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Alexandrine Pannard, Dolors Planas, Philippe Le Noac'H, Myriam Bormans, Myriam Jourdain, et al.. Contribution of the deep chlorophyll maximum to primary production, phytoplankton assemblages and diversity in a small stratified lake. *Journal of Plankton Research*, 2020, 42 (6), pp.630-649. 10.1093/plankt/fbaa043 . hal-03366344

HAL Id: hal-03366344

<https://hal.science/hal-03366344>

Submitted on 5 Oct 2021

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Contribution of the deep chlorophyll maximum to primary production, phytoplankton assemblages and diversity in a small stratified lake

Alexandrine Pannard¹, Dolors Planas, Philippe Le Noac'h, Myriam Bormans¹, Myriam Jourdain and Beatrix E. Beisner*

Department of Biological Sciences, Groupe Recherche Interuniversitaire en Limnologie, University of Quebec at Montreal, Montreal, Quebec, Canada

¹ present address: CNRS-UMR 6553 Ecobio, OSUR, University of Rennes 1, Campus de Beaulieu, bâtiment 14b, Av. General Leclerc, Rennes, F-35 042, France

*Corresponding author: alexandrine.pannard@univ-rennes1.fr

Abstract:

This six-month study characterized the contribution of deep chlorophyll maximum (DCM) to lake phytoplankton diversity and primary production, in relation to stratification during the ice-free season. Phytoplankton and zooplankton dynamics were examined with environmental drivers in a small stratified lake that presents vertical gradients of light and nutrients. The phytoplankton, first composed of diatoms and chrysophyceae, shifted to cyanobacteria in mid-July. With stratification increase, surface nutrient limitation appeared to favour motile species characteristic of oligotrophic environments above a deep layer of filamentous cyanobacteria, fueled by the vertical nutrient fluxes from sediment. The DCM contributed on average to 33% (but up to 60%) of total production during the strongest summer stratification period. In late summer, as stratification was eroding, the vertical gradient of nutrients was reduced, but light attenuation with depth increased. Distinct assemblages were identified between surface and deep layer with shade-adapted species. The contribution of DCM was reduced to 10%. Zooplankton community varied in conjunction with phytoplankton and stratification. Our study demonstrates no benefit of DCM for taxonomic and functional diversity and a limited contribution to total production. The depths over which phytoplankton use separate spatial niches may be lesser in a six-meters-deep lake compared with deeper stratified lakes.

Keywords: stratification, phytoplankton, cyanobacteria, zooplankton, diversity, succession

Abbreviated title: DCM contribution to production and diversity

Introduction

36 Spatial environmental heterogeneity is essential to sustain diversity in ecosystems (White *et al.*,
 37 2010; Stein *et al.*, 2014). The spatial structuring of habitats leads to segregation of niches and
 38 provision of refuges, allowing a greater coexistence of species. It is well studied in terrestrial
 39 ecosystems (Tews *et al.*, 2004; Lundholm, 2009; Tamme *et al.*, 2010; Pigot *et al.*, 2016), as well as
 40 in rivers (French and Chambers, 1996; Palmer *et al.*, 2010; Heino *et al.*, 2013; Massicotte *et al.*,
 41 2014), and to a lesser extent in lakes (Longhi and Beisner, 2009; Ouellet Jobin and Beisner, 2014).
 42 In temperate lakes a strong spatial heterogeneity occurs each year when they become thermally
 43 stratified, leading to strong vertical gradients of temperature ($> 10^{\circ}\text{C}$ change), dissolved oxygen,
 44 light and nutrient concentrations. Light decreases with depth dependent on wavelength (light
 45 colour), resulting in a structuring gradient for phytoplankton, both in terms of quantity and quality
 46 of light (Stomp, 2008). When internal nutrient loads of lakes are high, an inverse depth gradient of
 47 nutrients with releases via sediment mineralization often occurs simultaneously. Furthermore,
 48 thermal stratification itself leads to a gradient of water density with depth, allowing buoyant
 49 phytoplankton species to adjust their density to their optimal depth in terms of light and nutrients
 50 (Walsby, 1981). These trade-offs in light and nutrient gradients with consequences for
 51 phytoplankton community composition has been captured in the Algal Game (Klausmeier and
 52 Litchman, 2001). A consequence is the occurrence of deep chlorophyll maxima (DCM). DCMs are
 53 very common in stratified oligotrophic lakes, as soon as the epilimnion remains clear enough to
 54 allow photosynthetic activity in the metalimnion, sustained by upward nutrient fluxes from the
 55 hypolimnion (Fee, 1976). Deep lakes (maximum depth > 20 m) are widely studied with respect to
 56 this phenomenon, whether in terms of DCM species composition or their formation (Straile, 2000;
 57 Saros *et al.*, 2005; Anneville *et al.*, 2005; Salmaso and Padisák, 2007; Winder *et al.*, 2008; Pomati
 58 *et al.*, 2012; Padisák *et al.*, 2003).

59 More recently, studies have demonstrated that DCMs can also occur in small, shallow stratified
 60 lakes with clear oligotrophic epilimnia (Nõges and Kangro, 2005; Camacho, 2006; Selmeczy *et al.*,
 61 2016), although these are less studied. Lakes with smaller surface area also possess a shorter fetch
 62 and thus less energy input from wind, leading to greater thermal stability, counteracting the effect of
 63 shallower depth. Four non-exclusive processes have been advanced to explain DCMs: the inverse
 64 depth gradient of nutrient and light, allowing only shade-adapted species at intermediate depth
 65 (Camacho, 2006), the sedimentation hypothesis, with a depth accumulation of sinking
 66 phytoplankton species along the density gradient (Cullen, 1982), the behavioural hypothesis with
 67 mobile phytoplankton accumulating at depth, and a higher relative zooplankton grazing in the
 68 epilimnion over deep layers (Pilati and Wurtsbaugh, 2003; Pinel-Alloul *et al.*, 2008). None of these

processes is dependent on the size of the lake and DCMs can theoretically also occur in small, but relatively deep lakes. DCMs may thus occur more widely than previously thought, and should increase with the re-oligotrophication of lakes (increased epilimnetic clarity) and climate warming (increased stratification), as has been observed in deep lakes (Jacquet *et al.*, 2005; Pomati *et al.*, 2012).

While species composition of DCMs and the mechanisms causing their establishment have been widely studied, consequences of the presence of a DCM on phytoplankton assemblages and overall diversity across depths is less studied, particularly in smaller lakes. From productivity-diversity relationships, it is known that maintaining diversity is fundamental for biomass and production (Cardinale *et al.*, 2009; Korhonen *et al.*, 2011). DCMs segregate the phytoplankton community into a thin layer of a few tens of centimeters, and should have strong implications for the ecological functioning of lakes and for higher trophic levels (Fee, 1976; Yoshiyama *et al.*, 2009; Pannard *et al.*, 2011). Niche partitioning associated with vertical structuring of resources and microlayers may increase the species diversity at the scale of the water column and contribute to the maintenance of diversity as species are able to limit interspecific competition. Essentially, diversity is enhanced by taxa occupying separate niches defined by microlayers associated with different light intensities and nutrient concentrations. This could constitute one possible explanation for the Paradox of Plankton (Hutchinson, 1961). The objective of this study was to determine how the DCM shapes a lake phytoplankton community to influence the diversity and primary production levels observed. By examining through the ice-free season a small and moderately shallow stratified lake with an annual summer DCM, we characterized the spatial and temporal dynamics of the phytoplankton and zooplankton assemblages, in relation to stratification intensity.

In this study, we address four main hypotheses. First, we expect that it will be possible to distinguish the composition of the DCM as distinct from the surface water assemblage located just a few meters above and that this will be related to stratification. This is because surface plankton assemblages are likely to be controlled by the entrainment of deep waters with large wind events that enrich the epilimnion with phytoplankton cells and nutrients; without wind, settling surface species would be the main contributors to the DCM assemblage. Secondly, we hypothesize that a vertical structuring of assemblages should increase overall lake diversity. Specifically, we expect that beta and gamma diversities across depths increase when distinct assemblages are observed in the two layers. Third, we hypothesize that the surface phytoplankton assemblage will be photosynthetically active and growing, despite nutrient concentration limitation; but that the contribution of surface production will be less than that of the DCM. Finally, we expect that the

zooplankton community will change in conjunction with the presence of vertical structuring of phytoplankton community and with lake stratification.

Methods

Study site

Lake Bromont (45°16'N - 72°40'W) is a dimictic lake, located 80 km south-east of Montreal (QC, Canada). Despite its small surface area (0.45 km²), the lake is relatively deep for its size, with a mean depth of 4 m and a maximum one of 7.2 m due to a steep-sided basin. It has a volume of 10⁶ m³ and a catchment area of 23.47 km². A DCM is observed normally each summer at about 5 ± 0.5 m (Pannard *et al.*, 2011). Three stations less than 500 m apart were sampled at different depths in the pelagic zone, equidistant from each other and from the littoral banks (Fig. S1). A higher variation associated with depth for phytoplankton was expected during summer stratification. The small size of the lake (< 0.5 km²), allowed us to consider a reduced effect of horizontal advection of water masses.

