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Original Articles

Harmful blooms across a longitudinal gradient in central Europe during heatwave: Cyanobacteria biomass, cyanotoxins, and nutrients

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A B S T R A C T

Climate change has increased the frequency, duration and intensity of heatwaves in Europe. These extreme events result in alterations of physical, chemical, and biological properties of lakes that may synergistically promote cyanobacterial dominance. In our study we focused on cyanobacterial blooms in lakes distributed over a longitudinal gradient in Central Europe during one of the "top ten European heat waves" in summer 2015. 92 lakes were included in the study, located across three climatic subregions: cool northern lakes, situated in Lithuania, temperate northern lakes in Poland, and warm northern lakes in Croatia. The objective of the study was to determine if cyanobacterial biomass, predominant species, and cyanotoxin concentration differed, across the south-north gradient, as a function of water temperature, total phosphorus, and total nitrogen. Statistical significance of observed patterns was tested using the Kruskal-Wallis rank sum test and the generalized linear model. We found the lowest average epilimnion temperature, but the highest average cyanobacterial biomass in the northern, 'cool' lakes while the highest average temperature with the lowest average cyanobacterial biomass in the southern, 'warm' lakes. The concentration of cyanotoxins was also the highest in the 'cool' lakes. Total phosphorus and total nitrogen correlated significantly with cyanobacterial biomass, cyanotoxins concentration and biomass of some cyanobacterial species (mainly *Planktothrix agardhii*), regardless of the latitude. Only in the 'cool' lakes concentration of cyanotoxins (microcystins and anatoxin-a) correlated significantly with cyanobacterial biomass and the biomass of some dominant cyanobacterial species (*P. agardhii*). Our results emphasized the differences of heat weaves impact on lakes of various latitudes, with the strongest increase in toxic cyanobacterial blooms in northern 'cool' lakes, situated in high latitudes. On the other hand, nutrients directly enhanced blooms across all the studied latitudes of Central Europe. The cyanobacteria species dominating in blooms might be recognized as ecological indicators of climate change, especially in the north-eastern part of Europe.

1. Introduction

Cyanobacteria are unicellular, colonial or filamentous, gram-negative photosynthetic bacteria and are among the oldest organisms on the Earth (Castenholz, 2015). They are considered the earliest oxygen producers and are critical for global primary production and nitrogen fixation (Lyons et al., 2014; Paerl, 2017). The main macronutrients for which cyanobacteria compete are phosphorus (P) and nitrogen (N) (Paerl et al., 2020; Savadova-Ratkus et al., 2021). In addition, the N:P ratio (Howarth et al., 1988), inorganic carbon (Hamdan et al., 2018), and iron (Cole et al., 1993) can also play an important role in their growth.

The mass development of cyanobacteria is referred to as a 'cyanobacterial bloom'. The term 'bloom' is defined in many ways, but the simplest is 'a distinct visible discolouration of the water' (Huisman et al., 2018), usually with dominance (>80%) of one or a few cyanobacterial species (Humbert and Fastner, 2017). Cyanobacterial blooms are a well-known phenomenon worldwide, occurring in all types of water bodies, both warm (Paerl and Huisman, 2008) and cold (Reinl et al., 2023) temperate conditions. They are precarious to water ecosystems, since many cyanobacteria are capable of producing various types of bioactive metabolites, e.g., hepatotoxins, neurotoxins, lipopolysaccharides (LPS), β-methylamino-alanine (BMAA), non-ribosomal peptides, etc. (Gademann and Portmann, 2008), which pose a hazard to animals and humans (Chorus and Welker, 2021). Cyanotoxins are chemically diverse and have various effects, e.g. hepatotoxic, neurotoxic, dermatotoxic, cytotoxic, cancerogenic.

Hepatotoxic microcystins and other toxins, including cylindrospermopsins, neurotoxic anatoxins, saxitoxins, anatoxin-a(S), and dermatotoxins, are commonly found in freshwaters (Mantzouki et al., 2018a; Chorus and Welker, 2021). However, the problem caused by cyanobacterial blooms is not only the release of cyanotoxins and other biologically active metabolites. High biomass of cyanobacteria leads to deterioration of the underwater light climate, oxygen supersaturation in the upper water layers, due to intense photosynthesis, and temporary oxygen depletion at the bottom of lakes, due to the decomposition of organic matter (Dondajewska et al., 2020). None of these factors are beneficial to organisms or the ecosystem as a whole, leading to changes in the biological and functional diversity of aquatic communities (Krztoń et al., 2019) and a reduction in the quality and value of ecosystem services provided by freshwaters (Smith et al., 2019; Olokotum et al., 2020). In addition, an effect of decomposition of cyanobacterial blooms is the production of CO_2 and CH_4 (Bizic, 2021), the main greenhouse gases, promoting climate change over the globe.

In recent decades, the frequency and severity of cyanobacterial blooms in lakes and reservoirs have increased worldwide (Monchamp et al., 2018). The blooms might be recognized as ecological indicators of eutrophication but also as climate change. Because the spread of cyanobacteria is favored by increasing water temperatures (Paerl and Huisman, 2008), there is a global concern that climate change promotes the geographic dispersal of species, including some potentially harmful species (Salmaso et al., 2015). Climate change has also altered the timing and extent of precipitation, leading to changes in land–water connectivity and the physical, chemical, and biological properties of lakes (Creed et al., 2018), which may synergistically promote cyanobacterial development (Paerl and Paul, 2012; Budzyńska and Gołdyn, 2017; Paerl et al., 2020).

