Cyanobacteria and Toxic Blooms in the Great Mazurian Lakes System: Biodiversity and Toxicity

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Abstract The Great Mazurian Lakes System (GMLS), located in the northeastern part of Poland, is an extremely valuable area in terms of natural environment value, tourism, and local economy. The system is divided into two parts – the northern meso-eutrophic and the southern eutrophic. GMLS are lakes with very high taxonomic diversity of phytoplankton, and cyanobacteria are very often predominant in the species composition and biomass. The presence of cyanobacteria belonging to 14 different families from the orders of *Nostocales*, *Oscillatoriales*, *Synechococcales*, and *Chroococcales* was recorded throughout the system. The GMLS has undergone significant changes over the recent decades which affected the taxonomic composition and dominant species of cyanobacteria. Particularly the southern part was subject to significant changes, from rapid eutrophication in the 1970s and 1980s, resulting in massive blooms of cyanobacteria, to a significant improvement in water quality in the 1990s and a reduction of cyanobacteria biomass. However, cyanobacteria are the dominant component of phytoplankton up to the present, although there are no dense blooms in recent years. Many of the cyanobacteria taxa in the GMLS can potentially produce toxins. Hepatotoxic microcystins are the most common cyanotoxins in freshwater, and in GMLS

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they sometimes reached significant concentrations in water. Studies have shown that the main producers of microcystins in GMLS are genera *Microcystis* and *Planktothrix*.

Keywords Bloom · Cyanobacteria · Cyanotoxins · GMLS · Microcystins

1 Introduction

Cyanobacteria are one of the first forms of life that appeared on Earth [1, 2]. They are prokaryotic microorganisms, single cells, or colony-forming (like large aggregates, filamentous forms). Most cyanobacteria are aerobic photoautotrophs, some of them may also be mixotrophic, under certain environmental conditions (e.g., with insufficient light intensity) [3]. All cyanobacterial cells contain photosynthetic dyes like chlorophyll$_a$ and phycocyanin from phycobiliproteins group, which make them have a blue-green color. In addition, the cell may also contain auxiliary dyes such as carotenoids and other phycobiliproteins, e.g., phycoerythrin or allophycocyanin [4].

Cyanobacteria can live in very diverse environments, even with extreme conditions such as hot springs [5], snow, or ice [6, 7], as well as places with very high salinity [8]. However, their main habitat is water, both freshwater and marine ecosystems.

Cyanobacteria have some adaptations and features, which under certain conditions allow them to win a competitive advantage with other phytoplanktonic microorganisms. Auxiliary photosynthetic dyes cause that cyanobacteria can use in photosynthesis green, yellow, and orange part of the sunlight spectrum (500–650 nm), which are rarely used by other phytoplankton organisms. This enables living in deeper parts of water bodies, in turbid water with a large biomass of phytoplankton or other factors limiting the availability of light [8, 9].

Aerotopes (gas "vacuums") are cylindrical structures in the cytoplasm, filled with gas, which allows the regulation of the vertical position of cells in the water column [10]. Thanks to this ability, cyanobacteria can accumulate at depths with the most favorable conditions, e.g., with the appropriate intensity of light and carbon dioxide or biogenic compound availability. Aerotopes also contribute to the formation of dense blooms, because they can keep cyanobacteria cells on the surface [11].

Atmospheric nitrogen fixation is another process favoring the dominance of some cyanobacterial species. Vegetative cells of genera such as *Aphanizomenon*, *Cylindrospermopsis*, *Dolichospermum* (formerly *Anabaena*), *Nodularia*, or *Nostoc* can develop heterocysts in which molecular nitrogen (N_2) is reduced directly to ammonium nitrogen (NH_4^+) using the nitrogenase enzyme. In addition, the low ratio of nitrogen to phosphorus in water favors the development of cyanobacteria. The optimal ratio of TN/TP (total nitrogen to total phosphorus) for eukaryotic phytoplankton microorganisms is 16–23:1, while for cyanobacterial strains, it is 10–16:1 [12].

Cyanobacteria are also more resistant to zooplankton feeding than other phytoplankton microorganisms. Filamentous cyanobacteria (e.g., *Planktothrix* spp.) can clog the filtration apparatus of many species of zooplankton animals and thus reduce their efficiency of food intake [13, 14]. In addition, the nutritional value of cyanobacteria cells is low, due to the low content of unsaturated fatty acids [15].

