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Relationship between the quantitative development of phytoplankton and environmental factors in lakes of different trophic status in the Belarusian Lakeland

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ABSTRACT. This study examined 11 lakes of the Belarusian Lakeland, encompassing the range from mesotrophic lakes with oligotrophic features to highly eutrophic systems, to evaluate the impact of abiotic factors on the quantitative development of phytoplankton. Sampling was carried out during the growing seasons of 2023–2025 using standard hydrobiological and hydrochemical methods. Phytoplankton biomass showed an increase from 0.46–0.85 mg/L in mesotrophic lakes with oligotrophic features to 22.7–46.75 mg/L in hypereutrophic lakes. Among environmental factors, nitrogen compounds exerted the strongest influence, particularly nitrate nitrogen (r_s up to 0.7; $p < 0.001$), while the role of total phosphorus was less pronounced. The analysis did not consider the concentration of phosphate ions ($P–PO_4$) because it was mostly below the analytical detection limit, and the number of measurements with non-zero values was insufficient for statistically robust conclusions. Redundancy analysis (RDA) revealed that the combined effect of environmental factors explained up to 55% of the variation in phytoplankton, with the trophic gradient being the dominant driver. Both nitrate and ammonium nitrogen contributed significantly to phytoplankton development; however, the effect of nitrate nitrogen was more pronounced. This was likely due to the rapid uptake and oxidation of NH_4^+ under conditions of high oxygen concentration, which complicates the evaluation of its impact, whereas nitrate was consumed more slowly, allowing for a more reliable statistical evaluation of its role. The obtained results refine our understanding of the role of different nitrogen forms in shaping the productive state of lakes and may be applied in assessing their trophic status.

Keywords: phytoplankton, trophic status, lakes, total phosphorus, nitrate nitrogen, ammonium

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1. Introduction

Phytoplankton, as primary producers in aquatic ecosystems, play a crucial role in nutrient cycling, energy transfer, and the stability of aquatic ecosystems (Leng et al., 2024).

Freshwater phytoplankton communities are highly sensitive to a wide range of environmental variables (e.g., nutrients, light, temperature, and mixing), and therefore can serve as effective early indicators of changes in the structure and functioning of lake ecosystems (Filiz et al., 2020).

Numerous studies have demonstrated that both quantitative characteristics and taxonomic composition of phytoplankton are closely related to the trophic status of water bodies and to a complex of external drivers. Key factors for regulation phytoplankton development include water temperature (Leng et al., 2024), transparency (Gong et al., 2022; Kalinkina et al., 2024), dissolved oxygen content, pH (Zhu et al., 2021; Tsybekmitova et al., 2021), and concentrations of nutrients (Leng et al., 2024; Oğuz et al., 2020), particularly phosphorus (P) (Vollenweider, 1968; Schindler, 1977; Reynolds, 2006), which is traditionally considered the primary limiting element in freshwater ecosystems.

However, in some water bodies, especially under conditions of high phosphorus loading, nitrogen may become the limiting factor, as confirmed by previous studies (Smith, 1982; Guildford and Hecky, 2000). Thus, the dominant limiting role between these two nutrients remains context-dependent and cannot be answered unambiguously.

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Despite the widely recognized importance of these nutrients as key drivers of eutrophication, many studies indicate that the relative importance of limiting factors may vary depending on trophic conditions and season. In some cases, temperature, light availability, or other hydrochemical parameters may play a more decisive role than nutrient concentrations.

Existing approaches to assessing environmental effects on phytoplankton are often limited either to experimental conditions or to specific local lakes. This constrains our ability to fully understand the role of changes in individual factors along a trophic gradient. In the present study, we attempt to address this gap by investigating lakes of the Belarusian Lakeland that differ in trophic status.

Thus, the aim of this study is to evaluate which environmental factors most strongly influence the quantitative development of phytoplankton in lakes with different trophic statuses in the Belarusian Lakeland.

Understanding these mechanisms is essential both for predicting eutrophication processes and for developing approaches to diagnosing trophic status based on the relationship between key abiotic parameters and phytoplankton community structure.

2. Materials and methods

2.1. Study Area

The Belarusian Lakeland is a geomorphological region in northern Belarus that contains the majority of the country's lakes (474 in total). The total surface area of these lakes reaches ~2000 km^2, with a total water volume of ~6 km^3 (Vlasov, 2004).