The changes in summer weather in Europe include the increase in frequency, intensity and duration of heat waves (Lhotka and Kyselý, 2022). Overall, 83% of the European area experienced extremely hot summers (Lhotka and Kyselý, 2022). Modifications of air temperatures strongly impact lakes, with multiple effects including higher maximum temperatures, earlier onset of and stronger thermal stratification, and longer periods of high water temperature (Dokulil et al., 2021). However, even within the continent, the changes are not uniform. E.g., northern European lakes are warming faster than the global average (O'Reilly et al., 2015).

Climatic factors have also been identified as the major cause of cyanotoxin distribution at the European level (Mantzouki et al., 2018a), but no analyses have been performed on the distribution of biomass and diversity of cyanobacteria causing blooms. Therefore, we focused on the intensity, composition and toxin concentration of cyanobacterial blooms over a latitudinal gradient in Central Europe during the summer of 2015, which was one of the 'top ten European heat waves' (Russo et al., 2015) with a heat wave exceeding 100 days (Lhotka and Kyselý, 2022).

The aim of our study was to answer the question if cyanobacterial blooms differed among different climatic regions of Central Europe during one of the European heatwaves. Data from three regions of Europe in latitudinal gradient were compared (northern cool, northern temperate and northern warm). Cyanobacterial biomass, dominant species and cyanotoxin concentration were included in the analysis, along with parameters of climate warming (water temperature) and eutrophication (phosphorus and nitrogen concentration). The cyanobacterial blooms might be recognized as ecological indicators of climate change.

2. Material and methods

2.1. Lake selection

Ninety-two lakes located in Europe were sampled during one of the hottest summers in 2015 (https://www.visualcrossing.com/weather-data). The sampled lakes belonged to three types of northern lakes according to Maberly et al. (2020): 1) northern warm, localized in Croatia (CRO), 2) northern temperate, localized in Poland (PL), and 3) northern cool, localized in Lithuania (LT; Fig. 1.). The number of lakes in each of the types was as follows: fifteen northern warm lakes, sixty-two northern temperate lakes, and fifteen northern cool lakes. In each region we sampled a variety of lakes of various depths (Appendix A1 – data sources).

2.2. Sampling procedure

Samples were collected at the deepest point of each lake during the warmest, sunny and windless two-week period in summer 2015. To allow comparison of the results, all the samples were collected only from the part of the water column mixed by wind. In thermically stratified lakes, the mixed part meant from 0.5 m below the surface till the thermocline, with the thermocline determined in situ on the day of sampling. In shallow, non-stratified lakes, integrated samples were collected from 0.5 m below the surface to 0.5 m above the lake bottom. Samples were collected using a dedicated sampler made of a hose ('Anaconda') that allows collecting water samples from the whole water column, without intervals (Mantzouki et al., 2018a, Donis et al., 2021). The special sampler 'Anaconda' and its use was described in detail in Mantzouki et al., (2018b). All biological and environmental samples were collected in the same way, at the same time and in the same place. The phytoplankton samples were fixed with Lugol's iodine.

2.3. Analysis of samples

The samples for TP (total phosphorus), TN (total nitrogen) and cyanotoxins analysis were immediately transported to laboratory. The nutrient samples were frozen and shipped to a dedicated laboratory. A 50–250 ml subsample of each sample for cyanotoxins analysis was filtered through 47 mm Whatman glass fibre filters (GF/C) using a filtration device. The filters containing the cyanobacterial biomass were frozen at −20 °C and shipped to the appropriate laboratory where they were analyzed according to the methods described by Mantzouki et al. (2018a,b) and Donis et al. (2021). The analysis included anatoxin a (ATX), cylindrospermopsin (CYN) and various congeners of microcystins (MC-dmRR, MC-RR, MC-YR, MC-dmLR, MC-LR). For the statistical analyzes, we used the concentrations of the individual congeners (see above) and the sum of all congeners labeled as MC_tot.

The abundance, taxonomical composition and biovolume of phytoplankton and cyanobacteria in particular were counted according to the