On the other hand, there are several aspects in which cyanobacteria lose the competition with eukaryotic phytoplankton. Primarily the growth rate of cyanobacteria is usually much lower than in eukaryotic algae [16]. Slow growth rates require long water retention times to reach significant cell numbers. Therefore, cyanobacteria do not form blooms in flowing water, such as rivers.

The biomass and taxonomic structure of phytoplankton in water depend on the concentration of key biogenic elements, primarily nitrogen and phosphorus. At high concentrations of biogenic elements, the phytoplankton biomass increases, but also its biodiversity decreases. Species composition is dominated by cyanobacteria, especially large filamentous taxa such as *Aphanizomenon*, *Dolichospermum*, *Limnothrix*, *Microcystis*, or *Planktothrix* [17]. Advanced eutrophication is therefore closely related to the dominance of cyanobacteria in water [17, 18] and may eventually lead to the occurrence of mass cyanobacterial blooms, which are highly dangerous due to the possibility of release of cyanotoxins into the water.

The second most important factor, promoting the dominance of cyanobacteria is the elevated temperature. Cyanobacteria reach the maximum growth rate at a temperature higher than optimal temperatures for other phytoplankton species [19]. Global warming causes earlier stratification and later destratification of lakes in a temperate climate, which extends the period with optimal conditions for the development of cyanobacteria [11]. Climate change also significantly contributes to expanding the geographical coverage of some taxa. *Cylindrospermopsis raciborskii* was initially described as a species occurring in tropical or subtropical regions, but now is already widespread in lakes in northern Germany [20], and also appears in some Polish lakes [21]. Along with the predicted further climate warming [22, 23], cyanobacteria and the toxic blooms will become an increasingly important global environmental problem [24].

Cyanobacteria produce many metabolites that can be dangerous to animals and humans. Cyanotoxins are produced by a wide spectrum of cyanobacterial species, marine or freshwater, both colony and filamentous forms. Toxins produced by cyanobacteria are usually classified due to their effect on mammalian organisms, and there are three main groups distinguished: hepatotoxins (cyclic peptides, such as microcystins or nodularins, and alkaloids such as cylindrospermopsins), neurotoxins (e.g., anatoxin-a, saxitoxin, BMAA), and dermatotoxins (e.g., aplysiatoxin, lyngbyatoxin) [25]. The most widespread and most common type of cyanotoxins in freshwater ecosystems are hepatotoxic microcystins. These are cyclic heptapeptides which can be produced by many genera, e.g., *Aphanizomenon*, *Dolichospermum*, *Microcystis*, *Nostoc*, *Phormidium*, *Planktothrix*, *Pseudanabaena*, *Synechococcus*, and *Synechocystis* [8, 25–27]. Toxicity of microcystins for animal cells is associated with inhibition of the key cellular enzymes – protein phosphatases [25]. Microcystins are synthesized non-ribosomally by large enzymatic complexes, encoded by the *mcy* gene cluster. In cyanobacteria population toxic and nontoxic strains of one species can coexist, so the percentage of toxigenic cells indicates whether the bloom, if occur, will be toxic.

The Great Mazurian Lakes System (GMLS), which is part of the Mazurian Lake District, is located in the northeastern part of Poland (Fig. 1).

It is an extremely valuable area in terms of natural environment value as well as for the local fisheries economy. However, the basis of the region's economy is tourism. In recent years, over one million people visit Mazurian Lake District annually (Statistics Poland data for 2016). The GMLS includes glacial origin lakes of different size and depth, connected naturally or with channels built in the nineteenth century. This region was formed around 10–15 thousand years ago during the Baltic glaciation [28].

