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Regular build-up of the phytoplankton spring maximum before ice-break in a boreal lake

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Abstract

Development of phytoplankton biomass and composition was studied during the evolution of under-ice convection in spring in a eutrophic boreal lake. The results from eight years showed that, within a few weeks before ice-break, phytoplankton biomass increased by up to two or three orders of magnitude, reaching or exceeding that in summer, and this may be the most significant single annual phytoplankton episode in the lake. The development of phytoplankton was closely coupled with that of convection created by solar radiation at water temperatures < 4 °C. In addition to vertical convection which keeps phytoplankton suspended, there was also horizontal convection which transported water with evidently higher abundance of phytoplankton from the shallow lake margins. The effect of mechanical mixing, which was meant to prevent anoxia in the deep water layers of the study basin, was overridden by natural convection. Stochastic variations in weather played a key role controlling light penetration into the lake and hence the abundance and composition of under-ice phytoplankton. After snow melt the proportion of motile algae was at first higher, sometimes with a maximum nearest to the ice, but later diatoms flourished throughout the mixed layer. Only in the years of delayed ice melting did the proportion of motile algae remain higher until the end of ice cover.

Key index words: Convection, diatoms, motile algae, mechanical mixing, Enonselkä, Vesijärvi

Introduction

Boreal lakes are characterized by the alternation of ice-covered and open water seasons. Shifts between the seasons mean radical changes in physical and chemical conditions in the water column, which determine the development of phytoplankton biomass and the prevailing functional types (Reynolds et al. 2002). The ice-covered season has recently received increasing attention and several studies have demonstrated that phytoplankton may be active in the seemingly hostile under-ice environment (McKnight et al. 2000; Phillips and Fawley 2002; Straškrábová et al. 2005; Jewson et al. 2009; Üveges et al. 2012; Babanazarova et al. 2013). However, the harsh conditions in winter make sampling challenging and limit research possibilities. Particularly during the transition phases between the ice-covered and the open water seasons, access to lakes can be virtually impossible without expensive special vehicles.

Consequently these remain the least studied time periods in phytoplankton seasonal succession in lakes (Salonen et al. 2009; McKay et al. 2011; Bertilsson et al. 2013).

In mid-winter, snow cover reflects most of solar radiation and renders primary production of phytoplankton light-limited. However, in the absence of snow and snow-ice layers, phytoplankton might receive enough light to develop biomasses corresponding to those observed in the open water season (Eloranta 1982; Jewson et al. 2009; Twiss et al. 2012). Turbulence in the water column created by wind is largely eliminated in mid-winter, which favours under-ice phytoplankton able to avoid sedimentation or attach to the bottom of the ice cover (Jewson et al. 2009; Twiss et al. 2012). On the other hand, under-ice hydrodynamics in lakes which cool below 4 °C is not as quiescent as traditionally assumed (Kirillin et al. 2012). After the formation of ice, heat flux from the sediment creates density

gradient currents which affect the whole water column and may keep some phytoplankton species suspended (Kiili et al. 2009).

When snow, and finally also snow-ice, melt in late winter the penetration of light into water increases dramatically. If the water temperature is below 4 °C, the introduced heat generates convective mixing below a shallow boundary layer between ice and water (Matthews and Heaney 1987; Bengtsson 1996; Forrest et al. 2008). During such convective mixing, warmer water parcels sink to the depth at which density is similar. Accordingly, the depth of convection layer also increases along with temperature. Mixing keeps phytoplankton suspended, but also transports nutrients from deeper water layers (Kelley 1997). The few studies of phytoplankton under different under-ice mixing regimes are limited to relatively oligotrophic lakes, where phytoplankton biomass is low (Kiili et al. 2009; Vehmaa and Salonen 2009).

By using a hydrocopter (an air boat), we were able to monitor vertical distribution of phytoplankton biomass and community composition in a eutrophic boreal lake basin through the convective mixing period until ice-break. We expected that increased light availability after snow melt and nutrients made available by convective mixing would allow development of high phytoplankton biomass already before ice-break. We hypothesized that the development of phytoplankton biomass, their distribution in the water column and composition include notable variation due to interannually variable light and mixing conditions.

Materials

The study site was the southernmost Enonselkä basin of Lake Vesijärvi in southern Finland (Fig. 1; henceforward Enonselkä). The basin (area 26 km^2, max. depth 33 m, mean depth 6.8 m, residence time 5 years) has been heavily loaded by nutrients from anthropogenic activities. The water quality of Enonselkä has notably improved after sewage diversion in 1976, but blooms of harmful algae are still frequent in summer (Keto et al. 2005). To reinforce food web manipulation in the lake and management efforts in the catchment area, oxygenation by mechanical mixing was started in winter 2009-2010 to relieve oxygen depletion in the deepest water (Salmi et al. 2014b). One submerged 1.5 kW pump and eight 2.5 kW pumps were installed

at the deepest sites of Enonselkä (Fig. 1). Pumps located at 3 m depth pumped oxygen-rich surface water (approximately 1 m^3 s^{-1}) into deeper water layers through canvas tubes with a diameter of 1 m. To avoid resuspension of the sediment, the lower ends of the tubes were 8–10 m above the bottom (Lappalainen 1994; Bendtsen et al. 2013). In winter 2010–2011, the operation of only four pumps was tested (Fig. 1) to save energy. In 2010 and 2014 the pumps were kept on through the spring, but in 2011–2013 they were switched off 12, 34 and 15 days, respectively, before ice-break.
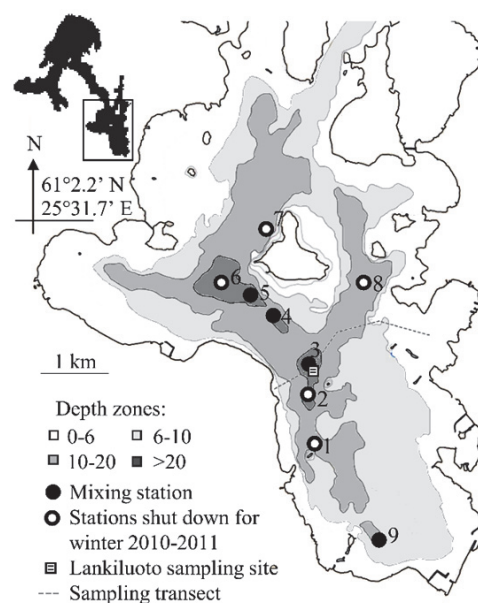

Figure 1. Map of the Enonselkä basin of Lake Vesijärvi (inset) in southern Finland. The sampling transect for horizontal oxygen distributions is shown by the broken line.

