Geographical and temporal patterns of cyanobacterial assemblages in the Danube Delta lake complexes

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Abstract

Danube Delta shallow lakes experience cyanobacteria blooms that can negatively affect the aquatic ecosystem. Although there are several studies on Danube Delta cyanobacteria, little is known about their spatial-temporal patterns and the potential predictive role they can offer. We therefore analyzed the distribution of cyanobacteria in 19 lakes belonging to three lake complexes, and tested whether their seasonal dynamics are in line with the predictions of the PEG model. Furthermore, we investigated to which extent cyanobacteria diversity and abundance were related to lake hydrogeomorphological characteristics such as: surface, water level, connectivity, water retention, flood risk, transparency. Although lakes had different seasonal cyanobacterial assemblages, the biovolume and genus richness had a geographical pattern, decreasing from south-east (lakes forming the fluvial delta) towards north-west (lakes forming the maritime delta). Cyanobacteria biovolume reflected largely the PEG model peaking in summer (the fluvial delta) and autumn (the maritime delta). Genus richness followed the same pattern. Cyanobacteria distribution was predicted by various abiotic (e.g. risk of flooding, connectivity) and biotic factors (e.g. submersed macrophytes, phytoplankton diversity, peat deposits). Our study contributes to the understanding of cyanobacteria diversity and distribution in shallow interconnected lakes by revealing the complexity of predictors for geographical and seasonal patterns.

Key words: freshwater cyanobacteria, RDA, assemblage, shallow lakes, spatial-temporal dynamics, hydrogeomorphological predictors

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Introduction

Deltas support high biodiversity and supply many ecosystem services ([Russi et al., 2013](#)). Water quantity and quality, as well as delta's biodiversity is affected by multiple use of these ecosystems by many stakeholders ([Erwin, 2009](#)). Biodiversity is used for monitoring the ecological state of environments ([Guerold, 2000](#); [Schmitz & Nagel, 1995](#)). Biodiversity decreases with environment degradation ([Botnariuc & Vădineanu, 1982](#); [Cardinale et al., 2012](#)), and is therefore a key measure of environmental quality in lake ecosystems ([Sayer et al., 1999](#)). The study of biodiversity in river deltas from temperate regions and in their associated human impacted lakes is of great importance ([Botnariuc & Vădineanu, 1982](#); [Kallis & Butler, 2001](#); [Penning et al., 2008](#)).

The Danube Delta, shared by Romania (80% of its surface) and Ukraine (20%), is a large and complex hydrological system through which water flows in three main branches (Chilia, Sulina and Sf. Gheorghe) and consist of hundreds of shallow lakes, connecting channels and floating reed beds ([Coops et al., 2008](#); [Găldean & Ruști, 2006](#)). At present, the Danube Delta represents one of the most valuable European natural wetlands. The mixture of several types of natural, partly modified, or man-made ecosystems ([Găstescu et al., 1999](#)), hosts over 1615 plant species and 3491 invertebrate and vertebrate species ([Oosterberg et al., 2000](#)), thus representing a global biodiversity hotspot ([Giosan, 2014](#)). It is characterized by a greater biodiversity compared to other European deltas due to its high habitat heterogeneity ([Buijse et al. 2002](#)). Unfortunately, the anthropic pressure, consisting of hydrotechnological interventions along the main Sulina branch between 1947 and 1989, led to significant changes in the water regime of the Danube Delta's natural hydrological network ([Irimuş, 2006](#)). The hydrological regime is strongly influenced by temporal water fluctuations due to weather events in the catchment (e.g. snow melt or high precipitations). This influx is subsequently returned to the adjacent secondary channels during summertime, having

ecological consequences in lakes. The Danube Delta comprises two sectors: a fluvial and a maritime one. The first sector includes the older lakes developed within the former gulf of the Danube river, with smaller and deeper lacustrine areas, partly subjected to an intensive siltation process. The second sector includes one of the most important lacustrine complex (Roşu-Puiu) affected by major morphohydrographic changes in the contact zone with the Black Sea ([Oosterberg et al., 2000](#)). Here also the last and most influencing dredging works were done ([Romanescu, 1999](#)). The maritime delta is composed of lagoons and sandy barriers created by long shore circulation ([Vespremeanu-Stroe et al., 2017](#)).

The Danube Delta underwent an accelerated eutrophication, triggered by heavy organic pollution that occurred throughout the Danube River Drainage Basin and altered the aquatic ecosystems ([Postolache et al., 2006](#); [Vădineanu et al., 2001](#)). As nutrient concentrations increased the dominance and abundance of phytoplankton, particularly cyanobacteria, also increases, often resulting in dense blooms, especially during summer ([Reynolds, 1984](#)). Cyanobacteria can provide several ecological services ([Díez & Ininbergs, 2014](#)). They fix nitrogen and release oxygen by photosynthesis, accumulate phosphorus and reflect the ecological state of the environment (i.e. bioindicator) ([Chaurasia, 2015](#); [Mateo et al., 2015](#)). But when cyanobacteria blooms occur, they are usually toxic and have severe consequences (release of toxins, organic material enrichment in sediment, negative impact on the food web and increased bacterial activity) for the entire ecosystem ([Havens, 2008](#)). In particular, algal blooms alter ecological services, such as water oxygenation and quality of drinking water. These problems seem to accentuate as a result of climate change ([Kleinteich et al., 2012](#); [Paerl & Huisman, 2008](#); [Paerl & Huisman, 2009](#)).

The spatial distribution of cyanobacteria taxa may depend on environmental conditions such as: climatic gradients and structural characteristics of the landscape (e.g. the presence or absence of lake vegetation) ([Stoch et al., 2016](#)). The hydrology of the Danube

Delta lakes is complex and the lakes are not isolated, but are parts of a large riverine system (Oosterberg et al., 2000). Therefore, connectivity and hydrogeomorphological features should also be taken into account when studying cyanobacteria distribution in the Danube Delta lakes. Water level can be used as a proxy for the hydrological regime (Irimuş, 2006) since water enters the lakes from the main channels into the secondary canals during spring with the rising of the water level and exits the lakes during summer dry season, when water level drops.

The Danube Delta is dominated by “flooded reed” (lakes with reduced exchange of water and partially covered with floating vegetation), “floating reed beds” (near the lakes with reduced exchange of water) and “lakes with large surface” or active change of water (Năstase & Năvodaru, 2008). The phytoplankton also plays an important role in the Danube Delta since it can cause rapid turbidity changes in shallow lakes by the water input from the main channels as revealed also by its spatial distribution observed on satellite images (Güttler et al., 2013). In contrast, macrophytes have an essential role in the maintenance of low turbidity (Vădineanu et al., 1992) and compete with the phytoplankton for nutrients. Previous studies investigated targeted some major aspects of the Danube Delta’s ecosystems, such as the impact of eutrophication and the consequent changes that occur in the Delta’s structure and functions (Postolache, 2003, 2006). Additionally, several publications describe cyanobacterial assemblages (Dumitrache et al., 2014; Moldoveanu & Florescu, 2013; Török, 2008b) indicating that bloom forming species, such as *Microcystis aeruginosa* (Kützing) Kützing 1846 or *Aphanizomenon flos-aquae* Ralfs ex Bornet & Flahault 1886, were frequently found in the shallow eutrophic lakes of the Danube Delta (Moldoveanu & Florescu, 2013; Török, 2008b).

The seasonal succession of phytoplankton in temperate (deep) lakes has been described with the PEG (Plankton Ecology Group) model (De Senerpont Domis et al., 2013).

In this model, two peaks of biomass occur: one in spring, involving small edible algae, and the other in summer, involving large or colonial algae resistant to zooplankton grazing. Phytoplankton dynamics in the Danube Delta are not fundamentally different from that in other temperate lakes. According to the PEG model, in the Danube Delta we might expect a high nutrients input during spring that can lead to diatoms blooms. This is followed by a clear water phase with a high grazer pressure and low nutrients availability and a shift to cyanobacteria in summer. Ultimately, increased water mixing, nutrient availability and predominance of filamentous algae and blooms are common in autumn ([Oosterberg et al., 2000](#)) ([Ibellings, 1992](#)).

Anthropogenic interventions have an important role in driving the seasonal variation of phytoplankton as well. Therefore, disturbances caused by changes in the external environment (e.g. pollution, nutrients), affect diversity ([Sommer et al., 1986](#)), which is an important aspect of community structure ([Xiao et al., 2011](#)). Anthropogenic-caused disturbances can alter cyanobacterial seasonality especially in those areas where the highest cyanobacteria biomass and diversity is observed (such as the Roşu-Puiu lake complex) ([Moldoveanu & Florescu, 2013](#)).

In this study, we analyzed the geographical distribution and seasonal dynamics of cyanobacteria in the Danube Delta lake complexes over a two-year period. Our study aims to test the following hypotheses: H (1) cyanobacterial assemblages differ among lake complexes with respect to biovolume and richness, being more dominant in the maritime delta, H (2) there is significant seasonal variation of cyanobacterial assemblages according to PEG model and H (3) cyanobacterial assemblages are influenced by the hydrogeomorphological characteristics that distinguish the Danube Delta lake complexes.

Material and methods

Study area and sampling

The Danube Delta is a Biosphere Reserve located at 45°0'N latitude and 29°0'E longitude in the eastern part of Romania. It comprises more than 300 water bodies, mainly shallow lakes, grouped in lake complexes, and interconnected by river branches and man-made canals ([Coops et al., 2008](#); [Romanescu, 2005](#)). The four major lake complexes (LCs) in the Danube Delta, are named after the two most representative lakes of each complex ([Oosterberg et al., 2000](#)). Listed from oldest to youngest, these are Șontea-Furtuna (LC1), Isac-Gorgova (LC2), Măța-Merhei (LC3) and Roșu-Puiu (LC4). The first three complexes belong to the fluvial delta and the fourth one to the maritime delta, being separated by the Caraorman sand dune and forest. Lakes in the most upstream complex Șontea-Furtuna have consistently low residence times, higher transparency and very good connection to the main branch. These lakes have therefore a high flooding risk. In the Măța-Merhei and Isac-Gorgova complex we find isolated lakes with a high residence time, organic bottom and high macrophyte coverage and phytoplankton diversity. In Roșu-Puiu on the other hand, the residence time in the large lakes is low, but increases in the small lakes (see Table S4 for more details) ([Friedrich et al., 2003](#); [Găstescu & Știucă, 2008](#); [Oosterberg et al., 2000](#)).

