Diurnal variation in the convection-driven vertical distribution of phytoplankton under ice and after ice-off in large Lake Onego (Russia)

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Abstract

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ABSTRACT
When sunlight penetrates the ice layer covering lakes in winter, it warms the top water layer and sets up convection, with several potentially contrasting effects on phytoplankton. While convective mixing keeps cells in suspension and prevents sedimentation losses, it may also transport phytoplankton well below the euphotic zone. We investigated diurnal variations in the vertical distribution of phytoplankton under ice and just after ice-off in Lake Onego (Russia), a lake with moderate to high colored dissolved organic carbon (CDOM) levels. We showed that diurnal variation in convection under ice restricts phytoplankton access to light in the morning hours to a narrow euphotic zone, whereas cells are mixed through a deep aphotic layer in the afternoon. After ice-off, low chlorophyll a was found on the open-water side of the thermal bar as convection distributed cells throughout the water column. By contrast, the inshore side had significantly higher concentrations of chlorophyll a (p < 0.001) because the mixing depth brought about by diurnal microstratification was reduced, resulting in greater access to light in the afternoon. Overnight, convective cooling broke down microstratification, which redeveloped the next day. Our work highlights the importance of studying diurnal variation in light availability for photoautotrophic growth, both under ice and after ice-off in lakes characterized by high CDOM.

Introduction
Interest is growing in the study of life under ice, including phytoplankton (Hampton et al. 2015, 2017). Many factors that control and drive early phytoplankton growth under ice and just after ice-off are not yet fully understood (Kelley 1997, Hampton et al. 2015, Bouffard et al. 2016). Sunlight penetrating the ice layer heats the water, increasing its density and setting up convection over the course of the day. Kelley (1997) described how, in Lake Baikal, convection maintains phytoplankton in suspension and within the euphotic zone, thereby promoting the development of algal blooms under the ice. When convection is sufficiently strong, even large and dense taxa, such as *Aulacoseira baicalensis* may thrive (Jewson et al. 2010, Jewson and Granin 2015). By contrast, Vehmaa and Salonen (2009) explained how under-ice convection in Lake Pääjärvi (Finland), a lake rich in colored dissolved organic matter (CDOM), drives phytoplankton below the shallow euphotic zone, hindering its development.

During the period of ice-off in spring, differential heating may cause the shallow near-shore areas of a lake to warm more quickly than its deeper central part, creating a thermal bar (Forel 1880, Holland and Kay 2003). On the inshore side of the thermal bar water is warmer and begins to stratify. By contrast, on the cold open-water side of the thermal bar, deep penetrative convection maintains full mixing and iso-thermal conditions. In a lake with steep light attenuation, such as a lake rich in CDOM, deep mixing would be prohibitive for phytoplankton growth in the open water (Talling 1971, Kirk 1994). By contrast, on the stratified inshore side of the thermal bar, the build-up of a spring phytoplankton bloom would be supported by maintaining the cells in the shallower mixed layer, allowing them to spend more time within the euphotic zone.

Although a number of studies on convection under ice and its effect on phytoplankton growth have been conducted, they have rarely investigated the significance...
of diurnal patterns of convection to phytoplankton development. In this study, we investigated the diurnal patterns of convection under ice and in open water, just after ice-off, on phytoplankton growth in the large and relatively high-CDOM Lake Onego in Russia (Fig. 1). Similar to the Finnish Lake Pääjärvi (Vehmaa and Salonen 2009), we assumed that deep convection limits phytoplankton growth. We also presumed that each day brief windows of opportunity for phytoplankton growth occur when light is sufficient for net growth but convection is not yet fully developed. Therefore, we expected contrasting patterns in diurnal variation in convection and phytoplankton distribution under ice and after ice-off. Considering these points, we aimed to test if:

(1) Deep convective mixing in a CDOM-rich lake leads to low phytoplankton biomass owing to light limitation; phytoplankton development requires a mechanism that allows cells to remain closer to the lake surface.

(2) Diurnal variation in the strength of convection limits access to light for photoautotrophic growth to specific time periods of the day (morning vs. afternoon), which are opposite under ice and after ice-off.

The 2 aims of the study were clearly linked. In CDOM-rich lakes, the same sunlight that maintains photosynthesis also sets up deep convection. Thus, we postulated that this deep convection drives phytoplankton into the deep aphotic zone and restricts opportunities for photoautotrophic growth to specific times of the day.

