton in the same sample, H′ is the Shannon-Wiener diversity index,

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

and Y represents the dominance, which indicates the frequency, f_i, of the species in the sample. When $Y \geq 0.02$, the species is classified as a dominant species.

Data analysis

Maps were created using QGIS software, and Excel 2019 was used to calculate phytoplankton abundance and dominance indices. R software was used to plot community structure, diversity indices, and dominance indices. Principal coordinate analysis (PCoA) was conducted to analyse the differences in phytoplankton community structure across different water layers during varying thermal stratification periods. Additionally, Variation Partitioning Analysis (VPA) was performed using the varpart function from the "vegan" package (version 2.6-4) in R software (version 4.4.2) to assess the explanatory power of phosphorus, nutrients, and temperature on community structure.

Results

Spatiotemporal variation in temperature parameters

In July, the thermal stratification structure of the Danjiangkou Reservoir exhibited significant spatial heterogeneity across the different reservoir regions. The thermal stratification structure of the Hanjing Reservoir (HJR) was characterised by an epilimnion-metalimnion-epilimnion-metalimnion-hypolimnion, with thermoclines at depths of 3 m and 30 m with thicknesses of 7 m and 7.8 m and temperature gradients of 1.04 °C/m and 1.07 °C/m, respectively (*Fig. 2a*). The RWCS/H index ranged from 10.61 to 14.03, with a mean value of 12.08. In contrast, the thermal stratification in DJR was less pronounced, with water temperatures ranging from 11.4 °C to 31.7 °C (*Fig. 2b*). In November, with a decrease in air temperature, the thermal stratification phenomenon in the Danjiangkou Reservoir gradually disappeared. Vertical temperature variations in both the HJR and DJR water columns were minimal. The water temperature in the HJR region ranged from 18.52 °C to 21.07 °C (*Fig. 2c*), while in the DJR region, it ranged from 19.08 °C to 20.88 °C (*Fig. 2d*).

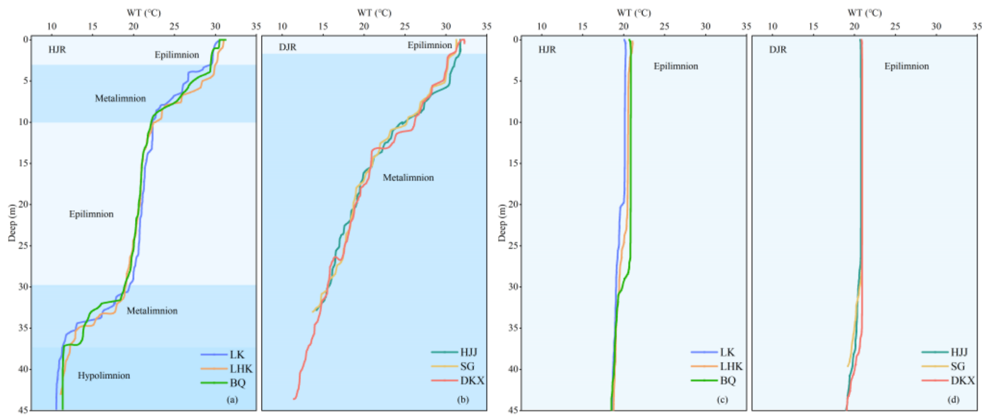

Figure 2. *Vertical temperature variation in the Han River Reservoir and Danjiang Reservoir*

In July, the heat exchange between the water column and the atmosphere caused the surface water temperature to increase with an increase in air temperature. A distinct temperature gradient forms within the water column owing to the limited impact of solar

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

radiation on deeper water layers, leading to thermal stratification in the vertical direction of the water column (Ficker et al., 2017; Woolway et al., 2018). The main factors influencing the thermal stratification structure of a reservoir include water temperature, lake morphology, inflow, and outflow (Liu et al., 2019; Geng et al., 2022). The HJR region, a canyon-type reservoir with a relatively deep-water column, exhibited rapid warming of the upper water layers during summer. The second thermocline formed at depths ranging from 30 m to 37 m. Additionally, longitudinal water flows generated by inflow and outflow, in combination with temperature-induced density stratification, resulted in the inflow moving along the thermocline in the water layers at temperatures close to the inflow temperature. This created a thermocline approximately 7 m thick in the surface layers, ranging from 3 to 10 m below the surface, which was distinguished from the deeper seasonal thermocline and was referred to as the surface thermocline. The DJR region, which is a lake-type reservoir, exhibited less pronounced thermal stratification.

