Oceanological and Hydrobiological Studies

International Journal of Oceanography and Hydrobiology

Volume 44, Issue 2, June 2015

pages (164-171)

ISSN 1730-413X
eISSN 1897-3191

Winter bloom of some motile phytoplankton under ice cover in a mesotrophic lake: vertical distribution and environmental factors

by

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DOI: **10.1515/ohs-2015-0016**
Category: **Original research paper**
Received: **November 28, 2014**
Accepted: **January 20, 2015**

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Abstract

The research was carried out in mesotrophic Lake Krasne during winter with thick ice/snow cover. Water samples for biological and physicochemical analyses were collected vertically from the water column. Several phytoplankton groups were identified during the study, however, only two main groups of motile phytoplankton, Cyanophyceae (the dominant species – *Planktothrix rubescens*) and Cryptophyceae (*Cryptomonas* spp. and *Plagioselmis nannoplanctica*), were analyzed in the gradient of nutrients, light and thermal conditions. In the studied water column, values of physicochemical parameters did not vary in a wide range. Nevertheless, high discrepancies were noted in the values of phytoplankton biomass and the concentration of chlorophyll-*a* which had shallower maxima and deeper minima. Statistically significant relationships were found between the biomass of two main phytoplankton groups, light conditions (PAR) and depth, however, no significant relationships were found between the biomass, biogenic compounds and water temperature. The studies showed that in the winter season with ice/snow cover, cryptomonads and *Planktothrix rubescens* occupied different ecological niches and the main factor determining their distribution were light conditions. The ice/snow cover probably plays an important role in protection of *P. rubescens* winter filaments against photoinhibition.

Key words: *Planktothrix rubescens*, cryptomonads, light conditions, physicochemical factors

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Introduction

During cold winters, the thickness and quality of ice, as well as the presence of snow cover on the ice play an important role in thermal and light conditions, nutrient recycling, oxygen content, water stability, phytoplankton growth and biodiversity (Phillips, Fawley 2002; Leppäranta et al. 2003).

The winter minima of the phytoplankton biomass under the ice cover in different types of lakes are commonly observed (Wetzel 2001), however, some phytoplankton species, like flagellate algae with active motility (e.g. cryptomonads) or planktonic cyanobacteria regulating their buoyancy with gas vesicles (e.g. *Planktothrix rubescens*), are able to maintain their position in a stable water column or move to places with favorable environmental conditions (Kiili et al. 2009, Nõges et. al 2010). Hence, their populations can be distributed at different depths and, in consequence, produce blooms under ice in winter (McKnight et al. 2000; Mitrofanova et al. 2007; Dokulil, Herzig 2009; Babanazarova et al. 2013).

The abundant occurrence of phytoplankton under the ice cover is often connected with their ability to effectively use low light conditions. For example, some cyanobacteria as filamentous *Planktothrix rubescens* can maximize light absorption by the presence of a red pigment – phycoerythrin – in their cell. Hence, *P. rubescens* may bloom in metalimnion of a deep lake during summer stratification (Walsby et al. 2001), as well as during autumn or winter (Walsby, Schanz 2002) in similar low light conditions. Other algae as cryptomonads (e.g. the genus *Cryptomonas* or *Plagioselmis*) contain phycobiliproteins, large and effective light harvesting complexes, which enable photosynthesis in low light and thermal conditions (Hammer et al. 2002).

The aim of this study was to determine the vertical distribution of selected taxa of motile phytoplankton under thick ice/snow cover in the gradient of environmental conditions, and to answer the following questions:

1) Whether species of flagellates and species with gas vesicles occupy the same or different ecological niche?

2) Do they compete for resources (biogenic compounds) or physical conditions (light, temperature)?

Materials and methods

The phytoplankton community was studied in mesotrophic and dimictic Lake Krasne (51°25’36” N, 22°57’35” E, 164.0 m a.s.l) located in the Łęczna-Włodawa Plain (West Polesie region), Eastern Poland. The lake area is 0.76 km^2 and the maximum depth is 33.0 m (Wilgat et al. 1991).

The research was performed in 2010 during the winter season (January – March) when Lake Krasne was basically covered with thick ice/snow cover.