The selection of study sites focused on covering a wide range of trophic conditions. The dataset included (Fig. 1): mesotrophic lakes with oligotrophic features (Krivoe "55.159630, 29.022555", Volos North "55.750034, 27.128764", Volos South "55.74172583, 27.13406265"); mesotrophic lakes (Vechelye "55.146131, 28.626658", Obsterno "55.609985, 27.374020"); eutrophic lakes (Potekh "55.685406, 27.166407", Otolovo "55.148056, 28.930657", Gorushka "55.6359, 27.3466"); and highly eutrophic water bodies subjected to significant anthropogenic pressure (Ilmenok "55.6798, 27.1881", Velikoe "55.155103, 27.675684", Cherstvyatskoe "55.200986, 28.853959").

The morphometric characteristics of the lakes are presented in Table 1.

2.2. Phytoplankton sampling

Sampling was carried out from May to September in 2023–2025. Samples from four lakes of the Usacy group (Lakes Cherstvyatskoe, Vechelye, Otolovo, and Krivoe) were collected three times during 2023: in the late spring, summer, and late summer periods.

Samples from five lakes of the Braslav group (Lakes Potekh, Gorushka, Obsterno, Volos North, and Volos South) were collected during the same periods in 2024. Samples from the hypereutrophic lakes Ilmenok and Velikoe were collected in the late spring, summer, and late summer periods of 2025.

Water samples were collected using an 8 L Molchanov bathometer sequentially from the surface layer, Secchi depth, and twice the Secchi depth, followed by mixing into an integrated sample. The samples were fixed with Utermöhl's solution. Phytoplankton was concentrated by sedimentation from an initial volume of 0.5 L. Overall, 66 phytoplankton samples were collected and analyzed.

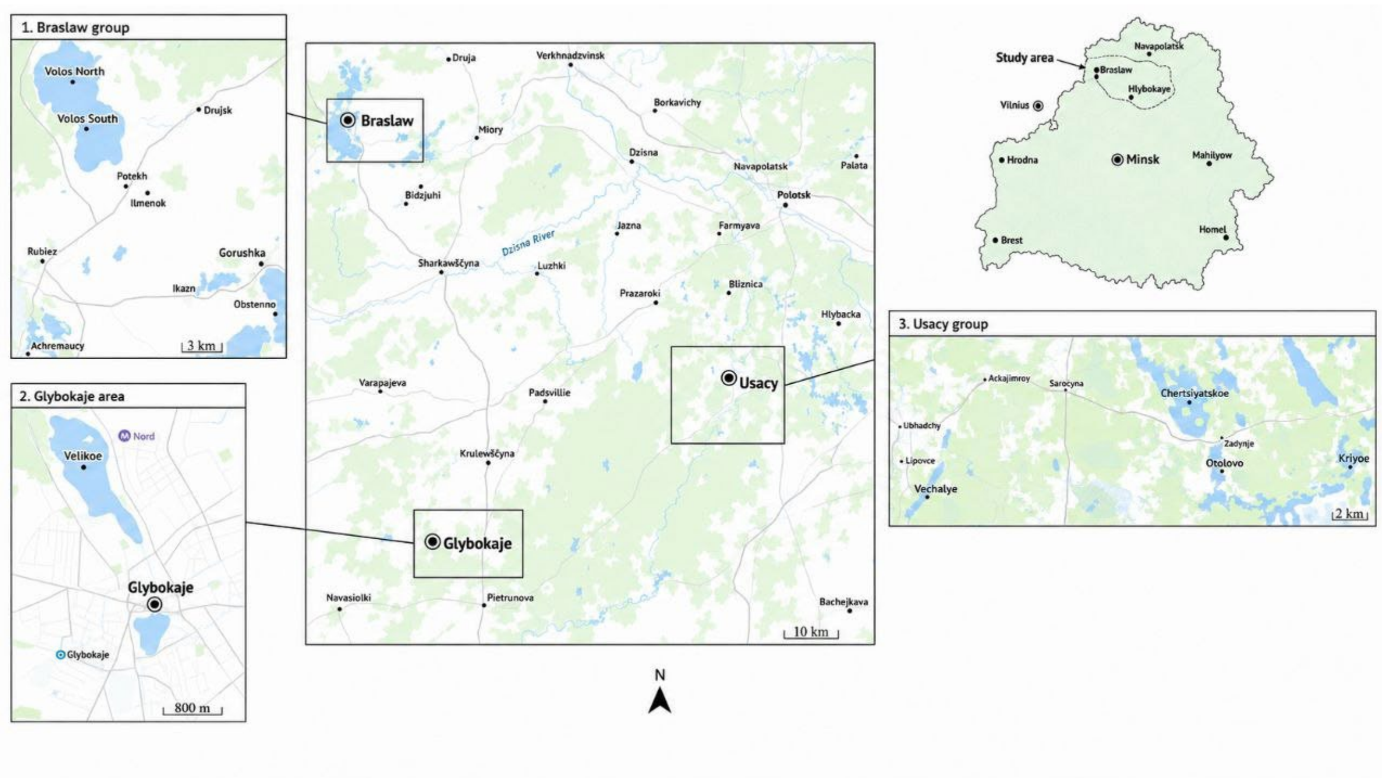

Fig.1. Lakes of different trophic statuses in the Belarusian Lakeland.

