

Article

Seasonal Dynamics of Planktonic Algae in the Danjiangkou Reservoir: Nutrient Fluctuations and Ecological Implications

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Abstract: Freshwater reservoirs serve as vital water sources for numerous residential areas. However, the excessive presence of nutrients, such as nitrogen and phosphorus, stimulates rapid algal proliferation, leading to the occurrence of algal blooms. To prevent this phenomenon, it is imperative to conduct regular ecological surveys aimed at assessing water quality and monitoring the dynamic composition of aquatic biological communities within the reservoir's ecosystem. In this study, seasonal changes in water quality parameters and the spatial and temporal distribution of planktonic algae at 14 sampling sites in the Danjiangkou reservoir were analyzed. A total of 136 taxonomic units of planktonic algae were identified, belonging to 8 phyla, 41 families, and 88 genera, with the dominant algae belonging to the phyla Chlorophyta, Bacillariophyta, and Cyanophyta. The order of abundance of the algae was summer > autumn > spring > winter and Hanku > Intake > Danku > Outflow. WT, pH, DO, COD_{Mn}, and Chl a were the primary drivers influencing the changes in the planktonic algal community within the reservoir. Two dominant algae, *Chlamydomonas debaryana* and *Scenedesmus quadricauda*, were isolated and cultured indoors to simulate the growth behaviors of algae in the Danjiangkou reservoir. The results show that the growth of *C. debaryana* was severely limited by the temperature, light, and nutrient concentration, whereas the growth of *S. quadricauda* was slightly affected under different temperature and light conditions and could occur at low concentrations of nitrogen and phosphorus nutrients. With excess nutrient levels, excessive proliferation of *S. quadricauda* could potentially cause algal blooms. This study examined the growth characteristics of the dominant algae in the Danjiangkou reservoir under laboratory conditions and delved into their interdependencies with environmental factors, aiming to furnish a theoretical and experimental foundation for investigating algal community dynamics and preventing algal blooms within the freshwater reservoir.

Keywords: Danjiangkou reservoir; planktonic algae; environmental factors; nitrogen and phosphorus; water quality monitoring



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1. Introduction

Planktonic algae, as the source of oxygen and food for all other life forms, play essential roles in aquatic ecosystems [1]. The community structure, species composition, and seasonal variations in phytoplankton exhibit exceptionally close correlations with water quality, significantly impacting the energy and material cycles within aquatic ecosystems [2]. Apart from its crucial function in sustaining these ecosystems, phytoplankton also responds most directly to alterations in the aquatic environment [3]. Consequently, phytoplankton occupies a pivotal role in monitoring water quality [4]. In eutrophic water bodies, the dynamics of phytoplankton are significantly affected, as nutrients such as nitrogen and phosphorus provide abundant sources of nourishment for their growth [5]. Phytoplankton utilize these nutrients for photosynthesis and metabolism, thereby accelerating their growth and reproduction rates, which alters the community structure and dynamic processes of phytoplankton. Additionally, excessive growth of phytoplankton can lead to over-proliferation, resulting in an imbalance in the biological community structure of the water body [6]. In freshwater ecosystems, phytoplankton overgrowth can lead to the deterioration of water quality and affect biodiversity, which, in turn, affects biomes [7]. At present, studies on phytoplankton in freshwater reservoirs start with the detection of plankton and physicochemical indexes and then begin to develop correlations between the phytoplankton and environmental factors [8].

The South-to-North Water Diversion Project (SNWDP) is an important systematic water management project to mitigate the drastic decline of water resources in northern China [9]. The Danjiangkou reservoir, located in central China, is the largest artificial freshwater lake in Asia with a capacity of $290.5 \times 10^8 \text{ m}^3$. It has become the main water source of China's SNWDP and is a vital source of drinking water [10]. However, surface water bodies have experienced a concerning deterioration in terms of water quality in recent years, particularly due to the increased frequency of algal blooms, which have led to an increased risk of potential health impacts of drinking water. The water quality of the Danjiangkou reservoir is strictly related to the water safety for the residents of the cities near the project. Therefore, it is crucial to protect the water quality and the ecological environment of the Danjiangkou reservoir to promote sustainable development. Reports have shown a high abundance of phytoplankton in the Danjiangkou reservoir [11]. Alterations in the algal density and diversity serve as a crucial determinant of ecosystem functional characteristics and as a significant indicator for evaluating the influence of external disturbances on ecosystems [12]. However, the growth and physiology of phytoplankton in the reservoir have been less studied. Shen investigated and analyzed the phytoplankton in the Danjiangkou reservoir and found a total of 8 phyla, 60 genera, and 110 species of phytoplankton, with Chlorophyta, Cyanophyta, and Bacillariophyta as the main species [13]. In 2017, Jia monitored the phytoplankton community in the Danjiangkou reservoir four times in different seasons, and a total of 7 phyla and 57 genera of phytoplankton were identified with Bacillariophyta, Cyanobacteria, and Chlorophyta as the main species [14]. The correlation between the phytoplankton and environmental factors was mainly studied by Wang, showing that the main environmental factors that affect the composition of phytoplankton in the Danjiangkou reservoir were dissolved oxygen (DO), pH, total phosphorus (TP), and water temperature (WT) [15]. Liu investigated the relationship between environmental factors and the phytoplankton community using typical correspondence analysis and found that the phytoplankton abundance was obviously dynamic and mainly regulated by DO, TP, and ammonia nitrogen ($\text{NH}_4^+\text{-N}$) [3]. Liu also investigated the eukaryotic phytoplankton structures using high-throughput sequencing technology in 2019, and found that pH, $\text{NH}_4^+\text{-N}$, and nitrate nitrogen ($\text{NO}_3^-\text{-N}$) were the

most crucial environmental factors affecting the structure of the phytoplankton community in the Danjiangkou reservoir [16].

Along with its rapidly expanding economy, China is also facing the increasingly serious problem of eutrophication, especially in aquatic ecosystems of lakes and reservoirs [17,18]. Water bloom is the worst result of lake or reservoir eutrophication [19]. The phenomenon of water blooms in Dianchi Lake, Chaohu Lake, and Taihu Lake has caused serious environmental problems [20]. The Han River and other rivers have also begun to show similar eutrophic problems [21]. Regional water security is seriously threatened [22]. Algae are an important part of water ecosystems and the basis for maintaining water quality and species diversity in freshwater reservoirs [23]. Previous studies have demonstrated that the algal community's diversity and structure vary with the seasons and are influenced by environmental factors [24]. The dominance of cyanobacteria in summer and autumn has been observed in various studies, with its seasonal succession being significantly influenced by nitrogen concentration [25]. Eutrophication increases the abundance of phytoplankton in water bodies [26]. Even in the oligotrophic state, when the concentrations of nitrogen and phosphorus in the water are at low levels, some dominant planktonic algae, such as *Scenedesmus quadricauda*, can still grow rapidly [27], which may become a potential source of algal blooms. It is obvious that monitoring ecological and algal growth in reservoirs plays a very important role in water resource management and environmental protection.

In the present study, seasonal variations in water quality indices and the spatiotemporal distribution of planktonic algae across 14 sites in the Danjiangkou reservoir were analyzed. The results showed that Chlorophyta, Bacillariophyta, and Cyanophyta were the main components of the algae population in the reservoir, and their abundance varied significantly among different seasons and spatial locations. Laboratory experiments on two dominant species, *C. debaryana* and *S. quadricauda*, revealed distinct growth responses to temperature, light, and nutrient availability, highlighting the potential risk of algal blooms even in oligotrophic freshwater systems. Our results help to clarify the dynamics of algal blooms and water quality associated with impoundments in eutrophic freshwater systems and may lead to more sustainable management of such ecosystems. These findings offer valuable insights into algal ecology and can inform the development of targeted strategies to mitigate algal blooms and ensure the sustainability of freshwater resources, providing more effective safeguards for environmental protection and human health.

