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CYANOBACTERIA AS KEY FACTORS IN STRUCTURING PLANKTONIC COMMUNITIES IN THE DANUBE DELTA

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Abstract

Cyanobacteria exert intense ecological pressure within aquatic systems of the Danube Delta, shaping both phytoplankton and zooplankton community dynamics. Their summer intense development can disrupt the balance between phytoplankton and zooplankton functional groups. Cyanobacteria dominated the phytoplankton, often outcompeting other algal taxa. Abundance indicated high concentrations of Cyanobacteria (10^7–10^8 cells L^{-1}), reflecting the high productivity. Their competitive advantage modifies species composition, reducing overall diversity and altering trophic interactions. The zooplankton displayed adaptive responses to shifts in phytoplankton, reflecting changes in food quality and availability. Among the dominant phytoplankton species were Anabaena variabilis, Aphanizomenon spp., and filamentous forms of the genera Microcystis spp., and Oscillatoria spp. In contrast, the zooplankton was predominantly structured by rotifers and cladocerans, among which Keratella cochlearis, Brachionus calyciflorus, and Bosmina longirostris were frequently found, indicating a high ecological tolerance. These temporal patterns highlight a complex interplay between communities, emphasising the regulatory role of cyanobacterial pressure in structuring aquatic community dynamics and influencing the trophic functioning of Delta ecosystems.

Key words*: cyanobacterial blooms, Danube Delta, phytoplankton, trophic interactions, zooplankton.*

INTRODUCTION

Cyanobacteria are a prominent group in aquatic phytoplankton that, under prolonged periods of high temperatures, proliferate and become dominant in many continental ecosystems (Paerl & Huisman, 2008). Their competitive success is explained by their functional traits, such as broad tolerance to temperature and light, the ability to efficiently exploit nutrient resources, buoyancy conferred by gas vacuoles and, in some cases, the production of secondary metabolites with allelopathic effect. In addition, adaptations such as the ability to fix atmospheric nitrogen and high tolerance to eutrophic conditions are also added (Reynolds, 2006; Paerl & Otten, 2013). The Danube Delta is a complex network of aquatic ecosystems characterised by high spatial heterogeneity and heightened sensitivity to anthropogenic and climatic pressures. Changes in the hydrological regime, increased nutrient input and climate change have favoured the intensification of eutrophication processes in many deltaic lakes (Dumitran et al., 2020). One of the most visible effects of these transformations is the increase in the frequency and intensity of algal blooms dominated by *Cyanobacteria*, with potential risks for ecosystems (Moza et al., 2021). Studies have shown that in recent decades, *Cyanobacteria* have contributed significantly to phytoplankton biomass with effects on trophic status (Török et al., 2017). This dominance is manifested either by the massive development of several cyanobacterial species or by high densities generated by one or two species (Dumitran et al., 2024). As a result of algal blooms, community structure is simplified, increasing the dominance of a few taxa and reducing evenness, even when overall richness remains relatively high. This imbalance in diversity is characterised by reduced abundances of species from other groups, temporary coexistence with *Cyanobacteria*, and subsequent competitive exclusion (Török, 2011).

The emergence and rapid expansion of *Cyanobacteria* have significant ecological

consequences, affecting both the structure of planktonic communities and trophic relationships in aquatic ecosystems (Moldoveanu & Florescu, 2011). In the lakes of the Danube Delta, these processes manifest differently depending on local environmental conditions, leading to contrasting responses from phytoplankton communities. Thus, studies have shown that in some ecosystems cyanobacterial dominance intensified, whereas in others competition with chlorophytes or diatoms limited the success of this group, generating unstable, seasonal community structures (Török et al., 2017).

The aim of our study is to evaluate the role of *Cyanobacteria* as key factors in structuring phytoplankton communities in Roșuleț, Puiu and Tătaru lakes, representative lakes of the Danube Delta. The objectives of the study are: 1. Analysing the taxonomic structure of phytoplankton communities and highlighting the position of *Cyanobacteria* relative to the main algal groups using multivariate methods; 2. Assessing variations in α and β diversity, in order to identify structural changes in communities between lakes and between seasons; 3. Identifying cyanobacterial taxa responsible for seasonal compositional changes by analysing their contribution to community dissimilarity; 4. Investigating competitive relationships between *Cyanobacteria* and other phytoplankton groups, through quantitative indicators of the competitive replacement rate, in order to highlight ecological hierarchies and community stability.

MATERIALS AND METHODS

Study site

The Danube Delta is characterised by a complex network of branches, channels and shallow lakes, developed on fluvial and marine beds, with active transformation processes. The inland lakes are generally shallow, with variable connectivity to the channel network, which results in low hydrodynamics and a strong influence on Danube level variations. From an ecological perspective, the Danube Delta is one of the most valuable wetlands in Europe, with high biodiversity and a wide range of aquatic ecosystems, including eutrophic and hypereutrophic lakes with rich phytoplankton communities (Pavel et al., 2009).

The lakes selected in our study, Puiu, Tătaru and Roșuleț (Figure 1), are part of the Danube Delta lacustrine complex, and are characterised by variable hydrodynamics and different connectivity with the river branches and secondary channels. The lakes are shallow, developed on fluvial beds and subject to clogging and morphological remodelling processes, characteristic of inland deltaic lakes. Lake Puiu is a large, relatively deep (2-2.5 m in our sampling campaigns) lake in the Danube Delta, with a moderate fluvial influence that determines the seasonal dynamics of nutrients and planktonic communities (Tudorancea & Tudorancea, 2006; Gâștescu, 2009). Lake Tătaru is shallower (approx. 1 m deep in our sampling campaigns) and less hydrologically connected, favouring nutrient accumulation and frequent eutrophic episodes, with seasonal algal dominance (Coops et al., 1999). Roșuleţul, a shallow lake (1.1-1-6 m in our sampling campaigns), is strongly influenced by internal processes, such as sediment resuspension and phosphorus recycling, which lead to high phytoplankton variability and unstable community structures (Oosterberg et al., 2000; Gâștescu, 2009).



