Research article

Cyanobacteria in winter: Seasonal dynamics of harmful algal blooms and their driving factors in boreal lakes

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A B S T R A C T

Lake cyanobacteria can overgrow and form blooms, often releasing life-threatening toxins. Harmful algal blooms (HABs) are typically caused by excess nutrients and high temperatures, but recent observations of cyanobacteria beneath the ice in boreal lakes suggest that the dynamics are more complex. This study investigates the seasonal dynamics of HABs in boreal lakes and identifies their driving factors. We study cyanobacteria assemblages in two boreal lakes in Abitibi-Témiscamingue (Quebec, Canada): Lake Fortune, noted for its under-ice cyanobacteria, and Lake Beauchamp, which has experienced recurrent summer-only cyanobacterial blooms. From June 2021 to July 2022, we identified monthly cyanobacterial communities and estimated water nutrients, organic carbon, temperature, oxygen, and pH. Cyanobacterial communities were dominated by the genus *Planktothrix* in Lake Fortune, and this genus was in a bloom state for each month of the year. Cyanobacterial abundance was highest (210 000 cells/mL) in November and lowest (28 000 cells/mL) in March. The abundance of *Planktothrix* correlated with total nitrogen and phosphorus and dissolved organic carbon concentrations. *Planktothrix* dominated even under ice cover, because of its ability to thrive in low-light and low phosphorus conditions. In Lake Beauchamp, *Aphanothece* was found throughout the year, highest (27 800 cells/mL) in August and lowest (2100 cells/mL) in March. In Lake Beauchamp, cyanobacterial blooms correlated with total dissolved phosphorus, nitrogen and organic carbon concentrations during summer and fall. The dominance of *Aphanothece* was especially pronounced during the summer and fall. Our study provides new knowledge about the seasonal dynamics of cyanobacterial blooms to help guide the future management of HABs in boreal lakes.

1. Introduction

Freshwater ecosystems have played a significant role in the growth of human civilizations [1]. The prevalence of harmful algal blooms (HABs) and their associated cyanotoxins in lakes is an increasing concern that poses an environmental and human health hazard. HABs are a significant challenge facing many water bodies in North America, with over 1161 lakes in the United States and 246

lakes in Canada being registered as having HABs [2]. Moreover, our understanding of HABs seasonal dynamics is underexplored in North America [3]. A clearer understanding is essential to reduce the impacts of cyanobacterial blooms on the health of humans and freshwater ecosystems.

Cyanobacteria are prokaryotic, phototrophic microorganisms, commonly known as blue-green algae, that play a crucial role as primary producers in freshwater and marine environments, contributing to approximately 20 %–30 % of the world's photosynthesis; thus, they are a crucial component for maintaining the global atmospheric balance and for the survival of humans and wildlife [4]. However, the rapid growth of cyanobacteria can be characterized by a sudden increase in cyanobacterial biomass and the dominance of one or a few species. These cyanobacterial blooms are known as HABs when harmful to humans and animals [5,6]. Some cyanobacterial species can produce secondary metabolites with toxic properties; these products include hepatotoxins, neurotoxins, and dermatoxins, collectively called cyanotoxins [7]. Many cyanobacteria produce intracellular cyanotoxins that harm humans [8–10]. Across the globe, cyanobacteria have been responsible for an increasing number of HABs that liberate cyanotoxins [11]. Among all cyanotoxins, microcystin is widely distributed (found on all continents except Antarctica) and potentially harmful to humans and animals [12–14]. The primary source of poisoning from cyanobacterial blooms for humans includes swimming in HAB-contaminated water and consuming HAB-contaminated food and drinking water [15] According to Health Canada, if 1 mL of lake water contains more than 5000 cells of *Microcystis* and chlorophyll-a is above 33 µg/L, microcystin is potentially present [16]. Toxins produced by cyanobacteria stem from a defence against grazers [17]; for example, cyanobacteria increase their toxin production to defend against *Daphnia magna* and *Moina macrocopa* [18–20]. In Quebec, 51 lakes have been contaminated by cyanobacterial blooms caused by 23 species of cyanobacteria [2]. In Missisquoi Bay, Québec, 14 different variants of cyanotoxins have been documented [21–25]. These variants differ in their nutritional and environmental requirements; therefore, it is crucial to learn about each to improve HAB management plans [26].

Cyanobacterial growth and bloom development are favored by several abiotic factors, including nutrient inputs (e.g., nitrogen above 0.3 mg/L, phosphorus above 20 µg/L), light availability for photosynthesis (Secchi depths deeper 2–3 m), temperature (optimal above 20 °C), water movement, pH changes (below 6–7) or trace metal concentrations [26]. Cyanobacterial blooms are more common in eutrophic lakes because of the nutrient enrichment, given the need for high nitrogen and phosphorus concentrations for cyanobacteria growth and development [27]. Increased eutrophication promotes the alkalization of lakes, which alters a lake's pH dynamics in different seasons. In general, pH seasonal dynamics are characterised by increased alkalinity during spring and early summer due to cyanobacterial photosynthesis, and a possible decrease in pH during fall, with a more stabilized environment in winter. This shift is thought to contribute to the growth of cyanobacterial blooms [28–30].

Phosphorus overload favours the eutrophication of freshwater ecosystems and promotes toxic cyanobacterial blooms [31–37]. The Downing et al. [38] model predicts that the probability of cyanobacterial blooms increases rapidly when total phosphorus is between 20 and 30 g/L, which corresponds to the water quality guidelines established by most provinces in Canada [39]. Phosphorus is considered an essential nutrient because it is a component of DNA (deoxyribonucleic acid), RNA (ribonucleic acid), ATP (adenosine triphosphate), and the phospholipids that form cell membranes [40].

Atmospheric nitrogen is also crucial because it is absorbed by cyanobacteria and other microorganisms [41]. Cyanobacterial blooms may be influenced by a species' seasonal dynamics and the nitrogen sources present in the lake. In warm months, when planktonic cyanobacterial blooms are most frequent, nitrogen limitation in freshwater systems has been most frequently recorded [42–45]. Glibert et al. [46] found a positive correlation between nitrogen availability and toxin liberation. However, there is still an ongoing debate in the scientific literature regarding the roles of phosphorus and nitrogen in blooms.

Temperature is considered the most critical factor for the growth and development of cyanobacteria because these taxa are well-adapted to warmer conditions in aquatic ecosystems [47–49]. The favourable in vitro temperature for cyanobacterial growth is around 20 °C with a maximum of 35 °C [50]. Global temperatures are expected to increase an additional 1.5° to 5.8 °C by the end of this century [51]. Therefore, the intensity of HABs may increase in the future because of climate change and eutrophication [52–54].

Cyanobacterial blooms are usually observed in late summer and autumn; however, several recent studies from Canada have also observed them in winter [5,55]. The seasonal dynamics of cyanobacterial blooms were believed to follow a gradual increase from spring to summer, with the highest abundance in fall and a decrease in winter. However, recent observations showed some unusual occurrences of the cyanobacterial genus *Planktothrix* under the ice cover at 4 °C [56]. This pattern contradicts the paradigm of cyanobacterial growth enhanced by warm water temperatures and high nutrients, such as in Chu et al. [57] and Suda et al. [58] and the scientific paradigm that consider most of aquatic life as dormant during winter [59]. These papers showed that the favourable thermal conditions required for the bloom of *Planktothrix* were between 15 and 30 °C. Although studies have shown that *Planktothrix* can grow in low light conditions, we do not know those factors influencing its presence under a thick ice cover in winter [60,61].