At the Lankiluoto sampling site (depth 30–31 m, WGS84 coordinates: 61°01.089' N and 25°36.211' E), located roughly 50 m from a mixing station (Fig. 1), temperature was measured every 30 min with Starmon Mini (Star-Oddi, Iceland, accuracy 0.05 °C) temperature recorders attached to a rope at 5 m intervals in winter 2007 and 2 m intervals in winters 2008–2014. Water column was taken to start convecting when temperature at 1 m depth equalled that at 5 m depth in 2007, and when temperature at 1–2 m equalled that at 3–4 m depth in other years. The

boundary layer between the layer of vertical convection and the water below was considered to be located at the depth interval where temperature changed the most. Heat content (Θ) for Enonselkä was calculated from the results from the temperature recorders as:

$$\Theta = \frac{1}{A_0} \int_0^{Zmax} c\rho A T dz$$

where A_0 [km^2] = lake surface area, c [J g^{-1} C^{-1}] = the specific heat capacity of water, ρ [kg m^{-3}] = density of the water layer, A [km^2] = lake area at depth z [m] and T = temperature [°C] (Johnson et al. 1978). Additional temperature profiles were measured with a Micro-CTD-3 (Falmouth Scientific, USA, accuracy 0.005 °C) in 2009 and with a CastAway-CTD (Yellow Springs Instruments, USA, accuracy 0.05 °C) in 2011. In 2013–2014 additional temperature profiles were measured with a XRX-620-CTD (RBR, Canada, accuracy 0.002 °C). In 2010–2013 relative light level both under the ice and on top of the ice was measured with Hobo Pendant Temperature/Light data loggers (Onset Computer Corporation, USA). For under-ice measurements, a light logger was installed at approximately 0.7 m depth, and to avoid any effect of phytoplankton growth on the measurements only the first 3–10 days are here taken into account. The appropriate number of days was estimated by comparing the increase in light level to increase in heat content. Directional values for light intensity were calculated according to Thimijan and Heins (1983).

Phytoplankton and oxygen samples were taken with a Limnos water sampler (volume 2.1 L, Limnos.pl, Poland) as vertical series with 2–10 m depth intervals. Samples immediately below the ice (denoted 0 m) were taken with a rectangular plastic tube (50 mm x 50 mm x 750 mm) to reduce the disturbance caused by drilling of the ice. The tube had plastic foam sides for floating and a rolling brush in front of its upper end to suspend phytoplankton possibly attached to the underside of ice. The tube was placed in a horizontal position at the edge of a hole sawed in ice and was moved against the underside of the ice until its rear end was at the margin of the hole. Its opening was then closed by the palm of a hand and the sample was rapidly transferred to a bucket. Phytoplankton samples were poured into 100 ml dark glass bottles and preserved with 1 ml of Lugol's solution. Unpreserved oxygen samples in ground glass stoppered bottles were covered with slush and transported to the laboratory in an insulated box. Oxygen concentrations were measured by Winkler titration using a DL 53 Titrator (Mettler-Toledo International Inc., USA). In late winters 2010-2012, oxygen profiles were also measured with a Pro-odo optical sensor (Yellow Springs Instuments, USA, accuracy 0.1 g m^{-3}) and in winters 2013-2014 with a Rinko III-sensor (JFE Advantech, Japan, accuracy 2 % of the full range) attached to the XRX-620-CTD (RBR, Canada) and the results were calibrated with the results from the Winkler titrations. Nutrient samples were taken into plastic bottles and filtered in the laboratory through 0.2 µm pore size syringe filters (Millipore, USA). Samples were stored at -20 °C until phosphate-phosphorus (PO_4-P) and nitrite- and nitrate-nitrogen (NO_2+NO_3-N) were determined with a QuickChem 8000 flow injection analyzer (Lachat Instruments, USA). Snow depth and ice thickness were measured with a wooden gauge. To measure the thicknesses of snow-ice and clear-ice layers, a block of ice was sawed out and lifted up. Secchi-depth was measured from the white lid of the Limnos water sampler (diameter 11 cm). The dates of freezing and ice-break of Enonselkä were obtained from the database of the Finnish Environment Institute.

Phytoplankton samples were counted using a settling chamber method (Utermöhl 1958). Counting was done with inverted light microscopes and phase contrast optics (Nikon Diaphot-TMD, Japan, Carl Zeiss, Germany, Olympus IX60, Japan or Wild M40, Switzerland). Depending on species composition, either two or three magnifications were used in counting. Small (< 10 µm) and medium–sized (10–20 µm) species were counted from randomly chosen microscopic fields with 300–600x magnification. Larger species were counted from transects of the counting chamber with 100–200x magnification. Dimensions of each counted cell were estimated with an eye-piece ocular micrometer. The biovolume of cells were determined according to their approximate geometric shape and converted to wet mass assuming them to be isopycnal with water (EN 15204 2006). The 95 % confidence limits (Cfl95) for the mean total wet mass were Cfl95 calculated as follows:

$$cfl\% = \frac{100 * t_{0.025} * \sqrt{\sum s^2/n}}{mean}$$

where $t_{0.025}$ = 97.5 % percentile of the t-distribution when the degrees of freedom are n–1, n = number of parallel microscopic views and s^2 = variance of biomass between microscopic views for a species; thus $\sum s^2$ = sum of the variances calculated for each species counted with a specific magnification. A

directional Cfl95 for the whole sample was calculated from the sum of the variances calculated for each magnification weighted by their proportions in total biomass. The target of Cfl95 $\leq$ 30 % was realized with a computer program which provided confidence limits of the results in real time during counting so that the number of replicate counts could be adjusted accordingly. In practice, typically 10–50 microscopic fields were counted with 400–600x magnification, 30–50 fields with 300x magnification and 3–4 transects were counted with 100–200x magnification. In sparse samples, wider confidence intervals were accepted.

Volume-weighted oxygen concentration and phytoplankton wet masses as well as abundances were calculated assuming the basin to have a shape of a frustum and dividing it into slices with each sample placed in the middle of a slice. The volume of the slice was multiplied by the biomass in the sample. The products were summed and finally divided by the volume of the basin. Phytoplankton samples taken from 30 m depth on 1st April 2009 were accidentally destroyed, but since the water volume of the 22.5–30 m deep water column is less than 1 % of the total water volume of Enonselkä the loss was ignored in calculations. Specific increase rate (r) between sampling dates was calculated from volume-weighted abundances as:

$$r = \ln(N_t/N_0)\,/t$$

where N_t = population size at the later sampling time, N_0 = population size at the earlier sampling time and t = time in days between samples.

To place our winter phytoplankton data in a wider seasonal context we used monthly phytoplankton results (database of the Finnish Environment Institute) of composite samples taken in May–October from the water layer that was twice the Secchi–depth. Statistical analyses were done with SPSS Statistics 20 (IBM, USA).

Results

Environmental conditions – The onset of convection could be rather precisely detected from the readings of temperature recorded twice per hour. The median start of vertical convection created by increasing penetration of solar radiation was 24 days before ice-break. The shortest durations of convection were 17 days in 2011 and 14 days in 2013. In these years, the period of ice cover was also longer (156 days in 2011

and 150 days in 2013) than in the other years (88–135 days). In 2008, convection had already started before the installation of the temperature recorders 19 days before ice-break. The longest duration of convection was 41 days in 2014. The increase in the heat content of the basin during the convection period was also highly variable (26–76 MJ, Fig. 2) reflecting interannual differences in snow and ice conditions (Figs. 2–3). Although reliable light results were obtained only during the early phase of convection, they clearly show that light was then already favourable for phytoplankton growth in the upper part of the water column (Table 1).

Table 1. Approximate mean irradiances (μmol m^{-2} s^{-1}) during the first 3–10 days of convection in water (at 0.7 m depth) and in air.