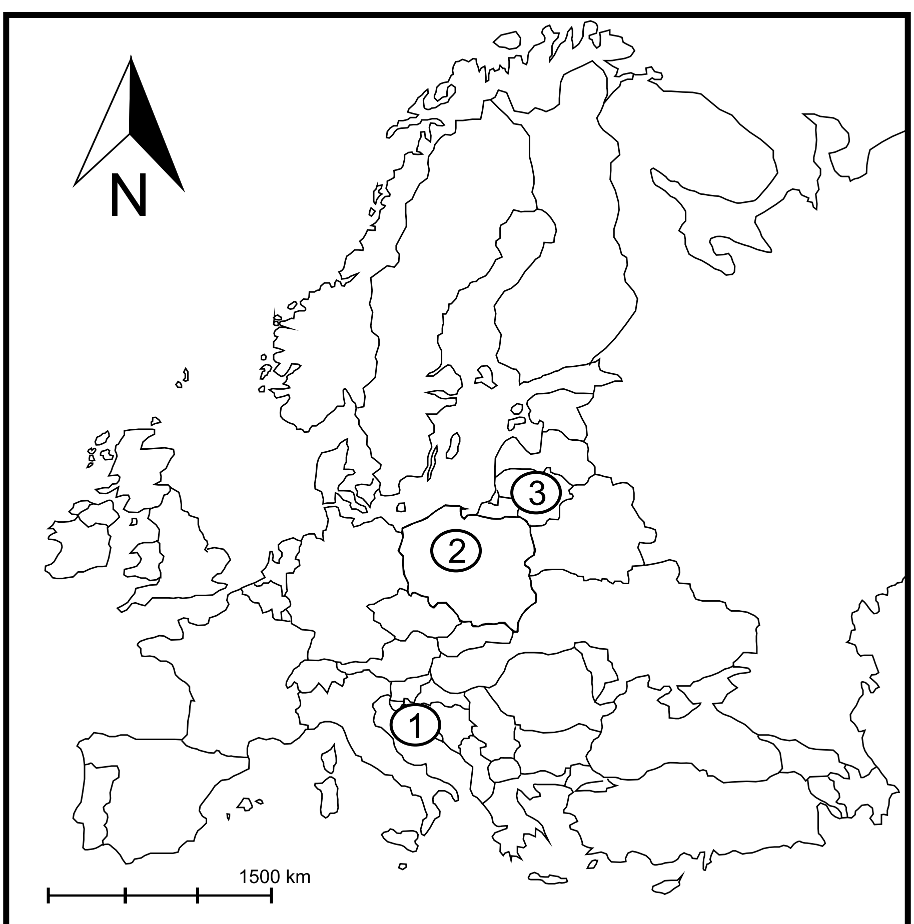

Fig. 1. Three regions in Europe in a north–south gradient in which lakes were sampled: 1. southern part, northern warm lakes (Croatia), 2. Northern temperate lakes (Poland), 3. Northern part, northern cool lakes (Lithuania).

rules described in 'Guidance on the quantitative analysis of phytoplankton in Freshwater Samples' (Brierley et al., 2007). The method was developed on the basis of Utermöhl technique (Lund et al., 1958; Utermöhl, 1958; CEN, 2004). The analysis was carried out using sedimentation chambers and an inverted microscope.

Species composition of cyanobacterial community was analysed using relevant taxonomic keys (Komárek, 2013; Komárek and Anagnostidis, 1999; 2005). Species with more than 20% share in the total phytoplankton biomass were considered the dominants.

2.4. Data analysis

TP, TN, and cyanotoxins data used for statistical analyses were obtained from the supplemental file of Manztouki et al. (2018a), available online https://www.mdpi.com/2072-6651/10/4/156/s1, https://portal.edirepository.org/nis/mapbrowse?packageid=edi.176.5 and Mantzouki et al. (2018). ***Environmental Data Initiative*** https://doi.org/10.6073/pasta/dabc352040fa58284f78883fa9debe37.

All *Microcystis* species were analysed as one entity, as these are only morphospecies, not supported by molecular analysis (Komárek et al., 2002). Also all *Dolichospermum* species were analysed in this way due to