Our study characterized the cyanobacterial community composition in two boreal lakes throughout one year, including under ice. Moreover, we aimed to determine the driving factors influencing cyanobacterial abundance, to fill the knowledge gap regarding the seasonal dynamics of cyanobacterial blooms, and help improve management plans for reducing atypical winter cyanobacterial blooms. We hypothesized that cyanobacterial communities will be detected at bloom levels in summer and fall in both lakes [47]. We also hypothesized that higher nutrients, including phosphorus and nitrogen availability, would drive cyanobacterial blooms [43,45,62,63].

2. Materials and methods

2.1. Study area

This study was conducted on two lakes of the Abitibi-Témiscamingue region of Quebec, Canada. This region of 64 878 km² has

more than 20 000 lakes. Regional climate is a cold and humid continental climate with a mean annual temperature of 2.5 °C and an average annual precipitation of 800–900 mm [64,65]. Lake Fortune is a medium-sized lake with a 0.75 km^2 surface and a 1.61 km^2 watershed. The maximum depth of this lake is around 17 m [66]. Lake Fortune is a headwater lake flowing into King-of-the-North Lake, which then flows into Mud Lake. Lake Fortune's drainage ratio is very small, inducing a low supply of nutrients given the small drainage area of the watershed. The lake is naturally clear and can be considered oligotrophic [66]. A total of 67 inhabitants live on the shores of Lake Fortune.

Lake Beauchamp is located in the Municipalité régionale de comté Abitibi territory, 8 km from the city of Amos, with a shared ownership among the municipalities of Amos, Trecesson, and Figuery [67,68]. Lake Beauchamp is situated near an esker and has a roughly circular shape. This lake lies in the sub-watershed system of the Davy and Harricana rivers (Fig. 1). Lake Beauchamp has 403 permanent inhabitants around the lake, and many visitors come to the municipal camping site and beach every year [67]. Both lakes Fortune and Beauchamp provide rich habitats for a diverse aquatic biodiversity and serve as popular recreational spots.

2.2. Experimental design

We sampled Lake Fortune and Lake Beauchamp between June 2021 and July 2022. We collected samples every month, except for December and April when sampling was impossible because of an insufficient ice thickness on the lake. A weekly sampling program was undertaken during the fall (mid-August to October), as this is the most significant period for cyanobacterial growth, according to multiple studies [69,70]. We collected samples from the deepest points of the lakes (14 m in Lake Fortune and 5 m in Lake Beauchamp) and from three different layers, including the epilimnion, metalimnion, and hypolimnion, when present [71].

3. Data collection

3.1. Physicochemical properties

We used a multi-parameter probe (RBR Concerto, Ottawa, Canada) to measure the temperature profile (°C), thermocline depth (m), dissolved oxygen saturation (%), specific conductivity (μS/cm), and pH. The Ruskin phone application determined the depth of each water layer during sampling. We estimated the maximum depth of the lake using a depth meter (Speedtech SM-5, Laylin, Unionville, Canada). We used a Secchi disk to measure the transparency of the water column. For each date during the 12-month sampling period, we used a Ruttner or a Van Dorn 2 L bottle [72] to collect water from the deepest point of each lake, sampling from the three layers: the epilimnion (1 m below the surface), the metalimnion, and the hypolimnion (1 m above the sediment). The metalimnion was determined as the mid-point of the estimated thermocline depth. In winter, samples were collected through a hole drilled through the ice using an ice corer.

3.2. Plankton sampling and enumeration

A total of 72 cyanobacteria samples were collected and identified. They were preserved in 250 mL brown glass or plastic bottles and
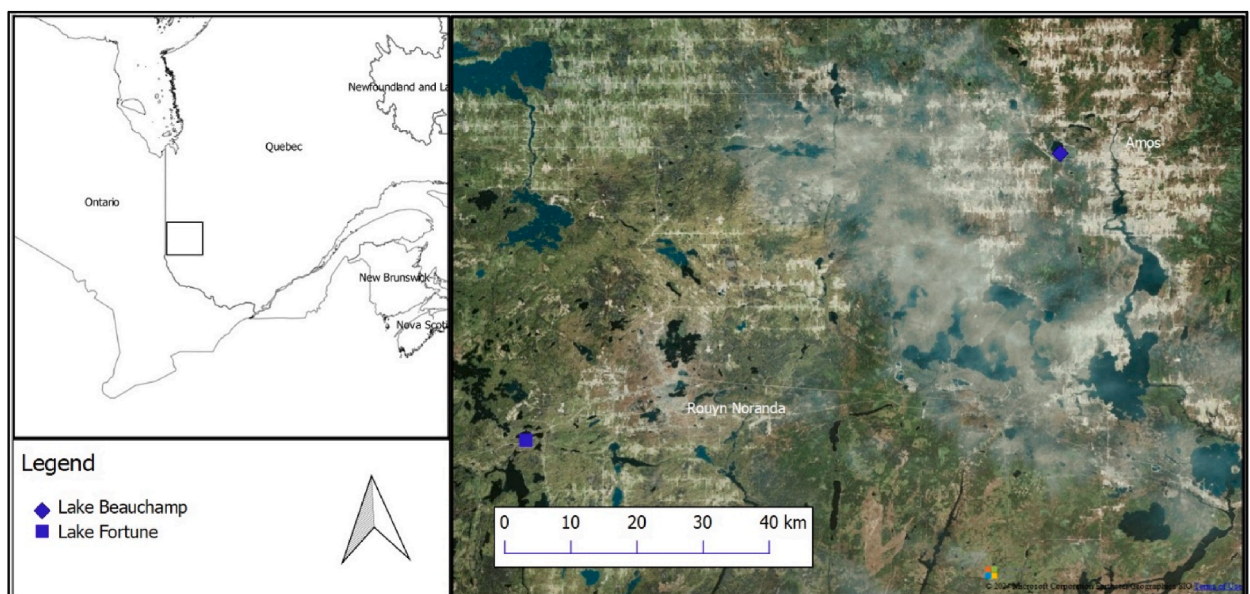

Fig. 1. Location of the lakes Fortune and Beauchamp in the Abitibi-Témiscamingue region.

then fixed with 1 % Lugol's solution. The samples from Lake Fortune were sent to the Direction générale du suivi de l'état de l'environnement of the Quebec Ministry of Environment and Climate Change for cell counting and identification. Samples from Lake Beauchamp were sent to Dolors Planas's laboratory at the University of Québec in Montreal. Phytoplankton identification was performed using a DM IRB Leica inverted microscope (Wetzlar, Germany) and an Utermöhl sedimentation chamber. The sub-sample volume was determined based on the density of organisms, debris, and sediments. Only live cells were counted. Using a 40X objective, identification and counting were conducted by traversing three sectors of the sedimentation chamber in a Z-pattern, continuing across up to 15 fields. All species observed in these fields were identified, measured, and recorded. Additionally, non-dominant species that were absent or too large to be counted at 40X were identified and counted at 10X. For each sample, 10X counting was performed by scanning the bottom of the sedimentation chamber vertically and horizontally, creating two cross-shaped transects.

We selected the five most abundant cyanobacterial genera from the cyanobacterial counts covering the entire year. Zooplankton communities were sampled to assess the potential predation pressure on the phytoplankton. For this, we collected an integrated-depth sample with a minimum of 15 L from the water column (from the surface to the maximum lake depth). The samples were sieved in a 50 μm plankton net, stored in 125 mL plastic bottles, and preserved in ethanol (≥70 % final concentration). Zooplankton samples were sorted and identified with a stereomicroscope (Discovery V.12, Zeiss, Oberkochen, Germany).

