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Research Article

Response of phytoplankton communities to environmental parameters in the rivers of the Khersan Sub-Basin in Chaharmahal and Bakhtiari Province

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Abstract

Understanding the influence of abiotic factors on the phytoplankton communities is essential for the effective management of aquatic ecosystems. This study was conducted in the Khersan sub-asin, encompassing the Marbareh, Bashar, and Khersan rivers. Seasonal sampling was carried out at five selected stations to assess physicochemical variables and phytoplankton community composition with the aim of evaluating the effects of abiotic parameters on these communities. A total of 55 phytoplankton taxa belonging to four phyla were identified, with Bacillariophyta representing 74.6%. of the total taxa. Non-metric multidimensional scaling (nMDS) revealed that phytoplankton community structure was primarily driven by seasonal variation, with samples clustering distinctly by season, whereas spatial differences among sampling stations had a comparatively minor influence. PERMANOVA confirmed a significant seasonal effect on phytoplankton composition (p<0.001). SIMPER analysis indicated that phytoplankton assemblages were more stable during the colder seasons, exhibiting higher within-season similarity in autumn (67.8%) and winter (51.8%) than in the more variable spring (34.7%) and summer (31.7%) communities. Diversity indices did not differ significantly among sampling stations, whereas species richness varied significantly across seasons (p<0.001). DistLM marginal tests identified six environmental variables that individually had a significant relationship with phytoplankton community structure (p<0.05), with pH showing the strongest individual effect and explaining 17.4% of the variation in the resemblance matrix. The optimal model, selected using the Akaike Information Criterion (AIC), included seven variables water temperature, dissolved oxygen, NH_3, NO_2^-, pH, total organic matter, and discharge, which together explained 71.0% of the total variation. Overall, the findings indicate that phytoplankton community structure in the Khersan sub-basin is jointly regulated by hydrological conditions, seasonal dynamics, and trophic status. The predominance of diatoms throughout most of the study period suggests a relatively stable ecosystem with no evidence of severe eutrophication. These findings provide a valuable baseline for future ecological monitoring, conservation planning, and sustainable management of the Khersan sub-basin.

Introduction

The Khersan River is located in southwestern Iran, and it is one of the most significant sub-basins of the Karun River in terms of flow volume. It is one of the most significant rivers that discharge into the Karun River. Flowing through the Zagros Mountains, the river supports a diversity of aquatic habitats and is of significant ecological and economic importance to the region. While hydraulic development in this area may be beneficial under certain circumstances, the risks may be significant (Zhang *et al*., 2019; Yaghoubzadeh *et al*., 2026). These may include alterations to the ecosystem as a result of changes to the flow of water, how long water stays in a specific area, the thermal regime of the water, the levels of Dissolved Oxygen, and the effects these changes may have on different living organisms (Nasrollahzadeh Saravi *et al*., 2017). When these alterations occur, concern about the relationship between changing environmental conditions and the structure of aquatic ecosystems is useful for the protection of the rivers and their ecosystems, as well as for managing these systems to ensure an adequate water supply.

River ecosystems, especially in developing countries, are under increasing pressure. Urban sprawl, industrial and agricultural development, and land-use changes have led to degraded river water quality in most regions (Ketola *et al*., 1988; Mustapha *et al*., 2013). Out of these pressures, the construction of dams has the most devastating impact on river ecosystems. This is because it disrupts the natural regime of river flow, severing river reaches, obstructs the movement of sediment, and replaces river ecosystems with stagnant water bodies and flow (Zhu *et al*., 2022). Climate variability, coupled with anthropogenic stressed ecosystems, also alters nutrient content and dissolved oxygen and the ecosystem equilibrium (Zhang *et al*., 2019).

Additionally, in Iran, freshwater ecosystems are becoming increasingly vulnerable to pollution. This is especially the case for rivers flowing through rural and urban settlements, because of increased population pressure and extensive human activities (Kamali *et al*., 2010). Unregulated human activities can compromise the ecological equilibrium of aquatic ecosystems, diminish their productivity, and change the composition and variety of life. Thus, to effectively manage a watershed system, the study of spatial and temporal changes of river water quality is crucial (Karimian *et al*., 2020).

Although water physico-chemical analyses provide essential data on the instantaneous state of water quality, they often fail to capture intermittent or long-term ecological shifts due to their snapshot nature. In contrast, biological assessments offer a more comprehensive perspective by integrating environmental stressors over extended periods. This is because aquatic organisms respond cumulatively to multiple stressors and habitat alterations, acting as continuous monitors of their environment. Consequently, biological assemblages serve as reliable indicators of long-term ecological health and can detect disturbances that transient chemical peaks might miss (Birk *et al*., 2020).

Phytoplankton are the primary producers in aquatic ecosystems. For this

reason, they are foundational to the food web. Changes in phytoplankton communities can signal changes in the aquatic system. Evidence has shown that nutrient enrichment in a water body can cause algal blooms and a change in the water's temperature, and anoxia can result in a reduction in diversity of the community and a change in the community structure (Protasov *et al.,* 2019; Kashani *et al*., 2025). In the interior waters of Iran, studies have shown that changes in temperature, total phosphorus, and water transparency can cause changes in the structure of the phytoplankton (Mohebbi *et al*., 2015; Fazli *et al*., 2022).

Due to the complexity of the systems, researchers have turned to multivariate statistical methods to study their functioning and ecological patterns. Most of the time, the PRIMER software package has been used to study the spatial distribution and seasonal changes of aquatic ecosystems and their connection to the environment. Methods such as nMDS, cluster analysis, SIMPER, PERMANOVA, DistLM, and dbRDA have proven useful for describing community patterns and identifying the environmental variables most strongly associated with them (Li *et al*., 2013; Mohebbi *et al*., 2015, 2016; Mirzajani *et al*., 2020; Gholizadeh, 2021; Fazli *et al*., 2022; Barroso *et al*., 2025; Gholizadeh *et al*., 2025). Despite the ecological importance of the Khersan sub-basin, research on plankton communities in this area remains limited, and no comprehensive study has yet examined the effects of environmental variables on phytoplankton community structure. Therefore, the present study aimed to investigate the spatial and seasonal distribution of phytoplankton communities in the Khersan sub-basin rivers and to assess the influence of environmental parameters on species diversity and community structure using a distance-based linear model (DistLM).

Materials and methods

Sampling Stations

The study was carried out along the Khersan River, downstream of the confluence of its two principal tributaries, the Marbareh and Bashar rivers. This reach has been identified as a priority zone for water abstraction and inter-basin transfer schemes intended to support local agriculture and industry. Field sampling covered four seasons: autumn 2023, winter, spring, and summer 2024, to capture temporal variability. Five sampling stations were established along the river corridor. Their locations (Fig. 1) were selected to maximize independence among sites and to represent the range of local conditions, taking into account surrounding land use, riverbank morphology, riparian vegetation, and ease of access.

Environmental Parameters

Sediment total organic matter (TOM) was determined gravimetrically, and grain size was analyzed using the sodium-hexametaphosphate dispersion method (Holme and McIntyre, 1984). Water temperature (W_T) was measured with a mercury thermometer. pH and electrical conductivity (EC) were measured with a WTW823 meter, and turbidity (Turb) with a turbidity meter. Dissolved oxygen (DO) and biochemical oxygen

demand (BOD_5) were determined by the Winkler method. Chemical oxygen demand (COD) was measured using the closed-reflux method (APHA, 2017). Nutrients (NH_4^+-N, NO_2^--N, NO_3^--N, PO_4^{3-}-P) were analyzed colorimetrically (indophenol blue, N-naphthylamine, cadmium reduction, and ammonium molybdate methods) with a CE2020 spectrophotometer (CECIL).