Physical forcing

Meteorological data for 2007 were obtained from the closest meteorological station located 25 km to the southwest of the lake (Frelighsburg, QC; Environment Canada 2007), in particular solar radiation, wind speed, and direction, rainfall, and air temperature. A thermistor chain, composed of ten HOBO Temp Pro Loggers, were deployed from May to the end of September in 2007 in the deepest part of the lake. The thermal structure was thus measured every 10 minutes from 1 m below the water surface to 0.5 m from the bottom.

The intensity of stratification of the water column was estimated as the potential energy in J m⁻³ (*PE*); representing the quantity of energy needed to homogenize the entire water column (Simpson *et al.*, 1979).

Field sampling and laboratory measurements

Chemical and biological parameters were measured twenty times between May and October 2007 at sampling intervals varying between 2 days and 2 weeks (Fig. 1), with more intensive sampling in August (7 sampling dates). Instantaneous PAR profiles were measured at the three stations at a 1-m interval. A submersible 4p quantum sensor (LICOR LI-193SA, Lincoln, NE, USA) was used for *in situ* light, while a 2p quantum sensor (LICOR LI-190SA) was used on boat

for incident light. The light extinction coefficient K was then calculated using Beer-Lambert law, while depth of the euphotic zone was calculated as the depth at which 1% of surface irradiance occurred. Dissolved oxygen (DO) and pH profiles were measured with a multiparameter probe (YSI 6920; YSI Environmental, San Diego, CA, USA). Nutrient concentrations were measured at the three stations at 2.5 ± 0.5 m and 5 ± 0.5 m from the surface : total dissolved phosphorus (TDP) and nitrogen (TDN) were analyzed through colorimetric methods (Cattaneo and Prairie, 1995), as well as total particulate phosphorus and nitrogen (TPP and TPN respectively).

Phytoplankton biomass and diversity

Phytoplankton was characterized at the three stations through fluorescence profiles (Fig. S1) of the four major spectral groups of phytoplankton measured with a Fluoroprobe (BBE Moldaenke GmbH, Kiel-Kronshagen, Germany): the GREENS (chlorophytes), the BLUE-GREENS (phycocyanin-containing cyanobacteria), the MIXED (cryptophyta and phycoerythrin-containing cyanobacteria) and the BROWNS (diatoms, dinoflagellates and chrysophytes) (Beutler *et al.*, 2002). To validate biomass measurements of the Fluoroprobe, chlorophyll *a* (Chl *a*) concentration was measured from water collected at 2.5 m and 5 m from surface, filtered, frozen and later analyzed in the lab using ethanol extraction and spectrophotometry (Sartory and Grobbelaar, 1984).

The community structure of Station A was characterized (Fig. S1) based on phytoplankton collected using a 1m integrated vertical bottle sampler at 2.5 m and 5 m depths. Aliquots were preserved in acid Lugol's solution. Identification and counting were performed using settling chambers and inverted microscope technique using the Utermöhl technique. At least 400 units (individual cells, filaments or colonies) were counted for each sample (Lund *et al.*, 1958). Phytoplankton assemblages were also sampled weekly at 1m intervals from the 7th of September to 11th of October. From the end of August until mid-September, two distinct DCM layers were observed in the Fluoroprobe profiles.

Phytoplankton biomasses were estimated from biovolumes based on size measurements during the study that enabled us to fit geometric shapes to each taxon (Hillebrand *et al.*, 1999). Species were then grouped together into the seven Morphologically Based Functional Groups (MBFG) (Kruk *et al.* 2010): group I contained small species with high Surface : Volume ratio (S:V), group II consisted of small siliceous flagellates, group III were filamentous species with large S:V, group IV were composed of medium size species without specializations, group V contained flagellates of medium to large size, group VI was composed of diatoms, and group VII consisted of large mucilaginous and low S:V colonies. Simpson's diversity was calculated based on

169 species biomasses and on the MBFG biomasses using the function *diversity* (Vegan package) in R
170 Studio version 1.2.5019 (R Core Team, 2019).

171 For each sampling date, gamma diversity (γ) was calculated as the total species richness,
172 while alpha diversity ($\bar{\alpha}$) corresponds to the mean number of species observed in each of the two
173 layers. Beta diversity corresponds to the species richness change between surface and deep layers,
174 compared with the average local diversity across all samples, and was calculated as follow: $\beta =$
175 $\gamma / \bar{\alpha} - 1$ (Tuomisto, 2010).

176

177 *Primary production*

178 To characterize the contribution of the different layers to the total primary production of the
179 lake, the net primary production of oxygen (NP) and community respiration (R) were measured by
180 changes in dissolved oxygen (DO) concentration (Carignan *et al.*, 1998), using a DO meter (YSI
181 5100 and YSI 5905-W; YSI Environmental). Water from three depths (2, 3.5, and 5 m) were
182 sampled using a 1m integrated vertical bottle sampler and divided across fifteen clear and six dark
183 glass biochemical oxygen demand bottles (300 mL) per depth for incubation. *In situ* incubations
184 were performed between 10:00 h and 15:00 h, with DO measurements taken initially and after
185 incubation. The gross photosynthetic production (GPP) was calculated as the sum of the net
186 photosynthetic production measured in light bottles and the respiration measured in dark bottles.
187 We considered similar respiration between light and dark incubations. To determine the relative
188 contribution of a specific layer to total production across the water column, GPP was then weighted
189 by the volume of each layer (calculated from the hypsographic curve of the lake) divided by the
190 total volume of the lake.

191

192 *Zooplankton*

193 Crustacean zooplankton were collected using a 30-L Schindler-Patalas sampler (61 μ m
194 mesh), at three depths (1 m, 3 m and 5 m from the surface) at the three stations. Zooplankton were
195 preserved in 70 % ethanol, after being narcotised with club soda (Black and Dodson, 2003).
196 Cladocera and copepod abundances were characterized under a stereoscopic microscope. The mean
197 abundance over depth was used for the following of the study. Simpson's diversity was calculated
198 on species abundances using the function *diversity* from Vegan package in R.

199

200 *Statistical Analyses*

201 To conduct the variation partitioning of the plankton assemblages in time and space, the
202 function *varpart* from Vegan in R was used with time (day), depth and stations (either A, B or C) as

explanatory matrices for the response variable matrices consisting of either the phytoplankton spectral group biomasses or of the zooplankton species abundances. We also characterized covariation of the phytoplankton and zooplankton assemblages over time using co-inertia coupling of the principal component analyses (PCA; following Hellinger transformation on the plankton matrices) for the phytoplankton and zooplankton species abundances. In both cases. The significance of the co-inertia coupling was tested with a Monte Carlo permutation test.

To compare surface and deep phytoplankton assemblages, a correspondence Analysis (CA) was performed on Hellinger transformed data with the ADE4 package in R. We also tested the dissimilarity between the two assemblages for each period separately using a permutation analysis: Bray-Curtis dissimilarities were calculated on Hellinger transformed data followed by a non-parametric multivariate analysis of variance using the Adonis algorithm in VEGAN, following Rodríguez-Pérez et Green (Anderson, 2001; Rodríguez-Pérez and Green, 2012).

One-way Analysis of Variance (ANOVA) with a post-hoc Tukey test was used when applicable, to compare seasonal periods. Linear regressions were used to determine which abiotic and biotic factors affected the biomass of DCM species and zooplankton taxa. For each variable response, the final model was obtained by performing an automatic backward variable selection procedure based on the corrected Akaike Information Criterion (AICc). This criterion is recommended when the number of sampling sites (28 in our study) is relatively low compared to the number of predictors considered in the models (Burnham and Anderson, 1998; Read *et al.*, 2018). This type of selection method does not involve sequentially dropping non-significant individual predictors, but rather aims at uncovering the most explicative model while maximizing parsimony. As a result, the variables of the final models are not necessarily all significant. To assess the validity of each model, the normality and the homoscedasticity of the residuals, as well as the absence of outliers were checked using diagnostic plots. To satisfy these requirements, response variables had to be systemically transformed using a logarithmic or a square-root function (see Table I).