The system is divided into two parts – the northern meso-eutrophic part, which includes the lakes Mamry (with a bay called Przystań Lake), Dargin, Łabap, and Kisajno, and the southern eutrophic part covering the lakes Niegocin, Boczne, Jagodne, Szymoneckie, Szymon, Tałtowisko, Ryńskie, Tałty, Mikołajskie, Bełdany, and Śniardwy (Fig. 1). The watershed is located around the Giżycki Canal and Lake Kisajno [29], although its location may be changeable [30]. The Pisa River is the

Fig. 1 Map of the Great Mazurian Lakes System area. The numbers indicate the lakes described in this chapter: 1, Przystań; 2, Mamry; 3, Kirsajty; 4, Dargin; 5, Łabap; 6, Kisajno; 7, Niegocin; 8, Boczne; 9, Jagodne; 10, Szymoneckie; 11, Szymon; 12, Tałtowisko; 13, Ryńskie; 14, Tałty; 15, Mikołajskie; 16, Bełdany; 17, Śniardwy

main outflow from the southern part of the GMLS; it flows into the Narew River, which connects with the Vistula River through the Zegrze Reservoir. Northern part belongs to the Pregoła catchment. Both parts of the GMLS substantially differ in anthropopressure level. Northern part of catchment basin is much less populated, while in the southern part, more towns, villages, and tourist centers are located.

In the species composition and biomass of phytoplankton in the GMLS, cyanobacteria are very often predominant [31, 32]. There is also a very high taxonomic diversity of cyanobacteria, morphologically different species appear, and many of them can also potentially produce toxins.

2 Biodiversity of Cyanobacteria in the Great Mazurian Lakes System

GMLS are lakes with very high taxonomic diversity of cyanobacteria (Table 1). The collected data from publications available from the 1970s allowed to state that the presence of cyanobacteria belonging to the orders of *Nostocales*, *Oscillatoriales*, *Synechococcales*, and *Chroococcales* was recorded throughout the system [31, 33–43]. Literature data indicate that cyanobacteria in GMLS belong to 14 different families and 26 genera (Table 1). It should be noted that the taxonomic classification of cyanobacteria and some species names have been changing over the years, and in this report, they are given according to the present arrangements (Algae.Base.org) [44].

Over the years, changes in the taxonomic composition and dominant species of cyanobacteria in the phytoplankton of Mazurian Lakes have been observed. They were different depending on the lake, its trophic state, surrounding area, or external conditions. Although all the lakes in the system are connected, the abundance of cyanobacteria can be very different, especially between the lakes of the northern and southern parts. The GMLS has undergone significant changes over the past few decades. In 1970s and 1980s, very fast eutrophication processes were observed, mainly in the southern lakes. The main reasons were bad agricultural practices (such as overfertilization and lack of vegetative riparian buffers around lakes), draining sewage to the lakes from urban areas and industry, as well as increasing tourism [45]. This had a devastating effect on the GMLS ecosystem, causing frequent and massive cyanobacterial blooms. The situation improved in the 1990s, when agriculture started to be less ecologically damaging, for example, the use of fertilizers decreased significantly [45]. The modernization of wastewater treatment plants in the region (e.g., in Giżycko) also contributed to the improvement. After modernization favorable changes were observed quickly in Lake Niegocin – a decrease in biomass of cyanobacteria and the dominance of other phytoplankton species [38]. This tendency, when cyanobacteria did not dominate in phytoplankton, remained only for a few years [38]. However, from that time to present, no dense, surface blooms are observed in GMLS, and the biomass of phytoplankton does not usually exceed 8 mg L^{-1}, which is considered a threshold limit for algal blooms.

Table 1 All species of cyanobacteria observed in the Great Mazurian Lakes System from the 1970s to present

Order	Family	Species
Nostocales	*Aphanizomenonaceae*	*Anabaenopsis* sp.
		Aphanizomenon flos-aquae
		Aphanizomenon gracile
		Aphanizomenon skujae
		Aphanizomenon yezoense
		Cuspidothrix issatschenkoi
		Dolichospermum sp.
		Dolichospermum affine
		Dolichospermum flos-aquae
		Dolichospermum lemmermanii
		Dolichospermum planctonica
		Dolichospermum spiroides
	Gloeotrichiaceae	*Gloeotrichia echinulata*
Oscillatoriales	*Microcoleaceae*	*Planktothrix agardhii*
		Planktothrix agardhii var. suspensa
	Oscillatoriaceae	*Lyngbya* sp.
Synechococcales	*Pseudanabaenaceae*	*Limnothrix redekei*
		Pseudanabaena catenata
		Pseudanabaena limnetica
		Pseudanabaena mucicola
	Leptolyngbyaceae	*Leptolyngbya thermalis*
		Planktolyngbya limnetica
	Romeriaceae	*Romeria gracilis*
	Coelosphaeriaceae	*Coelosphaerium* spp.
		Snowella lacustris
		Snowella litoralis
		Woronichinia naegeliana
	Merismopediaceae	*Aphanocapsa* spp.
		Merismopedia spp.
	Synechococcaceae	*Cyanobium* sp.
		Cyanodictyon spp.
		Lemmermanniella pallida
		Rhabdoderma lineare
		Synechococcus sp.
Chroococcales	*Aphanothecaceae*	*Aphanothece* spp.
	Chroococcaceae	*Chroococcus* sp.
		Chroococcus minimus
		Chroococcus turgidus
	Gomphosphaeriaceae	*Gomphosphaeria* sp.

