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DANS LES LACS BORÉAUX DE L'ABITIBI-TÉMISCAMINGUE

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TASNIM ANJUM MOU

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SEASONAL DYNAMICS OF HARMFUL ALGAL BLOOMS IN THE BOREAL
LAKES OF ABITIBI-TEMISCAMINGUE

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TASNIM ANJUM MOU

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FOREWORD

This master's thesis is divided into three chapters. The first chapter includes a general introduction that frames the research problem, presents a literature review, and states the objectives. Chapter II is presented in the form of a scientific article with the authors "Tasnim Anjum Mou, Miguel Montoro Girona, and Guillaume Grosbois." The article will be submitted to the journal *Environmental Research* in December 2023. The third chapter contains the general conclusion, limitations, and implications of this study to improve the health of boreal lakes. The project idea and the experimental design were conceptualized by Prof. Guillaume Grosbois and Prof. Miguel Montoro Girona before the start of my master's project. I was responsible for conducting the field and lab work, analyzing the data, and writing the article. My director and research committee members helped with the interpretation of the results and critically and constructively revised the content of the article. The project and my scholarship were funded by grants from MITACS obtained by Prof. Guillaume Grosbois and Miguel Montoro Girona. The part of the project focused on Lake Fortune was funded by a grant from the Fondation UQAT (FUQAT) obtained by Profs. Guillaume Grosbois and Miguel Montoro Girona. The second part of the project, focused on Lake Beauchamp, was funded through a grant from the Ville d'Amos obtained by Prof. Guillaume Grosbois. The Québec ministère de l'Environnement, de la Lutte contre les changements climatiques, de la Faune et des Parcs covered the laboratory costs for the cyanobacterial cell counts.

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RÉSUMÉ

Les cyanobactéries sont les plus anciens photoautotrophes de la Terre et sont responsables du niveau d'oxygène dont nous disposons actuellement. Cependant, lorsqu'elles prolifèrent et forment une efflorescence, elles provoquent une dégradation écologique et peuvent parfois produire des toxines qui mettent la vie aquatique et terrestre en danger. Ce phénomène est appelé "efflorescences d'algues nuisibles" et est généralement lié à un excès de nutriments dans l'environnement et à des températures élevées de l'eau. Des observations récentes de la présence d'algues nuisibles sous la couche de glace en hiver dans les lacs boréaux contredisent le fait que des températures plus élevées influencent toujours positivement la croissance des algues. La dynamique hivernale des cyanobactéries reste encore mal comprise, même si elle affecte la formation des efflorescences plus tard dans l'année en eau libre. Cette étude vise à mieux comprendre la dynamique saisonnière des proliférations d'algues nuisibles, y compris en hiver, dans les lacs boréaux en identifiant les facteurs moteurs potentiels responsables du développement des cyanobactéries. Notre design expérimental était composé de deux lacs boréaux de l'Abitibi-Témiscamingue (Québec, Canada): le lac Fortune qui présente une croissance inhabituelle de cyanobactéries sous la glace et le lac Beauchamp qui a connu des proliférations récurrentes de cyanobactéries en été seulement. Nous avons identifié la composition de la communauté cyanobactérienne à chaque mois, de juin 2021 à juillet 2022. Les communautés de cyanobactéries étaient dominées par le genre *Planktothrix* dans le lac Fortune dont les concentrations les plus élevées (210 milles cellules/mL) étaient au mois de novembre et les plus basses (28 milles cellules/mL) au mois de mars. Dans le lac Beauchamp, *Aphanothece* a été trouvé tout au long de l'année et était le plus abondant (27.8 milles cellules/mL) en août et le moins abondant (2,1 milles cellules/mL) en mars. Dans l'ensemble, nous avons constaté que la formation et le développement des fleurs d'eau de cyanobactéries étaient en corrélation avec la concentration d'azote et de carbone organique dissous pendant l'été et l'automne dans le lac Beauchamp et avec la disponibilité du phosphore, de l'azote dissous et du carbone organique dissous dans le lac Fortune tout au long de l'année. Le phosphore et le carbone organique dissous ont influencé de façon significative la formation de fleurs d'eau de cyanobactéries du genre *Planktothrix* dans le lac Fortune tout au long de l'année, y compris pendant les mois d'hiver sous la glace. Cette étude a étudié la dynamique saisonnière de proliférations d'algues nuisibles et les facteurs qui l'influencent. Elle émet des suggestions pour utiliser ces nouvelles connaissances dans une gestion des facteurs environnementaux qui peuvent contrôler l'occurrence des proliférations d'algues nuisibles.

ABSTRACT

Cyanobacteria, the oldest photosynthetic organisms on Earth, play a crucial role in producing the oxygen we breathe. However, when they grow excessively and form blooms, they can harm ecosystems and produce toxins that pose environmental risks. These blooms, known as harmful algal blooms (HABs), are typically associated with excess nutrients in the environment and high-water temperatures. Recent observations have challenged the notion algal growth require elevated temperature, as., HABs have been observed under ice covered of boreal lakes. Despite the influence of winter on bloom formation, our understanding of the winter dynamics of cyanobacterial community composition, nutrient and organic carbon concentrations, and environmental and climatic variables monthly from June 2021 to July 2022. In Lake Fortune, the dominant cyanobacteria study aimed to improve our understanding of the seasonal dynamics of HABs in boreal lakes, including lakes in during the winter. It focuses on two Abitibi-Témiscamingue, Quebec, Canada: Lake Fortune, which exhibits unusual cyanobacterial growth under the ice, and Lake Beauchamp, known for recurrent summer-only cyanobacterial blooms. We monitored cyanobacterial genus was *Planktothrix*, with its highest cell density in November (210 000 cells/mL) and its lowest density in March (28 000 cells/mL). In Lake Beauchamp, the dominant genus was *Aphanothece*, with the highest cell density observed in August (27 800 cells/mL) and the lowest in March (2 100 cells/mL). The study found that cyanobacterial bloom formation and development in Lake Beauchamp were strongly correlated with nitrogen and dissolved organic carbon concentrations during summer and fall. In Lake Fortune, nutrient availability—dissolved nitrogen and remains limited. This phosphorus concentrations—played a significant role throughout the year, even under ice cover. Specifically, phosphorus and dissolved organic carbon influenced the formation of cyanobacterial blooms, dominated by *Planktothrix*. Lake Fortune had a lower threshold

for total phosphorus, allowing *Planktothrix* to dominate year-round, even under the ice. This study investigated the seasonal dynamics of HABs and the factors that influence them. It makes suggestions for using this new knowledge for mitigating the occurrence of HABs.

Keywords: Algae, Cyanobacterial bloom, Climate change, Lake ecology, Public health, Seasonality, Water quality, Winter ecology.

CHAPTER 1

GENERAL INTRODUCTION

1.1 Research Context

Cyanobacteria are prokaryotic, phototrophic microorganisms, previously referred to as blue-green algae (Wejnerowski et al., 2018). Under particular conditions, cyanobacteria cells may proliferate, accumulate intensively, and form a bloom (Chorus & Bartram, 1999; Falconer & Humpage, 2005). Such cyanobacterial blooms are defined as harmful algal blooms (HABs) when they produce toxins and cyanobacterial abundance exceeds a predetermined threshold (for example, in Canada, this limit is above 50 000 cells/mL), threatening public health, fishing activities, aquaculture, and tourism (Ho & Michalak, 2015). HABs and the related toxicity in freshwater lakes are becoming global concerns by threatening public health and multiple aquatic environments (Huisman et al., 2018). According to the global HAB database, there were 519 reported cases of HABs around the world in 2019 (Enevoldsen, 2019). For example, studies from Lake Taihu in China (Chen et al., 2010), Lake Erie in North America (Michalak et al., 2013), and Lake Nieuwe Meer in The Netherlands (Jöhnk et al., 2008) highlight a concerning trend in global freshwater ecosystems (Huisman et al., 2018). The fishing and tourism industries have experienced considerable financial losses because of HABs, such as in fish farms where mass fish mortality caused by toxic blooms has caused losses as high as US \$24 million (Anderson et al., 2000). In

Canada, the commercial fishing industry in Lake Erie faces a loss of CDN \$93 million over 30 years because of HABs (Smith et al., 2019). Blooms can cause discoloration and foul odors in affected waterbodies, making them unattractive and sometimes dangerous for swimming, boating, and other recreational activities (Bechard, 2019).

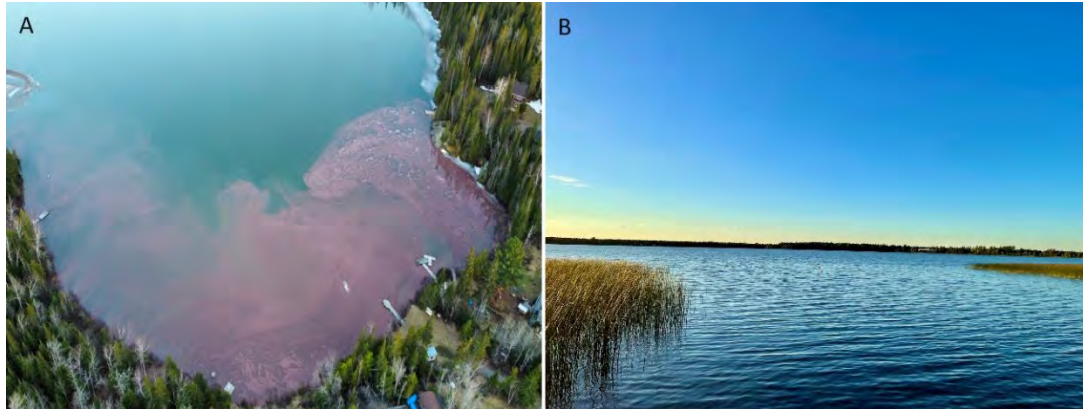


Figure 1.1 Cyanobacterial bloom in (A) Lake Fortune on May 11, 2022, and a photo of (B) Lake Beauchamp, taken July 3, 2019 (Image credits: A) Cédric Laplante, Radio-Canada, B) Le Citoyen).

However, as primary producers, cyanobacteria also play a vital role in maintaining the ecological balance in freshwater environments (Bownik et al., 2012). About 2600 species of cyanobacteria have been identified, although most remain to be found and identified, as they are microscopic and occur in a wide range of habitats (Tokodi et al., 2018). Among all existing microscopic organisms, cyanobacteria are considered a particularly crucial group because they were the first organisms to convert carbon dioxide to oxygen via photosynthesis at the beginning of the Earth's life history, and because they started maintaining nitrogen cycles (Bownik et al., 2012). Although cyanobacteria are a phylum of gram-negative bacteria, they contain chlorophyll-a, a green photosynthetic pigment that allows them to assimilate atmospheric carbon dioxide into biomass via photosynthesis. Because of this particularity, they are commonly found in aquatic ecosystems (Percival et al., 2013). Around 20% to 30% of global photosynthesis occurs through cyanobacteria, which makes them an essential

element for maintaining the global atmospheric equilibrium and for the survival of humans and wildlife (Tokodi et al., 2018).