In the current study, 19 shallow lakes situated on both sides of the Sulina branch and belonging to complexes 2-4 were sampled (Fig. 1). The locations of the studied lakes and a brief characterization of the lake complexes are given in Table 1. The lakes' limnological description was already detailed in previous papers ([Enache et al., 2019](#); [Fontana et al., 2018](#)). Sampling campaigns were carried out seasonally (except winter) for two years, in 2013 and 2014, in spring (May), summer (July) and autumn, (September/October), resulting in 114 phytoplankton samples.

Cyanobacteria analysis

Water samples were taken from the entire water column, from the center of each lake, using a Schindler – Patalas device (5 L). We extracted one sample (5 L) from the middle of the water column from lakes less than one meter deep, two samples (a “deep” and “less deep one”: 10 L) from lakes with a depth between one and two meters and three samples, one from each “meter layer” (15 L), from lakes deeper than two meters. From the final volume of mixed water a sample of 500 mL was taken, stored in a plastic container and fixed in the field with 4% formaldehyde.

In the laboratory, the phytoplankton samples were concentrated to 100 mL, by sedimentation for a few days, prior to cyanobacteria taxonomical identification at species level using specific keys ([Huber-Pestalozzi, 1938](#); [Komárek, 1998](#); [Komárek et al., 1998](#); [Komárek & Anagnostidis, 2005](#); [Komárek et al., 2014](#)).

Cyanobacteria total abundance, expressed as cells L⁻¹ (used for biovolume calculation), was estimated through direct count with a Zeiss inverted microscope using the Utermöhl technique ([Utermöhl, 1958](#)). Cyanobacteria total biovolume, expressed as µm³ L⁻¹, was determined according to a protocol described in ([Fontana et al., 2018](#)) based on a mean cell biovolume (calculated from geometric approximation of each species/genera cell shapes) ([Hillebrand et al., 1999](#); [Sun & Liu, 2003](#)).

The final value used for statistical analyses was divided by 10⁶, expressed as cubic micrometer per microliter (µm³ µL⁻¹) and was subsequently log-transformed (using natural logarithm) for normalization of the residuals in the univariate models and to evaluate relationships between response and explanatory variables on a multiplicative instead of an additive scale.

Identification of some cyanobacteria was not possible at species level, therefore some species are listed as “sp.” (Table S1). Thus, statistical analyses (using biovolume and richness) were

performed at the genus level, as it was done previously by Coops and his colleagues ([Coops et al., 2008](#)). For each of the hypotheses we considered three aspects of the cyanobacterial assemblage: total abundance (biovolume), genus richness and genus composition (i.e. biovolume of each genus in the assemblage) – each giving a different insight into the mechanisms of their spatio-temporal patterns.

Environmental variables

The assessment of the hydrogeomorphological variables (Table S4) and estimation of aquatic macrophytes were done as follows: (1) water level (depth) and transparency were measured in the center of the lake using a Secchi disk; this was done prior to water sampling in order to estimate how many Schindler-Patalas should be collected to cover the entire water column, (2) turbidity was measured with Hanna HI98713 turbidimeter, (3) water flow and water velocity were measured using a stream standard flow meter flow (MFP51 model from Geopacks), (4) surface, shore, main channel distance to lakes, elevation were measured using GoogleEarth Pro software and (5) macrophytes coverage was assessed based on photographs of the entire area of the lakes for total macrophytes and *in situ* directly from the boat based on direct visual observations of the floating and the submerged vegetation. For each lake and sampling campaign coverage was assigned to one of the following categories: low (0-25%), medium (25-50%) or high (50-100%) ([Radu et al., 2017](#)). The analyses were performed using the coverage mid-values of the three ranges (12.5, 37.5 and 75%) ([Lauridsen et al., 2015](#)) for each sampling campaign and the average values were used for statistical analyses. Water retention (or residence) time was provided by a one-dimensional flow model (SOBEK) ([Oosterberg et al., 2000](#)). SOBEK represents a dedicated hydrodynamic mathematical model for Danube Delta water circulation based on measurements made in 1996 ([Bondar & Panin, 2001](#); [Friedrich et al., 2003](#)). Based on the modelling results, the residence time appears to be

rather insensitive to seasonal water level fluctuations, even if the lakes within one complex can vary considerably in residence time ([Oosterberg et al., 2000](#)).

Statistical analyses

As response variables we included (1) biovolume, (used as a proxy for biomass ([Passy & Legendre, 2006](#))), (2) genus richness (the number of genera identified in each sample), as a measure of cyanobacteria alpha diversity) and (3) genus composition (biovolume of individual genera). As predictors we considered the lake complex, season, year, and the environmental variables (hydrogeomorphological and vegetation characteristics) of the lakes. Correlation was tested between the genus richness and biovolume, and between environmental variables. We used Shapiro-Wilk test to verify the normality assumption of parametric tests and linear mixed models. No significant deviation from the normal distribution was detected for the residuals of linear mixed models. In contrast, vegetation and hydrogeomorphological variables as well as genus biovolume and richness were not normally distributed. Univariate analyses were performed with R version 3.5.1 (*R Core Team 2018). For the mixed models we used „nlme” version 3.1-137 ([Pinheiro et al., 2018](#)). Multivariate analyses were performed with Canoco 5 ([Ter Braak & Šmilauer, 2012](#)).

For each of the hypothesis we considered all three characteristics of the cyanobacterial assemblage: total biovolume, genus richness and composition. Each characteristic offered a different insight into the mechanisms affecting cyanobacterial spatio-temporal patterns. While patterns of the total biovolume and genus composition can be tested using univariate methods (i.e. including only one response variable and one or more predictors), testing of patterns in genus composition needs a multivariate approach. This is the reason why for each hypothesis we used both mixed models and RDA. Mixed models were used instead of PERMANOVA because they are more general and may include as

predictors both factors and continuous variables. As a parametric method, mixed models are usually more powerful. To test the spatial-temporal patterns of cyanobacteria biovolume and genus richness ($H(1)$ and $H(2)$) we included lake complex, season and year, as well as their interaction, in a linear mixed model, considering lake as a random effect. For the comparison of mixed models, we used the likelihood ratio test (LR test). In addition, we tested the effect of space (lake complex) and time (season and year) on the biovolume in a redundancy analysis (RDA). We chose this linear ordination method over the unimodal method (canonical correspondence analysis, CCA) because in linear methods the raw abundance (biovolume) could be considered as response variable instead of relative abundance (standardized by sample total), and it includes also the empty samples. However, to apply linear ordination methods the genera turnover must be low (a gradient shorter than 4 units). Therefore, to shorten the gradient in our data we removed from the analysis 11 genera with less than 4 occurrences (Table S2). Significance of ordination axes was tested by the Monte-Carlo permutation test with 999 permutations per test. The permutations were restricted according to a hierarchical design ([Šmilauer & Lepš, 2014](#)) with lakes as freely exchanged whole plots and time series permutations of split-plots dependent across whole-plots.

A comparison between constrained and unconstrained analysis was performed to analyze the overall variation in biovolume with the fraction of variation explained by space and time variables. We used the three-group variation partitioning procedure to assess and compare the explanatory importance of the lake complex and time (year and season). Variation partitioning disentangles the unique and shared effects of two or more groups of explanatory variables representing distinct, interpretable phenomena, on the variation in the response data ([Šmilauer & Lepš, 2014](#)). Significance of individual genera to specific environmental variables was tested by means of t-value biplots ([Šmilauer & Lepš, 2014](#)).

To test the effect of the characteristics that define Danube Delta lake complexes on

the biovolume and genus richness of cyanobacteria (H (3)), we first verified differences in lake characteristics between lake complexes using the non-parametric Kruskal-Wallis test. Among the 27 environmental variables described in our study (Table 1 and S4) eight were collinear with the lake complex (e.g. delta type, formation age, water input), so they were not used in the analyses. Spearman correlation was used to identify strongly correlated variables and discard them from the predictors of biovolume and genus richness (Table S5 and S6). We set the selection threshold at Spearman correlation coefficient $\rho = 0.75$. Most correlations were either not significant or weak, thus we removed only two variables from the analyses: abundance of floating macrophytes (correlation between macroflo-macroto: $\rho = 0.95$, $p < 0.001$) and water flow (waterflow-watervelo: $\rho = 0.98$, $p < 0.001$). Additionally, in the univariate mixed models, multicollinearity of selected predictors was verified using the variance inflation factor, and all values were lower than three, indicating no severe multicollinearity in our models. Because turbidity and transparency may be both cause and effect of cyanobacteria biovolume, we did not use them as predictors.

In the multivariate analyses, interactive forward selection was applied to choose a parsimonious set of predictors for the RDA, using False discovery rate values to correct for the Type I error inflation. Using a partial RDA with lake complex as covariate we also tested the effect that vegetation and hydrogeomorphological lake characteristics had on biovolume of cyanobacteria genera in addition to lake complex. Partial ordinations focus on the influence of the variables of prime interest after having accounted for the effect of the covariates ([Ter Braak & Šmilauer, 2012](#)). In the partial RDA the permutations for Monte Carlo test were restricted to blocks defined by the covariate.

Results

Spatio-temporal patterns of cyanobacterial assemblages

Biovolume

The total biovolume of cyanobacteria assemblages showed a significant seasonality (LR = 32.977, df= 93, $p < 0.001$) and variation between lake complexes (LR = 25.180, df=16, $p < 0.001$). The effects of the year and the interaction between season and lake complex were however not significant (Fig. 2). Mean estimated biovolume in LC2 lakes during spring was 5.108 ($\mu\text{m}^3 \mu\text{L}^{-1}$), and the estimated variance of the random intercept was 0.124. From spring to summer, mean biovolume increased 16.46 times, and from spring to autumn 7.45 times. Mean biovolume in LC2 was 2.81 times lower than in LC3 and 48.94 times lower than in LC4 (Table S3). The total cyanobacteria biovolume was notably the highest in LC4 (especially in Mândra, Roşuleţ, Roşu, Puiu and Erenciuc), followed by LC3 (in Rădăcinoasele and Bogdaproste) (Fig. S1 and S2).