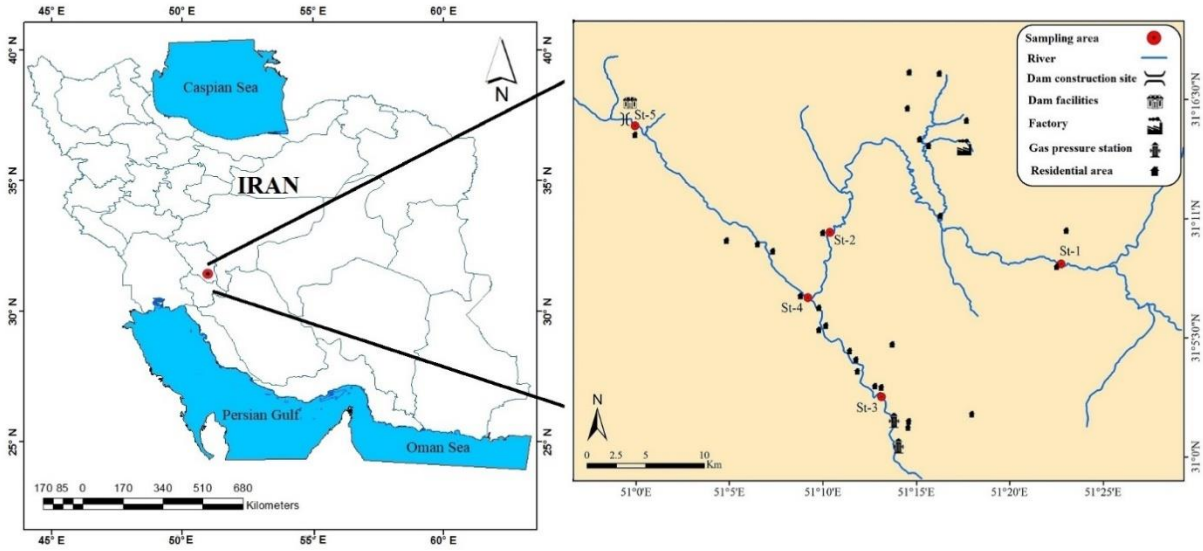

Figure 1: Location of sampling stations in the rivers of the Khersan sub-basin.

Phytoplankton sampling and analysis

At each station, three 1 L subsamples were combined to form a composite sample. A 500 mL aliquot was preserved in buffered neutral formalin (final concentration 0.5–2.0%). In the laboratory, samples were concentrated by dark sedimentation, careful siphoning of the supernatant, and centrifugation at 3000 rpm for 5 min, yielding a final volume of ~40–50 mL. After gentle decantation of the supernatant, 1–2 drops of the remaining concentrate were examined under a light microscope for qualitative assessment. Each sample was analyzed twice to determine species composition and obtain an approximate estimate of phytoplankton abundance. For quantitative counts, a 0.1 mL subsample was taken with a graduated piston pipette, mounted on a slide, and examined microscopically. Taxa were identified using standard floras (Wehr *et al*., 2015), and species-specific abundances were recorded. Phytoplankton density (individuals m^{-3}) was calculated from dilution and concentration factors following APHA (2017).

Statistical analysis

Data were first screened for errors and inconsistencies. Normality was evaluated with the one-sample Kolmogorov–Smirnov test, and data were transformed when necessary to satisfy parametric assumptions. Descriptive statistics and one-way ANOVA were used to analyze mean differences, followed by Duncan's multiple range test for significant results (Zar, 2010), with all analyses performed in SPSS v. 2024. Boxplots were generated to visualize

medians, quartiles, and extreme values, and Pearson's correlation coefficients were calculated to evaluate linear relationships among environmental variables. Graphical and correlation analyses were conducted in R using the packages ggplot2 (Wickham, 2016), gridExtra (Auguie, 2017), NADA (Helsel *et al*., 2020), corrplot (Wei and Simko, 2021), and Hmisc (Harrell, 2024), within the RStudio environment (RStudio 2025.09.0+387). Univariate diversity indices were calculated to evaluate phytoplankton community structure. Species richness (Margalef's index, *d*), Shannon–Wiener diversity index (*H'*), and Pielou's evenness index (*J'*) were computed for each sampling station and season using the DIVERS routine in the PRIMER software package (Clarke and Gorley, 2006). Multivariate analyses were performed to investigate spatial and seasonal patterns in community composition. Biological data matrices, consisting of species abundance values, were log (X+1) transformed prior to analysis to reduce the influence of highly abundant taxa. Bray–Curtis similarity coefficients were then calculated to quantify similarities among samples. Non-metric multidimensional scaling (nMDS) was applied to visualize spatial (among stations) and temporal (among seasons) patterns in phytoplankton community structure (Clarke and Warwick, 2001). PERMANOVA test with seasons was utilized to determine the reaction of these factors on phytoplankton species composition in the study area. Then, the significant test was analyzed with pairwise comparisons under 9999 permutations (Anderson *et al*., 2008). Similarity percentage (SIMPER) analysis was used to obtain information about changes in seasonal species composition (Clarke, 1993). A Distance-based Linear Model (DistLM) was used to analyze the relationships between phytoplankton taxa composition and environmental variables. Before the analysis, the highly correlated environmental variables were removed (Draftsman's plot> 0.8). DistLM was carried out based on the best procedure and Akaike's information criterion (AIC). The multivariate analysis was performed by PRIMER V.6 and PERMANOVA+ (Clarke and Warwick, 2001; Clarke and Gorley, 2006; Anderson *et al*., 2008).

Results

Environmental variables

Figure 2 and Table 1 highlight significant seasonal oscillations in environmental drivers, characterized by a strong interplay between hydrological regimes and water quality. Sediment dynamics showed a clear seasonal shift, with TOM increasing from 1.2±0.5 in spring to 2.6±1.4 in winter and 2.6±1.3 in autumn, while Sand fractions remained dominant overall and peaked in winter (93.3±9.3%) and autumn (92.9±9.0%). In contrast, S_C content was highest in summer (32.2 ± 28.1%) but declined sharply in winter (6.7±9.3%), indicating pronounced seasonal sorting of bed sediments. Turbidity showed the strongest variability, reaching 476.2±268.6 in spring, far above summer (4.1±2.6) and the colder seasons, suggesting episodic runoff-driven sediment pulses that may constrain light penetration and primary production. Water temperature ranged from 8.3±1.3°C in autumn to 21.9 ± 3.3 °C in

summer, while pH remained narrowly buffered between 8.2±0.1 and 8.6±0.1 across seasons. DO was highest in winter (10.9±0.4 mg L^{-1}) and lowest in spring (7.1±0.8 mg L^{-1}), whereas BOD_5 and COD increased to 4.4±0.9 mg $L^{-1}$and 21.1±2.5 mg L^{-1}, respectively, in summer and winter, reflecting seasonal shifts in organic loading. EC was relatively high throughout the year, peaking in autumn (515.2±49.2 ms/cm). Nutrient concentrations were generally low to moderate but exhibited distinct seasonal peaks: PO_4^{3-} reached 0.49±0.12 mg L^{-1} in summer, NH_4^+ was highest in autumn (0.208±0.14 mg L^{-1}), and NO_3^- peaked in winter (18.8±1.7 mg L^{-1}). Discharge was maximum in spring (54.9±8.7 m^3/sec) and lower in summer (29.8±7.8 m^3/sec), underscoring strong hydrological seasonality that likely regulates sediment transport, nutrient delivery, and overall river functioning.