Water samples for biological (concentration of chlorophyll-*a*, phytoplankton biomass) and chemical (concentration of biogenic compounds) analyses were collected once a month from the pelagic zone of the lake using a Ruttner water sampler (2.0 l capacity). Samples were collected vertically from the depth just beneath the ice cover (ca. 0.5 m) up to 8 m, at one-meter intervals.

Samples for phytoplankton analysis were fixed with Lugol’s iodine solution and a formalin glycerine mixture. The abundance of phytoplankton was determined according to Utermöhl’s (1958) method and algal biovolume was calculated using the formula described by Hillebrand et al. (1999). The water samples were transferred to a settling chamber with a 50 ml capacity; after sedimentation, the algal abundance was evaluated using an inverted microscope (Zeiss Axiovert 135). In each chamber, small phytoplankton species were counted on belts at 400× magnification (at least 200 specimens); larger forms (filamentous or coccal colonies) were counted over the entire bottom of the chamber at a magnification of 200×. The unit length of 100 μm and a surface of 300 μm^2 were considered to be one individual for filamentous and coccal colonies, respectively. Additionally, samples for taxonomic analysis of phytoplankton were collected using a plankton net (20 μm mesh size) and were left without fixation to observe live specimens under a light microscope (Nikon Eclipse 80i).

In the laboratory, spectrophotometric analyses were conducted to determine the concentration of chlorophyll-*a* (Nush 1980), soluble nutrients (N-NH_4, N-NO_3, P-PO_4) and total phosphorus (TP) and total nitrogen (TN, Hermanowicz et al. 1999).

Physicochemical parameters i.e. electrolytic conductivity (EC), water reaction (pH), water temperature, ice and snow thickness and light transmission through ice/snow cover were measured in situ. The light transmission (photosynthetically active radiation – PAR) was measured with a Li–Cor meter (Li–250A) with an underwater quantum sensor (Li–192SA).

Analysis of covariance (ANCOVA) was used to determine main factors affecting the development of particular phytoplankton groups. Fisher's test was used to estimate the significance of their effects. All data were log transformed prior to calculations to meet assumptions of the parametric test. Spearman's rank correlation coefficient (r) was also applied in the analysis. All calculations were performed according to Sokal and Rohlf (1995) using Statistica 10 software.

Results

During the studied winter season (2010), Lake Krasne was permanently covered with ice, with the maximum thickness (ca. 35 cm) in March. The thickness of snow cover did not differ in a wide range and was around 10 cm, however, it had the strongest effect on the under-ice light climate in February when 14-cm-thick snow cover lying on the ice absorbed almost 95% of the surface light (Table 1). Nevertheless, the highest intensity of light (PAR, 75.5 μmol m^{-2} s^{-1}) in water just beneath the ice cover was noted in March, which was coupled with the highest insolation (PAR above the ice, Table 1).

The mean values of most physicochemical parameters in the whole water column (0.5-8 m) did not vary in a wide range during winter (Table 2). The smallest differences were noted for soluble nutrients (N-NH_4, N-NO_3, P-PO_4), as well as for electrolytic conductivity, water reaction and temperature. The highest discrepancies were noted in the values of total nitrogen and total phosphorus (TN and TP). Mean values of TN in the water column in March were two times higher than in January, contrary to values of TP, which were the highest in January. It was confirmed by mean values of the TN:TP ratio, which were the lowest in January and the highest in March (Table 2).

During winter 2010, values of biological parameters greatly varied along the water column. In the studied water column (0.5-8 m), values of the phytoplankton biomass and the concentration of chlorophyll-*a* varied over a wide range, from 0.02 to 10.43 mg l^{-1} and from 1.1 to 28.6 μg l^{-1}, respectively. Both parameters were highly correlated ($r = 0.75$; $p < 0.05$; $n = 27$) and had shallower maxima in the water layer from 0.5 m (just beneath the ice cover) to 4 m,

Table 1

Values of snow and ice thickness and values of PAR (Photosynthetic Active Radiation) above and beneath the ice/snow cover in winter 2010 in Lake Krasne

