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Vertical distribution of phototrophs in the pelagic zone of three small *Lobelia* lakes

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Abstract

The community structure and biomass of pelagic phototrophs, with a particular focus on the picoplanktonic fraction, were studied in three small, soft-water lakes in the Pomerania Lake District (north Poland). The smallest phototrophs were usually dominated by picocyanophytes, both single-celled and colonial. Picochlorophytes were less frequent, and they formed dense populations only in one lake. The nano- and microplankton included many groups of organisms, but the main groups were comprised of dinoflagellates, chrysophytes and chroococcoid and/or filamentous cyanophytes and large raphidophytes. Community structure changed significantly with depth and in all lakes remarkable differences were observed between the epilimnion and both the meta- and hypolimnion. The hypolimnion was characterized by the presence of photosynthetic green sulfur bacteria or their symbiotic consortia.

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INTRODUCTION

Phototrophic communities vary in the vertical profiles of water bodies, even in relatively shallow ones. Variation in the pelagic zone is noted with regard to both phytoplankton taxonomic composition and cell size. However, only a few studies have described the abundance, distribution, and composition of the entire phototrophic community in consideration of all taxonomic groups and size fractions (Happey-Wood 1991; Beaty and Parker 1996; Szeląg-Wasielewska 1997, 2003). Size structure is a particularly important parameter in the characterization of phototrophic communities; however, recently increasing attention is being paid to the importance of the smallest cells, namely phototrophic picoplankton, as significant contributors to phototrophic biomass (Weisse 1993, Stockner et al. 2000). Generally, it is reported that the contribution of picoplankton to total phototrophic biomass is higher in oligotrophic environments (Stockner 1991).

The aim of this study was to characterize the phototrophic community in *Lobelia* lakes and to assess changes in its structure: (1) in the vertical profile, and (2) over a decade. Special attention was paid to picoplanktonic cells. In order to compare phototrophs, water samples were used that had been collected during the period of thermal stratification from three soft-water lakes with low trophic states.

STUDY LAKES

This study of phototrophs was carried out in three lakes, the Czarnówek, Piekiełko, and Iłowatka, which are located in the Pomerania Lake District (north Poland). Lake Czarnówek lies north of the village Złocieniec, while the others are west of Babolice. These lakes are protected as nature reserves and are called *Lobelia* lakes because of their specific vegetation. As reported by Kraska et al. (2006), Lake Piekiełko has the smallest area (9.9 ha) but is the deepest (max depth 28 m, volume 1.336 million m^3), with periodical flow-through. While the other two have no flow-through and have only slightly larger surface areas, they are much shallower (Lake Czarnówek - area 11.9 ha, max depth 9.5 m, 0.509 million m^3; Lake Iłowatka - 14.7 ha, max depth 8.7 m, 0.529 million m^3). They are all soft-water lakes with summer stratification and anoxic hypolimnions. Lake Czarnówek is experiencing progressing dystrophication and humification and Lake Iłowatka eutrophication and humification, but Lake Piekiełko was not strongly impacted by humans in the period between sampling sessions, so it remained “balanced” (Kraska et al. 2006).

MATERIALS AND METHODS

Water samples for the analysis of phytoplankton were taken in the deepest part of the pelagic zone of the lakes in August 1994 and 2003. The samples were collected with a Toń sampler at 1-meter intervals from the surface to the bottom, and integrated samples were made immediately on the basis of thermal stratification for three water layers (the epi-, meta- and hypolimnion). Water samples for picophytoplankton and bacterioplankton studies were preserved with glutaraldehyde, while the remaining size fractions of phytoplankton were preserved in Lugol's solution.

