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Vertical distribution of phytoplankton in two mesotrophic lakes

Pionowe rozmieszczenie fitoplanktonu w dwóch jeziorach mezotroficznych

ABSTRACT

In lakes Rogóžno and Zagłębcze located in the Łęczna-Włodawa Plain (E Poland), monthly and daily changes in the vertical distribution of phytoplankton biomass were investigated. In both lakes, phytoplankton biomass in metalimnion were two or three times higher than in epilimnion. In Rogóžno Lake, *Planktothrix rubescens* dominated in phytoplankton (> 80% of biomass), whereas in Zagłębcze Lake – *Ceratium hirundinella* prevailed (> 90% of biomass). The biomass maxima of *Pl. rubescens* (at 6 m depth – 43.5 mg dm⁻³ and at 7 m depth - 24.4 mg dm⁻³) were always below the lower limit of the euphotic zone, i.e. at the depth where the light was < 1%, and the water temperature was < 10 °C. Large biomass of *C. hirundinella* was observed always in metalimnion (up to 43.6 mg dm⁻³ in July) at the lower limit of the euphotic zone (transparency of Sd = 3.0 m). In August, when transparency of Sd = 2.5 m, biomass of *C. hirundinella* varied significantly during the day in the two thermal layers. In epilimnion, the largest increase of biomass was observed in daylight hours and the decrease at night. The reverse situation was observed in metalimnion – the decline in the daytime and the increase at night. The studies revealed that despite different mechanisms of motility (buoyancy or flagellar movement), vertical migrations of these species corresponded mainly to the changing light.

Keywords: deep lake, vertical distribution, *Ceratium hirundinella*, *Planktothrix rubescens*

STRESZCZENIE

W jeziorach Rogóžno i Zagłębcze położonych na Równinie Łęczyńsko-Włodawskiej (wsch. Polska) badano zmiany biomasy fitoplanktonu w pionowym rozmieszczeniu w skali miesięcznej i dobowej. W obu jeziorach biomasa fitoplanktonu w metalimnionie była dwa lub trzy razy wyższa

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niż w epilimnionie. W jeziorze Rogóžno w fitoplanktonie dominowała *Planktothrix rubescens* (> 80% biomasy), natomiast w jeziorze Zagłębcze – *Ceratium hirundinella* (> 90% biomasy). Maksima biomasy *Pl. rubescens* (na 6 m – 43,5 mg dm⁻³ i na 7 m – 24,4 mg dm⁻³) zawsze występowały poniżej dolnej granicy strefy eufotycznej, czyli na głębokości, gdzie światło było <1%, a temperatura wody wynosiła <10 ° C. Duża biomasa *C. hirundinella* występowała zawsze w metalimnionie (aż do 43.6 mg dm⁻³ w lipcu) przy dolnej granicy strefy eufotycznej (widzialność Sd = 3,0 m). W sierpniu, gdy widzialność krążka Sd = 2,5 m, biomasa *C. hirundinella* różniła się znacząco w ciągu doby w dwóch warstwach termicznych. W epilimnionie największy przyrost biomasy odnotowano w ciągu dnia, a spadek w nocy. Odwrotna sytuacja miała miejsce w metalimnionie – spadek w ciągu dnia i wzrost w nocy. Badania wykazały, że pomimo różnych mechanizmów ruchliwości (pławność lub aparat wiciowy), pionowe migracje tych gatunków związane były głównie ze zmieniającymi się warunkami świetlnymi.