2. Materials and Methods

2.1. Overview of the Sampling Area and the Setting of Sampling Points

The Danjiangkou reservoir (32°56'~32°82' N, 111°39'~111°61' E) is located in central China between Danjiangkou City, Hubei Province, and Xichuan County, Henan Province. It is Asia's largest artificial freshwater lake. The reservoir is V-shaped, consisting of two parts, Hanku and Danku, with a total water area of about 1050 Km² and a total capacity of 290.5×10^8 m³. Taking into account the varying degrees of influence from human activities and the unique geographic location characteristics of the Danjiangkou reservoir, along with the long-term monitoring of water quality and ecological conditions within the reservoir area, a comprehensive sampling strategy was devised, resulting in the establishment of a total of 14 sampling points. A total of 8 sampling points were established in Danku (Dashiqiao (DSQ), Zhangying (ZY), Caowan (CW), Heijizui (HJZ), Songgang (SG), Kuxin (KX), Taizishan (TZS), and Qushou (QS), of which DSQ and ZY are located at the inlet of Danku, and QS is located in the intake point of the SNWDP) and 5 sampling sites were established in Hanku (BS, LHK, TJL, MGC and GJC, of which LHK and MGC are located at the intake of Hanku). Another sampling site was set up 100 m downstream of the outlet of the Danjiangkou Dam: Baxia (BX) (Figure 1). Note that the 14 sampling points were all far

from shore or located at the corner of the lake to avoid disturbance from human activities. The GPS information of each sampling point is provided in Supplementary Data S1.

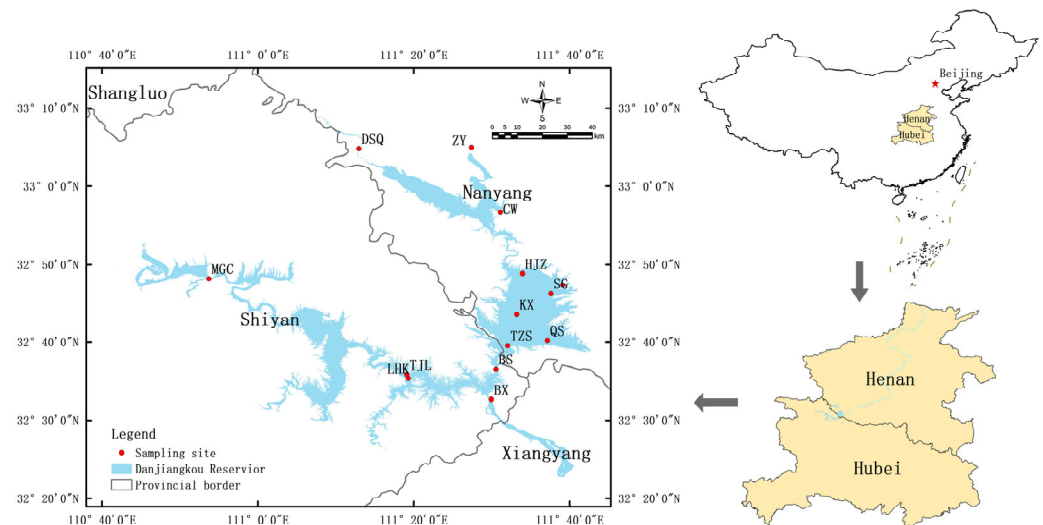


Figure 1. Overview of the distribution of the sampling points in the Danjiangkou reservoir.

2.2. Sample Collection and Data Processing

In this study, water samples and planktonic algae samples were collected six times in spring, summer, autumn, and winter from May 2021 to July 2022, respectively. According to the standard method [28], 2 L surface water samples were collected using a column water collector and stored at a low temperature and away from light. The permanganate index (COD_{Mn}), $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, TP, and TN in the water body were analyzed according to the Method of Monitoring and Analysis of Water and Wastewater [29]. The WT, pH, electrical conductivity (Cond), oxidation–reduction potential (ORP), and DO were determined on-site using a portable multi-parameter water quality tester (YSI Inc., Yellow Springs, OH, USA). The water transparency (SD) was measured using the Secchi disk method.

Planktonic algae samples were collected using a plankton net (with a mesh diameter of about 64 μm), which was dragged back and forth in the shape of “ ∞ ” at a water depth of 0.5 m from the surface for 5 min. The collected sample was placed in a 50 mL bottle. Formaldehyde was added, and the mixture was observed and photographed using a 400 $\times$ optical microscope (Olympus BX53, Japan). The morphology of the planktonic algae was identified by referring to an algae identification manual. The method used for collecting the quantitative planktonic algae samples was as follows: Surface water (2 L) was collected, and 30 mL of Lugol’s reagent was added. The mixture was well shaken and then kept still for 24 h. It was then concentrated to 100 mL, and the sediment was collected. Formaldehyde was used to fix the solution, and the cell number was counted under a microscope. Each sample was counted at least three times, and the average of these counts was calculated as the definitive result.

2.3. Analysis of Planktonic Algal Community Structure

The species dominance (Y) of the water samples was determined according to Mc-naughton’s dominance index, species was considered dominant when $Y \geq 0.02$. The Shannon–Wiener diversity index (H'), Margalef’s richness index (D), and Pielou’s evenness index (J) were used to characterize the diversity of the planktonic algae [15]. The formulae for each index were as follows:

$$Y = \frac{N_i}{N} * f_i \quad (1)$$

$$H' = -\sum_{i=1}^S P_i \ln P_i \quad (2)$$

$$D = (S - 1) / \ln N \quad (3)$$

$$J = H' / \ln S \quad (4)$$

where N_i is the total number of individuals of the species, N is the number of all species, f_i is the frequency of occurrence of the i th species at each point, P_i is the ratio of the number of individuals of the i th species to the total number of all individuals, and S is the total number of planktonic algal species in the sample.

Raw data collection and processing were performed using Excel 2019 (Microsoft, Redmond, DC, USA). Plots of changes in the planktonic algal abundance were drawn using Origin 2018 (Origin Lab, Northampton, PA, USA). Spatial and temporal differences in the environmental factors were explored using one-way ANOVA in SPSS 19.0 (IBM, Chicago, IL, USA). Heatmaps were plotted using R 3.6.2 (The R Programming Language, University of Auckland, New Zealand). The pheatmap package was used to depict the relationship between phytoplankton algae and the environmental factors, and boxplots were plotted using the ggplot2 package to depict the diversity of the phytoplankton algae.

2.4. Microalgae Isolation and Culture

The experimental algae were isolated using capillary separation techniques [30]. The dominant algae species were selected from the water samples under an inverted microscope and subsequently cultivated in 96-well plates, utilizing in situ water as the growth medium. As the cell density increased, the algal samples were progressively separated using the streak plate method, and liquid cultures were established using the BG11 medium. Under aseptic conditions, the algae inoculum was transferred into 250 mL conical flasks containing 100 mL of BG11 medium. The flasks were then sealed with sterile film and placed in a culture chamber maintained at 21 °C, with a light/dark cycle of 12 h each and a light intensity ranging from 15 to 50 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ for cultivation.

2.5. Identification of Dominant Algae in Water Samples

Samples of planktonic algae were collected, and the dominant algal cells were separated using the capillary separation method [31]. A single algal species was transferred to a 96-well plate containing BG11 medium and placed in an incubator set at 25 °C, with a light intensity of 30 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ under a light/dark cycle of 12 h/12 h. The sample was incubated for 10–15 d and then examined using a microscope. Single colonies of the algal samples were placed in a 2 L glass conical flask containing 500 mL of BG11 medium and incubated using a light incubator. The algae samples were centrifuged and washed with fresh BG11 medium, and then the morphological characteristics of the algal cells were observed and photographed using a light microscope and scanning electron microscope (SU8100, Hitachi). The genomic DNA of the algal cells was extracted using a plant genome kit, and the extracted genome was used as a template for PCR amplification of the 18S rDNA gene fragments, with the following primer sequences forward: 5'-CACCTGGTTGATCCTGCCAG-3' reverse: 5'-AGCTTGATCCTTCTGCAGGTTACCTAC-3'. The amplified DNA products were detected using electrophoresis, and the target DNA fragments were recovered and purified for sequencing. The sequencing results were applied online to Blast for sequence comparison. Based on the homologous similarity differences, the sequences with high similarity were downloaded from the National Center of Biotechnology Information (NCBI) database and analyzed using MEGA 7 software. A phylogenetic tree was constructed based on the neighbor-joining method to determine the taxonomic status of the alga.