Spatio-temporal patterns explained 24.71% (21.23% adjusted) of the variation in cyanobacteria biovolume (pseudo- $F = 7.1$, $p = 0.001$). The variation in the cyanobacterial assemblages was dominated by one gradient, from spring to summer to autumn and from LC2 and LC3 to LC4. All the cyanobacteria genera showed an increase in this direction along the first ordination axis (Fig. 3). Changes from 2013 to 2014 were correlated with the second axis, which showed also the difference between summer and autumn. Along this axis, different genera decreased in biovolume from summer to autumn and increased from 2013 to 2014. Other genera had an opposite trend, while certain genera showed no temporal trend (*Jaaginema*, *Aphanizomenon*, *Microcystis*) (Fig. 3). The t-value biplots revealed that only *Trichormus* decreased significantly in biovolume from summer to autumn and no genus increased significantly from 2013 to 2014. *Rhabdogloea*, *Wolleea* and *Aphcanocapsa* biovolume decreased significantly from 2013 to 2014 and increased from summer to autumn, while for *Snowella* and *Merismopedia* only the response to year was significant. The comparison between the unconstrained and the constrained ordination axes revealed that the

first constrained axis had a medium explanatory efficiency (51.71%), being highly significant (pseudo-F = 5.8, $p = 0.001$), while the second axis had a low explanatory efficiency (13.96%) and was not significant.

In the variation partitioning, lake complex counted for most part of the explained variation in biovolume (62%, pseudo-F = 11, $p = 0.001$), followed by season (32.1%, pseudo-F = 5.7, $p = 0.001$); the effect of year was marginally significant. Because the design was orthogonal and balanced, there was no overlap between these effects.

Genus richness

During our survey we found 48 species of Cyanobacteria belonging to 29 genera (Table S1), and 11 cyanobacteria genera were represented by only one species. On average, we found 2.5 species per genus, but the variation was very high (from 1 to 6 species per genus). Only *Chroococcus*, *Jaaginema*, *Merismopedia*, *Microcystis* and *Rhabdogloea* were found in all the studied lake complexes (even in all lakes), while some genera were specific for LC4: *Cylindrospermum* (in Roşu) and *Dolichospermum* (in Puiu) (Table S2). Following the same tendency as for biovolume, we found the highest genus richness in LC4, particularly in Roşu (Fig. S1 and S2), in which we recorded 14 cyanobacteria genera during the entire study period.

The cyanobacteria genus richness also displayed significant seasonality (LR = 58.742, $df = 86$, $p < 0.001$) in addition to variation between lake complexes (LR = 29.751, $df = 16$, $p < 0.001$) and years (LR=18.246, $df = 86$, $p < 0.001$) (Fig. 4 and 5). Mean estimated number of genera in LC2 lakes during spring 2013 was 1.46, and the estimated variance of the random intercept was 0.601. From spring to summer genus richness increased by 2.87 and from spring to autumn by 2.25. Related to the other LCs, in LC2 mean richness was by 0.5 lower than in LC3 and by 2.45 lower than in LC4. Genus richness decreased in 2014 by 0.42 compared with 2013. The interaction between season and lake complex (LR = 13.257, $df =$

86, $p = 0.010$) and interaction between season and year ($LR = 7.874$, $df = 86$, $p = 0.019$) had additional significant effects on cyanobacteria genus richness.

In each of the sampling campaigns cyanobacteria genus richness was significantly and positively correlated with biovolume (Fig. S3). The strongest correlation was found in autumn 2013 ($S = 100.15$, $df = 36$, $p < 0.001$, $\rho = 0.912$) and the weakest in spring 2014 ($S = 414.5$, $df = 36$, $p = 0.003$, $\rho = 0.636$). There was also a significant and strong correlation between the two response variables over the whole study period ($S = 44505$, $df = 112$, $p < 0.001$, $\rho = 0.819$).

Environmental variables

1. Characteristics defining the Danube Delta lake complexes

There were significant differences among the lake complexes between the median values of shoreline length, water level and velocity, abundance of submerse macrophytes, water retention time and transparency (Table 2, S5 and S6). LC4 has lakes with the highest shore length, which means they have a high degree of meandering, even if they have a big surface and the highest water level (Fig. S4), different wave intensities and lakebed type (Table S4). LC4 comprise lakes with a medium time of water retention and flood risk, highest water velocity and low phytoplankton diversity but the lowest transparency even if the macrophyte coverage is considerable. LC3, has most of the lakes situated farthest from main Sulina branch, with different degrees of connectivity, the lowest water levels, therefore a low flood risk in most of the lakes, medium water velocities, the smallest water retention time but the highest transparency due to their high macrophyte coverage and phytoplankton diversity. LC2 is the second oldest lake complex (after LC1, not included in this study). LC2 lakes are not so meandered, and they have the highest connectivity, since they are the closest to the main branch, exhibiting therefore a high flood risk. LC2 lakes have the highest phytoplankton

diversity and macrophyte coverage, medium water level and transparency. Due to their very good connectivity, LC2 lakes have medium water retention time. Phytoplankton diversity was strongly and negatively correlated with lake surface (Table S5 and S6) in the case of the LC4 lakes, the larger lakes from LC3 as well as Isac from LC2, all having low phytoplankton diversity. Transparency was strongly and negatively correlated with the water level. LC4 lakes had the highest water level and less than 50% transparency. The only exception was Erenciuc lake, which was also closer to the main branch and had a higher degree of connectivity (Table S4).

2. Predictors of cyanobacterial assemblages

Biovolume

In addition to season, some of the lake characteristics could be used as predictors of cyanobacteria biovolume, (LR = 34.97, df = 93, $p < 0.001$). Best model included: water level, abundance of macrophytes, flooding risk and phytoplankton diversity (Table 2). Cyanobacteria biovolume increased 6.96 times with the increase of water level by one meter and 1.03 times with the increase of abundance of macrophytes by one category. The biovolume decreased 2.35 times with the increase of risk of flooding from one category to another, and 2.53 times with the increase in diversity of phytoplankton by one category.

In the RDA (Fig. S5) vegetation and hydromorphological characteristics explained 16.34% (13.27 adjusted) of the variation in cyanobacteria biovolume. The first constrained axis (pseudo-F = 4.8, $p = 0.002$), given mainly by water level, negatively correlated with flood risk, and to a lesser degree with abundance of macrophytes and diversity of phytoplankton. Most genera (*Johanseninema*, *Leptolyngbya*, *Aphanocapsa*, *Microcystis*, *Trichoderma*, *Aphanizomenon*, *Jaaginema*, *Chroococcus*, *Planktolyngbya*) showed a significant positive response to water level. Few genera had a significant negative response to

flood risk (*Trichoderma*, *Jaaginema*, *Planktolyngbya*) and diversity of phytoplankton (*Jaaginema*, *Chroococcus*, *Planktolyngbya*, *Merismopedia*). Only *Jaaginema* responded positively to macrophytes.

In the partial RDA (Fig. 6), when accounting for the variation explained by the lake complex, best predictors were: *water velocity*, *peat deposits* and *flood risk*. Their effect was significant (pseudo-F = 2, $p = 0.001$), but their additional explanatory power was low (only 5.17%, 2.54 adjusted). Most genera were positively correlated along the first axis with the water velocity and peat deposits. Only *Planktolyngbya* had a significant response to peat deposits and both, *Planktolyngbya* and *Merismopedia*, had a significant response to water velocity. The negative response of *Planktolyngbya* to flood risk was also significant.

Genus richness

In the univariate models, in addition to season (LR = 63.494, $p < 0.001$) and year (LR = 19.536, $p < 0.001$), cyanobacteria genus richness was best predicted by surface, elevation, water level, water velocity, distance from the main channel and connectivity (Table 2). For example richness increased by 3.27 with the increase of water level by one meter, by 4.28 with the increase of water velocity with 0.1 m s^{-1} and decreased by 0.14 with the increase of distance from the main channel with one km and by 1.34 with the increase of connectivity by one category.

Discussions

Spatial distribution of cyanobacterial assemblages: Hypothesis 1

As hypothesized, the cyanobacterial assemblages of the studied lakes showed a heterogeneous structure, with different richness and biovolume among lake complexes (LCs) (Fig. 2-5). According to Bellinger and Sigee ([Bellinger & Sigee, 2010](#)), this aspect is characteristic of any delta floodplain with shallow lakes.

During our study, we identified 48 cyanobacteria species, out of which 77% are included in 19 genera with toxic potential (Table S1 and S2). In an earlier study, (Cărauş & Nicolescu, 2006) 1098 phytoplankton species were identified in the Danube Delta (> 400 lakes sampled between 1974-2000), containing 177 cyanobacteria species (17%) belonging to 34 genera. Our taxon list was shorter (48 out of 177) since we studied only 19 lakes over two years. Nevertheless, our results confirm that the Danube Delta still presents a high diversity of cyanobacteria.

All the genera were found in all lakes. Few genera were representative either for several lakes or for an entire LC, which highlight the Danube Delta ecosystems heterogeneity (Table S2). For example, *Anabaenopsis*, *Cylindrospermopsis*, *Cylindrospermum*, *Dolichospermum* and *Aphanothece* were observed only in LC4, confirming our hypothesis of higher richness in the maritime delta. However, comparing these findings with results available in the literature (Moldoveanu & Florescu, 2013; Moldoveanu et al., 2015; Török, 2005a, 2005b, 2005c, 2007, 2008a, 2009b, 2011) we see that some species (e.g. *Microcystis* sp.) are reported constantly. We conclude that these lakes were under high ecological stress, as they were dominated by cyanobacteria species which indicate increased eutrophication (Kauppila et al., 1995).

Our study revealed an increasing density of cyanobacteria from the West to the East, along the flow direction of the main channel (Fig. 5). This observation supports H (1) which states that cyanobacterial assemblages differ among lake complexes with respect to biovolume and richness, being more dominant in the maritime delta. Previous studies showed that between 2001 and 2007 few lakes experienced frequent cyanobacteria blooms (especially in summer and autumn) increasing in the same direction as we found: from LC2 to LC3 and LC4 (Török et al., 2008). This observation is similar to the biomass pattern that we found in our studied lakes (Fig. 2 and Table S3). We observed a synchrony between genus richness

and biovolume distribution concentrated at the southern part of the Danube Delta, with the highest recorded values throughout the study period in the Roşu-Puiu (LC4) (Fig. 2, 4, S1, S2 and Table S3). The lakes from Roşu-Puiu (LC4) were also more constant in terms of cyanobacteria abundance and genus compositions compared with the other two LCs. This was also reported in previous studies ([Nicolescu, 1992](#)), again supporting our hypothesis.