Figure 1. The sampling lakes: Roșuleț, Puiu and Tătaru (Google Earth app, 2026)

Phytoplankton sampling and analysis

Water samples were collected during two field campaigns, in August and September 2015. To capture the spatial variability of the studied ecosystems, 4 sampling stations were established in each lake. Phytoplankton sampling was performed on the entire water column using a Patalas-Schindler (5 litres) and stored in a bucket. From this volume, 500 ml of the water sample was taken, immediately fixed

with 4% formaldehyde, and stored in plastic containers. In the laboratory, the samples were sedimented for 14 days. Quantitative and qualitative analyses were performed according to the Utermöhl method (Edler & Elbrachter, 2010) using an inverted microscope (Zeiss Axiovert 40C, Germany).

Taxonomic identification of organisms was performed to the genus or species level, using specific determination keys for the main taxonomic groups: *Cyanobacteria, Euglenophyceae, Pyrrophyceae, Chrysophyceae, Bacillariophyceae, and Chlorophyceae* (Moldoveanu et al., 2025).

Statistical analysis

Statistical analyses were performed using Past 5.2.1 software (Hammer et al., 2001), including Discriminant Analysis (DA), diversity indicators α (Dominance_D, Shannon_H, Equitability_J) and β (Whittaker, Cody, Williams), and the construction of a dendrogram based on the Bray-Curtis coefficient. The structure of the communities was additionally assessed using ANOSIM (Permutation test, N=9999) and SIMPER. The Rate of Competitive Displacement (RCD) was also calculated according to the methodology described by Ji et al. (2017), which estimates the rate at which phytoplankton groups replace one another under competitive conditions. RCD as differences between September versus August, as ln(X1/X2), where: X1- *Cyanobacteria* and X2 – diatoms or green algae – the total abundances of group.

RESULTS AND DISCUSSIONS

The structure and distribution of phytoplankton communities

In the phytoplankton structure, *Cyanobacteria* recorded the highest share, followed by *Chlorophyceae* and *Bacillariophyceae*, with considerably lower abundances (Table 1). In Puiu and Tătaru lakes, all three groups showed significant increases in abundance during the monitoring period, with pronounced blue-green biomass peaks observed (in Tătaru − 9.22×10^7 cells/L; in Puiu − 8.04×10^7 cells/L). In contrast, at Roșuleț Lake, except for *Chlorophyceae*, most phytoplankton groups showed pronounced declines. *Chlorophyceae*, although the second group in weight, showed low abundances overall, reaching a maximum in Lake Tătaru in the month (2.79×10^7 cells/L). Diatoms recorded lower values than *Cyanobacteria*, but showed notable increases in September. The *Euglenophyceae, Pyrrophyceae*, and *Chrysophyceae* groups were present at low densities, reflected in episodic increases.

Table 1. The abundances of the phytoplankton taxonomic groups in the studied lakes

	Puiu		Tătaru		Roșuleț	
	VIII	IX	VIII	IX	VIII	IX
Cyanobacteria	$4.05x\ 10^7$	$8.04x10^7$	$1.45x10^7$	$9.22x10^7$	$4.08x10^7$	$2.04x10^7$
Euglenophyceae	$1.57x10^5$	$5.80x10^4$	$4.23x10^5$	$1.86x10^5$	$1.52x10^4$	$6.59x10^3$
Pyrrophyceae	$8.98x10^4$	$1.38x10^5$	$2.03x10^5$	$9.81x10^5$	$4.36x10^4$	$2.60x10^4$
Chrysophyceae	0	00	0	$8.84x10^5$	$1.23x10^5$	0
Bacillariophyceae	$1.54x10^6$	$5.75x10^6$	$4.89x10^5$	$2.48x10^6$	$1.92x10^6$	$3.94x10^5$
Chlorophyceae	$3.21x10^6$	$6.95x10^6$	$2.87x10^6$	$2.79x10^7$	$2.57x10^6$	$3.50x10^6$

The DA discriminant analysis revealed clear separation between the main phytoplankton groups, along with partial taxonomic overlap, reflecting functional similarities and convergent ecological responses (Figure 2). These indicate that taxonomic structure only partially explains community organisation. Discriminant axis 1 (61.72%), but also an evident separation of *Cyanobacteria* (positioned predominantly on the right side of the axis) from *Bacillariophyceae* and *Chrysophyceae* (located on the left). *Chlorophyceae* present an intermediate position, with a greater dispersion, which indicates a higher heterogeneity than diatoms. This spread suggests the presence of species that display both opportunistic strategies and adaptations to more stable conditions. The partial overlap between chlorophytes, *Cyanobacteria*, and diatoms indicates the

functional flexibility of this group. In contrast, diatom species showed a clearer delimitation compared to the other groups. Also, *Chrysophyceae* showed a strong separation from the other groups (observed on the left side of axis 1). Axis 2 (29.55%) contributes to further differentiation of the communities, especially by the distinct positioning of *Euglenophyceae*, which forms a separate group on the left side of the axis. Groups with reduced representation, such as *Pyrrophyceae* and *Chrysophyceae*, appear more poorly delimited, with limited dispersion and less obvious separation. This positioning suggests either a reduced contribution to the overall community structure or shared ecological features with other major groups. The other groups show a clear overlap on this axis, with no clear demarcations between them. This separation is more pronounced than the differences between ecosystems or months, indicating that the community structure is mainly dominated by the contrast between *Cyanobacteria* and the rest of the phytoplankton. However, habitat overlaps are also evident, especially among *Chlorophyceae*, *Cyanobacteria*, and *Euglenophyceae*, reflecting a complex, partially overlapping community structure.