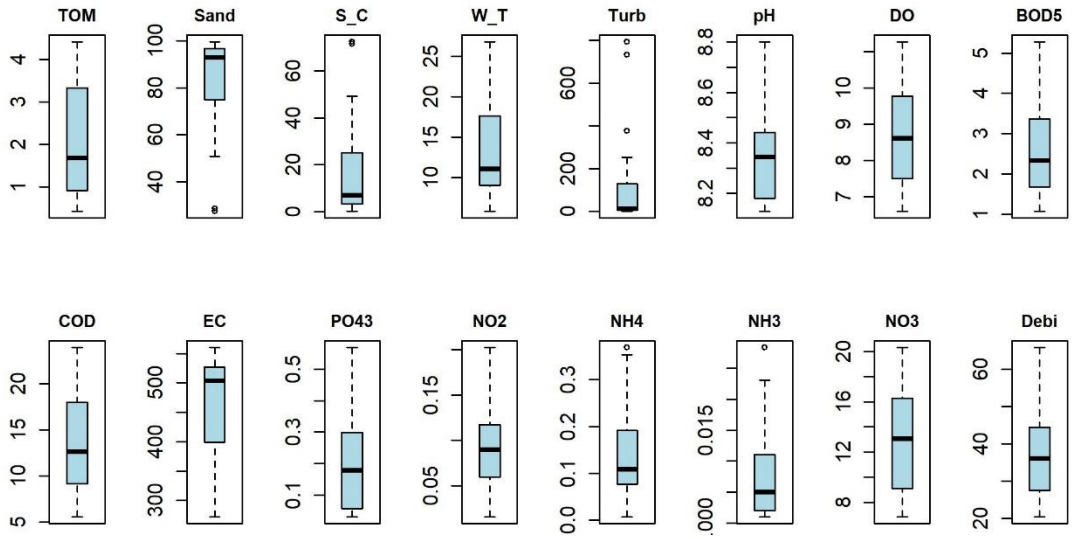

Figure 2: Box plots of variations in physical, chemical, and sediment parameters at sampling stations in the Khersan sub-basin rivers. See Table 1 for a key to environmental variables.

Correlation analysis of environmental variables

The correlation matrix (Fig. 3) showed several clear, strong relationships: sand was perfectly negatively correlated with S_C (r=–1.00); PO_4^{3-} was strongly positively correlated with W_T (r=0.92) and negatively correlated with NO_3^- (r=–0.75). DO and COD were strongly positively correlated (r=0.80), and discharge was strongly associated with turbidity (r=0.74). BOD_5 was strongly positively correlated with pH and NH_3 (r=0.82 and 0.81). NO_3^- had a moderate positive correlation with COD (r=0.66) and sand (r=0.48).

Spatial and seasonal phytoplankton community distribution

A total of 55 phytoplankton taxa were recorded across stations (Table 2), belonging to Bacillariophyta, Cyanobacteria, Chlorophyta, and Euglenozoa. Diatoms dominated the flora (74.6% of taxa), followed by Cyanobacteria and Chlorophyta (each 10.9%) and Euglenozoa (3.6%). nMDS ordination and

cluster analysis (Fig. 4) showed clear seasonal separation of communities, indicating strong sensitivity to changing conditions through the year.

Table 1: The seasonal mean (±SD) of environmental parameters in the rivers of the Khersan Sub Basin.

Parameter	Autumn	Winter	Spring	Summer	Total
TOM	2.6±1.3	2.6±1.4	1.2±0.5	1.8±1.5	2±1.3
Sand (%)	92.9±9	93.3±9.3	69.5±28.3	67.8±28.1	80.9±23
S_C (%)	7.1±9	6.7±9.3	30.5±28.3	32.2±28.1	19.1±23
W_T (°C)	8.3±1.3	9.7±2.5	14.1±3.5	21.9±3.3	13.5±6
Turb	11.9±12.2	12.3±3.6	476.2±268.6	4.1±2.6	126.1±241.3
pH	8.2±0.1	8.4±0	8.2±0.1	8.6±0.1	8.4±0.2
DO (mg L^{-1}l)	8.7±0.6	10.9±0.4	7.1±0.8	8.3±0.9	8.7±1.5
BOD_5 (mg L^{-1}l)	1.6±0.4	3.1±0.4	1.6±0.3	4.4±0.9	2.7±1.3
COD (mg L^{-1}l)	11.5±5.4	21.1±2.5	10.5±3.1	10.9±3.7	13.5±5.7
EC (ms/cm)	515.2±49.2	504.6±45	343.4±65.7	477.8±58.9	460.3±87
$PO4^{3-}$(mg L^{-1}l)	0.048±0.016	0.061±0.02	0.289±0.012	0.49±0.12	0.222±0.195
NO_2^-(mg L^{-1}l)	0.09±0.031	0.099±0.033	0.083±0.078	0.087±0.032	0.09±0.044
NH_4^+ (mg L^{-1}l)	0.208±0.14	0.136±0.091	0.099±0.054	0.122±0.076	0.141±0.097
NH_3 (mg L^{-1}l)	0.005±0.004	0.006±0.004	0.004±0.002	0.018±0.01	0.008±0.008
NO_3^- (mg L^{-1}l)	14.7±1.3	18.8±1.7	9.8±1.8	8.9±1.4	13±4.3
Discharge (m^3/sec)	33.7±9	32.2±8.6	54.9±8.7	29.8±7.8	37.7±13

TOM, total organic matter; S_C, silt & clay; W_T, water temperature; Turb, turbidity; DO, dissolved oxygen; BOD_5, biochemical oxygen demand; COD, Chemical oxygen demand; EC, electrical conductivity; $PO4^{3-}$, phosphate; NO_2^-, nitrite; NH_4^+, ammonium; NH_3, Ammonia; NO_3^- nitrate

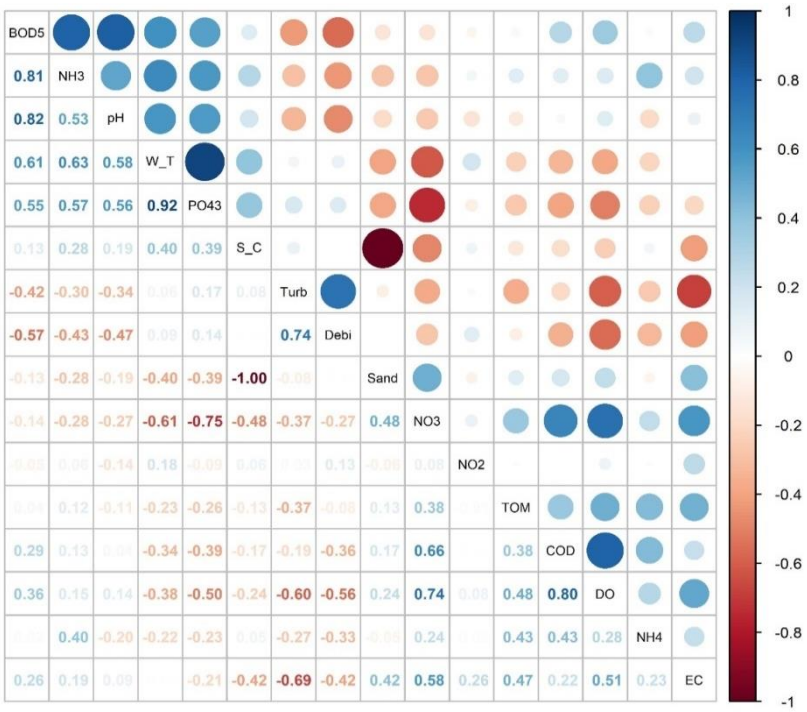

Figure 3: Circular correlation heatmap of physical, chemical, and sediment variables at sampling stations in the Khersan sub-basin rivers. Significant correlations (p<0.05) are highlighted in bold. See Table 1 for a key to environmental variables.