3.3. Nutrients

The collected water was analyzed for nutrients and dissolved organic carbon. Filtrate was added to the acid-washed glass vials (50
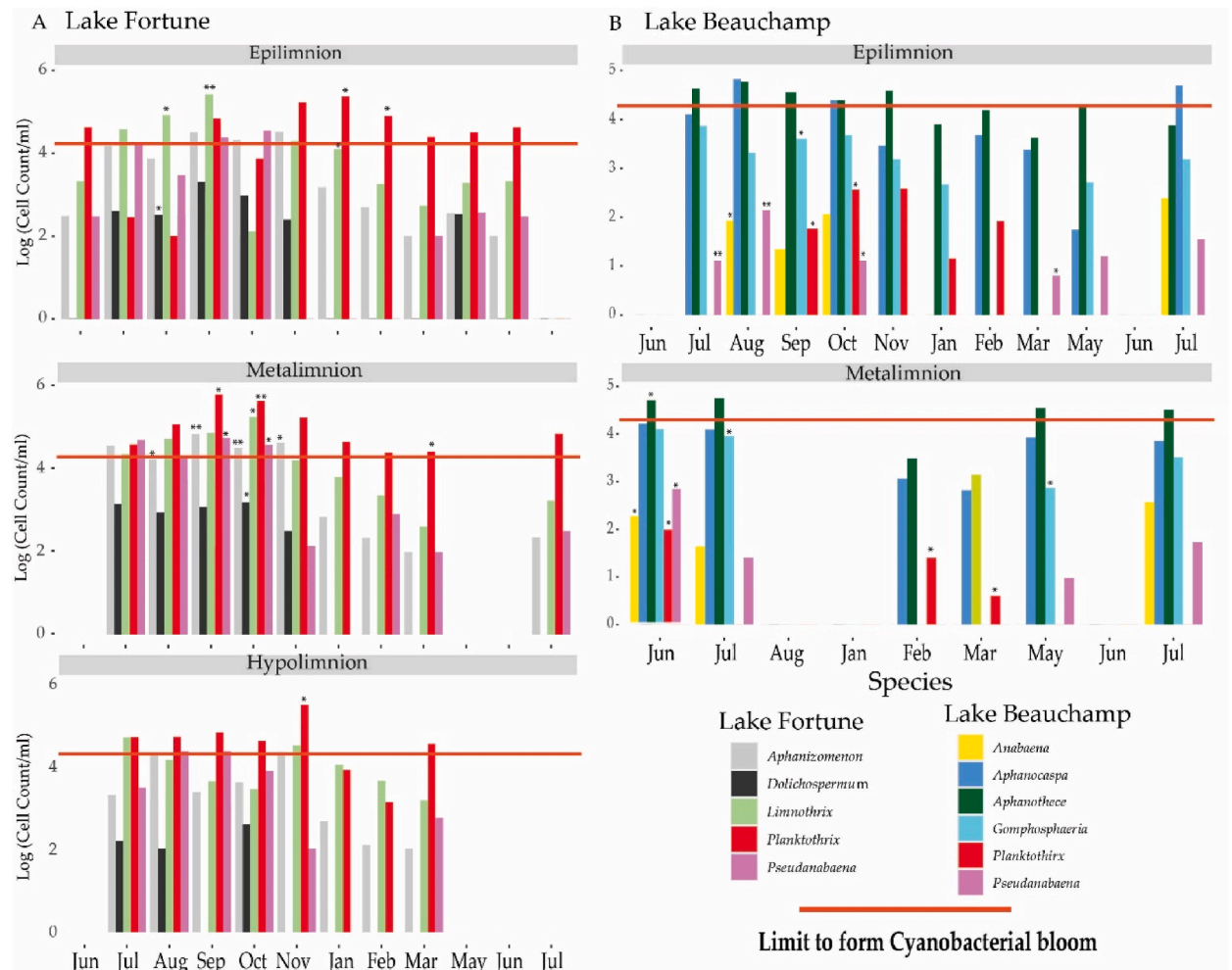
Fig. 2. Cyanobacterial cell counts of the dominant cyanobacteria genera of blooms in A) Lake Fortune and B) Lake Beauchamp in the epilimnion, metalimnion, and hypolimnion. The five genera from Lake Fortune and six from Lake Beauchamp showed a high abundance throughout the year. Missing months in the metalimnion and hypolimnion are months when the lake water column was not stratified. In these cases, the data are presented as epilimnion samples. December and April are not displayed, as it was logistically dangerous to sample on the thin ice in these months. P-values <0.05 are flagged with one star (*), <0.01 with two stars (**), and <0.001 with three stars (***).

mL) for each analysis: total phosphorus (TP) total nitrogen (TN) total dissolved nitrogen (TDN), and total dissolved phosphorus (TDP). Each vial was washed in a 10 % HCl bath for 24 h, rinsed, and then heated in an oven at 200 °C. To estimate dissolved elements, including dissolved organic carbon (DOC), TDP, and TDN, we used a 0.7 μm glass fibre filter (Cytiva, Marlborough, USA) to filter a 1 L water sample in the laboratory as in Grosbois, del Giorgio et al. [73]. All vials were kept at 4 °C until analysis. Nutrient samples were analyzed with a continuous flow analyzer (OI Analytical Flow Solution 3100) by an alkaline persulfate digestion method coupled with a cadmium reactor at the Interuniversity Research Group in Limnology (GRIL) analytical laboratory in Université du Québec à Montréal, following standard protocols [74]. To analyze DOC, we placed each vial in the oven at 400 °C for 4 h. Then, DOC samples were analyzed using the persulfate oxidation method via an OI Analytical Aurora 1030 W TOC analyzer at the GRIL analytical laboratory.

4. Statistical analysis

Data were tested for normality and homoscedasticity before any statistical analysis. The major cyanobacterial species from each lake were selected as those taxa found throughout the year and having the highest cell counts among the detected species [75]. The threshold of cell counts to form a bloom according to the WHO determined the dominant cyanobacterial genera from each lake [26]. We used Tukey's HSD to test for differences in the physicochemical and biological variables among layers and months [76]. To identify the relationship among physicochemical variables contributing to cyanobacterial blooms in different lakes and seasons, we ran principal component analysis using the R package factoextra [77]. To identify the environmental and biological variables responsible for cyanobacterial abundance throughout the year, we used a generalized additive model with months as the fixed effect and parameters as factors, using the gam function [78]. Data were log-transformed for each zooplankton species to observe their effect on cyanobacterial abundance [79]. All analyses were conducted using the statistical software R version 4.2.1 [80].

5. Results

5.1. Species abundance

We found cyanobacterial communities dominated by the genera *Planktothrix*, *Limnothrix*, and *Aphanizomenon* in Lake Fortune (Fig. 2A) and *Aphanothece*, *Aphanocapsa*, and *Gomphosphaeria* in Lake Beauchamp (Fig. 2B). In Lake Fortune, cyanobacteria abundance varied seasonally, with the highest values in summer (April–August) and fall (September–October) and the lowest values in winter (December–March). Five cyanobacterial species in Lake Fortune and six in Lake Beauchamp bloomed at least once during the year (Fig. 2, Table 1). Total cell counts of all these species combined were highest in June, September, and October in the epilimnion (*t*-test, $p < 0.1$). In Lake Fortune, the most dominant genus *Planktothrix* (*t*-test, $p < 0.05$) had the highest cell count in November (210 000 ± 52 915 cells/mL) and the lowest in March (28 000 ± 2450 cells/mL) with a yearly average of 81 800 ± 66 225 cells/mL (Fig. 5A). The second-most dominant genus in Lake Fortune, *Limnothrix*, had its highest cell counts in October (52 450 ± 67 780 cells/mL) and the lowest in March (790 ± 155 cells/L), with a yearly average of 19 655 cells/mL (Fig. 2A). The cell count of *Aphanizomenon*, another dominant genus (*t*-test, $p < 0.05$), was highest in November (33 166 ± 13 250 cells/mL) and lowest in March (100 ± 0 cells/mL) and had a yearly average of 9635 cells/mL (Fig. 2A).