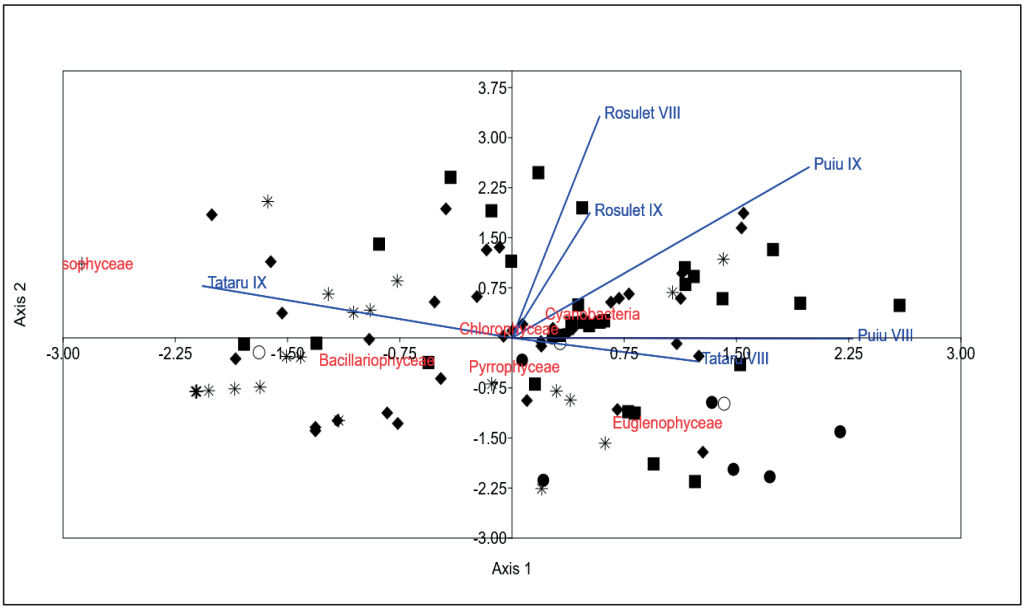


Figure 2. Biplot of the Discriminant Analysis showing the relationship between phytoplankton taxonomic groups and sampling sites (Lakes Roșuleț, Puiu, and Tătaru). ■ – *Cyanobacteria*; ● – *Euglenophyceae*, ○ – *Pyrrophyceae*, + – *Chrysophyceae*, * – *Bacillariophyceae*, ◆– *Chlorophyceae*, blue vectors– sampling points and months

α and β diversity traits

The α-diversity indices revealed clear differences in the structure of phytoplankton communities between the lakes and between the two periods analysed (Table 2). Although total species richness remained relatively high (44-60 species), the Shannon index values indicated differences in community diversity, reflecting changes in the relative distribution of taxa, especially in Puiu and Roșulet lakes. In these two ecosystems, the increase in the dominance index (D), concomitant with the decrease in evenness (J), suggests a more pronounced structuring of the community, characterised by the concentration of abundance within fewer groups or taxa. Thus, between the two periods, the diversity indices showed different changes in the structure of phytoplankton communities in the three ecosystems. Total species richness generally recorded higher values in September, with a maximum in Lake Tătaru (60 species), suggesting seasonal diversification of the communities, especially through increased contributions from

the *Bacillariophyceae* and *Chlorophyceae* groups. Lake Puiu showed an increase in total richness from 45 to 53 species, concomitant with an increase in *Cyanobacteria*, while Lake Roșuleț recorded a decrease in total richness in September, suggesting a possible simplification of the community structure. The Shannon index (H′) ranged from moderate to high (2.08-2.69), with the highest values observed in Lake Tătaru in both months, suggesting relatively well-structured and stable communities.

In contrast, the higher values of the dominance index (D), especially in September in Lake Puiu and Lake Roșuleț, indicate an increase in the dominance of a few taxa, probably favoured by trophic conditions. This trend is also supported by the decrease in evenness (J), which reflects a more unequal distribution of species abundances in the community.

Even if total species richness remains relatively high, the increase in the proportion of *Cyanobacteria*, associated with a decrease in evenness and effective diversity of the community, can lead to an "apparent diversity" in which other groups are present but contribute less to the total biomass.

Table 2. Diversity of phytoplankton in the studied ecosystems

	Puiu		**Tătaru**		**Roșuleț**	
	VIII	**IX**	**VIII**	**IX**	**VIII**	**IX**
Cyanobacteria	15	19	12	12	16	11
Bacillariophyceae	5	6	8	18	6	6
Chlorophyceace	17	23	20	25	19	20
Euglenophyceae	6	3	5	2	1	1
Pyrrophyceae	2	2	1	2	1	1
Chrisophyceae	0	0	0	1	1	0
Species richness (S)	45	53	46	60	44	39
Dominance (D)	0.11	0.30	0.11	0.11	0.14	0.26
Shannon (H′)	2.61	2.16	2.69	2.69	2.34	2.08
Equitability (J)	0.68	0.55	0.70	0.66	0.62	0.57

Spatial beta diversity among lakes (Table 3). showed a moderate to high overall species turnover among the lakes (Whittaker = 0.50; Cody = 46.00; Williams = 0.27). The pairwise comparisons showed the highest compositional dissimilarity between Lakes Puiu and Tătaru (Whittaker = 0.36; Cody = 25.50; Williams = 0.24), followed by the Puiu–Roșuleț pair (Whittaker = 0.31; Cody = 20.00; Williams = 0.19). The lowest beta diversity values were recorded between Tătaru and Roșuleț (Whittaker = 0.30; Cody = 20.50; Williams = 0.16). Similar spatial patterns were observed across all three indices, indicating consistent differences in species composition among the studied lakes.