Spatiotemporal distribution of phosphorus nutrients in Danjiangkou Reservoir

Prior to further analysis, a Mann-Whitney U test was conducted to assess differences between the HJR and DJR. No statistically significant differences were observed in key parameters ($p > 0.05$), and therefore, the two reservoirs were analyzed together in the following sections.

Based on the thermal stratification characteristics, this study primarily focused on the HJR region. In July, the average TP concentration in the HJR region was 0.018-0.024 mg/L, exhibiting a decreasing trend with depth, with the highest values observed in the surface layer (*Fig. 3a*). The average concentration of TDP was 0.011-0.017 mg/L, showing a fluctuating increase with depth (*Fig. 3b*). The average concentration of PP was 0.005–0.011 mg/L and exhibited a fluctuating decrease with increasing depth (*Fig. 3c*). Significant vertical differences in TP and TDP concentrations were not observed (*Figs. 4a* and *b*), whereas PP concentrations showed clear vertical differences between layers A, D, E, and B (*Fig. 4c*). In November, the average TP concentration was 0.022–0.033 mg/L, and the average TDP concentration was 0.011-0.0118 mg/L. Both TP and TDP concentrations fluctuated with depth, with the maximum concentrations observed in layer D (*Figs. 3a* and *b*). The average PP concentration was 0.007–0.018 mg/L, exhibiting an initial increase followed by a decrease with increasing depth (*Fig. 3c*). The TP concentrations in layers A, B, C, and E were significantly different from those in layer D (*Fig. 4d*), whereas the TDP and PP concentrations exhibited no significant vertical differences (*Figs. 4e* and *f*). Both the TP and PP concentrations were higher in November than in July.

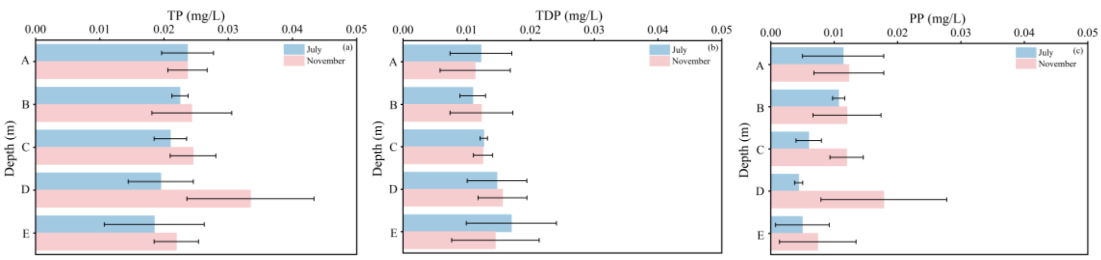

Figure 3. *Changes in phosphorous forms concentrations*

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

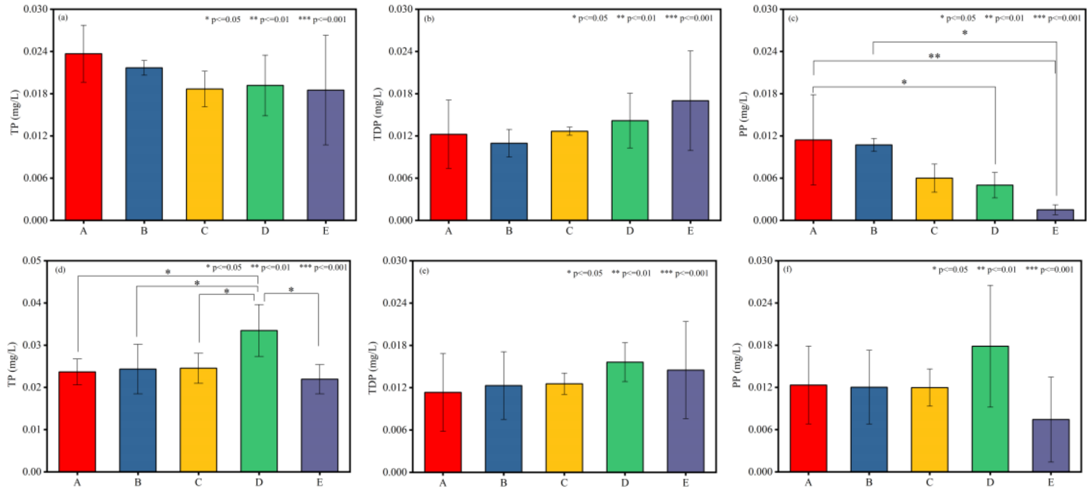

Figure 4. *Analysis of differences in phosphorous forms concentrations. Asterisks indicate statistically significant differences between layers ($p < 0.05$); error bars represent the standard deviation (SD) of the measurements for each layer*