In the laboratory, planktonic organisms were identified to the species level or, if this was impossible, they were only assigned to a genus. Several size fractions were taken into account, and phototrophic and heterotrophic plankters were identified based on the autofluorescence of photosynthetic pigments (MacIsaac and Stockner 1993) and second fluorescence (Porter and Feig 1980) under an epifluorescence microscope (Olympus BX-60). For the analysis of APP (0.2–2.0 μm), water samples of 5–10 ml in volume were collected by filtration on black Nuclepore filters of 0.2 μm pore size under low vacuum pressure. An HBO mercury lamp (100 W) and standard filter sets were applied to generate green, blue, blue-violet, and ultra-violet excitation light. The specimens were examined at a magnification of ×1500. Nanoplankton (2.0–20 μm), microplankton (20–200 μm), and larger phytoplanktonic organisms (>200 μm) were analyzed under an inverted microscope after sedimentation in settling chambers 14 ml in volume, at magnifications of ×40, ×150, and ×600. As the abundance and biomass of organisms larger than 200 μm were negligible, they were analyzed jointly with the microplankton. Abundance was expressed as the cell number per ml of water. The biovolume of each species was calculated based on cell shape, size, and number, while their biomass was expressed as wet weight assuming that the volume of 10^6 μm^3 is equivalent to 1 μg.

RESULTS

Lake Czarnówek

In Lake Czarnówek during both sampling periods the biomass of phototrophs was the highest in the metalimnion at 7.0 mg l^{-1} in 1994 and 1.9 mg l^{-1} in 2003 (Fig. 1). The mean biomass in the vertical profile was three times higher in the first period (4.3 mg l^{-1}) than in the second one (1.4 mg l^{-1}). In 1994 the main contributors to phototrophic biomass in the epilimnion were dinoflagellates (54%) and chrysophytes (45%), but in the

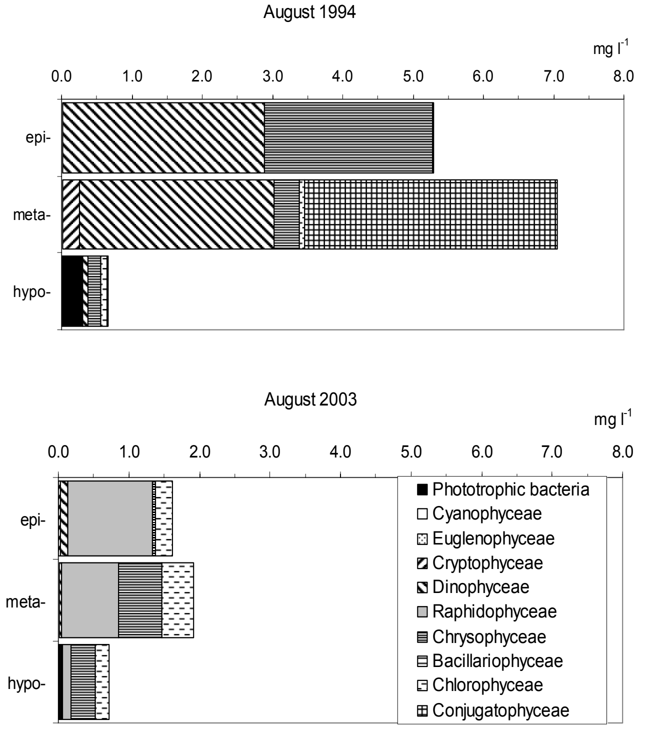

Fig. 1. Vertical variation in the biomass of taxonomic groups of phototrophs in Lake Czarnówek in August 1994 and 2003.

metalimnion conjugatophytes dominated (51%) and contributions of dinoflagellates and chrysophytes decreased to nearly 40% and 5%, respectively. In the hypolimnion, as much as 45% of biomass was contributed by the photosynthetic green sulfur bacteria (*Chlorobium* sp.) and their symbiotic consortia (*Pelochromatium* spp.). The same phototrophic bacteria were also noted there in 2003, but their contribution to the total phototrophic biomass did not then exceed 5% because the major contributors in that zone were chrysophytes (48%) of the genus *Dinobryon*. Biomass in the metalimnion was dominated by the raphidophyte *Gonyostomum semen* (43%), which accounted for 74% of the phototrophic biomass in the epilimnion.