Table 2: Occurrence (presence/absence) of phytoplankton species at sampling stations in the Khersan sub-basin rivers.

Phylum	Taxon	Stations				
		1	2	3	4	5
Bacillariophyta	*Actinocyclus* sp	+	-	-	-	-
	Amphora ovalis	+	+	-	-	-
	Amphora sp.	+	-	-	-	+
	Bacillaria paradoxa	-	-	-	+	-
	Caloneis amphisbaena	+	+	+	-	+
	Caloneis sp.	-	+	-	-	+
	Cocconeis placentula	+	+	+	+	+
	Cocconeis sp.	+	+	-	+	-
	Cyclotella menenghiniana	-	-	-	-	+
	Cymatopleura elliptica	+	-	-	-	-
	Cymbella cymbiformis	+	+	+	+	+
	Cymbella lanceolata	+	+	+	+	+
	Cymbella sp.	+	+	+	+	+
	Cymbella tumidae	+	+	+	+	+
	Diatoma sp.	+	+	+	+	+
	Diatoma vulgaris	+	+	+	+	+
	Encyonema sp.	+	-	-	-	-
	Fragilaria sp.	+	+	-	+	+
	Fragilaria sp2	-	+	-	-	-
	Gomphonema angustatum	+	-	+	+	+
	Gomphonema constrictum	+	+	+	+	+
	Gomphonema curtum	+	-	+	-	-
	Gomphonema sp.	-	+	+	-	+
	Melosira sp	-	-	+	-	+
	Navicula cryptocephala	+	+	+	+	+
	Navicula cuspidate	+	+	+	-	+
	Navicula sp.	+	+	+	+	+
	Navicula sp2	+	+	+	+	+
	Nitzschia acicularis	-	+	-	-	-
	Nitzschia Lanceolata	-	-	-	+	-
	Nitzschia plea	+	+	+	+	-
	Nitzschia reversa	-	-	-	+	-
	Nitzschia sigmoidea	+	+	+	+	+
	Nitzschia sp.	+	+	-	+	-
	Nitzschia sp2	+	+	+	+	+
	Nitzschia sp3	+	+	+	-	+
	Nitzschia tryblionella	-	-	+	+	-
	Pinnularia sp.	+	+	-	-	-
	Rhoicosphenia curvata	+	+	+	-	+
	Stephanodiscus sp.	+	-	+	-	+
	Surirella robustast	-	-	-	-	+
Cyanobacteria	*Anabaena* sp.	-	-	-	-	+
	Lyngbya sp.	+	+	-	+	+
	Merismopedia glausa	-	-	-	+	-
	Oscillatoria limosa	+	+	+	+	+
	Oscillatoria sp.	+	-	+	-	-
	Osillatoria Tenuis	+	-	+	+	+
Chlorophyta	*Crucigenia* sp.	-	+	-	-	-
	Monoraphidium sp.	-	+	-	-	-
	Oocystis parva	+	-	+	-	-
	Oocystis sp.	-	-	-	+	-
	Scenedesmus dimorphus	-	+	+	-	+
Euglenozoa	*Tetrastrum* sp.	+	-	-	-	-
	Euglena proxima	-	-	-	+	+
	Euglena sp.	+	+	-	-	-

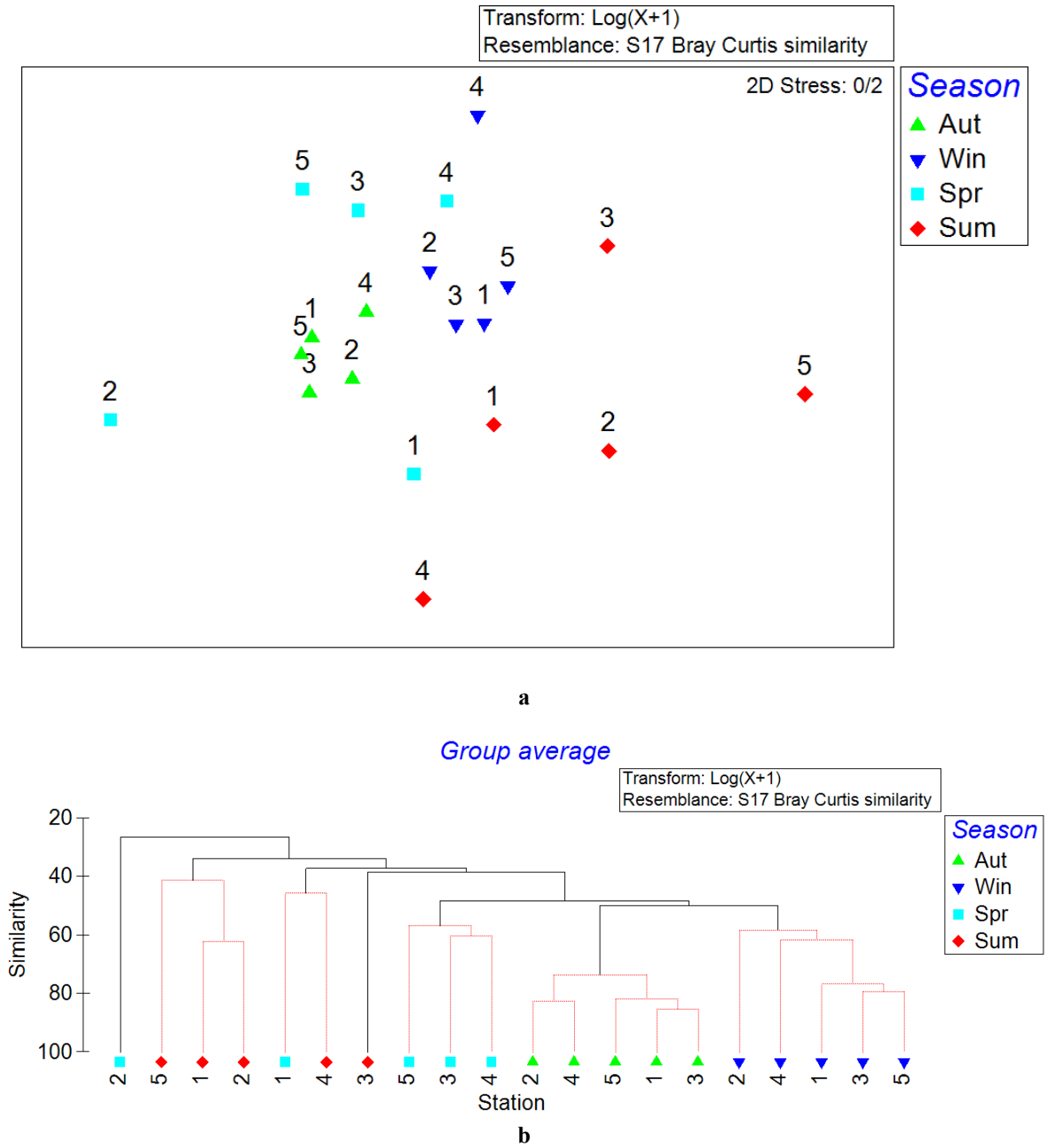

Figure 4: Multivariate analysis of phytoplankton community structure in the Khersan sub-basin rivers: (a) NMDS ordination plot based on Bray-Curtis similarity of transformed data, and (b) Hierarchical cluster analysis of the communities. Seasons are labeled as Aut (Autumn), Win (Winter), Spr (Spring), and Sum (Summer), and sampling stations are indicated by numbers 1–5.