In comparison with LC4, lakes from LC3 present only episodic peaks of cyanobacteria, otherwise having low diversity and abundance (Fig. S2). An explanation could be that reed, well represented in LC3 (Table S4), inhibits cyanobacteria development, notably via phenols produced by aquatic macrophytes that have allelopathic effects ([Antilla et al., 2015](#); [Watson, 2014](#); [Zhou et al., 2004](#)). The fluvial delta (Matiţa-Merhei and Gorgova-Uzlina LCs) is rich in stable reed ([Iordachi & Van Assche, 2014](#)). Our results therefore support the explanation that reed beds inhibit cyanobacteria development. The competition between cyanobacteria and macrophytes also exists in Danube Delta's shallow lakes ([Pantea, 1993](#)). This is why cyanobacteria's ability to float is a further advantage in their competition with other taxa ([Török, 2005b](#)). All these factors could explain high records of cyanobacteria in some lakes of LC3 (Fig. S2 and Table S2) for instance, which are nevertheless dominated by aquatic plants (Table S4). There is a clear longitudinal and latitudinal gradient of the cyanobacteria distribution (Fig. 5), with highest densities in its lower part, namely in LC4. This observation supporting H (1), since there are "significant differences between LCs, with LC4 being the most distinct among them".

Temporal distribution of cyanobacterial assemblages: Hypothesis 2

The PEG model predicts that cyanobacteria are predominant in summer-autumn, namely July and September ([De Senerpont Domis et al., 2013](#)). Generally, the phytoplankton in the Danube Delta is dominated in spring by diatoms and green algae, while the cyanobacteria

tend to develop to higher densities in all LCs in summer ([Enache et al., 2019](#)). In spring the composition of the diatoms indicates a mesoeutrophic status of the lakes. The occurrence of *Oscillatoria* blooms is for instance, characteristic for hypertrophic lakes, suggests a seasonal shift of the trophic status ([Năstase, 2009](#)). According to previous findings ([Dumitrache et al., 2014](#)), the most prevalent cyanobacteria genera in Roșu-Puiu (LC4) were *Anabaena*, *Lyngbya* and *Oscillatoria* in July, and *Microcystis* and *Oscillatoria* in September. According to our results, in LC2 most of the lakes reached their cyanobacteria biovolume peaks in summer, with the exception of lake Isac (spring). In LC3, six out of ten lakes had their peaks in summer, two in spring (Bogdaprote and Lung) and two in autumn (Matița and Merhei). In LC4 two lakes reached the peak in summer and three in autumn (Roșu, Mândra and Erenciuc) (Table S3). Following the same pattern, genus richness was the highest in summer, as expected in LC4, and lowest in spring (Fig. 4 and Table S3). Overall, the lowest values of biovolume and richness were recorded in lakes from LC2, which is part of the fluvial delta and well connected to the main channel. Therefore, our findings reveal that cyanobacteria assembly varied strongly between seasons (Fig. 2 - 4), largely in concordance with the PEG model at lake level, but fully fitted within the model as mean values per LCs. This could be very nicely seen in the RDA (Fig. 3), where all the vectors representing cyanobacteria genera are grouped in summer and autumn. Previous algal blooms were also observed in June of each year in LC2 (Uzlina) as well as in LC4 (Roșu and Roșuleț) during a survey performed between 1996-1998 ([Coops et al., 1999](#)). Earlier, in 1991, the cyanobacteria peak was registered in late summer-autumn in Erenciuc (LC4) ([Stancu-Stoianovici, 1992](#)).

Lake complex explained more than 60% of biovolume variation, while season accounted for 30% of this variation. Based on these observations we can conclude that local environmental condition of each lake complex influence two times more the patterns of cyanobacteria biovolume comparing to season. Lower biovolume of cyanobacteria was

recorded in spring for both years (Fig. 2 and Table S3) and was likely caused by the increased water level in this period, which predicted both genus richness and biovolume (Table 2). Sometimes spring blooms can also occur, when sunlight intensity increases, but those blooms do not lead to cyanobacteria surface accumulation, known as scum (Török, 2005b). Consistent with our results, the same tendency was also noticed during spring floods in 2013 (Florescu et al., 2015) in shallow lakes of a complex of wetland ecosystems, known as “inner Danube Delta”, located in Balta Mică a Brăilei Nature Park, upstream of the Danube Delta. In summer, densities of cyanobacteria increase because nutrients become more available (Török, 2005b). There are nonetheless situations in which the increase occurs in autumn, as it was the case of *Microcystis* blooms in the Isac (LC2) (Török, 2000-2001). Based on these assumptions, we presume that nutrients were released much later, since the cyanobacteria dominated alike in autumn, in at least Roșu-Puiu (Fig. 2, 4 and Table S3).

Environmental variables: Hypothesis 3

The Danube Delta is a mosaic of interconnected aquatic and terrestrial ecosystems with no strict boundaries between them, and is strongly dependent on seasonal water inflow, especially on floods (Armaș & Avram, 2009; Iordachi & Van Assche, 2014). The significant differences between lakes situated North and South from the Sulina main branch have already been outlined (Nicolescu, 1992): lakes from the northern part form the fluvial delta, comprise older lakes from the genesis point of view, and the sedimentation rate is higher here hence explaining why lakes have a lower water level. Lakes situated in the southern part form the maritime delta and are lakes formed before the northern lakes, with a much lower sedimentation rate since they are not situated so close to the main braches. Moreover, their lakes bed are mostly mineral and are separated by the Caraorman sand beam.

Testing 19 environmental variables (Table 1 and S4) within this study we showed that

the shore length of the lakes, water level, coverage of the submerse macrophytes, water transparency and velocity (Table 2, S5 and S6) are the most important predictors of LCs differentiation. Cyanobacteria biovolume and genus richness are significantly and positively correlated (Fig. S3), and we therefore expected to have similar predictors defining cyanobacteria assemblages. The three LCs from the Danube Delta are significantly different based on the biological and hydrogeomorphological characteristics of their lakes: LC2 comprises lakes with smallest shore length, medium water level and submerse macrophytes coverage, medium water retention time, higher transparency and low turbidity and water velocity. In contrast, LC4 includes lakes with the most meandering shorelines, highest water level, velocity and turbidity, longest retention time, largest natural submerse macrophyte coverage, and lowest water transparency. Lakes from LC3 are situated between the other two, with few exceptions already mentioned, that follow LC4 lakes tendency (Fig. S4). Surprisingly, only two of the tested from the best models tested on all significant hydrogeomorphological predictors which differentiate between LCs were involved as well in genus richness distribution: water level and velocity. More exactly, water level was involved in lake complex differentiation, biovolume and richness distribution (Table 2), therefore, contradicting partially hypothesis H (3) in which we assumed that “hydrogeomorphological characteristics that differentiate the lake complexes influence also the cyanobacteria assemblages in terms of biovolume and genera richness”.

Connectivity and water residence time seems to play an important role in the distribution of phytoplankton taxa in Danube Delta’s shallow lakes ([Guerold, 2000](#); [Jamil et al., 1999](#); [Postolache, 2003, 2006](#)). In addition, the development of cyanobacteria in relationship with the nutrient level and velocity of water circulation in the network of canals has a large impact on lakes and lake complexes ([Török, 2009a](#)). Therefore, in lakes with low residence time (Table S4), the cyanobacteria may be flushed away and have insufficient time

to fully develop. As a result, the water transparency is higher, allowing more submerged aquatic vegetation to grow ([Oosterberg et al., 2000](#)). During our study, some lakes of LC2 and LC3 experienced this situation.

Water level is the most important parameter that governs Danube Delta's shallow lakes, practically defining the ecosystems. Water level differs significantly among LCs and is a predictor in the best models of both cyanobacteria biovolume and genus richness (Table 2, S5 and S6). Elevation can also explain why we found the highest cyanobacteria diversity in LC4, as everything seems to be concentrated in the lower part of the Danube Delta, closer to the Black Sea. Beside these, other factors favor the highest cyanobacteria development in LC4 e.g. connectivity, distance from the main channel, water velocity and risk of flooding, all related to the water flowing direction to the sea after the flooding season (usually occurring in April-May).

The fact that flood risk was significant as predictor for cyanobacteria biovolume in our lake complexes is explained by the evidence that especially during flooding, there is a higher water input, and consequently of phytoplankton, from the main channel, ([Güttler et al., 2013](#)); this rises the diversity and biomass, in some cases. Flood risk was also negatively correlated with water level, implying that deep lakes had a lower flood risk and therefore a higher biomass. This was due to the low chance of washing, since the inflow and outflow of water is reduced. It is the case of most LC4 lakes and the biggest LC3 lakes (Fig. S4 and Table S4).

Beside the higher cyanobacteria biovolume registered in LC4 (Fig. S1), most of genera, both colonial and filamentous, were directly correlated with water level and flood risk (Fig. 6 and S5). Only three genera decreased in biovolume when the flood risk increased: *Trichormus* (former *Anabaena*), *Jaaginema* (former *Oscillatoria*) and *Planktolyngbya* (former *Lyngbya*), being flushed to LC4 (Table S2) which experienced the highest biovolume

and genera richness of these cyanobacteria. Lakes from LC3 have the highest water input from the main channel (Table S4), which can explain why most lakes present different cyanobacteria assembly patterns. Only some of LC3 big lakes, far from the main channel, namely Mătița and Merhei behave similarly to those from LC4 with regards to cyanobacteria biovolume and genus richness (Fig. S2).

Conclusions

In this study we compared cyanobacteria data from 19 Danube Delta lakes in which we identified 29 genera and found geographic and temporal patterns of cyanobacteria abundance (biovolume) and genus richness. We also found hydrogeomorphological characteristics that define the lake complexes and that act as predictors for cyanobacteria occurrence and distribution.