2.6. Measurement of Algal Growth Parameters

The cell growth was determined as follows: First, mL of algal culture was collected, centrifuged at $1000\times g$ for 1 min and the supernatant was discarded. The cell pellets were washed twice by adding 1 mL of fresh BG11 medium, and then resuspended and placed in quartz cuvettes. The absorbance of samples at 680 nm was measured with a UV light spectrophotometer (PERSEE TU-1900, PERSEE PGENERAL, Beijing, China), with 3 repeats for each sample. The determination of the algal pigments was conducted as follows: First, 3 mL of algal culture was centrifuged at $1000\times g$ for 10 min. The supernatant was discarded, and 3 mL of 90% acetone (acetone/H₂O = 9:1) was added to the culture and mixed well until the cell precipitate became pale white. After centrifugation at $1000\times g$ for 10 min, the supernatant was collected, and the absorbance of the supernatant at 750 nm, 663 nm, 645 nm, 630 nm, and 450 nm was measured using a UV light spectrophotometer. The concentrations of Chl a and carotenoid (Car) were calculated according to Sun's method [32]. The quantitative data are presented as the arithmetic means $\pm$ standard deviations (means $\pm$ S.Ds., $n = 3$). *, $p < 0.05$, **, $p < 0.01$ (Student's *t*-test).

3. Results

3.1. Spatial and Temporal Dynamics of the Water Quality in the Danjiangkou Reservoir

The dynamic changes in the water physicochemical parameters in different seasons in the Danjiangkou reservoir are shown in Table 1. The highest WT was observed in summer, with a mean value of 29.3 °C. The pH was significantly lower in autumn than in the other seasons ($p < 0.05$), and the mean values of pH ranged from 7.65 to 8.85. The DO concentration was the highest in winter, with a mean value of 11.20 mg/L. The ORP was significantly higher in winter than in the other seasons ($p < 0.05$). There was a significant difference in the NO₃[−]-N concentration between spring and autumn ($p < 0.05$). A significant difference in the TP occurred between summer and the other seasons. The COD_{Mn} in spring and winter was significantly different from that in summer and in autumn. The value of Chl a was significantly higher in winter than in the other seasons ($p < 0.05$). The Cond, NH₃-N, TN, and SD were not significantly different among the seasons ($p > 0.05$).

Table 1. Physicochemical factors of the Danjiangkou reservoir in different seasons.

Index	Spring	Summer	Autumn	Winter
WT (°C)	19.5 $\pm$ 2.31 ^b	29.3 $\pm$ 3.43 ^a	21.58 $\pm$ 1.54 ^b	16.82 $\pm$ 2.05 ^c
pH	8.85 $\pm$ 0.50 ^a	8.53 $\pm$ 0.41 ^{ab}	7.65 $\pm$ 0.31 ^c	8.31 $\pm$ 0.56 ^b
DO (mg/L)	10.26 $\pm$ 1.58 ^a	8.93 $\pm$ 0.94 ^b	8.24 $\pm$ 1.15 ^b	11.20 $\pm$ 1.04 ^a
Cond (μS/cm)	298.86 $\pm$ 103.33	279.03 $\pm$ 80.89	356.63 $\pm$ 237.24	275.27 $\pm$ 60.55
ORP (mV)	125.30 $\pm$ 29.18 ^a	122.22 $\pm$ 28.26 ^a	106.92 $\pm$ 72.24 ^a	211.55 $\pm$ 40.45 ^b
NO ₃ [−] -N (mg/L)	1.23 $\pm$ 0.89 ^b	0.81 $\pm$ 0.22 ^{ab}	1.03 $\pm$ 0.57 ^a	1.41 $\pm$ 0.83 ^{ab}
NH ₄ ⁺ -N (mg/L)	0.47 $\pm$ 0.09	0.32 $\pm$ 0.08	0.16 $\pm$ 0.09	0.30 $\pm$ 0.09
TN (mg/L)	1.84 $\pm$ 0.52	1.62 $\pm$ 0.62	1.96 $\pm$ 1.14	2.08 $\pm$ 0.93
TP (mg/L)	0.03 $\pm$ 0.01 ^b	0.04 $\pm$ 0.02 ^a	0.02 $\pm$ 0.01 ^b	0.04 $\pm$ 0.03 ^b
COD _{Mn} (mg/L)	2.57 $\pm$ 0.42 ^b	2.09 $\pm$ 0.68 ^a	3.01 $\pm$ 0.63 ^a	3.27 $\pm$ 0.85 ^b
Chl a (μg/L)	3.67 $\pm$ 2.72 ^a	3.49 $\pm$ 2.94 ^a	3.85 $\pm$ 3.65 ^a	5.90 $\pm$ 2.48 ^b
SD (m)	3.28 $\pm$ 2.23	2.32 $\pm$ 1.98	2.42 $\pm$ 1.88	3.06 $\pm$ 1.47

The values are the arithmetic means $\pm$ standard deviations of the samples, and lowercase letters represent significant differences at $p < 0.05$.

The dynamic characteristics of the water quality among the different sampling sites in the Danjiangkou reservoir are shown in Table 2. Differences were observed in the WT, TN, TP, and COD_{Mn}, but not in the other indexes. There were significant differences ($p < 0.05$) in the WT at the Intake, Danku, and Outflow, with the Outflow having the lowest

WT and a mean value of 16.07 °C. The highest TN value was found at the Intake and was significantly different ($p < 0.05$) from that of the Danku and Hanku reservoirs. There was an obvious difference in the TP between the Intake and Danku, and the highest TP value was found in the Intake.

Table 2. Physicochemical factors of the Danjiangkou reservoir in different locations.

Index	Intake	Danku	Hanku	Outflow
WT (°C)	21.93 ± 5.26 ^a	22.75 ± 3.43 ^a	21.32 ± 1.54 ^{ab}	16.07 ± 2.05 ^b
pH	8.14 ± 0.72	8.43 ± 0.47	8.46 ± 0.79	8.11 ± 0.58
DO (mg/L)	9.88 ± 1.37	9.58 ± 1.96	9.71 ± 1.19	9.08 ± 1.86
Cond (μS/cm)	325.76 ± 111.63	312.26 ± 180.98	267.61 ± 52.24	245.04 ± 34.21
ORP (mV)	153.87 ± 70.50	134.15 ± 65.31	135.76 ± 44.85	160.66 ± 28.61
NO ₃ ⁻ -N (mg/L)	1.67 ± 0.97	0.95 ± 0.49	0.84 ± 0.44	1.03 ± 0.25
NH ₄ ⁺ -N (mg/L)	0.37 ± 0.25	0.30 ± 0.26	0.25 ± 0.14	0.37 ± 0.12
TN (mg/L)	2.47 ± 1.18 ^a	1.67 ± 0.58 ^b	1.71 ± 0.85 ^b	1.94 ± 0.48 ^{ab}
TP (mg/L)	0.05 ± 0.03 ^a	0.02 ± 0.02 ^b	0.03 ± 0.02 ^{ab}	0.04 ± 0.04 ^{ab}
COD _{Mn} (mg/L)	3.06 ± 0.80	2.65 ± 0.83	2.70 ± 0.67	2.19 ± 0.36
Chl a (ug/L)	4.82 ± 2.66	3.27 ± 1.99	4.51 ± 2.10	1.31 ± 0.80
SD (m)	1.17 ± 1.18	4.39 ± 0.98	1.99 ± 1.38	2.20 ± 0.1

The values are the arithmetic means ± standard deviations of the samples, lower case letters represent significant differences at $p < 0.05$.