	2010	2011	2012	2013
Water	103	138	3	136
Air	798	1022	870	Lost

In the years without mechanical mixing (2007–2009), the under-ice convection layer deepened until it reached the chemocline at 20–25 m depth and overturn happened around the ice-break (Fig. 4). The prevention of chemical stratification by mixing during winter facilitated deepening of the convection layer so that the basin started to overturn roughly two weeks before ice-break in 2010 and 2014 (Fig. 4). In contrast, switching off mechanical mixing before ice-break in 2011–2013 led to a sufficient chemical gradient at 20–25 m depth to delay overturn until ice-break (Fig. 4). In 2010 and 2014, when mechanical mixing was continued through the ice-melting period, a distinct convection layer still developed, but without a chemocline.

In all study years, temperature increased in deep water before it was reached by vertical convection (Fig. 4), indicating heat input from shallow areas by horizontal flow of warmer water (horizontal convection, as described by Salonen et al. (2014). This was most distinct in the mixing year 2012 (Fig. 4) and was possibly facilitated by inflow from the River Joutjoki which receives warm cooling water from a power plant. In the years without mechanical mixing and when the mixing stations were switched off before ice-break, warming by horizontal convection was limited to the water layer above the chemocline.
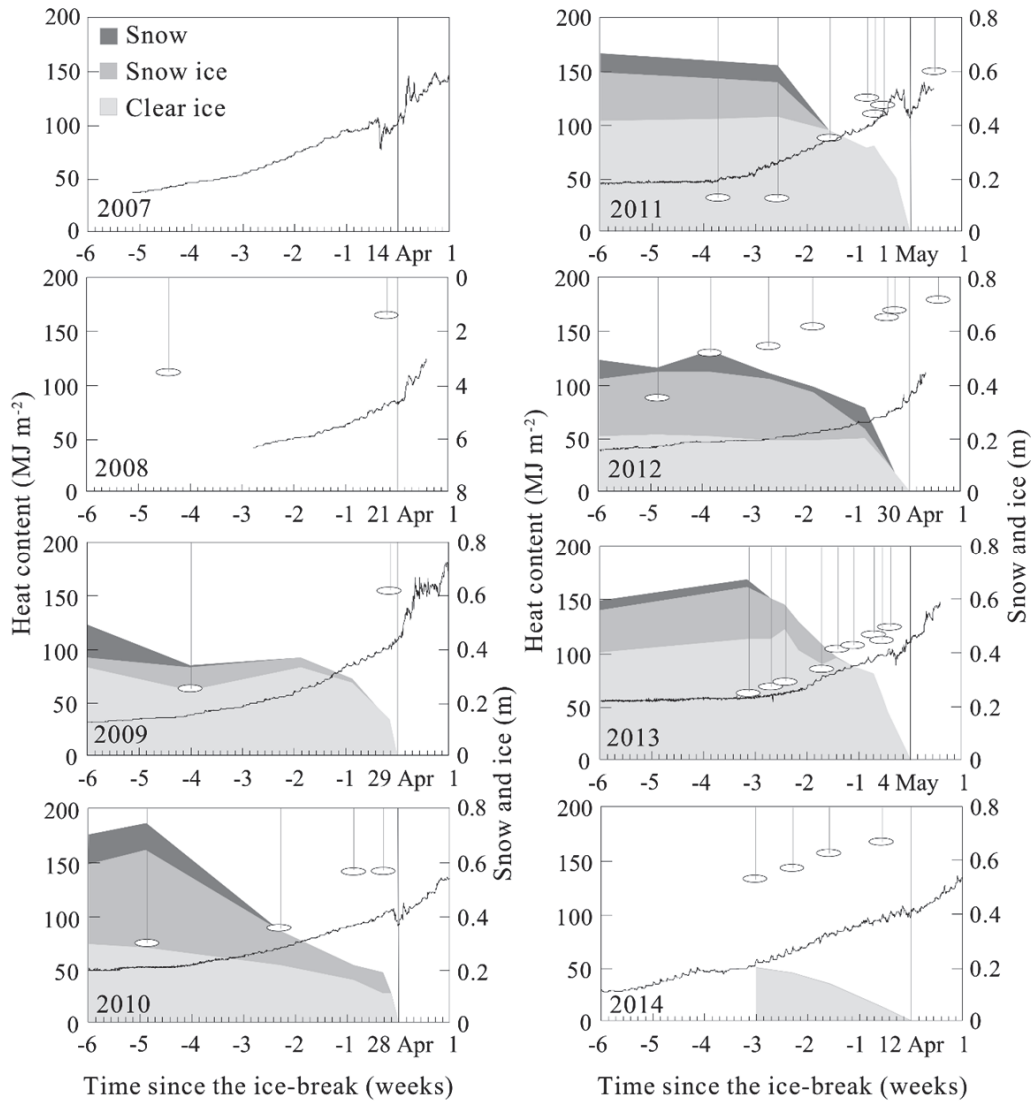
Figure 2. Ice and snow thickness, water column heat content and Secchi-depth in Enonselkä during late winter 2007-2014. Vertical lines at "0" denote the date of ice-break. The scale on the right y-axis in the panel of 2008 marks Secchi-depths (m). The sudden changes in heat contents were likely due to the breaking ice. The occurrence of decreases due to melting ice fragments occurring before ice-break in 2007 and 2013 was likely due to the fact that ice does not disappear simultaneously everywhere in the lake.
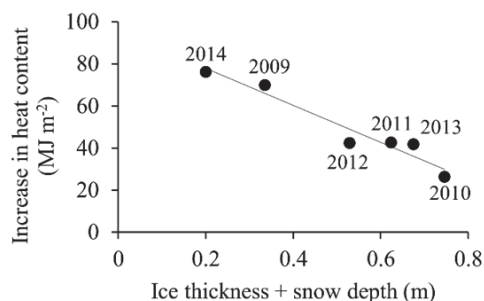
Figure 3. Relationship between the increase in heat content of Enonselkä during the under-ice convection period and the observed maximum thickness of ice and snow cover during the six weeks before ice-break ($R^2 = 0.94$).

In March 2007 and 2008, oxygen concentration at 30 m depth was 4 g m^{-3} and 2 g m^{-3}, respectively (more details in Salmi et al. 2014b), while in late winter 2009 anoxia developed below the chemocline at around 25 m depth (Fig. 4). In contrast, during mechanical mixing, the whole water column remained well oxygenated (> 6 g m^{-3}) through the winter. Oxygen measurements before the beginning of convection indicated that the effect of the mixing stations spread across the basin (Fig. 5) so that only the deeps behind shallow sills remained unaffected. After the mixing stations were switched off before ice-break in 2011–2013, oxygen concentration in the deepest water started to decrease and eventually diminished to < 2 g m^{-2} (Fig. 4).

Phytoplankton – Because we targeted favourable confidence limits for phytoplankton total biomass, counting effort was relatively more concentrated on diatoms and consequently the counts of other species generally include more uncertainty. On the other hand, this shortcoming is partly compensated by the rather frequent sampling as well as by the high vertical resolution of samples.

In mid-winter of 2009–2011 and 2013, volume-weighted wet mass of phytoplankton was low (0.05–0.09 g m^{-3}) and its vertical distribution was rather uniform even without mechanical mixing (Fig. 6–7).

