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RESEARCH ARTICLE

Changes in the quantitative relations of the phytoplankton in heated lakes

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Abstract. Long-term changes in phytoplankton biomass and structure were studied in three heated lakes that were included into a power plant cooling system in 1958 and 1970. Since the mid 1990s, the share of *Vallisneria spiralis* L., which is a thermophilic hydrophyte species that is alien to Poland, has been increasing. The phytoplankton biomass fluctuated in these basins in the 1992-2003 period from 0.2 to 49.3 mg dm^{-3}. Two phytoplankton assemblages were noted: one was typical of the cold season and the other of the warm season. The phytoplankton in the summer comprised cyanophytes, chlorophytes, dinoflagellates, and cryptophytes. Diatoms developed on a massive scale during cold periods. The results obtained indicate that the contemporary phytoplankton assemblages are shaped by the varied impact of water heating, increased flow rates, the highly productive waters, and the developing submerged hydrophyte phytocenosis along with the abundant growth of the epiphyte assemblage.

Keywords: algae, environmental monitoring, long-term succession, thermal pollution

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Introduction

This system of natural lakes, which is connected by canals and receives heated-water discharge from two power plants, is a unique subject for ecological studies. The discharged water heats the lakes substantially, contributes to the formation of specific spatial variation in temperature, and increases water movement considerably (Simm 1988, Zdanowski et al. 1988, Zdanowski and Prusik 1994, Socha 1997b, Socha and Zdanowski 2001, Stawecki et al. 2008). A phenomenon unique to the temperate zone that was observed in the heated lakes was the lengthening of the vegetative season to nearly the whole year, which caused substantial changes in the faunistic ratios and phytoplankton abundance (Dąmbska et al. 1976, Burchardt 1977, Spodniewska 1984, Sosnowska 1987, Simm 1988, Zdanowski 1994a, Socha 1994a, 1994b, Socha 1997a, 1997b, Socha and Zdanowski 2001). The most significant changes were observed in the winter, when the biomass of the varied phytoplankton species sometimes even with maximum development of nanoplanktonic diatoms, was decidedly higher than in lakes with ice cover.

According to Sosnowska (1987), adaptation to the new environmental conditions happened within the course of one year; however, Simm (1988) and Socha and Zdanowski (2001) contend that the impact of the rapid heating of the lake waters (to a maximum of 35°C) happened gradually during the first decade when the cooling system was functioning. This manifested in the tendency for intense planktonic alga development, short-term water blooms (maximum biomass to 210 mg dm^{-3}), and the accelerated tempo of seasonal changes in phytoplankton. Diatoms, which achieved maximum biomass in the cooler periods, dominated throughout the season (Dąmbska et al. 1976, Burchardt 1977, Spodniewska 1984, Sosnowska 1987). By the late 1970s and early 1980s, the influence of heating was counterbalanced by progressing nutrient depletion in the heated lakes (Hillbricht-Ilkowska and Simm 1988, Zdanowski et al. 1988, Zdanowski 1994b) and the intense water flow (Simm 1988, Zdanowski et al. 1988). The composition of the summer phytoplankton became homogeneous while simultaneously becoming similar in character to that in temperate zone eutrophic rivers. The biomass of planktonic alga decreased, no water blooms were noted, and there was no distinct dominant as the phytoplankton comprised various systematic groups (Simm 1988). As the eutrophic status of the lakes in the cooling system increased during the 1987-1993 period, the biomass of planktonic alga increased, long-term diatom biomass maxima occurred in the spring season, and the cyanophyte and chlorophyte alga biomass increased in the summer seasons (Socha 1994a, 1994b, Socha 1997a, 1997b). Lower values of phytoplankton biomass were noted again in the 1995-1999 period, most notably in the intensively heated Pątnowskie and Licheńskie lakes (Socha and Zdanowski 2001).

Vallisneria spiralis L., a thermophilic hydrophyte species with submerged leaves that is new to Polish flora, was noted in the heated lakes system. It overtook the phytolitoral zone in Lake Licheńskie, and much of the same in Lake Pątnowskie (Socha 1998, Hutorowicz 2006); both of these lakes are heated throughout the year. Single, small stands formed by this plant were noted in Lake Ślesińskie in 2002 (Hutorowicz et al. 2006).

Phytoplankton is regarded as a sensitive indicator of changes occurring in aquatic ecosystems (Reynolds 1980, Burchardt et al. 1994). Detailed analysis of changes in the abundance and frequency of particular taxa that comprise assemblages confirms their significance as indicators, especially with regard to changes in the trophic status of lakes (Burchardt et al. 1994, Hutorowicz and Napiórkowska-Krzebietke 2007). Phytoplankton has also been confirmed to be a very sensitive indicator of changes in the artificially heated Konin lakes (Dąmbska et al. 1976, Burchardt 1977, Spodniewska 1984, Sosnowska 1987, Simm 1988, Socha 1994a, 1994b, Socha 1997a, 1997b, Socha and Zdanowski 2001). The aim of the work was to compare the seasonal dynamics in biomass and seasonal changes in the phytoplankton structure in the 1992-1999 and 2000-2003 periods in three lakes that were heated to varying degrees. Of these three lakes, one exhibits distinct characteristics of a monomictic basin (Lake Licheńskie), which is mixing type that is typical of lakes in the sub-tropical zone, and one only receives heated water inputs in summer (Lake Ślesińskie).

