

Microbial and classic food web components under ice cover in eutrophic lakes of different morphometry and fisheries management

by

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DOI: [10.1515/ohs-2017-0029](https://doi.org/10.1515/ohs-2017-0029)

Category: **Original research paper**

Received: **November 28, 2016**

Accepted: **January 16, 2017**

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Abstract

The thickness and duration of ice cover are strongly influenced by global warming. The aim of this study was to determine chemical (organic carbon, total nitrogen and phosphorus concentrations) and biological (nanoflagellates, ciliates, phytoplankton, rotifers, crustaceans) parameters under the ice cover in three eutrophic lakes (Masurian Lake District, Poland), differing in their morphometry and fisheries management. All the studied groups of organisms showed high variability over a short time. Taxonomic composition of planktonic communities, except for rotifers and phytoplankton, was similar in all lakes. Nanoflagellates were dominated by autotrophic forms, while ciliates were primarily composed of small oligotrichs and prostomatids. Nano-sized diatoms and mixotrophic cryptophytes were the most important components of phytoplankton and they formed an under-ice bloom in one lake only. Rotifers were mainly represented by *Keratella cochlearis*, *Polyarthra dolichoptera* and *Asplanchna priodonta*. Among crustaceans, copepods clearly dominated over cladocerans. Our research suggests that winter was a very dynamic period. In the under-ice conditions, pelagic organisms were strongly dependent on each other. The shallow lake and the deeper, small lake differed significantly in nutrient and chlorophyll concentrations, ciliate and phytoplankton biomass and the ratio of autotrophic to heterotrophic biomass. These results suggest that morphometric parameters may affect planktonic organisms during the ice-covered period.

Key words: winter, ice cover, protists, phytoplankton, rotifers, crustaceans, fish stocking, eutrophic lakes

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Introduction

For many years, little attention has been paid to the winter ice-covered period in temperate lakes. The reason for this was not only the hard fieldwork conditions and methodological problems with sampling, but mainly the opinion that winter is a dormant season. It was assumed that the metabolic activity of planktonic organisms is reduced or even completely ceased due to low temperature, limited light availability and a short day (reviewed by Bertilsson et al. 2013).

Recent studies showed that aquatic communities can exist under the ice, showing adaptation to hard and unfavorable environmental conditions (Üveges et al. 2012). For example, phytoplankton may form massive under-ice blooms (e.g. Vehmaa & Salonen 2009; Babanazarova et al. 2013; Kalinowska & Grabowska 2016). In turn, the breakdown of phytoplankton blooms may cause extremely high bacterial abundance and biomass (Biżić-Ionescu et al. 2014). Intensive phytoplankton blooms as well as high abundance and activity of heterotrophic bacteria in ice-covered lakes are to a large extent a consequence of climate changes, leading to the decline or absence of ice/snow cover and the reduction of ice duration (Weyhenmeyer et al. 2011). On the other hand, snow, thick ice cover, low primary production and high decomposition of organic materials affect the oxygen depletion, subsequently influencing the winter fish kills and the cascading effect on lake food webs (Balayla et al. 2010; Sayer et al. 2016).

Studies that consider simultaneously all functional groups of aquatic food webs are still very scarce. The results of these studies showed that during the ice-covered period, nanoflagellates, ciliates and rotifers can reach high abundances, while crustaceans are usually few or even absent (Ventelä et al. 1998; Dokulil & Herzig 2009; Twiss et al. 2012; Kalinowska & Grabowska 2016). In addition, literature data show that primary producers can live not only in the water column below the ice cover, but also in liquid water pockets of lake ice sheets, where light conditions are more favorable than in the under-ice water (Kirillin et al. 2012).

It is well documented that winter conditions may significantly affect the functioning and structure of water ecosystems throughout the year (Adrian et al. 1999; Weyhenmeyer et al. 1999; Kirillin et al. 2012; Haberyan 2016), including spring phytoplankton (Yang et al. 2016), thermal regime, the amount of organic carbon production, summer hypoxia (Twiss et al. 2012), metabolic features of freshwater microorganisms, food web development (Bertilsson et al. 2013; Biżić-Ionescu

et al. 2014), and dynamics of planktonic organisms (Dokulil & Herzig 2009; Vehmaa & Salonen 2009). According to Haberyan (2016), a single strong climatic anomaly may affect a lake for several years, including a possible increase in winter fish kills (Sayer et al. 2016).

Although the number of studies on temperate ice-covered lakes increased in recent years, much more information about physical, chemical and biological processes is available for perennially ice-covered Arctic and Antarctic lakes than for seasonally ice-covered lakes (Kirillin et al. 2012). Therefore, much more studies of aquatic ecosystems in different parts of the world, focusing on all planktonic communities, are needed to better understand the structure and functioning of under-ice food webs (Twiss et al. 2012; Bertilsson et al. 2013; Biżić-Ionescu et al. 2014).

The aim of this study was to determine the abundance and composition of the microbial (nanoflagellates, ciliates) and classic (phytoplankton, rotifers, crustaceans) food webs' components in eutrophic Masurian lakes under the ice cover. Because only some species among various taxonomic groups of organisms can adapt to the under-ice conditions, e.g. low temperature and light intensities (Üveges et al. 2012; Biżić-Ionescu et al. 2014), we hypothesized that eutrophic temperate lakes, differing in morphometry and fisheries management, do not differ in abundance and structure of planktonic communities under the ice.

