



La prolifération de cyanobactéries en réservoir tempéré nordique (le Lac Saint-Charles, Québec, Canada): variabilité et facteurs de contrôle

Thèse

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Résumé

Les proliférations de cyanobactéries nocives dans les écosystèmes d'eau douce font l'objet d'une préoccupation grandissante dans la population et dans le milieu scientifique. Une meilleure compréhension des facteurs qui contrôlent ces proliférations est essentielle pour en améliorer leur prédition et leur gestion. L'objectif général de cette thèse est de comprendre les changements dans la structure de la communauté cyanobactérienne d'un réservoir d'eau douce. Le réservoir du lac Saint-Charles constitue une importante source d'eau potable pour la ville de Québec (Canada) et le signalement d'efflorescences de cyanobactéries y est de plus en plus fréquent depuis l'automne 2006. La collecte de données physiques, chimiques et biologiques pendant 5 années consécutives (2007-2011) a tout d'abord permis d'identifier l'état mésotrophique du lac et de mettre en évidence les importantes variations interannuelles des variables limnologiques, fournissant des conditions intermittentes favorables à la dominance des cyanobactéries. De larges variations spatiales – sur un gradient nord/sud – mais aussi interannuelles ont été révélées, à la fois en terme de concentrations observées et d'espèces dominantes (*Microcystis aeruginosa*, *Anabaena flos-aquae* et *Aphanocapsa/Aphanothece* sp.). Ces résultats ont souligné l'existence de contrôles environnementaux contrastés (phosphore, température, stabilité de la stratification) agissant sur les différents taxons de cyanobactéries et la forte sensibilité aux changements environnementaux des réservoirs à écoulement rapide tels que le lac Saint-Charles. L'analyse détaillée des sédiments du lac indique le faible potentiel d'inoculum sous forme de cellules en dormance. Cette observation contraste avec le cas de nombreux lacs touchés par les efflorescences de cyanobactéries et indique le potentiel d'une réponse rapide au contrôle de l'apport en sels nutritifs provenant du bassin versant. L'ensemble de ces recherches a permis de mettre en évidence la nature hautement dynamique des réservoirs d'eau douce, leur sensibilité à l'eutrophisation malgré un court temps de résidence, et la nécessité d'une surveillance continue afin de détecter au mieux l'apparition des taxons responsables pour les proliférations de cyanobactéries.

Abstract

The occurrence of harmful blooms of cyanobacteria in freshwater ecosystems is subject to growing public as well as scientific concern. An improved understanding of the factors controlling the proliferation of bloom-forming taxa is an essential requirement for the adequate prediction and management of this water quality problem. The overall objective of this thesis was to understand the cyanobacterial community dynamics of a north-temperate reservoir. The Lake St. Charles reservoir is a major source of drinking water for Quebec City, Canada, and cyanobacterial blooms have appeared episodically in the lake since autumn 2006. Physical, chemical and biological variables were measured over 5 consecutive summers (2007-2011). This confirmed the mesotrophic status of the lake, and underscored the large interannual variation in limnological conditions that provided intermittently favorable conditions for cyanobacterial growth and dominance. There were pronounced variations in cyanobacterial community biomass and structure among the 5 years, including in the dominant species (*Microcystis aeruginosa*, *Anabaena flos-aquae* and *Aphanocapsa/Aphanothecace* sp.). In addition, large differences in community biomass and composition were observed spatially, with significantly higher cyanobacterial concentrations in the north relative to south. These results indicated that there were contrasting environmental controls (phosphorus, temperature, stability of the stratification) acting on the different taxa of cyanobacteria. This large spatial and temporal variability also reflects the dynamic nature of high through-flow reservoirs such as Lake St. Charles. *In situ* sediment mapping implied that benthic resting cells, if present, were mostly below detection at all sites. This low potential to inoculate the water column from sediments contrasts with many lakes affected by cyanobacteria blooms and indicates the potential for a rapid response to nutrient loading control in the Lake St. Charles watershed. This research has highlighted the markedly dynamic nature of freshwater reservoirs, their potential sensitivity to eutrophication despite a short hydraulic residence time, and the need for continuous monitoring in order to detect the appearance of bloom-forming cyanobacteria.