Results

Seasonal thermal structure and vertical resource gradients:

To characterize the temporal stratification dynamics of the lake, we calculated the potential energy of the water column (energy to fully mix the water column) using temperature measured at different depths (Fig. 1a and 1b). The lake remained thermally stratified throughout the entire

summer, with a thick metalimnion reaching down to the bottom sediment (with no distinct hypolimnion). We now use the deep layer to refer to depths below the epilimnion, and surface layer for the epilimnion itself. Stratification intensity showed daily to weekly fluctuations associated with climatic forcing, with rapid increases controlled by solar radiation (not shown) and rapid decreases controlled by rainfall and cold fronts (Fig. 1a). With a few exceptions (31/05/2007, 09/07/2007 and 24/08/2007), all rainfall greater than 2 mm led to a decrease in the potential energy (Fig. 1a) and a temperature homogenization of the surface layers up to 3.5 m (Fig. 1b). Water temperature displayed short term fluctuations of temperature, which increased with depth (Fig. 1b). While surface layer fluctuations were associated with diurnal cycles, the large hourly temperature fluctuations of in deep layer revealed the occurrence of internal waves, with first, second and third vertical modes, as demonstrated in a previous study (Pannard et al. 2011). Water temperatures at depth increased linearly over time ($R^2 > 0.99$) between July 1st and the end of August, with the slope of the regression gradually decreasing with depth between 4 m and 5.5 m, reflecting the seasonal heat diffusion from the surface to the deep layer (Fig. 1b).

Stratification was associated with nutrient depletion in the epilimnion. Total dissolved phosphorus remained always $< 0.26 \mu\text{mol P L}^{-1}$ over the entire water column, and even $< 0.13 \mu\text{mol P L}^{-1}$ in the epilimnion from mid-June until August 28th (Fig. 1c). Total dissolved nitrogen remained $< 25 \mu\text{mol N L}^{-1}$ from mid-June, and was generally $< 18 \mu\text{mol N L}^{-1}$ in the epilimnion (Fig. 1d). On the 4th of August, all nutrient concentrations increased in response to the high rainfall on the previous day (Fig. 1a,c,d). The euphotic depth reached 7-m at the beginning of August but began to erode in depth by mid-August (data not shown).

Partitioning the plankton' variability into pure vertical, horizontal, temporal and shared components:

To define whether variables associated with time (Day), depth (surface and deep layer) or horizontal position (stations A, B, C) predominated in explaining plankton variation, variation partitioning was performed on the plankton assemblages (biomass of the phytoplankton spectral groups and zooplankton species abundances). At the seasonal timescale (May to October), time was the main component, as it explained most of the variation in the data for the two analyses: R^2_{adjusted} was 24% for zooplankton species and 47% for the spectral groups (Fig. 2). During the stratified period (July-August), depth explained more than time for the phytoplankton assemblages ($R^2_{\text{adjusted}} = 49\%$ vs. 33%; Fig. 2). The horizontal spatial component explained 2% of the zooplankton assemblage, but none for the phytoplankton spectral groups (Fig. 2). The three stations can thus be

270 considered similar in terms of phytoplankton assemblage structure, but with slightly greater
271 abundances of zooplankton in station C, close to the outlet of the lake.

272

273 *Four planktonic assemblage seasonal succession periods:*

274 To highlight successional periods and covariation in planktonic assemblages, a co-inertia
275 analysis on phytoplankton and zooplankton assemblages was performed (Fig. 3 – see Fig. S6 for
276 detailed plots), revealing four common periods: the spring period P1 (02/05/2007 to 10/07/2007
277 included) on the right of the plot, the early summer period P2 (24/07/2009 to 09/08/2007 included)
278 at the top of the plot, the summer P3 (21/08/2007 to 07/09/2007 included) and the late summer
279 period P4 (11/09/2007 to 11/10/2007 included). The shift from P1 to P2 (Fig. 3) corresponded to
280 the strong summer increase in stratification (Fig. 1a), coupled with lower concentrations of
281 dissolved phosphorus (DP) in the epilimnion (Fig. 1c) and a deep euphotic zone (ZE) reaching
282 almost the bottom of the lake, as discussed above. The shift from P2 to P3 (Fig. 3) corresponded to
283 a decrease in stratification intensity, so that P3 was thus intermediate in terms of stratification (Fig.
284 1a). The euphotic depth also eroded from 6 to 4.5 m. P4 (Fig. 3) marked the return of autumn
285 conditions and the mixing of the depth layers in late September. P1 (Fig. 3) was dominated by
286 chrysophyceae and diatoms (phytoplankton) and the copepod *Mesocyclops edax* (zooplankton).
287 Cyanobacteria on the left side of the plot, dominated for the rest of the summer (P2 to P4).
288 Filamentous phytoplankton species, such as *Dolichospermum* (*D. solitaria* and *D. spiroides*) and
289 *Aphanizomenon* (*A. flos-aquae* and *A. yezoense*), were associated on the second axis with the
290 zooplankton *Diaphanosoma birgei* (cladocera) and *Skistodiatomus oregonensis* (copepod), in
291 opposition to colonial phytoplankton species, such as *Woronichinia naegeliana* or *Coelosphaerium*
292 and the cladoceran *Daphnia dubia* (Fig. 3). The second axis corresponded to a change in
293 cyanobacterial succession, from *Aphanizomenon* and *Dolichospermum* (P2) to *Planktothrix* (P3)
294 and finally *Woronichinia* (P4).

295

296 *Seasonal dynamics of the DCM and surface assemblages:*

297 From mid-June to the seasonal overturn in mid-September, phytoplankton biomass was
298 concentrated in a DCM near the lake bottom (Fig. S2). Initially dominated by the BROWNS
299 spectral group (Chrysophyceae and diatoms), the DCM shifted to the BLUE-GREENs and MIXED
300 spectral groups mid-July until the autumn overturn (Fig. S2). In June the diatoms *Cyclotella* (*C.*
301 *comta* and *C. glomerata*) and the flagellate chrysophyceae *Synura uvella* dominated the DCM,
302 while the epilimnetic assemblage was largely dominated by *Cyclotella* only (Fig. S3). In mid-July,
303 the flagellate *Cryptomonas erosa* developed in the surface and the deep layers. For the rest of the

summer, the DCM was dominated by phycocyanin-containing cyanobacteria, such as *Aphanizomenon* (*A. flos-aquae* and *A. yezoense*), *Dolichospermum* and *P. agardhii* (Fig. S3). The epilimnion was composed of small flagellates, such as *Uroglena americana*, *Mallomonas* (mainly *M. bipunctuata*, *M. heterospina*, *M. pseudocoronata* and *M. tonsurata*), *Cryptomonas* (mainly *C. borealis*, *C. erosa*, *C. lucens*, *C. marssoni* and *C. ovata*) and *Trachelomonas* (mainly *T. aculeata*, *T. dybowskii*, *T. intermedia*, *T. hispida*, *T. planctonica*) until August (Fig. S3). Picocyanobacteria, such as *Aphanothece* (*A. bachmannii* and *A. clathrata*), were also observed in the epilimnion. At the end of August, the BLUE-GREENs spectral profile highlighted the presence of a double DCM, which persisted for two weeks (Fig. S2), with *Aphanizomenon* (*A. flos-aquae* and *A. yezoense*) in the uppermost layer and *Planktothrix agardhii* in the deeper layer (Fig. S4).

To compare the species assemblages in the surface (S) and the deep layers (D) over time, a correspondence analysis (CA) was performed on stratified periods P2, P3 and P4 (Fig. 4). P2 was distributed along the first axis, with surface phytoplankton (in red and italicized on Fig. 4) mixed on the plot with deep phytoplankton (in red and boxed on Fig. 4). During P3, the deep assemblage (in blue and boxed on Fig. 4) separated from surface assemblage (in blue and italicized in Fig. 4) along the second axis. During P4, both assemblages were grouped on the top right part of the plot (in green on Fig. 4). The deep and surface assemblages thus remained similar, except during P3, during which *Planktolyngbya pseudospirulina*, *Planktothrix agardhii* and *Limnothrix rosea* species increased in abundance at depth (Fig. 4). Based on non-parametric multivariate analysis of variance, the surface assemblage significantly differed from the deep assemblage only during P3 (pseudo-F = 4.44 ; P = 0.026), but not during P2 and P4 (pseudo-F = 0.957 ; P = 0.45 and pseudo-F = 1.13 ; P = 0.41 respectively). Thus, differentiation did not occur during the strongest stratification period (P2), but only afterwards (P3). The seasonal overturn and a mixing of the assemblages occurred during P4.

Global diversity in the lake:

Alpha (mean species richness) and gamma (total richness) were first calculated for each period and showed similar trends: a maximum diversity during P4 (seasonal overturn) and a minimum diversity during P3, although the differences between periods were not significant (Fig. 5a,b). When comparing beta diversity associated with the vertically distributed depth-layers, diversity increased with time, also being maximal during P4 (Fig. 5c).