Cyanobacterial blooms may cause toxicity in lakes, ponds, and rivers and be responsible for poisoning aquatic and human life. Toxin release from cyanobacteria may reflect a defense mechanism against grazers (Fiałkowska & Pajdak-Stós, 2014). For example, cyanobacteria defend themselves from the feeding pressure of *Daphnia magna* and *Moina macrocopa* by increasing their production of cyanotoxins (Jang et al., 2007; Sabart et al., 2010; Westrick et al., 2010). The specific cyanotoxin produced varies among cyanobacteria taxa (Table 1.1). Many cyanobacteria can produce intracellular cyanotoxins that harm the human body (Carmichael & Boyer, 2016; Chorus, Ingrid & Bartram, 1999; Otten & Paerl, 2015). For humans, the main source of toxicity from cyanobacterial blooms involves consuming contaminated food and drinking water or swimming in waters contaminated by HABs (Paerl, 2008). The health effects from HABs on humans are very diverse and include gastroenteritis, nausea, vomiting, fever, flu-like symptoms, sore throat, blistered mouth, ear and eye irritation, rashes, myalgia, abdominal pains, pulmonary consolidation, visual disturbances, and kidney and liver damage (Codd et al., 2005).

Table 1.1 Canadian surface waters having experienced harmful algal blooms (HABs), including the identified cyanobacteria species and the observed maximum concentrations.

| Site | Species | Maximum Concentration | Reference |
|--|--|---|--|
| Several freshwater lakes across Canada | <i>Microcystis</i> | 2153 µg/L | Orihel et al., 2012 |
| Freshwater lakes in Québec | <i>Dolichospermum</i> spp., <i>Anabaena</i> spp., <i>Aphanizomenon</i> spp., <i>Microcystis</i> spp., and <i>Worochinia</i> spp. | Mostly from 100–1000 µg/L | MDDEFP, 2014 |
| Missisquoi Bay, Québec | <i>Dolichospermum flosaquae</i> , <i>Gloeotrichia echinulata</i> and <i>Microcystis</i> spp. | | Blais, 2008, 2014, 2019 ; Bowling et al., 2015 ; Fortin et al., 2010 |
| The lower Great Lakes, Ontario | <i>Microcystis</i> | >200 µg/L | Carmichael & Boyer, 2016 |
| Lake Erie, Ontario | <i>Microcystis</i> and <i>Planktothrix</i> | 0.13–3.2 µg/L and 0.04–1.64 µg/L for <i>Microcystis</i> species and 0–0.14 µg/L for <i>Planktothrix</i> species | Dyble et al., 2008 |
| Lake of the Woods, Ontario/Manitoba | <i>Aphanizomenon flos-aquae</i> and <i>Dolicospermum</i> spp. (<i>Anabaena</i> spp.) | | Chen et al., 2007 |
| Freshwater lakes, Alberta | <i>Microcystis</i> | >200 000 cells/mL | Kotak et al., 1996 |

1.2 Problem Statement

Eutrophication from human activities and climate change have favored rapid cyanobacterial growth, leading to more frequent HAB events that liberate cyanotoxins (Li, 2020). Toxins released by cyanobacteria may persist both inside the cell and in aquatic ecosystems (Oudejans et al., 2015). The World Health Organization (WHO)

established a standard for the toxicity (20 000 cells/mL) of cyanobacterial blooms (World Health Organization, 2003). Microcystins are a group of hepatotoxins produced by various species of cyanobacteria. These hepatotoxins are highly toxic and harm aquatic organisms (Butler et al., 2009). Microcystins are widely distributed and can also harm human life in cases of long-term exposure, and the ingestion of water having a high level of microcystin can cause liver damage and liver cancer (Boyer, 2007; Williams et al., 2007; Winter et al., 2011). The WHO has implemented water quality guidelines for microcystin concentrations to protect human and animal health (0.3–1.6 µg/L for drinking water and ≤20 µg/L for recreational purposes; D'Anglada and Strong, 2015; Health Canada, 2019). According to Health Canada (2020), water containing more than 50 000 cells of cyanobacteria/mL is considered harmful for recreational activities such as swimming (Health Canada, 2020). Microcystins have been discovered in 246 waterbodies in Canada, a country with the world's largest number of freshwater waterbodies (Orihel et al., 2012). In Quebec, 51 lakes have been affected by cyanobacterial blooms, caused by 23 species of cyanobacteria (Orihel et al., 2012). Researchers found 14 variants of cyanotoxins in Missisquoi Bay, southern Quebec (Blais, 2008, 2014, 2019; Fortin et al., 2010; Bowling, Blais and Sinotte, 2015).

Like many other cyanobacteria, *Planktothrix* spp. tend to thrive in warm waters (Komárek & Komárková, 2004). During the summer, thermal stratification, abundant light energy, and higher nutrient concentrations create favourable conditions for the rapid growth and multiplication of *Planktothrix* spp. (Churro et al., 2017; Mankiewicz-Boczek et al., 2011). Recent observations in Lake Fortune (Quebec) found an unusual occurrence of *Planktothrix* under the ice cover in waters at 4 °C (Luneau, 2022). This observation contradicts the paradigm of cyanobacterial growth being enhanced through warm waters, e.g., (Chu et al., 2007; Jacquet et al., 2005) and Suda et al. (2002) stating that the optimal water temperature for cyanobacterial blooms is 15 to 30 °C. Although Luneau (2022) found that *Planktothrix* spp. can grow in low-light situations, the factors responsible for its presence under a thick ice cover in winter remain unknown (Mur,

Gons and van Liere, 1978; van Liere et al., 1979). Lake Beauchamp, also found in the Abitibi region, is situated along an esker fed by groundwater. This lake is poor in nutrients, as are most esker lakes in the region (Hasan et al. 2023). However, Lake Beauchamp has experienced summer cyanobacterial blooms during the last few years. In both lakes, the role of seasonality on bloom formation, especially under the winter ice cover, remains elusive. In this study, we aim to better understand the seasonal dynamics of cyanobacterial blooms in lakes of the Abitibi region of Quebec and identify their driving mechanisms.

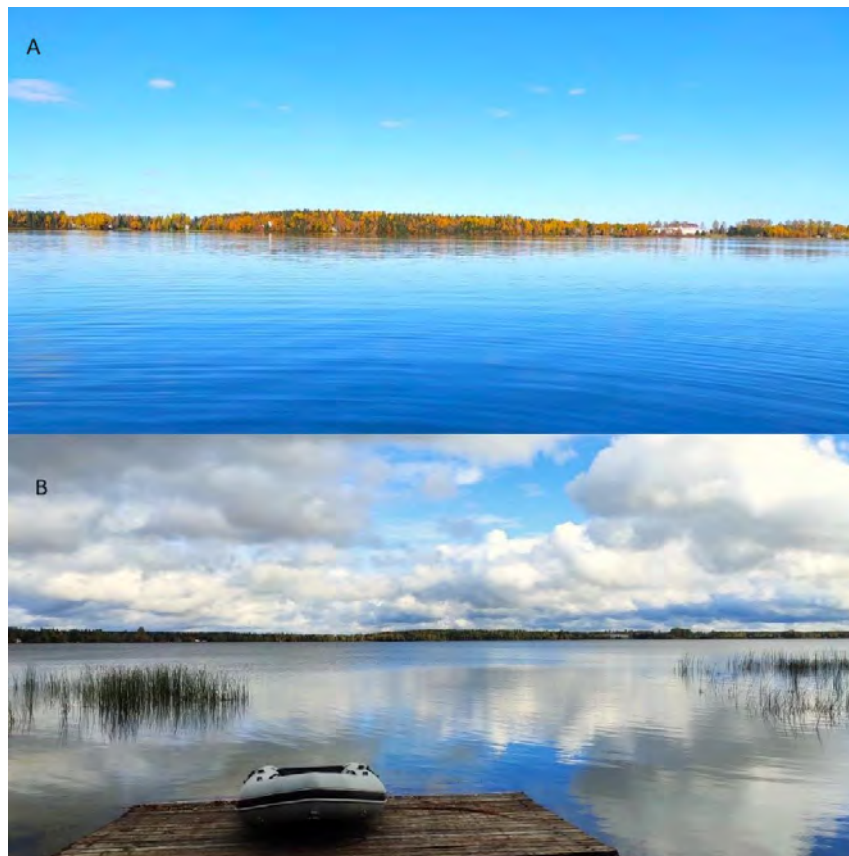


Figure 1.2 (top) Lake Fortune pictured from Rouyn-Noranda, Québec, a view of the Northern shore and (bottom) Lake Beauchamp as pictured from Amos, Québec. A view from the southern shore. Photo credits: Tasnim Anjum Mou, 2021.

1.3 State of Knowledge

1.3.1 Cyanobacteria: morphology, ecological function, and characteristics

Cyanobacteria are unicellular or colonial species that may form filaments, sheets, or hollow spheres. Their cell size ranges from 0.5 μm to 50–100 μm (Whitton, 2001), although filamentous cyanobacteria vary greatly in terms of cell size and shape (Chorus, Ingrid & Bartram, 1999; Falconer and Humpage, 2005). Cyanobacteria may grow in several forms, including spherical, bacillus, and fusiform, and even show pleomorphism (Herrero et al., 2004; Rippka et al., 1979). Many cyanobacterial species contain specialized cells called heterocysts that become functional when nitrogen is limiting from the environment (Kumar et al., 2010). A heterocyst is a differentiated cell, usually larger than vegetative cells, and either yellow or colourless, and its poles are adjacent to vegetative cells (Luz, 2018). Cyanobacteria also have another external layer called a mucilaginous sheath, a layer that protects cells from the damage caused by ultraviolet radiation (UV) (Gaysina et al., 2018). Cyanobacteria that grow and develop on the bottom of a waterbody are benthic cyanobacteria (Health Canada, 2020). Benthic cyanobacteria include genera such as *Oscillatoria*, *Phormidium*, and *Lyngbya*, which can produce toxins but are less hazardous for human health because of the more limited contact with humans given their benthic habitat preference (Lajeunesse et al., 2012; Quiblier et al., 2013; Vis et al., 2008).

1.3.2 Cyanobacterial blooms

Cyanobacteria can be found in all types of water and produce scum that floats on the water surface, causing a visible blue and green colouration of water and a rotten plant–

like odour (Huisman et al., 2018). According to Fallon and Brock (1979), when cyanobacterial cell lysis occurs, a blue opalescent sheen forms on the water's surface and results in the release of phycocyanin pigments, which are responsible for the blue colouring, whereas the green colour indicates chlorophyll persistency. Genera responsible for HABs include *Aphanizomenon*, *Planktothrix*, *Cylindrospermopsis*, *Dolichospermum*, *Microcystis*, *Nodularia*, and *Trichodesmium* (Huisman et al., 2018).

Cyanobacterial blooms are of great and increasing concern worldwide as atmospheric and water temperatures increase (Seneviratne et al., 2012). In Canada, cyanobacterial blooms are usually observed in late summer and autumn; however, recent studies have observed cyanobacterial growth in winter (Lavoie et al., 2007; Wejnerowski et al., 2018). In summer, Canadian lakes provide a favourable environment, including heat and nutrients essential for the growth and development of typical toxic and non-toxic cyanobacterial species. Remote sensing has revealed that cyanobacterial blooms are directly related to high temperatures and nutrient enrichment (Shi et al., 2017).