Methods

We conducted 2 field campaigns in Lake Onego, one in mid-March under the ice (winter expedition) and the other after ice-off in June 2017 (spring expedition). The lake surface area of 9700 km² makes it the second largest lake in Europe. Lake Onego has an average depth of 26.8 m and maximum depth of 119 m and is considered to be oligo-mesotrophic.

During the winter expedition, the sampling station P2, referred to as “Ice Camp,” was located ~2.6 km from Petrozavodsk port (Fig. 1, Table 1). For safety reasons, the station had to be located in Petrozavodsk Bay rather than the open-water part of the lake because of insufficient ice thickness. During the spring expedition, we added 2 more stations: T0708, referred to as the “inshore station” of the thermal bar; and C3, referred as the “open-water station” outside the thermal bar (Fig. 1, Table 1). These 2 stations, one on each side of the thermal bar, were the most intensively studied from a 10-station transect to locate the position of the thermal bar. Both in March and June 2017, water was sampled twice per day (Fig. 1, Table 1) using a Niskin bottle. Samples were taken at different depths (Table 1) according to the thermal structure of the water column, recorded with a conductivity, temperature, and depth (CTD) probe (RBR concerto CTD++, Canada), and the depth of the chlorophyll a (Chl-a) maximum from Fluoroprobe profiles (BBE Molsdauenke, Germany). At each depth, we collected 4 L of water for the following laboratory analyses: dissolved organic carbon (DOC), Chl-a, phytoplankton counts, and nutrients (Supplemental Table S1–S3).

Convectively mixed layer (CML)

The CML thickness and velocity were determined as described in Bouffard et al. (2019). Briefly, 10 fast
temperature sensors (10 s sampling period, TR-1060, RBR, Canada) positioned at 2.5 cm intervals for the first 25 cm under the ice allowed an accurate estimation of the upper boundary of the CML. The lower boundary of the CML was determined from hourly casts of CTD profiles (CTD 90 Sea & Sun Technology, Germany). The thickness of the CML, $h_{\text{CML}}$, was calculated as the difference between the upper and lower boundary. The convective velocity, $w_c$, scales with the buoyancy flux $B$ and the $h_{\text{CML}}$ as:

$$ w_c = (B h_{\text{CML}})^{1/3}. \quad (1) $$

Convection velocities were also measured directly by freezing acoustic Doppler current profilers (ACDP) (one 600 kHz Mode 11 Teledyne RDI ACDP unit [USA] and two High Resolution 2 MHz Nortek AquaDopp units [Norway]) in the ice for the duration of the field campaign.

In addition to the vertical profiling sensors, a thermistor chain (TR-1060, RBR, Canada) was installed below the ice, down to 25.56 m depth (0.36 m vertical spacing), to examine continuously (10 s sampling period) the temperature dynamics during the winter campaign.

The depth of the mixed layer in spring was calculated as the depth of the top of the thermocline using the R package “rLakeAnalyzer” by Read et al. (2011).

### Photosynthetically active radiation (PAR) profiles

The attenuation of solar radiation in the water was measured during both campaigns. In winter, the setup consisted of 8 PAR sensors (Ultra-miniature Light Intensity Recorder MDS-MkV/L, Alec electronics, Japan) installed under the ice at different depths (0, 0.35, 0.6, 0.85, 1.1, 1.6, 2.1, and 2.6 m, respectively). The sensors were programmed to record the light intensity ($\mu$mol m$^{-2}$ s$^{-1}$) for 3 consecutive days at 1 min intervals. In spring, PAR water column profiles were recorded at each sampling time and site using a multichannel CTD (RBRconcerto C.T.D+++, Canada).

Following the methodology described in Bouffard et al. (2016) for lakes under ice, we calculated the vertical light attenuation coefficient $K_w$ (equation 2) for different depths, and the euphotic zone $Z_{eu}$ (equation 3) as the depth where 1% of the surface PAR remains:

$$ K_w(Z_1, Z_2) = -\ln\left(\frac{\text{PAR}(Z_1)}{\text{PAR}(Z_2)}\right) \frac{1}{Z_1 - Z_2}, \quad (2) $$