Materials and Methods

The study was conducted in three eutrophic lakes with different stages of eutrophication (Napiórkowska-Krzebietke et al. 2012; Zakęś et al. 2015), situated in the Masurian Lake District (northeastern Poland). Lake Warniak is a shallow lake with submerged vegetation dominated by charophytes. Two other lakes are deeper and vary in area – Lake Dgał Wielki is a medium-sized lake, while Lake Dgał Mały – a small-sized one. Morphometric characteristics of the lakes are given in Table 1. Historically, all lakes were stocked with seston-filtering and herbivorous fish species – *Ctenopharyngodon idella* (Val.), *Hypophthalmichthys molitrix* (Val.), *Hypophthalmichthys nobilis* (Rich.) – with varying frequency, amounts and their subsequent exploitation, causing an increase in the trophic level and sporadic winter oxygen depletion (reviewed by Napiórkowska-Krzebietke et al. 2012). From 2000 until now, the stocking with predatory fish (e.g. *Esox lucius* L., *Silurus glanis* L., *Sander lucioperca* (L.), *Anguilla anguilla* L.) was carried out in all the studied lakes (Zakęś et al. 2015). In 2000-2010, the highest regularity (10 years) and the number of fish species stocked (6)

Table 1

Morphometric characteristics of the studied Masurian lakes.

Lake	Area (ha)	Max depth (m)	Mean depth (m)	Max length (m)	Max width (m)	Mixing type
Warniak	38.4	3.7	1.2	1000	500	polymictic
Dgał Wielki	93.9	18.8	5.7	1275	1110	dimictic
Dgał Mały	14.4	15.8	4.6	670	295	dimictic

were in Lake Dgał Wielki, followed by Lake Warniak (10 years, 3 fish species) and Lake Dgał Mały (5 years, 3 fish species), also varying in stocking doses per 1 ha and consecutive fish catches in each lake. In 2011-2014, all lakes were regularly stocked with *E. lucius* (Dgał Wielki and Warniak) and *S. lucioperca* (Dgał Mały), and the total annual stocking dose was 45 ind. per ha. Both fish species are very important in maintaining the proper structure of the fish community and appropriate balance in the food web.

Water samples were collected once a week in February 2016 (four occasions in each lake) from just beneath the ice cover. During the sampling period, the deepest parts of the lakes were not accessible due to thin or brittle and cracked ice. For this reason, our samples were collected from a site about 20 m away from the shore. On each sampling day, the thickness of the ice and snow were measured.

Temperature and oxygen concentrations were measured using a YSI oxygen meter (Model 57).

Total phosphorus (TP) concentrations were determined colorimetrically, after mineralization, using a Shimadzu UV 1601 spectrophotometer (Standard Methods 1999).

Nitrogen and organic carbon concentrations were measured by a Shimadzu TOC-VCSH with a TNM-1 module and automatic sample changer ASI-V using a NDIR detector, according to PN-EN 12260:2004 and PN-EN 1484:1999, respectively. To measure total nitrogen (TN) and total organic carbon (TOC), water samples were homogenized with a magnetic stirrer, while to measure dissolved organic carbon (DOC), water samples were filtered through 0.45- μm pore-size membrane filters. Particulate organic carbon (POC) was calculated as the difference between the TOC and DOC concentrations.

Chlorophyll *a* concentrations were determined by the spectrophotometric analysis of acetone extracts of algae and cyanobacteria retained on Whatman GF/C filters according to Golterman (1969).

Nanoflagellate (NF) samples were fixed with formaldehyde (final concentration 2%), stained with DAPI (Porter & Feig 1980), filtered through 0.8 μm pore size polycarbonate membrane filters (Millipore) and enumerated by epifluorescence microscopy

(Nikon Optiphot 2). The NF biovolume was calculated from measurements of cells size and their approximations to simple geometric forms. The carbon content was calculated by multiplying the biovolume with a conversion factor of 200 fg C μm^{-3} (Børsheim & Bratbak 1987). Autotrophic (ANF) and heterotrophic (HNF) nanoflagellates were differentiated on the basis of chlorophyll *a* autofluorescence.

Ciliate samples were fixed with Lugol's solution and examined under a light microscope (Nikon Eclipse E200). Biovolume was calculated from measurements of cell dimensions and simple geometric shapes and converted to carbon biomass using a conversion factor of 190 fg C μm^{-3} (Putt & Stoecker 1989). Species identifications of ciliates were based mainly on Foissner et al. (1999).

Phytoplankton samples were fixed with Lugol's solution and then ethanol, and enumerated by an inverted microscope (Nikon) according to Utermöhl (1958). Biomass was calculated from cell volume measurements, according to standard methods (Napiórkowska-Krzebietke & Kobos 2016). The content of phytoplankton cell carbon was calculated from cell volume according to the formula and coefficients given for freshwater phytoplankton species (Rocha & Duncan 1985). Phytoplankton composition was determined using a Carl Zeiss Jena "Jenamed" light microscope at 200 \times , 400 \times and 1000 \times magnifications with oil immersion. Taxa identifications followed the newest references (e.g. Huber-Pestalozzi 1983; Krammer & Lange-Bertalot 1986; 1988; 1991; Komárek & Anagnostidis 2005) and currently accepted taxonomic names were confirmed according to Guiry & Guiry (2016).