Vertical distribution of phytoplankton community structure

In July, the phytoplankton in the Danjiangkou Reservoir was primarily dominated by Cyanophyta and Chlorophyta (*Fig. 5a*), with a general decreasing trend in cell abundance with increasing water depth. The average cell abundance in layer A was the highest, at 16.50×10^6 cells/L, with Cyanophyta and Chlorophyta accounting for 53.91% and 38.24%, respectively. Layer B had an average cell abundance of 9.53×10^6 cells/L, with Cyanophyta and Chlorophyta accounting for 66.28% and 23.95%, respectively. The average cell abundances in layers C, D, and E were 3.46×10^6 cells/L, 4.88×10^6, and 2.22×10^6 cells/L, respectively. In layer C, Cyanophyta and Chlorophyta accounted for 60.39% and 27.56%, respectively; in layer D, they accounted for 60.48% and 23.88%, respectively, and in layer E, Cyanophyta and Chlorophyta accounted for 26.79%, respectively. The vertical Shannon-Wiener diversity index for the water column showed little variation, with values of 2.02, 2.30, 2.10, 1.89, and 2.24 for the A to E layers, respectively (*Fig. 5c*). Significant differences were observed between layers B and D ($P < 0.05$) (*Fig. 6a*). Fifteen dominant genera were identified: *Microcystis*, *Chlorella*, *Spirulina*, *Phormidium*, *Cylindrospermopsis*, *Anabaena*, *Merismopedia*, *Euglena*, *Staurastrum*, *Oscillatoria*, *Synedra*, *Closterium*, *Cryptomonas*, *Chlamydomonas*, and *Oscillatoria*. *Microcystis* was the dominant genus in layers A, B, and C, with cell abundances of 11.45×10^6 cells/L, 3.55×10^6 cells/L, and 11.55×10^6 cells/L, respectively. In layer D, *Phormidium* dominated, with a cell abundance of 9.90×10^6 cells/L. In layer E, *Merismopedia* dominated, with a cell abundance of 10.36×10^6 cells/L.

In November, the average phytoplankton abundance ranged from 1.12×10^6 to 2.24×10^6 cells/L, with minimal variation in vertical phytoplankton abundance across the water column. The phytoplankton community was primarily composed of Bacillariophyta (*Fig. 5b*). The proportions of Bacillariophyta in layers A, B, C, D, and E were 38.43%, 39.96%, 52.22%, 43.54%, and 45.54%, respectively. In November, 15 dominant genera were identified: *Chlorella*, *Oscillatoria*, *Chlorococcum*, *Euglena*, *Cryptomonas*, *Microcystis*, *Cyclotella*, *Oscillatoria*, *Chlamydomonas*, *Merismopedia*, *Synedra*, *Euglena*, *Merismopedia*, *Oscillatoria*, and *Peridinium*. Among them, *Chlorella*

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

dominated in layers A, D, and E; *Cryptomonas* dominated in layer B; and *Cyclotella* dominated in layer C. The Shannon-Wiener diversity indices for layers A to E were 1.81, 1.60, 1.67, 1.72, and 0.58, respectively (*Fig. 5d*). Significant differences were observed between layer E and all other layers (A, B, C, and D) (P < 0.001) (*Fig. 6b*).