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“An dour a red na ra droug da zen ebet...”

“L'eau qui court est bonne pour tout le monde...”

(Proverbe breton)

à Suzanne et Armelle

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Avant-propos

Cette thèse présente l'aboutissement de mes travaux de doctorat effectués sous la direction des professeurs Warwick F. Vincent du département de Biologie de l'Université Laval et Isabelle Laurion de l'Institut National de la Recherche Scientifique-Centre Eau, Terre, Environnement. La thèse est composée de 5 chapitres dont trois présentés sous forme d'articles, précédés d'un résumé en français. Le premier chapitre consiste en une introduction générale à la problématique de l'étude et se termine par une présentation de l'objectif général et des objectifs spécifiques. Le dernier chapitre présente les conclusions et perspectives de la recherche. Je suis première auteure de chacun des articles et responsable de la planification des travaux, de l'échantillonnage et mesures sur le terrain de 2009 à 2011, des analyses en laboratoire (à l'exception des analyses de pigments, des nutriments, de la granulométrie et de la radioactivité du ^{210}Pb) ainsi que du processus d'interprétation des données et de rédaction.

Chapitre 1: Introduction générale

Chapitre 2: *Limnological dynamics of a reservoir subject to harmful cyanobacterial blooms.* Ce chapitre a été soumis pour publication.

Chapitre 3: Rolland D. C., Bourget S., Warren A., Laurion I. and Vincent W. F. (2013) *Extreme variability of cyanobacterial blooms in an urban drinking reservoir.* Journal of Plankton Research. doi: 10.1093/plankt/fbt042.

Chapitre 4: *Phytoplankton seed banks in lake sediments: application of five methods to detect cyanobacterial resting stages in a drinking water reservoir.* Ce chapitre sera soumis sous peu pour publication.

Chapitre 5: Conclusion générale

Chapitre 1. Introduction générale

1.1 Introduction

L'eau est largement considérée comme la plus essentielle des ressources naturelles. Cependant, alors que la majorité de la planète est recouverte d'eau, seulement une toute petite portion est associée aux zones continentales. L'eau douce représente moins de 3% du volume global de la planète, mais n'en exerce pas moins un rôle vital pour les écosystèmes et les sociétés humaines. La majeure partie de cette eau (99%) est sous forme d'eau souterraine ou de glace et donc difficile d'accès (Dodds & Whiles, 2010). La croissance de la population sur la planète risque d'induire une forte augmentation de la demande en eau, ajoutée aux nombreuses incertitudes dues aux changements climatiques du futur (Vörösmarty et al., 2000). Les écosystèmes d'eau douce sont directement menacés par les activités humaines qui constituent les principaux facteurs de dégradation aussi bien du point de vue quantitatif en exploitant de façon désordonnée cette ressource, que qualitatif en perturbant ses caractéristiques chimiques et biologiques (Vörösmarty et al., 2010).

Une des principales causes de détérioration de la qualité de l'eau des lacs et réservoirs d'eau douce est le phénomène d'"eutrophisation", c'est-à-dire une augmentation excessive des apports externes de nutriments, qui a pour conséquence la prolifération de fortes biomasses de microalgues, de périphyton, de macrophytes et de bactéries photosynthétiques (Istvánovics, 2009; O'Sullivan, 1995). L'eutrophisation est un processus naturel de vieillissement des écosystèmes d'eau douce qui se déroule normalement sur plusieurs milliers d'années et qui dépend de perturbations naturelles ayant lieu dans le bassin versant telles que des variations climatiques (e.g. Brüchmann & Negendank, 2004; Istvánovics, 2009) ou des événements extrêmes comme des éruptions volcaniques (e.g. Larson, 1993) ou des ouragans (Köster & Pienitz, 2006). Cependant, l'augmentation des activités anthropiques a provoqué une accélération de ce processus dans les zones du globe modérément à très densément peuplées, un lac pouvant ainsi passer du stade oligotrophe (littéralement du latin "peu

nourrit") au stade eutrophe (littéralement du latin "bien nourrit") en une dizaine d'années (e.g. Pienitz et al., 2006).