Whether estimated as functional or taxonomic diversity, the surface assemblage (S) was always significantly more diverse than the deep assemblage (D) until P4 (Fig. 5 d,e). In addition to cyanobacteria, several other functional groups contributed to the increasing functional diversity in

the epilimnion (S), as observed in the CA of the seven MBFG (Fig. 6). The CA, which represents 74% of total inertia, distinguished groups II (small flagellates), V (medium and large flagellates) and VI (diatoms) from group III (filamentous cyanobacteria) on the first axis (Fig. 6b), with P1 and P3 situated at opposite extremes (Fig. 6a). The deep assemblage (D) was dominated by *Aphanizomenon*, *Dolichospermum* and *P. agardhii*, all from the same functional group (III), on the upper right quadrant of the CA (Fig 6). Group VII (mucilaginous colonies including both cyanobacteria and chlorophyceae) increased in the bottom portion of the plot (Fig. 6b), as did most of surface assemblages (Fig. 6a). The first axis thus separated spring (P1) from the rest of the summer, while the second axis separated the assemblages according to depth. Flagellates and mucilaginous colonies thus contributed to increased functional diversity in the epilimnion compared with the deep layer. The seasonal overturn (P4) increased both species diversity and richness (Fig. 5a,b,e), without a corresponding increase in functional diversity (Fig. 5d). Zooplankton taxonomic diversity was at its lowest during the seasonal overturn (P4) (Fig. 5f).

Contributions to primary production:

Primary production was measured at three depths for one to five dates per period (Fig. 7). The upper layer was the most productive compared to the deeper one during P1, P3 and P4, while the DCM was the most productive during P2. When the relative contribution to total primary production was calculated based on depth stratum volume, we observed a similar pattern for P1, P3 and P4, with the upper layer contributing at least 50% of total production (Fig. 7). During P2, higher production in the DCM was compensated for by the larger water volume of the upper layer, so that the DCM contributed approximately 30% of the total production (Fig. 7). Despite a very low phytoplankton biomass in the epilimnion compared to the DCM, surface assemblage production contributed most during all summer owing to higher light availability associated with the larger epilimnetic volume. During P3, surface assemblage contributing much more (>90%) than the deeper layer to overall production (Fig. 7). Total production was the highest relative to the other periods during P3 across depths (Fig. S7).

Controlling factors of the DCM species:

Cyanobacteria abundances were all positively explained by stratification intensity (PE) in the linear models (Table Ia). Abundance of the herbivorous zooplankton *Skistodiatomus oregonensis* was most related to variation in cyanobacteria, positively affecting epilimnetic species (*Aphanizomenon yezoense* and both *Dolichospermum*) and negatively affecting strictly deep-occurring species (*Planktothrix agardhii*). Several *Aphanizomenon* species were observed both in

the epilimnion in early summer and in the DCM in late summer (Fig. S3). The abundance of *Aphanizomenon flos-aquae* was negatively affected by temperature and by the concentration of dissolved nitrogen (DN), with a positive interaction between DN and temperature (Table Ia). *A. yezoense* was positively influenced by PE and its variation (Δ PE indicating rapid warming or cooling), negatively by the concentration in dissolved phosphorus (DP), and with a positive interaction of effects of temperature and DP. Both *Dolichospermum* species were also observed in the epilimnion and in the DCM in July, with *D. spiroides* occurring earlier in season than *D. solitaria*. For *D. solitaria*, most of the environmental parameters were selected in the final model, but the coefficients were not significant, so the result was similar for *D. spiroides*. Abundances of both species were significantly and positively related to stratification (PE) and to abundances of the zooplankton *S. oregonensis* (Table Ia). *Planktothrix agardhii* occurred in the deep layer during P3, at the same time that DP and DN increased over the entire water column (Fig. 1c,d). Its abundance was positively related (in order of importance) to DN concentration, PE and to zooplankton abundances *D. dubia* and negatively related to *S. oregonensis*. Stratification was the main driver of cyanobacterial abundance and composition.

387

388 *Macrozooplankton dynamics:*

389 The three dominant herbivorous zooplankton species were all explained by three parameters:
390 water temperature, biomass of the 'MIXED' spectral group and abundance of the predatory
391 copepod *Mesocyclops edax* (Table Ib). Abundances increased with water temperature and with
392 'MIXED' biomass, corresponding to cryptophyta, as no phycoerythrin-containing cyanobacteria
393 were observed in our microscopic analyses. Abundances of two cyanobacterial species were also
394 positively related to the abundances of two zooplankton species: *Aphanizomenon flos-aquae* with
395 *Diaphanosoma birgei* and *Planktothrix agardhii* with *Daphnia dubia*. However, coefficients were
396 very low, indicating a low contribution (Table Ib). *Daphnia dubia* was also negatively correlated to
397 potential energy PE (Table Ib) as it experienced increasing abundances in the fall when overturn
398 was occurring (Fig. S4).

399

400

401 **Discussion**

402

403 We addressed four main hypotheses in this detailed study of the vertical segregation of
404 phytoplankton assemblages, the repercussions for the diversity and primary production, and the
405 associated changes in zooplankton assemblages. In the study lake, which is moderately deep for its

size, the vertical temperature and resource gradients were strong and constrained the phytoplankton assemblages. We hypothesized that vertical structuring in phytoplankton assemblages would be controlled by lake stratification and that strong density stratification should reduce entrainment of deeper water and the incorporation of metalimnetic species into the epilimnion (Serra *et al.*, 2007). Different assemblages between the surface and the deep layers were expected, and predicted to result in increased beta diversity (along the vertical gradient) and in overall lake (gamma) diversity. We also expected the deep assemblage to contribute more to total primary production than the surface assemblage and that the zooplankton community would change in response to lake stratification and phytoplankton vertical structuring. We identified four periods of stratification intensity. Only one was associated with a vertical structuring of phytoplankton assemblages, without increase of either diversity or primary production. Instead, the period of maximal diversity corresponded to the seasonal transition. We first discuss the vertical structuring of phytoplankton assemblages in relation to stratification and resource gradients, followed by a discussion of the diversity and primary production responses.

We observed that surface and deep assemblages were similar during the strongest stratification period (P2), and then diverged into two distinct assemblages during P3, despite decreased stratification. Similar assemblages during strong stratification could result when the DCM represents an accumulation of surface-settling species (Cullen, 1982; Condie and Bormans, 1997) and/or when a portion of species in the DCM become entrained by internal waves and deep water upwelling (Bormans *et al.*, 2004). Both contributions were observed in our study, during P1 and P2 respectively. Indeed, until mid-July (P1), phytoplankton biomass was dominated by diatoms (especially *Cyclotella comta* and *C. glomerata*) in the epilimnion and in the deep layer. These small centric diatoms, would have been subject to sedimentation loss and accumulation in deeper waters (Fahnenstiel and Glime, 1983; Jackson *et al.*, 1990). Motile chrysophyta, with the spring species *Synura uvella* and *Dinobryon divergens*, also accumulated in the deep layer. *S. uvella* is also typical of small oligotrophic lakes and heterotrophic ponds, and may have accumulated at the bottom of the lake because of higher CO₂ levels (Reynolds, 2006) These species are also known to be mixotrophs (Reynolds, 2006) and able to benefit from likely higher bacterial populations at depth.

During P2, we observed the second period of similar deep and surface phytoplankton assemblages, in this case resulting from entrainment of deeper assemblages towards the surface. Recurrent internal waves associated with daily wind have been demonstrated in the study lake during the summer months (Pannard *et al.*, 2011). The DCM composition shifted to cyanobacteria at the end of July and for the rest of the summer, with dominance by *Aphanizomenon* (*A. flos-aquae* and *A. yezoense*) and *Dolichospermum* (*D. solitaria* and *D. spiroides*). *Aphanizomenon* and

440 *Dolichospermum* are representative of the functional group H1, in Reynolds' classification and are
441 sensitive to poor light and low phosphorus concentrations (Reynolds *et al.*, 2002). Epilimnetic
442 phosphorus concentrations remained low and consequently potentially limiting for growth at < 0.13
443 $\mu\text{mol P L}^{-1}$; most half-saturation constants for phosphorus uptake being above $0.16 \mu\text{mol P L}^{-1}$
444 (Reynolds, 2006; Edwards *et al.*, 2012; Bestion *et al.*, 2018). *Aphanizomenon* and *Dolichospermum*
445 were able to develop large biomasses in the DCM, most likely due to the upward input of P and N
446 from the anoxic sediment, possible as long as the euphotic zone reached the bottom of the lake. The
447 contribution of internal loading compared with external loading has been already highlighted in our
448 study lake (Planas and Paquet, 2016). A portion of the DCM species would have been entrained
449 into the epilimnion during P2 owing to shear stress associated with the occurrence of internal waves
450 (Pannard *et al.*, 2011). Anecdotally, we noted that cyanobacterial aggregates likely originating in the
451 DCM were regularly observed floating at the lake's surface, disappearing a few days later as
452 apparently low surface phosphorus concentrations precluded the growth of cyanobacteria in the
453 epilimnion.