After snow melt, Secchi-depth continuously decreased (Fig. 2). At the same time volume-weighted phytoplankton biomass increased exponentially in relation to the length of the convection period and was up to two or three orders of magnitude higher than in mid-winter (Fig. 8). The increases in carbon calculated from phytoplankton biomass assuming 10 % C of wet mass (Reynolds 2006) and assimilated carbon calculated from produced oxygen assuming a photosynthetic quotient of 1.2 between oxygen and carbon (Kirk 1994) corresponded closely (Fig. 9). In 2012, when the concentrations of inorganic phosphorus and nitrogen were studied more closely, PO$_4$-P concentration was depleted from the mixed layer before ice-break and NH$_4$-N remained at low level (Fig. 10), although light conditions (Table 1) due to late snow cover were not particularly favourable for phytoplankton primary production.

Without mechanical mixing, vertical distribution of phytoplankton biomass closely followed the deepening of the convection layer (Fig. 6). In 2010 and 2014, when the mixing stations were operated throughout the ice-covered period, the distribution of phytoplankton biomass in the convection layer was vertically most even (Fig. 7). We often observed high biomasses in the neighbourhood of the chemocline, or, during mechanical mixing, in the deepest water.

Mid-winter phytoplankton was mostly composed of cyanobacteria, particularly *Planktothrix agardhii* (Gomont) Anagnostidis & Komárek, and motile flagellates, but diatoms were also present. Later the proportion of motile species generally declined in favour of diatoms, but in 2011 and 2013, with the shortest duration of under-ice convection, their proportion remained high until ice-break (Fig. 6–7). No species was clearly specialized to conditions immediately under ice, but in 2013 *Uroglena* sp. was abundant in the 0-0.1 m sample (Fig. 6–7). Among diatoms small (cell diameter 4–6 µm) *Stephanodiscus* cf. *parvus* Stoemer & Håkansson was important or dominant every year. Only in 2008 was the biomass of *Asterionella formosa* Hassall and in 2009 that of *Aulacoseira* spp. also high (Fig. 6). Towards the end of ice cover, the mean depths of both non-motile diatom and motile flagellate populations were focused in the middle of the water column, indicating efficient mixing of the whole water column.
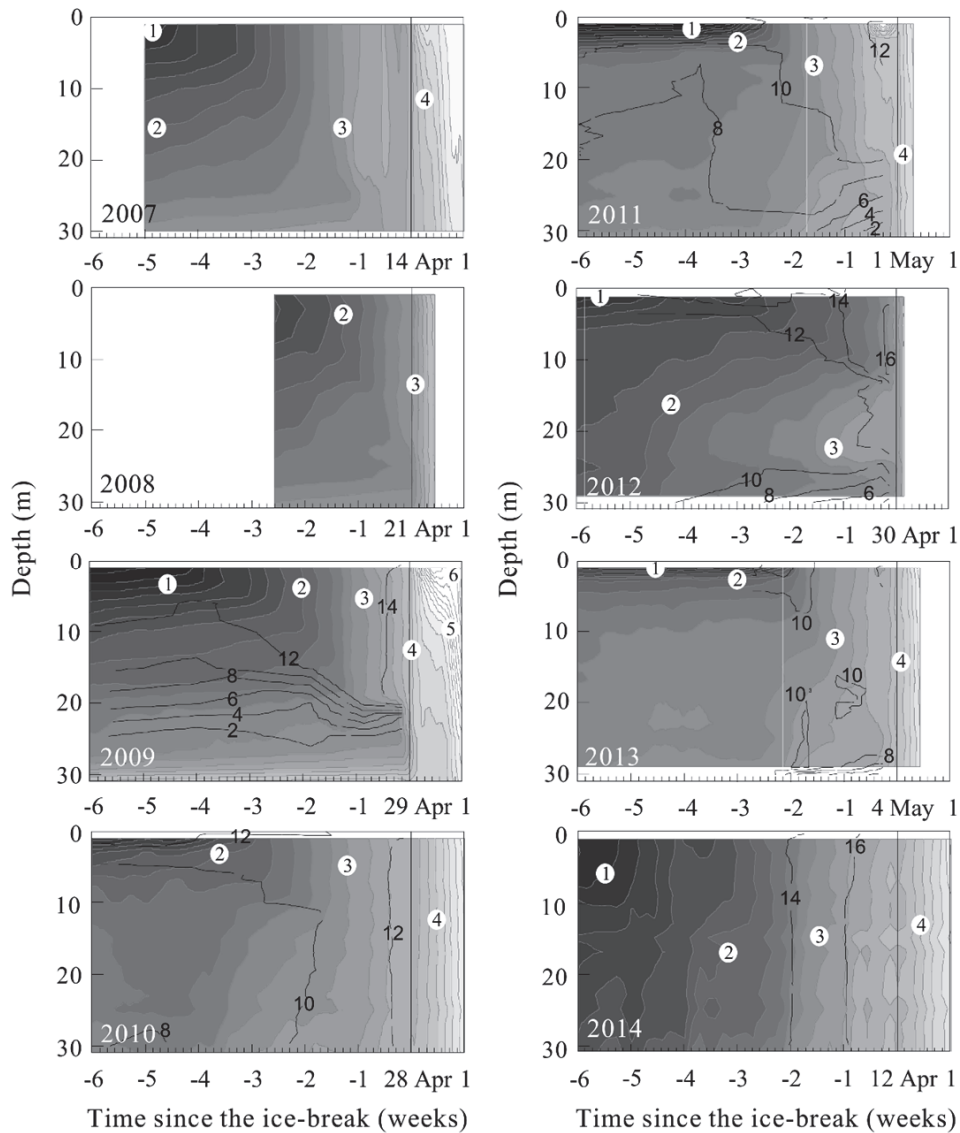
Figure 4. Development of temperature (°C, 24 h moving average, filled contours) and oxygen concentration (g m⁻³, black curves) in Enonselkä during late winter 207-2014. White vertical lines mark the dates when mixing stations were switched off before ice-break in 2011–2013. Black vertical lines at "0" denote the date of ice-break.
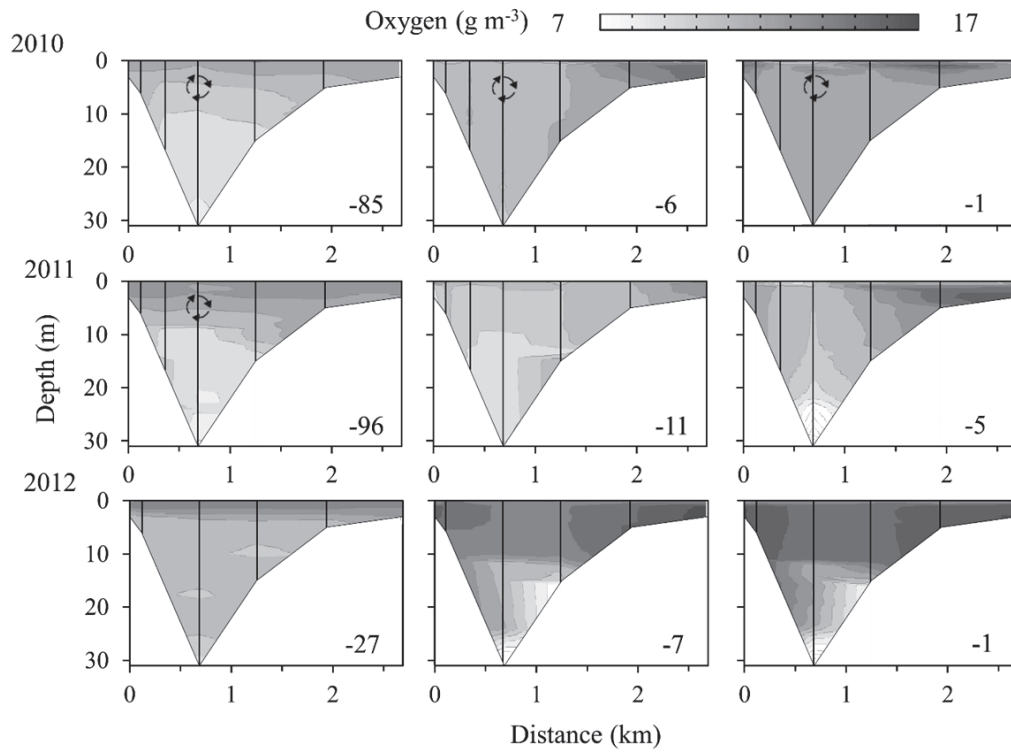
Figure 5. Horizontal distribution of oxygen concentration along the sampling transect in Enonselkä (Fig. 1) during convection in 2010–2012. Vertical lines mark the sampling points and circled arrows mark the dates when mechanical mixing was ongoing.
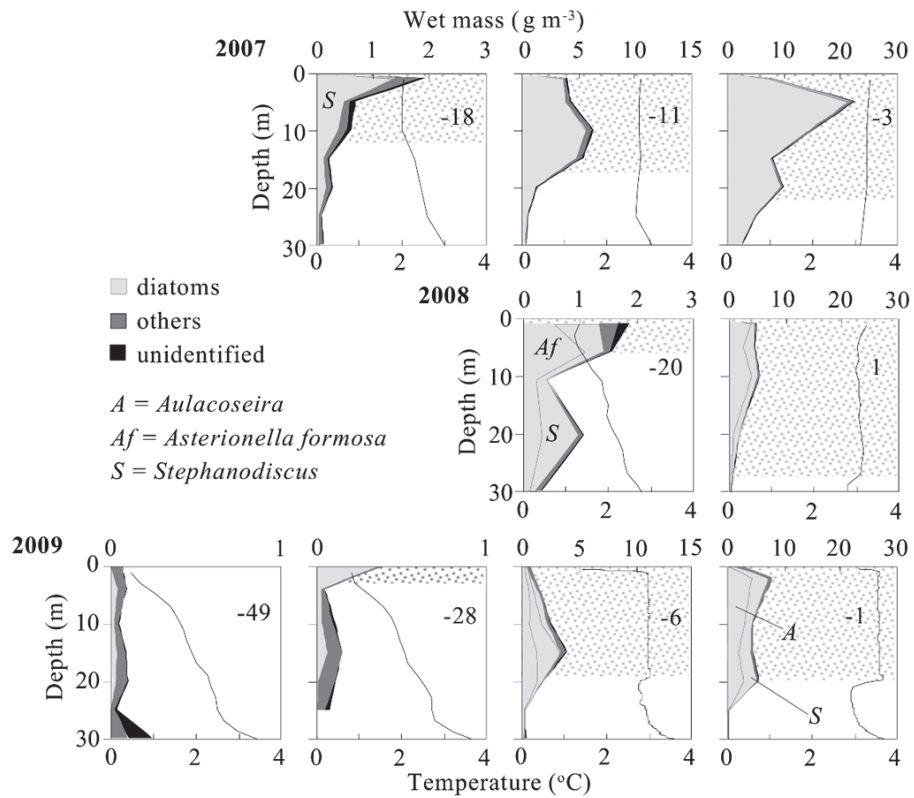
Figure 6. Vertical distributions of phytoplankton biomass and temperature (lines) in Enonselkä during late winter 2007-2009 without mechanical mixing. Shaded background – convection layer. The numbers indicate sampling time in days related to ice-break.