We found, in accordance with our expectation, higher values of cyanobacteria biovolume and richness in spring and autumn, especially in lake complexes from the southeastern part, revealing once again the heterogeneity of Danube Delta's shallow lakes. Our findings strengthen the hypothesis that there is a significant difference among the LCs and between the seasons regarding cyanobacteria assembly and supports earlier observations about the uniqueness of lakes concerning their cyanobacterial assemblages. We also showed that the PEG model can be applied to the Danube Delta. Furthermore, we showed that the biovolume variation in our lakes could be better explained by lake complex than by season. From the environmental variables water level, lakes connectivity and surface, channels distance and flooding risk, explained the best cyanobacteria abundance and diversity.

Our study was performed during 2 years and 3 seasons. However, to accurately capture the cyanobacteria dynamics in the Danube Delta Biosphere Reserve, studies that apply more frequent samplings during the all seasons and throughout many years would be needed.

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623 **References**

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830 for cyanobacteria genera *Anabaena* (*Anab*), *Anabaenopsis* (*Anas*), *Aphanizomenon* (*Apha*),
831 *Aphanocapsa* (*Aphca*), *Coelosphaerium* (*Coel*), *Chroococcus* (*Chro*), *Jaaginemo* (*Jaag*),
832 *Johanseninema* (*Joha*), *Lyngbya* (*Lyng*), *Leptolyngbya* (*Lepto*), *Microcystis* (*Micr*),
833 *Merismopedia* (*Meri*), *Oscillatoria* (*Osci*), *Planktolyngbya* (*Plan*), *Rhabdogloea* (*Rhab*),
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849 *Johanseninema* (*Joha*), *Lyngbya* (*Lyng*), *Leptolyngbya* (*Lepto*), *Microcystis* (*Micr*),
850 *Merismopedia* (*Meri*), *Oscillatoria* (*Osci*), *Planktolyngbya* (*Plan*), *Rhabdogloea* (*Rhab*),
851 *Snowella* (*Snow*), *Trichormus* (*Tric*) and *Wolleea* (*Spha*). Lake characteristics were: flooding
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886 *(MA)*, *Merhei (ME)*, *Merhei Mic (MM)*, *Lung (LU)*, *Dracului (DR)*, *Rădăcinoasele (RE)*,
887 *Babina (BA)* part of Matia-Merhei (LC3, yellow) and *Roşu (RO)*, *Roşuleţ (RT)*, *Mândra*
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899 *(Aphca)*, *Coelosphaerium (Coel)*, *Chroococcus (Chro)*, *Jaaginemoia (Jaag)*, *Johanseninema*
900 *(Joha)*, *Lyngbya (Lyng)*, *Leptolyngbya (Lepto)*, *Microcystis (Micr)*, *Merismopedia (Meri)*,
901 *Oscillatoria (Osci)*, *Planktolyngbya (Plan)*, *Rhabdogloea (Rhab)*, *Snowella (Snow)*,
902 *Trichormus (Tric)* and *Wolleea (Spha)*. Lake characteristics were: flooding risk (floodris), total
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905

Fig. 1 Danube Delta map (created in Google maps, May 2017) with sampled lakes and lake complexes (LC) indicated in different colors. Șontea-Furtuna (LC1), Isac-Gorgova (LC2), Matîța-Merhei (LC3) and Roșu-Puiu (LC4). Lakes from LC1, Isăscel from (LC2), Roșca from LC3 and Tătaru from LC4 were not included in this study

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Fig. 4 Seasonal variation of cyanobacteria genus richness (expressed as number of genera) in the Danube Delta lake complexes: Gorgova - Uzlina (LC2), Matița-Merhei (LC3) and Roșu-Puiu (LC4) among three seasons: spring (S1), summer (S2) and autumn (S3)

Fig. 5 Spatio-temporal pattern of cyanobacteria genus richness in the Danube Delta lake complexes displayed from West to East: Gorgova - Uzlina (LC2), Mătița-Merhei (LC3) and Roșu-Puiu (LC4). The overlaying discs represent the six samples taken from each lake during the study period (the top disc is autumn 2014) and the disc color intensity represent the cyanobacteria diversity (expressed as number of genera). Lake codes are given in Table 1

Fig. 6 Genera (in terms of biovolume) – lake characteristics biplot diagram from partial linear redundancy analysis (partial RDA) with lake complex as covariate. The codes for cyanobacteria genera are: *Anabaena* (*Anab*), *Anabaenopsis* (*Anas*), *Aphanizomenon* (*Apha*), *Aphanocapsa* (*Aphca*), *Coelosphaerium* (*Coel*), *Chroococcus* (*Chro*), *Jaaginemoia* (*Jaag*), *Johanseninema* (*Joha*), *Lyngbya* (*Lyng*), *Leptolyngbya* (*Lepto*), *Microcystis* (*Micr*), *Merismopedia* (*Meri*), *Oscillatoria* (*Osci*), *Planktolyngbya* (*Plan*), *Rhabdogloea* (*Rhab*), *Snowella* (*Snow*), *Trichormus* (*Tric*) and *Wollea* (*Spha*). Lake characteristics were: flooding risk (floodris), water velocity (watervel) and peat deposit (peat). Genera with less than four occurrences were not included in the analysis

Table 1 Description of the lakes sampled from Danube Delta between 2013 and 2014, with their surfaces and GPS coordinates of the sampling points; lakes are listed from West to East. Lake complex Șontea-Furtuna (LC1), part of the fluvial delta, was not included in this study. Bolded variables were used for statistical analyses

Lakes complex*** (W→E)	Lakes complex code	Lake name	Lake code	Latitude N (DDM)	Longitude E (DDM)	Delta type	Formation age	Surface (km ²)	Shore length** (km)	Water level** (m)	Transparency** (m)	Turbidity** (NFU)
Isac-Gorgova	LC2	Isac	IS	45°06.728'	29°17.056'	fluvial	old	11.79*	10.2	2.1	1.8	4.6
	LC2	Uzlina	UZ	45°05.524'	29°16.070'			4.83*	6.93	1.5	1.3	6.1
	LC2	Cuibul cu Lebede	CL	45°08.426'	29°20.589'			2.02**	5.16	1.5	1.5	6.7
	LC2	Gorgostel	GR	45°03.253'	29°19.692'			0.73*	5.73	2.0	1.4	7.4
Matița-Merhei	LC3	Trei Iezere	TI	45°14.769'	29°19.212'	fluvial	old	5.74*	18.6	1.7	1.6	6.6
	LC3	La Amiază	LA	45°13.887'	29°19.826'			0.81**	7.45	1.2	1.2	4.9
	LC3	Bogdaproste	BG	45°13.986'	29°20.935'			4.28*	11.9	1.5	1.5	3.2
	LC3	Matița	MA	45°17.862'	29°22.131'			6.87*	10.8	2.5	1.8	5.2
	LC3	Merhei	ME	45°19.020'	29°25.693'			12.27*	36.4	1.7	1.7	5.6
	LC3	Merhei Mic	MM	45°19.817'	29°28.596'			1.73*	8	1.3	1.3	4.1
	LC3	Lung	LU	45°18.220'	29°26.102'			0.74*	5.9	1.3	1.2	4.3
	LC3	Dracului	DR	45°19.508'	29°21.734'			1.83*	6.7	1.7	1.4	4.2
	LC3	Rădăcinoasele	RE	45°18.945'	29°21.287'			0.96*	10.9	1.6	1.2	5.8
	LC3	Babina	BA	45°18.090'	29°20.395'			4.99*	12.5	2.0	1.6	3.5
Roșu-Puiu	LC4	Roșu	RO	45°03.507'	29°35.198'	maritime	new	14.31*	15.1	3.0	0.9	14.1
	LC4	Roșuleț	RT	45°04.080'	29°36.801'			4.35*	13.1	2.2	0.9	14.0
	LC4	Mândra	MD	45°02.082'	29°31.068'			1.47**	7.57	1.9	1.0	9.9
	LC4	Puiu	PU	45°03.086'	29°28.372'			8.73*	13.3	3.1	0.9	8.2
	LC4	Erenciuc	ER	45°00.669'	29°24.850'			1.43*	14.3	2.6	1.6	20.9

*DDNIRD = Danube Delta National Institute for Research and Development

**this study; surface and shore measurements were done using GoogleEarthPro software

Table 2 Significant variables of the best models used to differentiate lake complexes and to explain the dynamics of cyanobacteria biovolume and genus richness

Variables that describe lakes*	Variable code	characteristics that differentiate lake complexes		predictors of cyanobacteria biovolume		predictors of cyanobacteria genus richness	
		<i>Kruskal-Wallis chi-squared (H)</i>	<i>p-value</i>	<i>Likelihood Ratio (LR)</i>	<i>p-value</i>	<i>Likelihood Ratio (LR)</i>	<i>p-value</i>
Lake surfaces (km ²)	surface					16.397	<0.001
Lakes shore (km)	shore	6.5068	0.03864				
Elevation (m)	elev					7.904	0.004
Main channel distance (km)	mcdist					12.529	<0.001
Connectivity with main channel (categories)	connect					6.072	<0.013
Water level (m)	depth	8.0693	0.01769	16.733	<0.001	26.373	<0.001
Submerse macrophyte (coverage units)	macrosub	8.4187	0.01486				
Total macrophyte (coverage units)	macrotot			4.879	0.027		
Water retention time (weeks)	retention	8.2514	0.01615				
Phytoplankton diversity (categories)	phpdiv			10.554	0.001		
Transparency (in % from the water level)**	trans_p	10.898	0.004301				
Flooding risk (categories)	floodris			17.484	<0.011		
Water velocity (m s ⁻¹)	watervelo	6.8217	0.03301			13.237	<0.001

*all the characteristics of lakes and lake complexes are detailed in Table 1 and Table S4

**transparency was considered both cause and effect of cyanobacteria biovolume and genus richness, therefore it was not included in the subsequent analyses

***water level was the only common predictor from all three sections

Electronic Supplementary Material

for the article cited as Moza *et al.*, 2020

Geographical and temporal patterns of cyanobacteria assemblages in the Danube Delta lake complexes

in *Hydrobiologia*, IF=2.05 , AI=0.69

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Table S1 Cyanobacteria genera and species identified in all 19 lakes from Danube Delta, over the entire study period (2013-2014)