454 During P2, the DCM was thus a source of species for the surface layer phytoplankton
455 assemblage and in particular, the filamentous cyanobacteria. However, small flagellated species,
456 specific to the epilimnion continued to be observed, albeit at low abundances: *Cryptomonas* (*C.*
457 *marssonii*, *C. erosa*), *Uroglena americana*, *Trachelomonas* (*T. intermedia*, *T. dybowskii*, *T.*
458 *aculeate*), *Scourfieldia cordiformis*, *Erkenia subaequiciliata*, *Ochromonas globosa*, *Mallomonas*
459 *acaroides*, and *Chlamydomonas* (*C. fusus*, *C. dinobryonii*). With a high surface : volume ratio,
460 small species are known to tolerate low nutrient concentrations and their ability to perform flagellar
461 movement reduces sinking loss (Reynolds, 2006). Their small cell size, buoyancy regulation and
462 motility associated with flagella are all functional traits related to preventing sinking loss (Salmaso
463 *et al.*, 2015). These species may have contributed to primary production in the surface layer,
464 keeping relative surface production higher than deep water production as observed. Such species
465 would likely also have benefitted the zooplankton assemblage: we observed a positive correlation
466 between the biomass of the 'MIXED' spectral group and the abundances of the three herbivorous
467 zooplankton. Finally, during the period of strong stratification (P2), surface nutrient limitation
468 favoured the occurrence of oligotrophic surface species above deep filamentous cyanobacteria, the
469 latter likely fueled by vertical nutrient fluxes from the anoxic sediments. However, it should be
470 noted that the two phytoplankton assemblages were not significantly distinguishable statistically.
471 Thus, stratification intensity may not have been sufficient to impede the vertical movement of DCM
472 species (Abbott *et al.*, 1984) and the shear stress associated with internal waves may have further
473 inhibited spatial segregation.

474 By mid-August, thermal stratification had decreased, following rainfall and wind events,
475 thereby reducing vertical gradients of nutrients and light (P3). At this point in time, the two
476 assemblages differed significantly with the development of shade-adapted species in the deep layer
477 and the continued presence of the epilimnetic species from the P2 phase at the surface. Some
478 picocyanobacteria (*Aphanothece clathrata*, *A. bachmannii*, *Aphanocapsa delicatissima*, *A. conferta*)
479 were also observed in the epilimnion. Metalimnetic species are well described in the literature, in
480 particular with respect to their chromatic adaptation to low light conditions and buoyancy regulation
481 capacities (Dokulil and Teubner, 2000; Walsby, 2005). Here we observed *Planktothrix agardhii*,
482 *Planktolyngbya pseudospirulina* and *Limnothrix* (*L. rosea* and *L. redekei*), which are known to
483 tolerate highly light-deficient conditions and are all known to be metalimnetic in distribution
484 (Reynolds, 2006). *Planktothrix rubescens*, a phycoerythrin species (the red *Planktothrix*), is known
485 to accumulate in the metalimnion of deep lakes (Walsby and Schanz, 2002; Oberhaus *et al.*, 2007)
486 where light is composed primarily of green wavelengths, thus forcing the species to use
487 phycoerythrin or another red pigment (Stomp, 2008). In our study lake, the DCM was located at a
488 depth of only five meters enabling dominance instead of the “green *Planktothrix*” (*Planktothrix*
489 *agardhii*); this “green” species more commonly in turbid well-mixed waters (Mantzouki *et al.*,
490 2016) where it can accumulate in DCMs (Utkilen *et al.*, 1985; Reichwaldt and Abrusan, 2007) at
491 similar depths as the “red” species (Halstvedt *et al.*, 2007). At the end of P3, two distinct layers
492 were observed within the DCM, with a peak of *Aphanizomenon* above a *Planktothrix* peak. Such a
493 spatial segregation, with two peaks of *Aphanizomenon* above *Planktothrix rubescens*, has already
494 been observed in a deep lake (69 m) and attributed to a spatial niche segregation of light and
495 nutrients (Selmeczy *et al.*, 2016). The seasonal overturn during P4 ended this vertical structuring of
496 assemblages.

497
498 We expected species richness to increase with vertical structuring of phytoplankton
499 assemblages, associated with the vertical resource gradient. The exploitation of the resource
500 gradients through the use of motility traits (flagella versus gas vacuoles) can reduce spatial overlap
501 between species, and sometimes lead to greater taxonomic and functional diversities (Beisner and
502 Longhi, 2013; Ouellet Jobin and Beisner, 2014). Instead, in our study, species richness did not
503 increase with vertical structuring of phytoplankton assemblages, but rather decreased during P3.
504 During this time light availability decreased in the deepest layer, resulting in more selective
505 environmental conditions and thus reduced diversity. Only shade-adapted species, such as
506 *Planktothrix*, *Planktolyngbya* and *Limnothrix*, were able to develop in deep layer during P3. Small,
507 motile species adapted to oligotrophic conditions increased surface taxonomic and functional

diversities, from P1 to P3. When focusing on functional diversity calculated with the seven morphologically based functional groups (MBFG) (Kruk et al. 2010) instead of the two hundred species of the entire community, the summer epilimnetic assemblages (P1, P2 & P3) were thus the most diverse with the presence of almost all groups, while the deep layer was dominated by filamentous cyanobacteria. The seasonal overturn (P4) mixed the surface and deep assemblages and was demonstrated to be the most diverse period for phytoplankton assemblages in taxonomic diversity, but without a corresponding increase in functional diversity. The erosion of thermal stratification led to epilimnetic increases in phosphorus availability and favoured the return of fall species, such as *Woronichinia naegeliana*. This seasonal disturbance enabled the highest alpha, beta and gamma diversities, favouring coexistence of late summer and fall species.

We also expected the DCM to contribute significantly to the overall lake production, especially in a relatively shallow and small lake. The vertical distribution of phytoplankton biomass was typical of a clear vertically stratified oligotrophic lake (Fee, 1976; Cullen, 1982), with a deep chlorophyll maxima (DCM). During summer (P1 to P3), epilimnetic biomass remained very low ($< 12 \mu\text{g chl}a \text{ L}^{-1}$) in contrast to the deep layer biomass ($> 200 \mu\text{g chl}a \text{ L}^{-1}$). It appears that the clear epilimnion allowed light to reach the deep layer. The control of DCM by stratification and light is already well described (Abbott *et al.*, 1984; Leach *et al.*, 2018), with vertical gradient in nutrients and light explaining DCM dynamics (Fee, 1976; Klausmeier and Litchman, 2001). During the most strongly stratified period, one could have expected a larger production by the DCM compared with the clear epilimnion, even when production is weighted by the volume of the two layers (based on data from a bathymetric map performed the same year). Because the area of the epilimnetic layer was larger, the volume of this layer is much bigger than that of the deep layer and this compensated for the concentrated deep layer production. Despite high deep layer primary production during P2, surface production integrated over the epilimnion was systematically higher. This epilimnetic production could have fueled zooplankton assemblage production, favouring competitive species able to grow at low resource concentrations and on small flagellates. The relative contribution to total production of the shade-adapted DCM species was even lower during P3 ($< 10\%$) than during P2, and could be considered negligible for lake primary production. There the occurrence of a DCM with a distinct phytoplankton assemblage did not lead to increases in diversity and its contribution to overall primary production remained limited.

Four periods were highlighted in the plankton assemblage compositions, differing mainly according to stratification intensity and surface dissolved phosphorus availability. Ice cover on the

study lake thawed in early May, but with rapid heating was already stratified by mid-May. It remained thermally stratified throughout the summer, with recurrent internal waves occurring every day (Pannard *et al.*, 2011). Other than the fall species, *Woronichinia naegeliana*, the abundances of cyanobacteria were all explained by stratification intensity, measured as potential energy. Stratification is known to be a critical driver of cyanobacteria blooms, either directly or through stratification-induced internal nutrient loading (Huber *et al.*, 2012). The four phytoplankton-determined periods were also reflected in the zooplankton assemblages. *Mesocyclops edax* characterized P1 (spring), with diatoms and chrysophyceae. *Diaphanosoma birgei* characterized P2 with *Dolichospermum* and *Aphanizomenon* during high stratification. *Daphnia dubia* showed the greatest biomass during P4 (overturn), co-occurring with mucilaginous phytoplankton species. Phytoplankton-zooplankton covariations were the result of common control factors, such as stratification and temperature, and of trophic interactions. Here, all the herbivorous species were explained by temperature, the abundance of the predator *M. edax* and the biomass of cryptophyceae prey. Temperature can have a direct effect on zooplankton growth (Shuter and Ing, 1997), and an indirect effect via stratification (Thackeray *et al.*, 2006). Disentangling the effects of biotic and abiotic factors and prioritizing them are not possible in observational field studies such as ours without further experimental manipulation. Experiments have shown that warmer temperatures accelerate *Daphnia* grazing and growth, but not growth of phytoplankton which are more controlled by depth stratification, through light availability (Berger *et al.*, 2006). We observed that the cryptophyceae occurred at greater biomass in the epilimnion than in the deep layer. Zooplankton, such as *Diaphanosoma* may feed selectively on cryptophyceae and it has been demonstrated that grazing rates by small zooplankton especially, is not reduced in presence of filamentous cyanobacteria (Kirk and Gilbert, 1992). *Daphnia* are also able to consume short filaments of *Planktothrix* (Reynolds, 2006) and in line with this, we observed that *Daphnia* abundances were correlated to *Planktothrix* by the linear models (although with a very small coefficient).