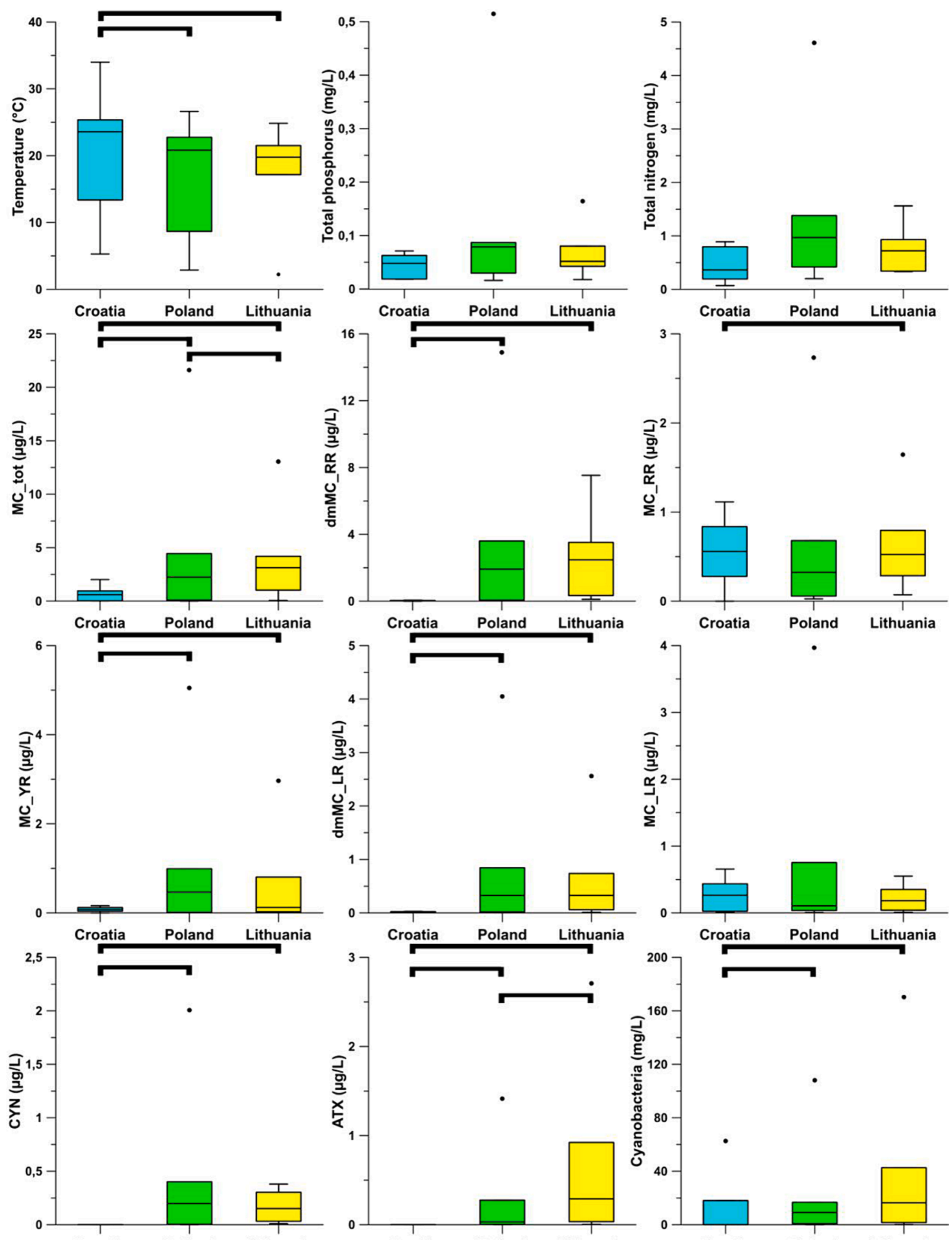

Fig. 2. Box-plot of environmental variables, cyanotoxins and total biomass of cyanobacteria among Croatian, Polish and Lithuanian lakes: horizontal lines at the top of each graph mark statistically significant differences between lakes in particular European regions (Kruskal-Wallis; $p < 0.05$); bars represent 25–75%; horizontal lines on the bars represent mean; dots represent outliers; whiskers represent ranges between minimum and maximum values. Abbreviations: Temperature – water temperature; MC_tot – concentration of total microcystins; MC_dmRR and MC_dmLR – concentration of desmethylic congeners of RR and LR microcystins; MC_LR, MC_RR, MC_YR – concentration of particular congeners of microcystins; CYN – concentration of cylindrospermopsins; ATX – concentration of anatoxin-a; cyanobacteria – total biomass of cyanobacteria.

their unclear intraspecific taxonomy (Zapomělová et al., 2011). The remaining species (*Aphanizomenon flos-aquae*, *A. gracile*, *Cuspidothrix issatschenkoi*, *Planktothrix agardhii*, *Raphidiopsis (Cylindropsermopsis) raciborskii*, *Sphaerospermopsis aphanizomenoides*) did not pose such taxonomic problem, hence analyses were possible for species.

Statistical significance of the differences in environmental variables, cyanotoxin concentration, and cyanobacterial biomass among the three groups of lakes were tested using the Kruskal-Wallis rank sum test with Dunn's test *post hoc*. To examine the relationships of environmental factors with concentration of cyanotoxins and the biomass of dominant species of cyanobacteria, the generalized linear model (GLMs) were employed. Statistical analyses were performed in R Studio version 4.0.2 (R Core Team, 2020). The *p*-value of 0.05 was considered the border value discriminating between the statistically significant and insignificant results.

3. Results

3.1. Environmental variables

Average water temperature in the epilimnion ranged from 20.48 °C in cool lakes group through 20.91 °C in temperate lakes groups, to 23.79 °C in warm lakes group (Appendix A2). Water temperature of the epilimnion of warm lakes differed significantly from the temperature noted in the temperate lakes and in the cool lakes. However, the difference in the temperature of temperate and cool lakes was not significant (Fig. 2).

The average values of TP and TN were the highest in the temperate lakes (0.079 mg/L and 1.035 mg/L, respectively) and the lowest in warm lakes (0.049 mg/L and 0.467 mg/L, respectively) (Appendix A2 – data sources), but no statistically significant differences were found (Fig. 2).

3.2. Concentration of cyanotoxins

Cyanotoxins were identified in all three groups of lakes, but CYN and ATX-a were noted only in temperate and cool lakes (Appendix A2). The average concentration of CYN was higher in temperate lakes than in cool lakes, but the difference was not statistically significant. The average concentration of ATX-a was higher in cool lakes than in the temperate lakes. Also the concentration of MC_tot was the highest in cool lakes, while the lowest in warm lakes, and the differences among three groups of lakes were significant (Fig. 2). The warm lakes contained the lowest average concentration of microcystin congeners MC-LR, dmMC-LR, MC-RR, dmMC-RR and MC-YR. The highest mean concentration of MC-YR was found in the temperate lakes, while all the other congeners (MC-LR, dmMC-LR, MC-RR and dmMC-RR) prevailed in the cool lakes (Appendix A2, Fig. 2).

Warm lakes differed significantly from the cool lakes and from temperate lakes in the concentration of dmMC-RR, MC-YR and dmMC-LR congeners. They also differed in the concentration of MC-RR congeners from the cool lakes. No statistical differences in the concentration of MC-LR, dmMC-RR, MC-RR, MC-YR, dmMC- LR was found between the temperate and cool lakes (Fig. 2).