Cyanobacteria genera (code)/species		
† <i>Anabaena</i> (<i>Anab</i>) <i>A. circinalis</i> (Kütz.) Hansgirg 1886 <i>A. spiroides</i> Klebahn 1895 <i>A. sp</i>	† <i>Chroococcus</i> (<i>Chro</i>) <i>C. dispersus</i> Lemmermann, E. 1904 <i>C. limneticus</i> Lemmermann, E. 1898 <i>C. minutus</i> Nägeli, C. 1849 <i>C. dimidiatus</i> <i>C. sp.</i>	† <i>Oscillatoria</i> (<i>Osci</i>) <i>O. limosa</i> C.Agardh ex Gomont 1892 <i>O. tenuis</i> C.Agardh ex Gomont 1892 <i>O. sp.</i>
† <i>Johanseninema</i> (<i>Joha</i>) <i>J.constrictum</i> (Szafer) Hasler, Dvorák & Poulícková 2014	<i>Rhabdogloea</i> (<i>Rhab</i>) <i>R. smithii</i> (Chodat & F.Chodat) Komárek 1983	† <i>Jaaginema</i> (<i>Jaag</i>) <i>J. minimum</i> Anagnostidis & Komárek 1988
† <i>Dolichospermum</i> (<i>Doli</i>) <i>D. flosaquae</i> (Brébisson ex Bornet & Flahault) P.Wacklin, L.Hoffmann & J.Komárek 2009 <i>D. scheremetie</i> (Elenkin) Wacklin, L.Hoffmann & Komárek 2009	<i>Gloeocapsa</i> (<i>Glsa</i>) <i>G. sp.</i>	† <i>Microcystis</i> (<i>Micr</i>) <i>M. aeruginosa</i> Kützing 1846 <i>M. flos-aquae</i> Kirchner, O. 1898 <i>M. pulverea</i> Forti, A. 1907 <i>M. smithii</i> Komárek & Anagnostidis 1995
† <i>Trichormus</i> (<i>Tric</i>) <i>T. variabilis</i> (Kützing ex Bornet & Flahault) Komárek & Anagnostidis 1989	<i>Gloeotece</i> (<i>Glce</i>) <i>G. sp</i>	<i>M. wessenbergii</i> Teiling 1941 <i>M. sp.</i>
† <i>Aphanizomenon</i> (<i>Apha</i>) <i>A. flos-aquae</i> Ralfs ex Bornet & Flahault 1886	† <i>Snowella</i> (<i>Snow</i>) <i>S. lacustris</i> Komárek, J. & Hindák, F. 1988	† <i>Leptolyngbya</i> (<i>Lepto</i>) <i>L. tenuis</i> Anagnostidis & Komárek 1988
† <i>Aphanocapsa</i> (<i>Aphca</i>) <i>A.sp.</i>	<i>Loriella</i> (<i>Lori</i>) <i>L. sp.</i>	† <i>Phormidium</i> (<i>Phor</i>) <i>P. sp.</i>
<i>Aphanothece</i> (<i>Aphce</i>) <i>A. sp.</i>	† <i>Planktolyngbya</i> (<i>Plan</i>) <i>P. contorta</i> Anagnostidis & Komárek 1988 <i>P. limnetica</i> Komárková-Legnerová & Cronberg 1992	<i>Rivularia</i> (<i>Rivu</i>) <i>R. sp.</i>
<i>Coelosphaerium</i> (<i>Coel</i>) <i>C. kuetzingianum</i> Nägeli 1849 <i>C. sp.</i>	† <i>Lyngbya</i> (<i>Lyng</i>) <i>L. sp.</i>	<i>Spirulina</i> (<i>Spir</i>) <i>S. sp.</i>
<i>Woronichinia</i> (<i>Woro</i>) <i>W. naegelianae</i> (Unger) Elenkin 1933	<i>Wolleea</i> (<i>Woll</i>)/ <i>Sphaerozyga</i> (<i>Spha</i>) <i>W. saccata</i> Bornet & Flahault 1886	† <i>Merismopedia</i> (<i>Meri</i>) <i>M. glauca</i> Kützing 1845 <i>M. punctata</i> Meyen 1839 <i>M. tenuissima</i> Lemmermann 1898 <i>M. sp.</i>
† <i>Cylindrospermum</i> (<i>Cylum</i>) <i>C. maius</i> Kützing ex Bornet & Flahault 1888	† <i>Anabaenopsis</i> (<i>Anas</i>) <i>A. elenkinii</i> V.V.Miller 1923	
† <i>Cylindrospermopsis</i> (<i>Cylis</i>) <i>C. sp.</i>		

†= genera of cyanobacteria with toxic potential; any genera that had at least one species mentioned in literature as toxic was classified as being with toxic potential

Table S2 Occurrence of cyanobacteria from Danube Delta lakes (expressed as genera number) studied in 2013-2014 period; bolded genera represent those with less than 4 occurrences and were not included in the analyses

Complex/ lake code		Cyanobacteria genera/species number																			Total
		Anab	Anas	Apha	Aphca	Chro	Cylis	Cylum	Doli	Jaag	Joha	Lepto	Lyng	Meri	Micr	Osci	Phor	Plan	Snow	Tric	
		(5)	(1)	(1)	(1)	(5)	(1)	(1)	(2)	(1)	(1)	(1)	(1)	(4)	(6)	(3)	(1)	(2)	(1)	(1)	
LC2	IS	1				1				1				1	1						5
	UZ					1				1				1	1						4
	CL	1				1				1			1	1	1						6
	GR	1				1				1	1		1	1	1		1	1		1	10
LC3	TI					1				1		1		1	1	1			1		7
	LA					1				1				1	1	1	1	1			7
	BG	1				1				1				1	1	1		1	1		8
	MA	1		1		1				1			1	1	1			1	1	1	10
	ME	1				1				1			1	1	1			1	1		8
	MM					1				1	1			1	1			1	1		7
	LU	1				1				1				1	1				1		6
	DR	1		1		1				1			1	1	1					1	8
	RE	1				1				1				1	1				1		6
	BA	1			1	1				1	1			1	1				1	1	9
	RO	1		1	1	1		1		1	1			1	1	1		1	1	1	13
LC4	RT	1		1	1	1				1	1	1	1	1	1			1	1	1	13
	MD	1	1	1	1	1	1			1			1	1	1	1	1	1	1	1	15
	PU	1	1			1	1		1	1	1	1	1	1	1		1	1		1	14
	ER	1		1	1	1	1			1	1	1	1	1	1	1			1	1	14
Total		15	2	6	5	19	3	1	1	19	7	4	9	19	19	6	4	10	12	9	

*legend: Anab=*Anabaena*, Anas=*Anabaenopsis*, Apha=*Aphanizomenon*, Aphca=*Aphanocapsa*, Chro=*Chroococcus*, Cylis=*Cylindrospermopsis*, Cylum=*Cylindrospermum*, Doli=*Dolichospermum*, Jaag=*Jaaginema*, Joha=*Johanseninema*, Lepto=*Leptolyngbya*, Lyng=*Lyngbya*, Meri=*Merismopedia*, Micr=*Microcystis*, Osci=*Oscillatoria*, Phor=*Phormidium*, Plan=*Planktolyngbya*, Snow=*Snowella* and Tric=*Trichormus*; (1-6) = species number for each genera signaled over the study period

Table S2 (continued) Occurrence of cyanobacteria genera from Danube Delta lakes (expressed as genera number) studied in 2013-2014 period; bolded genera represent those with less than 4 occurrences and were not included in the analyses

Lake complex/ Lake code		Cyanobacteria genera/species number									Total	
		Aphce	Coel	Rhab	Glsa	Glce	Lori	Rivu	Spir	Woro		Woll
		(1)	(2)	(1)	(1)	(1)	(1)	(1)	(1)	(1)		(1)
LC2	IS		1	1			1				1	4
	UZ			1								1
	CL			1								1
	GR			1					1			2
LC3	TI		1	1					1			3
	LA			1						1	1	3
	BG		1	1								2
	MA			1	1							2
	ME		1	1		1						3
	MM			1							1	2
	LU		1	1								2
	DR			1		1		1	1			4
	RE		1	1						1		3
	BA			1								1
	LC4	RO	1	1	1							1
RT				1							1	2
MD				1							1	2
PU			1	1							1	3
ER			1	1							1	3
Total		1	9	19	1	2	1	1	3	2	8	

*Legend: Aphce=*Aphanothece*, Coel=*Coelosphaerium*, Rhab=*Rhabdogloea*, Glsa=*Gloeocapsa*, Glce=*Gloeotece*, Lori=*Loriella*, Rivu=*Rivularia*, Spir=*Spirulina*, Woro=*Woronichinia*, Woll (Spha)= *Wolleea (Sphaerozyga)*; (1-2) = species number for each genera signaled over the study period

Table S3 Seasonal mean values (scientific number) of cyanobacteria biovolume and genus richness recorded over two years in Danube Delta shallow lakes

Lake	Cyanobacteria biovolume				Cyanobacteria genus richness			
	<i>Spring</i> ($\mu\text{m}^3 \text{ L}^{-1}$)	<i>Summer</i> ($\mu\text{m}^3 \text{ L}^{-1}$)	<i>Autumn</i> ($\mu\text{m}^3 \text{ L}^{-1}$)	<i>Mean per</i> <i>lake complex</i>	<i>Spring</i>	<i>Summer</i>	<i>Autumn</i>	<i>Total per</i> <i>lake complex</i>
Isac (IS)	9.E+08	2.E+07	2.E+07	4.E+09	2	4	2	14
Uzlina (UZ)	6.E+05	8.E+05	3.E+08		1	1	3	
Cuibul cu Lebede (CL)	2.E+05	8.E+08	4.E+07		1	4	2	
Gorgostel (GR)	3.E+07	2.E+09	6.E+07		2	6	3	
Trei Iezere (TI)	5.E+07	1.E+09	7.E+07	2.E+10	2	6	2	14
La Amiază (LA)	2.E+06	1.E+09	1.E+08		2	5	2	
Bogdaproste (BG)	2.E+09	9.E+08	3.E+07		1	5	3	
Matița (MA)	5.E+07	5.E+08	3.E+09		3	6	6	
Merhei (ME)	9.E+07	2.E+08	8.E+07		2	5	2	
Merhei Mic (MM)	2.E+08	8.E+07	3.E+08		4	4	5	
Lung (LU)	4.E+08	1.E+08	1.E+08		1	4	3	
Dracului (DR)	3.E+07	2.E+08	2.E+08		4	5	3	
Rădăcinoasele (RE)	5.E+04	2.E+09	2.E+09	1.E+11	1	6	4	19
Babina (BA)	4.E+07	4.E+08	2.E+08		1	7	4	
Roșu (RO)	3.E+08	8.E+09	3.E+10		6	11	9	
Roșuleț (RT)	5.E+08	1.E+10	7.E+09		3	9	8	
Mândra (MD)	2.E+08	7.E+09	9.E+09		4	8	7	
Puiu (PU)	2.E+08	9.E+09	7.E+09		5	9	7	
Erenciuc (ER)	4.E+06	1.E+09	4.E+09		2	5	9	