Słowa kluczowe: jezioro głębokie, pionowe rozmieszczenie, *Ceratium hirundinella*, *Planktothrix rubescens*

INTRODUCTION

During stratification in deep lakes, there are often differences in the abundance and species composition of phytoplankton between epi- and metalimnion (17). Sometimes it happens that concentration of phytoplankton is larger in the stable metalimnion than in turbulent epilimnion (3). Many phytoplankton species are able to move between those layers (2, 4, 30). Commonly called vertical migrations could be performed by taxa from different taxonomic groups, such as *Microcystis* (Chroococcales), *Volvox*, *Eudorina* (Volvocales), *Peridinium*, *Ceratium* (Dinophyceae) (9, 16, 27). Regular daily vertical migrations are characteristic of most flagellates. With the ability to move, they can maintain the position at depth in the water column, which allows them to avoid exposure to low nutrients levels, worse light conditions or high pressure of grazing (12, 28). For prokaryotic algae, it is common to move vertically due to presence of gas vacuoles and the buoyancy control may be even more efficient than in eukaryotic species with flagella (20, 23). An apparent difference in the number of some cyanobacteria species between epi- and metalimnion results mainly from their different preferences in relation to temperature and light (26). Both low temperature and low light intensity stimulate the growth of *Planktothrix rubescens* in metalimnion, and greater tolerance to temperature and light favors *Planktothrix agardhii*, which is more abundant in epilimnion (11, 13, 22).

The aim of the study was to determine the changes in phytoplankton biomass and in dominating taxa (*Planktothrix rubescens*, *Ceratium hirundinella*) between the epi- and metalimnion during a year. In the case of *Pl. rubescens*, the relationships between the biomass maxima and photosynthetic light, and temperature were considered. Daily migration between epi- and metalimnion was also analyzed for *C. hirundinella*.

MATERIAL AND METHODS

The studies were carried out in two lakes: Zagłębcze and Rogóžno, located in the Łęczna-Włodawa Plain (Eastern Poland) (Fig. 1). The area of the lakes is 57–59 ha and the maximum depth – 25 meters. The lakes are dimictic and mesotrophic.

Samplings were done in the deepest sites of lakes between May and August 2006 (Lake Rogóžno) and between June and September 2000 (Lake Zagłębcze). The studies included epilimnion and metalimnion, respectively extending to the depth of 3–4 and 8 m. Samples for the phytoplankton analyses were taken in both lakes, every 1 meter by the Ruttner sampler (2 dm³). Studies on diurnal vertical changes in phytoplankton biomass were performed in Lake Zagłębcze between June and



Fig. 1. Location of Łęczna-Włodawa Plain (E Poland)

September. Water samples were then collected every month for two consecutive days. During the day, samples were taken three times (at 5 a.m., 2 p.m. and 10.30 p.m.). Chlorophyll-a concentration was determined spectrophotometrically (21). Phytoplankton abundance was determined by the Utermöhl method (31), and fresh biomass of species was evaluated by calculating the volume in mm^3 (10).

Photosynthetically active radiation (PAR), Secchi disc visibility (Sd), temperature (T), oxygen concentration (O_2), pH and electrolytic conductivity (EC) were measured *in situ*. Measurements of temperature and oxygen were performed at 0.5 m intervals by means of WTW Oxi probe. Light was measured by the photometer Li-Cor meter (Li-250A) with the sensor Li-192SA. First, the light was measured just above the water surface to determine the amount of light reaching the water (I_0), and then every 0.5 m in the water column to a depth of ca. 9 m. Electrolytic conductivity and pH were measured in collected water during sampling with meters Elmetron C-411 and C-401.

Statistical analysis was performed with STATISTICA 9.0.

RESULTS

Basic physical-chemical parameters of water were demonstrated in Table 1. Between lakes those parameters did not show significant differences. During the whole study period in both lakes, the thermal-oxidative gradient was strong and stable (temperature: $F = 17.7\text{--}18.8$, $p < 0.005$, O_2 : $F = 8.63\text{--}14.7$, $p < 0.03$). Additionally, differences in water reaction values (mean pH: epi- 8.5, meta- 7.5) occurred in Lake Zagłębcze ($F = 69.3$, $p = 0.0002$).

Mean biomass in Lake Rogóžno amounted to 9.7 mg dm^{-3} , chlorophyll-a concentration up to $26.5 \text{ } \mu\text{g dm}^{-3}$, and in Lake Zagłębcze: 15.4 mg dm^{-3} and $6.9 \text{ } \mu\text{g dm}^{-3}$, respectively. For the whole period of stratification in both lakes, differences in the amounts of phytoplankton between epi- and metalimnion were identified

Table 1. Basic physical-chemical parameters of waters in the thermal layers of studied lakes.