$$ Z_{eu} = -\ln(0.01) \frac{1}{K_w}. \quad (3) $$

### Chlorophyll $a$ analysis

Two different instruments were used to measure Chl-$a$ in Lake Onego: a Fluoroprobe (BBE Moldaenke, Germany) for in situ measurements and a fluorometer (Trilogy, Turner Designs, USA) for lab-based Chl-$a$ fluorescence analysis of living cells (in vitro) and after extraction (in vitro) in lake water samples. Both instruments were calibrated for yellow substances and Chl-$a$ content with a certified standard solution prior to use. For the Chl-$a$ extraction, 1 L of each water sample was filtered using GF/F glass microfiber filters ($\phi$ 47 mm; 0.7 $\mu$m pore size; Whatman, UK). Two filters per depth were stored at $-80 \degree C$. The filters were cut into pieces and submerged in Falcon tubes with 10 mL of 90% acetone to extract the Chl-$a$. The tubes were vortexed and sonicated (Ultrasonic Vibra-Cell, Sonics, USA) at 60 W for 20 s, after which they were placed in an ultrasonic bath (Branson 5510MTH, Branson baths, UK) for 15 min. The samples were refrigerated for 1 h before the previous 2 steps were repeated and then refrigerated for 14 h. The extracted Chl-$a$ was centrifuged for 5 min (4000 rpm, 4 $\degree C$) and then measured in triplicate using the fluorometer (Chl-$a$ NA module-Turner Designs, USA).

### Phytoplankton counting and identification

On each sampling day, 1 L of water was preserved with 1% Lugol’s solution. After 10 days of sedimentation, the phytoplankton samples were individually concentrated 100-fold. Phytoplankton cells in each sample were counted and identified to species level using a Nageotte chamber (0.02 cm$^3$) under an optical microscope at 400× and 600× magnification. Species cell size was measured using an ocular micrometer (Hillebrand et al. 1999, Olenina et al. 2006). Cell biovolumes were calculated following Olenina et al. (2006) and Tikkanen (1986).

### Dissolved organic carbon (DOC) analysis

Water samples at 0.5, 15.5, and 27.5 m depth were filtered through 0.45 $\mu$m glass microfiber filters (GF/F filters, GE Healthcare Life Sciences, Switzerland) and acidified with 200 $\mu$L of HCL 2M to quantify DOC using a Shimadzu TOC-L analyzer.

### Sedimentation velocity

To estimate the sedimentation velocity of the dominant diatoms present in Lake Onego and to compare it with the convective velocity under ice, we measured the size of phytoplankton from a mesh net sample (55 $\mu$m)
using a 1.0 mL Sedgewick-Rafter counting chamber (Model 1801-G20, Wilco, USA) and a BX UCB microscope (Olympus, Japan) following IOC-UNESCO (2010). We focused on *Aulacoseira islandica* (filamentous diatom), the dominant species of Lake Onego in winter, to determine the sedimentation velocity by measuring the length, width, and orientation of the filaments. We used Stokes equation as corrected by McNown and Malaika (1950). The sinking rate of the filaments (cylinders) was considered to be the settling velocity of an ellipsoid with the same axial ratio, volume, and buoyant density (Walsby and Holland 2006):

\[v_s = \frac{2gr^2_e (\rho' - \rho)}{9\eta\phi},\]  

(4)

where \(g\) is gravity (9.8 m s\(^{-2}\)), \(\rho\) is water density (998.2 kg m\(^{-3}\) at 0.5 °C), and \(\eta\) is the corresponding dynamic viscosity (1.0019 × 10\(^{-3}\) kg m\(^{-1}\) s\(^{-1}\)). The effective radius \(r_e\), the density \(\rho'\), and the form resistance \(\phi\) are individual parameters of the filaments. We assumed that the density of *A. islandica* ranged between 1155 and 1182 kg m\(^{-3}\) as determined by Reynolds et al. (1984) for wide filaments of *A. subarctica*.

**Results**

Results are presented for the winter campaign first, followed by spring to separate the results during convective conditions in winter (i.e., under ice, water temperature <4 °C) from the results during stabilizing conditions in spring (i.e., water temperature >4 °C).

**Part A: winter campaign**

**Temperature profiles**

The vertical thermal structure (Fig. 2) consisted of 3 layers: (1) a thin under-ice layer from 0 to 0.36 m, (2) a CML from ~0.36 to 15 m, and (3) a layer down to the lake sediment at 26 m depth, where the temperature increased to 1.7 °C (Supplemental Fig. S1). The temperature at this bottom layer remained constant throughout the campaign.