3.2. Spatial and Temporal Distribution of Planktonic Algae

A total of 136 taxonomic units of planktonic algae were identified, belonging to 8 phyla, 41 families, and 88 genera (including varieties, Supplementary Data S2). Chlorophyta, Bacillariophyta, and Cyanophyta were found to be the dominant species. The order of species diversity was as follows: Chlorophyta > Bacillariophyta > Cyanophyta (Figure 2A). Among them, Chlorophyta had the maximum number of species, accounting for 42.65% of the total species identified. Bacillariophyta accounted for 29.41%, and Cyanophyta accounted for 13.24%, followed by Charophyta, Dinophyta, Euglenophyta, Cryptophyta, and Chrysophyta.

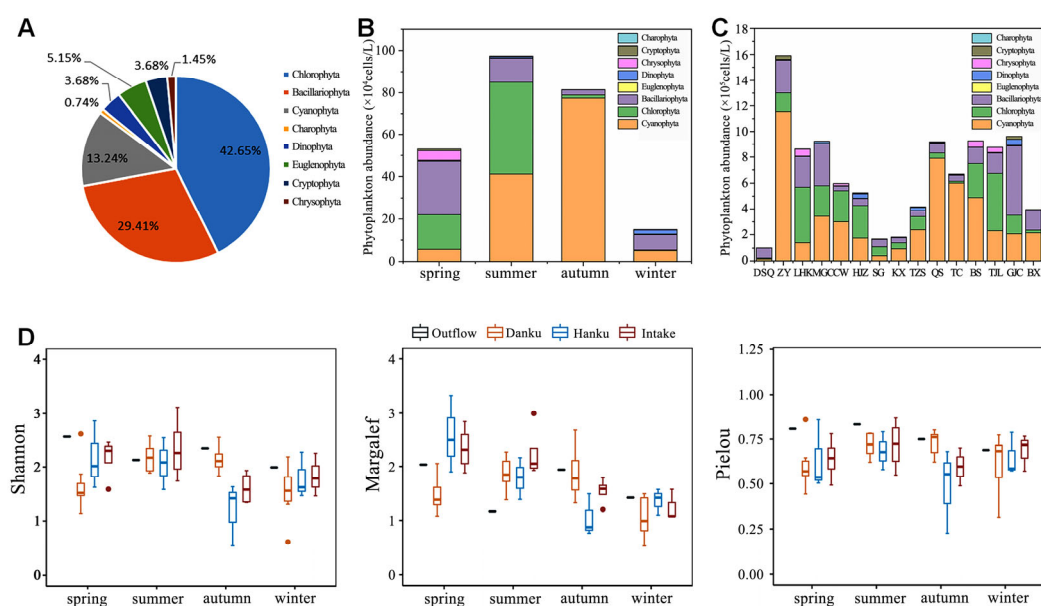


Figure 2. Characteristics of spatial and temporal distribution of planktonic algae in the Danjiangkou reservoir: Species composition (A). Temporal distribution characteristics (B). Spatial distribution characteristics (C). Diversity (D).

The abundance and relative composition of phytoplankton exhibited notable variations across different temporal and spatial scales. The average abundance of phytoplankton during the period of 2021–2022 was the highest in summer (9.74×10^5 cells/L), followed by that in autumn (8.14×10^5 cells/L), spring (5.31×10^5 cells/L), and winter (1.50×10^5 cells/L). In terms of community structure, the phytoplankton community structure fluctuated greatly among the different seasons (Figure 2B). In spring, Bacillariophyta was the dominant species, while in summer, Chlorophyta and Cyanophyta had the highest proportions, and Charophyta had the lowest proportion. In autumn, the phylum Cyanophyta was the most abundant. In winter, Bacillariophyta was the most abundant species. These results indicated that the dominant phytoplankton in the Danjiangkou reservoir were mainly Bacillariophyta in spring and winter, Chlorophyta and Cyanophyta in summer, and Cyanophyta in autumn.

Spatial analysis showed that the distribution of phytoplankton density in the Danjiangkou reservoir and tributaries showed significant differences (Figure 2C). The phytoplankton abundance in Hanku (BS-GJC) was significantly higher than that in the Intake (DSQ-ZY), and the phytoplankton abundance in Danku (LHK-QS) was significantly lower than that in the Outflow (BX). In terms of community structure, Bacillariophyta and Cyanophyta dominated in the Intake and Hanku reservoirs. Chlorophyta and Cyanophyta were the most abundant communities in the Danku reservoir.

Dynamic changes in phytoplankton community structures may lead to corresponding changes in the Shannon diversity index (H'), Margalef richness index (D), and Pielou evenness index (J). The phytoplankton diversity index H' in the Danjiangkou reservoir ranged from 0.61 to 3.12, and the richness index D ranged from 0.67 to 2.99. On the time scale, the phytoplankton diversity in spring and summer was higher than that in autumn and winter (Figure 2D). On the spatial scale, the phytoplankton diversity in the Danku reservoir was higher than that in the Hanku reservoir (Figure 2D). It is commonly accepted that higher values of the Shannon Wiener and Margalef indices indicate a more complex phytoplankton community structure, greater stability, and better water quality. Conversely, a smaller diversity index signifies a simpler community structure, poorer ecological stability, and poorer water quality. It is evident that the phytoplankton community structure in the Danjiangkou reservoir remained stable during spring and summer, and the water quality was superior to that of Hanku during autumn and winter.

3.3. Correlation Analysis Between Dominant Algae and Environmental Factors

Pearson correlation analysis was conducted between the dominant algae and environmental factors in the Danjiangkou reservoir (Figure 3). The results show that the WT was positively correlated with Cyanophyta, Chlorophyta, and Bacillariophyta. Chl a was positively correlated with Chlorophyta and Bacillariophyta, while pH was positively correlated with Bacillariophyta Chrysophyta, and Bacillariophyta, and negatively correlated with Cyanophyta. TP was positively correlated with Bacillariophyta but negatively correlated with Cyanophyta and Chlorophyta. TN was positively correlated with Chlorophyta and Bacillariophyta but negatively correlated with Chrysophyta.