Rotifers and crustaceans were collected using a 5 l Patalas sampler with five replicates (25 l in total). Samples were concentrated using a 30 μm mesh plankton net and preserved with Lugol's solution and 96% ethanol. The abundance of zooplankton was quantified using a Sedgwick-Rafter counting cell under an optical microscope. Identification of zooplankton species was based mainly on Flössner (1972), Radwan et al. (2004) and Rybak & Błędzki (2005). Length and length-dry mass relationships were used to determine the biomass of rotifers using Ejsmont-Karabin (1998)

and the biomass of crustaceans using Bottrell et al. (1976). The biomass of rotifers and crustaceans was converted to carbon units assuming that carbon content is 45% and 40% of the dry weight, respectively (Latja & Salonen 1978).

Statistical analyses of results were carried out using the STATISTICA software (StatSoft, Inc.). The differences in chemical and biological parameters between the studied lakes were analyzed using the nonparametric analysis of variance. The Kruskal-Wallis test followed by the Mann-Whitney *U*-test (post hoc test) was used to determine whether there were differences among three lakes. The biological, physical and chemical variables were correlated using principal component analysis (PCA) with a correlation matrix. The probability level at which statistical analyses were accepted as significant was ≤ 0.05 . The coefficient of variation (CV – % standard deviation of the mean) was used to compare variability of the studied parameters in the lakes.

Results

Physical and chemical characteristics

The studied lakes did not differ statistically (Kruskal-Wallis test, $P > 0.05$) in the thickness of the ice that declined gradually from 13-18 cm at the beginning of the study period to about 5 cm at the end. There was no ice cover on the surface of Lake Warniak on the 24th of February. In all the studied lakes, the ice was not covered with snow. Water temperature under ice was about 0-1°C. During the study period, water was always oxygenated (10.4-13.2 mg l⁻¹).

Dissolved organic carbon (DOC) concentrations were rather low (Table 2) and did not differ significantly between the studied lakes (Kruskal-Wallis test, $P > 0.05$). Although the mean concentration of particulate organic carbon (POC) was about two times higher in Lake Dgął Mały than in Lake Warniak, the differences

between the lakes were not statistically significant (Kruskal-Wallis test, $P > 0.05$).

The studied lakes were characterized by relatively high concentrations of total phosphorus (TP) and nitrogen (TN) (Table 2). The highest mean concentration of TP was recorded in Lake Dgął Mały, a slightly lower value was noted in Lake Dgął Wielki, while the lowest – in Lake Warniak. The mean values of TN in lakes Warniak and Dgął Wielki were similar and clearly lower than in Lake Dgął Mały. Statistical differences in TP and TN were significant between lakes Warniak and Dgął Mały (Kruskal-Wallis test, $P < 0.05$).

The mean concentration of chlorophyll *a* in Lake Dgął Mały was about two and five times higher than in lakes Dgął Wielki and Warniak, respectively (Table 2). Similarly as in the case of TP and TN, the differences in chlorophyll *a* were statistically significant between Lake Warniak and Lake Dgął Mały (Kruskal-Wallis test, $P < 0.05$).

Microbial food web components

The mean numbers and biomass of nanoflagellates were clearly higher in Lake Dgął Mały than in lakes Dgął Wielki and Warniak (Fig. 1A, B). However, the differences between the studied lakes, both in the numbers and biomass, were not statistically significant (Kruskal-Wallis test, $P > 0.05$). Autotrophic cells (ANF) formed a substantial part of both the total nanoflagellate numbers and biomass in lakes Warniak and Dgął Mały, while heterotrophic cells (HNF) dominated both in terms of their total numbers and biomass in Lake Dgął Wielki.

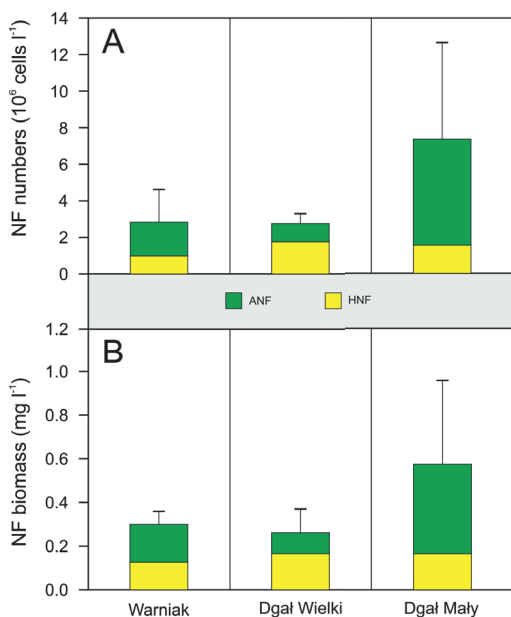
The ciliate assemblage was characterized by low numbers (Fig. 2A) and particularly low biomass (Fig. 2B). The mean numbers and biomass of ciliates were the highest in Lake Dgął Mały. In lakes Dgął Wielki and Warniak, the mean numbers of ciliates were about two times lower, while the mean biomass – three times lower. Oligotrichs, represented by small species from the genus *Rimostrombidium* (mainly *R. humile* (Penard)

Table 2

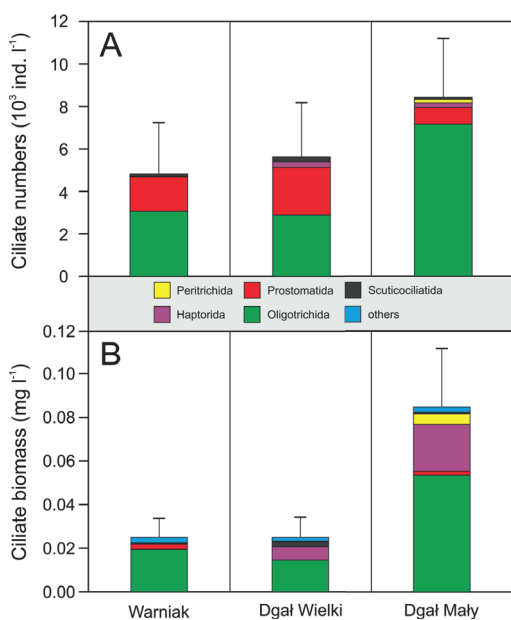
Chemical parameters during the ice-covered period in the eutrophic Masurian lakes. Mean values with standard deviations and ranges in parentheses.