Table 3. The spatial beta diversity among lakes

Global beta diversities			
Whittaker	0.50		
Cody	46.00		
Williams	0.27		
Whittaker	**Puiu**	**Tătaru**	**Roșulet**
Puiu	0.00	0.36	0.31
Tătaru	0.36	0.00	0.30
Roșulet	0.31	0.30	0.00
Cody			
Puiu	0.00	25.50	20.00
Tătaru	25.50	0.00	20.50
Roșulet	20.00	20.50	0.00
Williams			
Puiu	0.00	0.24	0.19
Tătaru	0.24	0.00	0.16
Roșulet	0.19	0.16	0.00

Regarding structural changes during the investigated period, β-diversity indices revealed moderate differences in phytoplankton composition (Table 4). The Whittaker index ranged from 0.40 to 0.47, indicating moderate temporal heterogeneity. The highest value was recorded in Lake Roșuleț (0.47), suggesting that this lake experienced the highest rate of species replacement from summer to autumn among the three. In contrast, the Cody index showed similar values across the lakes (19.5-21.0), suggesting a comparable rate of species replacement between months, with a slight maximum in Lake Tătaru. The Williams index values were relatively low (0.19-0.28), indicating low to moderate turnover (species change) between the two, but with a more pronounced differentiation in Lake Roșuleț.

Table 4. Temporal beta diversity within lakes

	Puiu	**Tătaru**	**Roșuleț**
Whittaker	0.41	0.40	0.47
Cody	20.00	21.00	19.50
Williams	0.23	0.19	0.28

The magnitude of structural changes reflected in diversity indices was assessed using a Bray-Curtis similarity dendrogram (Figure 3), which revealed distinct separation of the studied ecosystems, driven by both spatial and temporal factors.

The highest degree of similarity (approximately 67%) was found between Roșuleț and Puiu lakes in August (R-VIII, P-VIII), thus highlighting convergent trophic conditions that favour the same algal associations. In contrast, station Tătaru VIII showed the lowest similarity to the other ecosystems (below 50%), indicating a significant taxonomic divergence during the summer period. Also, in September, an association of Tătaru and Roșulet lakes were observed, forming a distinct cluster indicating a structural convergence of phytoplankton communities towards the end of the vegetation season and marking the transition from highly specialised summer associations to a more balanced structure, characteristic of the early autumn period.

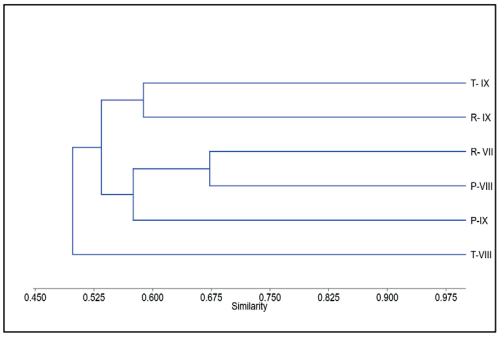


Figure 3. Similarity dendrogram of phytoplankton communities in lakes Roșuleț, Puiu and Tătaru (August-September), based on the Bray-Curtis index (Paired Group method)

Compositional shift at the level of phytoplankton groups

The ANOSIM test applied to identify structural changes during the tested period showed that the differences between the summer (VIII) and autumn (IX) periods were greater than the spatial variations between ecosystems (Table 5). Lake Roșuleț (R = 0.67, p = 0.008) showed the greatest and most significant seasonal change, indicating major structural changes during the investigated period. In Lake Puiu (R=0.47, p=0.03), the separation of communities was moderate, while in Lake Tătaru (R=0.30, p=0.05), the lowest seasonal differences but the highest spatial variation (12.08) were observed.

Table 5. ANOSIM analysis of structural changes among lakes and periods

	Puiu	**Tătaru**	**Roșulet**
Mean rank within:	10.67	12.08	11.75
Mean rank between:	17.38	16.31	23.9
R:	0.47	0.30	0.67
p (same):	0.03	0.05	0.008

By Simper analysis (Table 6), the species whose turnover was decisive in the phytoplankton structuring were identified. This analysis identifies the taxa that contributed the most to the taxonomic change from summer to autumn. In Puiu Lake the species *Oscillatoria minima* was the dominant species with the highest contribution (34.68%), achieved through a massive development reaching a peak of $1.06x10^8$ cells/L – in autumn. In contrast, other cyanobacterial species, *Aphanizomenon flos-aquae* (7.065) and Oscillatoria sp. (6.27%), showed a significant shift, but through a decline in abundance. In Tataru Lake, the strongest influences in the seasonal changes were also due to *Cyanobacteria*. *Gomphosphaeria lacustris* accounted for 16.84% of the difference, with an increase in the average in September, along with *Microcystis pulverea*, which also made a significant contribution (13.63%) due to its appearance and massive development in autumn. In contrast, *Oscillatoria limosa* showed a significant decline during this period. And in Lacul Roșuleț, *Cyanobacteria* were the taxa that contributed significantly higher values in the changes between the two periods. Thus, we mention, *Microcystis pulverea* (18.44%, with a significant increase in autumn), *Aphanocapsa grevillei* and *Aphanizomenon flos-aquae* (which together explained over 32% of the dissimilarity by completely disappearing in autumn), as well as *Oscillatoria minima* Gicklhom, which also underwent a decline in abundance. ANOSIM and Simper analyses confirm a strong turnover induced by *Cyanobacteria* species. While some summer species (such as *Aphanizomenon* spp. or *Aphanocapsa* spp.) tend to disappear or

decrease in September, others (such as *Oscillatoria minima* in Puiu or *Microcystis pulverea* in Tătaru and Roșuleț) take over dominance, generating changes in diversity.

Table 6. SIMPER analysis results of the major phytoplankton contributors to the average dissimilarity between seasons in: P – Puiu lake, T – Tătaru lake, R – Roșuleț. Av.d. - average dissimilarity, Contrib. (%) – percentage contribution to the average dissimilarity; Mean Aug – mean abundance in August; Mean Sep – mean abundance in September.