3.3. The cyanobacterial community

More than 110 cyanobacteria taxa were identified in the studied water bodies across the latitudes in Europe. Species which are potential toxins producers with a share over 20% of the total cyanobacteria biomass, were included in the analysis in this work: *Aphanizomenon flos-aqaue* Ralfs ex Bornet & Flahault, *Aphanizomenon gracile* Lemmermann, *Cuspidothrix issatschenkoi* (Usachev) Rajaniemi, Komárek, Willame, Hrouzek, Kastovská, Hoffmann & Sivonen, *Dolichospermum* spp. (*D. circinale* (Rabenhorst ex Bornet & Flahault) Wacklin, Hoffmann & Komárek, *D. flos-aquae* (Bornet & Flahault) Wacklin, Hoffmann & Komárek, *D. lemmermanii* (Richter) Wacklin, Hoffmann & Komárek, *D. spiroides* (Klebhan) Wacklin, L.Hoffmann & Komárek, *D. smithii* (Komárek) Wacklin, Hoffmann & Komárek), *Microcystis* spp. (*M. aeruginosa* (Kützing) Kützing, *M. viridis* (A.Braun) Lemmermann, *M. wesenbergii* (Komárek) Komárek ex Komárek), *Planktothrix agardhii* (Gomont) Anagnostidis & Komárek, *Raphidiopsis (Cylindrospermopsis) raciborskii* (Woloszynska) Aguilera & al., *Sphaerospermopsis aphanizomenoides* (Forti) Zapomelová, Jezberová, Hrouzek, Hisem, Reháková & Komárková.

The biomass of cyanobacteria differed significantly between warm lakes versus each of the other groups of lakes. There was no significant difference between cool and temperate lakes in the total biomass of cyanobacteria (Fig. 2), however the highest total cyanobacterial biomass was noted in Lithuanian lakes – 170.29 mg/L (Appendix A2).

The highest average biomass of *A. gracile*, *Dolichospermum* spp., *Microcystis* spp., and *P. agardhii* was found in cool lakes (Appendix A3 – data sources, Fig. 3). The average biomass of *A. flos-aquae*, *R. raciborskii*, and *C. issatschenkoi* was the highest in temperate lakes. *S. aphanizomenoides* as a dominant species was recorded only in temperate lakes (Appendix A3, Fig. 3). Statistically significant differences were found for *Dolichospermum* spp. and *Microcystis* spp. biomass when comparing each of the lakes groups with any of the other. Statistically significant difference was also found for the biomass of *A. gracile* between temperate and cool lakes. For the biomass of *P. agardhii*, a statistically significant difference was noted between warm and cool lakes, and between warm and temperate lakes, but not between temperate and cool lakes.

We did not find statistically significant differences for the biomass of the other species (*C. issatschenkoi*, *R. raciborskii*, *A. flos-aquae* and *S. aphanizomenoides*).

3.4. The impact of environmental variables on cyanobacterial community and cyanotoxin concentration

Statistical analysis (GLM) showed that TP and TN were significant factors affecting cyanobacterial biomass and some congeners of cyanotoxins (Table 1). Some significant relationships were also found for the latitude (Lithuania, the northern, cool part of Europe) and cyanobacterial biomass, latitude and concentration of ATX-a, and latitude and biomass of *P. agardhii* (Table 1).

4. Discussion

Rigosi et al. (2014) postulated that in eutrophic and hyper-eutrophic lakes, a significant interaction between nutrients, temperature, and cyanobacterial biomass exists. They showed that the relation between nutrients, water temperature and cyanobacterial development depends on the cyanobacterial species and the trophic state of the lake (Rigosi et al., 2014). Our studies highlighted that geographical location, TP and TN were statistically important factors for cyanobacterial biomass during the extremely hot summer of 2015 (a heat wave with a total extend of more than 100 days; Lhotka and Kyselý, 2022) in Central Europe. Water temperature was significantly higher in the 'warm' lakes than in the temperate and in the cool lakes. However, the opposite was true for cyanobacterial biomass in the regions studied: the highest average water temperatures coincided with the lowest cyanobacterial biomass, and lowest cyanotoxin concentrations. The lack of a relationship between the biomass of cyanobacteria and water temperature, in our study, does not mean that this factor is not important for cyanobacteria and their bloom development. Indirectly, temperature changes affect various processes inside and outside lakes, such as the extent of stratification (Paerl and Huisman 2008; Wilk-Woźniak et al., 2021) or light conditions (Donis et al., 2021). As we did not measure the extent of stratification or light conditions, so we cannot discuss these parameters and the synergy between them and water temperature affecting cyanobacterial blooms in this study.