Spring and summer samples were spread across multiple clusters, reflecting higher compositional variability under warmer conditions. Autumn and winter samples were more tightly grouped, forming distinct clusters that suggest greater community stability in cooler seasons. Bubble plots of key taxa (Fig. 5) illustrated contrasting ecological strategies. *Cocconeis placentula* and *Cymbella* sp. reached high abundance in only a few samples, with bubbles concentrated in restricted areas of the ordination, suggesting narrow habitat preferences. In contrast, *Cymbella tumidae* and *Diatoma vulgaris* occurred at high abundance across multiple samples and

seasons, indicating broader tolerance and the ability to dominate under diverse conditions. *Diatoma* sp. and *Navicula* sp.1 showed more localized peaks, pointing to dependence on specific environmental settings.

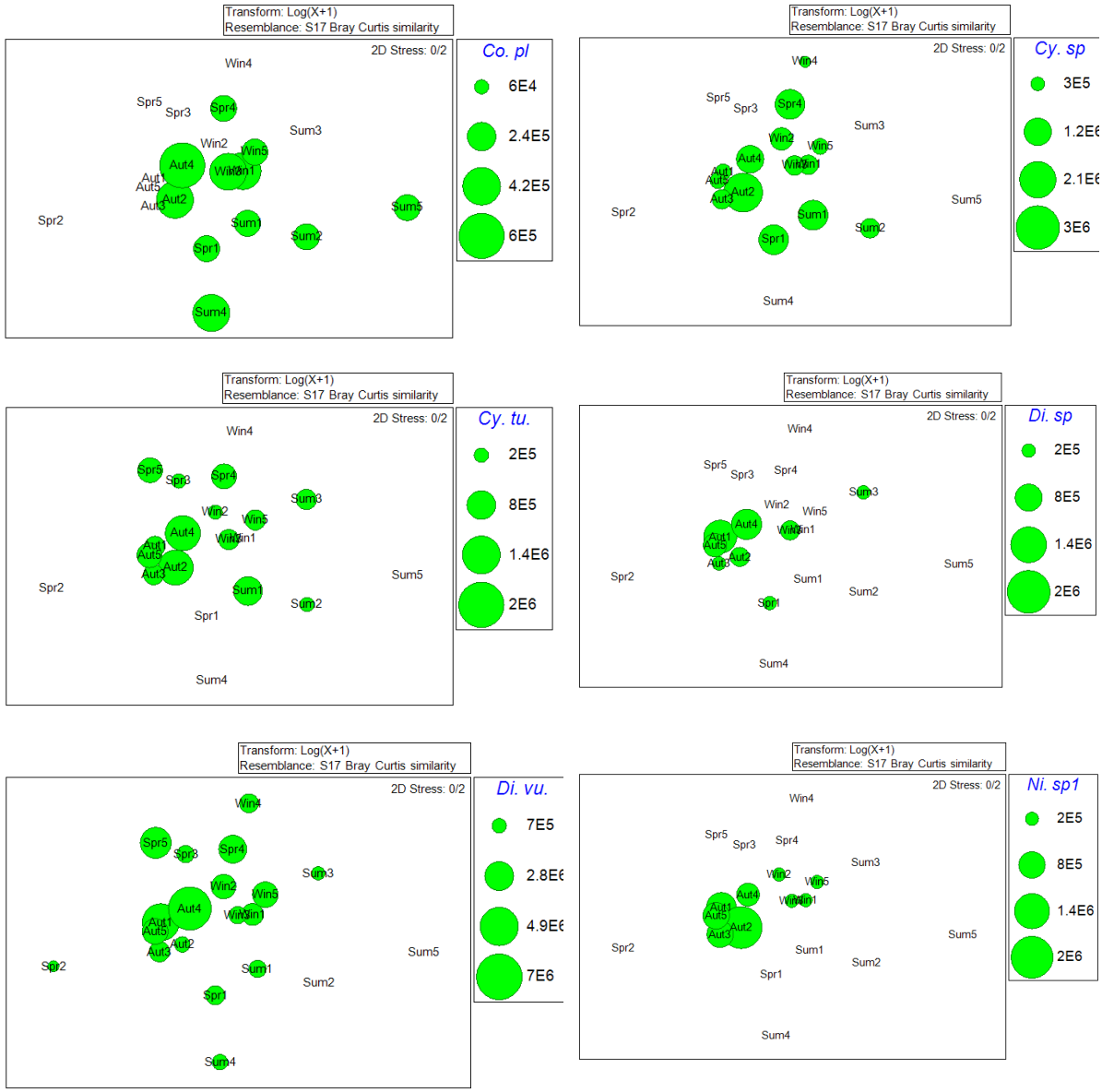

Figure 5: Bubble plots of dominant phytoplankton species in the Khersan sub-basin rivers. Species abbreviations are provided in parentheses: *Cocconeis placentula* (Co. pl.), *Cymbella sp.* (Cy. sp.), *Cymbella tumidae* (Cy. tu.), *Diatoma sp.* (Di. sp.), *Diatoma vulgaris* (Di. vu.), and *Navicula sp.* (Na. sp.).

PERMANOVA (Table 3) confirmed that season had a strong effect on phytoplankton composition (Pseudo F=4.20, $p<0.001$), whereas differences among stations were not significant (Pseudo F=0.96, $p>0.577$). Thus, temporal variation clearly outweighed spatial variation in shaping community structure.

SIMPER analysis showed strong seasonal shifts in assemblage composition:

within-season similarity was highest in autumn (67.8%) and winter (51.8%), but low in spring (34.7%) and lowest in summer (31.7%), indicating stable communities in colder seasons and highly variable assemblages in warm/transitional periods. Autumn similarity was mainly driven by several diatom taxa (e.g., *Diatoma*, *Cymbella*, *Nitzschia*, *Navicula*), winter by *Navicula* sp.1, *D. vulgaris*, *Cymbella* sp., and *Oscillatoria limosa*, spring largely by *Nitzschia* and *D. vulgaris*, and summer by *D. vulgaris*, *Cocconeis placentula*, and *Scenedesmus dimorphus* (Table 4).

Table 3: Results of the PERMANOVA test for phytoplankton communities among different seasons and sampling stations in the Khersan sub-basin rivers. Significant p-values (p<0.05) are highlighted in bold.

Source	d.f.	MS	Pseudo-F	P(perm)*
Season (Se)	3	5023.7	4.30	0.001
Station (Tr)	4	1119	0.96	0.577
Pair-wise test				
Season	t	P(perm) *		
Autumn-Winter	4.9	0.009		
Autumn-Spring	1.9	0.037		
Autumn-Summer	2.2	0.016		
Winter-Spring	1.9	0.054		
Winter-Summer	2.0	0.031		
Spring-Summer	1.7	0.069		

Table 4: Summary of SIMPER results for intra-seasonal similarity of phytoplankton community in the Khersan sub-basin rivers.