1.3.3 Toxins from cyanobacteria

Cyanotoxins, such as microcystins, nodularins, anatoxins, cylindrospermopsins, and saxitoxins are the most common toxins found in cyanobacteria (Singh, 2013). Although microcystins are relatively well studied, there is an incredible array of cyanotoxins; most have received very little attention and have unknown ecotoxicological risks (Janssen, 2019). Toxicity from algal blooms has been detected in many countries, including Canada. For example, in surveys between 2001 and 2011, several freshwater lakes across Canada had microcystin concentrations reaching a maximum of approximately 2150 µg/L (Orihel et al., 2012). In Quebec, surveys between 2007 and 2012 noted the presence of common cyanobacterial genera, including *Dolichospermum*

spp., *Anabaena* spp., *Aphanizomenon* spp., *Microcystis* spp., and *Worochinias* spp. (MDDEFP, 2014). Moreover, several toxin-producing cyanobacteria, such as *Dolichospermum flos-aquae*, *Gloeotrichia echinulata*, and *Microcystis* spp. have been detected in Missisquoi Bay, Quebec every year (Blais, 2008, 2014, 2019; Bowling et al., 2015). *Microcystis* spp. and *Planktothrix* spp. also appear throughout the year in Lake Erie, Ontario (Dyble et al., 2008). In Luanda and Mussulo bays from Angola, the poisoning of humans has been linked to the ingestion of shellfish contaminated by cyanotoxins (Vale et al., 2009). In Ohio, the drinking water supply was suspended for three days because of a bloom of *Microcystis aeruginosa* that covered the western basin of Lake Erie (US EPA, 2010). The specific cyanobacteria taxa undergoing blooms may vary, as observed in 12 lakes in South Korea that experienced hepatotoxic microcystins and neurotoxic anatoxin-a between 1992 and 1995 (Park et al., 1998). The pervasive presence of diverse cyanotoxins, coupled with the insufficient attention given to their ecotoxicological risks, highlights the urgent need for comprehensive research and effective management strategies to mitigate the potential health and environmental impacts of these toxins.

1.3.4 Impact of cyanobacteria on public health and ecosystems

Toxins synthesized by cyanobacteria are responsible for harming animal life and humans (Chorus, Ingrid & Bartram, 1999). Ingestion of water contaminated by cyanobacteria can cause gastrointestinal symptoms such as nausea, vomiting, diarrhea, and abdominal pain (Bell & Codd, 1994). Direct contact can also lead to skin irritation, rash, itching, and redness (Stewart et al., 2006). HABs liberating cyanotoxins also produce toxicity within the food web and bioaccumulate (Ibelings et al., 2005). They adversely affect the aquatic environment by deteriorating water quality and depleting oxygen (Wejnerowski et al., 2018). Thus, fewer resources are available for fish and

other aquatic life, and visibility in the water column is reduced. Consequently, aquatic life, including fish and crustaceans, must leave these less-oxygenated areas or die (Bartram, 1999; Duval et al., 2005; Rabalais et al., 2010).

1.3.5 The case of *Planktothrix*

Globally, there are over 2600 identified cyanobacterial species; however, this number is a small fraction of the actual number, which is estimated to be about 50 million species (Nabout et al., 2013). One of the most significant bloom-forming and harmful cyanobacteria is the genus *Planktothrix* (Olmsted et al., 2015; J. G. Winter et al., 2011). *Planktothrix* spp. are filamentous cyanobacteria produced from the binary division of cells in a single plane that form unbranched structures and have an average length of 4 µm. Their cells are usually cylindrical, with straight or slightly curved trichomes that can be attached or detached at the cross wall, oriented perpendicular to the long axis (Kurmayer et al., 2016). Their filaments may contain hundred to thousands of cells, and their length varies among species of the genus (Kurmayer et al., 2016). *Planktothrix* is a diverse genus and one of the most important in northern countries. *Planktothrix* spp. typically dominate cyanobacteria communities in the subalpine lakes of Europe, e.g., lakes Zurich and Lucern in Switzerland (Thomas & Marki, 1949), Lake Mondsee (Dokulil & Jagsch, 1992) in Austria, and lakes du Bourget (Jacquet et al., 2005) and Nantua (Feuillade, 1994) in France.

This genus can adapt and maintain its life cycle in low temperatures and at low irradiance (Feuillade et al., 1992; Van Liere & Mur, 1979). Species of this genus have a higher rate of growth than other algae at low light intensities, as they require less energy for their metabolic processes (Mur et al., 1978; van Liere et al., 1979). *Planktothrix* spp. can also produce toxins at higher concentrations than other

cyanobacteria (Hossain et al., 2012). Moreover, *Planktothrix* can be toxic to domestic animals or livestock if contaminated water having toxin concentrations exceeding 20 µg/L is consumed (Landsberg, 2002). The growth rate of *Planktothrix* is reduced for temperatures below 30 °C (Suda et al., 2002). Distinct temperature tolerances (from 10 to 35 °C) have been recorded among the different species of *Planktothrix* (Suda et al., 2002). For example, in Canada, *Planktothrix agardhii* occurs in many lakes and is found at its highest concentrations in autumn when average temperature stays between 10 to 20 °C (Chu et al., 2007).

1.3.6 Factors affecting cyanobacterial blooms

Human activities increase eutrophication, particularly through agricultural practices and fertilizer use, which are important sources of nutrients to aquatic environments (Carpenter et al., 1998; Geng et al., 2016). Nutrient inputs into lakes have significantly increased because of anthropological activities, such as agriculture, industry, and sewage disposal (Schindler, 1974). Cyanobacterial growth and bloom development is influenced by several abiotic factors, including nutrient input (e.g., nitrogen, phosphorus), light availability for photosynthesis, temperature, water movement, pH shifts, and trace metal concentrations (Mur et al., 1999). Cyanobacterial blooms are more common in eutrophic lakes because of nutrient enrichment, as cyanobacteria require high concentrations of nitrogen and phosphorus for their growth and development (Mur, Skulberg and Utkilen, 1999). Eutrophication, rising atmospheric levels of carbon dioxide, and global warming are provoking an increased number of cyanobacterial blooms in aquatic ecosystems around the world (Huisman et al., 2018; Park et al., 1998; Seneviratne et al., 2012). In North America and Europe, cyanobacterial blooms have increased noticeably in almost 60% of the lakes affected by HABs; these events are related to anthropogenic activities, and cyanobacterial

blooms have expanded disproportionately relative to other algal species. Nutrient inputs must therefore be minimized to control these blooms (Stroom & Kardinaal, 2016; Taranu et al., 2015).

Temperature is an important factor affecting the growth and development of cyanobacteria. The optimal in vitro temperature for cyanobacterial growth is around 20 °C with a maximum of 35 °C (Waterbury, 2006). Climate change is raising global and regional temperatures that will lead to an additional 1.5–5.8 °C of warming by the end of the century (Bernstein et al., 2007). Warmer temperatures from climate change could induce earlier lake water stratification in the spring and extend this stratification longer into the fall which facilitate cyanobacterial growth. Therefore, as global temperatures rise, more freshwater ecosystems are expected to be affected by toxic blooms by the end of this century.

Light is another important factor controlling cyanobacteria blooms because light is the primary source for energy through photosynthesis. However, when large concentrations of cyanobacteria occur in lakes and form a sheet at the water surface, light is blocked from passing into the water column, preventing primary producers in the water column from producing oxygen and thus reducing oxygen levels in the water (Chorus & Bartram, 1999). As a result, water quality and the overall environment in the lake are degraded. Cyanobacterial blooms usually absorb light through their photosynthetic and photoprotective pigments (Kahru et al., 1993; Paerl & Paul, 2012).

Phosphorus is an essential nutrient because it is a component of DNA (deoxyribonucleic acid), RNA (ribonucleic acid), ATP (adenosine triphosphate), and the phospholipids of cell membranes (Heaney & Graeff-Armas, 2018). Among the forms of phosphorus are organophosphate and dissolved inorganic phosphate, which are taken rapidly by all microalgae in a lake (EPA, 2002). Total phosphorus concentrations between 20 and 30 µg/L indicate excessive nutrient levels favourable for cyanobacterial blooms (Downing et al. 2001a). Phosphorus is directly linked to the

growth and development of cyanobacteria (Kramer et al., 2022). Total phosphorus concentrations under 20 $\mu\text{g/L}$ indicate a low probability of a cyanobacterial bloom in a lake (Carvalho, McDonald et al., 2013). Phosphorus loading increases in the summer, which strongly heightens the density of cyanobacteria (Nürnberg et al., 2012; Steinman et al., 2009). Sherman et al. (2000) reported a strong relationship between phosphorus concentrations in the hypolimnion in Australian lakes and the presence of cyanobacteria, indicating a strong dependency on internal phosphorus loading for cyanobacterial growth (Downing et al., 2001a; Ferrão-Filho et al., 2000; Fogg, 1969). HABs in Lake Erie have been linked to external phosphorus loading into the lake (Schindler et al., 2016).

Atmospheric nitrogen is also crucial, as it is absorbed by cyanobacteria and other microorganisms (Herrero et al., 2001). Simple organic compounds such as urea, amino acids, and some inorganic ions like nitrate or ammonium can be a nitrogen source in freshwater lakes (Herrero et al., 2001). Moreover, nitrogen is responsible for initiating toxicity from cyanobacterial blooms (Gobler et al., 2016). For example, non-diazotrophic cyanobacteria such as *Microcystis* cannot fix nitrogen; they produce toxins during blooms and are highly influenced by atmospheric nitrogen availability. In their review, Gilbert et al. (2016) reviewed multiple papers to show a direct correlation between nitrogen availability and the release of toxins. Some factors influence nitrogen input into lakes, such as animal waste, interspecific competition, and the sedimentation of phosphorus in lakes that contribute to nitrogen degradation by denitrification. Community competition increases nutrient demand and higher decomposition rates in lakes, resulting in more nitrogen accumulation. Ammonia is the preferred nitrogen source for many cyanobacteria, e.g., *Synechococcus elongates*, and ammonia uptake and retention processes play a vital role in the nitrogen metabolism of microorganisms (Ritchie, 2013).