Materials and methods

Study area

The Konin lakes are located in an urban area and comprise a group of five natural basins with varied morphology (Table 1). Lakes Gosławskie and Pątnowskie are large, shallow pond-like basins. Lakes Licheńskie, Wąsowsko-Mikorzyńskie, and Ślesińskie are trough basins with well-developed shorelines and different mean and maximum depths. Three of these lakes (Pątnowskie, Wąsowsko--Mikorzyńskie, Ślesińskie) comprise the central segment of the Ślesińskie Canal that connects the Warta River with Lake Gopło. Along with two other lakes, Gosławskie and Licheńskie, they comprise the cooling circuit for the Pątnów and Konin electric power plants. The Konin lakes are subjected to various anthropogenic pressures in addition to the electric power plants, including opencast mining (they are located in a depression pit and are recipients of post-mining waters), fisheries (pond and cages fish farming and commercial fisheries are conducted in the vicinity), tourism in various forms (the Warta-Gopło Canal tourist route, vacation resorts in

Table 1
Morphometric, hydrological, and thermal characteristics of the Konin lakes

Parameter	L. Gosławskie	L. Pątnowskie	L. Licheńskie	L. Mikorzyńskie	L. Ślesińskie
Area (ha)	454.5	282.6	147.6	251.8	152.3
Max. depth (m)	5.3	5.5	12.6	36.5	24.5
Mean depth (m)	3.0	2.6	4.5	11.5	7.6
Temperature in summer (°C)					
1965-1969[1]	20.4	24.7	27.4	21.2	20.8
1987-1992[1]	22.3	22.8	26.0	24.5	22.8
1995-1999	-		24.5	-	23.2
2000-2003	-		25.7	24.6[2]	23.3
Temperature in winnter (°C)					
1995-1999	-	-	7.5	-	4.3
2000-2003	-	-	6.6	-	4.9
Water retention 1999-2000 (days)	4-5	4-5	4-5	5-16	5-26

[1] accordind to Zdanowski and Prusik (1994)
[2] data from 2003 exclusively

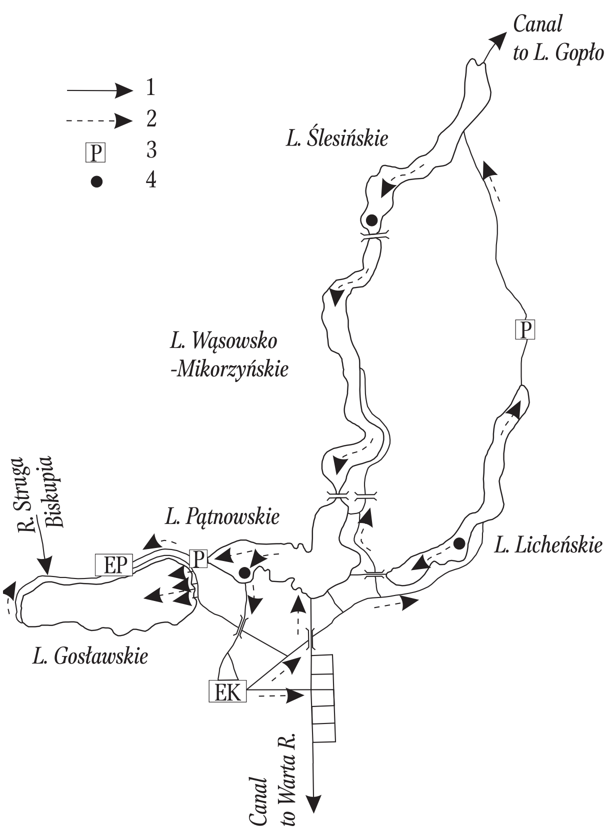

Figure 1. Map of the cooling systems of the Konin (EK) and Pątnów (EP) power plants. 1 – supply canals, 2 – direction of water flow, 3 – pumping stations (adapted from Hillbricht-Ilkowska and Zdanowski 1988).

Mikorzyn and Ślesin, the Sanctuary of Our Lady of Licheń).

Two different circulation circuits are used to cool the discharged heated waters from the power plants. The short circulation circuit is used in the cool season, and it includes lakes Gosławskie, Pątnowskie, Licheńskie and the southern part of Lake Wąsowsko-Mikorzyńskie (Fig. 1). During the summer season, the long circulation circuit is put into operation and includes Lake Ślesińskie and the northern part of Lake Wąsowsko-Mikorzyńskie. The lakes, which are connected by uptake and discharge canals (with a total combined length of 26 km), are a closed cooling system from the point of view of power plant exploitation. This method for cooling power plant waters increased the mean annual surface water temperature in Lake Licheńskie by about 5°C, and in Lake Ślesińskie by about 3°C (Table 1; Socha and Zdanowski 2001). Water retention times were also shortened. The trophic status of the Konin lakes has remained relatively stable. The total phosphorus concentration in the epilimnion of Lake Licheńskie in the 1995-2000 period ranged from 0.041 to 0.123 mg P_{Tot} dm^{-3}, and in the near-bottom layer it did not exceed 0.4 mg P_{Tot} dm^{-3}. In the second half of the 1990s, decreasing concentrations of nitrogen were noted in the waters of the epilimnion. In the 1995-1997 period, the mean nitrogen content in this layer in Lake Licheńskie was 1.59 mg N_{Tot} dm^{-3}, while in the 1998-2000 period, it was 1.13 mg N_{Tot} dm^{-3}. The decreases in the mean concentrations of nitrogen in the epilimnion of Lake Ślesińskie were analogous as they decreased from 1.30 mg N_{Tot} dm^{-3} in 1995-1997 to 1.13 mg N_{Tot} dm^{-3} in 1998-2000. In summer, nitrogen concentrations at the lake bottoms did not exceed 2.6 mg N_{Tot} dm^{-3} (Socha and Zdanowski 2001).

Phytoplankton studies

Phytoplankton samples were collected in the 1998-2003 period in the pelagic zone, in the epilimnion (in the 0-5 m layer) of lakes Pątnowskie, Licheńskie, and Ślesińskie. The samples were taken at times that are significant for the Konin system: in January and March when only the short circulation circuit is in operation; in May just after the long circulation circuit goes; in July when the power plants exploit both cooling circulation circuits (short and long); in September after the long circulation circuit is closed; and in November when only the short circulation circuit is functional.

Additionally, in May, July, and September of both 1998 and 1999, phytoplankton spatial differentiation studies were conducted in Lake Licheńskie, the most intensely heated of the basins (seven sampling stations were designated along the main water flow of the discharge waters) and at six stations in Lake Ślesińskie, the least heated basin.