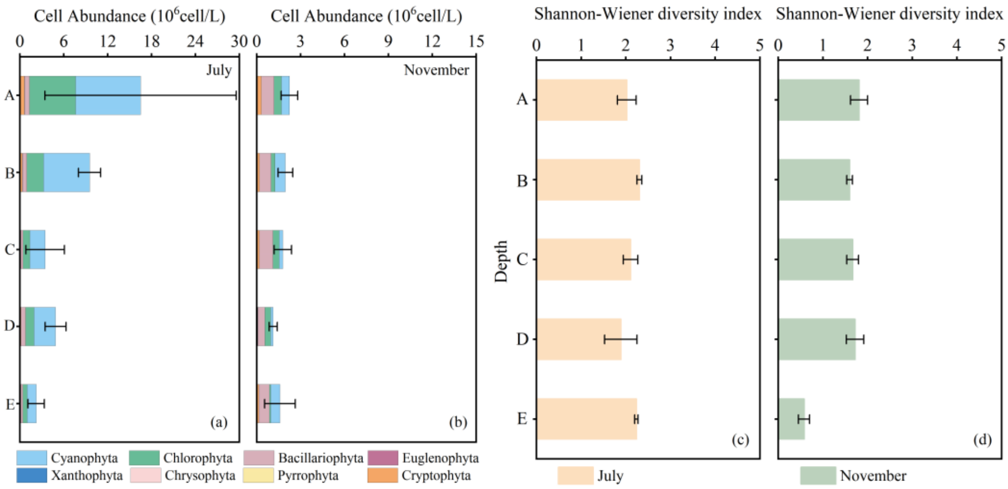

Figure 5. *Phytoplankton cell abundance and Shannon-Wiener diversity index*

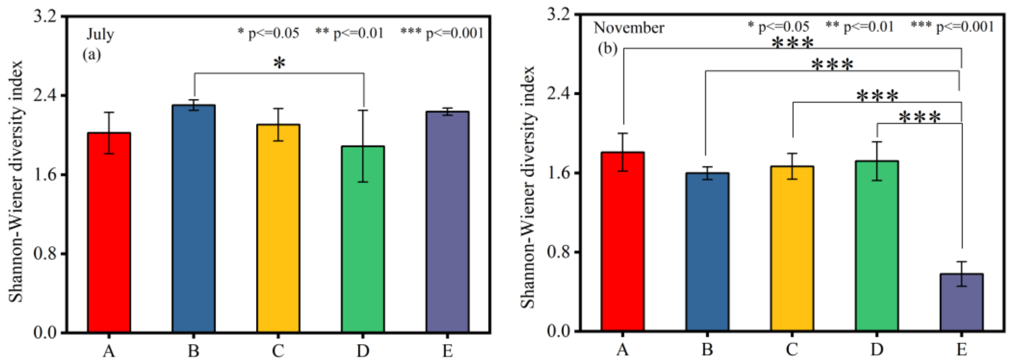

Figure 6. *Analysis of Shannon-Wiener diversity index differences*

In July, the PCoA analysis of the phytoplankton community (*Fig. 7a*) explained 87.01% of the variation in the phytoplankton community structure along the first and second axes. Layers A and B had similar community structures, and layers C, D, and E had similar phytoplankton communities. In November, the PCoA explained 71.89% of the variation in phytoplankton community structure (*Fig. 7b*). The phytoplankton community structures of layers B, C, and E were similar, with layers A, B, C, and D exhibiting greater similarity to each other, whereas a clear distinction was observed among layers A, B, C, and D.

VPA was further used to decompose the differences in the contributions of PP, TDP, and WT to the formation of the phytoplankton community structure in the Danjiangkou Reservoir (*Fig. 8*). The explained variance of PP (19.14%) was greater than that of TDP (0.15%), and that of WT was 14.34%. The unexplained proportion accounted for 50.58%.