Table 1. Morphometric characteristics of lakes with different trophic statuses in the Belarusian Lakeland.

Lake	Surface area, km²	Lake volume, km³	Maximum depth, m	Mean depth, m	Transparency, m
Chertsvyatskoe	9.93	0.021	4.30	2.20	0.70
Vechelye	1.36	0.025	35.90	18.50	2.37
Otolovo	8.2	0.028	16.40	3.50	2.67
Krivoe	4.5	0.043	31.50	9.60	5.17
Potekh	1.35	0.452	9.10	3.50	1.20
Gorushka	0.18	0.0005	6.90	2.80	1.83
Obsterno	9.89	0.05	12.00	5.10	2.37
Volos North	4.21	0.031	29.20	7.30	5.27
Volos South	1.21	0.015	40.40	12.50	6.17
Ilmenok	0.21	0.0006	6.40	3.00	1.00
Velikoe	0.89	0.003	5.70	2.50	0.36

2.3. Hydrochemical parameters

Secchi depth (SD) was measured using a standard white Secchi disk (d = 30 cm). Water temperature was measured at all sampled depths using a mercury deep-water thermometer with a resolution of 0.1°C.

pH values were determined using a pH meter (model pH-986). Dissolved oxygen (O_2) concentrations were measured using a portable oximeter (HANNA HI 9143).

Total nitrogen (TN) concentration was determined after oxidation of unfiltered water samples with potassium persulfate in an autoclave. Total phosphorus (TP) was measured photometrically using potassium persulfate digestion.

Nitrate nitrogen ($N–NO_3$) was determined photometrically using salicylic acid. Ammonium nitrogen ($N–NH_4$) was determined using the hypochlorite method with salicylate in the presence of sodium nitroprusside.

In addition to these parameters, phosphate ($P–PO_4$), Kjeldahl nitrogen, and nitrite ($N–NO_2$) were also measured; however, their concentrations were frequently below detection limits, preventing statistically reliable correlation analysis.

2.4. Phytoplankton abundance and biomass

Phytoplankton abundance was determined using standard hydrobiological methods (Mordukhai-Boltovsky, 1975). Biomass was estimated using the cell volume method (Mikheyeva, 1989).

Species composition was analyzed using a light microscope (Carl Zeiss, model Axiostar Plus) at magnifications of ×100, ×200, and ×400.

Species identification was performed using both regional (Gollerbach and Savich, 1951–1983) and international taxonomic keys (Komárek and Anagnostidis, 2005).

The classification and arrangement of algal divisions followed the system adopted in the reference “Algal Flora of Belarus” (Mikheeva, 1999).

The trophic statuses of lakes were determined based on phytoplankton biomass values according to Kitaev (1984).

2.5. Statistical analysis

Relationships between biotic and abiotic parameters were assessed using Spearman’s rank correlation coefficient.

To analyze the relationships between phytoplankton and environmental factors, redundancy analysis (RDA) was performed using Python and the NumPy, Scikit-learn, and SciPy libraries.

3. Results

3.1. General characteristics of the biotic and abiotic parameters of the studied lakes

Analysis of phytoplankton data revealed a clear relationship between biomass and the trophic status of the studied lakes (Table 2). Total phytoplankton biomass increased consistently with increasing trophic level of the water bodies.

Minimum biomass values ranged from 0.46 to 0.85 mg/L and were recorded in lakes with oligotrophic features (Volos North, Volos South, and Krivoe).

In mesotrophic and eutrophic lakes (Obsterno, Vechelye, Gorushka, Potekh, and Otolovo), total biomass ranged from 1.00 to 8.43 mg/L.

The highest biomass values were observed in highly eutrophic lakes: 22.7 mg/L in Lake Velikoe, 46.75 mg/L in Lake Ilmenok, and 48.65 mg/L in Lake Cherstvyatskoe.

Analysis of abiotic factors also revealed a wide range of values corresponding to the trophic gradient from mesotrophic lakes with oligotrophic features to highly eutrophic systems (Table 2).

Secchi depth (SD) decreased consistently from oligo-mesotrophic lakes (maximum 6.17 m in Lake Volos South) to highly eutrophic lakes (minimum 0.37 m in Lake Ilmenok), which is consistent with the concurrent increase in phytoplankton biomass.