Trace metals also affect cyanobacterial growth and bloom formation. Iron is crucial for cyanobacteria, as it directly influences chlorophyll-a synthesis, nitrogen fixation, and

photosynthesis (Alexova et al., 2011; Li et al., 2009). Excessive iron reduction diminishes the capacity of phycobilisomes to use the available energy from light (Alexova et al., 2011). The occurrence of cyanobacteria occasionally depends on the availability of iron, dominating over eukaryotic species such as N₂-fixing species (Davis et al., 2003; Molot et al., 2010, 2014; Sterner et al., 2004). Zinc plays a key role for various cyanobacteria and is associated with several physiological processes involved in cyanobacterial growth (Baptista & Vasconcelos, 2006; Downs et al., 2008). Zinc is a co-factor of many proteins, interferes with carbon dioxide transfer, and helps the enzyme carbonic anhydrase and alkaline phosphatase (Baptista & Vasconcelos, 2006; Sunda, 2006). Cobalt acts as a contributing factor for marine cyanobacterial distribution (Huertas et al., 2014). However, the role of cobalt in influencing cyanobacteria in freshwater ecosystems is not well studied (Facey et al., 2019). Manganese is not considered a limiting factor of cyanobacterial production because of its higher availability. However, changes in manganese concentrations can interfere with cyanobacteria's photosynthesis, such as observed for *Synechocystis* spp. (Kraemer et al., 2015; Salomon & Keren, 2011). Copper is used as an algacide to control cyanobacterial blooms because it kills cyanobacteria by decreasing their growth by creating a hyperoxidative state and chlorosis (Bishop et al., 2015; Pinto et al., 2003). Finally, lower molybdenum concentrations often decrease the efficacy of heterocystous cyanobacterial nitrogen fixation (ter Steeg et al., 1986; Zerkle et al., 2006).

There is considerable debate over how much zooplankton affect cyanobacterial growth (Gosselain et al., 1998; Sellner et al., 1993; Ventelä et al., 2002). Chow-Fraser et al. (1994) suggest that grazers, which are organisms that feed on cyanobacteria, may play a more significant role in the formation of blooms in oligotrophic lakes (nutrient-poor lakes) than in eutrophic lakes (nutrient-rich lakes). In oligotrophic lakes, where nutrients are limited, grazers may have a lower abundance and thus effect, allowing cyanobacterial populations to grow and potentially form blooms. In eutrophic lakes, on the other hand, high nutrient levels can support a diverse community of grazers that

consume the cyanobacteria and help regulate their populations, reducing the likelihood of blooms.

Cyanobacteria comprise a wide variety of species (distributed among 150 genera); however, most studies related to cyanobacterial blooms have focused on the genus *Microcystis* (Facey et al., 2019; Wilhelm, 2009). Therefore, other genera must be included in future studies to study cyanobacteria at the community level. Similarly, dissolved phosphorus, nitrogen, organic carbon, temperature, and trace metals can influence cyanobacterial blooms, although not all of these factors have received the same attention. This knowledge gap is even more significant in the context of climate change, where understanding the impact of disturbances on ecosystems will be essential (Aakala et al., 2023; Hof et al., 2021; Montoro Girona et al., 2023). Driving factors associated with winter cyanobacterial communities under the ice are also poorly studied. Therefore, it is essential to study cyanobacterial communities under the winter ice cover and the driving factors of their abundance in unfavourable conditions to properly understand the seasonal dynamics of HABs.

1.4 Objectives and Hypotheses

The main objective of this master's thesis is to describe the seasonal dynamics of cyanobacterial blooms in two boreal lakes and identify their driving factors. Our specific objectives are:

1. Characterize the cyanobacterial community abundance and composition in two boreal lakes over a year, including under lake ice in winter.
2. Determine the environmental factors influencing cyanobacterial abundance in these boreal lakes.

From these objectives, I hypothesize that:

1. The abundance of cyanobacterial species will vary over different months of the year but will experience a maximum in the summer and fall (Pick, 2016). At least one genus of cyanobacteria in each lake will be detected at bloom levels throughout the year, including under the ice in winter (Lavoie et al., 2007),
2. Higher nutrient availability (phosphorus and nitrogen), not water temperature, triggers cyanobacterial blooms in both lakes, as cyanobacteria can be observed in low temperatures and under low light conditions (Jöhnk et al., 2008).

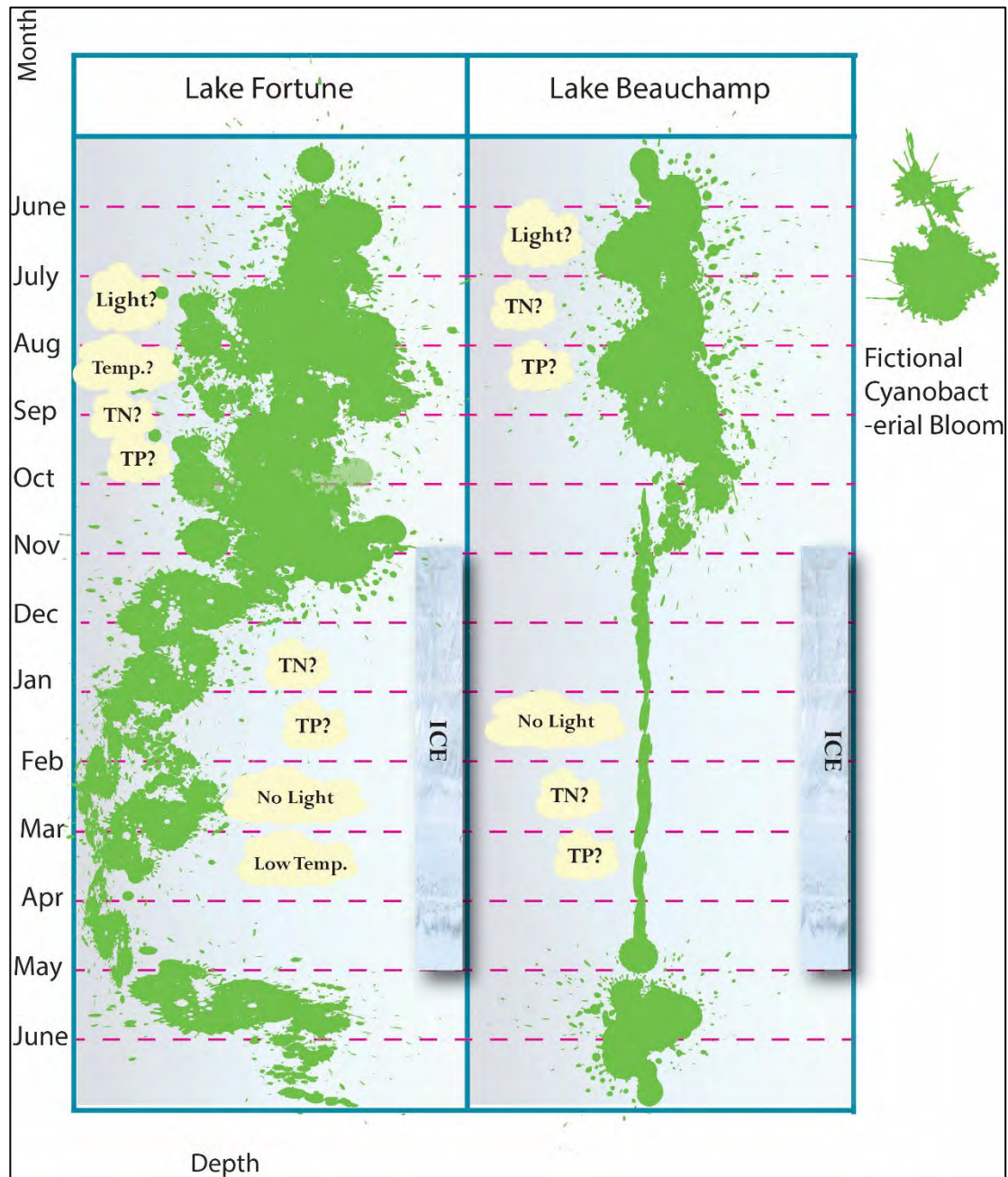


Figure 1.3 Conceptual framework representing cyanobacterial blooms over the year in both study lakes with the key controlling environmental and physicochemical variables (TN = Total Nitrogen, TP = Total Phosphorus and Temp = Temperature). (Credit: Tasnim Anjum Mou, Guillaume Grosbois, and Miguel Montoro Girona).

CHAPTER 2

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

Tasnim Anjum Mou^{1,2}, Guillaume Grosbois^{1,2*} and Miguel Montoro Girona^{1,3},

1. Groupe de recherche en écologie de la MRC Abitibi (GREMA), Université du Québec en Abitibi-Témiscamingue, 341 Rue Principale N, Amos, QC, J9T 2L8 Canada

2. Group for Interuniversity Research in Limnology and Aquatic Environments (GRIL), Université de Montréal, Montréal, QC, H3C 3J7 Canada

3. Grupo de Análisis y Planificación del Medio Natural, Universidad de Huelva, Huelva, Spain

*Correspondance: Guillaume.Grosbois@uqat.ca

Abstract

Lake cyanobacteria can overgrow and form blooms, often releasing life-threatening toxins and causing ecological degradation. These harmful algal blooms (HABs) are usually linked to excess nutrients and high-water temperatures. Recent observations of harmful algae under ice cover in winter in boreal lakes contradict this idea. This study investigates the seasonal dynamics of HABs in boreal lakes and identifies the driving factors responsible for cyanobacterial development. We study cyanobacteria assemblages in two boreal lakes in Abitibi-Témiscamingue (Quebec, Canada): Lake Fortune, which has unusual under-ice cyanobacterial growth, and Lake Beauchamp, which has experienced recurrent summer-only cyanobacterial blooms. Between June 2021 and July 2022, we identified monthly the lakes' cyanobacterial community and recorded nutrients (total phosphorus, total dissolved phosphorus, total nitrogen, and total dissolved nitrogen), organic carbon concentrations, water temperature, dissolved 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 nitrogen concentrations throughout the year, while phosphorus and organic carbon also influenced blooms. *Planktothrix* dominated even under ice cover, because it can also thrive in low-light conditions and lower concentrations of total phosphorus. 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 bloom formation and development correlated with total dissolved phosphorus and nitrogen and dissolved organic carbon concentrations during summer and fall. The dominance of *Aphanothece* was particularly marked 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 Abitibi-Témiscamingue.

Keywords: Boreal lakes; Harmful algal blooms; Ice cover; Phosphorus; *Planktothrix*; Winter bloom.

2.1 Introduction

Freshwater ecosystems have played a significant role in the growth of human civilizations (Wantzen et al., 2016). 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 (Orihel et al., 2012). Moreover, our understanding of HABs and their seasonal dynamics in Canadian boreal lakes is underexplored. 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% to 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 (Tokodi et al., 2018). However, the rapid growth of cyanobacteria can become 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 (Wejnerowski et al., 2018; Moreira et al., 2022). Some cyanobacterial species can produce secondary metabolites with toxic properties; these products include hepatotoxins, neurotoxins, and dermatotoxins, collectively called cyanotoxins (Bláha et al., 2009). Many cyanobacteria produce intracellular cyanotoxins that harm humans (Carmichael & Boyer, 2016; Chorus, Ingrid & Bartram, 1999; Otten & Paerl, 2015). Across the globe, cyanobacteria have been responsible for an increasing number of HABs that liberate cyanotoxins (Li, 2020). Among all cyanotoxins, microcystin is widely distributed (found on all continents except Antarctica) and potentially harmful

to humans and animals (Boyer, 2007; Williams et al., 2007; Winter et al., 2011). The primary source of poisoning from cyanobacterial blooms for humans includes swimming in HAB-contaminated water and consuming HAB-contaminated food and drinking water (Paerl, 2008). According to Health Canada, if 1 mL of lake water contains more than 5000 cells of *Microcystis* and chlorophyll-a is over 33 µg/L, microcystin is potentially present (Health Canada, 2020). Toxins produced by cyanobacteria stem from a defence against grazers (Fiałkowska & Pajdak-Stós, 2014); for example, cyanobacteria increase their toxin production to defend against *Daphnia magna* and *Moina macrocopa* (Jang et al., 2007; Sabart et al., 2010; Westrick et al., 2010). In Quebec, 51 lakes have been contaminated by cyanobacterial blooms caused by 23 species of cyanobacteria (Orihel et al., 2012). In Missisquoi Bay, Québec, 14 different variants of cyanotoxins have been documented (Blais, 2008, 2014, 2019; Bowling et al., 2015; Fortin et al., 2010). These variants differ in their nutritional and environmental requirements; therefore, it is crucial to learn about each to improve HAB management plans (Health Canada, 2019).