Lake	DOC (mg l ⁻¹)	POC (mg l ⁻¹)	TP (μg l ⁻¹)	TN (mg l ⁻¹)	Chl <i>a</i> (μg l ⁻¹)
Warniak	4.78 ± 0.77 (3.75-5.60)	0.23 ± 0.13 (0.10-0.37)	63 ± 7 (56-72)	0.97 ± 0.10 (0.87-1.10)	3.28 ± 1.12 (2.46-4.92)
Dgął Wielki	4.81 ± 0.61 (4.31-5.69)	0.34 ± 0.16 (0.19-0.57)	94 ± 19 (75-118)	1.04 ± 0.15 (0.91-1.22)	6.45 ± 1.09 (5.12-7.78)
Dgął Mały	5.71 ± 1.62 (4.23-7.50)	0.45 ± 0.11 (0.29-0.52)	105 ± 19 (81-128)	1.24 ± 0.08 (1.12-1.30)	15.47 ± 8.63 (5.32-24.78)

DOC: dissolved organic carbon; POC: particulate organic carbon; TP: total phosphorus, TN: total nitrogen, Chl *a*: chlorophyll *a*.

**Figure 1**

The numbers (A) and biomass (B) of nanoflagellates, with autotrophic (ANF) and heterotrophic (HNF) cells marked, during the ice-covered period in the eutrophic Masurian lakes. Mean values from four sampling datasets with standard deviations for the total numbers and biomass.

**Figure 2**

The numbers (A) and biomass (B) of ciliates, with taxonomic groups marked, during the ice-covered period in the eutrophic Masurian lakes. Mean values from four sampling datasets with standard deviations for the total numbers and biomass.

Petz & Foissner), constituted a substantial part of both the total numbers and biomass (52-85%) in all the studied lakes. Small prostomatids, such as *Balanion planctonicum* (Foissner, Oleksiv & Müller) Foissner, Berger & Kohmann and *Urotricha* spp. (primarily *U. furcata* Schewiakoff), dominated in Lake Dgał Wielki, accounting for 40% of the total numbers. Haptorida, composed mainly of mixotrophic *Cyclotrichium viride* Gajewskaja, were an important component of ciliate biomass in Lake Dgał Mały, accounting for 25% of the total biomass. Statistical analysis revealed significant differences in ciliate biomass only between lakes Warniak and Dgał Mały (Kruskal-Wallis test, $P < 0.05$).

Classic food web components

The numbers (Fig. 3A) and biomass (Fig. 3B) of phytoplankton differed markedly between the studied lakes. The highest mean numbers and biomass were noted in Lake Dgał Mały and about two times lower values were recorded in Lake Dgał Wielki. Lake Warniak was characterized by particularly low numbers and biomass of these organisms. However, statistical analysis revealed significant differences only in the phytoplankton biomass between Lake Warniak and Lake Dgał Mały (Kruskal-Wallis test, $P < 0.05$). Generally, the phytoplankton community was dominated by two taxonomic groups, namely diatoms and cryptophytes. However, the studied lakes differed in their mean percentage contribution. Diatoms (mainly nanoplanktonic *Cyclotella* sp. and colonial *Fragilaria construens* (Ehrenberg) Grunow, *Fragilaria capucina* Desmazières) dominated in the total numbers in lakes Dgał Wielki and Dgał Mały (66 and 60%, respectively) as well as in the total biomass in Lake Dgał Wielki (50%). Cryptophytes (represented by nanoflagellate *Plagioselmis nannoplanctica* (H. Skuja) G. Novarino, I. A. N. Lucas & S. Morrall and *Rhodomonas lens* Pascher & Ruttner in Lake Warniak and by *Rhodomonas lens* and microplanktonic *Cryptomonas curvata* Ehrenberg, *Cryptomonas erosa* Ehrenberg and *Cryptomonas marssonii* Skuja in Lake Dgał Mały) dominated in the total numbers in Lake Warniak (60%) and in the total biomass in lakes Warniak and Dgał Mały, accounting for 44% and 50% of the total biomass, respectively (Fig. 3A, B). Cyanobacteria (primarily filamentous *Limnothrix redekei* (Goor) Meffert) and dinoflagellates (primarily *Gymnodinium uberrimum* (G. J. Allman) Kofoid & Swezy, *Naiadinium polonicum* (Woloszynska) S. Carty and *Gyrodinium helveticum* (Penard) Y. Takano & T. Horiguchi) accounted for an important part of the total biomass in lakes Dgał Mały and Dgał Wielki, respectively (11 and 16%). Chlorophytes (primarily nanoflagellate