Cell counts of the genus *Aphanothece* were higher (*t*-test, $p < 0.05$) than other detected species over the year in Lake Beauchamp. In Lake Beauchamp, the cell count of *Aphanothece* was highest in May (27 850 ± 12 730 cells/mL) and lowest in March (2110 cells/mL) with a yearly average of 19 080 cells/mL (Fig. 2B). Cell counts were above the WHO threshold (20 000 cells/mL) in lakes Fortune and Beauchamp for *Planktothrix* in autumn and *Aphanothece* in summer, respectively. Cell counts of *Planktothrix* were higher (*t*-test, $p < 0.05$) throughout the year than for other species in Lake Fortune.

5.2. Physicochemical characteristics

Lakes Fortune and Beauchamp were covered by ice formed during November to December and melted during April to May in the year 2021–2022. Thermal stratification started in May and lasted until September in both lakes (Fig. 3). In Lake Fortune, the temperature was the highest in August and the lowest in January (Table 2, Fig. 3A). Specific conductivity was the highest in September and lowest in January (Table 2, Fig. 3C). The pH was highest in January and lowest in October (Table 2, Fig. 3E). Dissolved oxygen concentrations were highest in January to in the lowest September (Table 2, Fig. 3G). For Lake Beauchamp, water temperature was highest in August and lowest in January (Table 2, Fig. 3B). Specific conductivity was the highest in September to the lowest in May (Table 2, Fig. 3D). Lake pH was highest in November and the lowest in February (Table 2, Fig. 3F). Finally, the dissolved oxygen concentrations were highest in November and lowest in March (Table 2, Fig. 3H).

In Lake Fortune, the winter temperature of the epilimnion was 0.4 °C, and the temperature of the metalimnion fluctuated between 1.4 and 3.7 °C. Additionally, the summer temperature of Lake Fortune ranged from 15.8 to 19.1 °C at the surface and 5.2–7.6 °C in the hypolimnion. For Lake Beauchamp, the mean (January–February) winter surface temperature was 1.3 ± 0.3 °C, and the temperature in the metalimnion varied between 3.9 ± 0.3 and 4.0 °C. The summer temperature of Lake Beauchamp ranged from 19.1–21.1 °C at the surface. Specific conductivity in Lake Fortune for September (155.9 ± 9.3 μS/cm) in the hypolimnion was higher than the yearly average of 118.87 μS/cm and the average fall value of 121.46 μS/cm. In Lake Beauchamp, specific conductivity was higher during September (112.7 ± 66.9 μS/cm) in the epilimnion than the yearly (71.7 μS/cm) and seasonal (fall) (80.3 μS/cm) averages. During the winter, specific conductivity was higher in the hypolimnion in both lakes. Conductivity was highest in Lake Fortune in the

Table 1

Monthly average cyanobacterial cell counts (cells/mL) combining samples from all layers and months throughout the year in lakes Fortune and Beauchamp.

	Month	*Aphanizomenon*	*Dolichospermum*	*Limnothrix*	*Planktothrix*	*Pseudanabaena*	*Anabaena*	*Aphanothece*	*Gomphospharia*
Lake Fortune	Jan	888	0	9708	98617	0	0	0	0
	Feb	282	0	2767	36267	840	0	0	0
	Mar	100	0	788	28000	243	0	0	0
	May	325	340	1963	41750	364	0	0	0
	Jun	310	0	2100	43000	300	0	0	0
	Jul	9933	683	27325	41322	18345	0	0	0
	Aug	10258	450	33420	48775	9837	0	0	0
	Sep	16844	912	43930	160483	23035	8813	8700	0
	Oct	16844	585	52446	52446	18124	8733	1280	0
	Nov	33167	290	22167	21000	120	0	0	0
Lake Beauchamp	Jan	0	0	0	15	0	0	9127	490
	Feb	0	0	0	542	0	0	9265	0
	Mar	0	0	0	395	6332	0	2836	0
	May	0	0	0	0	1226	0	27850	639
	Jun	0	0	0	1076	0	2913	25021	9788
	Jul	0	0	0	3710	724	200	20472	5837
	Aug	0	0	0	0	1393	450	19562	2047
	Sep	415	0	10800	585	2849	3081	18083	2004
	Oct	1504	0	316	206	1769	7480	25483	5395
	Nov	0	0	949	386	0	2897	38982	15354
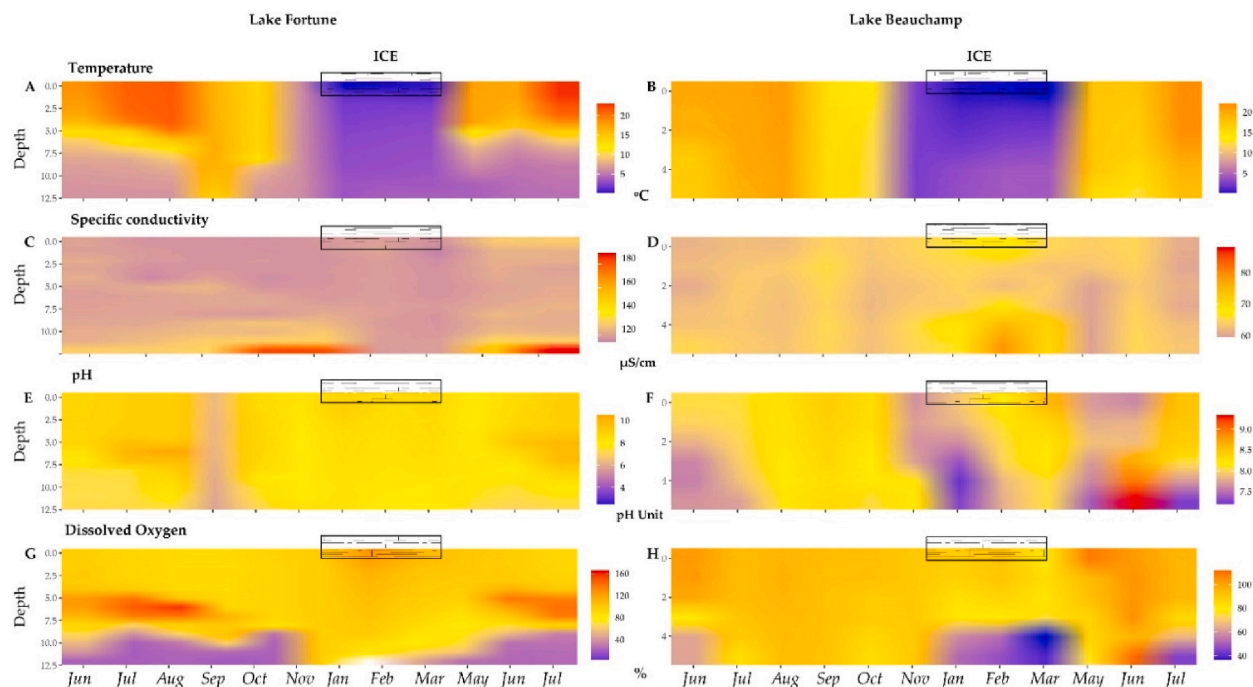
Fig. 3. Physicochemistry of lakes Fortune and Beauchamp with A and B) water temperature (°C); C and D) specific conductivity (µS/cm); E and F) pH; and G and H) dissolved oxygen saturation (%).