Variable	Unit	Month		
		January	February	March
Thickness of snow	cm	7	14	10
Thickness of ice	cm	11	24	35
PAR above the ice	μmol m^{-2} s^{-1}	222.1	514.9	841.2
PAR beneath the ice	μmol m^{-2} s^{-1}	36.3	28.6	75.5

Table 2

Mean values (and minimum-maximum range) of physicochemical parameters in the whole water column (0-8 m) in winter 2010 in Lake Krasne

Variable	Unit	Month		
		January	February	March
N-NH_4	mg l^{-1}	0.06 (0.04-0.09)	0.05 (0.04-0.08)	0.04 (0.03-0.06)
N-NO_3	mg l^{-1}	0.05 (0.04-0.06)	0.12 (0.10-0.15)	0.12 (0.10-0.15)
TN	mg l^{-1}	1.53 (1.24-2.06)	2.36 (2.29-2.53)	2.99 (2.57-4.05)
P-PO_4	mg l^{-1}	0.017 (0.014-0.027)	0.013 (0.010-0.015)	0.012 (0.010-0.015)
TP	mg l^{-1}	0.041 (0.033-0.054)	0.029 (0.023-0.040)	0.031 (0.026-0.041)
TN:TP		39:1 (29:1-61:1)	84:1 (58:1-114:1)	94:1 (98:1-117:1)
Conductivity	μS cm^{-1}	297 (295-301)	305 (300-310)	303 (298-306)
pH		7.8 (7.6-8.0)	7.7 (7.6-7.8)	8.0 (7.7-8.3)
Water temperature	°C	2.3 (1.4-2.7)	2.0 (1.1-2.3)	2.1 (1.0-2.4)

and deeper (5-8 m) minima (Fig. 1).

Several phytoplankton groups were identified during the study, although only two main taxonomic groups, Cyanophyceae and Cryptophyceae, had a considerable contribution in the total phytoplankton biomass. Both groups often represented above 80% of the total biomass, especially in the shallower water column, i.e. from 0.5 m to 4 m. Therefore, these two phytoplankton groups are presented in Figure 1, whereas the other groups are referred to as "others". The group of "others" includes phytoplankton species belonging to Euglenophyceae, Chrysophyceae, Bacillariophyceae and Chlorophyceae and had higher contribution in the phytoplankton biomass only at the deeper (5-8 m) part of the water column where values of the total biomass and chlorophyll-*a* were negligible (Fig. 1).

The difference between the dominant phytoplankton groups consists in their locomotion. *Cryptomonas marssonii* (Skuja), *Cryptomonas rostrata* Troitzkaja and *Plagioselmis nannoplanctica* (Skuja) Novarino, were included in the group of flagellated Cryptophyceae, whereas filamentous *Planktothrix rubescens* (DeCand. ex Gom.) Anagn. et Kom. equipped with gas vesicles was the most important species in the group of Cyanophyceae. Both groups dominated in the shallower water layers, however, they often occupied separate parts of the water column (Fig. 2). The highest differences in the biomass distribution between these two groups were observed in March when light conditions in the water under the thick ice/snow cover were relatively good, contrary to other winter months (Fig. 2). In such conditions, cryptomonads dominated near the ice cover (0.5 m, PAR = 30.6 µmol m^{-2} s^{-1}), whereas *P. rubescens* – at a depth of 1 m, in slightly lower light intensity (PAR = 21.7 µmol m^{-2} s^{-1}). Also the second peak of *P. rubescens* biomass was interesting –