Nanoplankton and/or microplankton dominated in the phototrophic size structure (Fig. 2). In 1994 the most abundant nanoplankter was the conjugatophyte *Cosmarium asphaerosporum*, while major microplankters were

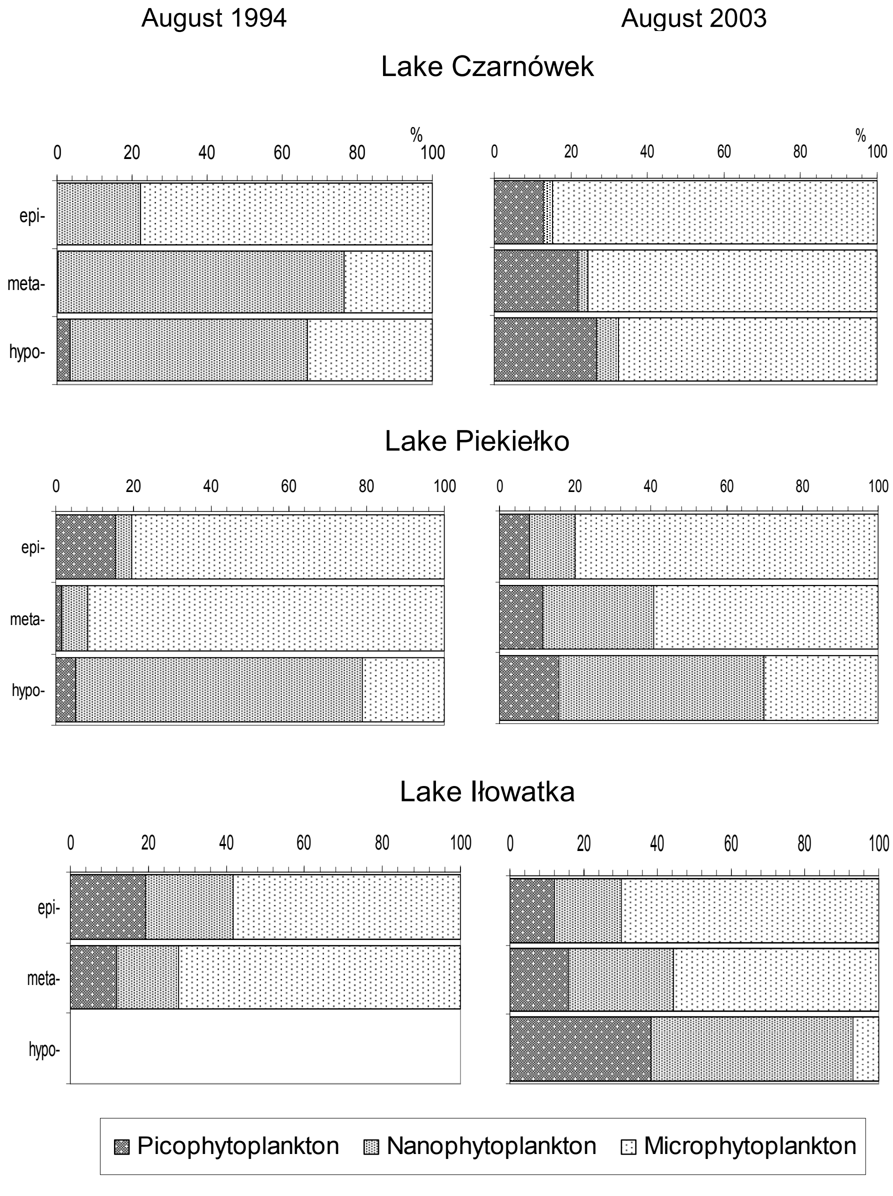

Fig. 2. Contribution of size fractions to phototrophic biomass in the studied lakes in August 1994 and 2003.

Dinobryon and *Gymnodinium* species (Table 1). In 2003 the contribution of microplankton, dominated by *Gonyostomum semen* and *Dinobryon pediforme*, was always the highest, although it decreased with increasing depth. The biomass contribution of the smallest phototrophs, picophytoplankton, increased with depth but was high only in the second study period when it reached 27% in the hypolimnion while in the vertical profile it amounted to 21%, on average. In the first period only eukaryotic cells were recorded, while in the second period large populations of the picochlorophytes *Choricystis minor* and *Chlorella* sp. were accompanied by picocyanophytes (Tables 1, 2). However, the contribution of picocyanophytes to total abundance did not exceed 2% and resulted from the presence of picoplanktonic cells forming characteristic, regular aggregations of cyanophytes (*Merismopedia tenuissima* Lemm).