	Rogóżno		Zagłębcze	
	E	M	E	M
Sd (m)	3.03 ± 0.97		2.87 ± 0.25	
T (°C)	20.1 ± 4.0	8.2 ± 3.3	17.7 ± 4.2	13.9 ± 2.4
O ₂ (mg dm ⁻³)	9.1 ± 1.2	7.3 ± 6.6	9.4 ± 1.4	4.85 ± 1.8
pH	8.5 ± 0.2	8.2 ± 0.5	8.2 ± 0.2	7.6 ± 0.1
EC (μS cm ⁻¹)	334 ± 9	351 ± 15	207 ± 30	244 ± 35

Sd – Secchi disc transparency, T – temperature, EC – electrolytic conductivity

(Table 2). In Lake Rogóżno, the phytoplankton biomass in metalimnion was about 3 times, and chlorophyll-a concentration 4 times higher than in epilimnion. Similarly, in Lake Zagłębcze, both parameters were approximately two times higher in metalimnion compared to epilimnion. In the studied lakes, the largest metalimnetic biomass and chlorophyll-a concentration was found between June and July for Lake Rogóżno, and between June and August for Lake Zagłębcze (Table 2).

In Lake Zagłębcze, the planktonic algal community was characterized by very low species diversity. From the beginning of June to September, dinoflagellate *Ceratium hirundinella* were the dominant species contributing

Table 2. The means of biomass (mg dm⁻³) and chl-a concentration (μg dm⁻³) in epi- (E) and metalimnion (M) of studied lakes.

Months	Rogóżno				Zagłębcze			
	Biomass		Chl-a		Biomass		Chl-a	
	E	M	E	M	E	M	E	M
May	5.8	11.5	14.2	35.6	-	-	-	-
June	2.6	26.9	4.0	71.2	8.6	17.3	4.5	9.3
July	0.8	16.5	3.4	50.3	3.1	45.5	4.4	11.0
August	5.1	8.31	5.3	27.9	22.4	17.5	10.4	18.7
September	-	-	-	-	4.3	4.7	8.3	7.5

even 90% of phytoplankton biomass (Fig. 2). Considering the seasonal changes of *C. hirundinella* biomass in metalimnion, the highest peak, 43.6 mg dm⁻³, in July was noted. At the same time, there was a significant decrease in total biomass of phytoplankton in epilimnion (Table 2).