(continued)

Table 1 (continued)

Order	Family	Species
	Microcystaceae	*Microcystis aeruginosa*
		Microcystis flos-aquae
		Microcystis ichtyoblabe
		Microcystis smithii
		Microcystis viridis
		Microcystis wesenbergii

Based on literature data [31, 33–43]

Rapid changes in phytoplankton structure or changes in dominant species are observed in many lakes of the system. They may indicate a low stability of the ecosystem and its high susceptibility to changes caused by various factors, such as the availability of nutrients. Temperature is also an important factor – an example can be the exceptionally hot summer of 2010, when there was practically the total domination of cyanobacteria in the phytoplankton structure, in contrast to the next year, when the water temperature was on average 2.6°C lower, and the cyanobacteria in most lakes did not dominate [43, 45].

The most visible taxonomic change in recent years concerns practically the entire system. Despite incomplete historical data, it can be stated that by the end of the first decade of the twenty-first century, the dominant taxa in different lakes were changing, but most often they were cyanobacteria from the genera *Aphanizomenon*, *Dolichospermum*, *Microcystis*, and *Planktothrix* [33–39, 41]. In recent years, however, the domination in summer of *Pseudanabaena limnetica* is observed [31, 42, 43]. Previously this species never had such a large share in the taxonomic composition.

2.1 Northern Part

The northern part of GMLS has been much less eutrophicated in the last decades than the southern part of the system. Available historical data, mainly from Lake Mamry, indicate that in the 1960s, 1970s, and 1980s of the twentieth century, the biomass of phytoplankton in these lakes was usually low (e.g., 0.7–2 mg L^{-1} in July 1976) and cyanobacteria were not dominant component of phytoplankton [35, 46, 47]. In the summer months in 1986–1989, the biomass of phytoplankton in Lake Mamry was still low (0.1–1.5 mg L^{-1}), cyanobacteria accounted for about 20% of biomass, and the dominant groups were diatoms, cryptophytes, and dinoflagellates [36]. The exception in the northern part was Lake Kirsajty, the only small, shallow, and polymictic lake in this part, in which both in 1976 and in 1988, cyanobacteria predominated in the summer in the phytoplankton structure (Table 2). In 1988, they were mainly *Aphanizomenon gracile* and *Leptolyngbya thermalis* [35, 39]. Data from the 1990s and the first decade of the twenty-first century are unfortunately very limited. However, research conducted in Lake Mamry

Table 2 The dominance of cyanobacteria (defined as >50% of the phytoplankton biomass) in the northern part of the Great Mazurian Lakes System in the last few decades and dominant taxa (if available)

Period	Lakes						References
	Przystań	Mamry	Kirsajty	Dargin	Łabap	Kisajno	
1960s, 1970s	nd	–	nd	nd	nd	nd	[36]
Summer 1976	nd	nd	+	nd	nd	nd	[35]
Summer 1986	nd	–	–	nd	nd	nd	[36, 39]
Summer 1987	nd	–	–	nd	nd	nd	[36, 39]
Summer 1988	nd	–	+ *Ag* *Lt*	nd	nd	nd	[36, 39]
Summer 1989	nd	–	nd	nd	nd	nd	[36]
Summer 2000	nd	+	+ *Lr* *Ag* *Lt*	nd	nd	nd	[36, 39]
Summer 2001	nd	+	+ *Ma* *Lt*	nd	nd	nd	[36, 39]
Summer 2010	+ *Psl*	+ *Psl*	nd	+ *Psl*	+ *Ge* *Ag*	–	[43]
Summer 2011	+ *Psl*	+ *Psl*	nd	–	–	–	[43]
Summer 2012	nd	+	nd	nd	nd	+	[42]