Table 1

The five most important taxa in the water column with regard to the phototrophic biomass of the studied lakes in August 1994 and 2003. The letters in brackets (e-epilimnion, m-metalimnion, h-hypolimnion) indicate the layer with the highest biomass of particular taxa

1994		2003	
Name of taxa	Biomass mg l^{-1}	Name of taxa	Biomass mg l^{-1}
Lake Czarnówek			
Cosmarium asphaerosporum Nordst.	3.580 (m)	*Gonyostomum semen* (Ehr.) Diesing	1.196 (e)
Dinobryon sertularia var. *protuberans* (Lemm.) Krieger	2.400 (e)	*Syncrypta* sp.	0.538 (e)
Peridinium inconspicuum Lemm.	1.517 (m)	*Pseudodictyosphaerium jurisii* (Hindák) Hindák	0.369 (m)
Gymnodinium sp.	1.093 (m)	*Dinobryon pediforme* (Lemm.) Steinecke	0.199 (h)
Peridinium sp.	0.744 (e)	*Choricystis minor* (Skuja) Fott	0.099 (h)
Lake Piekiełko			
Peridinium spp.	0.578 (m)	*Ceratium hirundinella* (F.B. Müller) Bergh	0.344 (e)
Tabellaria flocculosa var. *asterionelloides* Grunow	0.124 (e)	*Rhodospirillum rubrum* (Esmarch) Molisch	0.074 (h)
Romeria elegans (Wołosz.) Koczwara	0.109 (h)	*Sphaerocystis planctonica* (Korš.) Bourrelly	0.061 (m)
Rhodospirillum rubrum (Esmarch) Molisch	0.048 (h)	*Gonyostomum semen* (Ehr.) Diesing	0.049 (e)
Ceratium hirundinella (F.B. Müller) Bergh	0.042 (e)	*Peridinium* sp.	0.034 (m)
Lake Iłowatka			
Ceratium hirundinella (F.B. Müller) Bergh	0.168 (e)	*Ceratium hirundinella* (F.B. Müller) Bergh	0.248 (e)
Peridinium willei Huitfelt-Kaas	0.122 (m)	*Aphanizomenon gracile* Lemm.	0.104 (e)
Synechococcus sp.	0.095 (e)	*Aphanothece* sp.	0.081 (e)
Oscillatoria sp.	0.092 (e)	*Rhodospirillum rubrum* (Esmarch) Molisch	0.081 (h)
Aphanocapsa sp.	0.084 (e)	*Peridinium* sp.	0.078 (m)

Lake Piekiełko

In this lake, the mean phototrophic biomass in both periods was similar (0.409 and 0.412 mg l^{-1}, respectively), but its vertical distribution varied (Fig. 3). In the first period, it was the highest in the metalimnion and was characterized by the domination of dinoflagellates at 83%. In the epilimnion the major contributors to biomass were diatoms (40%), while in the hypolimnion, it was cyanophytes (54%). In the second period, phototrophic biomass was the highest in the epilimnion, and it decreased with increasing depth. In the

Table 2

Abundance and biomass of picophytoplankton in the studied lakes in August 1994 and 2003: single-celled picocyanophytes (S-Pcy), colonial picocyanophytes (C-Pcy) and eukaryotic picoplankton (E-PP)