Mean water temperature (t, °C) ranged from 11.0 to 16.9 °C. The highest values were recorded in shallow, highly eutrophic lakes Ilmenok and Velikoe, which can be explained by their morphometric charac-

Table 2. Mean values (± standard deviation) of phytoplankton parameters (abundance and biomass) and environmental variables (transparency (SD), temperature (°C), dissolved O_2, pH, TP, N–NH_4, and N–NO_2) for lakes of different trophic statuses in the Belarusian Lakeland.

Lake	N, $\times 10^6$ cells/L	B, mg/L	SD, m	t °C	O_2, mg/L	pH	TP, mg/L	N–NH_4, mg N / L	N–NO_3, mg N / L
Chertsvyatskoe (highly eutrophic lake)	171.9 ± 10.95	48.65 ± 14.9	0.7 + 0.00	15.2 ± 0.00	7.42 ± 0.00	8.03 ± 0.25	0.057 ± 0.007	0.063 ± 0.07	0.156 ± 0.068
Vechelye (mesotrophic lake)	10.26 ± 1.20	3.29 ± 1.24	2.37 ± 0.78	13.13 ± 1.58	10.96 ± 0.17	7.70 ± 0.50	0.049 ± 0.03	0.037 ± 0.013	0.26 ± 0.081
Otolovo (eutrophic lake)	18.44 ± 8.63	8.43 ± 3.84	2.67 ± 0.47	14.28 ± 0.55	10.66 ± 0.04	8.00 ± 0.36	0.027 ± 0.006	0.023 ± 0.012	0.065 ± 0.017
Krivoe (mesotrophic lake with oligotrophic features)	3.51 ± 0.92	0.85 ± 0.27	5.16 ± 0.24	11.03 ± 0.51	8.58 ± 0.15	8.00 ± 0.50	0.012 ± 0.0014	0.023 ± 0.018	0.033 ± 0.006
Potekh (eutrophic lake)	18.73 ± 12.9	6.29 ± 4.24	1.2 ± 0.08	14.48 ± 0.01	8.87 ± 0.95	7.47 ± 0.24	0.015 ± 0.01	0.0189 ± 0.0017	0.094 ± 0.016
Gorushka (eutrophic lake)	7.33 ± 3.48	4.85 ± 4.0	1.83 ± 0.12	15.4 ± 0.00	6.92 ± 0.00	7.3 ± 0.08	0.015 ± 0.006	0.023 ± 0.01	0.078 ± 0.005
Obsterno (mesotrophic lake)	3.25 ± 2.2	1.00 ± 0.78	2.37 ± 0.82	15.57 ± 0.97	7.92 ± 0.057	7.33 ± 0.12	0.022 ± 0.01	0.038 ± 0.02	0.075 ± 0.012
Volos North (mesotrophic lake with oligotrophic features)	3.98 ± 1.34	0.46 ± 0.16	5.27 ± 0.25	15.72 ± 0.00	7.72 ± 0.00	7.57 ± 0.17	0.009 ± 0.005	0.015 ± 0.0075	0.03 ± 0.012
Volos South (mesotrophic lake with oligo-trophic features)	3.38 ± 1.19	0.69 ± 0.50	6.17 ± 0.24	13.62 ± 0.34	9.099 ± 0.17	7.63 ± 0.26	0.007 ± 0.003	0.015 ± 0.009	0.027 ± 0.013
Ilmenok (highly eutrophic lake)	17.98 ± 7.91	46.78 ± 56.30	0.37 ± 0.12	16.93 ± 4.29	8.65 ± 0.55	7.83 ± 0.77	0.26 ± 0.13	0.27 ± 0.16	1.54 ± 1.60
Velikoe (highly eutrophic lake)	66.81 ± 34.65	22.6 ± 8.01	0.87 ± 0.38	16.75 ± 3.86	9.24 ± 1.16	7.67 ± 0.33	0.36 ± 0.38	0.32 ± 0.15	1.77 ± 1.88

teristics: weak stratification and warming of the entire water column result in higher average temperatures. In deep stratified lakes (down to 30 m in depth), colder hypolimnetic layers in sampling lead to lower mean temperature values.

Dissolved oxygen concentrations ranged from 6.92 mg/L (Lake Gorushka) to 10.96 mg/L (Lake Vechelye). Notably, relatively low oxygen levels were observed in the deep mesotrophic lake with oligotrophic features, Lake Krivoe (8.58 mg/L), which may indicate stratification.

The pH values were generally slightly alkaline (7.3–8.03).