Les activités humaines qui entraînent l'eutrophisation accélérée des écosystèmes aquatiques incluent l'épandage de fertilisants agricoles et de fumures organiques produites par le bétail, le rejet d'eaux usées, ainsi que toutes les activités favorisant l'érosion et donc l'apport en quantité importante de nutriments vers les écosystèmes aquatiques telles que le remembrement des champs, la déforestation et l'imperméabilisation des sols par la construction de surfaces goudronnées. En effet, il est généralement admis que les éléments clés impliqués dans l'eutrophisation sont l'azote (N) et le phosphore (P). Plusieurs études de grande envergure menées depuis les années 1960, ont mis en évidence que le P est l'élément qui détermine le plus souvent la capacité de support des lacs et réservoirs (OCDE, 1982; Schindler, 1974; Vollenweider, 1968). Le modèle initialement proposé par Vollenweider (1968) se base sur le fait que plus la charge externe en P est élevée, plus la production de biomasse chlorophyllienne est importante (Fig. 1.1). Cette relation a ensuite accrédité l'idée qu'il suffit de réduire les apports de P pour renverser le processus d'eutrophisation dans les lacs et réservoirs, même s'il y a beaucoup d'études qui indiquent que la limitation en N est courante dans les lacs (Dolman et al., 2012; Lewis & Wurtsbaugh, 2008). De fait, des opérations de contrôle des apports de P ont ainsi permis la "guérisson" spectaculaire de nombreux lacs, comme par exemple le Lac Washington aux États-Unis (Edmonson, 1977). D'autres expériences de gestion des apports de P montrent cependant que cette théorie est accompagnée d'incertitudes (Décamps, 2000) et qu'une diminution des apports de N doit parfois aussi être considérée (Conley et al., 2009).

Le premier signe d'eutrophisation perçu par la population est souvent l'apparition d'"efflorescences" (traduction littérale de "bloom") d'algues ou de cyanobactéries. Une augmentation de leur abondance est un signe de l'existence d'un problème d'eutrophisation accélérée (O'Sullivan, 1995). La relation entre la proportion relative de chaque groupe taxonomique composant le phytoplancton et la charge en P a ainsi

été décrite à partir de 91 lacs tempérés nordiques au Canada et a révélé un transfert de dominance vers les cyanobactéries lorsque le phosphore total (PT) augmente (Fig. 1.2. Watson et al., 1997). La prolifération des cyanobactéries engendre de lourdes conséquences sur la santé des écosystèmes, les risques sanitaires mais aussi sur la valeur économique et sociale des lacs et réservoirs touchés (Vincent, 2009a).

Cette thèse abordera ces problématiques dans le lac Saint-Charles, réservoir d'eau potable alimentant près de 300 000 résidents de la Ville de Québec. Ce chapitre présentera une revue de littérature de l'écologie et de la dynamique des cyanobactéries, des causes et conséquences de leur prolifération, une description du site d'étude et se terminera par une présentation des hypothèses, objectifs et démarches de recherche.

1.2 Description générale des cyanobactéries

1.2.1. Définition

Les cyanobactéries sont des eubactéries de type gram négatif particulières puisqu'elles sont capables d'utiliser le dioxyde de carbone (CO_2) comme source de carbone. A cet égard, les cyanobactéries sont similaires aux plantes supérieures, algues eucaryotes, bactéries photosynthétiques et bactéries chémolithotrophes (Smith, 1973). Puisque ce sont les premiers organismes capables de photosynthèse oxygénique apparus sur Terre (production de matière organique et d'oxygène à partir d'eau et de dioxyde de carbone), elles sont en grande partie à l'origine de l'augmentation de l'oxygène atmosphérique il y a 2 milliards d'années (Van den Hoek et al., 1995). Conformément aux organismes procaryotes, les cyanobactéries sont dépourvues de noyau délimité par une membrane et d'organites tels que les chloroplastes et mitochondries. Par conséquent, les cyanobactéries, communément appelées "algues bleues" ou "algues bleu-vert", ne sont pas des algues à proprement parler et ce terme doit être évité si l'on souhaite rester scientifiquement rigoureux.