The phytoplankton samples (volume of 1 dm^{-3}) were fixed immediately with Lugol's solution, and after being transported to the laboratory, they were concentrated through seston sedimentation to a volume of 2-5 cm^3. Quantitative and qualitative analyses of the phytoplankton were conducted in a Fuchs-Rozenthal chamber under a microscope at a magnification of 400x (Simm 1988). Fresh masses of algae were counted by multiplying the number of individual taxa by the volume of their chamber, which was calculated by comparing the shape of the algal cells to geometric figures (Pliński et al. 1984, Kawecka and Eloranta 1994). Randomly selected individuals of the dominant species from all the samples were measured. The nanoplankton fraction, comprising small organisms up to 30 μm, was identified. The phytosociological constancy for each species was (C) was determined in the samples collected throughout the year, in cooler periods (spring and fall) and summer using the Braun-Blanquet scale (Pawłowski 1959).

Some of the results obtained were published previously in Socha and Zdanowski (2001). Data from previous publications were used to describe long-term changes in phytoplankton structure and abundance (Sosnowska 1987, Spodniewska 1984, Simm 1988, Socha 1994a, 1994b, 1997a, 1997b, 1998, Socha and Zdanowski 2001).

Results

Phytoplankton biomass

In the 1992-2003 period the phytoplankton biomass in the Konin lakes changed within a very wide range from 0.2 mg dm^{-3} to a maximum of 29.5 mg dm^{-3} in Lake Pątnowskie, 46.7 mg dm^{-3} in Lake Ślesińskie, and 49.3 mg dm^{-3} in Lake Licheńskie. From 1992 to 1994, the mean total phytoplankton biomass in lakes Licheńskie, Ślesińskie, and Pątnowskie was about twice as high as that in the 1989-1991 period (Table 2). Similarly, the maximum values also increased in Lake Licheńskie by nearly 2.5 times, and in lakes Ślesińskie and Pątnowskie by about 1.5 times. In the 1995-1999 period, a similar tendency was maintained. While the mean algal plankton biomass was nearly twice as low in Lake Ślesińskie (5.6 mg dm^{-3}), and 1.5 times as low in Lake Pątnowskie (5.9 mg dm^{-3}), the maximum biomass in these three lakes was higher than it had been in the 1992-1994 period (Table 2). However, in the 2000-2003 period distinct decreases in the mean and maximum phytoplankton biomass were noted, as follows: in Lake Ślesińskim by 5.4 and 30.0 mg dm^{-3}; in Lake Pątnowskie to 4.9

Table 2
Overall phytoplankton biomass (annual means and ranges in mg dm^{-3}) in the Konin lakes in 1965-1984 (according to Sosnowska 1987, Spodniewska 1984, Simm 1988) and in 1987-2003 (according to Socha 1997a, 1997b, Socha and Zdanowski 2001, and current data)

Period	L. Gosławskie	L. Pątnowskie	L. Licheńskie	L. Mikorzyńskie	L. Ślesińskie
1965-1970			43.2	14.3	4.0[4]
			1.2-210.2	0.5-76.7	0.1-14.0
1977-1980	6.4		5.9	4.0	3.6
	3.9-10.2		2.4-12.0	0.9-11.7	0.6-7.2
1983-1984	1.3[1]		1.5[1]	1.8[1]	1.2[1]
	0.4-2.8		0.6-1.9	0.8-3.0	0.6-4.0
	3.0-11.0[2]				4.0-10.0[2]
1987-1988		2.0			
		0.1-15.3			
1989-1991	3.1	4.5	4.8		5.7
	0.2-14.8	0.4-18.7	0.4-17.9		0.2-24.0
1992-1994		7.6	9.4		10
		0.6-24.7	0.4-49.3		0.6-35.1
1995-1999	4.7[3]	5.9	4.2		5.6
	0.6-13.2	0.3-29.5	0.3-18.6		0.2-46.7
2000-2003		4.9	5.0	5.3[5]	5.4
		0.2-15.6	0.3-24.8	0.6-17.2	0.2-30.0

[1]summer season exclusively
[2]spring season
[3]1995-1996
[4]prior to connecting the lake to the cooling system
[5]data from 2003 exclusively

and 15.6 mg dm^{-3}, respectively. The tendencies of the changes in Lake Licheńskie were different. In the 1995-1999 period, the mean and maximum phytoplankton biomass values decreased more than twofold in comparison to the 1992-1994 period. These values were also distinctly lower than those from lakes Pątnowskie and Ślesińskie (Table 2). In subsequent years (2000-2003), contrary to the other two lakes, total and maximum biomass in Lake Licheńskie increased by 5.0 and 24.8 mg dm^{-3}, respectively.

The dynamics of the annual cycle of phytoplankton development also changed in the 1992-2003 period. Two biomass maxima with values exceeding 10 mg dm^{-3} were noted during the vegetative seasons from 1992 to 1994. In the subsequent period of 1995-1999, similarly high maxima (10 mg dm^{-3}) were noted in lakes Pątnowskie (Fig. 2) and Licheńskie (Fig. 3) only in spring (March), and in Lake Ślesińskie in September (Fig. 4). Two high phytoplankton biomass maxima (> 10 mg dm^{-3}) were again noted in Lake Licheńskie in the 2000-2003 period; the first was in the spring (March) and the second in early summer (June). A similar cycle of changes in plankton biomass was also observed in lakes Ślesińskie (summer peak < 10 mg dm^{-3}, in June) and Pątnowskie (summer peak < 10 mg dm^{-3}, in July). Spring biomass maxima formed at water temperatures within the range of 3.7-5.8°C in Lake Ślesińskie and at the range of 6.0-12.3°C in lakes Pątnowskie and Licheńskie.