	Taxon	Av. d.	Contrib. %	Mean august	Mean september
P	*Oscillatoria minima* Gicklhom	25.29	34.68	$8.36x10^6$	$5.01x10^7$
P	*Aphanizomenon flos-aquae* (L.) Ralfs	5.153	7.065	$7.29x10^6$	$2.14x10^6$
P	*Oscillatoria* sp.	4.576	6.273	$5.84x10^6$	0
R	*Microcystis pulverea* (Wood) Migula	15.01	18.44	$6.23x10^6$	$1.18x10^7$
R	*Aphanocapsa grevillei* (Hassal) Raben	14.44	17.73	9.78x106	0
R	*Aphanizomenon flos-aquae* (L.) Ralfs	12.08	14.83	$9.04x10^6$	0
R	*Oscillatoria minima* Gicklhom	10.94	13.44	$8.32x10^6$	$1.35x10^6$
T	*Gomphosphaeria lacustris* Chodat	13.73	16.84	$4.21x10^6$	$1.77x10^7$
T	*Microcystis pulverea* (Wood) Migula	11.11	13.63	0	$2.48x10^7$
T	*Aphanocapsa grevillei* (Hassal) Raben	8.998	11.04	$1.26x10^6$	$1.58x10^7$
T	*Merismopedia tenuissima* Lemm.	6.823	8.373	$3.27x10^6$	$7.58x10^6$
T	*Oscillatoria limosa* C.Agardh ex Gomont	4.825	5.92	$2.02x10^6$	0

Rate of Competitive Displacement (RCD). Although the results showed a decisive role of *Cyanobacteria* in the phytoplankton component in ecosystems, RCD highlighted that, with the arrival of autumn, the other two major groups (green algae and diatoms) showed tendencies toward recovery in their functionality. Thus, the negative values (Table 7) indicate an unfavourable exchange rate for the analysed blue-green algae group relative to the second one, diatoms or green algae. In the *Cyanobacteria* vs. *Chlorophyceae* testing, all ecosystems showed negative values: Puiu (-0.09), Tătaru (-0.43), and Roșuleț (-1.00), indicating that *Chlorophyceae* had a competitive advantage over *Cyanobacteria* in all three locations, with the impact being most pronounced in Roșuleț Lake. Also, the results regarding *Cyanobacteria* vs. *Bacillariophyceae* showed both a negative value in Puiu (-0.64) and positive values in Tătaru (0.22) and Roșuleț (0.89), which indicated that diatoms dominated competitively only in Puiu Lake, while in Tătaru and Roșuleț, *Cyanobacteria* managed to prevail over them even in autumn. Also, in Roșuleț, the most dynamic and unbalanced phytoplankton competition was recorded among all the studied locations, at the point where *Chlorophyceae* exerted the greatest pressure (-1), thus signalling a trend of competitive collapse on *Cyanobacteria*.

Table 7. Rate of Competitive Displacement (RCD) between *Cyanobacteria* and the other main phytoplanktonic groups

	Cyanobacteria vs *Chlorophyceae*	*Cyanobacteria* vs *Bacillariophyceae*
Puiu	-0.09	-0.64
Roșulet	-1	0.89
Tătaru	-0.43	0.22

This may indicate that the available resources in Roșuleț were accessed more efficiently by *Chlorophyceae* compared to the other groups, so *Cyanobacteria* could no longer maintain their population as in summer. However, *Cyanobacteria* maintained dominance despite competition with diatoms, even though the diatom replacement rate was the highest (0.89) among the three ecosystems (Table 7). Thus, in Roșuleț, *Cyanobacteria* were subjected to niche pressures.

The structural features of phytoplankton communities were also reflected in the zooplankton composition across the three lakes, indicating adaptive ecological responses shaped by interactions among environmental factors and trophic structure.

Thus, the pressure exerted by phytoplankton on primary consumer communities led to a prevalence of small, opportunistic forms, especially rotifers (*Trichocerca, Polyarthra, Keratella*) and juvenile copepods, along with microcrustaceans such as *Bosmina* spp. (Table 8).

Table 8. Dominant zooplankton species and their distribution in the studied ecosystems

Spercies	P- VIII	P- IX	T- VIII	T- IX	R-VIII	R-IX
Bosmina coregoni (Baird, 1857)	0.67	50.08	0.00	0.00	2.74	299.82
Copepoda g. sp. St Nauplial	99.17	239.58	238.20	471.91	78.70	86.70
Keratella cochlearis var. *tecta* (Gosse, 1851)	8.00	229.84	0.00	5.55	2.30	32.82
Lecane closterocerca (Schmarda, 1859)	0.00	7.54	0.55	0.66	639.13	0.70
Polyarthra remata Skorikow 1896	137.50	54.96	142.31	297.30	64.99	93.90
Synchaeta oblonga (Ehrenberg, 1832)	100.33	0.00	1.50	23.59	6.43	11.20
Trichocerca pussila (Jennings, 1903)	167.50	86.54	0.94	2.91	185.36	1.30
Trichocerca similis (Wierzejski, 1893)	231.50	86.82	0.00	2.00	180.80	12.32
Diflugia globulosa (Dujardin, 1837) Penard, 1902	1.33	260.42	0.00	3.04	1.30	0.00
Diflugia lobostoma (Leidy, 1879)	154.17	293.52	3.55	4.62	388.40	3.28

The Grubbs test identified statistically significant outliers ($p < 0.05$) for several species, indicating higher dominance relative to the rest of the zooplankton community and associated with a temporary reduction in competition. In Puiu Lake, Grubbs showed significant values for *Trichocerca similis* (August - 6.34) and *Difflugia lobostoma* (September - 5.75), indicating punctual dominance. In Tataru Lake, nauplial copepod stages were identified as dominant peaks in both August (9.14) and September (8.48), indicating maintenance of juvenile stages. In Roșuleț Lake, the rotifer *Lecane closterocerca* (August - 8.44) and the cladoceran *Bosmina coregoni* (September - 9.53) reflected pronounced seasonal structural changes as well as an alternation of dominant species. Thus, the results indicate a high spatio-temporal heterogeneity of zooplankton, with dominance patterns related to period and ecosystem, suggesting a differentiated response of taxa to local ecological conditions.