1.2.2. Distribution dans les écosystèmes

Les cyanobactéries sont des organismes ubiquistes qui peuvent coloniser tous les milieux (cf. revue de littérature; Whitton, 2012): les lacs, rivières, estuaires et océans mais aussi les sols et les environnements extrêmes tels que les sources géothermales (e.g. Banerjee et al., 2009; Becraft et al., 2011), les déserts (e.g. Hu et al., 2004; Kirkwood & Henley, 2006), les environnements polaires et alpins (e.g. Harding et al., 2011; Vincent et al., 2004), les eaux à pH élevé (e.g. Bañares-España et al., 2006) ou fortement salées (e.g. Sørensen et al., 2009). Lorsqu'elles colonisent la zone pélagique des écosystèmes aquatiques, les cyanobactéries font partie du phytoplancton au même titre que les microalgues. Les cyanobactéries formant des efflorescences dans les écosystèmes d'eau douce sont caractéristiques des eaux plutôt chaudes comme les lacs stratifiés des régions tempérées à chaudes (Vincent, 2009a). La distribution spatiale des cyanobactéries dans la colonne d'eau est très hétérogène. De larges variations peuvent apparaître, sur l'échelle de quelques millimètres, à plusieurs centaines de mètres et à travers l'ensemble du lac (Oliver et al., 2012) et diffèrent selon les paramètres environnementaux (vents, courants, conditions de croissance) et les capacités adaptatives des taxons considérés (motilité, capacité à former des colonies, forme de la cellule).

1.3 Les proliférations de cyanobactéries

1.3.1. Définition et occurrence

Le terme efflorescences (en anglais “*bloom*”) reste ambigu et les experts ne s'accordent pas sur une définition claire. Cependant, ce terme désigne en général le résultat d'une phase de prolifération massive de cyanobactéries, se traduisant par une importante biomasse, généralement sur une courte période de temps. En effet, la notion de taux de croissance élevé est importante (Smayda, 1997) et révèle d'une déviation de l'équilibre normal de l'écosystème (Roelke & Buyukates, 2002). Une perte de diversité spécifique du phytoplancton est alors constatée, à la faveur d'une ou deux espèces qui deviennent largement dominantes dans la colonne d'eau. On parle

d'efflorescence "nocive" (en anglais HAB : "*harmful algal bloom*") lorsque ce phénomène entraîne des conséquences néfastes pour l'écosystème, la santé publique et l'économie (Hudnell, 2010). Les principaux genres de cyanobactéries proliférantes sont *Anabaena*, *Aphanizomenon*, *Planktothrix* (filamenteuses) et *Microcystis* (coccoïde).

Il est préférable de ne pas confondre les efflorescences avec les "écumes", qui sont le résultat de deux mécanismes successifs: la migration des cellules cyanobactériennes à la surface de la colonne d'eau lorsque les conditions sont calmes, puis une accumulation de ces cellules au niveau des rives par l'intermédiaire de l'action du vent (Chorus & Bartram, 1999; Chorus & Cavalieri, 2000). Les écumes sont donc une conséquence de la prolifération de cyanobactéries qui forment des colonies flottantes (en général *Microcystis*, *Anabaena* et *Aphanizomenon*) et de conditions environnementales particulières. Ainsi, l'absence d'écume ne traduit pas une absence de prolifération de cyanobactéries. Par exemple, d'autres espèces filamentueuses telles que *Planktothrix agardhii* ou *Limnothrix redekei* ne forment pas de colonies flottantes mais peuvent tout de même proliférer et rester dispersées de façon homogène dans le métalimnion (Dokulil & Teubner, 2000). Dans ce cas, la prolifération se traduira par une augmentation de la turbidité de la colonne d'eau.