Season	Average Similarity (%)	Most Contributing Species (~70-80%)	Ecological Role/General Characteristic
Autumn	67.82	*Diatoma vulgaris*, *Nitzschia* sp1, *Cymbella cymbiformis*, *Cymbella tumidae*	Diatom dominance; a stable community with few dominant species showing relatively homogeneous structure.
Winter	51.81	*Diatoma vulgaris*, *Navicula* sp1, *Cymbella* sp., *Oscillatoria limosa*	Relatively stable community; dominance of diatoms and the presence of cyanobacteria, *Oscillatoria limosa*, in colder and more uniform environmental conditions.
Spring	34.66	*Diatoma vulgaris*, *Nitzschia* sp2, *Fragilaria* sp1, *Cymbella tumidae*	Lowest similarity; a transition season with high fluctuations and high variability, characterized by the rapid appearance and disappearance of species.
Summer	31.70	*Cocconeis placentula*, *Diatoma vulgaris*, *Scenedesmus* sp., *Cocconeis* sp.	A mixture of diatoms and green algae; the influence of high temperature and light on community structure and ecological instability.

Between-season dissimilarities (Table 5) underscored these shifts. The smallest difference occurred between autumn and winter (60.15%), mainly driven by *Nitzschia* sp.2, *Navicula* sp.1, *Navicula cryptocephala*, and *Cymbella cymbiformis*. Between autumn and spring (66.16%) was shaped by *Nitzschia* sp.1, *N. cryptocephala*, *C. cymbiformis*, and *Diatoma* sp., indicating loss or replacement of several

autumn dominants. Winter–summer dissimilarity (72.61%) was linked mainly to *O. limosa*, *Navicula* sp.1, *Nitzschia sigma*, and *Navicula cuspidate*, and winter–spring (65.89%) was linked to *Nitzschia* spp., *Cymbella* sp., and *O. limosa*. Autumn–summer dissimilarity (70.47%) captured the gradual shift from an autumn, diatom-dominated state to a summer assemblage including filamentous cyanobacteria (*Oscillatoria tenuis*).

Table 5: Summary of SIMPER results for dissimilarity between seasons of the phytoplankton community in the Khersan sub-basin rivers.

Seasonal Comparison	Average Dissimilarity (%)	Most Contributing Species (~70-80%)	Explanation
Winter-Autumn	60.15	*Nitzschia* sp2, *Cymbella cymbiformis*, *Navicula* sp1, *Navicula cryptocephala*	Change in the abundance of dominant diatoms; winter has a more uniform and stable structure compared to autumn.
Spring-Autumn	66.16	*Nitzschia* sp1, *Navicula cryptocephala*, *Cymbella cymbiformis*, *Diatoma sp.*	Elimination or decline of autumn indicator species and the formation of a new composition in spring, a transitional season.
Spring-Winter	65.89	*Nitzschia* sp2, *Nitzschia* sp1, *Cymbella sp.*, *Oscillatoria limosa*	Decline of winter-dominant species and increase in spring heterogeneity, reflecting changes in temperature and water flow.
Summer-Autumn	70.47	*Nitzschia* sp1, *Nitzschia* sp2, *Diatoma* sp., *Oscillatoria tenuis*	Transition from an autumn diatom-dominant community to a mixed summer composition including cyanobacteria.
Summer-Winter	72.61	*Oscillatoria limosa*, *Navicula* sp1, *Nitzschia sigmoidea*, *Navicula cuspidata*	High differentiation; an increase in the share of cyanobacteria and some diatoms in summer.
Summer-Spring	75.75	*Nitzschia* sp2, *Cocconeis* sp., *Scenedesmus dimorphus*, *Cocconeis placentula*	Highest dissimilarity; transition from an unstable spring community to a summer community dominated by *Cocconeis* and green algae.

The strongest contrast (75.75%) was between spring and summer, driven primarily by *Nitzschia* sp.2, *Cocconeis* sp., *Scenedesmus* sp., and *C. placentula*, indicating two particularly unstable transitional phases. Seasonal trends in diversity metrics are shown in Figure 6. Spatial differences in *d*, *H′*, and *J′* were small, and none of the indices varied significantly among stations ($p>0.05$). In contrast, *d* differed significantly among seasons ($p<0.05$), with the lowest values in spring, which were significantly lower than in autumn and winter ($p<0.05$). *H′* and *J′* did not vary significantly with season ($p>0.05$).

Relationship between environmental variables and phytoplankton community structure

The DistLM analysis identified that six of the twelve explanatory variables were significantly linked to the faunal resemblance matrix (DisTLM, $p<0.05$; Table 6). pH emerged as the strongest predictor, explaining 17.4 % of the multivariate variance, followed by NH_3, W_T, DO, NO_3^-, and discharge (16.3, 14.5, 13.0, 12.2, and 11.3%, respectively).

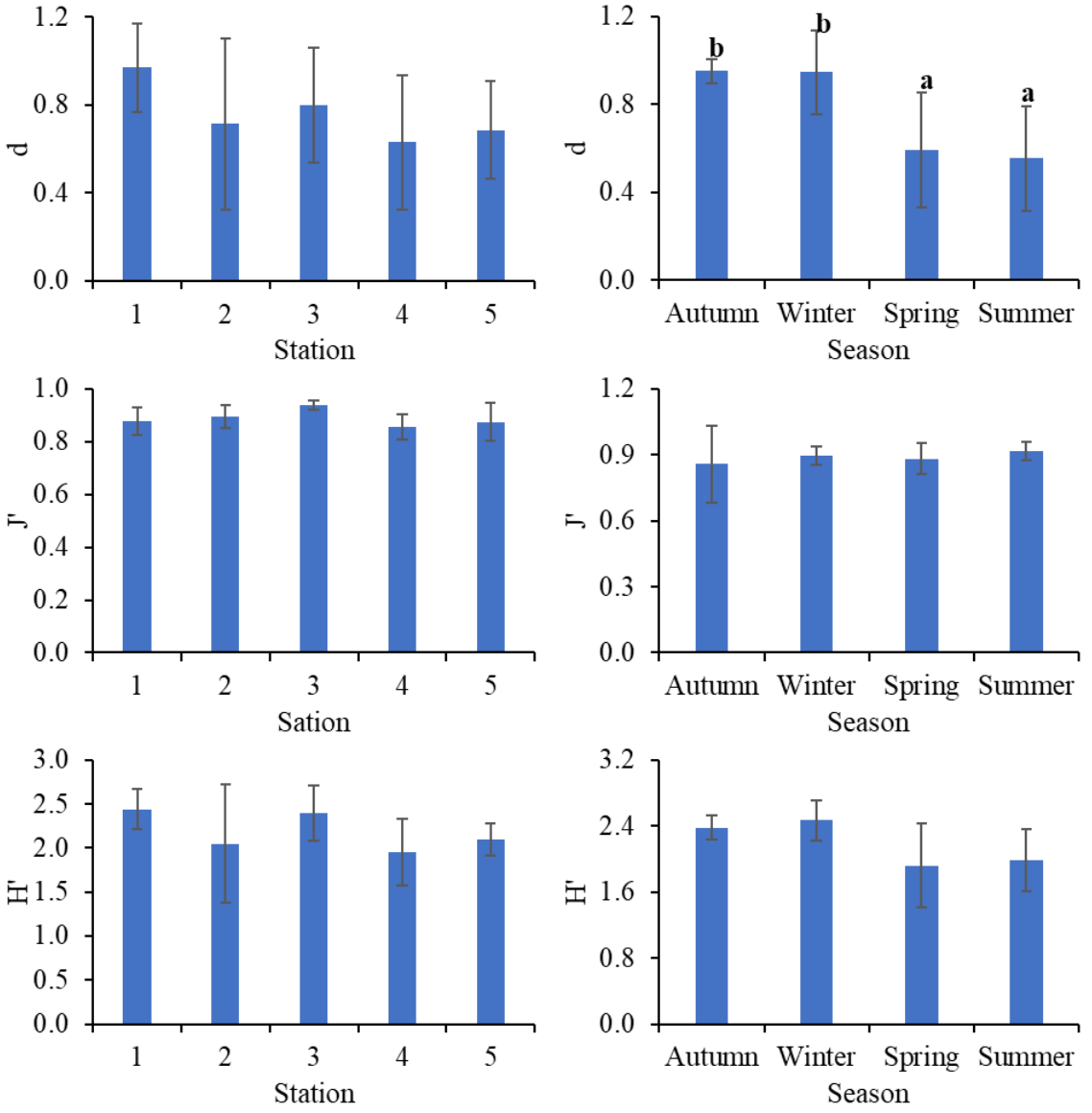

Figure 6: Mean values of phytoplankton community indices, Margalef richness (d), Shannon-Wiener diversity (H´), and Pielou's evenness (J´), across different seasons and sampling stations in the Khersan sub-basin rivers. Significant differences (p<0.05) are indicated by different lowercase letters.