The major aim of this study was to determine whether the vertical resource gradient in a small oligotrophic lake could lead to a spatial segregation of phytoplankton assemblages with benefits for overall depth-integrated diversity and production. The small size of the lake studied allowed us to ignore horizontal heterogeneity and horizontal advection. Our lake displayed a DCM, a common feature of deeper oligotrophic lakes and implying a vertical segregation of phytoplankton biomass, but our study demonstrated no benefit at the scale of the lake of the presence of this DCM for primary production and diversity, whether functional or taxonomic. Instead, phytoplankton diversity was favoured by mixing during the seasonal transition associated with succession. This

suggests that a shallower lake depth might negatively affect spatial segregation, although a previous multi-lake snapshot survey (MLSS) suggested that vertical spatial overlap of phytoplankton spectral groups is rather controlled by stratification, the optical depth (size of the light niche) and the lake trophicity (Beisner and Longhi, 2013). Compared to deeply stratified lake, the depth over which spatial segregation of phytoplankton could occur in our shallow lake is reduced, potentially increasing the overlap in competing spectral groups, with negative consequences for diversity (Ouellet Jobin and Beisner, 2014). Stratification, which is controlled by climatic forcing, is the prerequisite for DCM establishment. Light availability is also directly controlled by climate, as well as vertical nutrient fluxes which depend on wind forcing (MacIntyre et al., 2006). It is thus expected that the dynamics of DCM will change from year to year. However, the properties of the DCM can be well predicted from the euphotic depth and DOC concentration for DCM depth, and from lake size and maximum depth for DCM thickness (Leach et al., 2018). These parameters are quite stable between years, with some exceptions. An increase in turbidity due to glacial clay or volcanic ashes for instance make DCMs shallower (Modenutti et al., 2013). In another exception, a DCM does not occur each summer in Lake Erie despite strong stratification; depending on meteorological forcing and resuspension events (Bramburger and Reavie, 2016; Lick et al., 1994). Finally, light seems to be the main driver of DCM properties (biomass and depth), more so than stratification or phosphorus in southern lakes from Antarctica to the tropics (Burnett et al., 2006; Leach et al., 2018; Sanful et al., 2019)

Conclusion

In this study, we demonstrated a low contribution of the DCM to lake phytoplankton diversity and primary production, in a small but relatively deep lake (maximum depth of 7.2 m). The DCM production represented on average 33% of total production during the strongest summer stratification period, during which surface and deep assemblages were the same. When surface and deep assemblages diverged, the taxonomic and functional diversity at the scale of the water column decreased. The distinct surface and deep phytoplankton assemblages were within three meters of each other. Such lakes with intermediate depth represent good opportunity to study strong vertical clines over a small scale, which may allow both the niche partitioning but also facilitate the mobile species migration among habitats

Authors' contributions

609 A.P., D.P. and B.E.B. designed the study. A.P. and M.J. collected the data. A.P. assembled and
610 analyzed the data. P.LN. performed the linear models. A.P., B.E.B., D.P., P.LN and M.B. wrote the
611 manuscript.

612

613 **Acknowledgements**

614 We thank S. Paquet, C. Beauchemin, P. Marcoux, and K. McMeekin for field and laboratory
615 assistance and for the bathymetry of the lake (S. Paquet). We thank the Action de conservation du
616 bassin versant du lac Bromont for the infrastructure support, and for logistical help in the field and
617 the municipality for the bathymetric map. We thank the Interuniversity Limnology Research
618 Group/Groupe de recherche interuniversitaire en limnologie (GRIL) for providing funding to AP to
619 spend time in 2019 as an invited professor at UQAM to analyze the data from the field survey
620 performed in 2007. We thank John Dolan and two anonymous referees for helpful comments on an
621 earlier version of the manuscript.

622

623 **Funding**

624 This work was supported by a grant from the Fonds Québécois de la Recherche sur la Nature et les
625 Technologies to David F Bird, BEB, and DP and by the Groupe de Recherche Interuniversitaire en
626 Limnologie (GRIL).

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809 **Tables**

810 Table I: Summary statistics for the final regression models for (a) cyanobacteria abundances and (b) zooplankton abundances. Phytoplankton species
811 are A.f. (*Aphanizomenon flos-aquae*), A.y. (*Aphanizomenon yezoense*), D.so. (*Dolichospermum solitaria var planctonica*), D.sp. (*Dolichospermum spiroides*), P.a.
812 (*Planktothrix agardhii*) and W.e. (*Woronichinia egelia*). Zooplankton species are D.d. (*Daphnia dubia*), D.b. (*Diaphanosoma bergei*) and S.o. (*Skistodiatomus*
813 *oregonensis*). For each (a) and (b), the initial global models (top table) and their statistical parameters (bottom table) are shown. Bolded estimates
814 indicate those that were significant at $P < 0.05$. For each species, the real value of estimates has no meaning, as it depends on the data
815 transformation, but the relative value gives the proportional control of each factor over the biomass of the species. The Shapiro–Wilk normality test
816 (SWN test) on residuals are shown. Parameters are Day, Layer (deep versus surface), PE (potential energy), Δ PE (daily variation in PE), T° (water
817 temperature), Light, DP (dissolved phosphorus), DN (dissolved nitrogen, abundances of zooplankton D.d., D.b. and S.o., biomasses of dominant
818 cyanobacteria and biomass of the MIXED spectral group.

819

820 (a) cyanobacteria

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Species	(Intercept)	Day	Layer (deep)	PE	Δ PE	T°	light	DP	T° :DP	DN	T° :DN	TN:TP	D.d.	D.b.	S.o.
A.f.	44.22	-0.05		0.29		-1.53				-140.64	6.64				
A.y.	9.65	0.05	-1.03	0.49	2.49	-0.51	-0.01	-3.07	0.16	25.76	-2.41	-0.07		-0.35	0.19
D.so.	8246.34		-1201.83	330.10		-411.15	-17.45	1126.90	-67.21	-53637.62	2644.38	50.40		-86.06	89.19
D.sp.	-13.40	0.06	-1.41	0.39											0.12
P.a.	-16684.29	59.49	2038.71	497.93	-1552.12		-28.96	-580.91		21613.22			128.91		-253.19
W.e.	654.84	11.98	-805.62			-122.49									

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Species	Transformation	R ²	R ² (adjusted)	AICc	Shapiro test	LLik	DF	Residual Dev.
A.f.	log	0.54	0.44	141.76	0.98 (0.90)	-61.08	22	2.42
A.y.	log	0.94	0.89	115.17	0.97 (0.58)	-22.58	14	0.77
D.so.	sqrt	0.71	0.51	493.71	0.97 (0.47)	-220.85	16	852.79
D.sp.	log	0.48	0.39	124.62	0.97 (0.57)	-54.313	23	1.86
P.a.	sqrt	0.75	0.63	523.36	0.96 (0.37)	-242.43	18	1737.55
W.e.	sqrt	0.52	0.46	418.19	0.97 (0.70)	-202.73	24	364.49

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824 (b) zooplankton
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Species	(Intercept)	Layer (deep)	PE	temperature	TP	<i>Mesocyc edax</i>	<i>Aphanizomenon flos-aquae</i>	<i>Aphanothece</i>	<i>Dolichosper- mum</i>	<i>Planktothrix agardhii</i>	MIXED
<i>D.d.</i>	-1.64		-0.07	0.13		0.12				6.03E-09	0.05
<i>D.b.</i>	-8.85	0.85		0.46	-0.01	0.50	2.05E-08		-3.37E-08		0.14
<i>S.o.</i>	-1.33			0.08		0.15		3.10E-10			0.03

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Species	Transformation	R ²	R ² (adjusted)	AICc	Shapiro test	LLik	DF	Residual Dev.
<i>D.d.</i>	log	0.61	0.52	15.12	0.96 (0.32)	2.24	22	0.25
<i>D.b.</i>	sqrt	0.87	0.83	64.05	0.95 (0.16)	-18.03	20	0.54
<i>S.o.</i>	log	0.82	0.79	-17.07	0.96 (0.38)	16.54	23	0.15

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829 Table II: summary statistics for the dominant phytoplankton and zooplankton abundances depending on periods in surface and bottom.