1.3.2. Impacts des proliférations de cyanobactéries

La présence d'efflorescences de cyanobactéries affecte l'aspect esthétique d'un plan d'eau par l'augmentation de la turbidité, la couleur verte des écumes et la production de molécules malodorantes telles que la géosmine et le 2-méthylisoborneol (Izaguirre et al., 1982; Jüttner & Watson, 2007). Des concentrations importantes de cyanobactéries peuvent également causer une désoxygénéation de la colonne d'eau due à l'augmentation de la décomposition de la matière organique - induisant, entre autres, la mort de nombreux poissons et invertébrés - ainsi qu'une limitation de l'espace disponible pour les autres organismes et la diminution de la biodiversité (Oliver & Ganf, 2000; Paerl et al., 2001). L'inquiétude majeure demeure dans le domaine de la santé publique puisque certaines cyanobactéries synthétisent des

cyanotoxines qui peuvent avoir des effets nocifs sur la santé animale et humaine suite à leur ingestion ou à un contact cutané (Bownik, 2010; Codd et al., 2005). Les trois principaux groupes de cyanotoxines sont définis selon leurs effets sur la santé humaine; c'est-à-dire les neurotoxines (anatoxines, saxitoxines, et β -N-methylamino-L-alanine), les hépatotoxines (microcystines, cylindrospermopsine, et nodularines) et les dermatotoxines (lyngbyatoxines, aplysiatoxines, et lipopolysaccharides). Les microcystines, ayant environ 80 variantes différentes, sont les cyanotoxines les plus communes et sont synthétisées par les genres *Microcystis*, *Anabaena*, *Anabaenopsis*, *Planktothrix/Oscillatoria* et *Nostoc* (Carmichael et al., 2001; Huisman et al., 2005).

Tous les impacts mentionnés ci-dessus peuvent également avoir des conséquences économiques directes ou indirectes. En effet, les proliférations de cyanobactéries nocives peuvent augmenter considérablement les coûts de traitements de l'eau pour en éliminer la couleur, les odeurs et les toxines. Des proliférations excessives peuvent aussi obstruer les filtres et augmenter les coûts d'entretien des stations d'épuration, sans compter la fermeture de plans d'eau (Dodds et al., 2008; Steffenson, 2008). La diminution des activités récréatives (pêche, activités nautiques, baignade) en contact avec l'eau aura également pour conséquence une dégradation de la valeur récréative de certains plans d'eau et des terrains résidentiels environnants. Ainsi, le phénomène de prolifération des cyanobactéries dans les écosystèmes aquatiques est particulièrement préoccupant lorsqu'il touche d'importantes sources d'eau potable telles que le Lac Taihu en Chine, réservoir alimentant près de 33 millions de personnes (Guo, 2007).

1.3.3. Facteurs de contrôles et stratégies écologiques

Au même titre que tous les organismes phototrophes, la survie et la croissance des cyanobactéries est dépendante des ressources disponibles dans le milieu, plus particulièrement d'énergie lumineuse nécessaire pour la photosynthèse, de macronutriments biophiles (C, N, P) et d'éléments traces (Fe, Mn, Zn) nécessaires aux diverses activités métaboliques – entre autres, la transcription et la réPLICATION de l'ADN, la synthèse d'ATP, de NADPH, d'acides aminés et d'enzymes clés (Oliver et al.,

2012), – et une température optimale pour leur croissance (Paerl & Huisman, 2008; Reynolds, 2006). Cependant, la dynamique des différents taxons de cyanobactéries est très variable et dépendante de leurs propriétés écophysiologiques (Carey et al., 2012; Vincent, 2009a). Une compréhension de leur réponse face aux contraintes environnementales est donc nécessaire pour cibler les opérations de gestion et de restauration à mettre en œuvre. En effet, même si les cyanobactéries ne possèdent pas d'organites, la présence de structures cellulaires et d'inclusions ayant des fonctions spécialisées leur confèrent des avantages compétitifs qui contribuent largement à leur succès écologique. Plusieurs exemples sont listés ci-dessous :