Table 2. Mean specific increase rates (d^{-1}) of *Stephanodiscus* cf. *parvus*, small cryptophytes (cell length < 15 µm) and *Cryptomonas* sp. during under-ice convection.

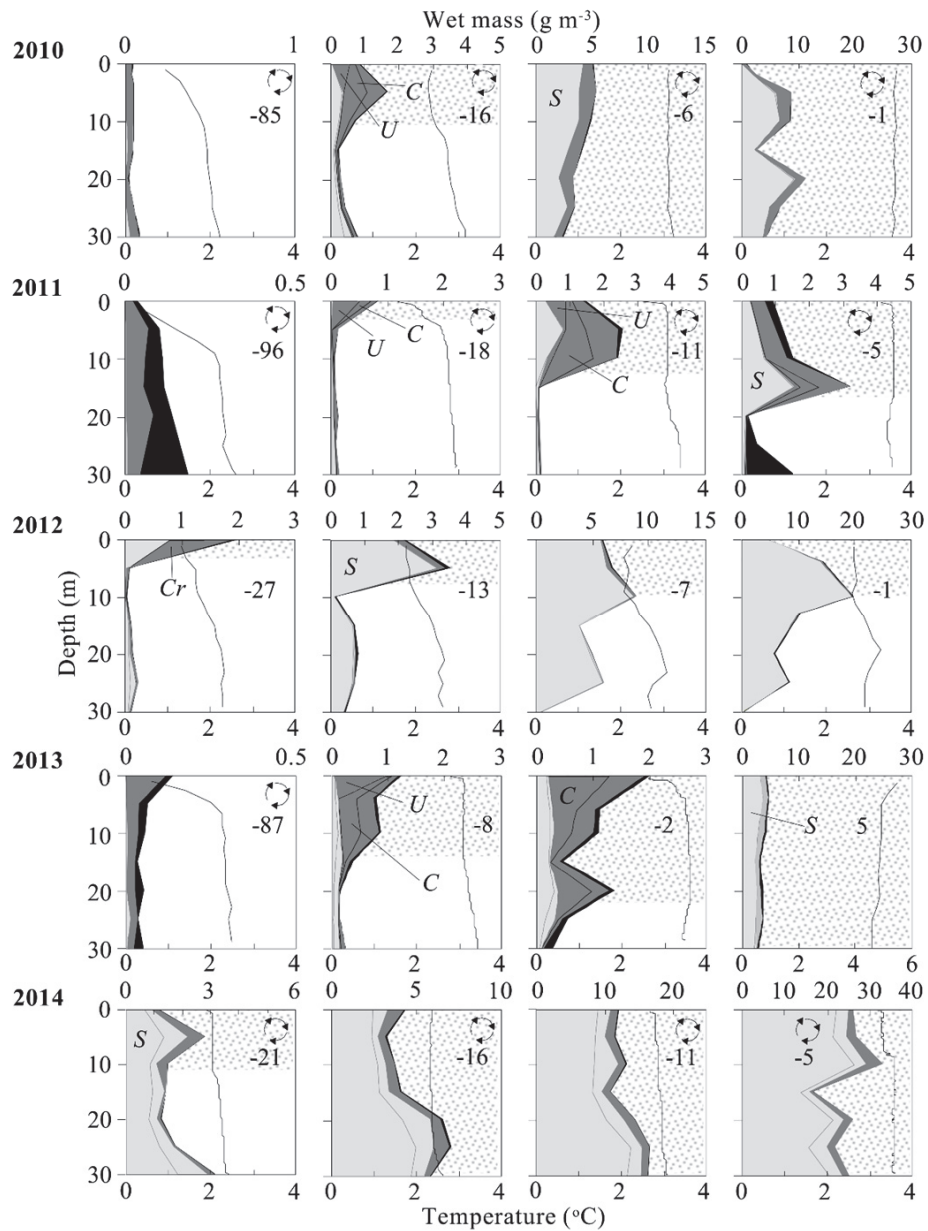| Taxon	2007	2008	2009	2010	2011	2012	2013	2014
S. parvus	0.20	0.11	0.23	0.19	0.28	0.14	0.22	0.19
Small cryptophytes	-0.02	-0.01	0.12	0.09	0.01	-0.05	0.16	0.06
Cryptomonas sp.	0.16	0.07	0.09	0.09	0.24	0.06	-0.08	0.01