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

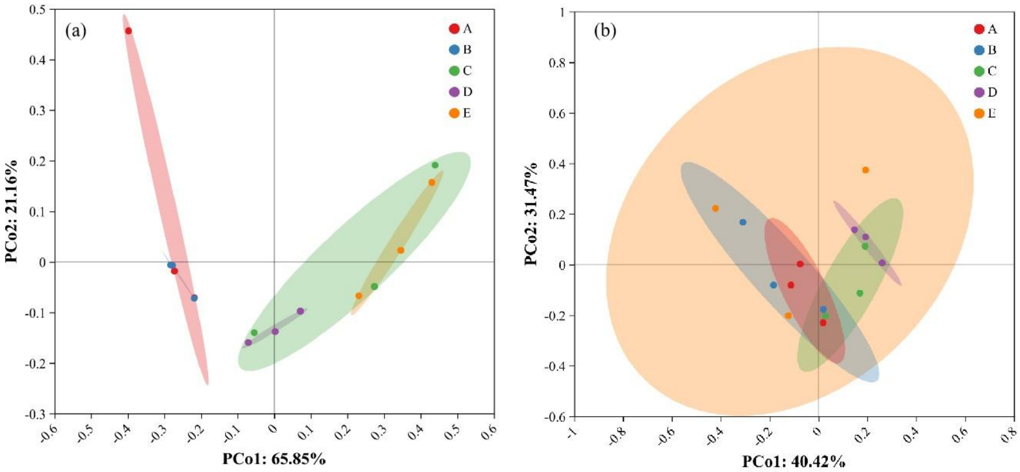

Figure 7. *PCoA of phytoplankton community structure*

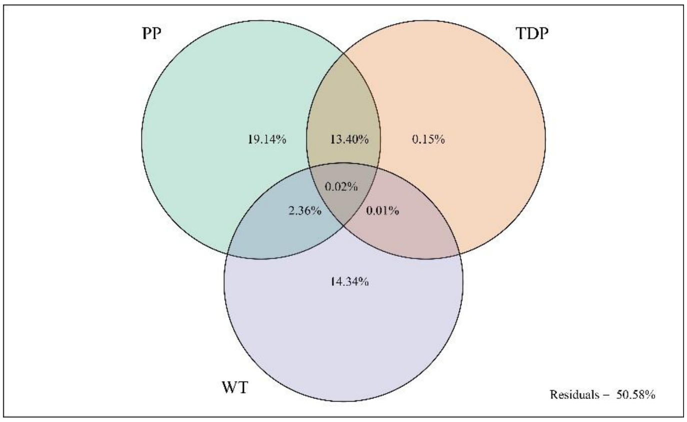

Figure 8. *VPA of phytoplankton community structure*

Discussion

Spatiotemporal distribution differences of phosphorus elements

In July, no significant vertical differences in the TP, TDP, and PP concentrations were observed in the HR region. The primary sources of phosphorus in reservoirs are pollutants carried by upstream inflows and the release of sedimentary phosphorus from sediments (Tang et al., 2014; Xin et al., 2015). Generally, the concentration of phosphorus in sediment pore water are higher, which leads to the transfer of phosphorus to the overlying water, thereby increasing phosphorus concentrations in the bottom layers. However, the TP concentration in the bottom layers of the Danjiangkou Reservoir did not increase significantly, which may have been because of the absence of hypoxic conditions at the bottom of the reservoir (Wang et al., 2024), hindering the release of phosphorus from the sediments. Furthermore, during the thermal stratification period, the bottom isothermal layer was undisturbed, and the overlying water exerted a minimal impact on the phosphorus concentration in the deep-water column. Additionally, sedimentary Ca-P contributes the most to the TP load in the Danjiangkou Reservoir, with inorganic active phosphorus accounting for no more than 20% of the sedimentary TP (Tang et al., 2014).

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

Therefore, sediments did not significantly influence the TP concentration in the bottom layers.

In November, the maximum concentrations of TP and PP were observed in layer D of the water column, whereas the TDP concentrations showed little variation. Additionally, temperature fluctuations were observed at a 20–30 m depth (C layer) in the water column (*Fig. 2c*). This may be due to colder upstream inflows, with the flow passing below layer C. During this period, the inflow river flow rate and velocity were relatively high, reducing the sedimentation rate of pollutants and leading to a notable increase in the TP concentration in layer D of the reservoir (Zhang et al., 2020). In the wet season (July), the reservoir primarily functions as a drainage system to prevent overflow, resulting in a relatively low inflow from the upstream tributaries. In contrast, during the normal water period (November), the reservoir regulates water levels through storage, increasing the inflow from the upstream tributaries. The Han River is the largest tributary of the Danjiangkou Reservoir. Previous studies have shown that the inflows from rivers into the reservoir are the primary sources of phosphorus, with the main stem of the Han River dominating the phosphorus flux into the reservoir (Yu et al., 2024). Based on TP concentration data from automatic monitoring stations of the Han River published by the Ministry of Ecology and Environment of the People's Republic of China and flow rate data published by the Ministry of Water Resources of the People's Republic of China, the calculated results showed that the TP flux in November was approximately 1.63 times higher than that in July (Since the second sampling time was in early November, the inbound flux of TP was calculated based on the inbound flux in October). Additionally, the entire flood season increases nutrient leaching from the soil, increasing the suspended particulate matter content in the upstream inflows (Yin et al., 2023). Therefore, the TP and PP concentrations in November were significantly higher than those in July.

Driving mechanisms of phytoplankton community structure

WT and PP were the main driving factors influencing vertical variation in phytoplankton community structure. WT plants exhibit clear seasonal characteristics that can directly affect the metabolic processes of phytoplankton, thereby influencing their growth (Dupuis et al., 2009). Seasonal differences in community composition and phytoplankton cell abundance were observed in Danjiangkou Reservoir. In July, owing to strong solar radiation, the thermal stratification of the water had a significant impact on the distribution of phytoplankton. Phytoplankton mainly occupied the surface layers and the thermocline, with the highest cell abundance in the surface layer, which decreased with water depth. The diversity index showed no significant differences, which was consistent with the findings of Wang et al. (2024). Cyanophyta dominated, likely because of their preference for summer growth at an optimal temperature of 25–35 °C, higher than other algae, and greater tolerance to high temperatures (Nalewajko et al., 2001). In November, with a decrease in temperature, the phytoplankton cell abundance significantly decreased, and the vertical variation in cell abundance was smaller, with Bacillariophyta becoming the dominant group. Bacillariophyta are better adapted to low water temperature and limited light availability (Sheng et al., 2016). Moreover, the water temperature in the reservoir during the monitoring period was ~20 °C, which is optimal for diatom growth. The cell abundance of phytoplankton in November was significantly lower than that in July, mainly because of the preference of algae, especially Cyanophyta and Chlorophyta, for higher temperatures and sufficient light. Additionally, in November,

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

the upstream inflow volume increased with the flow rate, leading to an increase in the diatom proportion in the unstable water column (An et al., 2000).