During the cool period (November, January), when the overall biomass of the phytoplankton in all three lakes studied was about 1.0 mg dm^{-3},

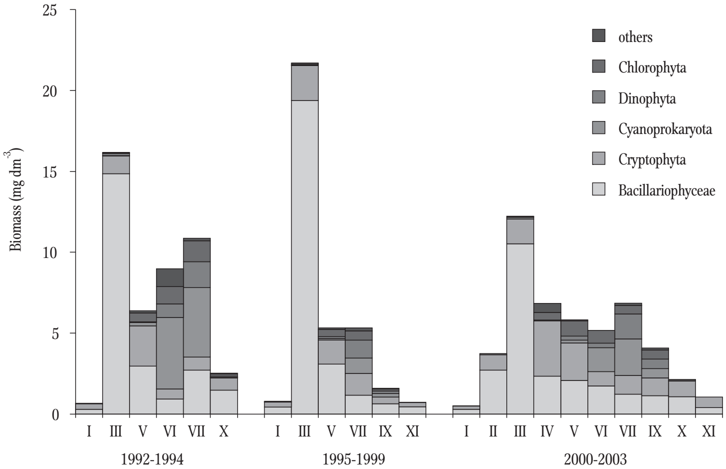

Figure 2. Phytoplankton biomass in Lake Pątnowskie in 1992-1994, 1995-1999 (according to Socha and Zdanowski 2001), and 2000-2003 (current data).

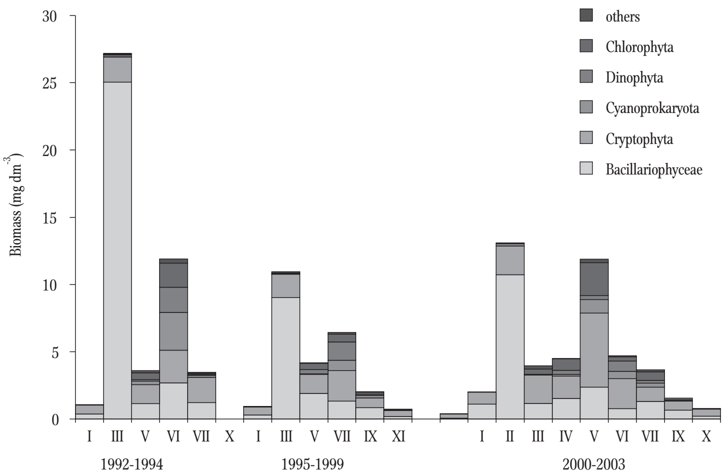

Figure 3. Phytoplankton biomass in Lake Licheńskie in 1992-1994, 1995-1999 (according to Socha and Zdanowski 2001), and 2000-2003 (current data).

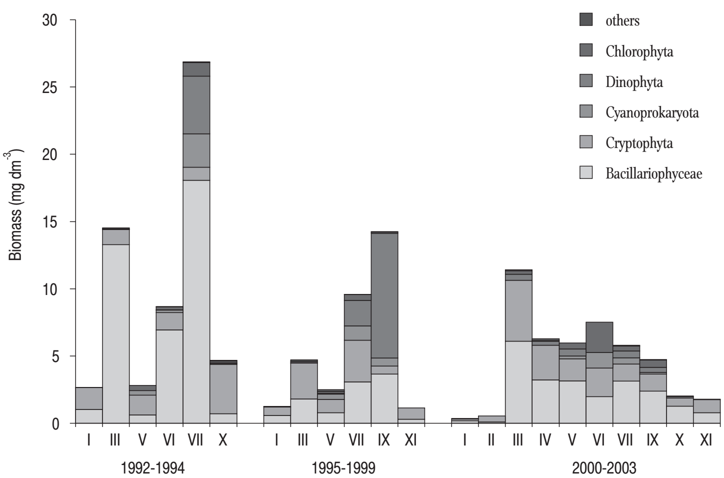

Figure 4. Phytoplankton biomass in Lake Ślesińskie in 1992-1994, 1995-1999 (according to Socha Zdanowski 2001), and in 2000-2003 (current data).

Table 3

Biomass (mean values and ranges) of species (in mg dm^{-3}) occurring with high constancy (C) throughout the year (Year), in cooler periods (Spring/Autumn), and in summer (Summer) in lakes Pątnowskie, Licheńskie, and Ślesińskie in the 1992-2003 period