The thin under-ice layer showed distinct diurnal changes in temperature from morning to afternoon (Fig. 2). For example, during the morning (0800 h) of 16 March, the coldest water, ~0.20 °C, was found at the top of the under-ice gradient. During the afternoon (1400 h) of the same day, the water temperature under the ice had increased from 0.20 to 0.33 °C, triggering convection and resulting in an isothermal mixed layer down to 15 m depth. During the night, the thin cold layer on the top of the water column redeveloped (Fig. 2), reestablishing the 3 stratified layers described earlier. The 24 h temperature readings directly under the ice and at 0.36 m depth confirmed the diurnal patterns (Fig. 3). During the morning sampling, the water column just under the ice was still stratified, with the temperature at 0 m lower than the temperature at 0.36 m depth. During the afternoon sampling, however, this difference in temperature at 0 and 0.36 m was no longer present. A similar vertical thermal structure was described by Bouffard et al. (2016) for Lake Onego.

![Figure 2](image-url)

**Figure 2.** Diurnal variation in the vertical water temperature profiles (0–20 m depth) from Lake Onego in March 2017 at the Ice Camp station. Each shade represents a different sampling day. The line types correspond to the time of day: morning = solid line, afternoon = dashed line.
Convection

The convective velocity, monitored continuously from 15 to 17 March 2017 (Fig. 4), showed a similar pattern for all days. Convection started at 0500 h, reached maximum values between 1300 and 1500 h (0.0038 m s$^{-1}$ average at 1300 h from 15 to 17 March), and stopped completely at 2000 h. ADCP measurements (data available in Bouffard et al. 2019) showed alternating downward and upward plumes with maximal values of 0.0075 m s$^{-1}$. The extent of the CML varied among the sampling days (Supplemental Table S4). The thin under-ice thermal layer warmed from the first to the third day of sampling (Fig. 3), which was reflected in the depth of the CML (Supplemental Table S4). In the afternoon of the first day, the CML was restricted to 12.84 m depth while on the last day reached 14 m depth.

Light profiles

The ice thickness in Lake Onego during the winter campaign was $\sim$0.38–0.40 m, the snow thickness varied

![Figure 3. Temperatures for a 24-hour period from 15 to 17 March 2017 at 0 m and 0.36 m under the ice at the Ice Camp station in Lake Onego. Each shade represents a different sampling day. The solid lines correspond to the under-ice layer and dashed lines to the 0.36 m depth layer.](image)

![Figure 4. Convective velocity over 3 days in Lake Onego, March 2017. Each shade represents a different sampling day: black line 15 March, yellow 16 March, and blue 17 March, respectively.](image)
between 0 to 0.05 m, and the snow cover varied between 50% and 80% at different locations in the lake. The absence of thick snow cover and the low albedo of the uncovered ice allowed good transmission of light, and therefore the value of downwelling solar irradiance under the ice exceeded upwelling solar irradiance above the ice (full results in Bouffard et al. 2019). PAR intensity varied between the sampling time and day (Fig. 5a). PAR was always higher for the afternoon sampling, especially on the second day when it reached 931 µmol m⁻² s⁻¹ under the ice. The percentage of light available, based on PAR, decreased steeply with depth (Fig. 5b). Only 25% of the surface PAR remained at 0.35 m depth (Fig. 5b). The depth of the euphotic zone varied from 1.69 (SD 0.02) m in the morning to 1.71 (SD 0.03) m in the afternoon (Table 2). The light attenuation coefficient, \(K_w\), was 2.71 (SD 0.05) m⁻¹ (Supplemental Table S5), indicating steep light attenuation. The ratio of euphotic to convective depth \(Z_{eu}/Z_m\) was only 0.13 with convection at maximum velocity at noon (Fig. 4, Table 2).

**DOC**

DOC concentration (as C) was 9.1 mg L⁻¹ at the top (0.5 m) and bottom (27.5 m) of the water column and 11 mg L⁻¹ in the middle of the water column (15.7 m).

![Figure 5](image-url)

**Figure 5.** Vertical profiles of Lake Onego in March 2017. (a) PAR values correspond to the average of 1 min PAR measurements at the indicated day and time. (b) Percentage of light available at depth under the ice from PAR profiles in (a). For both graphs, each shade represents a sampling day and solid versus dotted lines the time of sampling.
The Chl-a results obtained in vivo and after extraction in the lab were highly comparable (Fig. 6a–b); therefore, we only report the extracted Chl-a values here. The data showed a distinct difference between morning and afternoon vertical distribution. In the morning, the highest Chl-a concentrations were found in the under-ice thin layer, which was on average 0.59 (SD 0.09) µg L\(^{-1}\) for the 3 morning samplings. This concentration decreased rather abruptly with depth to 0.26 (SD 0.03) µg L\(^{-1}\) at 10 m (i.e., 56% reduction). In the afternoon, Chl-a concentrations were lower than in the morning and were more homogeneously distributed over the water column. The average Chl-a concentration in the afternoon samplings between 0 and 10 m depth was 0.25 (SD 0.08) µg L\(^{-1}\) (Fig. 6b).