(a)	surface								bottom							
	period 1		period 2		period 3		period 4		period 1		period 2		period 3		period 4	
	mean	±stand. dev.	mean	±stand. dev.	mean	±stand. dev.	mean	±stand. dev.	mean	±stand. dev.	mean	±stand. dev.	mean	±stand. dev.	mean	±stand. dev.
<i>Aphanizomenon flos-aquae</i>	10	17	300	540	41	60	21	21	0	0	9	13	89	197	3	5
<i>Aphanizomenon yezoense</i>	460	754	1 865	1 517	2 707	1 688	406	291	96	166	10 879	8 945	468	901	712	1 033
<i>Aphanocapsa conferta</i>	7	12	195	306	298	222	2	4	0	0	194	198	41	52	2	4
<i>Aphanocapsa delicatissima</i>	262	454	1 968	2 001	64	105	0	0	0	0	21 612	38 365	682	1 102	618	892
<i>Aphanothece bachmannii</i>	37	51	264	353	26 068	21 662	27 239	31 893	2 186	3 511	26 372	24 381	39 905	22 664	12 411	13 039
<i>Aphanothece clathrata</i>	0	0	740	1 152	2 233	3 833	2 700	4 443	1 702	2 716	2 085	3 842	23 698	51 873	10 648	12 670
<i>Botryococcus braunii</i>	4 834	7 150	6 540	9 380	26 770	24 874	47 804	53 581	2 789	3 981	20 664	17 802	6 754	9 648	26 467	44 970
<i>Chroococcus sp.</i>	53 727	17 621	50 015	67 749	138 642	139 148	61 639	48 394	32 257	6 894	89 910	171 385	49 576	38 092	121 112	148 782
<i>Coelosphaerium kuetsingianum</i>	0	0	41 828	69 063	140 151	215 882	16	28	0	0	23 416	22 421	28 202	39 968	7 529	13 041
<i>Cyanodiction imperfectum</i>	0	0	384	777	360	785	0	0	0	0	681	1 022	210	469	0	0
<i>Desmerella brachycalyx</i>	57	46	52	79	207	239	142	142	16	24	53	78	297	102	422	438
<i>Dictyosphaerium pulchellum</i>	701	921	204	300	16 835	11 218	33 195	11 093	1 179	1 922	2 373	3 294	33 156	23 550	8 242	8 596
<i>Dolichospermum flos aquae</i>	0	0	3 438	4 924	14 826	33 153	159 154	345 103	0	0	320	715	0	0	67 258	99 224
<i>Dolichospermum solitaria</i> <i>var. planctonica</i>	51	60	43	75	203	213	0	0	96	96	127	240	116	97	163	65
<i>Dolichospermum spiroides</i>	6	11	7	16	0	0	13	22	0	0	10	22	0	0	0	0
<i>Limnothrix rosea</i>	2	3	0	0	0	0	11	19	46	63	2	5	3 693	5 500	0	0
<i>Merismopedia tenuissima</i>	0	0	0	0	34	76	0	0	0	0	0	0	864	1 484	195	218
<i>Microcystis wesenbergii</i>	22	38	460	789	341	329	342	560	540	935	343	324	12 051	26 948	17 561	23 797
<i>Planktolyngbya pseudospirulina</i>	172	187	69	79	4 754	4 872	3 112	2 304	5 397	7 201	8 829	9 274	51 624	30 500	3 297	2 457
<i>Planktothrix agardhii</i>	1	1	0	0	905	1 999	0	0	550	953	4	10	14 226	18 827	224	388
<i>Snowella septentrionalis</i>	0	0	0	0	0	0	256	443	0	0	0	0	1 007	2 251	3 557	4 346
<i>Woronichinia naegeliana</i>	0	0	124	165	676	591	5 716	2 245	23	39	298	291	682	320	823	724

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832 (b)

	period 1		period 2		period 3		period 4	
	mean	±stand. dev.	mean	±stand. dev.	mean	±stand. dev.	mean	±stand. dev.
<i>Diaphanosoma birgei</i>	22	13	1357	938	479	213	110	36
<i>Skistodiaptomus oregonensis</i>	698	699	819	459	720	415	634	145
<i>Daphnia dubia</i>	1384	1837	679	657	1758	754	3352	2305
<i>Eubosmina coregoni</i>	131	126	1	2	6	6	4	2
<i>Daphnia ambigua</i>	0	0	147	88	214	61	420	37
<i>Mesocyclops edax</i>	1021	1159	99	70	113	54	75	35

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Figures

Figure 1: Time series of (a) rainfall (histogram) and potential energy of the water column (black curve), (b) temperature at different depths measured every ten minutes, (c) dissolved total phosphorus and (d) dissolved total nitrogen. Slopes of the daily increase in temperature depending on time (Day) are shown in (b) at 4.5, 5.0 and 5.5 m depth during the stratification. Regression coefficients are $0.055 \cdot \text{Day}$ for S1, $0.085 \cdot \text{Day}$ for S2, and $0.104 \cdot \text{Day}$ for S3, with all $R^2 > 0.99$.

Figure 2: Variance partitioning of spectral phytoplankton groups and of zooplankton community structure by: station (A, B and C), depth (epilimnion and deep layer) and time (Day). The top row shows the results from across the ice-free season (top row), while the bottom row shows results restricted to time points in the stratification period of July and August only. The number of observations (n) is indicated below each plot.

Figure 3: Sample plot of the co-inertia analysis performed on the PCA of the phytoplankton assemblage and the PCA performed on the zooplankton assemblage. The most dominant taxa are underlined for phytoplankton and in italic for zooplankton. Time periods (P1 to P4) are grouped by their barycenter, with periods seen from zooplankton (blue points) and from phytoplankton (grey squares). Detailed plots of co-inertia with all plankton taxa are shown in Fig. S4.

Figure 4: Correspondence analyses (CA) of the phytoplankton assemblages, from surface (S) and deep layer (D) during periods P2, P3 and P4. Plot (a) shows samples by date from the CA with B assemblages (names in framed) and S assemblages (names in italic). Periods are indicated by names in red, in blue and in green for P2, P3 and P4 respectively. In (b), the CA plot with species is shown (only the most contributing species are indicated). The black dotted arrow shows the divergence of B assemblage during P3.

Figure 5: Boxplots of (a) mean alpha ($\bar{\alpha}$) and (b) gamma (γ) diversities, as well as (c) beta diversity ($\beta = \gamma/\bar{\alpha} - 1$) by time period, for surface (S) and deep layer (D). Simpson diversity indices are calculated using (d) biomasses of the seven MBFG by period, (e) biomasses of phytoplankton species and (f) abundances of zooplankton species. Similar results are observed with Shannon and Evenness indices. Boxplots show the median, first and third quartiles, with minimum and maximum values at both ends. Boxes within each period that have different letters indicated are significantly different ($p < 0.05$).

Figure 6: CA performed on the seven Morphologically Based Functional Groups (MBFG) of phytoplankton (Kruk et al. 2010), with (a) plot of the samples and (b) plot of the MBFG.

Figure 7: Boxplots of (a) gross primary production (GPP) in the epilimnion (2m and 3.5m depths) and the deep layer (5m depth) and (b) relative contributions to the total production of the lake. Boxplots show the median, first and third quartiles, with minimum and maximum values at both ends. Sampling occurred on one date in P1, four dates in P2 and five dates in P3 and P4. Boxes within each period that have different letters indicated are significantly different ($p < 0.05$).

Supplementary data:

Figure S1: Bathymetric map of the study site, with the three stations A, B, C located in the pelagic area.

Figure S2: Biomasses of the four spectral groups, with (a) the GREENS (chlorophyceae), (b) the BLUE-GREENS (phycocyanin-containing cyanobacteria), (c) the BROWNS (diatoms, dinoflagellates and chrysophyceae) and (d) the MIXED group (cryptophyceae and phycoerythrin-containing cyanobacteria; the latter of which were never observed in our lake). Colour intensity scales are shown on the right and were adapted to the biomass of the group. Stars at the top indicated dates for which detailed assemblage data are shown (Fig. S3).

Figure S3: Composition at the genus level of the phytoplankton assemblages in the epilimnion and in the deep layer, over five dates showed by asterisks on Fig. S2. Data are expressed as percent of total biovolume ($\text{mm}^3 \text{L}^{-1}$).

Figure S4: Vertical profile of the dominant cyanobacteria genus measured on September 7th 2007.

Figure S5: Time series of zooplankton abundances for the dominant species.

The figure consists of two ordination plots. The left plot is a vector plot showing the relationship between environmental variables (vectors) and species composition (points) along the first two axes of Co-inertia. The x-axis is labeled 'First Axis of Co-inertia (76.9% of inertia)' and the y-axis is labeled 'Second Axis of Co-inertia (11.0% of inertia)'. The right plot is a biplot showing the relationship between environmental variables (vectors) and species composition (points) along the first axis of Co-inertia (76.9% of inertia) and the first axis of Correspondence Analysis (76.9% of inertia). The x-axis is labeled 'First Axis of Co-inertia (76.9% of inertia)' and the y-axis is labeled 'First Axis of Co-inertia (76.9% of inertia)'. The scale of the right plot is indicated as $d = 0.1$.