		1992-1999						2000-2003					
		L. Pątnowskie		L. Licheńskie		L. Ślesińskie		L. Pątnowskie		L. Licheńskie		L. Ślesińskie	
		Biomass	C	Biomass	C	Biomass	C	Biomass	C	Biomass	C	Biomass	C
	Year	(n = 48)		(n = 48)		(n = 44)		(n = 30)		(n = 29)		(n = 36)	
k	*Cryptomonas erosa*	547 (22-3615)	V	832 (13-2740)	V	957 (40-6720)	V	1029 (10-6012)	V	1392 (30-7000)	V	1193 (31-5966)	V
k	*Rhodomonas minuta*	449 (77-2475)	V	418 (96-2120)	V	467 (20-2940)	V	314 (60-2080)	V	300 (12-2800)	V	540 (10-7300)	V
o	*Stephanodiscus hantzschii*	.		.		194 (11-856)	V	1340 (4-13623)	V	965 (10-5850)	V	306 (4-1650)	V
o	*Aulacoseira granulata*	.		.		.		319 (15-1300)	IV	379 (30-1665)	III	2403 (20-9600)	IV
z	*Scenedesmus quadricauda*	.		.		.		125 (4-615)	IV	113 (10-600)	V	89 (1-354)	III
s	*Chroococcus minor*	.		.		.		.		48 (3-300)	III	35 (2-200)	III
z	*Coelastrum microporum*	.		.		.		.		150 (20-412)	III	99 (20-400)	III
o	*Cyclotella* sp.	.		.		118 (20-220)	II	140 (12-384)	II	96 (3-234)	III	548 (5-2544)	II
z	*Scenedesmus spinosus*	.		.		.	.	.		31 (8-100)	III	48 (6-170)	II
b	*Peridinium* spp.	.		.		.	.	.		382 (10-2600)	III	206 (56-434)	I
z	*Tetrastrum staurogeniaeforme*	.		.		.	.	.		29 (5-150)	III	22 (5-100)	I
z	*Planktonema lauterbornii*	.		.		.	.	.		102 (8-300)	III	.	
	Spring/Autumn	(n = 27)		(n = 27)		(n = 23)		(n = 19)		(n = 18)		(n = 22)	
o	*Stephanodiscus hantzschii*	2643 (10-18090)	V	1188 (4-12810)	V	.		.		.		.	
o	*Stephanodiscus minutulus*	1622 (30-6740)	III	870 (20-4810)	III	309 (15-1510)	III	1830 (40-10800)	II	1865 (31-18280)	II	1190 (18-2680)	I
o	*Navicula tripunctata*	66 (10-170)	III	89 (6-240)	II	35 (30-40)	I	220 (30-600)	II	120 (100-140)	I	325 (50-600)	I
o	*Fragilaria ulna*	405 (70-1124)	II	264 (40-920)	III	173 (34-370)		224 (36-500)	II	199 (18-750)	II	.	
o	*Nitzschia kutzingiana*	74 (10-325)	III	.		.		.		.		.	
o	*Stephanodiscus neoastraea*	90 (90)	I	75 (75)	I	290 (25-1000)	III	120 (40-250)	I	.		1570 (10-15000)	II
o	*Asterionella formosa*	.		38 (5-120)	II	48 (1-166)	III	34 (10-70)	II	35 (10-132)	II	199 (7-1200)	II
	Summer	(n = 21)		(n = 21)		(n = 21)		(n = 11)		(n = 11)		(n = 14)	
b	*Ceratium hirundinella*	1207 (500-2120)	V	140 (140)	I	5513 (130-42680)	II	1355 (500-2000)	I	230 (230)	I	690 (100-1200)	I
z	*Scenedesmus quadricauda*	34 (4-190)	IV	47 (4-142)	IV	26 (4-127)	IV	.		.		.	
o	*Aulacoseira granulata*	423 (24-1835)	II	209 (10-940)	III	1409 (10-11840)	IV	.		.		.	
b	*Peridinium* sp.	178 (20-410)	III	498 (40-2470)	III	147 (30-350)	III	288 (20-670)	II	.		.	
s	*Chroococcus minor*	49 (6-112)	III	40 (5-143)	III	26 (2-94)	III	91 (3-330)	II	.		.	
z	*Coelastrum microporum*	75 (5-190)	II	58 (19-150)	III	42 (19-131)	III	214 (40-1000)	III	.		.	
z	*Tetrastrum staurogeniaeforme*	14 (30-30)	II	19 (3-70)	III	165 (5-33)	II	27 (9-75)	II	.		.	
z	*Crucigenia tetrapedia*	16 (1-74)	III	16 (2-50)	II	6 (1-15)	II	31 (5-50)	II	.		19 (4-50)	I
z	*Scenedesmus ecornis*	31 (4-94)	II	21 (1-50)	III	26 (3-72)	II	41 (20-66)	I	.		10 (10)	I
z	*Scenedesmus spinosus*	22 (4-43)	I	21 (6-62)	III	11 (2-30)	II	75 (6-300)	III	.		.	
z	*Scenedesmus intermedius*	5 (2-10)	II	17 (4-81)	III	7 (2-12)	I	9 (6-12)	I	10 (10)	I	.	
e	*Euglena* sp.	23 (20-30)	I	136 (5-245)	III	52 (12-124)	I	142 (30-200)	I	112 (20-200)	II	40 (25-56)	I
z	*Pediastrum duplex*	90 (50-150)	I	54 (13-100)	III	63 (14-150)	II	130 (60-260)	I	99 (30-230)	I	170 (60-450)	I
o	*Nitzschia palea*	.		22 (3-84)	III	.		.		.		.	

o – diatoms, k – cryptomonads, z – green algae, s – blue-green algae, b – dinoflagellates, e – euglenophytes cryptophytes and diatoms dominated. The mean share of cryptophytes in the phytoplankton biomass in the 1992-2003 period was 68% in Lake Licheńskie, 56% in Lake Ślesińskie, and 46% in Lake Pątnowskie, while the shares of diatoms were 26, 42, and 52%, respectively. The spring peak in biomass in Lake Licheńskie (11.0-27.0 mg dm^{-3}) and Lake Pątnowskie (12.2-21.7 mg dm^{-3}) was formed by diatoms (86 and 89% of the biomass, respectively) at a quite significant share of cryptophytes (13 and 10%), while cryptophytes (61%) comprised a greater share than did diatoms (35%) in Lake Ślesińskie (4.7-14.5 mg dm^{-3}). The significantly lower phytoplankton biomass during its maximum development during spring in lakes Licheńskie and Ślesińskie in the 1995-1999 period was due to the lower biomass (by 60-67%) of diatoms from the genus *Stephanodiscus* than had been noted in previous years.

Phytoplankton structure

Quite distinct changes in the structure of the phytoplankton were observed in May, after the collapse of the spring biomass maximum (up to 3-6 mg dm^{-3}), when the long cooling circuit began running. The water temperature reached 10.0-18.9°C in Lake Ślesińskie, and 21.3-29.1°C in Lake Licheńskie. Although the greatest contribution to the phytoplankton biomass remained diatoms (36-47%) and cryptophytes (36-40%), the share of other systematic groups was often greater than 10%. Generally, chlorophytes attained the highest share in the general biomass (in Lake Licheńskie – 15%, Lake Pątnowskie – 11%, Lake Ślesińskie – 9%), dinoflagellates (6, 2, and 4%, respectively), chlorophytes (4, 3, and 10%, respectively), and chrysophytes (2, 1, and 2%, respectively). However, the shares achieved by algae classes in particular years were as high as follows: cyanophytes 31 %; chlorophytes – 34%; dinoflagellates – 17%; chrysophytes – 19%.