Cyanobacterial growth and bloom development are influenced 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 (Health Canada, 2019). 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 (Mur et al., 1999). Increased eutrophication also promotes the alkalization of lakes, which alters lake pH dynamics across different seasons. In general, pH seasonal dynamics are characterised by increased alkalinity during spring and early summer due to algal 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 (Kaushal et al., 2017; Raven et al., 2020; Verspagen et al., 2014).

Phosphorus enrichment results the eutrophication of freshwater ecosystems and promotes toxic cyanobacterial blooms (Glibert et al., 2002; Johnson & Chase, 2004; Liu et al., 2009; Perkins & Underwood, 2002; Smith et al., 2006; Vadeboncoeur et al., 2003; Zhang et al., 2008). The Downing et al. (2001) 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 (Pick, 2016). 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 (Heaney & Graeff-Armas, 2018).

Atmospheric nitrogen is also crucial because it is absorbed by cyanobacteria and other microorganisms (Herrero et al., 2001). 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 (Chaffin et al., 2013; Davis et al., 2015; Gobler et al., 2007; Xu et al., 2010). Glibert et al. (2016) found a positive correlation between nitrogen availability and toxin liberation.

Temperature is one of the most critical factor for the growth and development of development of cyanobacterial blooms because cyanobacteria are well-adapted to warmer conditions in aquatic ecosystems (Jöhnk et al., 2008; Kosten et al., 2012; Paul, 2008). The favourable in vitro temperature for cyanobacterial growth is around 20 °C with a maximum of 35 °C (Waterbury, 2006). Global temperatures are expected to increase an additional 1.5 ° to 5.8 °C by the end of this century (Bernstein et al., 2007). Therefore, the intensity of HABs may increase in the future because of climate change

and eutrophication (Jensen, Lomstein and Sørensen, 1990; De Figueiredo et al., 2006; Chen et al., 2010; Chuai et al., 2011).

Cyanobacterial blooms are usually observed in late summer and autumn; however, several recent studies from Canada have also observed them in winter (Lavoie et al., 2007; Wejnerowski et al., 2018). 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 (Babanazarova et al., 2013). This pattern contradicts the paradigm of cyanobacterial growth enhanced by warm water temperatures and high nutrients, such as in Chu et al. (2007) and Suda et al. (2002) and the scientific paradigm that consider most of aquatic life as dormant during winter (Grosbois & Rautio, 2018). 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 the factors influencing its presence under a thick ice cover in winter (Mur et al., 1978; van Liere et al., 1979).

Our study characterizes 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 would be detected at bloom levels in summer and fall in both lakes (Jöhnk et al., 2008). We also hypothesized that higher nutrients, including phosphorus and nitrogen availability, would drive cyanobacterial blooms (Davis et al., 2015; Dokulil & Jagsch, 1992; Kramer et al., 2022; Xu et al., 2010).

2.2 Materials and Methods

2.2.1 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 (Beaulne et al. 2012). 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 to 900 mm (Blouin & Berger, 2002; Rey et al., 2018). Lake Fortune is a medium-sized lake with a 0.75 km² surface and a 1.61 km² watershed. The maximum depth of this lake is around 17 m (Firlotte et al., 2007). 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 (Firlotte et al., 2007). 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 (Hasan et al., 2023; Organisme de bassin versant Abitibi-Jamésie, 2014). Lake Beauchamp is situated near an esker and has a roughly circular shape. This lake lies in the subwatershed system of the Davy and Harricana rivers. Lake Beauchamp has 403 permanent inhabitants around the lake, and many visitors come to the municipal camping site and beach every year (Organisme de bassin versant Abitibi-Jamésie, 2014). Both lakes Fortune and Beauchamp provide rich habitats for a diverse aquatic biodiversity and serve as popular recreational spots.

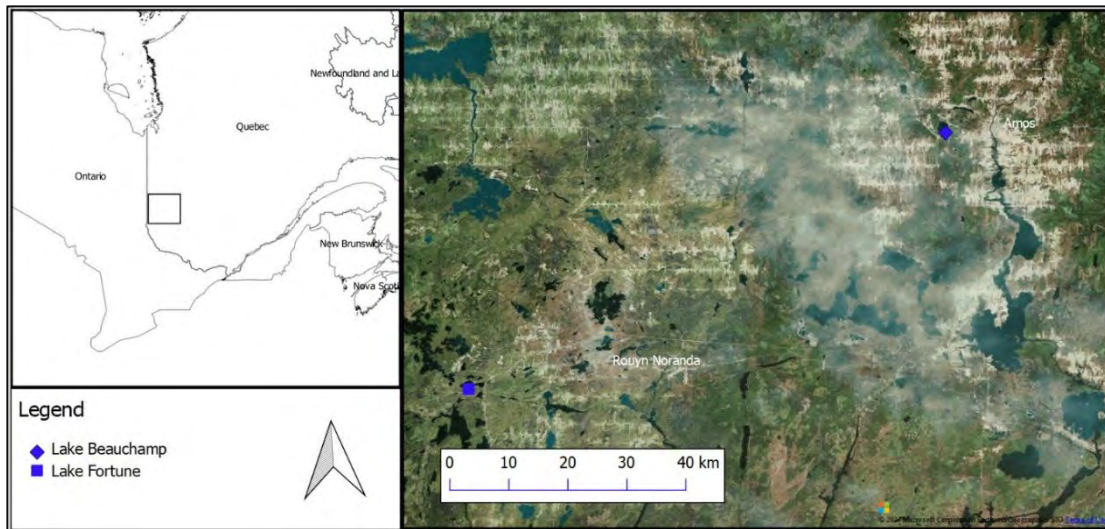


Figure 2.1 Location of the lakes Fortune and Beauchamp within the MRC Abitibi and Rouyn-Noranda regions.

2.2.2 Sampling 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 (Kong et al., 2019; Paquette-Struger et al., 2018). We collected samples from the deepest point of the lake (14 m depth in Lake Fortune and 5 m depth in Lake Beauchamp) and from three different layers, including (when present) the epilimnion, metalimnion, and hypolimnion.

2.2.3 Data collection

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 ($\mu\text{S}/\text{cm}$), 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. At the deepest point of the lake, we used a Ruttner or a Van Dorn 2 L bottle (Fernández Severini et al., 2019) to collect water from the three layers, including the epilimnion (1 m below the surface), metalimnion, and 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.

Cyanobacteria abundance

Cyanobacteria samples were collected in 250 mL brown glass or plastic bottles and then fixed with 1% Lugol's solution. The samples were sent to the Quebec Ministry of Environment and Climate Change and the University of Montreal for cell counting and identification. 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 integrated 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 ($\geq 70\%$ final concentration).

Nutrients

The collected water was analyzed for nutrients and dissolved organic carbon. Acid-washed glass vials (50 mL) were used to collect water for each analysis: total phosphorus (TP), total nitrogen (TN), total dissolved nitrogen (TDN), and total dissolved phosphorus (TDP). 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., 2017). Each vial was washed in a 10% HCl bath for 24 h, rinsed, and then heated in an oven at 200 °C. 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 (Wetzel & Likens, 1991). 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 1030W TOC analyzer at the GRIL analytical laboratory.

2.2.4 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 (Wickham, 2011). The threshold of cell counts to form a bloom according to the WHO determined the dominant cyanobacterial genera from each lake (Health Canada, 2019). We used Tukey's HSD and ANOVA followed by a post-hoc to test for differences in the physicochemical and biological variables among layers and months (Zhang et al., 2016). To identify the relationship among physicochemical variables contributing to

cyanobacterial blooms in different lakes and seasons, we ran principal component analysis (PCA) using the R package *factoextra* (Kassambara & Mundt, 2020). To identify the environmental and biological variables responsible for cyanobacterial abundance throughout the year and to identify non-linear responses, we used a generalized additive model with months as the fixed effect and parameters as factors, using the *gam* function (Wood, 2001). Data were log-transformed for each zooplankton species and cyanobacterial abundance to observe their effect on cyanobacterial abundance (Bolker et al., 2009). All analyses were conducted using the statistical software R version 4.2.1 (R Core Team, 2021).

2.3 Results

2.3.1 Species abundance

Cyanobacterial communities were dominated by the genera *Planktothrix*, *Limnothrix*, and *Aphanizomenon* in Lake Fortune (Figure 2.2A) and by *Aphanothece*, *Aphanocapsa*, and *Gomphosphaeria* in Lake Beauchamp (Figure 2.2B). 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 (Figure 2.2). 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 ($210\,000 \pm 52\,915$ cells/mL) and the lowest in March ($28\,000 \pm 2\,450$ cells/mL) with a yearly average of $81\,800 \pm 66\,225$ cells/mL (Figure 2.5A). The second-most dominant genus in Lake Fortune, *Limnothrix*, had its highest cell counts in October ($52\,450 \pm 67\,780$ cells/mL) and the

lowest in March (790 ± 155 cells/L), with a yearly average of 19 655 cells/mL (Figure 2.2A). The cell count of *Aphanizomenon*, another dominant genus (*t*-test, $p < 0.05$), was highest in November ($33\,166 \pm 13\,250$ cells/mL) and lowest in March (100 ± 0 cells/mL) and had a yearly average of 9635 cells/mL (Figure 2.2A).

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 ($27\,850 \pm 12\,730$ cells/mL) and lowest in March (2110 cells/mL) with a yearly average of 19 080 cells/mL (Figure 2.2B). 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.