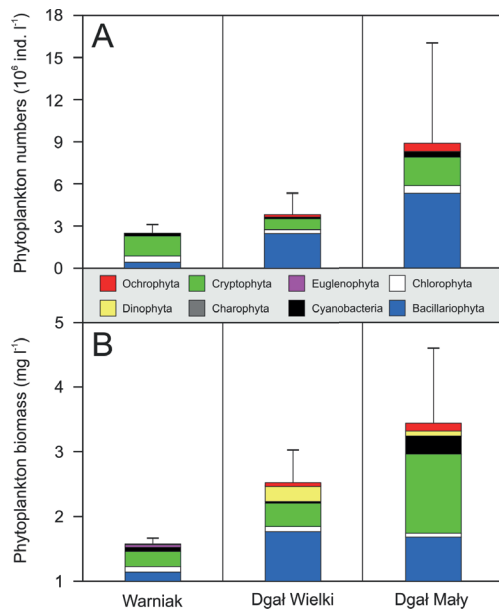


Figure 3

The numbers (A) and biomass (B) of phytoplankton, with taxonomic groups marked, during the ice-covered period in the eutrophic Masurian lakes. Mean values from four sampling datasets with standard deviations for the total numbers and biomass.

Chlamydomonas) contributed a significant portion to the total numbers and biomass in Lake Warniak (18 and 14%, respectively). Other groups of phytoplankton, such as euglenophytes, ochrophytes and charophytes accounted for a small part (< 7%) of the total numbers and biomass.

The numbers (Fig. 4A) and biomass (Fig. 4B) of rotifers were low in the studied lakes. The highest mean numbers was recorded in Lake Dgał Wielki and slightly lower values were noted in Lake Dgał Mały. In contrast, the highest mean rotifer biomass was observed in Lake Dgał Mały. Lake Warniak was characterized by a relatively low numbers and biomass of rotifers. There were no statistical differences in the numbers and biomass of rotifers between the studied lakes (Kruskal-Wallis test, $P > 0.05$). In terms of the numbers, the dominance structure was very similar in all the studied lakes, where *Keratella cochlearis* (Gosse) dominated, accounting for 80, 82 and 58% of the total numbers in lakes Warniak, Dgał Wielki and Dgał Mały, respectively. The second most abundant species were: *Filinia terminalis* (Plate) in Lake Warniak (7% of the total numbers) and *Polyarthra dolichoptera* Idelson in lakes Dgał Wielki and Dgał Mały (15 and 26%, respectively). Taking into account the total biomass, different species of rotifers were dominant in different lakes. Species from the genus *Keratella* (mainly *K. cochlearis*)

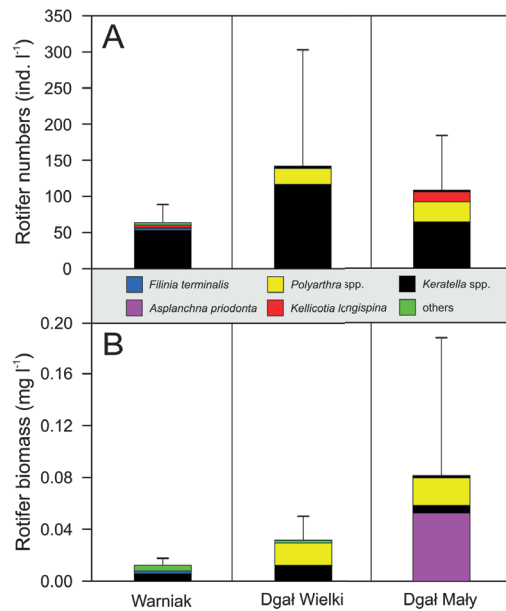


Figure 4

The numbers (A) and biomass (B) of rotifers, with dominant taxa marked, during the ice-covered period in the eutrophic Masurian lakes. Mean values from three sampling datasets with standard deviations for the total numbers and biomass.

dominated in Lake Warniak (48% of the total biomass), *Polyarthra* spp. (primarily *P. dolichoptera*) dominated in Lake Dgał Wielki (55%), whereas large predatory *Asplanchna priodonta* Gosse was a dominant species in Lake Dgał Mały (65% of the total biomass).

The highest mean numbers of crustaceans was noted in Lake Dgał Mały (Fig. 5A). The values were similar in the two other lakes, Warniak and Dgał Wielki, and about two times lower compared to Lake Dgał Mały. The mean biomass of crustaceans was the highest in Lake Warniak, while the slightly lower value was noted in Lake Dgał Mały (Fig. 5B). Lake Dgał Wielki was characterized by extremely low biomass, which was about 6 and 8 times lower compared to two other lakes. The differences in the crustacean biomass between the studied lakes were not statistically significant (Kruskal-Wallis test, $P > 0.05$). Copepods clearly dominated over cladocerans in all lakes, both in terms of the numbers and biomass. Their contribution to the total numbers and biomass was 62-94%. During the study period, copepods were mainly represented by cyclopoid and calanoid nauplii, *Cyclops scutifer* G.O. Sars and *C. strenuus* Fischer. Among cladocerans, *Alona intermedia* G.O. Sars, *Bosmina coregoni* Baird, *B. longispina* Leydig and *Chydorus sphaericus* (O.F. Müller) were the most important species.