Nutrient concentrations exhibited the most pronounced trophic gradient. Total phosphorus (TP) increased from 0.007 mg/dm^3 (Lake Volos South) to 0.36 mg/dm^3 (Lake Velikoe), with an over 50-fold variation. Ammonium nitrogen ($N–NH_4$) and nitrate nitrogen ($N–NO_3$) followed a similar trend, reaching maximum values in the hypertrophic lakes Ilmenok and Velikoe ($N–NH_4$ up to 0.32 mg N/dm^3; $N–NO_3$ up to 1.77 mg N/dm^3).

3.2. Influence of environmental factors on the quantitative development of phytoplankton

Correlation analysis (Spearman's rank coefficient) revealed statistically significant relationships between quantitative phytoplankton indicators and physicochemical environmental parameters (Fig. 2).

The strongest positive relationship was observed between phytoplankton abundance and total biomass ($r_s = 0.94$; $p < 0.001$), indicating a synchronous variation of these parameters and suggesting that an increase in cell abundance is accompanied by a proportional increase in total community biomass.

One of the most pronounced patterns is the negative correlation between phytoplankton quantitative indicators and water transparency. The correlation coefficients were $r_s = –0.77$ ($p < 0.001$) for abundance and $r_s = –0.83$ ($p < 0.001$) for biomass. This indicates that increasing phytoplankton development is associated with decreasing water transparency, which is a typical pattern in freshwater ecosystems (Carlson, 1977; Brezonik et al., 2019).

Among chemical environmental factors, the most significant positive relationships were found between phytoplankton quantitative characteristics and nitrogen compounds. The highest correlation coefficients were obtained for nitrate nitrogen ($N–NO_3$): $r_s = 0.65$ ($p < 0.001$) for abundance and $r_s = 0.70$ ($p < 0.001$) for biomass.

Total phosphorus (TP) also showed positive correlations with phytoplankton quantitative indicators; however, these were slightly lower ($r_s = 0.58$; $p = 0.0004$ for abundance and $r_s = 0.65$; $p < 0.001$ for biomass).

An interesting feature is the difference in the strength of relationships between different forms of nitrogen and phytoplankton quantitative characteristics. Ammonium nitrogen ($N–NH_4$) demonstrated a statistically significant correlation mainly with phytoplankton biomass ($r_s = 0.41$, $p = 0.01$), whereas its

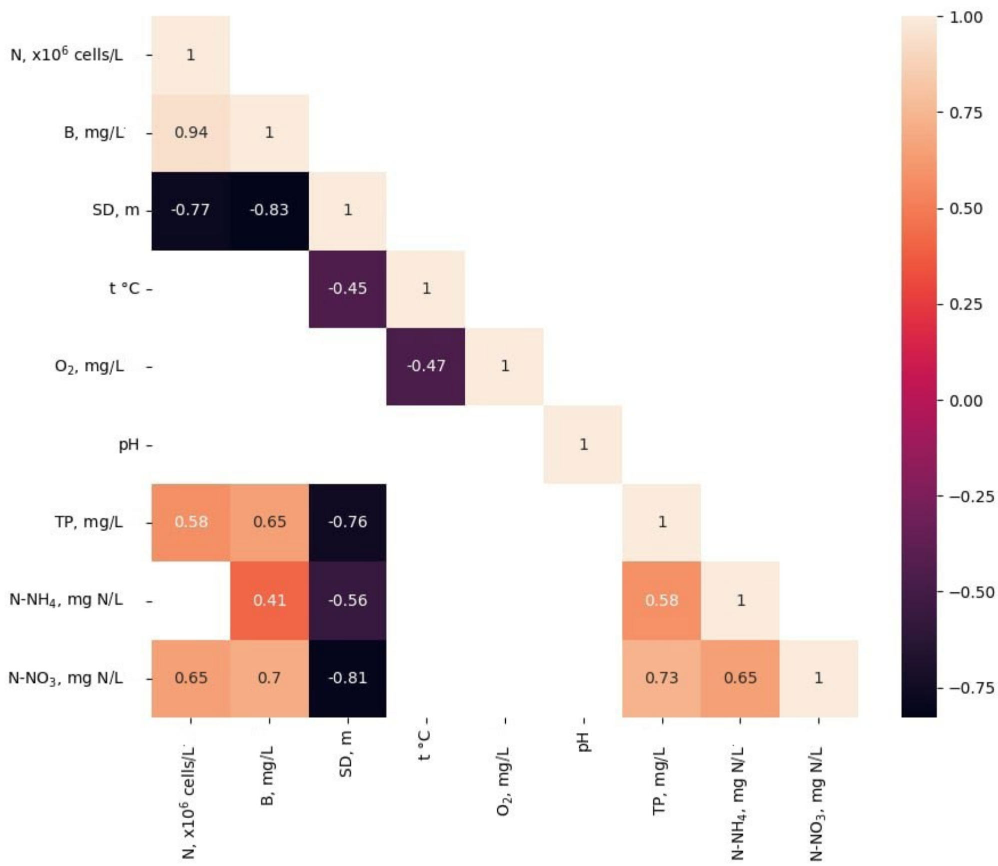

Fig.2. Correlation matrix relationships between quantitative phytoplankton characteristics and environmental factors.

relationship with abundance was much weaker and not statistically significant ($p = 0.052$).