	Abundance (10^3 cells ml^{-1})				Biomass (mg l^{-1})			
	1994		2003		1994		2003	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Lake Czarnówek								
S-Pcy	nd	-	nd	-	nd	-	nd	-
C-Pcy	nd	-	0.4-4.2	1.8	nd	-	0.001-0.003	0.001
E-PP	0.6-5.9	3.7	58-135	86.9	0.002-0.020	0.012	0.187-0.418	0.271
Total	0.6-5.9	3.7	62.2- 136	88.7	0.002-0.020	0.012	0.190-0.418	0.273
Lake Piekiełko								
S-Pcy	9.8-32.2	17,7	11.4-50.0	36.0	0.004-0.013	0.007	0.005-0.025	0.017
C-Pcy	2.9-34.9	14.6	6.5-26.4	19.2	0.001-0.028	0.012	0.006-0.022	0.017
E-PP	0.2-1.7	0.8	0.4-1.6	1.0	0.001-0.006	0.003	0.001-0.006	0.004
Total	12.9-68.8	33.0	18.3-75.1	56.1	0.006-0.048	0.022	0.013-0.050	0.037
Lake Iłowatka								
S-Pcy	152-247	199	19.1-61.6	37.9	0.058-0.095	0.076	0.010-0.026	0.017
C-Pcy	141-245	188	17.3-112	77.4	0.054-0.109	0.081	0.010-0.093	0.064
E-PP	nd	0	0-0.8	0.4	nd	0	0-0.003	0.001
Total	293-492	393	78.9-136	116	0.112-0.203	0.158	0.038-0.106	0.082

nd – not detected

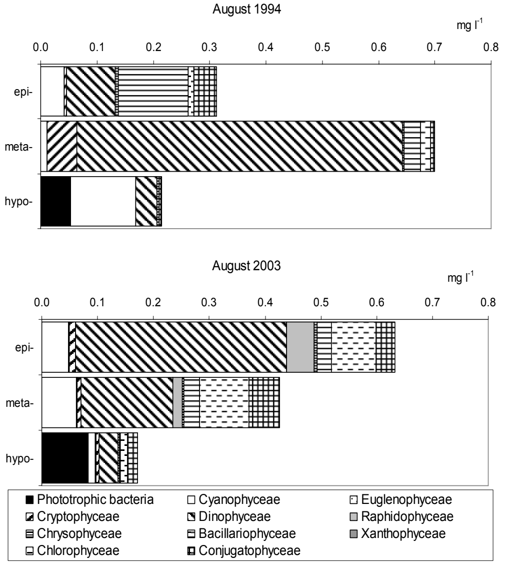

Fig. 3. Vertical variation in the biomass of taxonomic groups of phototrophs in Lake Piekiełko in August 1994 and 2003.

epilimnion, in addition to the domination of dinoflagellates (60%), chlorophytes were also characterized by a considerable contribution to biomass (18%). In the metalimnion, although phototrophic biomass was about 30% lower, contributions of these taxonomic groups were similar. Phototrophic bacteria were noted in the hypolimnion in both periods and were mainly *Rhodospirillum rubrum*, *Chlorochromatium aggregatum* Lauternborn, and *Chlorobium* spp. In the first period their contribution to phototrophic biomass reached 25%, but cyanophytes dominated (54%). In the second period, the contribution of phototrophic bacteria doubled (48%), but dinoflagellates (20%) and chlorophytes (18%) were also important contributors.

In the phototrophic biomass of Lake Piekiełko, microplankton dominated in the epi- and metalimnion (Fig. 2). In the first period their contribution to phototrophic biomass was not lower than 80%, whereas in the second period it was not lower than 60%. Deeper down, in the hypolimnion, the importance of microplankton declined in favor of nano- and picoplankton. Within microplankton, the highest biomass was produced by the diatom *Tabelaria flocculosa* var. *asterionelloides* and flagellates *Ceratium hirundinella, Gonyostomum semen* and members of the genus *Peridinium.* The most important nanoplanktonic species were the cyanophytes *Romeria elegans* and chlorococcal green algae of the genera *Crucigenia* and *Tetraedron* (Table 1). The mean contribution of picoplanktonic cells to phototrophic biomass was higher in the second period (11.2%) than in the first (7.4%), but the maximum values in both periods, recorded in the hypolimnion and epilimnion, respectively, were similar at about 16%.