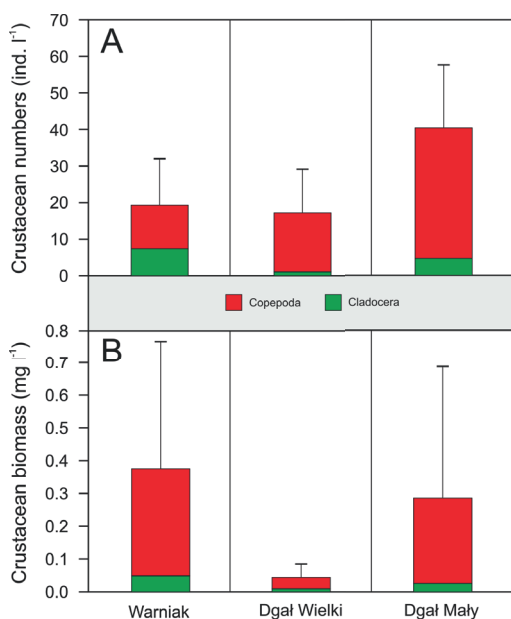


Figure 5

The numbers (A) and biomass (B) of crustaceans, with cladocerans and copepods marked, during the ice-covered period in the eutrophic Masurian lakes. Mean values from three sampling datasets with standard deviations for the total numbers and biomass.

Discussion

Field studies in ice-covered freshwater systems are hazardous, logistically difficult and expensive, especially during the thin ice period or the final phase of ice melting. At that time, the deepest sites of the lakes are usually not accessible either by ship or by car. Samples usually collected from the deepest parts of lakes are treated by hydrobiologists as representative for the whole lake. However, lakes are far from being homogenous in a horizontal plane (Laybourn-Parry 1992). Heterogeneity in the environment and in the distribution of aquatic organisms seems to be particularly evident during the winter when the deepest part of lakes are covered with thick ice, while the parts of lakes closer to the shoreline are without ice or covered with thin ice. However, further studies are needed to confirm this assumption. In this study, we investigated both abiotic and biotic parameters under thin and brittle ice. Similarly to the studies conducted by Kalinowska & Grabowska (2016) in eutrophic Lake Mikołajskie, our samples were collected from a site about 20 m away from the shore. Thus, our results are mainly compared with those noted by the above authors.

Our studies showed low variability (CV < 20%) of chemical parameters, especially TP and TN whereas

high variability (CV ranged from 20% to 141%) of biological parameters in all the studied lakes over the short time span. Such large fluctuations, both in the numbers and biomass of all the studied groups of organisms, suggest that winter is a very dynamic period.

The high dissolved oxygen concentrations during the whole ice-covered period suggested good conditions for fish survival in all the studied lakes. Such oxygen conditions in winter were also recorded in 2011-2014, thus, no winter fish kills were observed (Zakęś et al. 2015). The concentrations of dissolved organic carbon (DOC) were relatively low (below 7.5 mg l⁻¹), approximately constant (CV did not exceed 28%) and similar in all the studied lakes. In winter, the vast majority of organic matter in lake waters is of autochthonous origin due to the reduction of dissolved and particulate matter from the atmosphere and the surface runoff from the surrounding watershed by ice cover (Bertilsson et al. 2013). The autochthonous organic matter released by phytoplankton is easily utilized and decomposed by bacteria (Chróst 1986). This fact may explain low DOC concentrations in lake water during winter.

Similarly to the results of other studies (Agbeti & Smol 1995; Toporowska et al. 2010; Babanazarova et al. 2013), we recorded relatively high TP and TN concentrations in all lakes. It seems that such high concentrations of nutrients could be responsible for the massive development of phytoplankton. Another factor contributing to the growth of phytoplankton could be the lack of snow on the ice (Bolsenga & Vanderploeg 1992). Unfortunately, contrary to the results reported by many authors (e.g. Vehmaa & Salonen 2009; Üveges et al. 2012; Babanazarova et al. 2013; Wojciechowska & Lenard 2014; Kalinowska & Grabowska 2016), we did not observe such massive phytoplankton blooms.

The numbers and biomass of phytoplankton did not exceed 16 m ind. l⁻¹ and 4 mg l⁻¹, respectively. Both the maximum and mean phytoplankton numbers were similar to those noted by Kalinowska & Grabowska (2016), while the biomass was about 4 times lower because of nanoplanktonic taxa dominance. However, these maximal values as well as high chlorophyll *a* content observed in Lake Dgał Mały can be assessed as a winter bloom event. Similarly, Guinder et al. (2015) recorded the chlorophyll concentration of up to 25 µg l⁻¹ and phytoplankton abundance of up to 8 × 10⁶ cells l⁻¹ during a phytoplankton winter bloom in a shallow estuary. In comparison with the results reported by several authors (Agbeti & Smol 1995; Danilov & Ekelund 2001; Dokuli & Herzig 2009; Vehmaa & Salonen 2009; Toporowska et al. 2010), the phytoplankton

communities of all the studied lakes were primarily composed of nanoplanktonic diatoms from the genus *Cyclotella* and mixotrophic nanoflagellate cryptophytes from the genera *Plagioselmis* and *Rhodomonas* or slightly larger taxa (microplankton in size class above 20 μm) from the genus *Cryptomonas*.