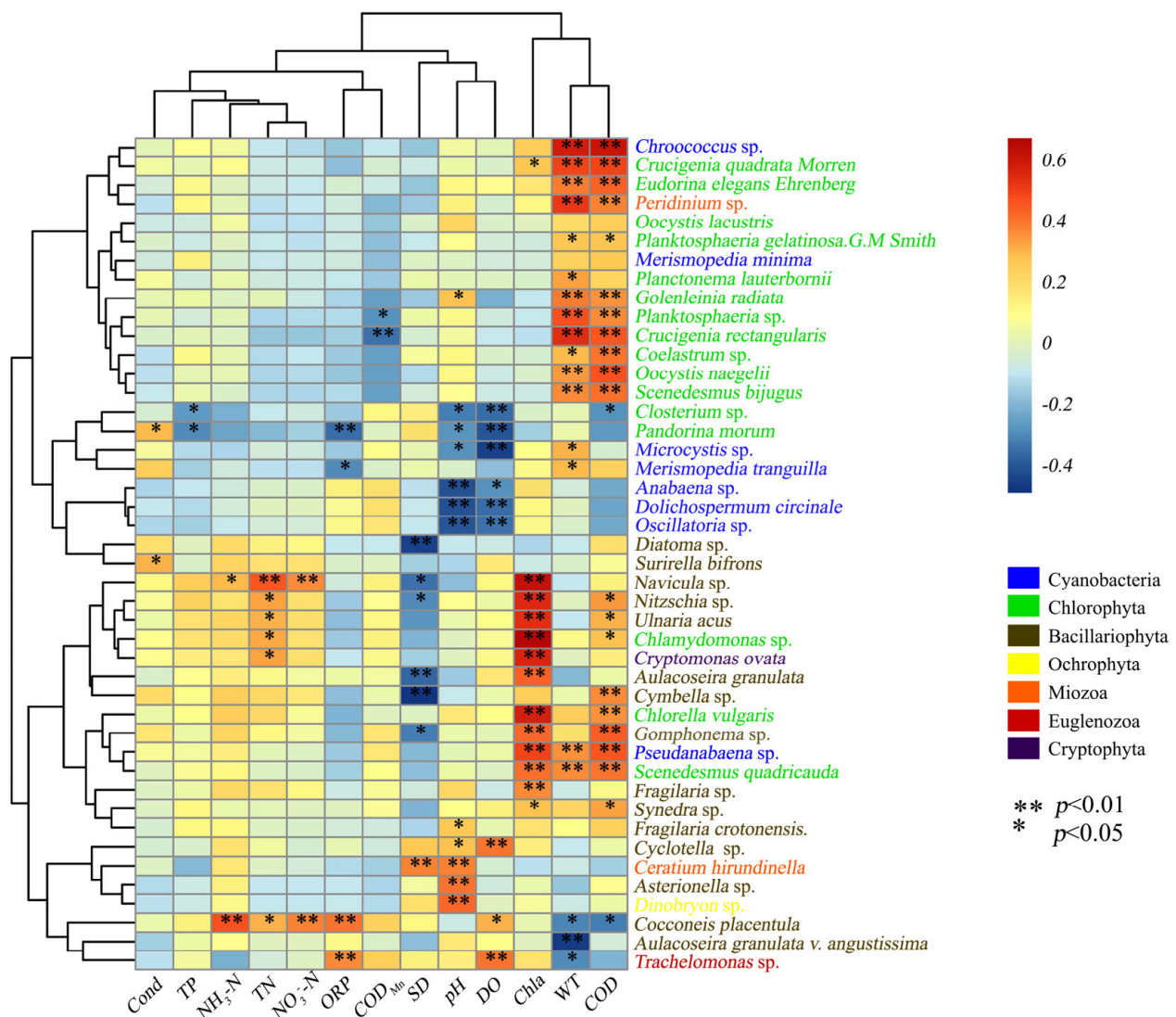


Figure 3. Correlation analysis between dominant algae and environmental factors.

3.4. Isolation and Identification of Dominant Algae Species from Danjiangkou Reservoir

The algae in the Danjiangkou reservoir were collected. Two strains, named CH–1 and CH–2, were isolated and cultured indoors. CH–1 displayed a unicellular, spherical, or ovate shape, with dimensions varying between 2.7 and 8.37 μm in length and between 2.17 and 7.8 μm in width. At the anterior end of the cells, two equal-length flagella were present, with the telescopic vesicles located at their bases. Additionally, near the anterior end of the cells, red eyespots were visible. Upon examination, large cup-shaped chromoplasts and amyloid nuclei were observed within the cells (Figure 4A,B). The CH–2 cells exhibited a spindle-shaped or oblong morphology, with dimensions ranging from 3.6 to 5.7 μm in length and from 2.1 to 4.1 μm in width. Predominantly, these cells occurred as singles, but they could also be found in groups of two or four. Inside the cells, lamellar or cup-shaped chromatophores were abundant, accompanied by one or two pyrenoids. Spines were visible at the upper and lower ends of the cell's outer surface (Figure 4D). The cell wall was characterized by granules, spines, or elevated lines (Figure 4D,E). The 18S rDNA analysis showed that CH–1 was in a clustered branch with 100% self-expansion support with the *Chlamydomonas debaryana* strain SAG26.72, indicating that CH–1 was close to *C. debaryana* (Figure 4C). The *Scenedesmus quadricauda* isolate SB40-3 was clustered into a single unit with 100% self-expansion support with CH–2, suggesting that CH–2 was the closest relative to *S. quadricauda* (Figure 4C). Based on the cell morphology observations and molecular

comparison, the dominant algal species CH-1 and CH-2 were identified as *C. debaryana* and *S. quadricauda*, respectively.

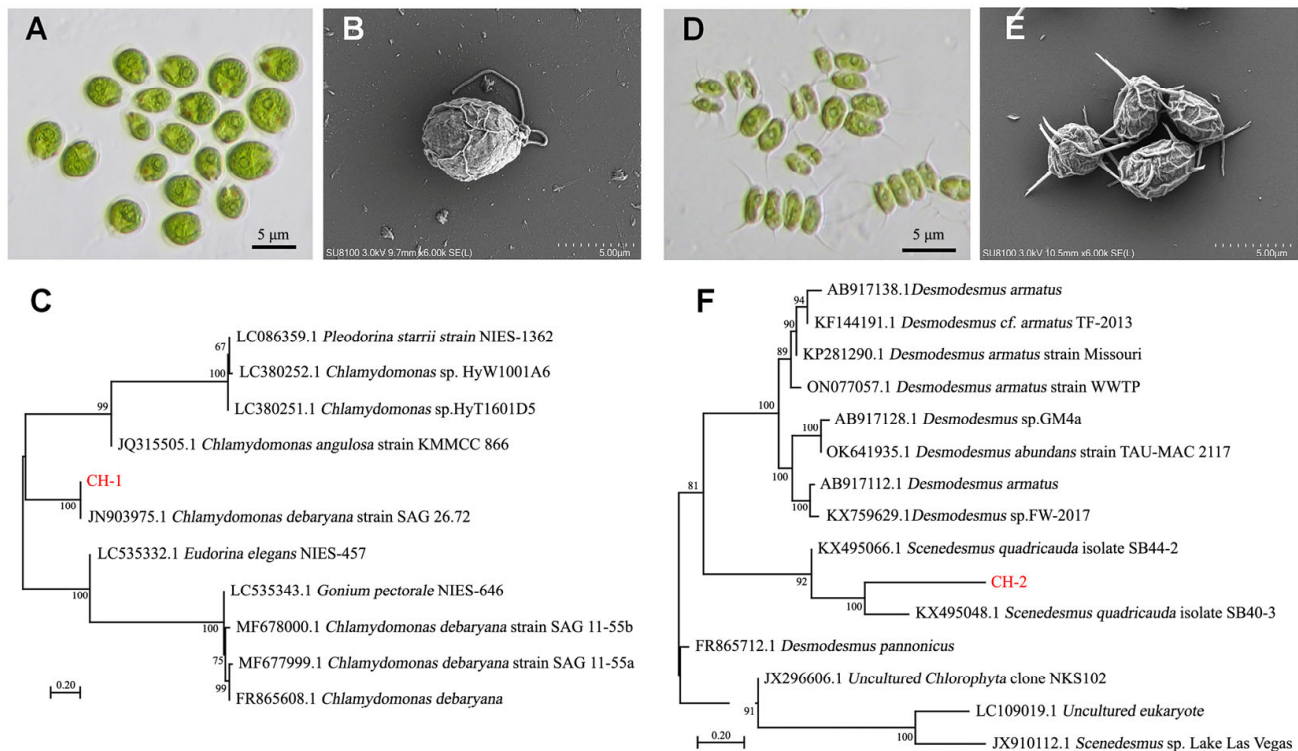


Figure 4. Microscopic observation and molecular identification of two dominant algal species: Microscopic observation (A,B) and evolutionary tree analysis (C) of CH-1. Microscopic observation (D,E) and evolutionary tree analysis (F) of CH-2.

3.5. Effects of Environmental Factors on the Growth of Dominant Algae

In order to better study the growth characteristics of planktonic algae in the reservoir, the growth conditions of two isolated algae were simulated under laboratory conditions. According to the physicochemical characteristics of the water in the Danjiangkou reservoir (Tables 1 and 2), the incubation temperature gradient was set at 15–35 °C, and the light intensity was set at 10–120 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$.