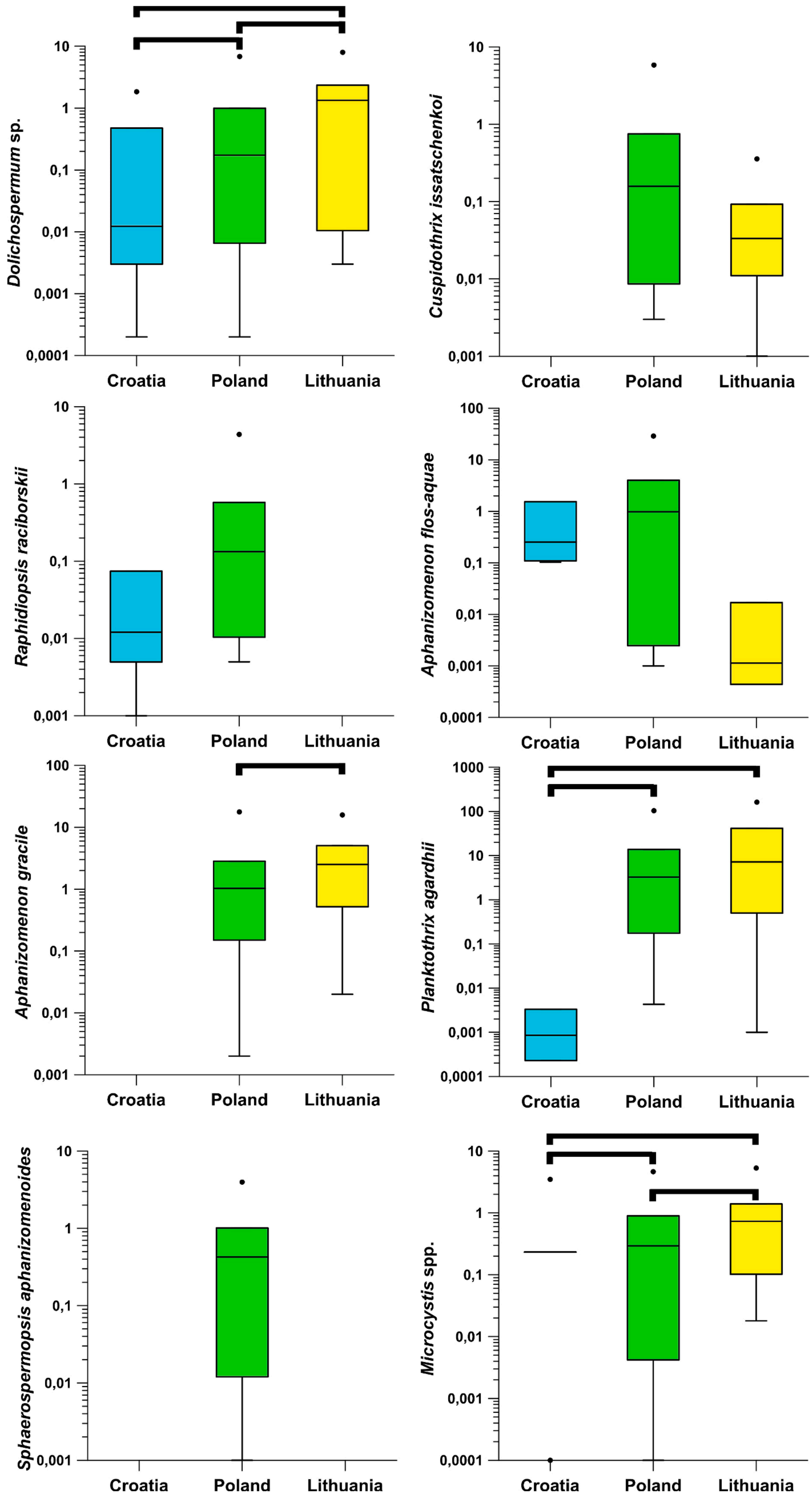

Fig. 3. The biomass of dominant cyanobacterial taxa among Croatian, Polish and Lithuanian lakes (log scale): horizontal lines at the top of each graph mark statistically significant differences between lakes in particular European regions (Kruskal-Wallis, $p < 0.05$); bars represent 25–75%; horizontal lines on the bars represent mean; dots represent outliers; whiskers represent ranges between minimum and maximum values.

Table 1
Significant relationships between different environmental parameters, cyanobacteria and lake groups.

Relationships	Estimate	Std error	T value	Pr (>/t/)	Significance
Cb – TP	159.28	42.173	3.777	0.000	***
Cb – TN	10.22	4.608	2.217	0.033	*
Cb – LT	16.79	7.644	2.196	0.017	*
Cb – TP/TN	108.69	34.355	3.164	0.003	**
Cb – LT – TP	−1122.10	217.051	−5.170	5.79e-06	***
Cb – LT – TP/TN	1669.63	226.964	7.357	3.93e-09	***
Cb – MC_{tot}	0.11	0.014	8.052	7.47e-12	***
$MC_{\_tot}$ –TP	25.99	5.078	5.119	5.37e-06	***
$MC_{\_tot}$ –LT	1.85	0.978	1.986	0.064	#
dmMC-RR – TP	21.62	3.975	5.439	1.27e-06	***
dmMC-RR – TN	1.04	0.374	2.777	0.007	**
dmMC-LR – TP	2.71	1.247	2.172	0.035	*
dmMC-LR –TN	0.34	0.117	2.879	0.006	**
ATX-a – LT	0.14	0.057	2.497	0.156	*
Dspp. – LT	1.21	0.420	2.888	0.056	**
AGb – LT	2.65	0.988	2.681	0.009	**
PAb – TP	174.93	39.399	4.440	4.84e-05	***
PAb – LT	13.27	7.291	1.821	0.075	#

Abbreviations: Cb – total cyanobacterial biomass; TP – total phosphorus; TN – total nitrogen; TP/TN – total phosphorus to total nitrogen ratio; LT – Lithuania; $MC_{\_tot}$ – total microcystins concentration; dmMC-RR, dmMC-LR – concentration of microcystins congeners; ATX – concentration of anatoxin-a; Dspp. – *Dolichospermum* spp. biomass; AGb – *Aphanizomenon gracile* biomass; PAb – *Planktothrix agardhii* biomass.
Kruskal-Wallis test; significance code: 0.001 – ***; 0.01 – **; 0.05 – *; 0.1 – #.