As shown by Dokulil & Herzig (2009), if food quality and quantity are good (cryptophytes prevail during winter), some eurythermal rotifer species can quickly reach high densities. In our study, however, both the numbers and biomass of rotifers (maximum of 326 ind. l^{-1} and 0.2 mg l^{-1} , respectively) were relatively low – about 6-7 times lower than maximal values recorded by Kalinowska & Grabowska (2016). In contrast, the numbers and biomass of crustaceans (maximum of 58 ind. l^{-1} and 0.82 mg l^{-1}) were much higher compared to values observed by above authors. The dominance of detritophagous *Keratella cochlearis*, algivorous *Polyarthra dolichoptera* and predatory *Asplanchna priodonta* may indicate that rotifers exploited various food resources, depending on their availability in a particular lake. The clear dominance of copepods over cladocerans is also a characteristic feature of crustacean zooplankton (Agbeti & Smol 1995; Ventelä et al. 1998; Twiss et al. 2012; Kalinowska & Grabowska 2016). In this study, copepods accounted for 62-94% of the total numbers and biomass of crustaceans. They are selective feeders that can graze on protists, mainly nanoflagellates, in addition to algae and rotifers (Sanders & Wickham 1993). Results obtained by several authors (Bastviken et al. 2003; Rellstab & Spaak 2009) have shown that bacteria may also constitute a primary food resource for zooplankton during winter, especially in a situation where the availability of algae is reduced. The maximum nanoflagellate numbers of 12.37×10^6 cells l^{-1} and biomass of 0.95 mg l^{-1} in Lake Dgał Mały were about 2 times higher than maximal values recorded by Kalinowska & Grabowska (2016). The relatively high nanoflagellate abundance resulted from the availability of bacterial food. On the other hand, the grazing pressure by rotifers and crustaceans was not strong enough to reduce the nanoflagellate abundance. Predominance of autotrophic/mixotrophic nanoflagellates over heterotrophic ones in lakes Warniak and Dgał Mały may indicate low light limitation.

Although the maximum numbers and biomass of ciliates, 10.6×10^3 ind. l^{-1} and 0.12 mg l^{-1} , were about 2 and 6 times, respectively, lower than those noted by Kalinowska & Grabowska (2016), their taxonomic composition and dominance structure were very similar. Under-ice ciliate communities were mainly represented by small species from the genera *Rimostrombidium* and *Urotricha*, indicating that these

small species can well adapt to harsh environmental conditions. Thus, they can reach extremely high abundance during the spring period (Kalinowska et al. 2013). The results of PCA analysis confirmed that only the numbers and biomass of phytoplankton and nanoflagellates, concentrations of chlorophyll *a* and all forms of organic carbon were positively and strongly correlated with PC1 (41.4% of the total variability) and between each other (Fig. 6A). Slightly weaker correlations were also observed with TN and ciliate biomass. Regarding PC2 (28.6% of the total variability),

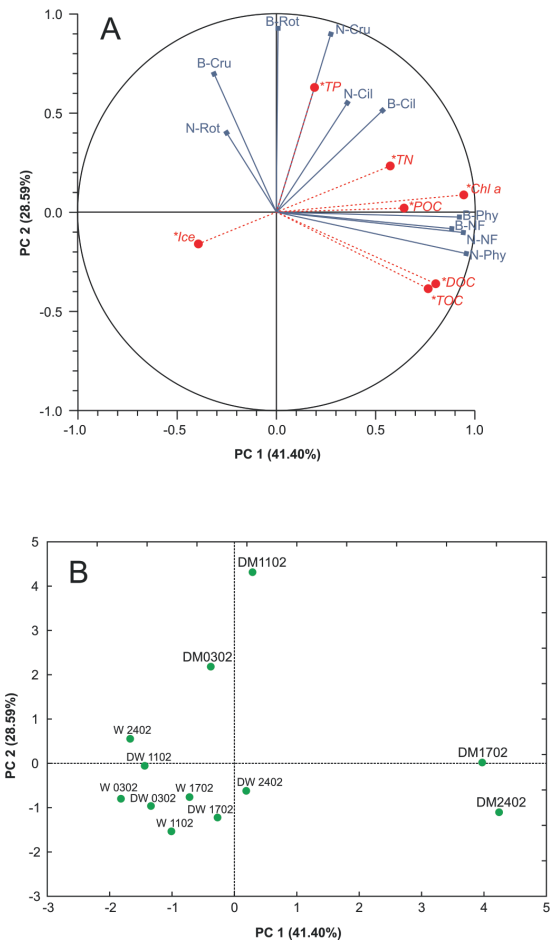


Figure 6

The relationships between abiotic and biotic components based on Principal Component Analysis (PCA). A – ordination diagram, B – classification of samples. Ice – ice cover, DOC, POC, TOC – forms of carbon, TP, TN – total phosphorus and nitrogen, Chl *a* – chlorophyll *a*, N-NF, B-NF, N-Cil, B-Cil, N-Phy, B-Phy, N-Rot, B-Rot, N-Cru, B-Cru – the numbers and biomass of nanoflagellates, ciliates, phytoplankton, rotifers, and crustaceans, respectively. W, DW, DM – lakes Warniak, Dgał Wielki and Dgał Mały with sampling dates

strong correlations were found with the numbers and biomass of crustaceans, the biomass of rotifers and TP, which had insignificant impact on phytoplankton and nanoflagellates. The analysis of such relationships requires further studies, however, our results may imply that in harsh environmental conditions, pelagic organisms are strongly dependent on each other (bottom-up versus top-down control).

Ecosystem size affects the phytoplankton nutrient status (Guildford et al. 1994), photosynthesis (Fee et al. 1992), distribution (Agbeti et al. 1997) and composition (Borics et al. 2016) and determines food-chain length (Post et al. 2000) in lakes during the ice-free periods. In contrast, the morphometry of lakes does not seem to play an important role in determining the phytoplankton communities during the period of ice cover, with depth being the only determinative factor (Danilov & Ekelund 2001). Information on the effect of lake size on other groups of planktonic organisms under the ice/snow cover is very scarce. That is why in the present study we investigated both microbial and classic food web components in three lakes of almost the same trophic level, but different morphometry. It should be emphasized that only a few studies have so far simultaneously focused on various groups of organisms (Agbeti & Smol 1995; Ventelä et al. 1998; Dokulil & Herzig 2009).