The explanatory power of PP on the phytoplankton community structure was greater than that of TDP. Related studies have shown that most of the organic phosphorus in suspended particulate matter in the water column is released during sedimentation or after settling, thereby providing a major source of bioavailable organic phosphorus for algae. Although the TDP concentrations in some water columns are low, the risk of algal blooms remains (Jin et al., 2023). In this study, 50.58% of the variance could not be explained. This may be because some limiting factors, such as zooplankton grazing and hydrological dynamics, were not included in the study scope, which can also influence the structure of phytoplankton communities (Wu et al., 2023). Moreover, VPA cannot quantitatively explain the effects of species interactions (Huang et al., 2023), indicating the need for further analysis of interspecies relationships among phytoplankton.

Conclusions

(1) The community structure of the Danjiangkou Reservoir exhibited differences during different thermal stratification periods. During the stable thermal stratification period, Cyanophyta and Chlorophyta were dominant, with cell abundance decreasing vertically with increasing depth. Additionally, significant differences in community structure were observed between layers A and B and layers C, D, and E. During the thermal stratification breakdown period, Bacillariophyta dominated and vertical changes in cell abundance were minimal, with significant differences in community structure between D and other water layers.

(2) WT and PP were the main driving factors influencing the vertical variation in phytoplankton community structure, with explanatory rates of 14.34% and 19.14%, respectively.

Funding. This research was funded by the Major Science and Technology Project of the Ministry of Water Resources (SKS-2022058).

REFERENCES

[1] An, K.-G., Jones, J. R. (2000): Factors Regulating Bluegreen Dominance in a Reservoir Directly Influenced by the Asian Monsoon. – Hydrobiologia 432: 37-48.

[2] Becker, V., Huszar, V. L. M., Naselli-Flores, L., Padisak, J. (2008): Phytoplankton Equilibrium Phases during Thermal Stratification in a Deep Subtropical Reservoir. – Freshwater Biology 53(5): 952-963.

[3] Cabecinha, E., Cortes, R., Cabral, J. A., Ferreira, T., Lourenço, M., Pardal, M. Â. (2009): Multi-Scale Approach Using Phytoplankton as a First Step towards the Definition of the Ecological Status of Reservoirs. – Ecological Indicators 9(2): 240-255.

[4] Cui, Z., Gao, W., Li, Y., Wang, W., Wang, H., Liu, H., Fan, P., Fohrer, N., Wu, N. (2023): Dissolved Oxygen and Water Temperature Drive Vertical Spatiotemporal Variation of Phytoplankton Community: Evidence from the Largest Diversion Water Source Area. – International Journal of Environmental Research and Public Health 20(5): 4307.

[5] Dupuis, A. P., Hann, B. J. (2009): Warm Spring and Summer Water Temperatures in Small Eutrophic Lakes of the Canadian Prairies: Potential Implications for Phytoplankton and Zooplankton. – Journal of Plankton Research 31(5): 489-502.