Picophytoplankton structure in both sampling periods was similar and was dominated by picocyanophytes, which accounted for 97-99% of the total abundance and 79-94% of the total picophytoplankton biomass (Table 2). Mean abundance of picoeukaryotes did not exceed 10^3 cells per ml but their mean contribution to biomass was higher than to abundance of picophytoplankton at 13.1% and 2.2%, respectively. In both periods the maximum abundance of picocyanophyte cells occurred in the epilimnion at similar values (67×10^3 cells ml^{-1} in 1994 and 74×10^3 cells ml^{-1} in 2003), but the mean value for the vertical profile was higher in the second period. Picocyanophytes were dominated by single-celled forms, and the mean contribution of colonial forms to total picocyanophyte abundance in the water column of both sampling periods was similar at 37% and 35%, respectively.

Lake Iłowatka

The epilimnion was characterized by the highest biomass in Lake Iłowatka during both study periods (Fig. 4). In the first period its value slightly exceeded

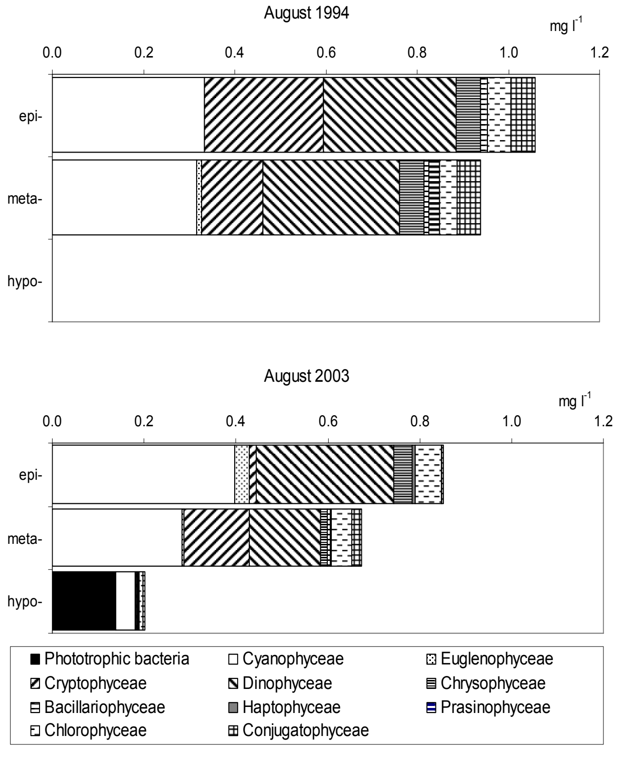

Fig. 4. Vertical variation in the biomass of taxonomic groups of phototrophs in Lake Iłowatka in August 1994 and 2003.

1 mg l^{-1}, but in the second period it was about 20% lower. Phototrophic biomass gradually decreased with increasing depth, but both in the epilimnion and in the metalimnion the major contributors to biomass were cyanophytes, dinoflagellates, and/or cryptophytes. As for differences between the two study periods in relation to taxonomic groups, the mean contribution of cyanophytes in the water column increased by about 15%, but contributions of cryptophytes and dinoflagellates decreased by 10%. In the hypolimnion, which was studied only in 2003, biomass was several times lower, and the structure of phototrophs was different as photosynthetic bacteria were the dominant group. Their contribution to total phototrophic biomass was nearly 70%, and the most abundant taxa were *Rhodospirillum rubrum* and *Chlorochromatium glebulum*. These bacteria were accompanied by cyanophytes which contributed 20% of the biomass.

The most important microplanktonic species in Lake Iłowatka were *Aphanizomenon gracile*, *Ceratium hirundinella*, *Peridinium willei*, *Closterium acutum* var. *variabile* (Lemm.) W. Krieg., and *Dinobryon* spp. (Table 1). The contribution of microplankton was the highest in the epilimnion (58-70%) and the metalimnion (56-72%). The mean contribution of nanoplankton in those layers was similar in both periods at 19% in 1994 and 23% in 2003, while the picoplankton reached 16% and 14%, respectively. While phototrophic biomass was very low (0.2 mg l^{-1}) in the hypolimnion in 2003, the contribution of picoplankton to the biomass was high (nearly 40%) and the mean contribution of picoplankton to the whole water column was 22% (Fig. 2).