Table 2
Physicochemical values from lake Fortune and lake Beauchamp. Maximum and minimum values are monthly means ± standard deviations calculated for the water column profile from lake surface to bottom. Yearly mean values are calculated from the mean of each water column monthly means.

Lake name	Variable (unit)	Month of highest value	Highest average value (mean ± SD)	Month of lowest value	Lowest average value (mean ± SD)	Yearly average value (mean ± SD)
Fortune	Temperature (°C)	August	13.7 ± 6.1	January	2.6 ± 0.5	8.6 ± 1.1
	Specific conductivity (µS/cm)	September	127.2 ± 16.9	January	113.1 ± 0.6	118.8 ± 2.1
	pH	January	8.6 ± 0.1	October	7.7 ± 0.5	8.1 ± 0.1
	Dissolved oxygen (µmol/L)	January	322.3 ± 28.2	September	62.1 ± 81.4	203.7 ± 81.4
Beauchamp	Temperature (°C)	August	20.7 ± 0.1	January	2.2 ± 1.1	12.3 ± 0.5
	Specific conductivity (µS/cm)	September	112.8 ± 47.3	May	53.5 ± 0.5	71.7 ± 7.8
	pH	November	8.2 ± 0.3	February	7.3 ± 0.1	7.9 ± 0.1
	Dissolved oxygen (µmol/L)	November	387.4	March	225.0	262.6 ± 15.1

hypolimnion in the fall. In Lake Fortune, the water was more acidic (6.8 ± 0.5) in the fall than the yearly average (8.1 ± 0.4), whereas in Lake Beauchamp, pH was higher in the metalimnion during the summer (8.1 ± 0.6) than the yearly average (7.7 ± 0.7). Lake Fortune showed metalimnetic oxygen maxima from June to September. In Lake Fortune, transparency measurements varied from 2.8 m in summer to 1.4 m in winter and 2.3 m in fall, whereas in Lake Beauchamp, transparency varied from 2.8 m in summer to 1.9 m in winter and 2.1 m in fall.

In Lake Fortune, TP concentrations varied from 35.1 mg/L in June (2021) to 10.3 mg/L in August (2020). TDP concentrations varied from 36.1 mg/L in August (2021) to 5.48 mg/L in June (2021). The TN and TDN concentrations were higher during the fall (September–October) than the yearly average. The TN and TDN concentrations were 56 % and 30 % higher, respectively, than the yearly average, and the concentrations were four times higher in the metalimnion. Similarly, TP and TDP were 80 % higher in August in the metalimnion relative to the epilimnion and hypolimnion. TN concentrations varied from 1.9 mg/L in September to 0.2 mg/L in July. TDN varied from 0.8 mg/L in September to 0.2 mg/L in June, combining all layers. Additionally, the DOC concentration was higher during the fall (August–October) when combining all layers, although this was not significantly different ($F = 1.4$ $p = 0.2$). TN and TDN were 40 % higher in June relative to March concentrations. DOC varied from 7.2 mg/L in September to 3.7 mg/L in June.

In Lake Beauchamp, TP varied from 35.8 mg/L in July in the metalimnion to 14.3 mg/L in September in the epilimnion. TDP varied from 29.1 mg/L in August from epilimnion samples to 5.2 mg/L in the June metalimnion samples. TDP was higher (6.2 mg/L) in the

epilimnion (21.1 mg/L) than in the metalimnion (14.9 mg/L) (Fig. 4D). TN varied from 0.6 μg/L in August for the epilimnion to 0.3 μg/L in June for the metalimnion. TN was higher in the epilimnion (0.6 μg/L) than in the metalimnion (0.4 μg/L) (Fig. 4F). TDN varied from 0.4 μg/L in March in the epilimnion to 0.2 μg/L in May in the hypolimnion. For yearly average, it was only 0.02 μg/L higher in the epilimnion (0.4 μg/L) than the hypolimnion (0.4 μg/L) (Fig. 4H). DOC varied between 12.07 mg/L in June for the epilimnion and 5.5 mg/L in March for the metalimnion. DOC was higher in the epilimnion (12.1 mg/L) than in the metalimnion (6.3 mg/L) (Fig. 4J).

5.3. Factors explaining cyanobacterial communities

Each standardized cell counts of dominant cyanobacterial genus were tested with environmental variables such as TP, TDP, TN, TDN, temperature, specific conductivity, pH, dissolved oxygen using principal component analysis (PCA). The first two axes of the PCA of *Planktothrix* cell densities in Lake Fortune explained 56 % of the variation (Fig. 5A). The PCA of *Limnothrix* described 55 % of the variation with the first two axes, and the cell count of *Limnothrix* revealed a correlation between pH and specific conductivity ($r > 0.4$, $p < 0.05$) (Fig. 5C). The PCA of *Pseudanabaena* cell densities described 56 % of the variation within the first two axes. The cell count of *Pseudanabaena* correlated with TDP and temperature ($r > 0.5$, $p < 0.05$) (Fig. 5E). The cell counts of *Aphanizomenon* correlated with temperature and specific conductivity ($r > 0.4$, $p < 0.05$), and the PCA of *Aphanizomenon* explained 56 % of the variation in the first two axes (Fig. 5G).

In Lake Beauchamp, PCA of *Planktothrix* cell counts defined 66 % of the variation in the first two axes, and the total cell count of *Planktothrix* did not correlate with any variables ($r < 0.3$, $p > 0.1$) (Fig. 5B). The individual PCAs for *Gomphosphaeria*, *Aphanothece*, and *Aphanocapsa* explained 67 %, 66 %, and 67 % of the variation, respectively, and did not show any relationship with the variables ($r < 0.4$, $p > 0.1$; Fig. 5D–F, H).

To observe the effects of physicochemical variables on cyanobacterial genera through a generalized additive model, we used the cell counts of 10 species from both lakes as dependent variables, and the physicochemical variables served as explanatory variables. In Lake Fortune, we found that DOC significantly affected the *Dolichospermum* cell counts ($p < 0.05$; Table 3). Similarly, DOC and TP significantly affected the *Planktothrix* cell counts ($p < 0.01$; Table 3). For Lake Beauchamp, TDN significantly affected ($p < 0.05$) *Anabaena* cell counts. TDN significantly affected the *Gomphosphaeria* ($p < 0.01$) and *Aphanothece* cell counts ($p < 0.01$) (Table 3).