Figure 7. Vertical distributions of phytoplankton biomass (areas) and temperature (black curves) in Enonselkä during late winter 2010-2014 with mechanical mixing. Light grey – diatoms, dark grey – others, black – unidentified, *S* – *Stephanodiscus*, *Cr* – Cryptophyceae, *C* – *Chlamydomonas* sp., *U* – *Uroglena* sp. and shaded background – convection layer. Circled arrows mark the dates when mechanical mixing was ongoing.

Although the biomass of motile species typically increased during convection (Figs. 6–7), diatoms increased faster (Table 2). The average specific increase rates of *Stephanodiscus* were remarkably similar from year to year irrespective of whether the basin was mechanically mixed (median 0.20 d^{-1}) or not (median 0.19 d^{-1}, Table 2). The results calculated for shorter time intervals indicated that during the convection period the rate of increase was originally stable and then finally probably decreasing (Fig. 11; Related–Samples Wilcoxon Signed Rank Test for two last determinations, p = 0.046, *n* = 6).
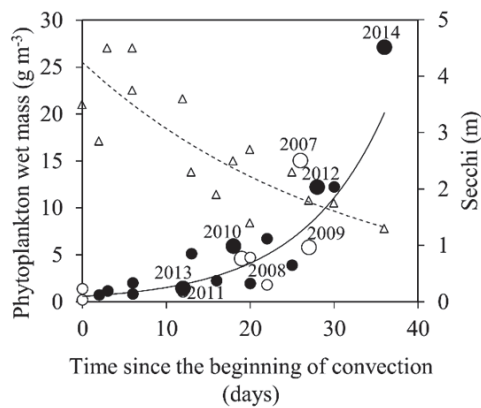

Figure 8. Volume weighted under-ice biomasses of total phytoplankton (solid exponential curve, R^2 = 0.75) and Secchi-depths (triangles, broken exponential curve, R^2 = 0.72) in relation to the estimated date of the beginning of vertical convection in Enonselkä. Dots – with mechanical mixing; circles – without mechanical mixing; larger dots mark the last observed under-ice biomasses of specified years.

The first open–water samples were taken 9 to 27 days after ice-break when the dominant phytoplankton groups were typically the same as under ice (Fig. 12). The highest biomass in summer was often observed after a minimum in June, but during the study years it never exceeded that observed in late winter (Fig. 12). In contrast to the dominance of small diatoms in late winter and early summer, cyanobacteria and larger diatoms, such as *A. formosa*, *Aulacoseira islandica* (O. Müller) Simonsen or *Tabellaria fenestrata* (Lyngbye) Kützing, contributed most to the late summer biomass.
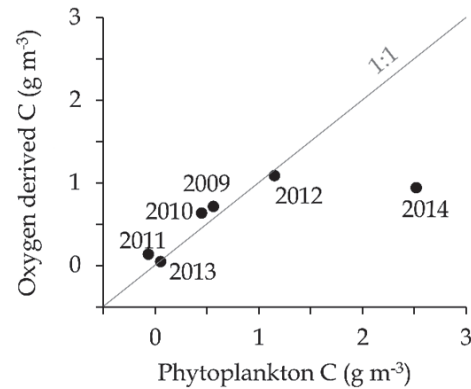

Figure 9. Relationship between the increase of phytoplankton carbon and net production calculated from the increase of oxygen concentration during the convection period in Enonselkä.
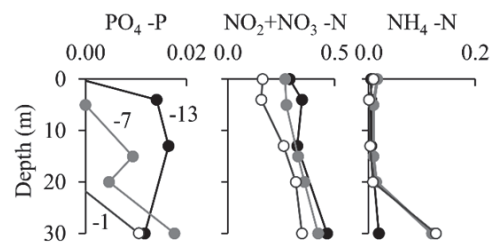

Figure 10. Vertical distribution of concentration (mg m^{-3}) of phosphate-phosphorus (PO_4 –P), nitrite- and nitrate-nitrogen (NO_2 + NO_3 –N) and ammonium-nitrogen (NH_4 –N) in Enonselkä in late winter 2012. Numbers shown within the first panel indicate days before ice-break. Each x –axis starts from the detection limit (0.003 mg m^{-3} for PO_4, 0.01 mg m^{-3} for NO_2 + NO_3 and 0.005 mg m^{-3} for NH_4).

Discussion

Development of under-ice phytoplankton

In boreal lakes, the annual oscillatory cycle of phytoplankton is characterized by a spring maximum followed by a clear water phase during stratified water column and a late summer maximum (Lampert et al. 1986; Sommer et al. 2012). Kalff and Knoechel (1978) and Weyhenmeyer et al. (1999) suggested that in dimictic lakes the phytoplankton spring maximum, which can be the single most important

phytoplankton episode in the lake, typically reaches its full strength after ice-break. However, it is difficult to assess phytoplankton biomass just before ice-break. Apart from difficulties due to sometimes partial ice-break, it is seldom possible to take samples at the last moment of ice cover. Even if a suitable vehicle is available, it would necessitate daily sampling, because the precise time of ice-break is difficult to predict. Therefore, in practice, sampling can often be made with only a few days precision in relation to ice-break time, which due to the exponential growth of phytoplankton may result in marked underestimation of the final under-ice biomass. On the basis of our results from Enonselkä and literature (Pettersson 1985, Kiili et al. 2009, Vehmaa and Salonen 2009) we suggest that both in oligotrophic and eutrophic lakes phytoplankton can often deplete nutrients and develop the bulk of their spring maximum already before ice-break.
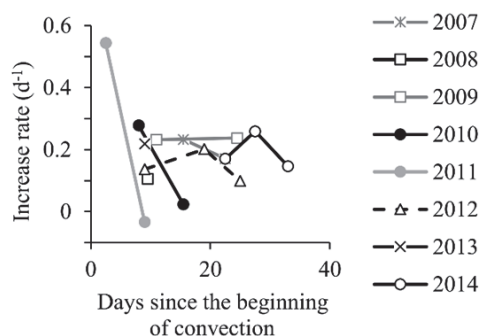

Figure 11. Growth rate of *Stephanodiscus* cf. *parvus* during convection before ice-break in Enonselkä during the study years.