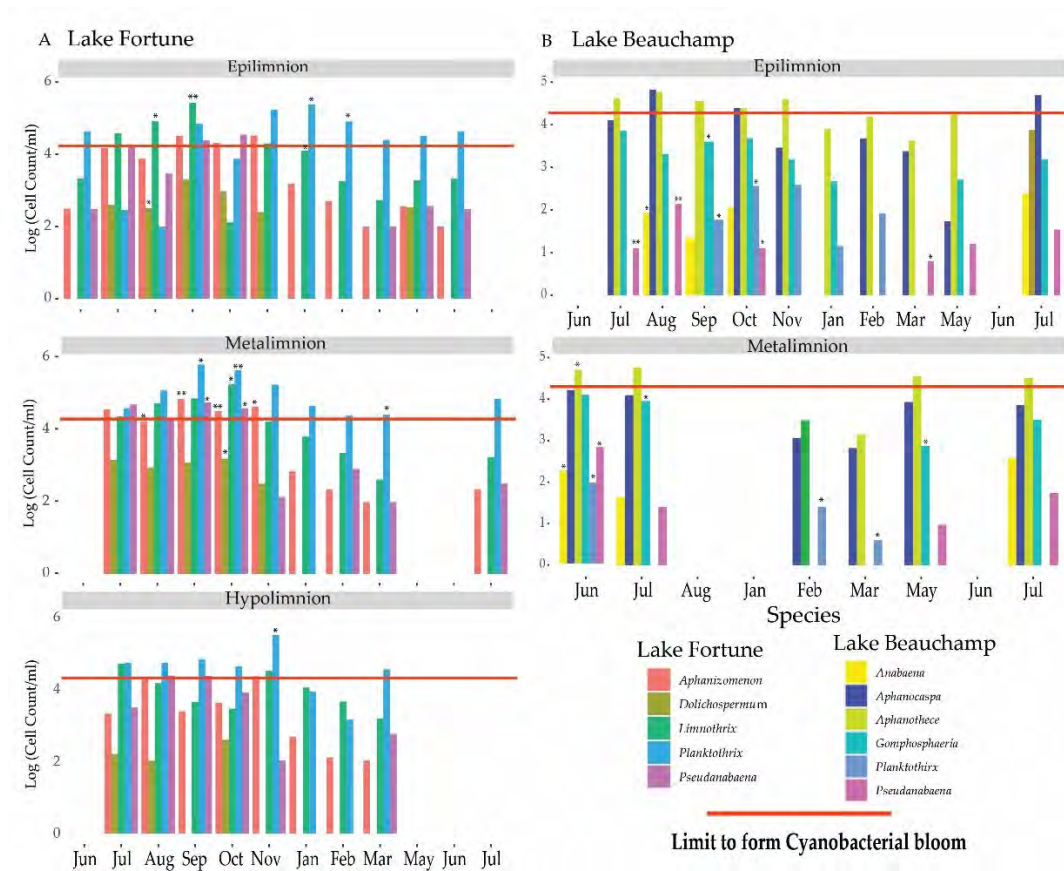


Figure 2.2 Cyanobacterial cell counts of the dominant cyanobacteria genera of blooms in A) Lake Fortune and B) Lake Beauchamp in the epilimnion, metalimnion, and hypolimnion. The five genera from Lake Fortune and six from Lake Beauchamp showed a high abundance throughout the year. Missing months in the 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.

Table 2.1 Monthly average cyanobacterial cell counts (cells/mL) combining samples from all layers and months throughout the year in lakes Fortune and Beauchamp.

| | Month | <i>Aphanizomenon</i> | <i>Dolichospermum</i> | <i>Limnothrix</i> | <i>Planktothrix</i> | <i>Pseudanabaena</i> | <i>Anabaena</i> | <i>Aphanothece</i> | <i>Gomphosphaeria</i> |
|----------------|-------|----------------------|-----------------------|-------------------|---------------------|----------------------|-----------------|--------------------|-----------------------|
| 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 |

2.3.2 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 (Figure 2.3). In Lake Fortune, temperature was highest (13.7 ± 6.1 °C) in August and lowest (2.6 ± 0.5 °C) in January, with a yearly average of 8.6 ± 1.1 °C (Figure 2.6A). Specific conductivity ranged from 127.2 ± 16.9 $\mu\text{S}/\text{cm}$ in September to 113.1 ± 0.6 $\mu\text{S}/\text{cm}$ in January, with a yearly average of 118.8 ± 2.1 $\mu\text{S}/\text{cm}$ (Figure 2.3C). The pH was highest (8.6 ± 0.1) in January and lowest (7.7 ± 0.5) in October, with a yearly average of 8.1 ± 0.1 (Figure 2.3E). Dissolved oxygen concentrations ranged from 322.3 ± 28.2 $\mu\text{mol}/\text{L}$ in January to 62.1 ± 81.4 $\mu\text{mol}/\text{L}$ in September, with a yearly average of 203.7 ± 81.4 $\mu\text{mol}/\text{L}$ (Figure 2.3G).

For Lake Beauchamp, water temperature was highest (20.7 ± 0.1 °C) in August and lowest in January (2.2 ± 1.1 °C) with a yearly average of 12.3 ± 0.5 °C (Figure 2.3B). Specific conductivity varied from 112.8 ± 47.3 $\mu\text{S}/\text{cm}$ in September to 53.5 ± 0.5 $\mu\text{S}/\text{cm}$ in May, with a yearly average of 71.7 ± 7.8 $\mu\text{S}/\text{cm}$ (Figure 2.3D). Lake pH was highest (8.2 ± 0.3) in November and lowest (7.3 ± 0.1) in February, with a yearly average of 7.9 ± 0.1 (Figure 2.3F). Finally, the dissolved oxygen concentrations were highest (387.4 $\mu\text{mol}/\text{L}$) in November and lowest (225.0 $\mu\text{mol}/\text{L}$) in March, with a yearly average of 262.6 ± 15.1 $\mu\text{mol}/\text{L}$ (Figure 2.3H).

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 to 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 ± 1.7 to 21.1 °C at the surface. Specific conductivity in Lake Fortune for September (155.9 ± 9.3 $\mu\text{S}/\text{cm}$) in the hypolimnion was higher than the yearly average of 118.87 $\mu\text{S}/\text{cm}$ and the average fall value of 121.46 $\mu\text{S}/\text{cm}$. In Lake Beauchamp, specific conductivity was higher during September (112.7 ± 66.9 $\mu\text{S}/\text{cm}$) in the epilimnion than the yearly (71.7 $\mu\text{S}/\text{cm}$) and seasonal (fall) (80.3 $\mu\text{S}/\text{cm}$) averages. During the winter, specific conductivity was higher in the hypolimnion in both lakes. Conductivity was highest in Lake Fortune in the 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). Oxygen saturation varied between 80% and 100% in the epilimnion and declined to a minimum of 5% during the summer and fall in Lake Fortune. In Lake Beauchamp, the oxygen saturation varied between 70% and 100% in the epilimnion and never declined below 40% in the metalimnion and hypolimnion. 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.

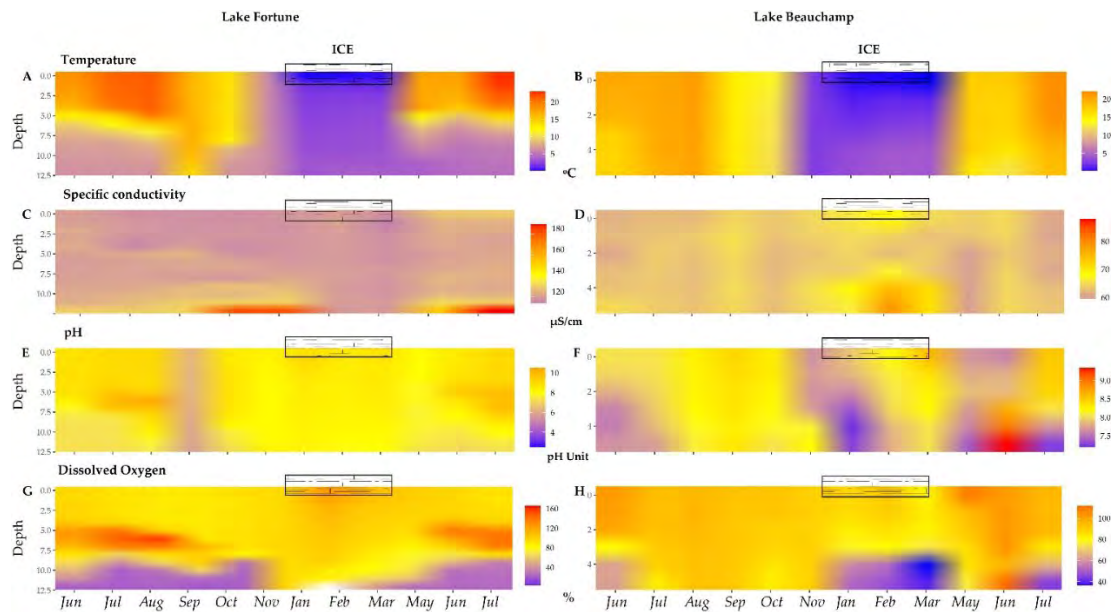


Figure 2.3 Physicochemistry of lakes Fortune and Beauchamp with A and B) water temperature ($^{\circ}\text{C}$); C and D) specific conductivity ($\mu\text{S}/\text{cm}$); E and F) pH; and G and H) dissolved oxygen saturation (%).

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) (Figure 2.4D). TN varied from 0.6 $\mu\text{g/L}$ in August for the epilimnion to 0.3 $\mu\text{g/L}$ in June for the metalimnion. TN was higher in the epilimnion (0.6 $\mu\text{g/L}$) than in the metalimnion (0.4 $\mu\text{g/L}$) (Figure 2.4F). TDN varied from 0.4 $\mu\text{g/L}$ in March in the epilimnion to 0.2 $\mu\text{g/L}$ in May in the hypolimnion. For yearly average, it was only 0.02 $\mu\text{g/L}$ higher in the epilimnion (0.4 $\mu\text{g/L}$) than the hypolimnion (0.4 $\mu\text{g/L}$) (Figure 2.4H). 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) (Figure 2.4J).

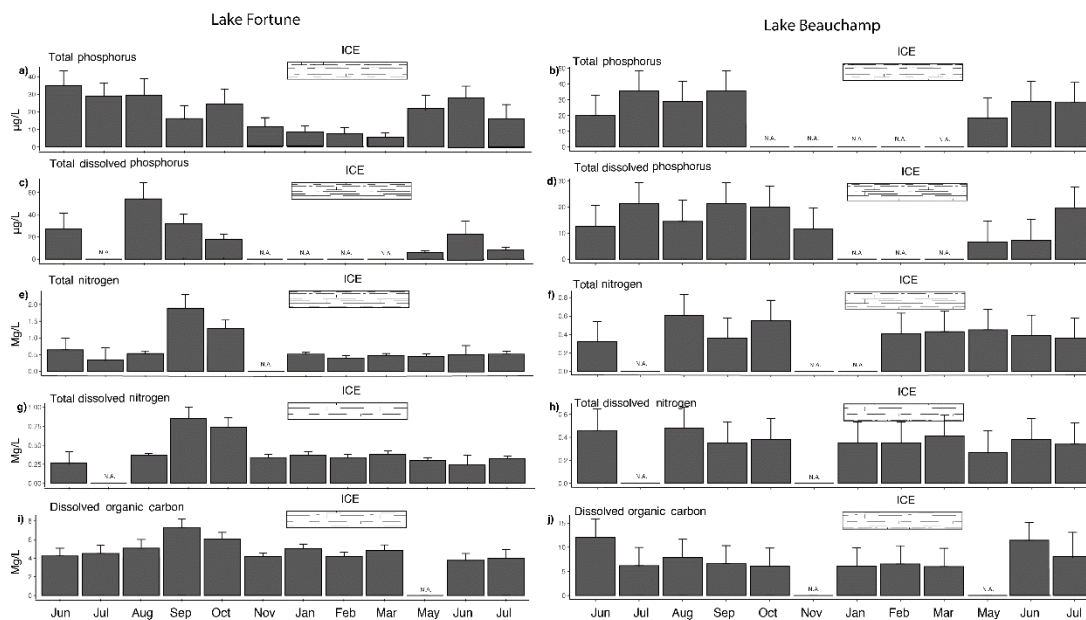


Figure 2.4 Total nutrient and carbon concentrations in lakes Fortune and Beauchamp over a year. Data represent the means and standard deviations from the three lake layers (epilimnion, metalimnion, and hypolimnion) combined. Here, N.A. means the data is not available.