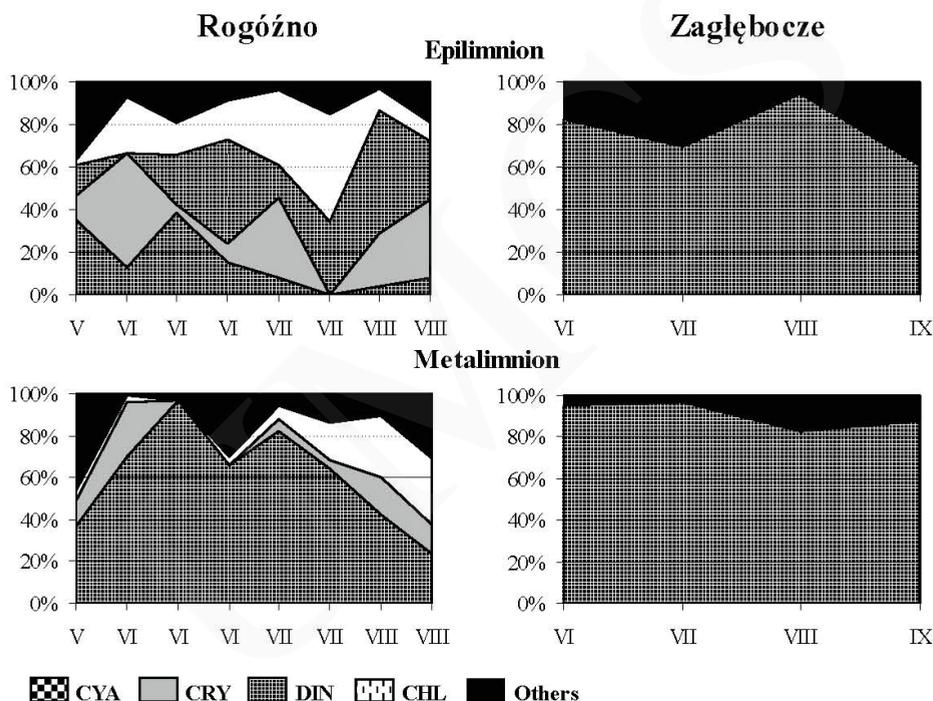


Fig. 2. Relative abundance of algal groups (in total biomass) in studied lakes. Explanations: CYA – Cyanoprokaryota, CRY – Cryptophyta, DIN – Dinophyceae, CHL – Chlorophyta

High values of *C. hirundinella* biomass in metalimnion continued in almost all the study periods. The range of daily variation in biomass of that species was also much higher in meta-than in epilimnion. The exception was the month August, when the biomass in the two thermal layers was similar and its daily fluctuations were comparatively high (Fig. 3). In June and August, the epilimnetic increase of biomass was observed in daylight hours and the decrease at night (Fig. 4). Converse patterns of biomass changes were observed in metalimnion – the decline in daytime and the increase at night. Interestingly, similar pattern of *C. hirundinella* biomass changes in both thermal layers was not observed in July, despite the fact that the biomass of this species significantly varied in metalimnion.

Much greater phytoplankton diversity was in Lake Rogóźno. In epilimnion, cryptomonads, dinoflagellates and green algae had a relatively high contribution

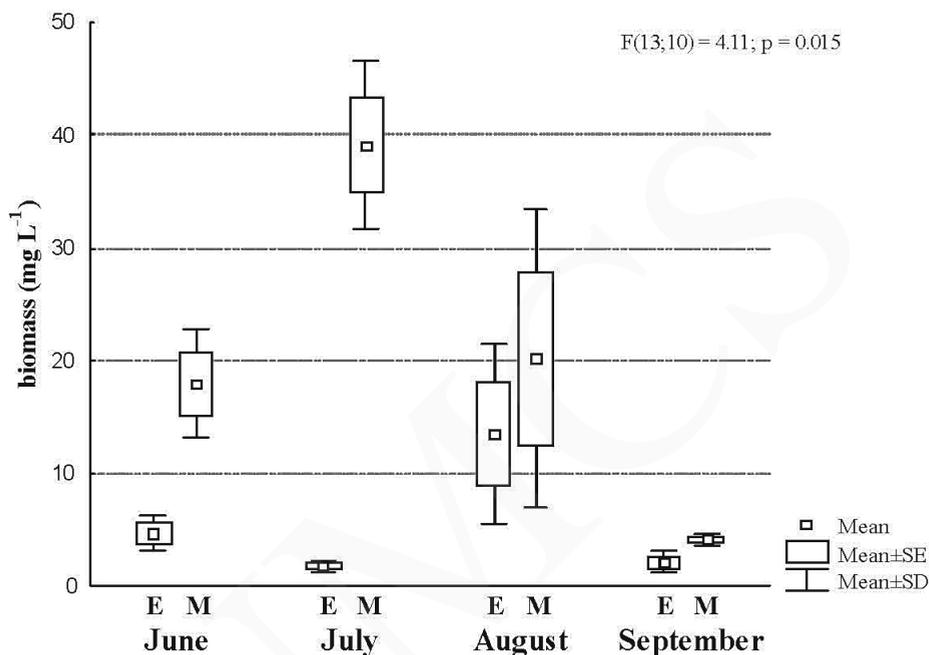


Fig. 3. Range of diurnal changes in biomass of *C. hirundinella* in two thermal layers. Explanations: E – epilimnion, M – metalimnion, F – value of F-test, SE – standard error, SD – standard deviation