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

[6] Falkowski, P. G., Laws, E. A., Barber, R. T., Murray, J. W. (2003): Phytoplankton and Their Role in Primary, New, and Export Production. – In: Fasham, M. J. R. (ed.) Ocean Biogeochemistry. Global Change, The IGBP Series (closed). Springer, Berlin, Heidelberg pp. 99-121.
[7] Ficker, H., Luger, M., Gassner, H. (2017): From Dimictic to Monomictic: Empirical Evidence of Thermal Regime Transitions in Three Deep Alpine Lakes in Austria Induced by Climate Change. – Freshwater Biology 62(8): 1335-1345.
[8] Fornarelli, R., Antenucci, J. P., Marti, C. L. (2013): Disturbance, Diversity and Phytoplankton Production in a Reservoir Affected by Inter-Basin Water Transfers. – Hydrobiologia 705: 9-26.
[9] Geng, M., Niu, Y., Liao, X., Wang, K., Yang, N., Qian, Z., Li, F., Zou, Y., Chen, X., Deng, Z., Xie, Y. (2022): Inter-annual and intra-annual variations in water quality and its response to water-level fluctuations in a river-connected lake, Dongting Lake, China. – Environmental Science and Pollution Research 29: 14083-14097.
[10] Habib, O., Tippett, R., Murphy, K. (1997): Seasonal Changes in Phytoplankton Community Structure in Relation to Physico-Chemical Factors in Loch Lomond, Scotland. – Hydrobiologia 350: 63-79.
[11] Hecky, R., Kilham, P. (1988): Nutrient Limitation of Phytoplankton in Freshwater and Marine Environments: A Review of Recent Evidence on the Effects of Enrichment. – Limnology and Oceanography 33(4part2): 796-822.
[12] Huang, Z., Pan, B., Zhao, X., Liu, X., Liu, X., Zhao, G. (2023): Hydrological Disturbances Enhance Stochastic Assembly Processes and Decrease Network Stability of Algae Communities in a Highland Floodplain System. – Science of the Total Environment 903: 166207.
[13] Jia, H. Y., Xu, J. F., Lei, J. S. (2019): Relationship of community structure of phytoplankton and environmental factors in Danjiangkou Reservoir. – Yangtze River 50(5): 52-58.
[14] Jin, Z., Liao, P., Jaisi, D. P., Wang, D., Wang, J., Wang, H., Jiang, S., Yang, J., Qiu, S., Chen, J. (2023): Suspended Phosphorus Sustains Algal Blooms in a Dissolved Phosphorus-Depleted Lake. – Water Research 241: 120134.
[15] Kraemer, B. M., Anneville, O., Chandra, S., Dix, M., Kuusisto, E., Livingstone, D. M., Rimmer, A., Schladow, S. G., Silow, E., Sitoki, L. M., Tamatamah, R. (2015): Morphometry and Average Temperature Affect Lake Stratification Responses to Climate Change. – Geophysical Research Letters 42(12): 4981-4988.
[16] Lagus, A., Suomela, J., Weithoff, G., Heikkilä, K., Helminen, H., Sipura, J. (2004): Species-Specific Differences in Phytoplankton Responses to N and P Enrichments and the N: P Ratio in the Archipelago Sea, Northern Baltic Sea. – Journal of Plankton Research 26(7): 779-798.
[17] Lindholm-Lehto, P. C., Vielma, J. (2019): Controlling of Geosmin and 2-Methylisoborneol Induced off-Flavours in Recirculating Aquaculture System Farmed Fish: A Review. – Aquaculture Research 50(1): 9-28.
[18] Liu, M., Zhang, Y., Shi, K., Zhu, G., Wu, Z., Liu, M., Zhang, Y. (2019): Thermal Stratification Dynamics in a Large and Deep Subtropical Reservoir Revealed by High-Frequency Buoy Data. – Science of the Total Environment 651: 614-624.
[19] McNaughton, S. J. (1967): Relationships among Functional Properties of Californian Grassland. – Nature 216(5111): 168-169.
[20] Nalewajko, C., Murphy, T. P. (2001): Effects of Temperature, and Availability of Nitrogen and Phosphorus on the Abundance of Anabaena and Microcystis in Lake Biwa, Japan: An Experimental Approach. – Limnology 2: 45-48.
[21] O'Keeffe, J. (2004): Measuring biological diversity. – Journal of the Limnological Society of Southern Africa 29(2): 285-286.
[22] Padisák, J., Borics, G., Grigorszky, I., Soróczki-Pintér, É. (2006): Use of Phytoplankton Assemblages for Monitoring Ecological Status of Lakes within the Water Framework Directive: The Assemblage Index. – Hydrobiologia 553: 1-14.