Based on literature data [35, 36, 39, 42, 43]
+ cyanobacteria predominate in phytoplankton biomass, – cyanobacteria do not dominate in phytoplankton biomass, *nd* no data, *Ag Aphanizomenon gracile*, *Ge Gloeotrichia echinulata*, *Lr Limnothrix redekei*, *Lt Leptolyngbya thermalis*, *Ma Microcystis aeruginosa*, *Psl Pseudanabaena limnetica*

in 2000 and 2001 indicates that there has been a significant change in the structure of phytoplankton in this lake. The total biomass of phytoplankton in these years was about two times higher than at the end of the 1980s, and the share of cyanobacteria (mainly *Microcystis aeruginosa*, *Aphanizomenon flos-aquae*, *Limnothrix redekei*, and *Leptolyngbya thermalis*) in the summer reached even 80% biomass [36]. In these years, surface blooms of *Gloeotrichia echinulata* were also observed [36]. Lake Kirsajty was studied in the same years and cyanobacteria predominated there and also the summer phytoplankton. In August 2000 the dominant species were *Limnothrix redekei*, *Aphanizomenon gracile*, and *Leptolyngbya thermalis*, in August 2001 *Microcystis aeruginosa*, and in September 2001 *Microcystis aeruginosa* and *Leptolyngbya thermalis* (Table 2) [39].

Studies concerning a larger number of lakes from the northern part were conducted in 2010 and 2011 on Przystań, Mamry, Dargin, Łabap, and Kisajno lakes (Table 2) [43]. In the summer months, the biomass of cyanobacteria reached high values only in Lake Łabap (average 12.8 mg L^{-1}), while in the other lakes, it did not exceed 2 mg L^{-1}. Cyanobacteria usually dominated in the phytoplankton during the summer months, especially in August, often reaching over 90%. One exception was the Lake Kisajno, in which in these 2 years, there was no dominance of cyanobacteria. At that time, there was a change in the taxonomic structure of cyanobacteria in comparison to previously analyzed periods. The most frequently dominant species was *Pseudanabaena limnetica*, which reached even about 90% share in the biomass of cyanobacteria in Przystań and Mamry lakes. The dominance of this species is a significant change compared to previous studies that have never shown a large biomass of this taxon in the northern lakes before. In addition to *Pseudanabaena limnetica*, in Lake Łabap in the summer of 2010, higher numbers also reached *Gloeotrichia echinulata* and *Aphanizomenon gracile* [43].

The most recent studies on the composition of phytoplankton in the northern lakes concern years 2011–2013, when the lakes Mamry and Kisajno were studied (Table 2) [42]. The average share of cyanobacteria in the total phytoplankton biomass was 43–44% in the summer months, and the maximum value was 83% in Lake Kisajno in July 2012. Lake Kisajno, in which in 2010 and 2011 there was no dominance of cyanobacteria, in 2012 completely changed the structure of phytoplankton. In 2012 and 2013, the most dominant species in the northern lakes was still *Pseudanabaena limnetica* [42].

2.2 Southern Part

The southern part of the GMLS differs significantly in trophic status from the northern part. While the northern lakes are mainly classified into meso-eutrophy, southern lakes in the last decades were defined as eutrophic or sometimes even hypereutrophic [43, 45, 48]. For this reason, the abundance and taxonomic structure of cyanobacteria in these lakes differs from those of the northern part.

Already in the 1970s and 1980s, it was reported that the biomass of phytoplankton often exceeded 8 mg L^{-1}, which is a characteristic value for eutrophic lakes [34, 35, 38, 49]. However, historical data on the taxonomic composition of cyanobacteria in these lakes are quite limited. The report by Chróst [33] describing Lake Mikołajskie indicates that in the early autumn of 1972 and 1973, cyanobacteria dominated the phytoplankton. *Microcystis aeruginosa*, *Microcystis wesenbergii*, and *Dolichospermum flos-aquae* reached the highest numbers, and *Aphanizomenon flos-aquae* also appeared in smaller quantities. Data from Lake Niegocin show that in the 1970s and 1980s, summer phytoplankton was dominated by filamentous species, mainly *Planktothrix agardhii* and *Aphanizomenon flos-aquae* [38].