Structure and distribution of phytoplankton communities. The dominance of *Cyanobacteria* in all three lakes studied during the summer period underlines their role as key factors in structuring phytoplankton communities in the Danube Delta. This dominance is consistent with numerous studies showing that, under conditions of high temperatures, hydrodynamic stability and increased nutrient availability, *Cyanobacteria* are favoured over other algal groups (Paerl & Huisman, 2008; Moza et al., 2021; Dokulil & Teubner, 2023). The high cyanobacterial abundance in Puiu and Tătaru lakes, as well as the persistence of this group in Roșuleț, indicate a meso- to hypereutrophic trophic status, characteristic of many deltaic lacustrine ecosystems. In Puiu and Tătaru, the simultaneous increase of *Cyanobacteria*, *Chlorophyceae* and diatoms suggests a general intensification of primary production in the late summer period, while in Roșuleț the decline of most groups, except *Chlorophyceae*, indicates a pronounced structural instability. Such spatiotemporal patterns are frequently reported for shallow lakes, where sediment resuspension and internal nutrient recycling can amplify fluctuations in phytoplankton communities (Oosterberg et al., 2000; Gâștescu, 2009).

Taxonomic structure and interpretation of discriminant analysis. Discriminant analysis revealed a clear separation of *Cyanobacteria* from the other major groups, highlighting the functional contrast between this group and the rest of the phytoplankton. The intermediate positioning and high dispersion of *Chlorophyceae* indicate increased ecological flexibility, reflecting the ability of this group to occupy varied niches and to respond rapidly to environmental changes. Diatoms and *Chrysophytes* showed clearer delimitation, suggesting stricter ecological requirements and greater sensitivity to changes in physicochemical conditions. The overlaps observed among *Chlorophyceae*, *Cyanobacteria*, and *Euglenophyceae* indicate convergent ecological responses and common functional traits, especially in unstable

ecosystems. This type of community structure is typical of eutrophic lakes, where competition for resources is intense, and advantages are quickly redistributed among groups depending on seasonal conditions (Jia et al., 2022; Tóth-Krasznai et al., 2022).

α and β diversity: ecological implications. Although total species richness remained relatively high in most cases, α-diversity indices showed a clear trend toward increasing dominance and decreasing evenness, especially in Puiu and Roșuleț lakes. This combination suggests the emergence of an "apparent diversity", in which numerous taxa are present but their contribution to total biomass is reduced, eclipsed by *Cyanobacteria*'s dominance. The phenomenon is frequently reported in eutrophic ecosystems and is considered an indicator of the functional degradation of phytoplankton communities (Vasconcelos et al., 2020; Ahoutou et al., 2021).

The moderately high spatial β diversity reflects the pronounced heterogeneity of the studied lakes, determined by differences in hydrological connectivity, morphology and nutrient supply. At the same time, temporal β-diversity indicates significant seasonal turnover, especially in Roșuleț Lake, confirming the structural instability of this ecosystem. These results suggest that seasonal variations may have a greater impact on community composition than spatial differences, a finding also confirmed by ANOSIM tests. Seasonal dynamics of *Cyanobacteria*: ANOSIM and SIMPER. ANOSIM results confirm that seasonal differences explain a significant proportion of the variation in phytoplankton communities, especially in Lake Roșuleț. SIMPER analysis showed that these changes are mainly driven by a small number of cyanobacterial species, including *Oscillatoria minima, Microcystis pulverea, Gomphosphaeria lacustris,* and *Aphanizomenon flos-aquae*. The alternation between dominant summer and autumn species reflects the seasonal succession described by the PEG model, where non-nitrogen-fixing *Cyanobacteria* can take over dominance towards the end of the growing season (Moza et al., 2021).

The persistence and dynamics of these taxa indicate a high adaptability to eutrophic conditions and variations in the hydrological regime. At the same time, the disappearance or decline of some species in autumn suggests increased sensitivity to temperature drops and increased water turbulence, factors known to limit cyanobacterial blooms (Jiang et al., 2023; Lenard & Ejankowski, 2024).

Relationships between the main phytoplankton groups. Even though *Chlorophyceae* occupied a secondary position in the phytoplankton structure, they demonstrated a competitive role, especially in Lake Roșuleț, where they exerted the greatest pressure on *Cyanobacteria* during the autumn period. The negative values of the Rate of Competitive Displacement (RCD) for the *Cyanobacteria-Chlorophyceae* comparison across all lakes confirm the competitive advantage of green algae at lower temperatures and under changing light and nutrient conditions. This behaviour is well documented in the literature, showing that many *Chlorophyceae* exhibit high growth rates at moderate temperatures and can efficiently exploit available phosphorus, thereby limiting cyanobacterial development (Briddon et al., 2022; Vasconcelos et al., 2020).

In contrast, the relationship between *Cyanobacteria* and diatoms was more nuanced. In Puiu Lake, diatoms had a competitive advantage in autumn; in Tătaru and Roșuleț, *Cyanobacteria* remained dominant, even as diatom replacement rates increased. This capacity suggests that *Cyanobacteria* exhibit functional adaptations to persistent eutrophic conditions, including tolerance to variations in the N:P ratio and changes in the mixing regime (Zou et al., 2025; Reynolds, 2006).

The Rate of Competitive Displacement analysis adds an important functional dimension to the interpretation of results, highlighting not only the competitive relationships among phytoplankton groups but also the degree of community stability. Strongly negative RCD values indicate unstable competitive hierarchies and reduced cyanobacterial capacity to maintain dominance, while mixed values suggest seasonal resilience, with alternations between dominant groups.

Also, the fact that seasonal differences are more pronounced than spatial ones emphasises the role of seasonality as an integrating factor of physicochemical and biological variations.

This predominance of the temporal signal suggests that climate change and changes in the hydrological regime may have a stronger impact on phytoplankton community structure than local spatial differences between lakes.

Overall, the results confirm the central role of *Cyanobacteria* in structuring phytoplankton communities in the studied lakes, but also highlight a clear dissociation between taxonomic diversity and ecological functionality of the communities. Although the specific richness remains relatively high, the pronounced dominance of *Cyanobacteria* leads to functional simplification, with the effective contribution to biomass and ecosystem processes concentrated in a small number of opportunistic taxa. This situation reflects what can be defined as an "apparent diversity", characteristic of shallow eutrophic ecosystems.