In the range of 15–25 °C, the growth of *C. debaryana* accelerated with increases in temperature, but its growth was inhibited when the temperature was higher than 30 °C. The optimum growth temperature for *C. debaryana* was 25 °C (Figure 5A–C). Meanwhile, the growth of *S. quadricauda* increased as the temperature increased (Figure 5D–F).

The growth of *C. debaryana* was strongly affected by light intensity. In the light intensity range from 10 to 90 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$, the growth of *C. debaryana* intensified with the increase in light intensity, and the concentrations of Chl a, and Car were increased (Figure 6A–C). The growth of *S. quadricauda* showed the same behavior at different light intensities, and the maximum growth was obtained at 30 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ (Figure 6D–F).

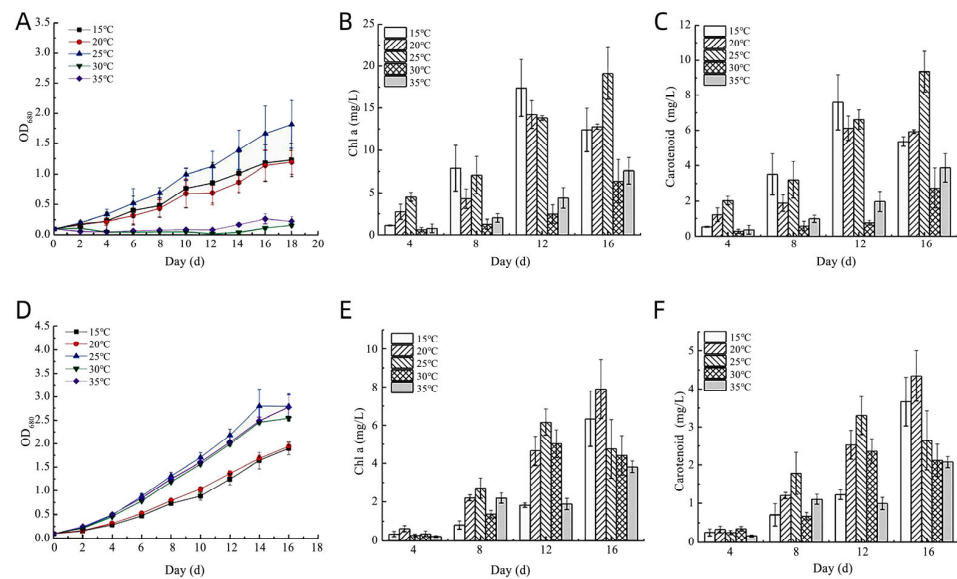


Figure 5. Effects of temperature on the growth behavior of *C. debaryana* and *S. quadricauda*. The cell density OD 680 (A,D), The content of Chl a (B,E), The content of Carotenoid (C,F). The quantitative data are presented as the means ± S.Ds. (n = 3).

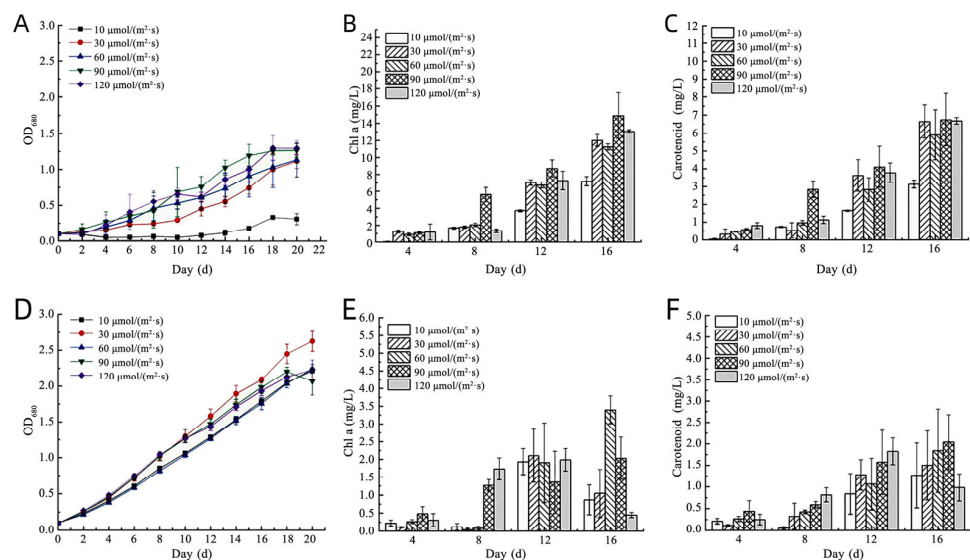


Figure 6. Effects of light on the growth behavior of *C. debaryana* and *S. quadricauda*. The cell density OD 680 (A,D), The content of Chl a (B,E), The content of Carotenoid (C,F). The quantitative data are presented as the means ± S.Ds. (n = 3).

3.6. Effects of Nutrient Concentrations on the Growth of Dominant Algae

Nutrient concentrations, particularly those of nitrogen and phosphorus, play a pivotal role in supporting algal growth and metabolism. To gain a deeper understanding of the growth behavior of planktonic algae in reservoirs in response to varying nutrient concentrations, a laboratory simulation was conducted to observe the growth of two isolated algae species under different levels of nitrogen and phosphorus nutrients. Five nitrogen concentrations of 0, 0.6, 1.2, 1.8, and 2.4 mg/L were set for NaNO_3 as the nitrogen source, and five phosphorus concentrations of 0, 0.01, 0.03, 0.05, and 0.25 mg/L were set for K_2HPO_4 as the phosphorus source. The results show that the growth of *C. debaryana* was inhibited in all three experimental groups with nitrogen concentrations lower than 1.8 mg/L. The highest cell density was even lower than the initial inoculum density (Figure 7A), and *C. debaryana* grew more slowly with increases in the nitrogen concentration, while the

cell pigments were still affected (Figure 7B,C). *S. quadricauda* grew slowly in the range of the set nitrogen concentrations. The cell density and pigment contents intensified with increases in the nitrogen concentration (Figure 7D). *C. debaryana* hardly grew at a 0~0.05 mg/L phosphorus concentration (Figure 8A) but started to grow when the phosphorus concentration increased to 0.25 mg/L (Figure 8). Meanwhile, the cell pigments also accumulated significantly only when the phosphorus concentration was higher than 0.05 mg/L (Figure 8B,C). *S. quadricauda* grew slowly in the set range of phosphorus concentration (Figure 8D), and the cell pigments reached a maximum value on the eighth day of incubation (Figure 8E,F). These results indicate that low nitrogen and phosphorus concentrations inhibited the growth of *C. debaryana* but did not affect the growth of *S. quadricauda*.

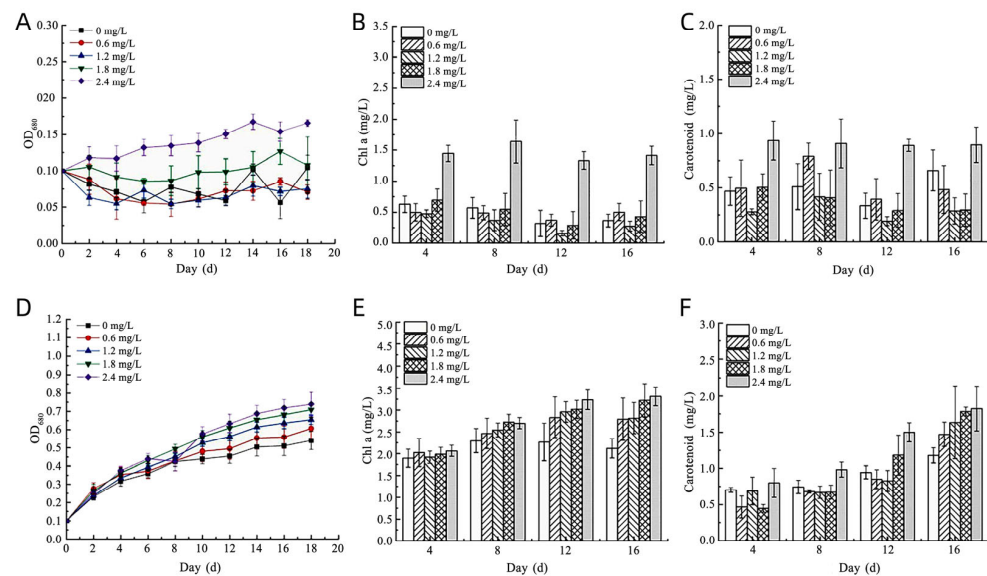


Figure 7. Effects of nitrogen on the growth behavior of *C. debaryana* and *S. quadricauda*. The cell density OD 680 (A,D), The content of Chl a (B,E), The content of Carotenoid (C,F). The quantitative data are presented as the means $\pm$ S.Ds. ($n = 3$).