Available data from the last decade of the twentieth century mainly concern Lake Niegocin (Table 3). Changes in the biomass of phytoplankton and its taxonomic composition during this period were largely related to the modernization of the wastewater treatment plant, from which sewage was discharged into the lake. Before the modernization, until 1994, the biomass of phytoplankton reached even 8.2 mg L^{-1}, while after this process, in the years 1995–1999, it never exceeded 2.9 mg L^{-1} [38]. Until 1995, cyanobacteria most often dominated in the summer and autumn phytoplankton, reaching even 96% of biomass. The dominant species were

Table 3 The dominance of cyanobacteria (defined as >50% of the phytoplankton biomass) in the southern part of the Great Mazurian Lakes System in the last few decades and dominant taxa (if available)

Period	Lakes											References
	1	2	3	4	5	6	7	8	9	10	11	
1970s–1980s	+ *Pa* *Afa*	nd	nd	nd	nd	nd	nd	nd	+ *Dfa* *Ma* *Mw*	nd	nd	[33, 38]
S 1991	+ *Pa*	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	[38]
S-A 1992	+ *Pa* *Afa* *Lt*	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	[38]
S-A 1993	+ *Pa* *Afa*	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	[38]
A 1994	+	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	[38]
S-A 1995	+ *Dfa* *Pa* *Lt*	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	[38]
S-A 1996	–	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	[38]
S 1997	–	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	[38]
A 1998	–	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	[38]
S-A 1999	+ *Asp* *Dsp* *Lsp*	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	[38]
S-A 2000	–	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	[38]
S-A 2001	+ *Asp* *Dsp* *Lp*	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	[38]
S 2002	nd	nd	+ *Pa*	+ *Pll* *Lr* *Asp*	+ *As* *Lr*	+ *Afa* *Ag* *Pa* *Psl*	nd	nd	nd	nd	nd	[37]
S 2007	+ *Ma*	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	[41]

(continued)

Table 3 (continued)

Period	Lakes											References
	1	2	3	4	5	6	7	8	9	10	11	
S 2010	+ *Ag*	+ *Ma*	+ *Psl*	+ *Psl*	+ *Psl*	+ *Psl*	+ *Psl*	+ *Psl* *Ge*	+ *Psl*	+ *Ag* *Psl*	+ *Psl*	[43]
S 2011	–	–	–	–	+ *Ag*	–	+ *Psl*	+ *Psl*	–	–	+ *Psl*	[43]
S 2012	–	nd	nd	nd	+	+	nd	+	+	+	+	[42]

Based on literature data [33, 37, 38, 41–43]

Lakes (numbers according to Fig. 1): 7, Niegocin; 8, Boczne; 9, Jagodne; 10, Szymoneckie; 11, Szymon; 12, Tałtowisko; 13, Ryńskie; 14, Tałty; 15, Mikołajskie; 16, Bełdany; 17, Śniardwy. S, summer; A, autumn; S-A, summer-autumn

+ cyanobacteria predominate in phytoplankton biomass, – cyanobacteria do not dominate in phytoplankton biomass, *nd* no data. *Afa*, *Aphanizomenon flos-aquae*; *Ag*, *Aphanizomenon gracile*; *As*, *Aphanizomenon skujae*; A_{sp}, *Aphanizomenon* sp.; *Dfa*, *Dolichospermum flos-aquae*; D_{sp}, *Dolichospermum* sp.; *Ge*, *Gloeotrichia echinulata*; *Lt*, *Leptolyngbya thermalis*; L_{sp}., *Leptolyngbya* sp.; *Lr*, *Limnothrix redekei*; *Ma*, *Microcystis aeruginosa*; *Mw*, *Microcystis wesenbergii*; *Pll*, *Planktolyngbya limnetica*; *Pa*, *Planktothrix agardhii*; *Psl*, *Pseudanabaena limnetica*

filamentous *Planktothrix agardhii*, *Aphanizomenon flos-aquae*, and *Leptolyngbya thermalis*. Since 1996 in summer more often occurs the dominance of dinoflagellates or the codominance of dinoflagellates-cyanobacteria. In autumn the domination of diatoms has been more frequent [38]. At the turn of the century, the situation in the Lake Niegocin again began to change (Table 3). Already in 1999 there was a re-dominance of cyanobacteria in the summer, mainly of the genera *Aphanizomenon*, *Dolichospermum*, and *Leptolyngbya*. In the next 2 years, the increase of phytoplankton biomass to a similar level as before the modernization of the sewage treatment plant was observed, and the predominant taxa of cyanobacteria were *Aphanizomenon* sp., *Dolichospermum* sp., *Leptolyngbya* sp., as well as *Microcystis aeruginosa* [38]. Further studies of cyanobacteria in Lake Niegocin were made in the summer of 2007 and confirmed their domination in phytoplankton biomass (over 90%) [41]. Analysis at that time showed a large taxonomic diversity of cyanobacteria, but the dominant species was *Microcystis aeruginosa*. Besides this species, cyanobacteria from the genera *Chroococcus*, *Aphanizomenon*, *Dolichospermum*, and *Planktolyngbya* also occurred in significant numbers [41].