Phytoplankton counts
Microscopic analysis showed that the phytoplankton was dominated by diatoms (Bacillariophyta), which accounted for 82.8–98.8% of the total biomass of the samples. The other taxa, such as dinoflagellates (Dinophyceae), cryptophyta (Cryptophyceae), golden algae (Chrysophyceae), and cyanobacteria (Cyanophyta), accounted for <5% of the total biomass. *Aulacoseira islandica* and *A. islandica* subsp. *helvetica* were identified as the most dominant species, accounting for 70–99% of the total biomass based on biovolume. Subdominant diatoms observed were *Asterionella formosa*, *Nitschia acicularis*, *Tabellaria fenestrata*, and *Cyclotella* spp.

Sedimentation velocity
*Aulacoseira* filaments had a mean width of 13.53 (SD 2.6) µm \((n = 50)\) and mean length of 247.2 (SD 95.3) µm \((n = 50)\) in the samples analyzed by microscopy. The sedimentation velocities were calculated for each of the 50 individual filaments we measured. The mean sinking velocity was 62.0 (SD 25.15) µm s\(^{-1}\) for the vertically oriented filaments \((u_v)\) and 41.1 (SD 16) µm s\(^{-1}\) for the horizontally oriented filaments \((u_h)\), an overall average of 51.6 (SD 23.7) µm s\(^{-1}\). Vertically and horizontally oriented filaments have different sinking velocities because the form resistance factor, \(\varphi\), in Stokes law changes with the orientation of the diatoms, resulting in filaments that can sink at different angles (Walsby and Holland 2006).

Part B: spring campaign
Temperature profiles
During the spring campaign the vertical thermal structure was radically different between the 2 stations (Fig. 7a). For the inshore station during the morning, the water column was mostly isothermal with the temperature varying by only 0.35 °C from the top to 26 m depth. By contrast, in the afternoon we distinguished 3 layers:

### Table 2. Average values (standard deviation) for light attenuation coefficient \((K_w)\), mixing depth \((Z_m)\) and euphotic zone \((Z_{eu})\) in Lake Onego 2017 campaigns. For Ice Camp, the average corresponds to the 3 sampling days from 15 to 17 March 2017.

<table>
<thead>
<tr>
<th>Station</th>
<th>Time</th>
<th>(K_w) (m(^{-1}))</th>
<th>(Z_m) (m)</th>
<th>(Z_{eu}) (m)</th>
<th>(Z_{eu}/Z_m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ice Camp</td>
<td>0800 h</td>
<td>2.74 (0.03)</td>
<td>13.39 (0.48)</td>
<td>1.69 (0.02)</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>1400 h</td>
<td>2.69 (0.05)</td>
<td>13.42 (0.68)</td>
<td>1.71 (0.03)</td>
<td>0.13</td>
</tr>
<tr>
<td>Spring</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inshore side</td>
<td>0800 h</td>
<td>1.04 (0.41)</td>
<td>19.87</td>
<td>4.44</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>1500 h</td>
<td>3.07 (0.46)</td>
<td>4.29</td>
<td>1.5</td>
<td>0.35</td>
</tr>
<tr>
<td>Open water</td>
<td>0800 h</td>
<td>0.80 (0.14)</td>
<td>36.48</td>
<td>5.77</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>1500 h</td>
<td>1.31 (0.29)</td>
<td>41.92</td>
<td>3.63</td>
<td>0.09</td>
</tr>
</tbody>
</table>

**Figure 6.** Chlorophyll a profiles of Lake Onego water column in winter 2017. (a) Chlorophyll a in vivo; each point represents the average of 4 water samples. (b) Chlorophyll a after extraction in acetone; each measurement represent the results from the extraction of 2 filters. The error bars represent standard error; line types correspond to time of day: morning = black solid line, afternoon = blue dashed line.
(1) a near-surface mixed layer of 6.5 °C, extending from the surface to ∼5 m depth;
(2) a transition layer, from 5 to 10 m depth, where temperature decreased from 6.5 to 5 °C; and
(3) a deep layer, from 10 m down to the bottom, where the water temperature decreased slowly to ∼4.6 °C.

At the open-water station, no sign of thermal stratification was observed (Fig. 7a). The daily average temperature in the isothermal water column was 2.5 (SD 0.04) °C, below the critical 4 °C limit where water reaches its highest density, so that any daytime warming would strengthen convective mixing.