2.3.3 Factors explaining cyanobacterial communities.

Standardized cell counts of each dominant cyanobacterial genus were tested with environmental variables including TP, TDP, TN, TDN, DOC, temperature, specific conductivity, pH, dissolved oxygen, depth using principal component analysis. The first two axes of the principal components analysis (PCA) of *Planktothrix* cell densities in Lake Fortune explained 56% of the variation (Figure 2.5A). 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 ($r > 0.4$, $p < 0.05$) (Figure 2.5C). 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 ($r > 0.5$, $p < 0.05$) (Figure 2.5E). 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 (Figure 2.5G).

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 ($r < 0.3$, $p > 0.1$) (Figure 2.5B). 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 ($r < 0.4$, $p > 0.1$; Figures 2.5D, F, H).

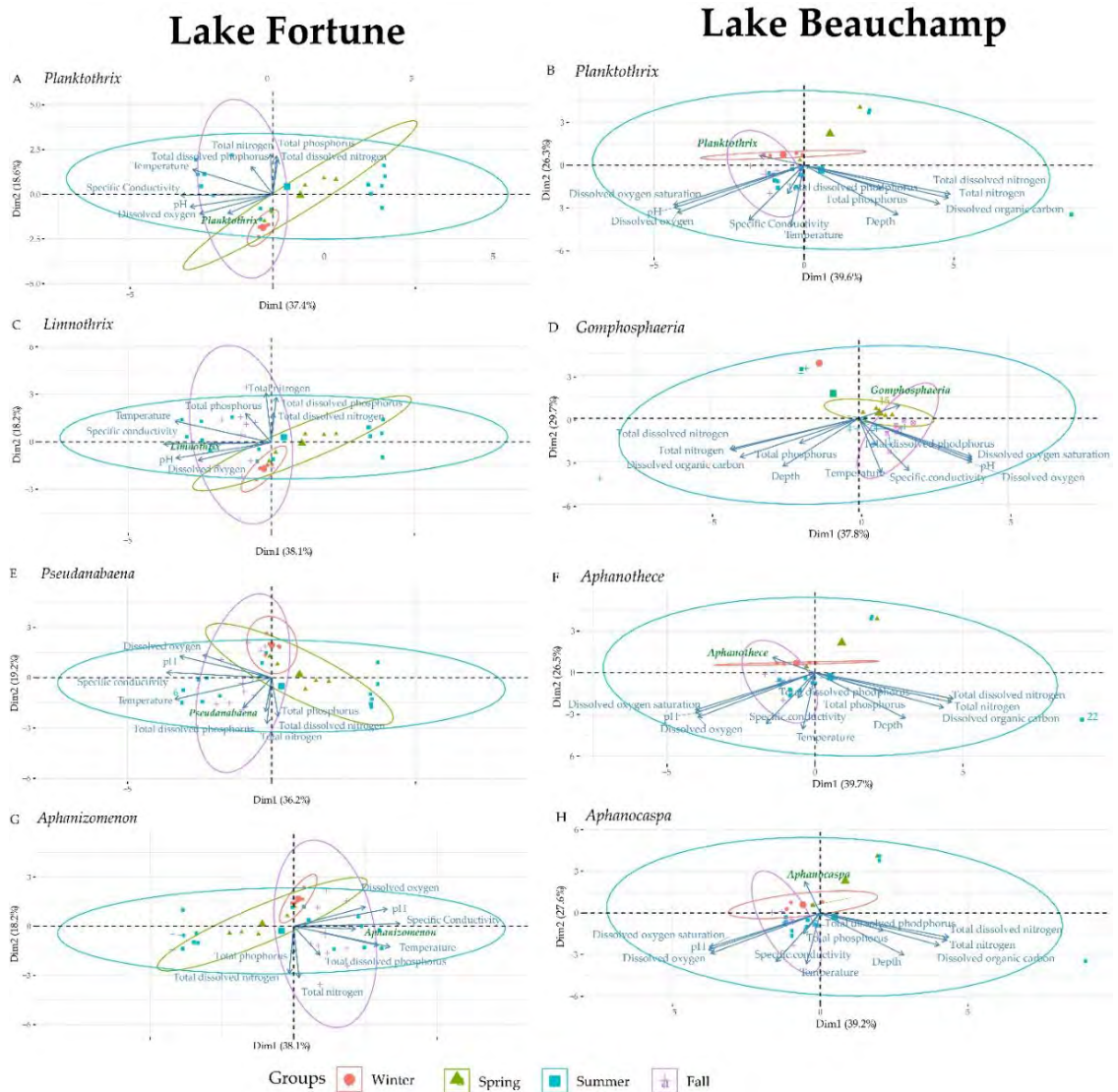


Figure 2.5 Principal component analysis (PCA) of the measured environmental variables and cyanobacterial cell densities in lakes Fortune and Beauchamp.

Table 2.2 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 | | | | |
|-----------|----------------------------|--------------------------|---------------------------|------------------------|---------------------------|--------------------------|----------------------|---------------------------|-------------------------|----------------------------|
| | <i>Dolichospermum</i> spp. | <i>Planktothrix</i> spp. | <i>Aphanizomenon</i> spp. | <i>Limnothrix</i> spp. | <i>Pseudanabaena</i> spp. | <i>Planktothrix</i> spp. | <i>Anabaena</i> spp. | <i>Pseudanabaena</i> spp. | <i>Aphanothece</i> spp. | <i>Gomphosphaeria</i> spp. |
| TP | 0.52 | 0.02* | 0.16 | 0.02* | 0.36 | 0.22 | 0.4 | 0.36 | 0.42 | 0.1 |
| TDP | 0.18 | 0.79 | 0.35 | 0.63 | 0.76 | 0.5 | 0.05 | 0.43 | 0.3 | 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* | 0.2 | 0.04* | 0.02* |
| DOC | 0.005** | 0.04* | 0.33 | 0.08. | 0.92 | 0.67 | 0.32 | 0.7 | 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* | 0.1 | 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 | 0.008** | 0.02* | 0.79 | 0.93 | 0.1 |
| June | 0.91 | 0.8 | 0.86 | 0.39 | 0.55 | 0.008** | 0.04* | 0.38 | 0.12 | 0.009** |
| July | 0.2 | 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.

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 2.2). Similarly, DOC and TP

significantly affected the *Planktothrix* cell counts ($p < 0.01$; Table 2.2). 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 2.2).

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 2.3).

Table 2.3 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 | | | | | | | |
|--------------------|------------------------------|-------------------------------|---------------------------|-----------------------------|------------------------------|-----------------------------|------------------------------|-------------------------|------------------------------|-------------------------------|
| | <i>Aphanizomenon</i> spp. | <i>Dolichospermum</i> spp. | <i>Limnothrix</i> spp. | <i>Planktothrix</i> spp. | <i>Pseudanabaena</i> spp. | <i>Planktothrix</i> spp. | <i>Aphanizomenon</i> spp. | <i>Anabaena</i> spp. | <i>Pseudanabaena</i> spp. | <i>Gomphosphaeria</i> spp. |
| <i>Bosmina</i> | 0.16 | 0.63 | 0.75 | 0.92 | 0.24 | 0.4 | 0.86 | 0.52 | 0.72 | 0.93 |
| <i>Daphnia</i> | 0.7 | <0.05** | 0.31 | 0.18 | 0.87 | 0.71 | 0.64 | 0.75 | 0.65 | 0.89 |
| <i>Calanoid</i> | 0.65 | 0.78 | 0.25 | 0.04* | 0.85 | 0.69 | 0.57 | 0.82 | 0.88 | 0.96 |
| <i>Cyclopoid</i> | 0.83 | 0.88 | 0.98 | 0.52 | 0.68 | 0.68 | 0.34 | 0.66 | 0.74 | 0.86 |
| <i>Nauplii</i> | 0.04* | 0.92 | 0.4 | 0.3 | 0.15 | 0.75 | 0.42 | 0.71 | 0.83 | 0.79 |
| <i>Keratella</i> | 0.69 | 0.91 | 0.49 | 0.17 | 0.71 | 0.73 | 0.97 | 0.73 | 0.67 | 0.83 |
| <i>Kellicottia</i> | 0.59 | 0.95 | 0.75 | 0.31 | 0.47 | 0.59 | 0.39 | 0.75 | 0.92 | 0.87 |

2.4 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. Each study lake had different cyanobacterial bloom patterns. 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 influenced the cyanobacterial blooms. Nutrients and organic carbon significantly influenced the dominance of *Planktotrix* in Lake Fortune and *Aphanothece* in Lake Beauchamp. Thus, we confirmed our hypothesis that predicted that a higher availability of dissolved phosphorus and nitrogen favours the formation of cyanobacterial blooms.

2.4.1 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 (e.g., Chu et al., 2007; Suda et al., 2002). For example, in Lake Zurich (Thomas & Marki, 1949), Lake Mondsee in Austria (Dokulil & Jagsch, 1992), and lakes du Bourget (Jacquet et al., 2005) and Nantua (J. Feuillade, 1994) 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 (Feuillade et al., 1992; Van Liere & Mur, 1979). Moreover, *Plankthotrix* can have higher growth rates than other algae in low light intensities because they require relatively less energy for their metabolic processes (Mur et al., 1978; van Liere et al., 1979).

The genus *Aphanothece* dominated the cyanobacterial community in Lake Beauchamp throughout the year, even in the unfavourable winter months. These taxa can survive in winter using mixotrophy and by assimilating organic matter (Anneville et al., 2015). This strategy allows *Aphanothece* to persist below the photic zone and in light-limited conditions. Moreover, *Aphanothece* is a gram-negative bacteria able to fix atmospheric nitrogen in the water (Maçik et al., 2020). 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 (Halstvedt et al., 2007). The dominance of *Planktothrix* in Lake Fortune may have been influenced by reduced grazing from *Daphnia*. Rohrlack et al. (2005) found that many inhibitors of the *Daphnia* digestive enzyme trypsin are produced by *Planktothrix*, causing the death of *Daphnia*. Moreover, Oberhaus et al. (2007) 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 (Eskinazi-Sant'Anna et al., 2013). *Calanoida* are known for ingesting large amounts of cyanobacterial cells such as *Planktothrix* (Gliwicz, 1990) and several species are known to stay active during winter (Grosbois

et al., 2020; Grosbois, Mariash, et al., 2017; Schneider et al., 2016, 2017). However, future work is needed to understand the complex relationship between algal and zooplankton population dynamics in these boreal lakes.