Four lakes of the southern part of the GMLS (Jagodne, Szymoneckie, Szymon, and Tałtowisko) were examined for biomass and taxonomic composition of phytoplankton in the summer of 2002 [37]. In all lakes, cyanobacteria predominated, reaching 53.5% (Tałtowisko) to over 92% (Jagodne, Szymoneckie) of phytoplankton biomass. In lakes Jagodne and Szymoneckie, cyanobacteria reached at that time a very high biomass, 9.8 and 15.5 mg L^{-1}, respectively. The taxonomic composition was dominated by filamentous genera, primarily *Planktothrix*, *Planktolyngbya*, *Limnothrix*, *Aphanizomenon*, and *Pseudanabaena* spp. (Table 3).

Extensive analysis of biomass and diversity of cyanobacteria in the southern part of GMLS in 2009–2011 is described by Siuda et al. [43]. There were 11 lakes studied – Niegocin, Boczne, Jagodne, Szymoneckie, Szymon, Tałtowisko, Ryńskie, Tałty, Mikołajskie, Bełdany, and Śniardwy. The average summer biomass of cyanobacteria in these years was very different in individual lakes and ranged from 0.7 mg L^{-1} in Lake Niegocin to almost 11 mg L^{-1} in Lake Tałty. The dominance of cyanobacteria in the phytoplankton composition was visible primarily in the summer of 2010, when they accounted for 75–100% of the phytoplankton biomass in almost all lakes, except for lakes Niegocin and Boczne (Table 3). The predominant species of cyanobacteria was the filamentous *Pseudanabaena limnetica*, which dominated almost all lakes, again with the exception of lakes Niegocin and Boczne, where *Aphanizomenon gracile* and *Microcystis aeruginosa* were predominantly observed. In the summer of 2011, cyanobacteria were less abundant, and their share in the phytoplankton biomass did not exceed 70%, with the exception of Lake Śniardwy. The dominance of cyanobacteria was not observed in lakes Niegocin, Boczne, Jagodne, Szymoneckie, Tałtowisko, Mikołajskie, and Bełdany (Table 3). Again, the most frequently occurring species was *Pseudanabaena limnetica*, although the dominance of *Aphanizomenon gracile* was observed in Lake Szymon [43].

The latest study on six southern lakes (Niegocin, Tałtowisko, Tałty, Mikołajskie, Bełdany, Śniardwy) shows that the average summer biomass of phytoplankton in 2011–2013 did not exceed 6 mg L^{-1} in any of the lakes, and the average share of cyanobacteria in phytoplankton was 16–57% [42]. In the summer of 2012, the highest share of cyanobacteria was recorded in Lake Tałtowisko (82%). Again, the most common taxa were *Pseudanabaena limnetica*, but *Planktolyngbya limnetica*, *Limnothrix redekei*, *Planktothrix agardhii*, and *Planktothrix agardhii* var. suspensa also appeared sometimes in large numbers (Table 3).

3 Toxic Cyanobacteria in the Great Mazurian Lakes System

Most of the data about cyanobacterial toxins in GMLS is related to hepatotoxic microcystins, which are the most common cyanotoxins in freshwaters. The first study on microcystin concentration was carried out in 2002 on the lakes Jagodne, Szymoneckie, Szymon, and Tałtowisko [37]. The HPLC analysis showed quite high toxin concentrations, 4.8–12.1 μg L^{-1}, while the safe limit value for recreational waters is 5 μg L^{-1} according to the World Health Organization [50]. The highest concentration was recorded in Lake Szymoneckie, and the detected variants of microcystins were dmMC-RR (desmethyl-RR), MC-YR, and MC-LR [37].