Based on AIC criteria, the best fit with the lowest AIC value, the combination of W_T, NH_3, NO_2^-, DO, pH, TOM, and discharge was selected to build the parsimonious DisTLM model to explain 71.0% of the total variability (Table 7). The first axis was mainly negatively dependent on pH, NH_3, and W_T (−0.88, −0.83, and −0.64), and positively associated with discharge and turbidity (0.40 and 0.49, respectively), while the second axis is related to DO and NO_2^- (-0.67 and −0.55, respectively). Seasonal patterns in sample scores support this interpretation. Autumn samples cluster mainly in the right and upper ordination space, consistent with higher discharge and relatively favorable DO conditions. Spring samples occupy the central region with greater scatter, indicating enhanced environmental heterogeneity. Summer samples are concentrated in the upper left quadrant and are closely associated with

higher W_T, pH, and NH_3. In contrast, winter samples are positioned mainly in the central and lower parts of the plot, where lower DO and NO_3^- prevail (Fig. 7).

Table 6: Results of the DistLM model, containing the Sum of Squares (SS), Pseudo-F statistic, *p*-value, and proportional and cumulative explained total variance. See Table 1 for a key to environmental variables.

Variable	SS	Pseudo-F	P value	Proportion %
pH	5836.4	3.79	0.001	17.4
NH_3	5465.7	3.5	0.002	16.3
W_T	4874.1	3.06	0.003	14.5
DO	4372.5	3	0.003	13.3
NO_3^-	4092.1	2.5	0.012	12.2
Discharge	3793.1	2.29	0.019	11.3
Turb	3219.4	1.91	0.061	9.6
EC	3204.6	1.9	0.069	9.5
TOM	2718.6	1.59	0.131	8.1
NO_2^-	2032.4	1.16	0.346	6.1
NH_4^+	1803.7	1.02	0.451	5.4
Sand	656.95	0.36	0.922	1.9

Table 7: Summary of the best-fit model selected by DistLM based on the Akaike Information Criterion (AIC) for phytoplankton communities in the Khersan sub-basin rivers. See Table 1 for a key to environmental variables.

Number of Variables	AIC	R^2	RSS	Selected variables
1	148.7	0.174	27716	pH
2	147.3	0.301	23433	Do, pH
3	145.9	0.409	19813	Do, W_T, Discharge
4	143.9	0.516	19229	NH_3, DO, pH, Discharge
5	142.2	0.599	13431	NH_3, DO, pH, W_T, Discharge
6	140.8	0.662	11333	NH_3, DO, pH, W_T, TOM, Discharge
7 (The best model)	139.7	0.710	9717	NH_3, NO_2^-, DO, pH, W_T, TOM, Discharge
8	140.4	0.729	9089	NH_3, NO_2^-, DO, Turb, pH, W_T, TOM, Discharge
9	141.3	0.743	8619	NH_3, NO_2^-, DO, EC, pH, W_T, TOM, Discharge, Sand
10	142.1	0.759	8092	NO_3^-, NH_3, NO_2^-, DO, EC, pH, W_T, TOM, Discharge, Sand

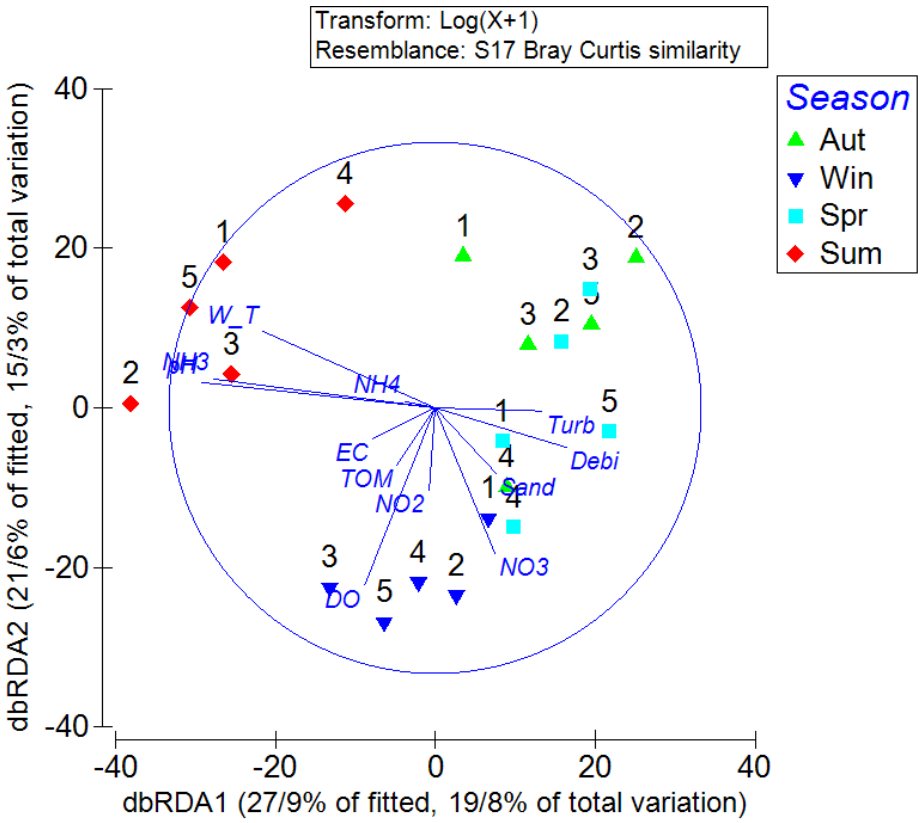

Figure 7: Distance-based redundancy analysis (dbRDA) plot based on Bray-Curtis similarity, showing the relationship between phytoplankton community structure and environmental variables in the Khersan sub-basin. Symbols represent seasons (Aut: Autumn, Win: Winter, Spr: Spring, Sum: Summer) and sampling stations (1–5). Vectors indicate the direction and magnitude of environmental variables influencing the community composition. See Table 1 for a key to environmental variables.

Discussion

Phytoplankton are key primary producers across aquatic ecosystems; in freshwater river systems, they underpin nutrient cycling, energy transfer, and overall ecosystem functioning. Their short life cycles, rapid growth, and high sensitivity to environmental change make them widely accepted bioindicators of water quality and ecological status (Wehr *et al*., 2015; Kuturo *et al*., 2024). Community composition is shaped by interacting physical, chemical, and hydrological drivers, including temperature, flow regime, light and transparency, residence time, and nutrient supply (Litchman *et al*., 2007). Shifts in phytoplankton structure, therefore, provide a direct signal of both natural variability and human pressures.