Eloranta (1982) demonstrated that maximum phytoplankton biomass developed already between mid–February and end of March in a pond which received warm cooling waters so that temporary ice cover appeared only during the coldest weather episodes. Under natural conditions, light attenuation by snow and ice cover typically delay development of phytoplankton in the same district by about two months. Our results also emphasize the importance of snow and ice conditions in late winter, which determine the availability of light and the length of the under-ice convection period. Despite high variation due to stochastic weather conditions, during the under-ice convection period the bulk of the phytoplankton spring maximum developed under ice. This was demonstrated by depletion of PO_4-P concentration (Fig. 10) in a year with moderate light conditions. Under-ice depletion of PO_4-P was also observed by Pettersson (1985) in Lake Erken. The under-ice phytoplankton maximum in Enonselkä was typically slightly higher, but of similar magnitude to that in Lake Erken (Pettersson 1985). Volume weighted maximum biomasses in Enonselkä were up to two orders of magnitude higher than in lakes Pääjärvi (Vehmaa and Salonen 2009) or Päijänne (Kiili et al. 2009). The difference can be explained by oligotrophy of the latter lakes and by their much deeper under-ice convection layer. The total P concentration in Enonselkä (Salmi et al. 2014b) is similar to that in Lake Erken (~0.02 g m^{-3}), but higher than in the two oligo–mesotrophic Finnish lakes. In addition to higher trophic state, lower water colour and shallower convection in Enonselkä might have helped to sustain the higher phytoplankton biomass.

Increase in oxygen concentration under the ice-cover correlated well with that of phytoplankton biomass (Fig. 9), which suggests that oxygen determinations made in sufficient scale might provide a straightforward method to complement laborious microscopic counting. The anomaly of the carbon assimilation value calculated for late winter 2014 might be related to the strong oxygen supersaturation (109–122 %) of the mixed layer at that time.
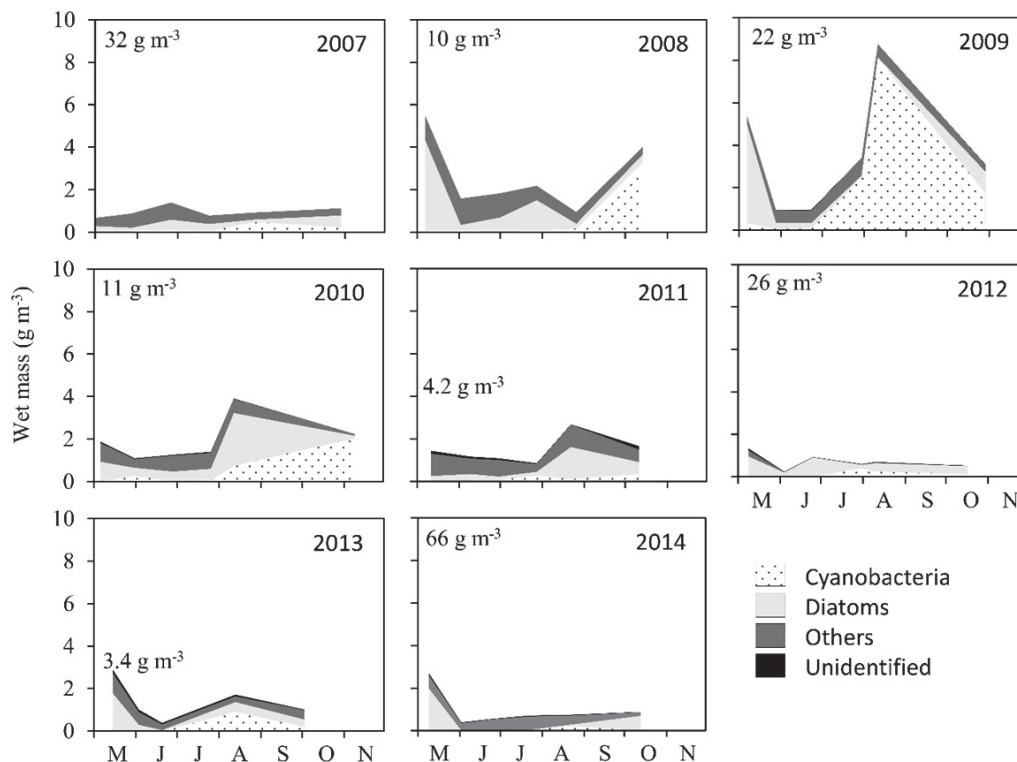
Figure 12. Development of phytoplankton in Enonselkä during the open water seasons of 2007–2013. Values on the left side of each panel indicate the observed under-ice maximum biomass that has been scaled to the depth of the epilimnion in August. The thickness of the euphotic zone was estimated to be twice the Secchi–depth.

Water shallower than 12.5 m comprises 90 % of total water volume in Enonselkä. In March 2000–2009 without mechanical mixing (Salmi et al. 2014b) a median of 88 % (range from 46 % in 2003 to 89 % in 2006) of total phosphorus in the water mass was in this layer < 12.5 m deep, so that the role of the deepest water remains small in the phytoplankton phosphorus budget. This means that mechanical mixing probably had no marked influence on inorganic or organic phosphorus concentrations in the uppermost water layers (Salmi et al. 2014b). In line with that, under-ice phytoplankton biomasses and rates of increase were not markedly affected by mechanical mixing. The rate of increase of *Stephanodiscus* sp. in Enonselkä (Fig. 11, Table 2) was an order of magnitude higher than those of the diatoms, *Urosolenia longiseta* (O.Zacharias) Edlund & Stoermer (previously *Rhizosolenia longiseta* O.Zacharias) and *Aulacoseira* sp., in the deep and

oligotrophic lake Pääjärvi during under-ice convection (0.02 d^{-1}, Vehmaa and Salonen 2009). In Lake Erken, Pechlaner (1970) found a similar rate of increase (0.21 d^{-1}) of *Stephanodiscus hantzschii* v. *pusillus* Grunow. In shallow Lough Neagh, the mean rate of increase of *Stephanodiscus astraea* Kütz. during spring blooms was similar (0.11 d^{-1}, Foy and Gibson 1993) despite the much more eutrophic nature of the lake (total P ca. 0.100 g m^{-3}). Somewhat higher increase rates (average 0.24–0.88 d^{-1}) than in Enonselkä have been reported from laboratory experiments at low temperatures and continuous light of 46–220 µmol m^{-1} s^{-1} for different psychrophilic diatoms from Antarctic lakes (Fiala and Oriol 1990). Different conditions make comparison between lakes and experiments crude, but rates of increase derived from under-ice field observations in Enonselkä can still be considered reasonable. The abundance of diatoms increases first and after some delay is

followed by their grazers (Adrian et al. 1999). With the exception of calanoid copepods, which overwinter actively in the water column (Vanderploeg et al. 1992), crustacean zooplankton cannot efficiently respond to the development of under-ice phytoplankton (Pechlaner 1970).

The availability of light was no doubt key to the development of under-ice phytoplankton biomass maxima in Enonselkä. However, due to temporally variable weather conditions light availability in the water was never increasing smoothly and the time span from the beginning of convection to ice-break varied. Nevertheless, the results showed exponential development of phytoplankton after the beginning of convection (Fig. 8). Because the increase rates of *Stephanodiscus* remained quite similar until the end of ice cover (Fig. 11), increasing light penetration into water was probably compensated by increasing mixing depth and decrease of nutrient concentrations.