**Light profiles**

PAR profiles in spring varied between sampling stations and time of the day (Fig. 7b). At both stations, PAR was higher during the morning than in the afternoon. The open-water station had the lowest $K_w$, both in the morning and in the afternoon, and thus the deepest euphotic zone (Table 2). The biggest difference between the 2 sites was observed in the afternoon, with a 2.13 m deeper $Z_{eu}$ at the open-water station than at the inshore station. However, $K_w$ for both sites increased during the day as euphotic zones became shallower. This increase was especially striking at the inshore station, with $K_w$ in the afternoon tripling in value compared to the morning. Potential causes for the diurnal variation in light extinction are part of a further investigation by the Karelian Research Center.

**DOC**

DOC concentrations for the open-water stations varied from 6.36 mg L⁻¹ at 1 m depth to 6.48 mg L⁻¹ at 40 m depth. Petrozavodsk Bay had higher DOC concentrations, 12.8 mg L⁻¹ from the surface to the bottom of the water column.

**Chlorophyll a profiles**

The Chl-a profiles were different between the 2 spring sampling stations ($t = -16.45, p < 0.001$; Fig. 8). At the open-water station, Chl-a was low and homogeneously distributed over the water column, with a nonsignificant difference between morning and afternoon concentrations ($t = -1.02, p = 0.169$). The average Chl-a concentration at this station was 1.66 (SD 0.08) µg L⁻¹. At the inshore station of the thermal bar, the vertical
distribution of Chl-a in the water column changed with depth and with the time of the day (Fig. 8). In the morning, Chl-a concentrations were significantly lower than in the afternoon ($t = -2.64, p = 0.012$), with average values of 6.35 (SD 0.97) and 7.82 (SD 0.79) $\mu$g L$^{-1}$, respectively. At this inshore station we found the highest Chl-a concentrations from all samplings, both for spring and winter. Chl-a reached a maximum value at 8 m depth (7.31 $\mu$g L$^{-1}$) in the morning and at 4 m depth (8.90 $\mu$g L$^{-1}$) in the afternoon.

**Phytoplankton counts**

The dominant phytoplankton group in the lake was again diatoms, accounting for 77–99% of the biomass based on biovolume, followed by Cryptophyceae (0.3–12.1%), Dinophyceae (0–16.6%), and Chrysophyceae (0–2.8%). The diversity of species changed between the stations. At the open-water station, we mainly found *Aulacoseira islandica* accounting for 36–68% of the total biomass, followed by *Asterionella formosa* (4–16%) and *Aulacoseira islandica* subsp. helvetica (3–13%). At the inshore station the diatom diversity was higher (*Asterionella formosa* 45%, *Cyclotella* spp. 22%, *Tabellaria fenestrata* 11%, among others), but *Aulacoseira islandica* remained most dominant (maximum 49%).

**Discussion**

Given the narrow euphotic zone of Lake Onego (Fig. 5b, Table 2), a mechanism is needed to maintain algal presence in a restricted layer close to lake surface where the light intensity is sufficient to support net photoautotrophic growth (Granin et al. 2000). In this study we investigated the role of light as the key limiting factor for phytoplankton development in Lake Onego (aim 1). In particular we focused on the diurnal aspects of sunlight driving convection and therefore phytoplankton distribution under ice and after ice-off (aim 2). We provided new support for the critical role of mixing on limiting access to light under ice in the colored lake Onego, plus a direct comparison with the continued prominent role of convection and steep light attenuation directly after ice-off.

**Light limitation in a lake with moderate to high CDOM levels**

The importance of light for phytoplankton development in lakes is well known, as is the critical role of mixing depth (Sverdrup 1953, Talling 1971, Huisman et al. 1999). Light also plays a prominent role among the factors that limit under-ice phytoplankton growth (Kelley 1997, Granin et al. 2000, Katz et al. 2015). A clear lake like Lake Baikal exhibits distinctive positive effects of under ice convection (e.g., Katz et al. 2015). Convection maintains phytoplankton cells in suspension, preventing large sedimentation losses. Convection also enhances nutrient availability for blooms that form under the ice. By contrast, we found that in a turbid lake like Lake Onego, the effect of convection was primarily negative by driving cells well below the euphotic zone. Evidently, the importance of diurnal aspects of under ice convection is more significant in a turbid than in a clear lake. Whereas under the ice in Lake Baikal phytoplankton remains in the illuminated part of the water column for most of the day, in Lake Onego sufficient access to light is restricted to a brief time in the morning, just before surface heating triggers convection.