Capture de la lumière

Le complexe de capture de la lumière (en anglais LHC ou *light-harvesting complex*) au sein des cellules cyanobactériennes comprend de la chlorophylle *a* et des caroténoïdes tous contenus dans les thylacoïdes, siège de la photosynthèse. Mais contrairement aux microalgues, les pigments majeurs sont les phycobiliprotéines et se situent dans des complexes distincts appelés phycobilisomes attachés à la surface externe de la membrane des thylacoïdes (Grossman et al., 1995). Les chromophores des phycobiliprotéines sont la phycocyanine (A_{\max} 620 nm) et l'alophycocyanine (A_{\max} 650 nm) qui confèrent un aspect bleuté aux cyanobactéries et la phycoérythrine, pigmentée rouge (A_{\max} 560 nm; Bryant, 1991). Les phycobiliprotéines permettent d'exploiter la lumière visible (en anglais PAR ou *photosynthetically available radiation*) à travers un spectre plus large de longueurs d'ondes que l'antenne pigmentaire des micro-algues et permettent un transfert efficace de l'énergie lumineuse vers les centres réactionnels de la photosynthèse; les photosystèmes I et II (Glazer et al., 1994). Si l'on ne tient pas compte de la division des Prochlorophytes, toutes les cyanobactéries contiennent de la phycocyanine et alophycocyanine mais seulement une partie contient en plus de la phycoérythrine. Ces espèces ont la possibilité de s'adapter chromatiquement, c'est-à-dire de passer de la couleur bleu-vert au rouge-brun et ainsi peuvent s'adapter aux différentes longueurs d'onde disponibles (Stomp et al., 2004).

Protection contre les UV

Des niveaux élevés de lumière peuvent photoinhiber ou endommager les centres réactionnels de la photosynthèse mais aussi affecter la fixation de l'N atmosphérique, l'activité de certaines enzymes (e.g. RuBisCO, ATP synthétase), la différenciation cellulaire ou l'assimilation d'ammonium (NH_4^+) et de nitrate (NO_3^-), endommager les phospholipides ou des parties de l'ADN (Castenholz & Garcia-Pichel, 2012). Cependant, les cyanobactéries ont développé un très grand nombre de stratégies de protection contre les méfaits des rayons ultraviolets (UV; cf. revue exhaustive Castenholz & Garcia-Pichel, 2012). Par exemple, plusieurs espèces de cyanobactéries (notamment *Nostoc*, *Calothrix* et *Gloeocapsa*) présentent des écrans anti-UV au niveau de leur membrane externe, incluant la scytonemine (pic d'absorption dans les UV-A) et des acides aminés de type mycosporine (pic d'absorption dans les UV-B; Proteau et al., 1993). De plus, les pigments caroténoïdes (β -carotène, myxoxanthophylle, échinénone, oscilloxanthine et canthaxanthine) sont très efficaces pour la protection vis-à-vis de la photooxydation par les UV et les PAR trop intenses (Vincent and Quesada, 2012). En anglais, on parle de "*carotenoid quenching*" qui est la neutralisation des espèces réactives oxydées par l'activité réductrice des caroténoïdes. Il existe aussi des défenses de type enzymatique contre la photooxydation (e.g. catalase-peroxydase; Tichy & Vermaas, 1999) et des mécanismes de réparation des dommages causés par les UV au niveau des centres réactifs et de l'ADN (Vincent & Quesada, 1993). Cette diversité de méthodes de protection et de réparation contre les UV contribue au succès des cyanobactéries dans une grande variété d'habitats tels que la surface de la colonne d'eau au sein des efflorescences, au niveau des zones benthiques littorales et dans la zone pélagique des lacs très transparents (Vincent, 2009a).