In Lake Fortune, the correlation between zooplankton species and cyanobacterial cell counts in Lake Fortune reveals key insights into aquatic ecosystem dynamics. Copepod larvae (Nauplii) were significantly related to the cell counts of *Aphanizomenon* ($r = -0.4$, $p < 0.05$). Calanoid (adult) significantly and positively affected the cell count of *Planktothrix* ($r = 0.6$, $p < 0.05$), whereas *Daphnia* (adult) significantly and negatively ($r = -0.7$, $p < 0.05$) affected the cell count of *Dolichospermum* (Table 4).
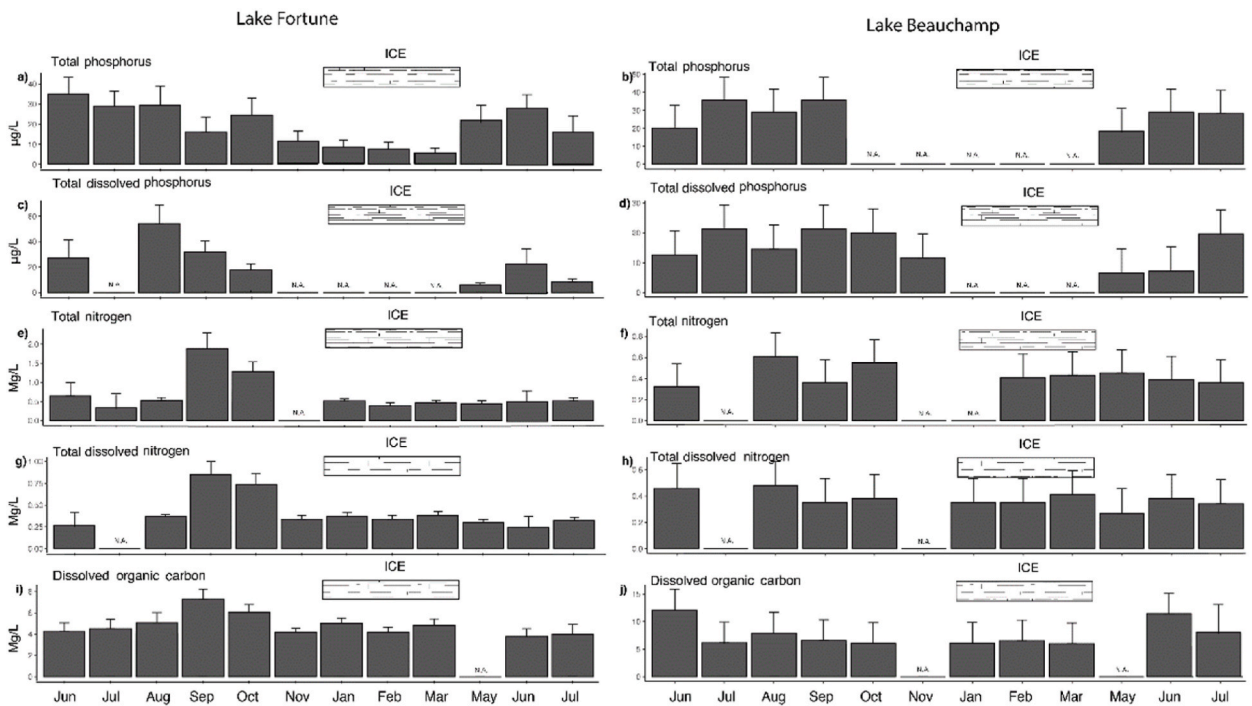

Fig. 4. Total nutrient and carbon concentrations in lakes Fortune and Beauchamp over a year. Data represent the means and standard deviations from the three lake layers (epilimnion, metalimnion, and hypolimnion) combined.
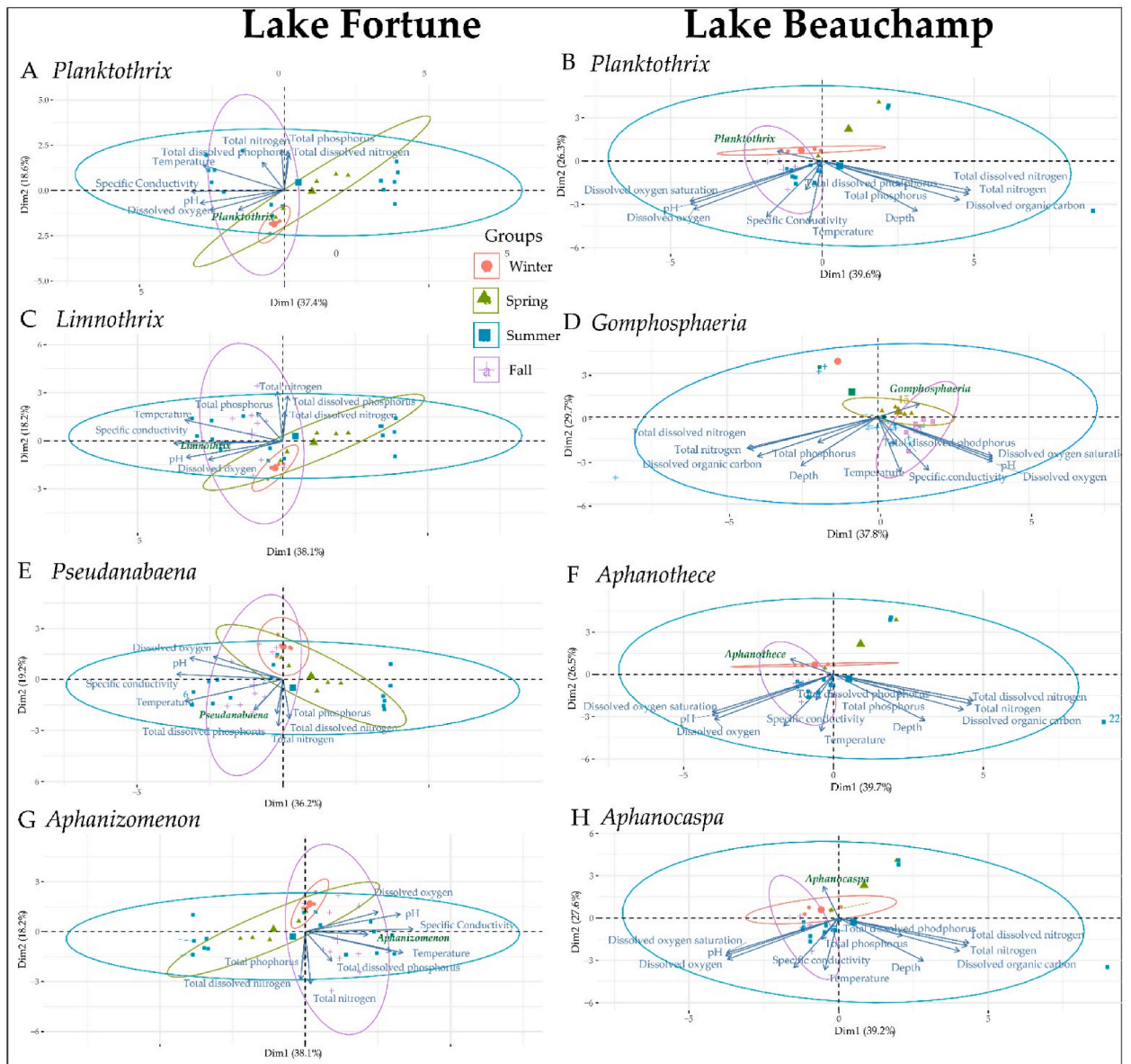
Fig. 5. *Principal component analysis (PCA) of the measured environmental variables and cyanobacterial cell densities in lakes Fortune and Beauchamp.*

6. Discussion

Studying cyanobacterial blooms during winter is crucial for understanding their impact throughout the year, as these blooms can have significant consequences on water quality and ecosystem dynamics. Both studied lakes had different cyanobacterial bloom patterns. For both lakes, we observed at least one genus of cyanobacteria that remained in a state of bloom over the year in Lake Fortune and only in summer in Lake Beauchamp. *Planktothrix* was present throughout the year in Lake Fortune; most of the time, including during winter, its concentration was above the level recommended by the WHO for recreational water quality and human health (20 000 cells/mL). This observation confirmed our hypothesis that in Lake Fortune, the cyanobacteria community would be detected at bloom levels throughout the year, even under ice in winter. We also found that higher nutrients in lakes generally positively influenced the cyanobacterial blooms. Nutrients and organic carbon significantly positively influenced the dominance of *Planktotrix* in Lake Fortune and *Aphanothece* in Lake Beauchamp. Thus, we confirmed our hypothesis that a higher availability of dissolved phosphorus and nitrogen favors the formation of cyanobacterial blooms.