2.4.2 Environmental drivers

Planktothrix in Lake Fortune was influenced by TP and DOC concentrations in the water. Phosphorus concentrations directly affect cyanobacterial genera such as *Planktothrix* (Downing et al., 2001b; Ferrão-Filho et al., 2000; Fogg, 1969). Moreover, Hampel et al. (2019) 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 (Zotina, Köster and Jüttner, 2003). Hence, *Planktothrix* can remain dominant in Lake Fortune throughout the year, including during the winter.

Nutrient concentrations were higher in Lake Fortune than in Lake Beauchamp. Lake Fortune was originally oligotrophic, but its trophic status changed recently to oligomesotrophic, as recent surveys found increased phosphorus and chlorophyll-*a* concentrations (unpublished data, [Voluntary Lake Monitoring Network](#)). Lake Beauchamp lies near 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 (Hasan et al., 2023) but are more often connected to the groundwater system. Eskers also have sandy soils and are found at higher elevations than other surrounding lakes (Winter et al., 1998). TP concentrations were highest in July in Lake Beauchamp. This mid-summer increase may be due to warmer waters favour the release of phosphorus from sediments and increase dissolved phosphorus levels in the water column (Jiang et al., 2008). Additionally, human activities, such as increased tourism or recreational activities during summer, may lead to higher nutrient inputs into lakes (Girona, Aakala, et al., 2023; Li et al., 2022). 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 from the land.

Atmospheric weather patterns may alter physicochemical parameters throughout the water column (Kraemer et al., 2015). In particular, Lake Fortune showed a wide variation in pH, which can be related directly to the higher cyanobacterial activity during the fall (Zhang et al., 2019). 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 (Hasan et al., 2023).

2.4.3 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 (Eilers, 2019). Studies have shown correlations between faulty septic systems and cyanobacterial blooms in many lakes in North America, e.g., Lake Chaplin, USA (Dove & Chapra (2015) cited in Lapointe et al., 2017). 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 (Reynolds, 2006). 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 (Carvalho, McDonald, et al., 2013a; Downing et al., 2001b; Maileht et al., 2013). Although the WHO set a health threshold for TP at 20 $\mu\text{g/L}$ (World Health Organization, 2004), *Planktothrix* can thrive at concentrations of 10 to 15 $\mu\text{g/L}$ (Steinberg & Hartmann, 1988; Vuorio et al., 2020). For almost the entire year, TP concentrations in Lake Fortune were around or above 20 $\mu\text{g/L}$, 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., Carvalho et al., 2011; Carvalho, McDonald, et al., 2013b). Nonetheless, knowledge about genera-specific nutrient thresholds is necessary to reduce cyanobacteria blooms initiated by specific taxa (Vuorio et al., 2020). Both 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 helps provide information for adapted management tools to reduce cyanobacterial blooms.

2.5 Conclusions

Our research revealed the seasonal dynamics of cyanobacterial blooms in two Canadian boreal lakes. We demonstrated that higher nutrients in both lakes influenced 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 higher total phosphorus concentrations and due to its ability to absorb dissolved organic carbon (DOC) 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.

CHAPTER 3

GENERAL CONCLUSION

3.1 Study Contribution

This study provided new knowledge about the seasonal dynamics of harmful algal blooms (HABs), including dynamics under the ice in winter, and identified the driving factors behind these HABs in the Abitibi-Témiscamingue region. We hypothesized that the cyanobacterial community in Lake Fortune would be found over the entire year, including under ice during winter and that in Lake Beauchamp, the presence of cyanobacteria would be limited to the summer months. Additionally, we expected that the higher nutrient concentrations in Lake Fortune would facilitate cyanobacterial blooms. In contrast, the nutrient-poor conditions of the Lake Beauchamp ecosystem would lead to peak cyanobacterial abundance primarily during the summer months, mainly because of summer temperatures. Our study showed that nutrient concentrations in both lakes influenced cyanobacterial blooms, confirming our first hypothesis, although not directly the second hypothesis related to temperature. In Lake Fortune, total phosphorus, dissolved nitrogen, and dissolved organic carbon influenced cyanobacterial abundance, whereas in Lake Beauchamp, dissolved nitrogen and total nitrogen influenced cyanobacterial growth. The genus *Planktothrix* dominated the cyanobacteria community in Lake Fortune and was favoured by the high phosphorus concentrations maintained throughout the year. The genus *Aphanothece* dominated the cyanobacterial community in Lake Beauchamp with a higher number of cells than the health limit recommended by the WHO.

Phosphorus and organic carbon played a significant role in forming cyanobacterial blooms, particularly for *Planktothrix*. *Planktothrix*, known for its lower TP threshold required for bloom formation, was consistently dominant in Lake Fortune throughout the year, even when the lake was covered by ice and snow. *Planktothrix* can adapt and thrive in unfavourable temperatures by adapting to fewer resources and low light intensities over its life cycle. The high concentration of *Planktothrix* may relate to reduced grazing by zooplankton, as *Planktothrix* filaments are difficult for zooplankton to ingest. In Lake Fortune, however, the abundance of *Planktothrix* experienced relatively low grazing by the zooplankton genus *Daphnia* but instead were grazed by order Calanoida, known for its ability to ingest cyanobacteria (Eskinazi-Sant'Anna et al., 2013; Gliwicz, 1990; Kozłowsky-Suzuki et al., 2003).

Our study identified cyanobacterial blooms during each month of the year, particularly in late summer and autumn, and *Planktothrix* blooms in winter. To our knowledge, ours is the first observation of a lake having a metalimnetic bloom throughout the year. During winter, abiotic conditions change significantly in lakes. Water temperatures drops to 4 °C, ice cover disconnects the water column from the atmosphere, which lowers the dissolved oxygen and nutrient concentrations in the water, and biological activity is reduced because many organisms, including phytoplankton and bacteria, enter a state of dormancy or reduced activity (Grosbois et al., 2020; Grosbois & Rautio, 2018). In contrast, *Planktothrix* in Lake Fortune could adapt to unfavourable temperatures (near 4 °C) and maintain its life cycle by relying on fewer resources at low temperatures and irradiance. The genus can absorb dissolved organic carbon and survive in low light conditions, explaining its year-round presence in Lake Fortune, including the winter months. Moreover, the dominant cyanobacterial genus in Lake Beauchamp, *Aphanothece*, was observed throughout the year, employing mixotrophy for its winter survival (Mur et al., 1999).

3.2 Managerial Recommendations

Minimizing nutrient inputs from sewage and septic systems through effective management practices can reduce nitrification in Lake Fortune, whereas minimizing agricultural runoff and repairing faulty sewage systems would limit nitrification and phosphorus inputs in Lake Beauchamp. One of the most effective practices is to update septic system infrastructures to control the leaking of anthropogenic nutrients into lakes. Moreover, regional and local authorities should limit the number of residences around each lake to minimize the damage to the ecological resources of the lakes and not exceed the lakes' carrying capacity. Removing excessive nutrients from the sediments can potentially reduce HABs. One success story is from Lake Trummen, Sweden, where suction-dredging of the upper half of sediments significantly decreased cyanobacterial blooms (Welch & Naczka, 2021). However, this process is very expensive and time-consuming and can only apply to relatively small and shallow lakes. Moreover, this method can also deteriorate the water quality temporarily. Applying algaecides with copper components or hydrogen peroxide can offer a solution for reducing HABs (Matthijs et al., 2012). However, there is a risk of copper toxicity in the food webs, which can have severe long-term consequences. Both solutions can be applied in all seasons (Visser et al., 1996).

Aquatic environments are complex and influenced by multiple factors at different scales. Seasonal dynamics of cyanobacterial blooms are also challenging to understand, as they include complex interactions among different communities within the food web. Finding a solution to HABs must thus be adapted to each lake; hence, solutions remain a challenge, as one-for-all solutions risk failing in many cases. Relying on the existing literature and this study, we can propose several management practices to

reduce bloom formation in these two lakes; however, the effectiveness and suitability of each management practice must be tested for each lake before any implementation.

The driving factors influencing cyanobacterial blooms in Lake Fortune are phosphorus, nitrogen, and organic carbon, whereas dissolved nitrogen was most important for explaining cyanobacterial densities in Lake Beauchamp. The existing land-use patterns around the lakes likely induce the heightened influence of these parameters. Limiting excessive nutrient inputs from external sources is often the key to reducing cyanobacterial blooms in lakes. Moreover, controlling chemical fertilizer use around Lake Beauchamp is vital for reducing nitrogen input. Lake Fortune and Lake Beauchamp require proper management plans for the safety of the communities dependent on these water bodies. In short, a sustainable management approach is vital for conserving biodiversity, improving water quality, supporting ecosystem services, and ensuring the well-being of communities and the environment dependent on these lakes.

From our observations and results, we propose several managerial recommendations to protect boreal lakes from harmful algal blooms.

1. Every septic system must be evaluated periodically to reduce anthropogenic nutrient inputs to the lake, following provincial guidelines.
2. Anthropogenic disturbances must be reduced around the lake to limit pollution (Gauthier et al., 2023; Grosbois et al., 2023; Montoro Girona et al., 2023).
3. The injection of algaecides, such as aluminium compounds, chlorine, potassium permanganate, and copper-based algaecides, can be a solution to reduce phosphorus concentrations in the water body; however, their use may

bring other environmental problems. Moreover, such algaecides harm humans and animals if swallowed or absorbed through the skin.

4. Riparian forests should be maintained to intercept the runoff of pollutants and excess nutrients.
5. Adopting partial harvesting rather than clearcutting of forest around a lake can reduce DOC inputs (Bose et al., 2023; D'Amato et al., 2023; Girona, Moussaoui, et al., 2023; Montoro Girona et al., 2023; Moussaoui et al., 2020) and reduce nutrient concentrations in the lake.
6. Avoid the construction of new houses along the shores of the lakes.

Moving forward, an exciting avenue for further research involves a more nuanced investigation into microbial interactions within the food web. Understanding the intricate relationships among microbial communities, including bacteria and other algae, and their role in moderating the initiation, growth, and recession of harmful cyanobacterial blooms across seasons could provide crucial insight. Future research should extend to exploring the influence of climate change on the temporal patterns of blooms and bloom intensity, evaluating the impact of anthropogenic activities on cyanobacterial dynamics, conducting genomic analyses to identify genetic factors contributing to the success of cyanobacterial strains in different seasons, and examining the interactions among microbial metabolism, nutrient availability, and cyanotoxin production during bloom events. Answers to these research questions will broaden our understanding and have important implications for developing targeted and sustainable management strategies to effectively mitigate the impact of cyanobacterial blooms on public health and foster the overall health of aquatic ecosystems.

APPENDIX A

Table S.1 Average Secchi depth in lakes Fortune and Beauchamp over the year

| Month | Secchi depth in Lake Fortune (m) | Secchi depth in Lake Beauchamp (m) |
|-----------|-------------------------------------|--|
| January | 2.4 | 2.3 |
| February | 0.6 | 1.9 |
| March | 2.1 | 2.9 |
| May | 2.6 | 3.9 |
| June | 3.2 | 2.5 |
| July | 3.3 | 1.9 |
| August | 2.9 | 1.9 |
| September | 1.7 | 1.9 |
| October | 2.4 | 2.3 |
| November | 1.3 | 1.7 |

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