In the summer of 2007, concentration of microcystins was analyzed in Lake Niegocin [41]. The highest concentration was noted at the beginning of September;

however, it was much lower than in the lakes analyzed in 2002 (<0.2 μg L^{-1}). The microcystin variants detected during these studies were MC-LR, MC-RR, and MC-YR.

Subsequent analyses of the microcystin concentration in the GMLS were conducted from spring to autumn in 2012 and 2013 and concerned with both lakes of the northern (Mamry, Kisajno) and southern part (Niegocin, Tałtowisko, Ryńskie, Tałty, Mikołajskie, Bełdany, Śniardwy) [42]. Also, in these years, the concentration in water was low (0–0.3 μg L^{-1} in 2012 and 0–0.6 μg L^{-1} in 2013). Microcystins were practically not detected in Lake Mamry (except one sample in which the concentration was 0.1 μg L^{-1}), while the highest concentration was recorded in Lake Ryńskie. In addition to the dissolved microcystin, the total concentration of microcystins (together dissolved in water and present in cyanobacteria cells) was also tested. This analysis showed that the total concentration of microcystins may be 2–20 times higher than dissolved microcystins. The highest total concentration was recorded in September 2013 in Lake Mikołajskie (2.1 μg L^{-1}). In 2012 and 2013, seven variants of microcystin were detected in GMLS, the most common was demethylated variant [Asp3]MC-RR [42].

Because in the population of one cyanobacteria species, both toxic and nontoxic strains can occur, and toxic and nontoxic cells cannot be distinguished by microscopic methods, until recently it was not known which taxa in GMLS are responsible for the production of toxins. Among many taxa occurring in the Mazurian Lakes, microcystins can produce the genera *Anabaenopsis*, *Aphanizomenon*, *Aphanocapsa*, *Dolichospermum*, *Limnothrix*, *Microcystis*, *Planktothrix*, *Pseudanabaena*, *Snowella*, *Synechococcus*, and *Woronichinia* [8, 24, 51–56]. However, only the molecular methods allow to determine which of them actually have genes responsible for toxin production. In the summer and early autumn of 2011, *mcy*A gene sequences from four lakes were obtained (Mamry, Tałtowisko, Mikołajskie, Bełdany). Sequences showed that in Lake Mamry toxicity genes belong to cyanobacteria from genus *Microcystis* while in the other three lakes to the *Planktothrix* genus [31].

In the publication from Bukowska et al. [42], it was found that the *mcy*A, *mcy*D, and *mcy*E genes, responsible for microcystin production, occur in all lakes studied in 2012 and 2013 (Mamry, Kisajno, Niegocin, Tałtowisko, Ryńskie, Tałty, Mikołajskie, Bełdany, and Śniardwy). In the whole GMLS, the main producers of microcystins were genera *Planktothrix* and *Microcystis*, which at that time were not the dominant taxa in the biomass of cyanobacteria. The participation of toxic cells in the populations of these genera was also investigated by real-time PCR method. In the case of *Planktothrix*, in all samples almost the entire population consisted of toxic cells (75–100%), and the highest average share was recorded in Lake Mikołajskie (95%). It was different in the case of *Microcystis* – there was a very large variation in the proportion of toxic cells between samples (0–100%). The highest average share was recorded in Lake Mamry (21%) and the lowest in Lake Mikołajskie (0.2%). The proportion of *Microcystis* cells in the population was also variable over time; no seasonal pattern was observed [42].

There are no studies on the presence of cyanotoxins other than microcystins in the GMLS. One of the harmful toxins is cylindrospermopsin, also classified as hepatotoxin. One of its producers – *Cylindrospermopsis raciborskii* – is quite rapidly spreading in temperate climate lakes, although it was recently considered as a tropical or subtropical species [20]. Studies conducted in the summer of 2014 did not show the presence of this species in Mazurian Lakes [57]. However, cylindrospermopsins may be also produced by other genera (e.g., *Aphanizomenon*, *Dolichospermum*, *Planktothrix*), which are sometimes present in the GMLS in large numbers; thus they can potentially be dangerous [8, 24, 56, 58]. It is similar with neurotoxins such as anatoxin-a or saxitoxin, which potential producers are also cyanobacteria found in the GMLS (*Aphanizomenon*, *Cuspidothrix*, *Dolichospermum*, *Planktothrix*) [26, 58–60].

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