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

[23] Paerl, H. W., Gardner, W. S., Havens, K. E., Joyner, A. R., McCarthy, M. J., Newell, S. E., Qin, B., Scott, J. T. (2016): Mitigating Cyanobacterial Harmful Algal Blooms in Aquatic Ecosystems Impacted by Climate Change and Anthropogenic Nutrients. – Harmful Algae 54: 213-222.
[24] Pan, Y., Guo, S., Li, Y., Yin, W., Qi, P., Shi, J., Hu, L., Li, B., Bi, S., Zhu, J. (2018): Effects of Water Level Increase on Phytoplankton Assemblages in a Drinking Water Reservoir. – Water 10(3): 256.
[25] Shannon, C. E. (1948): A mathematical theory of communication. – Bell System Technical Journal 27: 379-423.
[26] Sheng, X., Xu, H., Deng, P., Mao, J., Liu, W. (2016): Temporal and spatial pattern of phytoplankton community and its affected factors of Shiyan Reservoir. – Ecological Science 35(01): 17-26.
[27] Shi, J., Wang, L., Yang, Y., Huang, T. (2022): A Case Study of Thermal and Chemical Stratification in a Drinking Water Reservoir. – Science of The Total Environment 848: 157787.
[28] State Environmental Protection Administration (2002): Water and Wastewater Monitoring and Analysis Methods (Fourth Edition). – Editorial Board of the Water and Wastewater Monitoring and Analysis Methods. Bei Jing: China Environmental Science Press.
[29] Stockwell, J. D., Doubek, J. P., Adrian, R., Anneville, O., Carey, C. C., Carvalho, L., De Senerpont Domis, L. N., Dur, G., Frassl, M. A., Grossart, H.-P., Ibelings, B. W. (2020): Storm Impacts on Phytoplankton Community Dynamics in Lakes. – Global Change Biology 26(5): 2756-84.
[30] Tang, X., Wu, M., Dai, X., Chai, P. (2014): Phosphorus Storage Dynamics and Adsorption Characteristics for Sediment from a Drinking Water Source Reservoir and Its Relation with Sediment Compositions. – Ecological Engineering 64: 276-284.
[31] Wang, Y. H., Chen, L., Niu, Y., Yu, H., Luo, M. K. (2016): Spatio-temporal variation in phytoplankton community and its influencing factors in Danjiangkou Reservoir. – Lake Sci 28(5): 1057-1065.
[32] Wang, F. (2020): Impact of a Large Sub-Tropical Reservoir on the Cycling of Nutrients in a River. – Water Research 186: 116363.
[33] Wang, H., Li, Y., Li, Y., Liu, H., Wang, W., Zhang, P., Fohrer, N., Li, B.-L., Zhang, Y. (2024): Phytoplankton Communities' Response to Thermal Stratification and Changing Environmental Conditions in a Deep-Water Reservoir: Stochastic and Deterministic Processes. – Sustainability 16(7): 3058.
[34] Woolway, R. I., Simpson, J. H., Spiby, D., Feuchtmayr, H., Powell, B., Maberly, S. C. (2018): Physical and Chemical Impacts of a Major Storm on a Temperate Lake: A Taste of Things to Come? – Climatic Change 151: 333-347.
[35] Wu, Z., Liu, M., Lan, J., He, J., Yu, Z. (2012): Vertical distribution of phytoplankton and physico-chemical characteristics in the lacustrine zone of Xin'anjiang Reservoir (Lake Qiandao) in subtropic China during summer stratification. – Journal of Lake Sciences 24(03): 460-465.
[36] Wu, S., Dong, Y., Stoeck, T., Wang, S., Fan, H., Wang, Y., Zhuang, X. (2023): Geographic Characteristics and Environmental Variables Determine the Diversities and Assembly of the Algal Communities in Interconnected River-Lake System. – Water Research 233: 119792.
[37] Xin, X., Li, K., Finlayson, B., Yin, W. (2015): Evaluation, Prediction, and Protection of Water Quality in Danjiangkou Reservoir, China. – Water Science and Engineering 8(1): 30-39.
[38] Xu, Y., Li, A. J., Qin, J., Li, Q., Ho, J. G., Li, H. (2017): Seasonal Patterns of Water Quality and Phytoplankton Dynamics in Surface Waters in Guangzhou and Foshan, China. – Science of the Total Environment 590: 361-369.

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669

[39] Yin, W., Wang, C., Wang, L., Xin, X., Liu, G. (2023): Spatial and temporal distribution characteristics and influencing factors of total phosphorus in Danjiangkou Reservoir. – Yangtze River 54(01): 1-7+10.
[40] Yu, Q., Lin, L., Jin, H., Chen, L. (2024): Features of spatial and temporal distribution of nitrogen and phosphorus in the Danjiangkou Reservoir and safeguarding measures for water quality. – China Water Resources, pp. 1-8.
[41] Yue, Z., Chen, Y., Wu, Z., Cheng, X., Bao, Z., Deng, X., Shen, H., Liu, J., Xie, P., Chen, J. (2024): Thermal Stratification Controls Taste and Odour Compounds by Regulating the Phytoplankton Community in a Large Subtropical Water Source Reservoir (Xin'anjiang Reservoir). – Journal of Hazardous Materials 466: 133539.
[42] Zhang, C., Song, D., Lian, T. (2020): The influences of the water diversion structure change on total phosphorus retention and implication for ecological flows in Yugiao Reservoir, Tianjin. – Journal of Lake Sciences 32(02): 370-379.
[43] Zhang, C., Nong, X., Behzadian, K., Campos, L. C., Chen, L., Shao, D. (2024): A New Framework for Water Quality Forecasting Coupling Causal Inference, Time-Frequency Analysis and Uncertainty Quantification. – Journal of Environmental Management 350: 119613.
[44] Zhao, Z., Wang, J., Zhang, Y., Jing, Z., Hou, Y., Sun, W., Wang, X. (2022): Phytoplankton community structure and biodiversity in the water source area along the middle route of South-to-North Water Transfer Project. – South-to-North Water Transfers and Water Science & Technology 20(05): 914-924.

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2306_1065510669