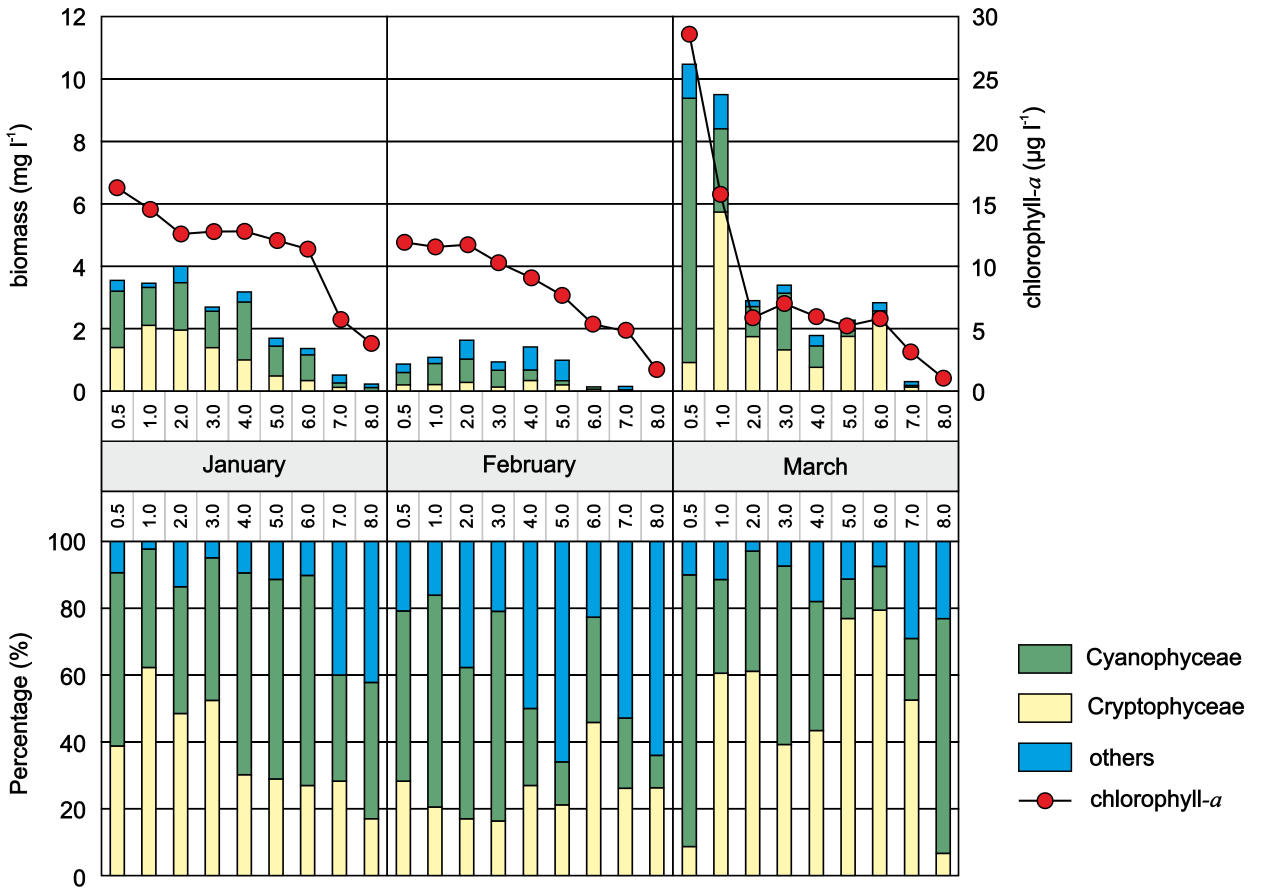

Figure 1

Vertical variations of chlorophyll-*a*, phytoplankton biomass (upper panel) and percentage of the main phytoplankton groups based on the biomass (bottom panel) in winter 2010 in Lake Krasne