To date, the role of DOC under ice, a topic of growing attention in open water linked to brownification of lakes, has received little attention (Granelli 2012). DOC contains both chromophoric and nonchromophoric components, but given the dark color of Lake Onego and strong wavelength dependence of $K_{uv}$ from 1.2 m$^{-1}$ at 700 nm to 5 m$^{-1}$ at 450 nm (Bouffard et al. 2019), a large fraction of DOC behaves as CDOM. DOC concentrations in Lake Onego exceeded the median DOC values (~5 mg L$^{-1}$) of a 7500 lakes dataset (Sobek et al. 2007). At Ice Camp for example, DOC concentrations exceeded 9 mg L$^{-1}$. However, given the spatial heterogeneity in Lake Onego, we would classify it as moderately high (open-water station) to high (Ice Camp) in DOC. These conditions can have a negative effect on phytoplankton development, as shown in experiments in 3 lakes in Wisconsin, USA, where they demonstrated a significant reduction in the primary production and Chl-a levels when DOC concentrations were >5 mg L$^{-1}$ (Carpenter et al. 1998).

**Diurnal patterns in temperature and biomass gradients under ice and after the ice-off**

Winter campaign results demonstrated a beneficial top-down distribution in the morning when the peak in phytoplankton biomass was located in the uppermost layers of the lake (i.e., within $Z_{eu}$; Fig. 6a–b). This result can be explained by looking at the morning temperature profiles, showing a narrow cold layer on top of a denser slightly warmer water layer (Fig. 2, 3). In this narrow cold layer, Chl-a values were 2–3-fold higher (albeit small in absolute terms) than in the water underneath. In the afternoon, radiatively driven convection had removed the thermal stratification, and the Chl-a gradient became more homogeneously distributed (Fig. 2, 4, 6). Hence, the vertical phytoplankton distribution under the ice is only beneficial for photoautotrophic growth in the morning when cells are positioned within the euphotic zone. This opportunity is lost in the
afternoon. Maximum convection values were observed around noon and stayed on a plateau for 2–3 h (Fig. 4). Convection is set up by the same sunlight that the algae need for energy and growth, and hence sunlight clearly has a double effect, both positive and negative, on phytoplankton development in Lake Onego. The dominant phytoplankton species in winter in Lake Onego are *Aulacoseira islandica* and *A. islandica* subsp. *helvetica* (70–99% of total biomass). They are representative species of the cold season, particularly of large and high altitude lakes (Le Coju 1996), and are known to form blooms under the ice (Babanazarova et al. 1996, Likhoshway et al. 1996). Literature values known to form blooms under the ice (Babanazarova et al. 1996, Likhoshway et al. 1996). Literature values for sinking velocities of similarly large diatoms vary from 34.7 to 69.4 µm s$^{-1}$ for *Aulacoseira baicalensis* to 1.2–69.4 µm s$^{-1}$ for *Rhizosolenia* (Smayda 1974, Kelley 1997, Walsby and Holland 2006). Our estimates for *A. islandica* and *A. islandica* subsp. *helvetica* revealed that the peak convection velocity was much higher than the estimated sedimentation velocity ($V_c = 3800$ µm s$^{-1}$, $V_s = 51.6$ µm s$^{-1}$ for convection and sedimentation velocities, respectively). This finding means that convection, when present, easily entrains diatoms under the ice, preventing sedimentation, but through the downwelling component of convection also forces them into deep, unproductive layers. For Lake Baikal, Jewson and Granin (2015) observed that *A. baicalensis* cells concentration was reduced by half from 1200 to 0400 h in the morning because of deep convection. They suggested that cell distribution was dependent not only on the snow cover but also on the time of day as the intensity of vertical mixing varied on a diel time scale. In Lake Baikal, where the euphotic zone can reach 25 m depth under ice, convection sustains cells in the illuminated part of the lake, in contrast to turbid Lake Onego where convection drives phytoplankton well below the narrow euphotic zone.