Table 3

Generalized additive model showing relationships between cyanobacterial cell counts and physicochemical variables for lakes Fortune and Beauchamp. P-values <0.05 are flagged with one star (*), <0.01 with two stars (**), and <0.001 with three stars (***).

Variable	Lake Fortune					Lake Beauchamp				
	Dolichospermum spp.	*Planktothrix* spp.	*Aphanizomenon* spp.	*Limnothrix* spp.	*Pseudanabaena* spp.	*Planktothirx* spp.	*Anabaena* spp.	*Pseudanabaena* spp.	*Aphanothece* spp.	*Gomphosphaeria* spp.
TP	0.52	**0.02***	0.16	**0.02***	0.36	0.22	0.40	0.36	0.42	0.10
TDP	0.18	0.79	0.35	0.63	0.76	0.50	**0.05**	0.43	0.30	0.44
TN	0.99	0.81	0.77	0.65	0.32	0.13	**0.09**	0.38	0.38	0.14
TDN	0.51	0.25	**0.03***	**0.01***	0.14	0.06	**0.03***	0.20	**0.04***	**0.02***
DOC	**0.005****	**0.04***	0.33	0.08.	0.92	0.67	0.32	0.70	0.83	0.61
Temp	0.39	0.23	0.22	**0.82**	0.68	0.59	0.33	0.16	0.08	0.17
January	0.86	0.19	0.10	0.05	0.92	**0.09**	**0.77**	0.42	0.31	0.15
February	0.84	**0.04***	0.19	0.11	0.39	0.21	0.12	0.42	0.49	**0.02***
March	0.77	**0.03***	0.31	0.18	0.05	**0.06.**	**0.07**	0.68	0.48	**0.01***
May	0.36	0.75	0.46	0.76	0.17	**0 0.008****	**0.02***	0.79	0.93	0.10
June	0.91	0.80	0.86	0.39	0.55	**0.008****	**0.04***	0.38	0.12	**0.009****
July	0.20	0.09	0.19	0.48	0.07	**0.02***	0.24	0.99	0.46	0.15
August	**0.02***	0.13	**0.03***	0.08	**0.001****	**0.007****	**0.07**	0.53	0.29	**0.01***
September	0.13	**0.0005*****	**0.003****	**0.001****	**0.003****	**0.02***	0.21	0.36	0.32	**0.03***
October	**0.05***	**0.002****	**<0.001*****	**0.003****	**0.01***	0.21	0.59	0.36	0.83	0.24
November	0.11	**0.02***	**0.02***	**0.14**	0.29					

TP: total phosphorus, TDP: total dissolved phosphorus, TN: total nitrogen, TDN: total dissolved nitrogen, DOC: dissolved organic carbon, Temp.: temperature.

Table 4
Effect of zooplankton communities on cyanobacteria cell counts in lakes Fortune and Beauchamp using generalized linear models. P-values <0.05 are flagged with one star (*), <0.01 with two stars (**), and <0.001 with three stars (***).

	Lake Fortune					Lake Beauchamp				
	Aphanizomenon spp.	*Dolichospermum* spp.	*Limnothrix* spp.	*Planktothrix* spp.	*Pseudanabaena* spp.	*Planktothrix.* spp.	*Aphanizomenon* spp.	*Anabaena* spp.	*Pseudanabaena.* spp.	*Gomphosphaeria.* spp.
Bosmina	0.16	0.63	0.75	0.92	0.24	0.4	0.86	0.52	0.72	0.93
Daphnia	0.7	< **0.05****	0.31	0.18	0.87	0.71	0.64	0.75	0.65	0.89
Calanoid	0.65	0.78	0.25	**0.04***	0.85	0.69	0.57	0.82	0.88	0.96
Cyclopoid	0.83	0.88	0.98	0.52	0.68	0.68	0.34	0.66	0.74	0.86
Nauplii	**0.04***	0.92	0.4	0.3	0.15	0.75	0.42	0.71	0.83	0.79
Keratella	0.69	0.91	0.49	0.17	0.71	0.73	0.97	0.73	0.67	0.83
Kellicottia	0.59	0.95	0.75	0.31	0.47	0.59	0.39	0.75	0.92	0.87

6.1. Seasonal dynamics of cyanobacteria

Cyanobacterial cell counts differed among seasons. The genus *Planktothrix* was present during the winter months in contrast to previous conclusions regarding cyanobacterial blooms and the optimal temperatures being in warmer waters [57,58]. For example, in Lake Zurich [81], Lake Mondsee in Austria [62], and lakes du Bourget [82] and Nantua [83] in France, *Plankthotrix* was detected and thrived at higher temperatures (20–30 °C). However, our observation of this genus at unfavorable temperatures (near 4 °C) likely relates to its ability to adapt and maintain its life cycle using fewer resources at low temperatures and low irradiance [84,85]. Moreover, *Plankthotrix* can have higher growth rates than other algae in low light intensities because they require relatively less energy for their metabolic processes and harvest a different part of the solar spectrum [60,61].

The genus *Aphanothece* dominated the cyanobacterial community in Lake Beauchamp throughout the year, even in the unfavorable winter months. These taxa can survive in winter using mixotrophy and by assimilating organic matter [86]. This strategy allows *Aphanothece* to persist below the photic zone and in light-limited conditions. Moreover, *Aphanothece* is a gram-negative bacterium able to fix atmospheric nitrogen in the water [87]. We observed that dissolved nitrogen concentrations significantly affect the cell counts of *Aphanothece* in Lake Beauchamp.

We found that the total cyanobacteria cell counts were higher in the metalimnion than in the epilimnion and hypolimnion. A similar phenomenon was observed by Halstvedt et al. (2007), as they detected *Planktothrix* throughout the year with the highest concentrations observed during the fall (September–November) and the highest *Planktothrix* biovolume found in the metalimnion. The higher concentrations of *Planktothrix* may result from less grazing because the filamentous *Planktothrix* are difficult for zooplankton to ingest [88]. The dominance of *Planktothrix* in Lake Fortune was influenced by reduced grazing from *Daphnia*. Rohrlack et al. [89] found that many inhibitors of the *Daphnia* digestive enzyme trypsin were produced by *Planktothrix*, causing the probable death of *Daphnia* as a consequence. Moreover, Oberhaus et al. [90] concluded that *Daphnia*-related control of *Planktothrix* blooms is effective only during the early stages of its bloom when the filament lengths of *Planktothrix* are shorter. *Calanoida* abundance has been shown to correlate positively with the *Planktothrix* abundance [91]. Calanoida are known for ingesting large amounts of cyanobacterial cells such as *Planktothrix* [92] and several species are known to stay active during winter [93–96]. However, future study is needed to understand the complex relationship between algal populations and zooplankton population dynamics in these boreal lakes.