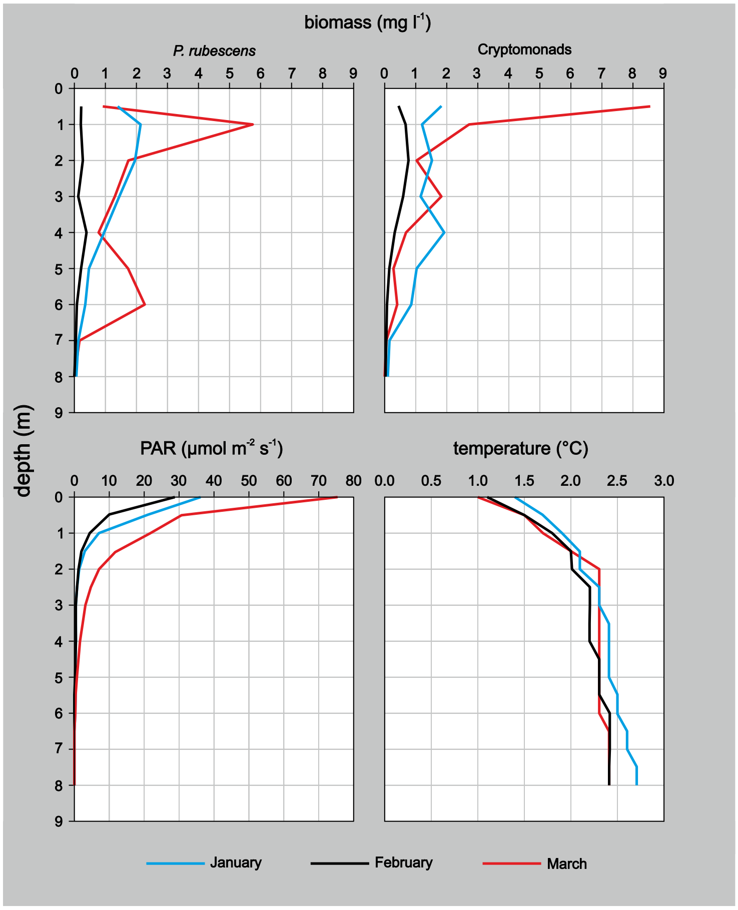

Figure 2

Vertical distribution of light (Photosynthetic Active Radiation, PAR), water temperature and biomass of selected motile phytoplankton under the ice cover in winter 2010 in Lake Krasne

recorded in March at a depth of 6 m, with extremely low values of light intensity (PAR, 0.8 µmol m^{-2} s^{-1}). Values of water temperature at different depths only slightly varied in the following months (Fig. 2).

The relationships between the physicochemical parameters and the values of the Cryptophyceae and Cyanophyceae biomass were tested using Fisher's test (ANCOVA). Statistically significant relationships were found between the biomass of both phytoplankton groups, light conditions (PAR) and depth, however, no significant relationships were found between the biomass, biogenic compounds (TN and TP) and water temperature (Table 3). Thus, the water layer just beneath the ice cover and relatively good light conditions led to a greater biomass of the Cryptophyceae group, whereas slightly lower light conditions and depth were coupled with the development of Cyanophyceae groups.

Table 3

The results of ANCOVA (F-test) for relationships between the biomass of the Cyanophyceae and Cryptophyceae group and the main physicochemical parameters

Parameters	Cyanophyceae		Cryptophyceae	
	df	F-test	*df*	F-test
PAR beneath the ice		4.58^{a}		10.56^{a}
Depth		19.45^{b}		44.07^{b}
Temperature	1	1.09	1	1.29
Total nitrogen (TN)		0.72		0.23
Total phosphorus (TP)		0.96		2.64

^{a} $p<0.05$; ^{b} $p<0.001$

Discussion

Small values of phytoplankton biomass and poor species composition with the dominance of cryptomonads, diatoms, chrysophytes or small green algae are often reported in the winter season (Wetzel 2001; Barone, Naselli-Flores 2003; Mitrofanova et al. 2007). In shallow eutrophic or hypertrophic lakes, however, the filamentous cyanobacteria i.e. *Limnothrix* spp., *Pseudoanabaena* spp. or *Planktothrix* spp. could develop in great numbers under the ice cover, even during the coldest winters (Wiedner, Nixdorf 1998; Toporowska et al. 2010; Babanazarova et al. 2013).

In Lake Krasne, the values of biogenic compounds were generally high, and they were not a limiting factor for the phytoplankton growth. Hence, their role in the phytoplankton development was statistically insignificant. This is consistent with the observations of Wiedner&Nixdorf (1998) that the role of nutrients during the winter season may be secondary. The ratio of TN:TP in Lake Krasne greatly varied, although it was never below 29:1. Low values of the TN:TP ratio is considered favorable to the dominance of cyanobacteria (Smith 1983, Havens et al. 2003), which are more capable of competing for nitrogen than other algae. Nevertheless, the abundant occurrence of cyanobacteria *Planktothrix rubescens* under the ice cover was observed in Lake Krasne, which supports the hypothesis of Teubner&Dokulil (2002) that highly fluctuating TN:TP ratios in mesotrophic lakes can also favor cyanobacterial dominance.