in the phytoplankton throughout the whole study period (Fig. 2). Among them, *Cryptomonas rostrata*, *Peridinium aciculiferum* and *Coenococcus planctonicus* were the most abundant taxa. At the beginning of stratification in May, both in epi- and metalimnion, about 40% of phytoplankton biomass was composed of the cyanobacterium *Planktothrix rubescens*. Next, between June and August, it dominated only in metalimnion, contributing 80% of phytoplankton biomass (Fig. 2). The highest values of *Pl. rubescens* biomass were recorded at the depth of 6 m (19.06 – 43.5 mg dm⁻³) and at the depth of 7 m (13.07 – 24.4 mg dm⁻³) (Fig. 5). The biomass maxima of this cyanobacterium were always observed below the euphotic layer, i.e. at the depth where PAR intensity was < 1% (Fig. 5), and water temperature was < 10 °C.

DISCUSSION

Gas-vacuolate cyanobacterium *Pl. rubescens* and dinoflagellate *C. hirundinella* are often important components of phytoplankton in the metalimnetic waters of deep, stratified lakes (8, 14, 19). According to classification of phytoplankton

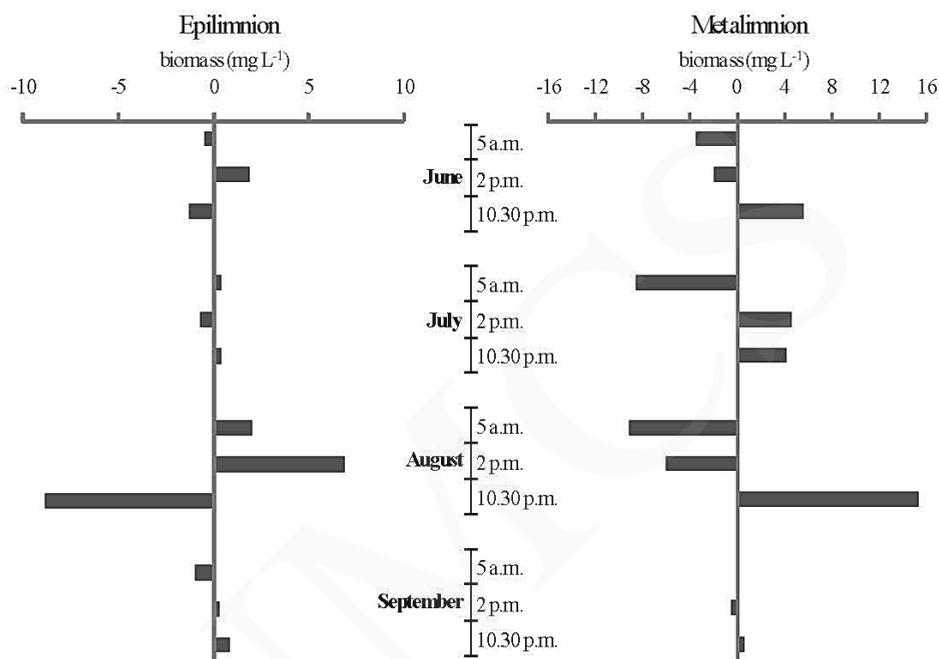


Fig. 4. Daily changes in biomass of *C. hirundinella* (expressed as deviation from the average daily of biomass)