Under-ice phytoplankton assemblage

The size range of phytoplankton extends from pico- to microplankton. Picoplankton biomass has often been neglected although it can significantly contribute to total phytoplankton biomass (Callieri 2008). However, from comparison between the increase in microscopically counted picophytoplankton biomass and oxygen concentration, Salmi et al. (2014a) suggested low importance of picophytoplankton in Enonselkä. Here we found that during the convection period in 2009–2011 picophytoplankton biomass was only 0.2-3.3 % of that of nano- and microphytoplankton, which confirms the earlier conclusion. In Lake Baikal, where picophytoplankton are important during summer, they showed only a similarly small contribution to total phytoplankton biomass in spring (Belykh and Sorokovikova 2003; Popovskaya 2000).

After snow melt light conditions in Enonselkä at first markedly improved, but the increasing phytoplankton biomass as well as deepening convection soon started to decrease average light availability for phytoplankton. Foy and Gibson (1993) concluded that many diatom species are capable of growing at low irradiances and their growth is weakly affected by the length of photoperiod at low temperatures. Therefore non-motile diatoms suspended by convection currents (Kelley 1997) were probably least affected by the reduction of light availability during deep mixing of Enonselkä. Indeed, diatoms can maintain relatively high division rates, which can explain why they are generally responsible for the

spring maximum of phytoplankton in boreal and temperate lakes (Reynolds 1984; Richardson et al. 2000; Padisák et al. 2003). Although in the years with short duration of convection phytoplankton groups other than diatoms were relatively more abundant, there was no support for the suggestion of Weyhenmeyer et al. (1999) that the proportion of diatoms is low when spring phytoplankton maximum occurs below ice. However, information from a wider variety of lakes is clearly needed to understand better the factors behind species composition of under-ice phytoplankton.

Small *Stephanodiscus* diatoms have been found typical of eutrophic and phosphorus-replete conditions (Anderson 1989; Stoermer et al. 1985) and according to the sediment records from Enonselkä (Liukkonen et al. 1993; Liukkonen et al. 1997) they have been a dominant component of phytoplankton spring maximum in Enonselkä for decades. However, in agreement with our study, the diatoms *Asterionella formosa* and *Aulacoseira islandica* have also been found. Mechanical mixing did not seem to affect the species composition of the diatom assemblage, which is not surprising because natural convection overrode mechanical mixing in late spring. Liukkonen et al. (1997) reported that small *Stephanodiscus* cells comprised < 20 % of the total annual accumulation of diatom wet mass in the Enonselkä sediments, which were mainly composed of larger species. Our results confirm the deduction that large, heavily silicified species are more typical of late summer than winter (Liukkonen et al. 1997; Sicko-Goad et al. 1989).

Based on correlations with the North Atlantic Oscillation indexes (NAO), Weyhenmeyer et al. (1999) suggested that phytoplankton species composition in Lake Erken is determined early in winter. However, because many episodic type factors occurring in autumn (Salonen et al. 2014), winter and spring can be in decisive role for the development of under-ice phytoplankton, the low (50% or less) degree of explanation by the correlations of Weyhenmeyer et al. (1999) hardly makes NAO indexes useful for the prediction of phytoplankton or its species composition.

Under-ice distribution of phytoplankton

Despite little difference between the vertical distributions of diatoms and motile phytoplankton in Enonselkä, the higher contribution of the latter to early under-ice phytoplankton biomass suggests that

their motility initially allowed better access to light. Later high light intensity and dilution of nutrient concentrations by melt water made living in the boundary layer next to ice unfavourable. This might explain the generally lower phytoplankton biomass within the first 0.1 m under the ice. The few observed exceptions probably depended on the strength of convection (i.e. solar radiation) at the moment of sampling. In the more than twice as deep and oligo–mesotrophic Lake Pääjärvi, Vehmaa and Salonen (2009) found that cryptophytes and chrysophytes were partly able to maintain their highest abundance in the uppermost water layers (no samples above 1-m depth) during vertical convection while diatoms were not. Instead, in even larger Lake Päijänne, where horizontal convection dominated, water movements were evidently too strong and led to uniform distribution of motile phytoplankton in the late phase of ice-cover (Kiili et al. 2009). Horizontal convection currents, which prevailed in the Enonselkä basin in 2014, are more continuous than diurnal vertical convection (Salonen et al. 2014) and leave phytoplankton no possibility to recover their vertical distribution during night. Thus vertical distributions of different phytoplankton species may vary greatly according to momentary conditions and the mixing regime.

Compared to wind–induced turbulent mixing, under-ice convective mixing is weak and (with the exception of horizontal convection) diurnally intermittent, which may provide an advantage to small diatoms over larger ones in avoidance of sedimentation. Large *Aulacoseira baikalensis* can dominate under ice in Lake Baikal (Kozova 1987) where it may be favoured by wind, which often drives snow away so that increased light penetration into the lake amplifies under-ice convection currents. Because little is known about under-ice horizontal convection in late winter, its consequences for phytoplankton and particularly for diatoms are unclear. Under the ice of Enonselkä, the transport mechanism moving diatoms to the pelagial cannot be simply vertical convection, as diatoms appeared before vertical convection had reached the deepest water layers. As many diatoms, including *Stephanodiscus*, have been suggested to be meroplanktonic (Sicko-Goad et al. 1989), horizontal convective currents likely have a key role in the development of under-ice diatoms (Vehmaa and Salonen 2009).

Because we have no horizontal phytoplankton data from under the ice of Enonselkä the occurrence of higher deep-water biomasses might in isolation be interpreted as simply random variation. However, the coincidence with temperature and oxygen results (Fig. 4) makes interpretation more convincing. Particularly in 2012, when mechanical mixing was already switched off, the remarkable increase in deep-water phytoplankton biomass must have been due to horizontal convection (Fig. 7). The similarity of the species composition with that in the upper water layers does not support a possibility that warmer water originated from the River Joutjoki. Instead, because water heated by solar radiation is mixed by convection through a smaller depth in the shallow than in the offshore regions, it warms more rapidly (Fig. 4) and tends to intrude below the vertical convection layer of the pelagial (Salonen et al. 2014). At the same time higher oxygen concentrations in the shallower areas indicated higher primary production, and consequently also phytoplankton biomass, than in the middle of the basin (Fig. 5). Furthermore, there was no increase in biomass at 30 m depth (Fig. 7), which excludes the possibility that increased deep-water biomass was due to sedimentation. Thus, variation in the melting of ice and snow over the shallow areas (Salonen et al. 2014) can significantly contribute to the interannual differences in diatom biomass in the middle of the basin.

Conclusions

During the last few weeks of ice cover, phytoplankton in Enonselkä undergoes rapid growth, which is closely coupled with the development of vertical and horizontal convection typical of lakes in which water temperature drops well below 4 °C before freezing. Because the development is coupled with highly stochastic, mainly weather-related, factors, under-ice phytoplankton can be interannually variable. It seems that the bulk of phytoplankton spring maximum often develops under ice and may reach values corresponding to or even exceeding the highest summer values. During the last few weeks of ice-cover, circulation induced by solar radiation is so strong that it masks the effects of mechanical mixing. Variation in the development of the phytoplankton spring maximum is likely important for trophic dynamics of lake ecosystems in the following summer. Better understanding of spring phytoplankton requires high frequency areal observations of temperature, oxygen, photosynthetic pigments and sedimentation over the transition period between winter and summer.

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