In the Khersan sub-basin, we recorded 55 phytoplankton taxa from four divisions (Bacillariophyta, Cyanobacteria, Chlorophyta, Euglenozoa). Diatoms (Bacillariophyta) were overwhelmingly dominant, contributing 74.6% of total richness. This pattern mirrors reports from other rivers, floodplains, and river–lake continua worldwide (Li *et al*., 2019; Yang *et al*., 2021; Gao *et al*., 2024; Huang *et al*., 2025). Diatoms typically outcompete other groups in running waters owing to efficient nutrient acquisition, tolerance of flow

variability, and resilience to hydrological disturbance. The strong diatom dominance in the Khersan system suggests relatively stable flow, sufficient light, and moderate nutrient availability. Previous work indicates that such conditions, with intermediate disturbance and balanced nutrient ratios, favour diatom-led assemblages (Giri *et al*., 2022; Bayramova *et al*., 2023). Many species can attach to substrates, withstand strong currents, and maintain high photosynthetic rates even in turbid, mixed water columns, making them particularly successful in lotic habitats.

Most taxa recorded were typical riverine diatoms associated with flowing, moderately nutrient-rich waters, including *Cocconeis*, *Cymbella*, *Diatoma*, *Navicula*, *Nitzschia*, *Gomphonema*, *Cyclotella*, and *Stephanodiscus*. The frequent occurrence of *Cocconeis placentula*, *C. cymbiformis*, *C. tumidae*, *D. vulgaris*, *N. cryptocephala*, and multiple *Nitzschia* species across stations and seasons points to broad ecological tolerance and an ability to cope with continuous mixing and seasonal change. Consistent with other studies, *Navicula*, *Nitzschia*, and *Cymbella* function here as indicators of moderately to highly enriched and hydrodynamically dynamic conditions (Li *et al*., 2019; Yang *et al*., 2021). Periodic occurrences of *Cyclotella* and *Stephanodiscus* likely mark episodes of enhanced water-column stability and altered nutrient regimes.

In addition to diatoms, the occurrence of Cyanobacteria (*Anabaena*, *Lyngbya*, *Oscillatoria*) and green algae (*Scenedesmus*, *Monoraphidium*, *Oocystis*, *Tetrastrum*) indicates that conditions periodically favored more opportunistic taxa. The recurrent detection of *O. limosa* and *S. dimorphus* at several stations during warm periods is likely linked to higher temperatures, reduced flow, longer residence time, and locally elevated nutrients. Similar seasonal shifts toward Cyanobacteria and Chlorophyta have been reported in urban and semi-arid rivers, where summer increases in temperature, NO_3^-, turbidity, and suspended solids promote their growth (Dong *et al*., 2022; Gao *et al*., 2024). However, the overall low contribution of cyanobacteria in the Khersan system suggests that the river has not yet reached an advanced eutrophic state and that conditions remain generally unsuitable for large, persistent algal blooms.

Multivariate analyses (nMDS, cluster analysis, PERMANOVA) showed that seasonality, rather than site-to-site variation, was the main factor structuring phytoplankton communities. The clear seasonal clustering in the nMDS ordination and the strong PERMANOVA signal for seasonal effects point to temporal dynamics as the dominant driver. This pattern is consistent with findings from other rivers and floodplain systems, where temperature, discharge, light climate, and nutrient availability act as key filters shaping phytoplankton composition (Yang *et al*., 2021; Huang *et al*., 2023, 2025).

Community composition within each season revealed a pronounced successional pattern. In autumn, typical riverine diatoms, such as *D. vulgaris*, *C. tumidae*, *C. cymbiformis*, *Navicula* spp., and *Nitzschia* spp. contributed most to within-season similarity, indicating a well-established, diatom-dominated assemblage. Diatoms

also prevailed in winter; yet the occurrence of *O. limosa* shows that some cyanobacteria tolerated colder conditions and relatively enriched nutrients. Spring and summer were transitional periods with rapid community reorganization and high species turnover, with the pronounced spring–summer dissimilarity indicating major environmental change and replacement of cold-season dominants by warm-adapted opportunistic taxa.

Bubble plots indicated that *D. vulgaris* and *C. tumidae* were widespread due to their broad ecological tolerance, with *D. vulgaris* specifically serving as an indicator of moderately impacted, β- to oligo-mesosaprobic water quality (Abiyev *et al*., 2025). In contrast, *C. placentula*, *Navicula* spp., and *Cymbella* taxa showed more restricted distributions, reflecting higher sensitivity and a preference for turbulent, turbid, and nutrient-enriched conditions (Zhang *et al*., 2019; Gao *et al*., 2024). DistLM analysis confirmed that a suite of physical, chemical, and hydrological variables (such as W_T, NH_3, NO_2^-, DO, pH, TOM, and discharge) jointly structure phytoplankton assemblages in the Khersan sub-basin. This highlights that phytoplankton dynamics arise from interacting environmental drivers, and shifts in any one of these axes can alter both species composition and overall community structure. Among these drivers, W_T emerged as a key control. Warmer conditions enhance algal metabolism and photosynthesis, favouring fast-growing Chlorophyta and Cyanobacteria, whereas diatoms generally peak under cooler to moderate temperatures and thus dominate many mountain and semi-mountain rivers. The temperature signal detected by DistLM likely reflects seasonal thermal cycles in the Khersan system and is consistent with numerous riverine studies that identify temperature as a primary seasonal regulator of phytoplankton dynamics (Yang *et al*., 2021; Gao *et al*., 2024).

Nutrients like nitrogen and phosphorus are crucial regulators of freshwater primary production and community composition, with the N:P ratio often determining taxonomic dominance (Hecky and Kilham, 1988). Deviations from optimal N:P ratios, especially during high discharge, can suppress phytoplankton growth (Liu *et al*., 2023). In this study, DistLM analysis identified nitrogen species as key predictors of variability, a pattern consistent with findings that nutrient enrichment favors opportunistic taxa and cyanobacterial blooms (Amorim and Moura, 2021).
Hydrological conditions, especially discharge and turbulence, strongly influence phytoplankton by altering residence time, mixing, and nutrient transport: high flows tend to limit population growth, whereas slower flows favor biomass accumulation, and the DistLM relationships likely reflect seasonal flow-driven changes in these processes (Schmutz and Moog, 2018).

Our results are consistent with regional studies in Iranian waters, such as the Azad Dam reservoir, where temperature, nutrients, and transparency were identified as primary drivers of phytoplankton structure (Fazli *et al*., 2022). Similar patterns, emphasizing the roles of sediment abrasion, light penetration (Yuli Herawati *et al*., 2024), and seasonal dynamics, have been reported in the Maroon and Kardeh

reservoirs, confirming that temperature, hydrology, and nutrient interactions are central to shaping diatom-dominated communities across the region (Salavatian *et al*., 2018).

Conclusion

In summary, phytoplankton structure in the Khersan sub-basin is governed by the combined effects of hydrological regime, seasonal variability, and nutrient status. The persistent dominance of diatoms across most seasons points to a relatively stable system and the absence of advanced eutrophication. Nonetheless, the occasional occurrence of Cyanobacteria and Chlorophyta may signal gradual nutrient enrichment and emerging ecological change. The predominance and high richness of Bacillariophyta suggest that substrates and ambient conditions favor diatom communities over other microalgae, such as cyanobacteria and green algae. Finally, the stronger seasonal than spatial signal indicates that temporal fluctuations in temperature, discharge, light, and nutrient concentrations are the main forces driving phytoplankton dynamics in this river network.

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Conflicts of interest

The authors declare that they have no conflict of interest.

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