Left Plot: First two axes of Co-inertia

- X-axis:** First Axis of Co-inertia (76.9% of inertia)
- Y-axis:** Second Axis of Co-inertia (11.0% of inertia)
- Species (Points):** Anabaena, Uroglena, Monoraphidium, Kirchneriella, Navicula, Dinobryon, Desmerella, E. Cammulina, Anaphanethos, Chironomus, Katablepharis, Aphanizomenon, Plectonilla, Salpingoeca, Microcystis, Trachelomonas, Asterionella, Melosira, Ankirodesmus, Scenedesmus, Cyclotella, Quagga, Surire, Coelosphaerium, Euglena, Woronichinia, Chroococcus, Fragilaria, Malcomsonas, Comptonas, Tetradion, Schrodedia, Melosira.
- Environmental Variables (Vectors):** Aphanizomenon, Uroglena, Monoraphidium, Kirchneriella, Navicula, Dinobryon, Desmerella, E. Cammulina, Anaphanethos, Chironomus, Katablepharis, Aphanizomenon, Plectonilla, Salpingoeca, Microcystis, Trachelomonas, Asterionella, Melosira, Ankirodesmus, Scenedesmus, Cyclotella, Quagga, Surire, Coelosphaerium, Euglena, Woronichinia, Chroococcus, Fragilaria, Malcomsonas, Comptonas, Tetradion, Schrodedia, Melosira.

Right Plot: First axis of Co-inertia vs. First axis of Correspondence Analysis

- X-axis:** First Axis of Co-inertia (76.9% of inertia)
- Y-axis:** First Axis of Co-inertia (76.9% of inertia)
- Species (Points):** Diapha. birrelli, Skisto. oregonensis, Mesocyc. edax, Daph. parvula, Lepto. kindti, Daph. dubia, Daph. ambigua.
- Environmental Variables (Vectors):** Diapha. birrelli, Skisto. oregonensis, Mesocyc. edax, Daph. parvula, Lepto. kindti, Daph. dubia, Daph. ambigua.

Figure S7: Average gross photosynthetic production (GPP) integrated across the water column by time period. Differences were not significant.

Table S1: List of phytoplankton taxa (Cyan Cyanobacteria, Crypt Cryptophyceae, Diat Diatoms, Eugl Euglenophyceae, Dino Dinoflagellates, Chlor Chlorophyceae, Chrys Chrysophyceae)

group	genus species	authority	abbreviations	group	genus species	authority
Cyan	<i>Dolichospermum solitaria</i> var. <i>planctonica</i>	Komarek			<i>Tabellaria fenestrata</i>	Lyngbye
	<i>Dolichospermum spiroides</i>	Klebs	<i>Dolichospermum</i>		<i>Tabellaria flocculosa</i>	Roth
	<i>Dolichospermum flos-aquae</i>	(Lyngbye) Brebisson		Eugl	<i>Euglena acus</i>	Ehrenberg
	<i>Aphanizomenon flexuosum</i>	Komarek			<i>Euglena minuta</i>	Prescott
	<i>Aphanizomenon flos-aquae</i>	Ralfs			<i>Euglena pisciformis</i>	Klebs
	<i>Aphanizomenon gracile</i>	Lemmermann	<i>Aphanizo</i>		<i>Euglena viridis</i>	Ehrenberg
	<i>Aphanizomenon yezoense</i>	M. Watanabe			<i>Phacus caudatus</i>	Hubner
	<i>Aphanocapsa conferta</i>	W. & G.S. West	<i>Aphanoca</i>		<i>Trachelomonas volvocina</i>	Ehrenberg
	<i>Aphanocapsa delicatissima</i>	W. & G.S. West		Dino	<i>Ceratinum hirundinella</i>	(Mueller) Schrank
	<i>Aphanothece bachmannii</i>	Komárková-Legnerová		Chlor	<i>Ankistrodesmus falcatus</i>	(Corda) Ralfs
	<i>Aphanothece clathrata</i>	W. & G.S. West	<i>Aphanoth</i>		<i>Chlamydomonas fusus</i>	Ehrenberg
	<i>Aphanothece clathrata brevis</i>	Bachmann			<i>Chlamydomonas globosa</i>	Snow
	<i>Chroococcus dispersus</i>	(Keissler) Lemmermann			<i>Elakatothrix gelatinosa</i>	Wille
	<i>Chroococcus minimus</i>	(Keissler) Lemmermann			<i>Gyromitus cordiformis</i>	Skuja
	<i>Chroococcus minutus</i>	(Kuetzing) Naegeli			<i>Kirchneriella lunaris</i> var. <i>dianae</i>	(Kirchner) Moebius
	<i>Chroococcus prescottii</i>	Drouet & Daily			<i>Micractinium pusillum</i>	Fresenius
	<i>Coelosphaerium kuetsingianum</i>	Naegeli			<i>Monoraphidium contortum</i>	Pascher & Korshikov
	<i>Cyanodiction imperfectum</i>	Cronberg & Weibull			<i>Monoraphidium dybowskii</i>	(Woloszyriska) Hindak & Kom.
	<i>Limnothrix rosea</i>	Utermöhl	<i>Limnoth</i>		<i>Oocystis submarina</i> var. <i>variabilis</i>	Skuja
	<i>Lyngbia limnetica</i>	Lemmermann			<i>Quadrigula lacustris</i>	Chodat
	<i>Merismopedia tenuissima</i>	Lemmermann			<i>Salpingoeca frequentissima</i>	Zacharias
	<i>Microcystis flos-aquae</i>	(Wittrock) Kirchner	<i>Microcys</i>		<i>Scenedesmus ecomis</i>	(Ralfs) Chodat
	<i>Microcystis wesenbergii</i>	Komarek			<i>Scenedesmus incrassatulus</i>	Bohlin
	<i>Oscillatoria tenuis</i>	Agardh			<i>Schroederia setigera</i>	(Schroeder) Lemmermann
	<i>Plankthotrix agardhii</i>	Gomont	<i>Plankto</i>		<i>Scourfieldia cordiformis</i>	Takeda
	<i>Planktolyngbya pseudospirulina</i>	Pascher	<i>Planktol</i>		<i>Sphaerocystis schroeteri</i>	Chodat
	<i>Snowella septentrionalis</i>	Komarek			<i>Tetraspora gelatinosa</i>	(Wahlb.) Agardh
	<i>Woronichinia naegeliana</i>	Unger	<i>Woronichinia</i>	Chrys	<i>Bicoeca socialis</i>	Lauterborn
Crypt	<i>Cryptomonas borealis</i>	Skuja			<i>Chromulina elegans</i>	Doflein
	<i>Cryptomonas erosa</i>	Ehrenberg			<i>Chromulina mikrop plankton</i>	Pascher
	<i>Cryptomonas marssonii</i>	Skuja			<i>Desmerella brachycalyx</i>	Skuja
	<i>Chroomonas nordstedtii</i>	Hansgirg			<i>Dinobryon divergens</i>	Imhof
	<i>Chroomonas acuta</i>	Utermöhl			<i>Erkenia subaequiciliata</i>	Skuja
	<i>Katablepharis ovalis</i>	Skuja			<i>Mallomonas acaroides</i>	Perty
Diat	<i>Asterionella formosa</i>	Hassall			<i>Mallomonas tonsurata</i>	Teiling
	<i>Cyclotella comta</i>	(Ehrenberg) Kuetzing			<i>Ochromonas elegans</i>	Doflein
	<i>Cyclotella glomerata</i>	Bachmann			<i>Ochromonas globosa</i>	Skuja
	<i>Fragilaria crotonensis</i>	Kitton			<i>Salpingoeca frequentissima</i>	(Zacharias) Lemmermann
	<i>Melosira italica</i> var. <i>subarctica</i>	Ehrenberg			<i>Stichgloeia doederleinii</i>	(Schmidle) Wille
	<i>Rhizosolenia longiseta</i>	Zacharias			<i>Synura uvella</i>	Ehrenberg
	<i>Synedra acus</i> var. <i>radians</i>	Ktitzing			<i>Uroglona americana</i>	Catkins

Table S2: dominant macrozooplankton species during summer 2007 in Lake Bromont.

Genre	Espèce	Authority	Suborder	diet
<i>Diaphanosoma</i>	<i>birgei</i>	Korinek	Cladocera	herbivorous
<i>Daphnia</i>	<i>dubia</i>	Herrick	Cladocera	herbivorous
<i>Skistodiaptomus</i>	<i>oregonensis</i>	Lilljeborg	Copepoda	herbivorous
<i>Ceriodaphnia</i>	<i>sp.</i>		Cladocera	herbivorous
<i>Bosmina (Eubosmina)</i>	<i>coregoni</i>		Cladocera	herbivorous
<i>Acanthocyclops</i>	<i>(vernalis)</i>	Fischer	Copepoda	predator
<i>Leptodora</i>	<i>kindtii</i>	Focke	Cladocera	predator
<i>Mesocyclops</i>	<i>edax</i>	Forbes	Copepoda	predator