During the summer maximum of phytoplankton development, the temperature ranges in the lakes studied was as follows: Ślesińskie – 20.0-26.2°C; Pątnowskie – 21.7-28.6°C; Licheńskie – 24.7-31.5°C. The biomass in Lake Licheńskie (in 1992-1994 at 11.9 mg dm^{-3}; in 1995-1999 at 6.4 mg dm^{-3}; in 2000-2003 at 11.9 mg dm^{-3}) comprised cryptophytes (mean 34%), diatoms (20%), dinoflagellates (18%); cyanophytes (16%); chlorophytes (10%). In Lake Pątnowskie the biomass maxima (in 1992-1994 at 10.9 mg dm^{-3}; in 1995-1999 at 5.3 mg dm^{-3}; in 2000-2003 at 6.9 mg dm^{-3}) comprised cyanophytes (30%), ditaoms (22%), dinoflagellates (19%), cryptophytes (17%), and chlorophytes (19%); however, the co-dominants in Lake Ślesińskie (in 1992-1994 at 26.8 mg dm^{-3}, in 1995-1999 at 9.6 mg dm^{-3}, in 2000-2003 at 7.5 mg dm^{-3}) were diatoms (51%, primarily *Aulacoseira granulata* (Ehr.) Simonsen, cryptophytes (19%), and dinoflagellates (15%). The share of cyanophytes and chlorophytes did not exceed 10% (at 9 and 5%, respectively).

In September, when the water temperature remained high (18.0-24.0°C in Lake Licheńskie and 15.0-21.0°C in lakes Pątnowskie and Ślesińskie) and the overall biomass ranged from 2-5 mg dm^{-3}, the phytoplankton comprised the same alga groups as those that occurred during the summer maximum, but with a distinctly higher share of diatoms (34-39%), and cryptophytes (16-32%) were also numerous. In Lake Ślesińskie dinoflagellates (36%) were abundant, while in Lake Pątnowskie cyanophytes (14%), dinoflagellates (12%), and chlorophytes (11%) were abundant, but in Lake Licheńskie it was chlorophytes (12%). In September 1998, after Lake Ślesińskie had been disconnected from the cooling circuit, the dinoflagellate *Ceratium hirundinella* (O.F. Müll.) Dujard. developed intensively and reached a biomass of 42.6 mg dm^{-3}, which was 91% of the total biomass.

Spatial variation

The spatial variation of phytoplankton abundance in Lake Licheńskie, the most intensely heated basin, and in Lake Ślesińskie, the least heated basin, was quite small in 1998 and 1999. In May the mean biomass of algae in Lake Licheńskie comprised from 3.7-7.7 mg dm $^{-3}$, and in Lake Ślesińskie it was approximately 1.0 mg dm^{-3}. Undoubtedly, the different biomass of the phytoplankton in the two lakes resulted from the different water temperatures in these basins during the winter-spring periods. In summer (July) in Lake Licheńskie the mean biomass of algae ranged from 5.4 to 6.1 mg dm^{-3}, and in Ślesińskie from 5.6 to 8.0 mg dm^{-3}. Exceptionally high variation in phytoplankton biomass was observed among the various stations in July 1999 in Lake Ślesińskie. In the northern deep part of the basin, where the water exchange is not intensive, the biomass of the cryptophyte *Cryptomonas erosa* Ehr. was 27.5 mg dm^{-3}. At the same time in the central part of the basin where the water is mixed from the surface to the bottom, the algal biomass was again significantly lower (1.4-3.9 mg dm^{-3}). Similar phytoplankton biomass differentiation in Lake Ślesińskie was confirmed in September 1998. The greatest biomass of algal plankton was confirmed in the southern deep part of the basin (46.7 mg dm^{-3}), but the abundance was much lower in the central and northern parts of the lake (6.9-18.9 mg dm^{-3}). At this time, blooms comprised the dinoflagellate *C. hirundinella*. However, in Lake Licheńskie the mean algal biomass in September ranged from 1.8 to 2.4 mg dm^{-3}. In 1999, abundant euglenids from the genus *Euglena* appeared in this basin and reached a biomass of about 1.0 mg dm^{-3}.

Among the species identified in lakes Pątnowskie, Licheńskie, and Ślesińskie, one group of taxa occurs throughout the year (Table 3). In the 1992-1999 period, *C. erosa* and *Rhodomonas minuta* Skuja were noted at a high frequency and biomass (to 2-6 mg dm^{-3}); additionally, *Stephanodiscus hantzschii* Grun. was noted in Lake Ślesińskim. In the 2000-2003 period, the number of taxa that were noted frequently in the samples collected throughout the year was decidedly larger. In addition to the cryptophytes (*C. erosa* and *R. minuta*) that occurred at the fifth degree of permanence and at a high biomass (up to 7 mg dm^{-3}), the diatoms *S. hantzschii* (up to 13.6 mg dm^{-3} in Lake Pątnowskie) and *A. granulata* (4th degree; 9.6 mg dm^{-3} in Lake Ślesińskie) were noted, as were diatoms and chlorophytes *Scenedesmus quadricauda* (Turp.) Bréb. (3rd and 4th degree). In lakes Licheńskie and Ślesińskie the chlorophyte *Coelastrum microporum* Näg. in A. Br. and the cyanophyte *Chroococcus minor* (Kütz.) Näg. were noted often (3rd degree), while in Lake Licheńskie there were an additional five taxa: chlorophytes – *Scenedesmus spinosus* Chod., *Tetrastrum staurogeniaeforme* (Schröd.) Lemm., *Planktonema lauterbornii* Schmidle, and dinoflagellates of the genus *Peridinium*.