Table S4 Characterization of the lake complexes from Danube Delta based on their biological and hydro-geomorphological features

Lakes complex * (W→E)	Lake name and code	Main channel distance** (km)	Connectivity with the main river branch Sulina ^{#,1}	Water input from the main channel*** (m ² /s)	Lake complex mean altitude ¹ (m)	Lakes complex surface ¹ (thousands ha)	Elevation** (m)	Flooding risk ^{#,2,3,4,5}	Transparency** (%)
Isac-Gorgova (LC2)	Isac (IS)	10.4	good	8	0.16	23.2	-1	very high	85.7
	Uzlina (UZ)	13.8	good				-1	very high	89.9
	Cuibul cu Lebede (CL)	7.24	good				-2	high	93.3
	Gorgostel (GR)	21.75	poor				-2	low	66.3
Matița-Merhei (LC3)	Trei Iezere (TI)	11.5	good	27.6	0.7	20.5	-1	medium	97.3
	La Amiază (LA)	13.24	medium				-2	low	95.7
	Bogdaprote (BG)	4.95	good				-2	low	95.4
	Matița (MA)	25.3	good				-1	low	70.9
	Merhei (ME)	19.5	poor				-1	high	98.5
	Merhei Mic (MM)	22.68	poor				-1	high	97.0
	Lung (LU)	17.7	poor				-2	low	88.4
	Dracului (DR)	30.21	poor				-1	low	83.3
	Rădăcinoasele (RE)	31.79	poor				0	low	74.7
	Babina (BA)	28.1	medium				-1	medium	78.6
Roșu-Puiu (LC4)	Roșu (RO)	13.48	medium	9.4	0.22	33.1	-1	low	26.3
	Roșuleț (RT)	11.15	medium				-1	low	37.0
	Mândra (MD)	18.26	medium				0	low	50.9
	Puiu (PU)	20.95	medium				-1	medium	25.9
	Erenciuc (ER)	29.55	good				-2	high	62.8

*lakes complex Șontea-Furtuna (LC1), part of the fluvial delta, was not included in this study

**this study; measurements were done using GoogleEarthPro software

***DDNIRD = Danube Delta National Institute for Research and Development

****bolded characteristics were included in hydro-geomorphological analyses as well

#for each category a number from 1 to 6 was attributed for statistical analyses

Table S4 (continued 1) Characterization of the lake complexes from Danube Delta based on their biological and hydro-geomorphological features

Lakes complex * (W→E)	Lake name and code	Water retention ^{6,7} (weeks)	Water velocity ^{**} (m/s)	Floating macrophyte ^{**} (average coverage units)	Submerse macrophyte ^{**} (average coverage units)	Total macrophyte ^{**} (average coverage units)
Isac-Gorgova (LC2)	Isac (IS)	4-6	0.07	12.5	35.6	48.1
	Uzlina (UZ)	4-6	0.08	35.8	35.8	71.6
	Cuibul cu Lebede (CL)	< 2	0.08	35.4	35.3	70.7
	Gorgostel (GR)	4-6	0.07	36	35.9	71.9
Matița-Merhei (LC3)	Trei Iezere (TI)	< 2	0.07	35	35	70
	La Amiază (LA)	< 2	0.06	35.2	35.2	70.4
	Bogdaproste (BG)	< 2	0.07	35.2	35.3	70.5
	Matița (MA)	< 2	0.11	12.5	12.5	25
	Merhei (ME)	< 2	0.13	12.5	35	47.5
	Merhei Mic (MM)	< 2	0.09	34.9	34.8	69.7
	Lung (LU)	< 2	0.07	34.7	34.9	69.6
	Dracului (DR)	< 2	0.10	12.5	35	47.5
	Rădăcinoasele (RE)	< 2	0.08	12.5	35	47.5
	Babina (BA)	< 2	0.10	12.5	35	47.5
Roșu-Puiu (LC4)	Roșu (RO)	2-4	0.14	12.5	36.3	48.8
	Roșuleț (RT)	2-4	0.11	36.3	36.3	72.6
	Mândra (MD)	2-4	0.11	12.5	36.3	48.8
	Puiu (PU)	2-4	0.11	12.5	12.5	25
	Erenciuc (ER)	> 4	0.09	37.5	36	73.5

*]akes complex Șontea-Furtuna (LC1), part of the fluvial delta, was not included in this study

**this study; measurements were done using GoogleEarthPro software

***DDNIRD = Danube Delta National Institute for Research and Development

****bolded characteristics were included in hydro-geomorphological analyses as well

#for each category a number from 1 to 6 was attributed for statistical analyses

Table S4 (continued 2) Characterization of the lake complexes from Danube Delta based on their biological and hydro-geomorphological features

Lakes complex * (W→E)	Lake name and code	Lake bottom type ⁸	Thickness of peat deposits ⁸ (cm)	Reed beds presence**, #	Phytoplankton diversity ^{#,9}	Water birds colonies presence ^{#,10}
Isac-Gorgova (LC2)	Isac (IS)	mineral	50-130	high	low	medium
	Uzlina (UZ)	organic	20-50	medium	medium	
	Cuibul cu Lebede (CL)	organic	20-50	high	high	
	Gorgostel (GR)	mineral	20-50	high	high	
Matița-Merhei (LC3)	Trei Iezere (TI)	organic	20-50	high	medium	high
	La Amiază (LA)	organic	20-50	high	high	
	Bogdaproste (BG)	organic	20-50	high	medium	
	Matița (MA)	mineral	130-200	high	low	
	Merhei (ME)	organic	20-50	high	low	
	Merhei Mic (MM)	organic	50-130	high	low	
	Lung (LU)	organic	50-130	high	high	
	Dracului (DR)	organic	20-50	high	medium	
	Rădăcinoasele (RE)	organic	20-50	high	high	
	Babina (BA)	mineral	20-50	high	medium	
Roșu-Puiu (LC4)	Roșu (RO)	mineral	130-200	high	low	low
	Roșuleț (RT)	mineral	50-130	very high	low	
	Mândra (MD)	organic	20-50	medium	low	
	Puiu (PU)	mineral	130-200	high	low	
	Erenciuc (ER)	organic	20-50	high	high	

*lakes complex Șontea-Furtuna (LC1), part of the fluvial delta, was not included in this study

**this study; measurements were done using GoogleEarthPro software

***DDNIRD = Danube Delta National Institute for Research and Development

****bolded characteristics were included in hydro-geomorphological analyses as well

#for each category a number from 1 to 6 was attributed for statistical analyses

Table S4 References

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Table S5 Regression analysis using Spearman multiple correlation nonparametric for the 19 lakes describing variables (bolded and in orange color are variables strongly correlated)

<i>Variables*</i>	kmp	shore	elev	mcdist	connect	depth	macroflo	macrosub	macrotot	peat	reed	retention	phpdiv	trans_m	trans_p	floodrisk	turb	waterflo	watervelo
kmp	1	0.62	0.38	-0.25	0.62	0.5	-0.45	-0.08	-0.44	0.42	0.07	0.37	-0.72	0.25	-0.04	0.37	0.06	0.5	0.53
shore	0.62	1	0.31	0.03	0.21	0.52	-0.21	-0.01	-0.21	0.18	0.29	0.37	-0.45	0.1	-0.11	0.13	0.26	0.45	0.46
elev	0.38	0.31	1	0.32	0.25	0.26	-0.64	-0.07	-0.57	0.15	-0.24	0.12	-0.59	-0.17	-0.24	0	0.09	0.48	0.54
mcdist	-0.25	0.03	0.32	1	-0.53	0.2	-0.32	-0.37	-0.42	-0.07	-0.09	-0.14	0.11	0.05	-0.28	-0.11	-0.05	0.31	0.32
connect	0.62	0.21	0.25	-0.53	1	0.38	-0.11	0.22	-0.07	0.27	-0.12	0.1	-0.47	0.01	-0.25	0.13	0.18	0.2	0.23
depth	0.5	0.52	0.26	0.2	0.38	1	-0.22	0.22	-0.23	0.44	0.22	0.53	-0.45	0.02	-0.78	-0.02	0.57	0.58	0.59
macroflo**	-0.45	-0.21	-0.64	-0.32	-0.11	-0.22	1	0.43	0.95	-0.3	0.17	0.12	0.48	-0.05	0.12	0.12	0.28	-0.35	-0.44
macrosub	-0.08	-0.01	-0.07	-0.37	0.22	0.22	0.43	1	0.63	-0.25	-0.11	0.6	0.04	-0.23	-0.34	-0.05	0.56	0.04	0.03
macrotot	-0.44	-0.21	-0.57	-0.42	-0.07	-0.23	0.95	0.63	1	-0.34	0.08	0.22	0.43	-0.11	0.1	0.11	0.33	-0.35	-0.42
peat	0.42	0.18	0.15	-0.07	0.27	0.44	-0.3	-0.25	-0.34	1	0.33	0.17	-0.59	-0.26	-0.42	-0.09	0.11	0.36	0.38
reed	0.07	0.29	-0.24	-0.09	-0.12	0.22	0.17	-0.11	0.08	0.33	1	0.03	-0.02	0	-0.09	-0.22	-0.01	0.13	0.04
retention	0.37	0.37	0.12	-0.14	0.1	0.53	0.12	0.6	0.22	0.17	0.03	1	-0.4	-0.13	-0.37	0.24	0.62	0.43	0.44
phpdiv**	-0.72	-0.45	-0.59	0.11	-0.47	-0.45	0.48	0.04	0.43	-0.59	-0.02	-0.4	1	0.05	0.21	-0.12	-0.06	-0.63	-0.67
trans_m**	0.25	0.1	-0.17	0.05	0.01	0.02	-0.05	-0.23	-0.11	-0.26	0	-0.13	0.05	1	0.47	0.45	-0.38	-0.19	-0.19
trans_p**	-0.04	-0.11	-0.24	-0.28	-0.25	-0.78	0.12	-0.34	0.1	-0.42	-0.09	-0.37	0.21	0.47	1	0.36	-0.61	-0.47	-0.49
floodrisk	0.37	0.13	0	-0.11	0.13	-0.02	0.12	-0.05	0.11	-0.09	-0.22	0.24	-0.12	0.45	0.36	1	-0.01	-0.08	-0.04
turb**	0.06	0.26	0.09	-0.05	0.18	0.57	0.28	0.56	0.33	0.11	-0.01	0.62	-0.06	-0.38	-0.61	-0.01	1	0.4	0.37
waterflo**	0.5	0.45	0.48	0.31	0.2	0.58	-0.35	0.04	-0.35	0.36	0.13	0.43	-0.63	-0.19	-0.47	-0.08	0.4	1	0.98
watervelo	0.53	0.46	0.54	0.32	0.23	0.59	-0.44	0.03	-0.42	0.38	0.04	0.44	-0.67	-0.19	-0.49	-0.04	0.37	0.98	1