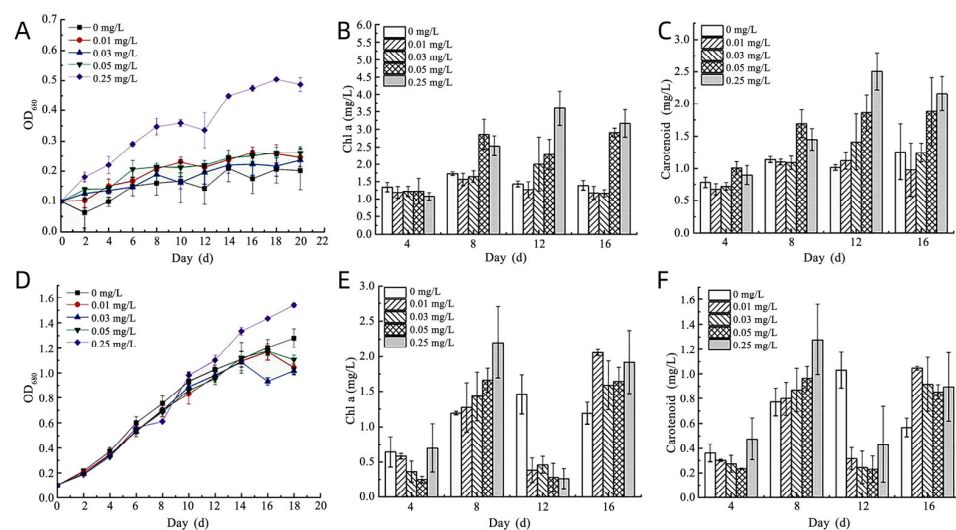


Figure 8. Effects of phosphorus on the growth behavior of *C. debaryana* and *S. quadricauda*. The cell density OD 680 (A,D), The content of Chl a (B,E), The content of Carotenoid (C,F). The quantitative data are presented as the means $\pm$ S.Ds. ($n = 3$).

4. Discussion

4.1. Spatial and Temporal Variation Patterns of Phytoplankton Community Structure and Their Interaction

The composition and structure of phytoplankton communities are directly influenced by the nutrient concentration, hydrodynamic properties, grazing pressure from zooplankton, and hydrological dynamics within the water body [8]. Furthermore, the impact of temporal and geospatial variations, which are significant factors, should not be overlooked [33]. In the present study, spanning the period from 2021 to 2022, a diverse array of 41 species of phytoplankton belonging to eight different phyla were observed. Notably, 44 species distributed across 7 phyla emerged as dominant species within the sampled ecosystem (Supplementary Data S2). Jia found that the community composition of the Danjiangkou reservoir was dominated by Bacillariophytas, Cyanobacteria, and Chlorophyta [14], which is consistent with the results of this study, indicating that the dominant species were Chlorophyta (42.65%), Bacillariophyceae (29.41%), and Cyanobacteria (13.24%) (Figure 2). The abundance and dominant species of phytoplankton in the Danjiangkou reservoir showed obvious differences among the seasons. Recent studies have shown that in reservoir areas, Bacillariophyta dominate the phytoplankton community primarily in spring, while Cyanophyta, Bacillariophyta, and Chlorophyta are all abundant in summer and autumn. During winter, Bacillariophyta and Cryptophyta are dominant [34]. In this study, 27 dominant species were found in spring, mainly in the phyla of Bacillariophytas and Chlorophyta (Supplementary Data S2), of which the main dominant species were *Cyclotella* sp., *Dinobryon* sp., and *Oocystis naegelii*. In summer, the dominant species were Cyanophyta, Chlorophyta, and Bacillariophyceae, and the main dominant species were *Cyclotella* sp., *Synedra* sp., and *Navicula* sp. In autumn, Cyanophyta and Bacillariophyceae dominated, with *Oscillatoria* sp. being the most dominant cyanobacteria. In winter, the dominant phylum was Bacillariophyceae, and the dominant species were *Cyclotella* sp., *Cocconeis placentula*, and *Navicula* sp. This is generally consistent with the fluctuation trend of the phytoplankton community structure in the Danjiangkou reservoir over the past decade. Spatially, the phytoplankton density in Hanku was significantly higher than that in Danku. The structure of phytoplankton in Danku was dominated by Bacillariophyceae, Cyanophyta, and Chlorophyta, and the community structure was relatively stable. The dominant phytoplankton groups in Hanku were more variable, and the dominant group structure of Cyanophyta, Chlorophytae, and Bacillariophyceae varied greatly (Figure 3). Although the storage capacities of Danku and Hanku are comparable, they exhibit significant differences in their respective shapes. Danku is a lake-type area with a wide water surface and short shoreline, while Hanku is a canyon-type reservoir with a long and narrow surface and many tributaries and winding banks, which receive a wide range of exogenous nutrients from surface runoff [35]. As the duration of impoundment continues, Hanku becomes increasingly conducive to the growth and reproduction of various types of algae. Consequently, the phytoplankton density observed in Hanku was notably higher than that in Danku.

The variations in the structure and diversity of phytoplankton communities are intricately intertwined with fluctuations in environmental factors. Notably, the environmental parameters that influence these communities exhibit varying degrees of significance, highlighting the multifaceted nature of their interactions [36]. Currently, researchers are focusing their efforts on elucidating the mechanisms by which environmental factors predominantly influence the structure of phytoplankton communities. This exploration primarily encompasses the following key aspects: In 2013, Jin conducted a redundancy analysis based on the relative frequency and abundance of phytoplankton in typical Baiyangdian waters and found that the TP, TN, pH, and DO concentrations were the key factors affecting the

distribution of phytoplankton [37]. In an experimental study conducted by Lijun Fang in 2014 that investigated the influence on phytoplankton community structure in a Xiangxi River cove, it was discovered that WT was the primary factor driving the succession of the phytoplankton community [38]. Increases in temperature can also impact the physical and chemical properties of the water, potentially affecting nutrient availability and oxygen levels. Xiaohong Zhang found that Bacillariophytas were adapted to grow in water at lower temperatures, with an optimum temperature of about 20 °C, while blue-green algae were suitable to grow in water at higher temperatures and an optimum temperature was 25–35 °C [39]. In the present study, *C. debaryana* grew better when the temperature increased to between 15 and 25 °C compared to higher temperatures between 30 and 35 °C. *S. quadricauda* grew faster in higher-temperature conditions from 30 to 35 °C, which indicates that *S. quadricauda* is more tolerant to high temperatures than *C. debaryana*. Light is a necessary condition for algal growth. When the external environmental conditions are certain, the optimal light intensities for different types of Chlorophytae are slightly different. This study found that low light conditions were not favorable for the growth and reproduction of *C. debaryana* and that its optimal light intensity was 90–120 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ (Figure 6). *S. quadricauda* was more adaptable to light intensity, and its growth was normal at 10–120 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$.