The results of our study showed that the lakes, although similar in the ice cover thickness, differed significantly in the concentrations of TP, TN and chlorophyll *a* as well as in the biomass of ciliates and phytoplankton groups. The most visible differences were observed between shallow Lake Warniak and deeper, small-sized Lake Dgał Mały. The lakes also differed clearly in the ratio of autotrophic to heterotrophic biomass (Table 3). It should be stressed that this ratio was calculated from three sampling

dates and did not include bacterial biomass. In lakes Dgał Wielki and Dgał Mały, autotrophic biomass was higher than the heterotrophic one. The low autotrophic/heterotrophic biomass ratio (0.7) in Lake Warniak may imply that the grazing pressure of consumers was substantially stronger in the shallow lake than in the two other deeper lakes (the ratio of 3.6 and 3.0 for lakes Dgał Wielki and Dgał Mały, respectively). Heterotrophic biomass in lakes Warniak and Dgał Mały was dominated by crustaceans (79 and 56% of the total biomass, respectively), while in Lake Dgał Wielki – by HNF (51%) (Table 3). Consequently, the biomass of phytoplankton and autotrophic nanoflagellates in the shallow lake was rapidly grazed.

In conclusion, shallow Lake Warniak was characterized by the lowest concentrations of DOC, POC, TP, TN, chlorophyll *a* and the numbers and biomass of ciliates, phytoplankton (total and its main groups) and rotifers. In contrast, in the deeper, small Lake Dgał Mały, the concentrations of DOC, POC, TP, TN, chlorophyll *a*, the biomass of ciliates and phytoplankton, and the numbers of crustaceans were clearly higher than in the two other lakes. The deeper, medium-sized Lake Dgał Wielki had the highest numbers of rotifers, while the lowest crustacean biomass. However, the PCA analysis indicated a close relationship between lakes Warniak and Dgał Wielki, and a large difference from Lake Dgał Mały (Fig. 6B). Additionally, such differentiation between the studied lakes could be the result of recent stockings with predatory fish, the keystone species in freshwater food webs, adequately to different environmental conditions. The lakes Warniak and Dgał Wielki were stocked with pike (*E. lucius*) and had good environmental conditions (including both morphometry and food resources) for natural reproduction and growth of juvenile stages. In contrast, Lake Dgał Mały was stocked with pikeperch (*S. lucioperca*) whose

Table 3

Mean (from three sampling dates) biomass (in $\mu\text{g C l}^{-1}$) of autotrophic (A) and heterotrophic (H) organisms during the ice-covered period in the eutrophic Masurian lakes.

Organisms	Warniak	%	Dgał Wielki	%	Dgał Mały	%
Autotrophic biomass						
Phytoplankton	100.7	76.2	255.5	91.5	501.6	82.3
ANF	31.4	23.8	23.6	8.5	107.6	17.7
TOTAL	132.1		279.1		609.2	
Heterotrophic biomass						
HNF	30.8	16.0	39.8	51.3	40.2	19.6
Ciliates	5.1	2.7	5.7	7.4	13.7	6.7
Rotifers	5.2	2.7	13.9	17.9	36.6	17.8
Crustaceans	151.2	78.6	18.1	23.4	114.8	55.9
TOTAL	192.3		77.5		205.3	
A/H biomass ratio	0.7		3.6		3.0	

growth rate was probably slow, mainly because of unfavorable oxygen conditions as well as relatively low availability and quality of food (dominance of bream (*Abramis brama* (L.)), which due to its body size and structure does not belong to prey preferentially consumed by pikeperch) (Zakęś et al. 2015). All of these facts may suggest that morphometric parameters (size, depth) may also influence planktonic organisms during the period of ice cover. In addition, summer/autumn conditions in lakes of different morphometry may have a decisive impact on chemical and biological variables during winter (Dokulil & Herzig 2009; Haberyan 2016).

Conclusions

The studied lakes were characterized by low organic carbon and chlorophyll *a* concentrations while relatively high total phosphorus and nitrogen content. All the studied groups of organisms were present at moderate densities and showed high variability over the short time span, suggesting that winter is a very dynamic period. Taxonomic composition of planktonic communities, except for rotifers and phytoplankton, was more or less similar in all lakes. The phytoplankton winter bloom, primarily due to high numbers and biomass of small-sized diatoms and cryptophytes, was recorded in deeper, small Lake Dgał Mały only. The results of the present study showed that pelagic organisms under ice were strongly dependent on each other (bottom-up versus top-down control). The low autotrophic/heterotrophic biomass ratio (0.7) in Lake Warniak may indicate higher grazing pressure in the shallow lake than in the deeper ones. The studied lakes differed significantly in nutrient and chlorophyll *a* concentrations as well as in ciliate and phytoplankton biomass, suggesting that the lake morphometry may have an impact on planktonic communities during winter.

Acknowledgements

We are grateful to Waldemar Kozłowski, Adam Mańko, Jan Rola for their help in the field sampling and Stanisław Sidorski for chlorophyll *a* analysis. This research was financed through the Stanisław Sakowicz Inland Fisheries Institute in Olsztyn within its statutory research activity (topic no. S-011). We thank two anonymous reviewers for valuable comments, which helped us to improve the manuscript.

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