*kmp=surface (kmp), shore=shore length (km), elev=elevation (m), mcdist=main channel distance (km), connect=connectivity with the river branch Sulina (categories), depth=water level (m), macroflo=floating macrophytes coverage (coverage units), macrosub= submerse macrophytes coverage (coverage units), macroto=total macrophytes coverage (coverage units), peat= thickness of peat deposits (cm), reed= reed beds presence (categories), retention= water retention time (weeks), phpdiv= phytoplankton diversity (categories), trans_m=water transparency (m), trans_p= water transparency (% from water level), floodrisk=flooding risk (categories), turb=water turbidity (NTF), waterflo= water flowing rate, watervelo=water velocity (m/s)

**variables were not included in further tests either because there are considered both cause and effect (transparency) or because there are strongly correlated with other variables

Table S6 Regression analysis using Spearman multiple correlation nonparametric for the 19 lakes describing variables (bolded and in orange color are variables strong correlated)

– *p* values

<i>Variables*</i>	kmp	shore	elev	mcdist	connect	depth	macroflo	macrosub	macrotot	peat	reed	retention	phpdiv	trans_m	trans_p	floodrisk	turb	waterflo	watervelo
kmp		0.0048	0.11	0.3002	0.0044	0.0294	0.0532	0.7452	0.0617	0.0726	0.7656	0.1166	0.0005	0.3019	0.8866	0.1232	0.8028	0.0305	0.02
shore	0.0048		0.1923	0.9035	0.3788	0.0236	0.3889	0.9712	0.3885	0.451	0.2233	0.1196	0.0547	0.6896	0.6524	0.6067	0.2864	0.0557	0.0452
elev	0.11	0.1923		0.182	0.2937	0.2764	0.0033	0.771	0.0112	0.5376	0.3155	0.6143	0.0076	0.4786	0.3243	0.993	0.7	0.039	0.0179
mcdist	0.3002	0.9035	0.182		0.0209	0.4054	0.1815	0.1199	0.0763	0.7774	0.7103	0.5667	0.6526	0.8294	0.2537	0.6542	0.8529	0.1995	0.183
connect	0.0044	0.3788	0.2937	0.0209		0.1073	0.6444	0.3732	0.7806	0.2598	0.6168	0.698	0.0437	0.9682	0.296	0.6037	0.4732	0.4011	0.3491
depth	0.0294	0.0236	0.2764	0.4054	0.1073		0.3553	0.3631	0.3419	0.0566	0.3699	0.0183	0.0505	0.9368	0.000	0.9394	0.0113	0.009	0.0073
macroflo**	0.0532	0.3889	0.0033	0.1815	0.6444	0.3553		0.0692	0.000	0.2062	0.48	0.6125	0.0363	0.8419	0.6201	0.6149	0.2453	0.1476	0.0611
macrosub	0.7452	0.9712	0.771	0.1199	0.3732	0.3631	0.0692		0.0036	0.3078	0.6484	0.0067	0.8822	0.351	0.1569	0.8242	0.012	0.8824	0.8892
macrotot	0.0617	0.3885	0.0112	0.0763	0.7806	0.3419	0.000	0.0036		0.1563	0.7558	0.365	0.0661	0.6588	0.6822	0.661	0.1703	0.141	0.0715
peat	0.0726	0.451	0.5376	0.7774	0.2598	0.0566	0.2062	0.3078	0.1563		0.173	0.4906	0.0081	0.2826	0.0726	0.7134	0.6498	0.1349	0.1106
reed	0.7656	0.2233	0.3155	0.7103	0.6168	0.3699	0.48	0.6484	0.7558	0.173		0.9051	0.9403	0.9955	0.7145	0.3572	0.9686	0.6037	0.8617
retention	0.1166	0.1196	0.6143	0.5667	0.698	0.0183	0.6125	0.0067	0.365	0.4906	0.9051		0.0908	0.5883	0.1196	0.3316	0.005	0.0684	0.0598
phpdiv**	0.0005	0.0547	0.0076	0.6526	0.0437	0.0505	0.0363	0.8822	0.0661	0.0081	0.9403	0.0908		0.8375	0.3998	0.6102	0.7957	0.0037	0.0017
trans_m**	0.3019	0.6896	0.4786	0.8294	0.9682	0.9368	0.8419	0.351	0.6588	0.2826	0.9955	0.5883	0.8375		0.0428	0.0529	0.1105	0.4261	0.4275
trans_p**	0.8866	0.6524	0.3243	0.2537	0.296	0.000	0.6201	0.1569	0.6822	0.0726	0.7145	0.1196	0.3998	0.0428		0.1285	0.006	0.0425	0.0331
floodrisk	0.1232	0.6067	0.993	0.6542	0.6037	0.9394	0.6149	0.8242	0.661	0.7134	0.3572	0.3316	0.6102	0.0529	0.1285		0.9659	0.7349	0.8683
turb**	0.8028	0.2864	0.7	0.8529	0.4732	0.0113	0.2453	0.012	0.1703	0.6498	0.9686	0.005	0.7957	0.1105	0.006	0.9659		0.0935	0.1162
waterflo**	0.0305	0.0557	0.039	0.1995	0.4011	0.009	0.1476	0.8824	0.141	0.1349	0.6037	0.0684	0.0037	0.4261	0.0425	0.7349	0.0935		0.000
watervelo	0.02	0.0452	0.0179	0.183	0.3491	0.0073	0.0611	0.8892	0.0715	0.1106	0.8617	0.0598	0.0017	0.4275	0.0331	0.8683	0.1162	0.000	

*kmp=surface (kmp), shore=shore length (km), elev=elevation (m), mcdist=main channel distance (km), connect=connectivity with the river branch Sulina (categories), depth=water level (m), macroflo=floating macrophytes coverage (coverage units), macrosub= submerse macrophytes coverage (coverage units), macroto=total macrophytes coverage (coverage units), peat= thickness of peat deposits (cm), reed= reed beds presence (categories), retention= water retention time (weeks), phpdiv= phytoplankton diversity (categories), trans_m=water trasnparancy (m), trans_p= water transparency (% from water level), floodrisk=flooding risk (categories), turb=water turbidity (NTF), waterflo= water flowing rate, watervelo=water velocity (m/s)

**variables were not included in further tests either because there are considered both cause and effect (transparency) or because there are strongly correlated with other variables

Fig. S1 Cyanobacteria biovolume (a) and genus richness (b) for every studied lake (displayed from West to East): *Isac* (IS), *Uzlina* (UZ), *Cuibul cu Lebede* (CL), *Gorgostel* (GR) part of Gorgova- Uzlina (LC2, green), *Trei Iezere* (TI), *La Amiază* (LA), *Bogdaproste* (BG), *Matița* (MA), *Merhei* (ME), *Merhei Mic* (MM), *Lung* (LU), *Dracului* (DR), *Rădăcinoasele* (RE), *Babina* (BA) part of Matița-Merhei (LC3, yellow) and *Roșu* (RO), *Roșuleț* (RT), *Mândra* (MD), *Puiu* (PU), *Erenciuc* (ER) part of Roșu-Puiu (LC4, purple)

Fig. S2 Scatterplot of cyanobacteria genus richness and biovolume (ln value) in the Danube Delta lakes during the study period. The two parameters are significantly ($p < 0.001$) and positively and strongly correlated according to Pearson correlation coefficient ($\rho = 0.819$)

Fig. S3 Danube Delta lake parameters that significantly: (a) describe the lake complexes (LC2 = Gorgova- Uzlina, LC3=Matia-Merhei and LC4=Roșu-Puiu), (b) predict cyanobacteria biovolume and (c) cyanobacteria genus richness. The hydro-geomorphological features are described in Table S5

Fig. S4 Genera (in terms of biovolume) – lake characteristics biplot diagram from linear redundancy analysis (RDA) with lake complex as covariate. The codes for cyanobacteria genera are: *Anabaena* (Anab), *Anabaenopsis* (Anas), *Aphanizomenon* (Apha), *Aphanocapsa* (Aphca), *Coelosphaerium* (Coel), *Chroococcus* (Chro), *Jaaginemoia* (Jaag), *Johanseninema* (Joha), *Lyngbya* (Lyng), *Leptolyngbya* (Lepto), *Microcystis* (Micr), *Merismopedia* (Meri), *Oscillatoria* (Osci), *Planktolingbya* (Plan), *Rhabdogloea* (Rhab), *Snowella* (Snow), *Trichormus* (Tric) and *Wolleea* (Spha). Lake characteristics were: flooding risk (floodris), total macrophyte coverage water velocity (macrotot), water level (depth) and phytoplankton diversity (phpdiv). Genera with less than four occurrences were not included in the analysis