In this study, Pearson's correlation analysis was conducted to examine the relationships between three phytoplankton community indices (the Shannon–Wiener diversity index H' , the Pielou homogeneity index J , and Margalef species richness D) and environmental factors. It was found that the factors affecting the phytoplankton community characteristics were the WT, pH, DO, COD, and Chl *a*. Canonical correspondence analysis (CCA) highlighted the pH, nitrate levels, and dissolved oxygen as influential factors [40]. However, variations in phytoplankton indicators and analytical approaches may yield disparate results [41]. Phytoplankton rely on absorbing inorganic nutrients, including nitrate, nitrite, silicate, and phosphate, from the water for their growth and reproduction. Consequently, nutrient concentration plays a pivotal role in shaping phytoplankton communities [42]. Nitrogen and phosphorus, as the primary essential elements contributing to the primary productivity of aquatic ecosystems, have a direct impact on the productivity level of phytoplankton, are crucial limiting factors in the eutrophication process of water bodies, and play a pivotal role in sustaining the normal metabolic processes of algae [43]. In different water bodies and seasons, the sources and concentrations of nutrient salts can vary, resulting in changes in the type and amount of phytoplankton communities. Certain experimental findings have indicated that at elevated phosphorus concentrations, green algae tend to dominate phytoplankton communities [44]. In this study, an initial nitrogen concentration of 0.1 mg/L hindered the normal growth of the algae; however, when the nitrogen concentration was maintained within the range from 1.8 mg/L to 2.4 mg/L, the algae were able to grow normally. Similarly, when the phosphorus concentration ranged from 0.05 mg/L to 0.25 mg/L, a higher phosphorus concentration was observed to positively enhance the algal growth. This indicates that the alga has a high demand for both nitrogen and phosphorus. *C. debaryana* grew slowly within the given ranges of nitrogen and phosphorus concentrations, while the biomass of *S. quadricauda* increased significantly, suggesting that *S. quadricauda* has a relatively low demand for phosphorus.

4.2. Characterization of Algal Growth and Monitoring of Algal Blooms in Oligotrophic Water Bodies

The trophic state of a lake significantly influences the composition of its phytoplankton community. In oligotrophic lakes and reservoirs characterized by extremely low nutrient contents (especially nitrogen and phosphorus), the distribution of algae is notably sparse and limited in species diversity. Nevertheless, even a small number of algae is still a

potential threat that may have a significant impact on the water quality. In this experiment, it was noteworthy that *S. quadricauda* demonstrated the ability to grow normally even under conditions of low nutrient contents.

According to the Harmful Algal Events Database (HAEDAT), harmful algal blooms occur annually in over 200 countries and regions globally [45], giving rise to a myriad of environmental, social, and economic challenges. Presently, red tide outbreaks are prevalent in numerous domestic water sources, including Taihu [46], Dianchi [47], and Erhai Lakes [48]. These blooms not only drastically deteriorate water quality by compromising the transparency, dissolved oxygen content, and pH but also pose a severe threat to aquatic organisms by depleting vital nutrients and oxygen from the water. Following the demise of algal cells, the decomposition of the algal biomass remaining consumes substantial amounts of dissolved oxygen, resulting in oxygen depletion and the demise of aerobic organisms [49]. Additionally, they can cause fish kills, emit unpleasant odors in water bodies, and diminish the aesthetic appeal and water quality indicators of landscapes [50]. Lastly, some deceased algal cells release copious amounts of phycotoxins, significantly impacting drinking water quality and posing health risks to humans and animals [51]. Hence, the management and protection of oligotrophic lakes and reservoirs are paramount. It is imperative to intensify the monitoring and regulation of nutrients in water bodies, minimize external nutrient inputs, and be vigilant of factors such as climate change, which may adversely affect aquatic ecosystems. Through scientific management and effective conservation measures, by constructing artificial wetlands and restoring aquatic vegetation, we can enhance the self-purification capacity of water bodies and promote the recovery and development of phytoplankton communities. We can safeguard the stability of water quality and the well-being of aquatic ecosystems in oligotrophic lakes and reservoirs, thereby averting potential water bloom threats [52]. Thus, the mechanisms of nutrient regulation and algal outbursts in water, along with their prevention and control, have emerged as critical areas of water environment research and are critical issues currently being addressed worldwide [12].

4.3. Algal Surveys and Research Endeavors Within the Framework of Global Warming and Carbon Neutrality

Climate change and environmental pollution are among the most pressing issues confronting the globe [53]. In recent years, harmful algal blooms have emerged as a significant environmental challenge, with their frequency, intensity, duration, and spatial extent all intensifying in tandem with rising carbon dioxide (CO₂) levels and global temperatures [54]. Therefore, it is potentially valuable to reduce algal blooms by suppressing environmental factors (such as CO₂) that promote algal growth [55]. Algal blooms are seasonal in nature and require suitable conditions of temperature, light, and nutrients to reproduce [56]. As temperatures continue to rise, it is possible that the nutrient-rich conditions may be altered, leading to changes in the composition and abundance of phytoplankton populations [57]. This could potentially have cascading effects on the overall ecosystem. In this study, we found that *S. quadricauda* exhibited remarkable adaptability, particularly to high-temperature and oligotrophic aquatic environments, where it demonstrated swift growth (Figures 5 and 6).

Concurrently, human-induced water eutrophication creates conducive conditions for algae's explosive proliferation. Consequently, temperature fluctuations and increases in nutrient concentrations may collude to trigger algal blooms in water sources, posing a significant threat to water safety. *S. quadricauda* showed broad temperature tolerance and swift growth in oligotrophic waters, which would make it a significant potential contributor to algal blooms in reservoirs under future climate change scenarios. This study, by delving into algae species, distribution, growth characteristics, and their environmental interactions

in reservoir areas, revealed that temperature, light, and nutrient levels significantly impact algae growth. Based on the results of this study, measures to decrease nutrient (TN and TP) levels may help to limit algal blooms [58], and to provide a scientific foundation for water quality protection and reservoir management. Furthermore, closely monitoring and accurately predicting the occurrences and trends of algal blooms are actions that can be taken toward sustainable development to mitigate their detrimental impacts on water quality and human health [59]. Incorporating these insights into both policy formulation and practical applications will enable us to strive for the sustainable management of water resources amidst the challenges posed by climate change.

5. Conclusions

The present study conducted a comprehensive analysis of seasonal variations in water quality parameters and the spatial–temporal distribution of planktonic algae in the Danjiangkou reservoir. A total of 136 taxonomic units of planktonic algae were identified, belonging to 8 phyla, 41 families, and 88 genera. The dominant algae species were found to be closely correlated with factors such as the WT, pH, DO, COD_{Mn}, Chl a, and nutrients including TN and TP. Through indoor cultivation and simulation experiments, it was observed that *S. quadricauda* exhibited slight sensitivity to fluctuations in temperature and light conditions and could thrive under low concentrations of TN and TP. However, when the nutrient levels surpassed a certain threshold, excessive proliferation of *S. quadricauda* could occur, potentially triggering algal blooms. Our findings contribute to a deeper understanding of algal community dynamics in freshwater reservoirs and provide a theoretical and experimental basis for monitoring algal blooms. In particular, this study underscores the importance of TN and TP in stimulating algae growth and their role in shaping phytoplankton communities. Monitoring algal blooms in oligotrophic lakes, such as the Danjiangkou reservoir, is crucial for maintaining water quality and ensuring water safety. Given the adaptive capabilities of certain algae species, such as *S. quadricauda*, to high-temperature and oligotrophic conditions, a multifaceted approach is required to effectively manage and mitigate algal blooms. Developing integrated management strategies, exploring biological control measures, and considering the impacts of climate change will be pivotal in maintaining the ecological health of oligotrophic lakes and ensuring the sustainability of water resources for future generations.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/su17020406/s1>, Data S1. The GPS information of the sampling point in the study; Data S2. Dominant phytoplankton species and their dominance in the Danjiangkou Reservoir in different seasons.

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