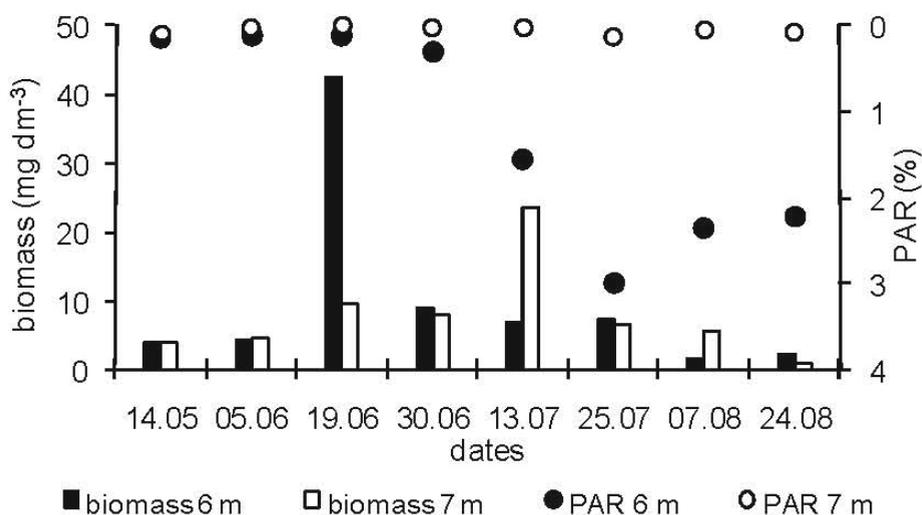


Fig. 5. Biomass values of *Pl. rubescens* and percentage values of PAR at two depths in Lake Rogóžno

to functional groups (24), *Pl. rubescens* belongs to R and *C. hirundinella* to L₀ group. Both groups comprised taxa typical of rather deep, oligo- and mesotrophic lakes.

The abundance of *Pl. rubescens* is strongly associated with illumination in metalimnion and also less with low temperature, phosphate depletion and high nitrogen loads (6). In metalimnion of Lake Rogóźno, below the euphotic layer, *Pl. rubescens* reached the high biomass. Good conditions for mass development of that species in deeper water are often associated with low biomass of phytoplankton, low light absorption and then high transparency in upper water layer (25). This is also found in Lake Rogóźno, i.e. the low biomass of phytoplankton (0.8–2.6 mg dm⁻³) and the low attenuation coefficient ($K_d = 0.7\text{--}0.9$) in epilimnion were noted. When the light intensity is too high or too low, *Pl. rubescens* may migrate downward or upward of the water column (18, 32). In the studied lake, the shift of biomass maxima between 6 and 7 m was observed which was related to searching of optimal light, often below 1% of PAR intensity. Possibility to carry out an intensive photosynthesis at extremely low light intensity is connected with high amount of ficoerythrin (29). Exposure to very high light intensities can often damage photosynthetic apparatus (5).

Dinophyte *C. hirundinella* occurs preferentially in lakes characterized by stable epilimnion and low nutrients concentrations (15). In Lake Zagłębcze, *C. hirundinella* was the species with the highest biomass in metalimnion. Many studies have shown that the biomass maxima of this species are often observed within the deeper part of the euphotic layer, where ca. 10 % of the light penetrates into the water (7). Most of the time during the study, the metalimnion of Lake Zagłębcze reached the depth of 5–7 m and it overlapped with the lower limit of the euphotic zone (SD = 3 m). In August, in varying light conditions because of the reduction of water transparency up to 2.5 m, the distribution of *C. hirundinella* biomass was more homogeneous in both thermal layers. During that month, also diurnal migrations of this species between epi- and metalimnion were observed. Part of the *C. hirundinella* population migrated at noon toward the surface, and the late afternoon and at night – toward deeper water layers (metalimnion). The movement of this species toward the upper water layer resulted from searching well illuminated water, while the movement toward the deeper water resulted from searching water with higher amounts of nutrients (1, 33).

The presented studies proved that in the conditions of the permanently sustained thermal gradient, the phytoplankton was dominated by two species: *Planktothrix rubescens* and *Ceratium hirundinella*. Despite different mechanisms responsible for motility (buoyancy or flagellar movement) and different time scale (day–night, between months) of migration, a shift of position in the water column corresponded mainly to changing light conditions.