In the 1992-1999 period, the diatom *Stephanodiscus minutulus* (Kütz.) Cl. occurred only in spring and fall in all the lakes at fairly high permanence (3rd degree) and biomass, while in Lakes Pątnowskie and Licheńskie *S. hantzschii* was noted at the fifth degree of permanence. This species was noted systematically throughout the year in Lake Ślesińskie, and in 2000-2003 it was noted in all the lakes. In the 1992-1999 period, the diatom *Nitzschia kutzingiana* Hilse was noted often (3rd degree) in Lake Pątnowskie, and *Fragilaria ulna* (Nitzsch) Lange-Bertalot was noted in Lake Licheńskie, and *Stephanodiscus neoastraea* Håkansson & Hickel and *Asterionella formosa* Hass. in Lake Ślesińskim. In the 2000-2003 period, these species occurred much less frequently (at the most at the 2nd degree).

The list of taxa noted at high permanence during the warm season in the 1992-2003 period in all the lakes comprises just three species: *S. quadricauda* (4th degree); *Chroococcus minor* (3rd degree); *Peridinium* sp. (3rd degree). Additionally, individuals of *C. hirundinella* (5th degree) and *Crucigenia tetrapedia* (Kirchn.) (3rd degree) were noted frequently. Frequent species in the other lakes included *C. microporum* in lakes Licheńskie and Ślesińskie, and *T. staurogeniaeforme*, *Scenedesmus ecornis* (Ehr.) Chod., *S. spinosus*, and *S. intermedius* Chod. as well as *Pediastrum duplex* Meyen, *Nitzschia palea* (Kütz.) W. Smith and *Euglena* sp. only in Lake Licheńskie. In the 2000-2003 period the species that occurred only in Lake Pątnowskie at fairly high permanence were *C. microporum* Näg. in A. Br. and *S. spinosus*. However, as many as seven species were noted throughout the year in at least one of the lakes studied (Table 3).

Correlation analysis between the biomass of particular systematic groups comprising the phytoplankton in the studied lakes indicated that there was a significant relationship between the intensity of the development between cyanophytes and chlorophytes (r = 0.68-0.85; P < 0,05). Various taxa from these systematic groups form the phytoplankton assemblages that are typical of the summer season and which develop in warm, productive waters, and move through the system of lakes when the long cooling circulation circuit is in operation. The assemblages in Lake Licheńskie were enriched further by taxa of dinoflagellates, cryptophytes, and euglenids, which formed significant and strict correlative relationships among each other. In addition to cyanophytes and chlorophytes, diatoms (*A. granulata*, *S. hantzschii*) were also typical.

Discussion

According to Reynolds (1980), the cyclical development of phytoplankton assemblages in lakes is controlled by just two environmental factors that are mutually influential, namely the availability of nutrients and water stability. Because in a given ecosystem of a particular trophic status in which the intensification of ecological factors (biocenotic dependencies, intensification of the influence of physico-chemical factors) is usually relatively stable, the dynamics of changes in phytoplankton structure are typical (Burchardt et al. 1994). According to Reynolds (1980), the most typical seasonal succession of phytoplankton in eutrophic lakes runs from diatoms to Volvocales and Nostocales then to dinoflagellates or cyanophytes from the genus *Microcystis*; however, in mesotrophic lakes succession runs from diatoms through chrysophyte/*Sphaerocystis* to dinoflagellates. Increased water movement in lakes causes, among other things, reduced water column stability, which disturbs succession (Reynolds 1980). Long-term phytoplankton studies conducted in lakes impacted by discharges of heated waters indicate that these two factors were decisive in determining the seasonal succession of phytoplankton in these basins.

During the first decade in which the cooling system was in operation (late 1960s and early 1970s), the most significant factor was increased water temperature (Sosnowska 1987). The impact of the thermal shock was expressed in the accelerated development of algae, the extension of the vegetative season, and the occurrence at separate locations of short-term algal biomass peaks often comprising a single species. Although diatoms dominated throughout the entire vegetative season and achieved maximum biomass during the cold periods, a large number of green alga species occurred in the phytoplankton (Dąmbska et al. 1976, Burchardt 1977, Sosnowska 1987).

Relative balance was noted in the phytoplankton assemblages during the second decade in which the cooling system was operational. This was possible thanks to the regular working cycle of the cooling system and the relatively limited influence from other anthropogenic factors. This manifested in the fairly distinctly drawn tendency for the overall phytoplankton biomass to decrease in subsequent years (Table 2), which, according to Spodniewska (1984) and Simm (1988), was related to the high water flow rates in the basins. The low biomass of summer phytoplankton was also due to the low bioavailability of phosphorus sorbed on mineral molecules in an alkalized environment (Zdanowski et al. 1988).

In the late 1980s, in addition to the impact of heated water discharge and opencast mining, the lakes were also impacted by fish farming in the discharge canals of the power plants, tourism, and recreation (Socha and Zdanowski 2001). This increased the trophic status of the lakes. Several phenomena were noted, namely, decreasing oxygen in the hypolimnion in the deeper lakes, the accumulation of mud and consequently decreasing depth of the artificial basins in the cooling system, increasing salinity of the waters, and worsening of the sanitary state of the waters (Świątecki 1994, Zdanowski 1994a). The overall biomass of the phytoplankton increased (Table 2), but the share of nanoplankton decreased, and most importantly the type of seasonal succession changed. In summer the assemblages formed were characteristic of very productive waters with the domination of cyanophytes, dinoflagellates, and cryptophytes. The early spring blooms of diatoms of the genus *Stephanodiscus* also lasted longer (Socha 1994b, Socha 1997a).

Previous research by Socha (1997a) permitted identifying two types of phytoplankton seasonal succession: the first is typical of lakes that are part of the cooling system circulation circuit throughout the year (lakes Pątnowskie and Licheńskie); the second is typical of lakes that are periodically part of the cooling system (Lake Ślesińskie). Only two phytoplankton assemblages form in the strongly mixed lakes that are heated throughout the year and have no permanent ice cover in winter. In the warm season, the assemblage comprised abundantly occurring species of cyanophytes, chlorophytes, diatoms, dinoflagellates, and chrysophytes, while the only component of the phytoplankton during the cold period was diatoms. Variations in these patterns stemmed mainly from changes in the strength and direction of water flow in the basins. Diatoms dominated throughout the vegetative season in Lake Ślesińskie, which is only periodically connected to the power plant cooling system. However, two variants were noted in the phytoplankton assemblages: the first had a greater share of chlorophytes, cyanophytes, and dinoflagellates (summer period), and the second had a larger share of cryptophytes (cool period). The relatively stable dynamics of seasonal changes in the phytoplankton structure in Lake Ślesińskie indicated that, despite everything, the impact of the heated waters that reached this lake only in the summer period was fairly limited.