6.2. Environmental factors

Planktothrix in Lake Fortune was influenced by TP and DOC concentrations in the water. Phosphorus concentrations directly affect cyanobacterial genera such as *Planktothrix* [38,97,98]. Moreover, Hampel et al. [99] found that *Planktothrix* thrives in low-nitrogen environments, partly explaining this genus's dominance in Lake Fortune. Furthermore, *Planktothrix* can absorb DOC and survive in low light conditions, as observed in Lake Zurich [100]. Similar results were obtained from phytoplankton community studies in Sandusky Bay, where *Planktothrix* thrives in waters due to its ability to tolerate a wide range of temperatures and its adaptability to grow under low light conditions [101]. The shallow depth of Sandusky Bay leads to suspended sediment particles, creating turbidity and low light conditions that promote the growth of *Planktothrix* [99]. The low requirements of *Planktothrix* for irradiance and temperature have been observed in other studies [102,103] Likewise, similar low light conditions occur beneath the ice cover in winter at Lake Fortune. Hence, *Planktothrix* can remain dominant in Lake Fortune throughout the year, including during the winter.

The metalimnetic oxygen maximum is strongly associated with the dominance of *Planktothrix* in the metalimnion of Lake Fortune (Figs. 2 and 3). Metalimnetic oxygen maxima can be observed in many lakes and are linked to the presence of phytoplankton, as indicated by deep chlorophyll maxima [104]. *Planktothrix* populations typically form in the metalimnion because their gas vesicles enable them to adjust their position to optimal growth conditions [105]. Consequently, metalimnetic blooms are usually dominated by the genus *Planktothrix* as seen in the Norwegian lake Steinsfjorden, where both *P. rubescens* and *P. agardhii* have been observed forming metalimnetic blooms in summer [106]. Similar to Lake Fortune, the ability of *Planktothrix* to grow in low irradiance has also been observed during autumn and winter in other lakes, including Lake Zurich, Switzerland [107].

Nutrient concentrations were higher in Lake Fortune than in Lake Beauchamp. Lake Fortune was originally oligotrophic, but its trophic status changed recently to oligo-mesotrophic, as recent surveys found increased phosphorus and chlorophyll-*a* concentrations (unpublished data, Voluntary Lake Monitoring Network). Lake Beauchamp lies on an esker and was also originally oligotrophic. Esker lakes receive few nutrients from the watershed because they are usually not connected to the surface hydrological network [68] but are more often connected to the groundwater system. Eskers also have sandy soils and are found at higher elevations than other surrounding lakes [108]. TP concentrations were highest in July. Warmer waters favour the release of phosphorus from sediments and increase dissolved phosphorus levels in the water column [109]. Human activities, such as increased tourism or recreational activities during summer, sometimes lead to higher nutrient inputs into lakes [110,111]. For example, wastewater treatment plants, septic systems, detergents, fertilizers, decaying plants, and direct sewage discharge release phosphorus-containing compounds and contribute to elevated phosphorus levels in adjacent lakes. Moreover, warmer temperatures usually increase the solubility of inorganic and organic components, which leads to more nutrients entering the water column.

Physicochemical variables such as temperature, pH, conductivity, dissolved oxygen, and nutrient levels vary with the seasonal dynamics of the lakes. Atmospheric weather patterns affect the water temperature and alter the physicochemical parameters throughout the water column [112]. In particular, Lake Fortune showed a wide variation in pH, which can be related directly to the higher cyanobacterial activity during the fall [113]. Similarly, dissolved oxygen concentrations were highest in Lake Fortune during peak cyanobacterial activity. Of concern, Lake Beauchamp experienced hypoxia despite being a lake probably influenced by dissolved oxygen–rich groundwater from the esker sediments; normally, esker lakes show higher oxygen concentrations [68].

6.3. Management

Lake Beauchamp and Lake Fortune are influenced by anthropogenic disturbances throughout the year stemming from permanent houses along the lakes' shores. Faulty septic systems can favour nutrient accumulations in the lake that may trigger HABs in all seasons. The input of excessive nutrients is recognized as one of the primary causes of algal bloom formation in North American lakes [114]. Studies have shown correlations between faulty septic systems and cyanobacterial blooms in many lakes in North America, e.g., Lake Chaplin, USA (Dove & Chapra [115] cited in Lapointe et al., [116]. Although the primary cause of higher nutrients in Lake Fortune and Lake Beauchamp is likely faulty septic systems and anthropogenic pressure, further research must confirm the nutrient sources for both lakes.

Cyanobacterial genera differ in their environmental preferences for rapid development [117]. Therefore, managing cyanobacterial blooms for a given genus requires knowledge specific to the genus undergoing the bloom. Limiting HABs depends on reducing the supply of phosphorus and DOC, and phosphorus is considered to have the strongest influence on growth [38,118,119]. Although the WHO set a health threshold for TP at 20 µg/L [120], *Planktothrix* can thrive at concentrations of 10–15 µg/L [121,122]. For almost the entire year, TP concentrations in Lake Fortune were around or above 20 µg/L, favouring the persistence of *Planktothrix*. Lakes dominated by *Planktothrix* are not safe for recreational activities, such as swimming or fishing, or the drinking of the lake water. Reducing phosphorus inputs is an effective means of reducing the danger from cyanobacterial blooms initiated by *Planktothrix*. On the other hand, Lake Beauchamp, an esker lake possessing unique characteristics and having lower nutrient concentrations, also has issues with cyanobacterial blooms. Similar to Lake Fortune, reducing the nutrient loading of both phosphorus and nitrogen and controlling the early summer eutrophic conditions are essential for limiting cyanobacterial blooms in Lake Beauchamp.

Limiting excessive nutrient input to lakes by controlling the nutrient source can reduce seasonal bloom formation (e.g., Refs. [123, 124]. Nonetheless, knowledge about genera-specific nutrient thresholds is necessary to reduce cyanobacteria blooms initiated by specific taxa [122]. Lakes Fortune and Beauchamp are significant for the region, providing essential cultural, economic, and ecological benefits. Our study reduces the existing knowledge gap, including the winter dynamics of cyanobacterial communities, and provides information for adapted management tools to reduce cyanobacterial blooms. Future sustainable management of lake ecosystems must also consider terrestrial disturbances from both anthropogenic sources, such as harvesting pressure, recreation, and mining extraction [125–127], and natural sources, including fire, beaver activity, and insect outbreaks, which are expected to increase in frequency and severity due to climate change [128–130]. Therefore, it is crucial to develop further research that integrates aquatic and terrestrial ecosystems [131] to better understand these complex ecological interactions and mitigate future impacts.

7. Conclusions

Our research revealed the seasonal dynamics of cyanobacterial blooms in two Canadian boreal lakes. We demonstrated that higher nutrients in both lakes favored the formation of cyanobacterial blooms, however nutrient requirement varies within different species. The genus *Planktothrix* was dominant in Lake Fortune throughout the year, related to relatively higher phosphorus concentrations and due to its ability to absorb dissolved organic carbon in winter. The genus *Aphanothece* dominated the cyanobacterial community in Lake Beauchamp over the year at levels higher than the recommended limit. Limiting nutrient inputs is key to reducing cyanobacterial blooms in both lakes and applies to all boreal lakes. Moreover, understanding the dynamics of winter cyanobacterial blooms provides crucial insights into a more holistic comprehension of bloom patterns, aiding the development of effective strategies for proactively managing and conserving boreal lake ecosystems.

CRediT authorship contribution statement

Guillaume Grosbois: Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Tasnim Anjum Mou:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Miguel Montoro Girona:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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