REFERENCES

1. Alexander R., Imberger J. 2009. Spatial distribution of motile phytoplankton in a stratified reservoir: the physical controls on patch formation. *J. Plan. Res.* 31 (1): 101–118.
2. Barbosa L. G., Barbosa P. M. M., Barbosa F. A. R. 2011. Vertical distribution of phytoplankton functional groups in a tropical shallow lake: driving forces on a diel scale. *Acta Limnol. Brasil.* 23 (1): 63–73.
3. Beamud S. G., Diaz M. M., Baccala N. B., Pedrozo F. L. 2010. Analysis of patterns of vertical and temporal distribution of phytoplankton using multifactorial analysis: Acidic Lake Caviahue, Patagonia, Argentina. *Limnologica* 40: 140–147.
4. Becker V., de Souza Caedoso L., Huszar V. L. M. 2009. Diel variation of phytoplankton functional groups in a subtropical reservoir in southern Brazil during an autumnal stratification period. *Aquat. Ecol.* 43: 285–293.
5. Dubinsky Z., Stambler N. 2009. Photoacclimation processes in phytoplankton: mechanisms, consequences and applications. *Aquat. Microb. Ecol.* 56: 163–176.
6. Ernst B., Hoeger S. J., O'Brien E., Dietrich D. R. 2009. Abundance and toxicity of *Planktothrix rubescens* in the pre-alpine Lake Ammersee, Germany. *Harmful Algae*: 8: 329–342.
7. Gervais F., Siedel U., Heilmann B., Weithoff G., Heisig-Gunkel G., Nicklisch A. 2003. Small-scale vertical distribution of phytoplankton, nutrients and sulphide below the oxycline of a mesotrophic lake. *Journ. of Plan. Res.* 25 (3): 273–278.
8. Grabowska M., Górnjak A., Krawczuk M. 2013. Summer phytoplankton in selected lakes of the East Suwałki Lakeland in relation to the chemical water parameters. *Limnol. Rev.* 13 (1): 21–29.
9. Hart R.C., Wragg P. D. 2009. Recent blooms of the dinoflagellate *Ceratium* in Albert Falls Dam (KZN): History, causes, spatial futures and impacts on a reservoir ecosystem and its zooplankton. *Water SA (online)* 35 (4): 455–468.
10. Hillebrand H., Dürschen C. D., Kirschtel D., Pollinger U., Zohary T. 1999. Biovolume calculation for pelagic and benthic microalgae. *J. Phycol.* 35: 403–424.
11. Jacquet S., Briand J. F., Leboulanger C., Avois-Jacquet C., Oberhaus L., Tassin B., Vincon-Leite B., Paolini G., Druart J. C., Anneville O., Humbert J.F. 2005. The proliferation of the toxic cyanobacterium *Planktothrix rubescens* following restoration of the largest natural French lake (Lac du Bourget). *Harmful Algae* 4: 651–672.
12. Johansson K. S. L., Trigel C., Vrede T., Johnson R. K. 2013. Community structure in boreal lakes with recurring blooms of the nuisance flagellate *Gonyostomum semen*. *Aquat. Sci.* 75: 447–455.
13. Konopka A. 1989. Metalimnetic cyanobacteria in hard-water lakes: Buoyancy regulation and physiological state. *Limnol. Oceanogr.* 34 (7): 1174–1184.
14. Krupa D., Czernaś K. 2003. Mass appearance of Cyanoprokaryota *Planktothrix rubescens* as degradation symptom of Lake Piaseczno, Eastern Poland. *Wat. Qual. Res. J. Can.* 8 (1): 141–152.
15. Lopez N. L., Rondon C. A. R., Zapata A., Jimenez J., Vilamil W., Arenas G., Rincon C., Sanchez T. 2012. Factors controlling phytoplankton in tropical high-mountain drinking-water reservoirs. *Limnetica* 31(2): 305–322.
16. Medrano E. A., Uittenbogaard R. E., Dionisio Pires L. M., van de Wiel B. J. H., Clercx H. J. H. 2013. Coupling hydrodynamics and buoyancy regulation in *Microcystis aeruginosa* for its vertical distribution in lakes. *Ecol. Mod.* 248: 41–56.
17. Mellard J. P., Yoshiyama K., Litchman E., Klausmeier Ch. A. 2011. The vertical distribution of phytoplankton in stratified water columns. *J. Theor. Biol.* 269: 16–30.