There are some opinions that increasing the seasonal length of days with high temperature (due to climate change) could lead to a shorter duration of blooms in lakes with nutrient limitation (e.g., Free et al., 2022). However, another hypothesis was proposed by Bonilla et al. (2023) who suggested that in the Americas, nutrients (eutrophication) are more conducive to cyanobacterial development compared to the climatic gradient. Previous studies in Canada have also shown that nutrients (phosphorus and nitrogen) best predict cyanobacteria biomass, with no significant regional differences (Beaulieu et al., 2014). It was also found that nutrient availability affected the reaction of cyanobacteria on temperature (Thomas and Litchman, 2016). Statistical analyses showed that TP, TN and climatic region (latitude) were significantly important for cyanobacterial biomass, a production of specific congeners of toxins, and biomass of a particular cyanobacterial species mainly *P. agardhii*, a species known for its high demand for phosphorus (Hašler et al., 2003).

Climatic region (latitude) was a statistically significant factor related to the biomass of cyanobacteria, especially the biomass of *Dolichospermum* spp., *Aphanizomenon gracile*, and *P. agardhii*. All these species had the highest average biomass in northern Lithuanian lakes. *Dolichospermum* spp. and *A. gracile* are diazotrophic (N-fixing) species. Their high biomass in Lithuanian lakes is consistent with the finding that diazotrophic species are increasing in northern lakes (Przytulska et al., 2017). Likely the high biomass of *A. gracile* and *Dolichospermum* spp. may be indirectly related to increasing temperatures in the northern zone, but could not demonstrate this as a direct effect and point to a necessary direction for future research. Cremona et al. (2022) indicated that rising temperatures lead to altered ice phenology that disrupts hydrological and thermal regimes. In addition, Freeman et al.(2020) showed that rising temperatures are responsible for the lengthening of the growing season. This is also because an increase in water surface temperature leads to prolonged stratification and reduces the depth of the mixed layer (Stockenreiter et al., 2021; Wilk-Woźniak et al., 2021). Longer growing seasons are well suited for N-fixing filamentous cyanobacteria because they have more time to elongate their filaments sufficiently to produce specialized heterocytes (Freeman et al., 2020). Some relationships between *Dolichospermum* and *P. agardhii* were found in earlier studies. Toporowska et al. (2016) showed that mass development of *Dolichospermum* spp. in a highly eutrophic lake affected by prolonged *P. agardhii* blooms depended on water temperature, but could also be controlled by the DIN /DIP ratio. The periodic dominance of certain N-fixing species, especially of the genus *Dolichospermum*, can change very rapidly (Pawlik-Skowrońska et al., 2013; Toporowska et al., 2016). This relationship would also be worth investigating further in northern cool lakes.

The biomass of cyanobacteria was significantly related to the concentration of cyanotoxins, especially $MC_{\_tot}$. Although no statistical correlation of ATX-a with total cyanobacterial biomass or biomass of a particular species was found, a significant relationship between the concentration of neurotoxins (ATX-a) and latitude was found. Indeed, the highest concentration of neurotoxins was found in Lithuanian lakes, as was the highest average biomass of *Dolichospermum* spp. and *A. gracile*. Both the species are known ATX-a producers (Chorus and Welker, 2021). In contrast to cool lakes, ATX-a was not present in warm lakes. Interestingly, lakes in the Alps showed a similar trend of increasing importance of ATX-a (Cerasino and Salmaso, 2020), suggesting that ecosystems of cool lakes are more threatened by neurotoxins than warm lakes. Cool lakes are more vulnerable to changes observed due to climate warming (Pilla and Williamson, 2022), and we might expect adverse phenomena to occur much more frequently and with greater severity in these lakes than in warmer lakes.

In the present study $MC_{\_tot}$ was associated with TP, TN and cyanobacterial biomass, whereas demethylated variants of MC-RR and MC-LR were significantly associated with TP and TN, respectively. The obtained results are consistent with a study on microcystins from 190 Canadian lakes (MacKeigan et al., 2023) and an experimental study on *Microcystis* blooms in a lake and tidal tributary (Vézie et al., 2002), where microcystin production was also associated with phosphorus and nitrogen levels.

MC-LR was the only congener found in our study with no statistically significant difference in concentration between analysed regions This congener is known to be most abundant one in aquatic ecosystems (Mantzouki et al., 2018a; MacKeigan et al., 2023), so we did not expect differences in distribution between lakes. The third type of cyanotoxin – CYN was found in cool and temperate, but not warm lakes. However, we found no relationships with cyanobacterial species, including *R. raciborskii*, a species known to produce CYN, outside Europe (Kokociński et al., 2013; Chorus and Welker, 2021). Moreover, CYN is produced in European waters by other species, e.g., *Aphanizomenon klebahnii*, *A. gracile*, *A. flos-aquae*, *Chrysosporum ovalisporum* (syn. *Aphanizomenon ovalisporum*), *Anabaena planctonica* (syn. *Dolichospermum planctonicum*), *A. lapponica*, *Oscillatoria* sp. (Rzymski and Poniedziałek, 2014), and when they co-occur with *R. raciborskii*, misinterpretation of results may occur. It is very likely that CYN was produced by several various species in our lakes, which is why we found no correlations. However, the most important finding is the absence of this toxin in warm lakes.