At the same time, several environmental factors, including pH and dissolved oxygen concentration, did not show statistically significant correlations with phytoplankton quantitative indicators.

In addition to correlation analysis, redundancy analysis (RDA) was performed to assess the influence of environmental factors on phytoplankton quantitative characteristics. The constructed model for phytoplankton abundance and biomass yielded a coefficient of determination of $R^2 = 0.55$, indicating that the included hydrochemical and physical parameters explain ~55% of the variation in phytoplankton characteristics. The adjusted coefficient of determination was Adjusted $R^2 = 0.41$, which is expected when multiple predictors are used, indicating a relatively high explanatory power of the model for natural ecosystems.

Multicollinearity diagnostics showed that variance inflation factor (VIF) values for all environmental variables did not exceed 5, indicating the absence of strong intercorrelations among predictors and confirming the robustness of the model.

The RDA ordination diagram demonstrates that the first axis (RDA1) explains 79.1% of the variation, whereas the second axis (RDA2) accounts for 20.9%, indicating the dominant role of the primary ecological gradient (Fig. 3).

Analysis of the direction and length of environmental factor vectors indicates that the first axis represents a gradient of increasing trophic status of the water bodies. In the positive direction of RDA1, vectors of nitrate nitrogen ($N–NO_3$), ammonium nitrogen ($N–NH_4$), and total phosphorus (TP), as well as phytoplankton biomass and abundance, are oriented, indicating a positive relationship among these variables.

The relationship between phytoplankton biomass and nitrate concentration ($N–NO_3$) is particularly pronounced. Vector of ammonium nitrogen ($N–NH_4$) is oriented in a similar direction, suggesting a moderate influence of reduced nitrogen forms on phytoplankton development. Total phosphorus (TP) vector is also directed in the same direction; however, its shorter length and larger angle relative to phytoplankton variables indicate a comparatively weaker influence.

In contrast, vectors of water transparency (SD) and dissolved oxygen are oriented in the opposite direction along the first axis, indicating a negative relationship with phytoplankton biomass and abundance.

The distribution of lakes on the ordination diagram confirms a pronounced trophic gradient. Lakes in the lower-left part of the diagram are associated with the direction of transparency and dissolved oxygen vectors. These are primarily mesotrophic lakes (Obsterno and Vechelye) and mesotrophic lakes with oligotrophic features (Krivoe, Volos North, and Volos South). Their position reflects conditions of high transparency, relatively low nutrient concentrations, and low phytoplankton biomass, which are characteristic of such systems.

In the opposite part of the diagram are lakes associated with the vectors of nitrate, ammonium, and phosphorus, as well as with phytoplankton biomass and abundance. Their position indicates elevated nutrient concentrations and higher productivity, typical of some mesotrophic (especially in the late summer period) and eutrophic lakes.