The shallow nature of the analysed lakes amplifies the role of internal sediment-nutrient-phytoplankton feedbacks, favouring the persistence of *Cyanobacteria* even under conditions of seasonal instability. In this context, Lake Roșuleț is characterised by a more unstable community structure, driven by intense internal nutrient recycling and high competitive pressure from *Chlorophyceae*, suggesting an ecosystem in an ecological transition.

The species with high abundances identified by the Grubbs test ($p < 0.05$) reflect episodes of massive development of resistant and opportunistic species, characteristic of shallow, highly dynamic aquatic ecosystems such as the lakes of the Danube Delta. The specialised literature describes the punctual dominance of the rotifers *Trichocerca similis* and *Lecane closterocerca* as opportunistic taxa with high reproduction rates and increased tolerance to eutrophic or unstable conditions (Allan, 1976; Wallace et al., 2006). Regarding the nauplial stages of Copepoda in Lake Tătaru, the persistent outlier values observed in both months suggest an unbalanced stage structure, with juveniles dominating. This pattern is typical of ecosystems where conditions favour continuous reproduction, but the survival of adult stages is limited by stressors or predators (Sommer et al., 2012; Hirst & Kiørboe, 2002). This may reflect another effect of bottom-up phytoplankton pressures. Also, the dominance of *Bosmina coregoni* in Lake Roșuleț in September reflects seasonal changes in the structure of the cladoceran community, which are recognised for their sensitivity to temperature, phytoplankton availability, and grazing pressure (Lampert, 1987). These episodes of dominance of some zooplankton species were directly reflected in the values of diversity indices, in particular the decrease of Shannon and Pielou indices and the increase of dominance (Simpson). The literature emphasises that such temporary imbalances are an intrinsic component of planktonic community function and provide essential information about the processes of community assembly and the stability of ecosystems (Magurran, 2013; Borics et al., 2021).

CONCLUSIONS

Cyanobacteria proved to be the dominant ecological factor in the structure and dynamics of planktonic communities in Puiu, Tătaru, and Roșuleț lakes, profoundly influencing both phytoplankton composition and zooplankton responses. During the summer, blue-green algae reached very high densities, dominating the phytoplankton and affecting the diversity and functional balance of the other communities. Thus, the phytoplankton structure was strongly shaped by the competition between *Cyanobacteria* and the other major groups (chlorophytes and diatoms). With the onset of autumn, recovery trends in diatoms and chlorophytes were observed, reflected in negative values of the competitive replacement rate (RCD). However, the intensity of these processes varied among the lakes, with Roșuleț exhibiting the greatest structural instability and the most pronounced seasonal turnover. Seasonal changes were stronger than spatial ones, and cyanobacterial species were the main contributors to dissimilarity between periods characterised by variations in community structure, either through massive development or sudden disappearances. The impact on zooplankton was evident in the dominance of small, opportunistic forms (rotifers and juvenile copepod stages), indicating the trophic pressure exerted by a phytoplankton community dominated by *Cyanobacteria* and the reduced quality of the food resource. Overall, our study

highlights the central role of *Cyanobacteria* in regulating the functioning of lacustrine ecosystems in the Danube Delta. In the context of climate change and eutrophication, these processes are increasingly common, accentuating the vulnerability of deltaic ecosystems.

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REFERENCES

Ahoutou, M. K., Djeha, R. Y., Yao, E. K., Quiblier, C., Niamen-Ebrottié, J., Hamlaoui, S., Tambosco, K., Perrin, J.-L., Troussellier, M., Bernard, C., Séguis, L., Bouvy, M., Pédron, J., Konan, F. K., Humbert, J. F., & Coulibaly, J. K. (2021). Assessment of some key indicators of the ecological status of an African freshwater lagoon (Lagoon Aghien, Ivory Coast). *PLoS ONE, 16*(5), e0251065. https://doi.org/10.1371/journal.pone.0251065

Allan, J. D. (1976). Life history patterns in zooplankton. *The American Naturalist, 110*(971), 165–180. https://doi.org/10.1086/283056

Briddon, C. L., Szekeres, E., Hegedűs, A., Nicoară, M., Chiriac, M., Stockenreiter, M., & Drugă, B. (2022). The combined impact of low temperatures and shifting phosphorus availability on the competitive ability of cyanobacteria. *Scientific Reports, 12*(1), 16409. https://doi.org/10.1038/s41598-022-20580-2

Borics, G., Abonyi, A., Salmaso, N., & Ptacnik, R. (2021). Freshwater phytoplankton diversity: Models, drivers and implications for ecosystem properties. *Hydrobiologia, 848*, 53–75. https://doi.org/10.1007/s10750-020-04332-9

Coops, H., Hanganu, J., Tudor, M., & Oosterberg, W. (1999). Classification of Danube Delta lakes based on aquatic vegetation and turbidity. *Hydrobiologia, 415*, 187–191. https://doi.org/10.1007/s10452-007-9108-8

Dokulil, M. T., & Teubner, K. (2023). Long-term adjustment of phytoplankton structure to environmental traits at timescales during lifetime development and over generations. *Hydrobiologia, 851*(4), 823–839. https://doi.org/10.1007/s10750-023-05365-6

Dumitran, G. E., Vuță, L. I., & Popa, B. (2024). Overview of the eutrophication in Romanian lakes and reservoirs. *Limnological Review, 24*(1), 76–104.

Dumitran, G. E., Vuță, L. I., Popa, B., & Popa, F. (2020). Hydrological variability impact on eutrophication in a large Romanian border reservoir, Stânca–Costești. *Water, 12*(11), 3065. https://doi.org/10.3390/w12113065

Edler, L., & Elbrächter, M. (2010). The Utermöhl method for quantitative phytoplankton analysis. In B. Karlson, C. Cusack, & E. Bresnan (Eds.), *Microscopic and molecular methods for quantitative phytoplankton analysis* (pp. 13–20). Paris, FR: UNESCO.