18. Messyasz B., Lücke A., Schleser G. H. 2003. Dominance of cyanobacteria *Planktothrix rubescens* in Lake Holzmaar, Germany – an indication of the trophic status? Acta Bot. Warmiae and Masuriae 3: 21–31.
19. Messyasz B., Czerwik-Marcinkowska J., Lücke A., Uher B. 2012. Differences in the ultrastructure of two selected taxa of phytoplankton in thermally stratified Lake Holzmaar (Germany). Biodiv. Res. Conserv. 28: 55–62.
20. Messineo V., Mattei D., Melchiorre S., Salvatore G., Bogialli S., Salzano R., Mazza R., Capelli G., Bruno M. 2006. Microcystin diversity in a *Planktothrix rubescens* population from Lake Albano (Central Italy). Toxicon 48: 160–174.
21. Nush E.A. 1980. Comparison of different methods for chlorophyll and pheopigment determination. Arch. Hydrobiol. Beih. Ergebn. Limnol. 14: 14–36.
22. Oberhaus L., Briand J. F., Lebourlanger C., Jacquet S., Humbert J. F. 2007. Comparative effects of the quality and quantity of light and temperature on the growth of *Planktothrix agardhii* and *P. rubescens*. J. Phycol. 43: 1191–1199.
23. Padisak J., Barbosa F., Koschel R., Krienitz L. 2003. Deep layer cyanoprokaryota maxima in temperate and tropical lakes. Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 58: 175–199.
24. Padisak J., Crossetti L. O., Naselli-Flores L. 2009. Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. Hydrobiologia 621: 1–19.
25. Salmasso N. 2010. Long-term phytoplankton community changes in a deep subalpine lake: responses to nutrient availability and climatic fluctuations. Fresh. Biol. 55: 825–846.
26. Serizawa H., Amemiya T., Kiminori I. 2010. Effects of buoyancy, transparency and zooplankton feeding on surface maxima and deep maxima: Comprehensive mathematical model for vertical distribution in cyanobacterial biomass. Ecol. Model. 221: 2028–2037.
27. Solari C., Michod R. E., Goldstein R. 2008. *Volvox barberi*, the fastest swimmer of the Volvocales (Chlorophyceae). J. Phycol. 44: 1395–1398.
28. Trigal C., Hallstan S., Johansson K.S.L., Johnson R. K. 2013. Factors affecting occurrence and bloom formation of the nuisance flagellate *Gonyostomum semen* in boreal lakes. Harmful Algae 27: 60–67.
29. Tooming-Klunderud A., Soggea H., Ballestad-Roungea T., Nederbragta A. J., Lagesena K., Glöckner G., Hayes P. K., Rohrlack T., Jakobsena K. S. 2013. From green to red: Horizontal gene transfer of the Phycoerythrin gene cluster between *Planktothrix* strains. Appl. Environ. Microbiol. 79 (21): 6803–6812.
30. Yaoyang Xu, Qinghua Cai, Lan Wang, Linghui Kong, Daofeng Li 2010. Diel vertical migration of *Peridiniopsis niei*, Liu et al., a new species of dinoflagellates in an eutrophic bay of Three-Gorge Reservoir, China. Aquat. Ecol. 44(2): 387–395.
31. Vollenweider R. A. 1969. A Manual on Methods for Measuring Primary Production in Aquatic Environments. Blackwell, Oxford–Edinburgh.
32. Walsby A. E., Dubinsky Z., Kromkamp J. C., Lehmann C., Schanz F. 2001. The effects of diel changes in photosynthetic coefficients and depth of *Planktothrix rubescens* on the daily integral of photosynthesis in Lake Zürich. Aquat. Sci. 63: 326–349.
33. Whittington J. B., Sherman B., Green D., Oliver R.L. 2000. Growth of *Ceratium hirundinella* in a subtropical Australian reservoir: The role of vertical migration. J. Pl. Res. 22: 1025–1045.