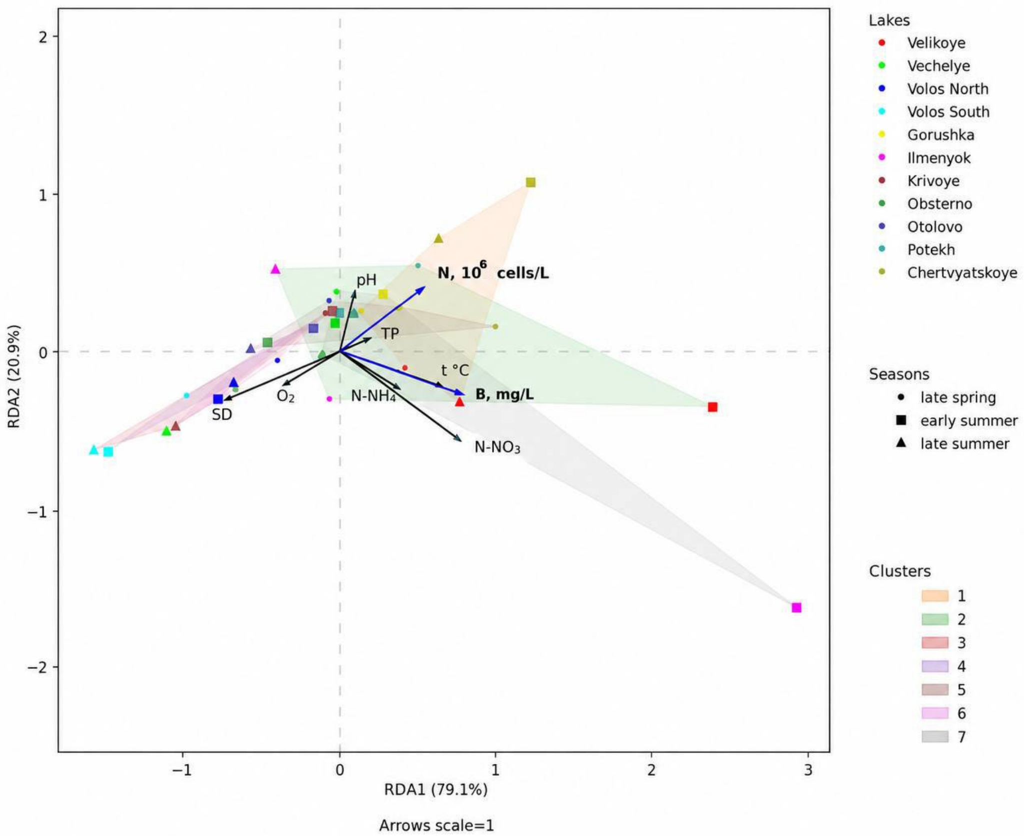

Fig.3. RDA ordination of lakes with different trophic statuses in the Belarusian Lakeland depending on environmental factors.

The second ordination axis explains a substantially smaller proportion of the variation (20.9%) and reflects additional differences among water bodies. The main factor associated with this gradient is pH, whose vector is oriented predominantly in the vertical direction. This suggests that acid–base conditions exert an additional influence on the distribution of phytoplankton quantitative characteristics; however, their role is considerably less pronounced compared to that of nutrients.

4. Discussion

The obtained results demonstrate that the influence of different forms of nutrients on phytoplankton development in the studied lakes varies significantly along the trophic gradient and, in some cases, deviates from the classical phosphorus-limitation paradigm.

According to the classical concepts of eutrophication by Vollenweider (1968) and Schindler (1977), phosphorus is considered the primary limiting nutrient in freshwater ecosystems. Indeed, in the studied lakes, an increase in total phosphorus (TP) from 0.007–0.012 mg/dm^3 in mesotrophic lakes with oligotrophic features to 0.26–0.36 mg/dm^3 in hypereutrophic systems is accompanied by an increase in phytoplankton biomass, which is consistent with classical theory, forming the basis of Carlson's trophic state index (Carlson, 1977). However, this relationship alone does not imply that TP remains the determining factor of phytoplankton variability across all conditions.

First, total phosphorus does not directly represent the bioavailable fraction of the element. As shown in fundamental studies (Rigler, 1973; Lean, 1973), there is often no direct functional relationship between TP and phytoplankton production rates, since a substantial portion of phosphorus exists in organic or particulate forms and is involved in slow internal cycling. In the studied lakes, this is supported by extremely low orthophosphate concentrations, indicating rapid uptake and maintenance of phytoplankton through regeneration processes rather than through the instantaneous TP pool.

Second, at high phosphorus concentrations, the system may reach saturation, where further increases in TP do not result in proportional increases in phytoplankton biomass. This effect was repeatedly reported in classical reviews (e.g., Smith, 1982; Hecky and Kilham, 1988), showing that under eutrophic and hypereutrophic conditions, limitation often shifts toward nitrogen or becomes co-limited. Thus, at high TP levels, its variability loses the controlling significance for phytoplankton production.

Third, internal phosphorus loading and rapid cycling play an important role. In shallow and productive lakes (such as Velikoe and Ilmenok), bottom sediments can act as a significant phosphorus source, compensating for low concentrations of dissolved forms in the water column (Wetzel, 2001). Under such conditions, phytoplankton effectively exists in an environment with a constant but "hidden" phosphorus supply, weakening statistical relationships between TP and biomass.

Thus, a combination of factors explains why TP does not act as the key driver of phytoplankton variability in the studied lakes.

Against this background, nitrogen becomes particularly important. Unlike phosphorus, its bioavailable forms, especially nitrates, show a stronger relationship with production characteristics. RDA results indicate that nitrate nitrogen (N–NO_3) contributes most to the variation in phytoplankton biomass and abundance, as evidenced by the longest vector aligned with productivity indicators.

This shift in limiting control from phosphorus to nitrogen is consistent with modern concepts of freshwater ecosystem functioning. Studies by Smith (1982), Guildford and Hecky (2000), and Elser et al. (2007) demonstrate that under high trophic conditions and phosphorus excess, nitrogen often becomes the limiting nutrient.