Of the three lakes studied, the picophytoplankton was most abundant in Lake Iłowatka. Its mean abundance to the water column was 3.9×10^5 cells ml^{-1} in the first period and 1.2×10^5 cells ml^{-1} in the second period, while biomass was 0.158 and 0.082 mg l^{-1}, respectively. Picocyanophytes dominated with respect to both abundance and biomass, and they were characterized by a high contribution of colonial forms to the total number of cells at an average of 49% in 1994 and 61% in 2003. In the second period, when the hypolimnion was taken into account, the contribution of colonial forms decreased from 85% in the epilimnion to 22% in the hypolimnion. Picoeukaryotes were detected only in 2003 (Table 2). Their maximum abundance was recorded in the metalimnion and reached 0.8×10^3 cells ml^{-1}. However, the maximum proportion of picoeukaryotes to the total picophytoplankton abundance did not exceed 1% (mean 0.4%) or 5% in biomass (mean 2.2%).

DISCUSSION

The dependence of phytoplankton structure on depth has been known for a long time, and it is of great importance for understanding the functioning of aquatic ecosystems (Reynolds 1984). Despite the recognition of the role of some plankton components in the food web and the contribution of microorganisms to the functioning of the pelagic zone in lakes, knowledge regarding the depth distribution of phototrophs is still poor with regard to *Lobelia* lakes (Szeląg-Wasielewska 1994, 2005).

Flagellates often played an important role in the total biomass of phototrophic communities in the investigated lakes. These were mainly species from the genera *Dinobryon*, *Gymnodinium, Peridinium* and *Ceratium hirundinella.* These are mixotroph microplanktonic organisms which are capable of both phototrophic and phagotrophic nutrition (Turpin 1988, Arvola et al. 1999). According to Reynolds (1984), *Ceratium hirundinella* forms high biomass concentrations in summer and fall in water bodies that are categorized from mesotrophic to eutrophic states, but they prefer warm and transparent waters. The highest phototrophic biomass in the water column is usually recorded in the metalimnion. Such a distribution of biomass in the water column is regarded as characteristic of lakes with a lower trophic state (Moll and Stoemer 1984). However, in Lake Iłowatka, where concentrations of nutrients in the water were higher than in the other investigated lakes (Kraska et al. 2006), phototrophic biomass was concentrated in the epilimnion. The higher trophic state of the lake, as compared with the other two, was confirmed by the presence and larger abundance of filamentous cyanophytes. The hypolimnion of the studied lakes was characterized by the presence of photosynthetic green sulfur bacteria or their symbiotic consortia. These bacteria occurred in stratified lakes with a hydrogen sulphide zone and then anoxygenic photoassimilation can contribute substantially to the organic matter production during the stratification period (Camacho et al. 2001).

The smallest phototrophs were present in all studied lakes, but in various amounts and proportions, as regards prokaryotic and eukaryotic cells. Picochlorophytes were less frequent and formed dense populations only in Lake Czarnówek during the second sampling period. As reported by Kraska et al. (2006), the characteristic feature of the pelagic zone of the lake was the acid reaction of water (pH 5.6 in the epilimnion), which confirms reports (e.g. Stockner and Shortreed 1991) about the elimination of picocyanophytes resulting from decreasing water pH. The picophytoplankton of the other lakes were dominated by cyanophytes. Despite their small size, picophytoplankton contributed substantially to phototrophic biomass, which was usually, on average, more than 10% (range 1.3-22%). On the whole, the proportion of picophytoplankton to total phototrophic biomass was not too great in comparison with *Lobelia* lakes in the Bytów Lakeland (Szeląg-Wasielewska 2005), but they were within the range found in lakes with low trophic levels (Stockner 1991, Stockner et al. 2000).

CONCLUSIONS

In stratified *Lobelia* lakes with a low trophic state, phototrophic picoplankton are abundant and significant contributors to the phototropic biomass in some water layers. Moreover, the total phototrophic biomass may be even higher because of the presence of phototrophic bacteria in the anoxic hypolimnion. The size structure of phototrophs is an important parameter in the characterization of food resources in the pelagic zone of lakes. Many consumers feed on the smallest organisms, as they are abundant in open waters and sedimentation is slower than it is with the larger microorganisms. Thus, it is important to distinguish between the larger phytoplankton and picophytoplankton.

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