5. Conclusions

Cyanobacterial blooms and cyanotoxin concentration were the highest in the northern, cool lakes, despite the lowest temperature of water. Nutrients concentration showed a much stronger effect on cyanobacterial biomass, cyanotoxins, and the biomass of some cyanobacterial species (*Planktothrix agardhii*) than water temperature.

Certain cyanobacterial species dominated the cyanobacterial community only in some climatic groups of lakes: *Sphaerospermopsis aphanizomenoides* in temperate lakes, *Cusphidothrix issatschenkoi* and *Aphanizomenon gracile* in cool and temperate lakes, and *Raphidopsis raciborskii* in warm and temperate lakes. *Dolichospermum* spp., *Aphanizomenon flos-aquae*, *Planktothrix agardhii* and *Microcystis* spp. were found as dominant species in all the three regions.

Our study suggests that northern aquatic ecosystems are the most threatened by the blooms of cyanobacterial species that produce ATX-a, especially diazotrophic species (*Aphanizomenon gracile* and *Dolichospermum* spp.).

We demonstrated that changes in summer climate in Europe, particularly periods of heat waves, promote an increase in toxic cyanobacterial blooms in northern cool lakes more than in lower latitudes. Nutrients directly enhance blooms across all latitudes in central Europe during heat weaves. The cyanobacteria species that dominate in blooms might be recognized as ecological indicators of climate change, especially in the north-eastern part of Europe.

CRediT authorship contribution statement

Elżbieta Wilk-Woźniak: Writing – review & editing, Validation, Investigation, Data curation. **Wojciech Krztoń:** Writing – review & editing, Validation, Investigation, Data curation. **Martyna Budziak:** Writing – review & editing, Visualization, Validation, Software. **Edward Walusiak:** Writing – review & editing, Validation, Investigation, Data curation. **Petar Žutinič:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Investigation. **Marija Gligora Udovič:** Writing – review & editing, Validation, Investigation, Data curation. **Judita Koreivienė:** Writing – review & editing, Validation, Software, Investigation, Data curation. **Jūratė Karosienė:** Writing – review & editing, Validation, Investigation, Data curation. **Jūratė Kasperovičienė:** Writing – review & editing, Validation, Investigation, Data curation. **Justyna Kobos:** Writing – review & editing, Validation, Investigation, Data curation. **Magdalena Toporowska:** Writing – review & editing, Validation, Investigation, Data curation. **Agnieszka Bańkowska-Sobczak:** Writing – review & editing, Validation, Investigation, Data curation. **Agnieszka Budzyńska:** Writing – review & editing, Validation, Investigation, Data curation. **Piotr Domek:** Writing – review & editing, Validation, Investigation, Data curation. **Julita Dunalska:** Writing – review & editing, Validation, Investigation, Data curation. **Magdalena Frąk:** Writing – review & editing, Validation, Investigation, Data curation. **Ryszard Gołdyn:** Writing – review & editing, Validation, Investigation, Data curation. **Magdalena Grabowska:** Writing – review & editing, Validation, Investigation, Data curation. **Natalia Jakubowska-Krepska:** Writing – review & editing, Validation, Investigation, Data curation. **Iwona Jasser:** Writing – review & editing, Investigation, Data curation. **Maciej Karpowicz:** Writing – review & editing, Investigation, Data curation. **Mikołaj Kokociński:** Writing – review & editing, Validation, Investigation, Data curation. **Anna Kozak:** Writing – review & editing, Validation, Investigation, Data curation. **Hanna Mazur-Marzec:** Writing – review & editing, Validation, Investigation, Data curation. **Beata Mądrecka-Witkowska:** Writing – review & editing, Validation, Investigation, Data curation. **Beata Messyasz:** Writing – review & editing, Validation, Investigation, Data curation. **Agnieszka Napiórkowska-Krzebietke:** Writing – review & editing, Validation, Investigation, Data curation. **Michał Niedźwiecki:** Writing – review & editing, Investigation, Data curation. **Barbara Pawlik-Skowrońska:** Writing – review & editing, Validation, Investigation, Data curation. **Agnieszka Pasztaleniec:** Writing – review & editing, Validation, Investigation, Data curation. **Aleksandra Pełechata:** Writing – review & editing, Validation, Investigation, Data curation. **Mariusz Pełechaty:** Writing – review & editing, Validation, Investigation, Data curation. **Wojciech Pęczuła:** Writing – review & editing, Validation, Investigation, Data curation. **Joanna Rosińska:** Writing – review & editing, Validation, Investigation, Data curation. **Elżbieta Szeląg-Wasielewska:** Writing – review & editing, Validation, Investigation, Data curation. **Joanna Mankiewicz-Boczek:** Writing – review & editing, Validation, Investigation, Data curation. **Michał Wasilewicz:** Writing – review & editing, Investigation, Data curation. **Filip Stević:** Writing – review & editing, Investigation, Data curation. **Dubravka Špoljarić Maronić:** Writing – review & editing, Validation, Investigation, Data curation. **Tanja Žuna Pfeiffer:** Writing – review & editing, Validation, Investigation, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.111929.

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