Despite the high productivity of the lake and elevated water temperature, a distinct decrease in algal plankton biomass was noted in the second half of the 1990s. According to Socha and Zdanowski (2001), this could have been the result of the development of subtropical *V. spiralis*, which is *a* new species among Polish flora. This plant formed dense, single-species stands along the shores of the most intensely heated lakes, including Lake Licheńskie (Gąbka 2002, Hutorowicz 2006), and supplanted the submerged hydrophytes that had grown there previously. The leaves of *Vallisneria* turned out to be an excellent substrate for the development of abundant epiphyte algae (Luścińska et. al. 2005). Likely this plant was well-suited to the phytolittoral zone and it became an excellent competitor with phytoplankton. This conclusion is also confirmed by the greatest decrease in the overall biomass of plankton algae in Lake Licheńskie, a basin in which *V. spiralis* almost totally supplanted other species of submerged hydrophytes (Table 2).

The lengthening of the period of species occurrence is important information regarding the changes occurring in the functioning of the aquatic ecosystems of heated lakes, and this indicated in the 1992-1999 period that they preferred waters that were heated to a greater degree (Table 2). These included the cyanophyte *Ch. minor*, the chlorophytes *C. microporum*, *S. quadricauda*, *S. spinosus*, and *T. staurogeniaeforme*, the diatom *A. granulata*, and the dinoflagellate from the genus *Peridinium*. The changes in the phytoplankton structure that were noted during the cold period concurred temporally with the appearance of the *Vallisneria spiralis* in the littoral of Lake Ślesińskie (Hutorowicz et al. 2006). Since the operation of the cooling system did not change substantially during this period, this can be attributed to global climate change, and most of all to the lack of long winters with sub-freezing temperatures. This is confirmed by the mean water temperature which was higher by 0.6°C during the January-March period in 2000-2003 than it was in 1995-1999 (Table 1). Many authors maintain that the effect of increased water temperature is most pronounced during cooler periods, mainly in winter (Vinogradskaja 1971, Noton 1975), and determines the distribution of, among other things, the vegetation in a certain area (Kornaś and Medwecka-Kornaś 2002).

The systematic phycological studies presented in the current paper permitted identifying three abiotic factors that shape the phytoplankton of the Konin lakes. Increased water temperature, especially during the winter period, and the productivity of the lakes stimulate the growth of algae and the development of large assemblages of diatoms in early spring.

However, the fast water flow rates in the lakes are the primary limiting factor for the development of abundant algae (including the problematic cyanophytes) in the summer season. The studies suggest the development of submerged macrophytes (*Vallisneria spiralis*) and the accompanying abundant epiphyte algae (which compete with phytoplankton) that have been noted in recent years are important to the functioning of the heated lakes ecosystems.

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Streszczenie

Zmiany struktury fitoplanktonu w podgrzewanych jeziorach

Celem badań było zbadanie długookresowych (1992-2003) sezonowych zmian biomasy i struktury fitoplanktonu w trzech ogrzewanych jeziorach, które w 1958 i 1970 roku zostały włączone do systemu chłodzenia elektrowni cieplnych, w których od połowy lat dziewięćdziesiątych XX wieku rośnie *Vallisneria spiralis* L. – obcy we florze Polski ciepłolubny gatunek hydrofitu. W latach 1992-1994 ogólna biomasa fitoplanktonu była stosunkowo duża i wynosiła średnio od 7,6 mg dm^{-3} w Jeziorze Pątnowskim do 9,4-10,0 mg dm^{-3} w jeziorach Licheńskim i Ślesińskim (tab. 2). W następnym pięcioleciu (1995-1999) obserwowano około dwukrotnie mniejszą średnią (tab. 2) i maksymalną biomasę planktonu roślinnego w okresie lata w J. Pątnowskim (rys. 2), w J. Licheńskim (rys. 3) i w J. Ślesińskim (rys. 4). Taka tendencja zmian utrzymywała się w J. Ślesińskim do 2003 roku. Nieco słabiej rysowała się ona w J. Pątnowskim. W latach 2000-2003 w podgrzanych jeziorach można było wyodrębniać dwa zbiorowiska fitoplanktonu. Pierwsze, charakterystyczne dla lata, o biomasie 10,0 mg dm^{-3} budowały sinice, zielenice, bruzdnice i kryptofity. W okresach chłodnych masowo rozwijały się okrzemki z rodzaju *Stephanodiscus*, osiągając biomasę nawet 27,0 mg dm^{-3}. W latach 2000-2003 wyraźnie wydłużył się okres występowania kilku gatunków, które w latach 1992-1999 notowano wyłącznie latem. Były to sinica *Chroococcus minor*, zielenice: *Coelastrum microporum, Scenedesmus quadricauda, S. spinosus i Tetrastrum staurogeniaeforme*, okrzemka *Alaucoseria granulata* i bruzdnice z rodzaju *Peridinium* (tab. 3). Opisywane zmiany struktury fitoplanktonu w okresach chłodnych zbiegły się w czasie z pojawieniem się *Vallisneria spiralis w* litoralu tego zbiornika. Przeprowadzone badania potwierdziły decydujący wpływ na strukturę i obfitość fitoplanktonu trzech czynników abiotycznych. Rozwój okrzemek wczesną wiosną stymuluje temperatura wody i żyzność jezior. Duży przepływ wody ogranicza rozwój glonów (w tym uciążliwych sinic) w sezonie letnim.