One issue that remains somewhat of an enigma is the means by which a Chl-a peak forms in the thin under-ice layer, and seems to do so recurrently. Whereas Chl-a profiles were homogeneous over depth in the afternoon, a distinct top-down Chl-a distribution was reestablished the next morning (Fig. 6a–b). Given the short time available between sunrise and sampling, it seems unlikely that most of what we see is in situ photoautotrophic growth. *Aulacoseira*, the dominant genus in Lake Onego, is known for growing attached to the ice in long strings in other lakes (Straškrabová et al. 2005, Bondarenko et al. 2006). However, a Trilux fluorometer positioned facing the underside of the ice for a number of days provided no evidence for the presence of Chl-a. A third possibility would be that motile taxa disentrain from weakening convection toward the end of the afternoon and at night and simply move back to the surface. Large diatoms that dominated phytoplankton have no mechanisms for motility, although they are known to reduce their sedimentation velocity (Reynolds and Irish 1997). Yet, on one of the sampling dates, 12% of the phytoplankton community under the ice was identified as the dinoflagellate *Peridinium pusillum*, which is able to form dense populations under ice (Spilling 2007) and, being motile, could reposition itself in the top layer after convection subsides. The final possibility, which we cannot discount, is advection of cells from the shallowest areas around the edge of the Petrozavodsk Bay, driven by the convection set up by additional warming in the more shallow littoral zone (Vehmaa and Salonen 2009).

In spring after ice-off, the results also support a crucial role of light for phytoplankton growth in Lake Onego, and once more diurnal patterns seem relevant (Fig. 7b, 8). On the inshore side of the thermal bar, we found Chl-a values $>$5-fold higher than at the open-water station (Fig. 8), just a short distance away. The availability of nutrients on either side of the thermal bar showed no difference (Supplemental Table S3). Rather, the key difference between the 2 stations seemed to be in the thermal structure and its diurnal variation (Fig. 7a, Table 2). After ice-off on the open-water side of the thermal bar, water temperature remained $<$2 °C in June while at the inshore station the lake had already warmed to $>$5 °C. At the open-water station, a thermal structure was virtually absent, resulting in unrestricted and deep mixing, while on the inshore side mixing was shallower, restricted by temperature stratification (Table 2). This finding may well explain the difference in Chl-a (Fig. 8, Table 2). When morning versus afternoon temperature profiles were compared (Fig. 7a), surface heating during the day created denser water and hence deep penetrative mixing at the cold open-water side of the thermal bar, maintaining isothermal conditions. By contrast, warming enhanced water-column stability through microstratification at the warmer inshore side where lake temperature was $>$4 °C. With deep mixing, Chl-a levels remained low and homogeneous over depth. Under conditions of microstratification, Chl-a distribution showed a more beneficial pattern, with a peak approaching 9 µg L$^{-1}$, building near the lake surface in the afternoon. Thus, the best conditions for photoautotrophic growth are found when the ratio of $Z_{eq}/Z_m$ is high, which for Lake Onego was found at the inshore station in the afternoon (Supplemental Fig. S2; Table 2).

Although the existence of a thermal bar and the stark contrast it creates between nearby sampling stations has
already been investigated for Lake Onego (Tekanova and Syarki 2015), in this study we added diurnal variation in temperature and phytoplankton biomass gradients on either side of the thermal bar. This early in the season, near-surface microstratification that builds during the day on the inshore side is too weak to survive convective cooling at night but is demonstrably strong enough to create important differences in biological activity, expressed as Chl-\(a\) (Fig. 7a, 8). In a lake like Lake Onego, where a vertical position inside the euphotic zone seems restricted to parts of the day, the diurnal time scale is crucial for phytoplankton development. Studies that only focus on longer time scales (e.g., seasons) would risk overlooking this possibility.

Conclusions

Under-ice convective heating in clear-water lakes can be a decisive factor in promoting blooms, like Aulacoseira bicaliensis, because it maintains cells in suspension and brings up nutrients from the deep. In (moderately) high CDOM lakes, however, there is a clear trade-off to these benefits as convection forces cells well beyond the euphotic zone. The dark color of Lake Onego and the resulting shallow euphotic zone imply that light is the key resource limiting phytoplankton in the lake (aim 1 of the study). Particularly striking is the difference in Chl-\(a\) on either side of the thermal bar, 2 stations with nearly identical nutrient levels but different in the degree of thermal stratification. In late winter, sufficient under-ice sunlight for net photoautotrophic growth is only available early in the morning before sunlight sets up convection, resulting in distinct diurnal patterns in phytoplankton distribution and growth in high CDOM lakes like Lake Onego (aim 2). After ice-off, net phytoplankton growth is promoted by the development of diurnal microstratification that limits mixing depth at the inshore side of the thermal bar. Our results, with a focus on diurnal variation in phytoplankton distribution, show that windows of opportunity occur for a more beneficial top down distribution, when a majority of the cells remain in the euphotic zone. These diurnal windows of opportunity are seemingly essential for early development of phytoplankton at the end of the winter and early spring in Lake Onego.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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