In Lake Krasne, only several species belonging to Cyanophyceae (i.e *Planktothrix rubescens*) and Cryptophyceae (i.e. *Plagioselmis nannoplanctica*, *Cryptomonas marssonii*, *C. rostrata*) found favorable conditions for their abundant occurrence under the ice cover. During winter, the light intensity in the water column was low, however, it was more important to the development of cryptomonads. They were present in the whole examined water column, but they dominated in the phytoplankton biomass just beneath the ice cover with the highest availability of light, which is consistent with the observations of Danilov&Ekelund (2001), Mitrofanova et al. (2007) Vehmaa&Salonen (2009) or Wojciechowska&Lenard (2014) in lakes of different trophic conditions. A similar effect of cryptomonads distribution was reported from a Finnish humic lake in the summer season. Cells of cryptomonads responded to light – in daylight they usually concentrated at the surface or subsurface of the lake and migrated downward the water column at night (Jones 1988, Smolander&Arvola 1988).

During the winter season, the presence of filamentous cyanobacteria is often observed in lakes with a high trophic status (Toporowska et al. 2010, Babanazarova et al. 2013), however, their abundant occurrence under thick ice cover is occasionally reported from mesotrophic lakes (Halstvedt et al. 2007). Large numbers of *P. rubescens* in winter were reported from Poland only once. It was in 1989 in mesotrophic Lake Piaseczno (Eastern Poland) when the lake was free of ice cover throughout the winter (Krupa, Czernaś 2003). Therefore, in some deep lakes in Italy, *P. rubescens* is called a "winter species" (Messineo et al. 2006) because its dominance is generally observed during mild winters when lakes are completely devoid of ice cover.

On the other hand, the abundant occurrence of *P. rubescens* in Lake Krasne was reported in winter with thick ice/snow cover. The highest biomass of *P. rubescens* was recorded in March at a depth of 1 m, just below the layer of abundant occurrence of cryptomonads. The reverse effect of cryptomonads and filamentous cyanobacteria coexistence was observed during the summer season in a Finnish humic lake. Cryptomonads usually gathered at greater depths of the water column (at a depth of 1.5 m), under the layer with a dense cyanobacterial bloom that restricted their migration to the water column with better light conditions (Smolander&Arvola 1988). In March, *P. rubescens* dominated in Lake Krasne at a depth of 1 m when values of light were around 21 μmol m^{-2} s^{-1} and at 6 m at extremely low light intensity (0.8 μmol m^{-2} s^{-1}). Hence, winter development of "shade tolerant" *P. rubescens* seems to be more resistant to insufficient light conditions. Light intensity around 20 μmol m^{-2} s^{-1} is even better than the values of light measured in metalimnion during summer stratification in *P. rubescens*-like subalpine lakes of Europe (Walsby et al. 2001, Legnani et al. 2005, Jacquet et al. 2005). Laboratory experiments (Kromkamp et al. 2001, Oberhaus et al. 2007) confirmed that low light intensity (around 10 μmol m^{-2} s^{-1}), especially the fraction of green light at a temperature of 15°C, effectively supports the *P. rubescens* development. Thermal conditions under the ice/snow cover in Lake Krasne were different (mean water temperature around 2°C), however, light conditions in the layer with high biomass of *P. rubescens* were at similar levels compared to those obtained in laboratory experiments. On the other hand, high light intensity (above 200 μmol m^{-2} s^{-1}) can cause photoinhibition of the photosynthetic apparatus in *P. rubescens* (Oberhaus et al. 2007). Hence, the thick ice/snow cover probably plays an important role in the protection of *P. rubescens* filaments against photoinhibition, especially in late winter (March) when the light intensity above the ice cover can be high.

Conclusions

Light conditions played the most important role in the winter development of both groups: Cyanophyceae and Cryptophyceae.

In stable conditions of winter stagnation, flagellated species and species with gas vesicles occupied different water layers and in consequence, separate ecological niches.

Development of both motile phytoplankton groups seems to be independent of nutrient concentration under the ice cover.

The ice/snow cover probably plays an important role in the protection of *P. rubescens* filaments against photoinhibition.

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