One key factor explaining this phenomenon is the rapid uptake of ammonium nitrogen by phytoplankton. According to Wetzel (2001), N–NH_4 is the most energetically favorable nitrogen form and is rapidly assimilated by algae. In conditions of high biomass, as observed in lakes Cherstvyatskoe, Velikoe, and Ilmenok (up to 48.65 mg/L), ammonium is intensively consumed and does not accumulate in the water column. This is confirmed by relatively moderate concentrations of N–NH_4 (0.27–0.32 mg N/dm^3) even under high trophic status.

An additional factor is the dominance of cyanobacteria, particularly species of the genus *Limnothrix* (M.-E. Meffert, 1987) and *Aphanizomenon flos-aquae* (L.) Ralfs ex Bornet & Flahault, 1888, in hypereutrophic lakes. Cyanobacteria are known to efficiently assimilate ammonium and switch between different nitrogen sources (Blomqvist et al., 1994; Glibert et al., 2016). When N–NH_4 is available, it is preferentially utilized, leading to its rapid depletion. Thus, ammonium functions as a rapidly cycling component that does not fully reflect nitrogen availability for phytoplankton.

In contrast, nitrate nitrogen is a more stable form and is less subject to immediate uptake. In the studied lakes, its concentrations reach 1.54–1.77 mg N/dm^3 in hypereutrophic systems, significantly exceeding those in mesotrophic lakes (0.027–0.26 mg N/dm^3). At the same time, nitrate consistently dominates over ammonium, which contrasts with classical assumptions about the accumulation of reduced nitrogen forms in eutrophic conditions (Quirós, 2002).

The oxygen regime plays a crucial role in maintaining high nitrate concentrations. In all studied lakes, dissolved oxygen levels remain relatively high (6.9–10.9 mg/L), including hypereutrophic systems. This indicates the absence of strongly reducing conditions in the pelagic zone and promotes active nitrification. As a result, ammonium entering the system or produced during organic matter mineralization is rapidly oxidized to nitrate, leading to its accumulation.

Moreover, nitrate nitrogen may reflect substantial external loading from the catchment area. Unlike phosphorus, which is often retained in sediments or exists in less accessible forms, nitrates remain dissolved and readily available for phytoplankton uptake. This makes them a more reliable indicator of nitrogen availability in the system.

Thus, the stronger influence of nitrate nitrogen on phytoplankton development in the studied lakes is explained by a combination of factors: rapid ammonium uptake, high nitrification rates, stable oxygen conditions, and significant external nitrate inputs. Under these conditions, nitrate acts as the primary controlling factor of production processes, despite the traditionally leading role of phosphorus in freshwater ecosystems.

5. Conclusions

The present study confirmed a well-defined trophic gradient in the lakes of the Belarusian Lakeland, reflected in both phytoplankton quantitative characteristics and hydrochemical parameters of the aquatic environment. Phytoplankton biomass increases consistently from mesotrophic lakes with oligotrophic features (0.46–0.85 mg/L) to hypereutrophic systems (up to 46.75 mg/L), accompanied by decreasing water transparency and increasing nutrient concentrations.

Analysis of environmental factors showed that nitrogen compounds, particularly nitrate nitrogen ($N–NO_3$), play the most significant role in shaping phytoplankton quantitative characteristics. Moderate positive correlations were found between nitrate concentration and biomass ($r_s = 0.7$), whereas the influence of total phosphorus was slightly weaker ($r_s = 0.65$).

Ordination analysis (RDA) confirmed the leading role of nitrate nitrogen, demonstrating its maximum contribution to explaining variation in phytoplankton indicators along the trophic gradient.

Ammonium nitrogen plays a less significant role compared to nitrate, despite its high bioavailability. This is due to its rapid uptake by phytoplankton, especially in highly eutrophic lakes dominated by cyanobacteria. Hence, ammonium functions as a rapidly cycling form of nitrogen that does not accumulate in the water column, reducing its contribution to statistically detectable relationships.

The oxygen regime significantly influences the balance of nitrogen forms. Relatively high dissolved oxygen concentrations in all studied lakes promote active nitrification, leading to nitrate accumulation and its dominance over ammonium even under high productivity conditions.

Thus, a complex interplay of factors governs phytoplankton development in the lakes of the Belarusian Lakeland. Among them, both phosphorus and nitrogen are important, although the influence of nitrogen appears to be more pronounced. The results indicate that under conditions of high trophic status and sufficient aeration, nitrate nitrogen may act as a key controlling factor in production processes. This should be taken into account when assessing the ecological status of lakes and developing management strategies for eutrophication control.

Conflict of interest

The authors declare no conflict of interest.

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