Gâștescu, P. (2009). *Delta Dunării – geneză și evoluție, hidrologie, peisaj*. București, RO: Editura Fundației România de Mâine.

Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica, 4*(1).

Hirst, A. G., & Kiørboe, T. (2002). Mortality of marine planktonic copepods: Global rates and patterns. *Marine Ecology Progress Series, 230*, 195–209. https://doi.org/10.3354/meps230195

Ji, X., Verspagen, J. M. H., Stomp, M., & Huisman, J. (2017). Competition between cyanobacteria and green algae at low versus elevated CO_2: Who will win, and why? *Journal of Experimental Botany, 68*(14), 3815–3828.

Jia, J., Chen, Q., Ren, H., Lu, R.-J., He, H., & Gu, P. (2022). Phytoplankton composition and their related factors in five different lakes in China: Implications for lake management. *International Journal of Environmental Research and Public Health, 19*(5), 3135. https://doi.org/10.3390/ijerph19053135

Lampert, W. (1987). Laboratory studies on zooplankton-cyanobacteria interactions. *New Zealand Journal of Marine and Freshwater Research, 21*(3), 483–490. https://doi.org/10.1080/00288330.1987.9516244

Lenard, T., & Ejankowski, W. (2024). Ice phenology as a predictor of *Planktothrix rubescens* bloom in the vegetation season in temperate lakes. *Frontiers in Microbiology, 15*, 1384435. https://doi.org/10.3389/fmicb.2024.1384435

Magurran, A. E. (2013). *Measuring Biological Diversity*. Wiley-Blackwell. 272 pp. ISBN 978-1-118-68792-5.

Moldoveanu, M., & Florescu, L. I. (2011). Long-term analysis of cyanobacterial blooms in Lake Roșu (Danube Delta). *Scientific Annals of the Danube Delta Institute*, 17, 89–98.

Moldoveanu, M. M., Florescu, L. I., Dumitrache, C. A., & Cătana, R. D. (2025). Assessing urban river health: Phytoplankton as a proxy for resource use efficiency and human impact. *Phycology, 5*(4), 72.

Moza, M. I., Postolache, C., Benedek, A. M., Moldoveanu, M., & Spaak, P. (2021). Geographical and temporal patterns of cyanobacterial assemblages in the Danube Delta lake complexes. *Hydrobiologia, 848*, 753–771. https://doi.org/10.1007/s10750-020-04466-w

Oosterberg, W., Staras, M., Bogdan, L., Buijse, A. D., Constantinescu, A., Coops, H., Hanganu, J., Ibelings, B. W., Menting, G., & Navodaru, I. (2000). *Ecological gradients in the Danube Delta lakes: Present state and man-induced changes*. Lelystad, NL: RIZA Report 2000.015.

Paerl, H. W., & Huisman, J. (2008). Blooms like it hot. *Science, 320*(5872), 57–58.

Paerl, H. W., & Otten, T. G. (2013). Harmful cyanobacterial blooms: Causes, consequences, and controls. *Microbial Ecology, 65*(4), 995–1010.

Pavel, A., Durisch-Kaiser, E., Balan, S., Radan, S., Sobek, S., & Wehrli, B. (2009). Sources and

emission of greenhouse gases in Danube Delta lakes. *Environmental Science and Pollution Research, 16*(Suppl. 1), 86–91.

Reynolds, C. S. (2006). *The ecology of phytoplankton*. Cambridge, UK: Cambridge University Press.

Sommer, U., Adrian, R., De Senerpont Domis, L. N., Elser, J. J., Gaedke, U., Ibelings, B. W., Jeppesen, E., Lürling, M., Molinero, J. C., Mooij, W. M., van Donk, E., & Winder, M. (2012). Beyond the Plankton Ecology Group (PEG) model: Mechanisms driving plankton succession. *Annual Review of Ecology, Evolution, and Systematics, 43*, 429–448. https://doi.org/10.1146/annurev-ecolsys-110411-160251

Török, L. (2011). The trend of phytoplankton development in Danube Delta lakes. *Scientific Annals of the Danube Delta Institute*, 17, 89–98.

Török, L., Török, Z., Cârstea, E. M., & Savaștru, D. (2017). Seasonal variation of eutrophication in some lakes of the Danube Delta Biosphere Reserve. *Water Environment Research, 89*(1), 86–94. https://doi.org/10.2175/106143016X14733681696248

Tóth-Krasznai, E., Török, P., Borics, G., Lukács, Á., Kókai, Z., Lerf, V., Görgényi, J., & B-Béres, V. (2022). Functional dynamics of phytoplankton assemblages in hypertrophic lakes: Functional- and species diversity is highly resistant to cyanobacteria*Cyanobacteria*l blooms. *Ecological Indicators, 145*, 109583. https://doi.org/10.1016/j.ecolind.2022.109583

Tudorancea, C., & Tudorancea, M. M. (2006). *Danube Delta: Genesis, biodiversity and conservation*. Leiden, NL: Backhuys Publishers.

Vasconcelos, H. C., Lopes, J. A., Pereira, M. J., & Pinto, A. S. (2020). Fluorescence behavior of phytoplankton blooms by time-correlated single-photon counting (TCSPC). In *IntechOpen eBooks*. https://doi.org/10.5772/intechopen.93292

Wallace, R. L., Snell, T. W., Ricci, C., & Nogrady, T. (2006). *Rotifera. Volume 1: Biology, Ecology and Systematics* (2nd ed.). Backhuys Publishers, Leiden. 299, ISBN 90-5782-178-8.

Zou, B., Hu, H., Jia, J., Wu, W., Li, X., Chen, X., Zeng, H., Wang, Z., & Wu, C. (2025). Temporal variation of plankton community in a typical lake in the middle reaches of the Yangtze River: Structure, environmental response and interactions. *Water, 17*(7), 1021. https://doi.org/10.3390/w17071021