Fixation d' N_2

Les cyanobactéries possédant le gène *nif* ont la capacité de synthétiser la nitrogénase, enzyme responsable de la fixation d' N_2 atmosphérique et de la conversion de N_2 en NH_4^+ puis en acides aminés. Cependant, cette fixation d'N ne peut se faire qu'en

conditions réductrices et est donc sensible à la présence d'oxygène. Les cyanobactéries appartenant aux genres des Nostocales et Stigonematales se sont adaptées pour pouvoir effectuer la fixation d'N en conditions aérobie, par la formation de cellules spécialisées (5 à 10%) appelées "hétérocystes" (ou hétérocyte), lorsque les concentrations en azote dissous inorganique sont faibles (Wood et al., 2010). Cela leur permet ainsi de séparer spatialement la fixation d'N et la photosynthèse. Cependant, certaines souches de cyanobactéries sans hétérocystes, notamment du groupe de *Synechococcus*, sont capables aussi de fixer l'N en conditions aérobie. Ces souches ont été séparées taxonomiquement en *Cyanothece*. L'hypothèse la plus probable est que la séparation de la photosynthèse et de la fixation d'N se ferait de façon temporelle. (jour/nuit). Des inclusions de protéines et/ou d'hydrates de carbone produites pendant le jour et utilisées pendant la nuit permettraient une protection contre l'oxydation (Sherman et al., 1998). Cette capacité de fixation de N, confère aux cyanobactéries un avantage compétitif lorsque l'azote dissous devient limitant dans la colonne d'eau, tel qu'à la fin de l'été.

Réserves

Les cyanobactéries contiennent plusieurs formes d'inclusions leur permettant de stocker des nutriments en excès lorsque les conditions sont favorables. L'azote en excès peut être stocké sous forme de phycocyanine ou de cyanophycine, un copolymère de l'aspartate et de l'arginine (Kolodny et al., 2006). Ces réserves d'N sont ensuite puisées en priorité, avant la fixation d'N₂ atmosphérique, lors des périodes d'insuffisance des ressources (Kolodny et al., 2006). Le phosphore en surplus peut aussi être accumulé dans des granules de polyphosphates, phénomène qui est toutefois observé chez plusieurs microalgues. Le carbone est stocké dans les granules de glycogènes, premier produit résultant de la photosynthèse (Šejnohová & Maršálek, 2012). Ces réserves peuvent ensuite être utilisées pour le maintien de la viabilité et la croissance lorsque les conditions de ressources sont inadéquates.

Flottabilité

Plusieurs espèces de cyanobactéries planctoniques peuvent migrer verticalement de façon active par l'intermédiaire de vacuoles de gaz qui leur fournissent un potentiel de flottabilité (cf. revue de littérature Carey et al., 2012). Ces vacuoles sont des structures cylindriques creuses et rigides, perméables aux gaz mais imperméables à l'eau du fait de la présence de molécules hydrophobes au niveau de leur paroi interne (Šejnohová & Maršálek, 2012). De cette façon les cyanobactéries peuvent migrer vers la surface de la colonne d'eau, là où les conditions de luminosité sont plus avantageuses pour effectuer la photosynthèse (Walsby & McCallister, 1987). Ce pouvoir de flottabilité leur confère un avantage compétitif comparé à de nombreux groupes de microalgues qui subissent la sédimentation. La régulation de cette flottabilité s'effectue en réponse aux différents stimuli environnementaux et peut s'ajuster par des changements dans la densité de gaz ou la proportion de constituants cellulaires plus ou moins denses (e.g. hydrates de carbone, protéines, granules de polyphosphates; Brookes & Ganf, 2001; Romans et al., 1994).

Dormance

Les cyanobactéries ont la capacité de rester en dormance dans les sédiments lorsque les conditions sont défavorables à leur survie et leur croissance, par exemple pendant l'hiver. Cette "hivernation" est rendue possible par l'intermédiaire de la formation de cellules spécialisées aux parois épaissies appelées akinètes (dans le cas des Nostocales) ou par la formation de cellules végétatives (Kaplan-Levy et al., 2010). Lors de cette phase benthique, les conditions physiologiques et la structure des cellules sont conservées et restent comparables à celles des formes planctoniques (Latour et al., 2007). Ces cellules de dormance, peu sensibles à la photoinhibition, peuvent former une banque de graines dans les sédiments et ainsi permettre une recolonisation rapide de la colonne d'eau quand les conditions redeviennent favorables. Cette recolonisation par activation des vacuoles de gaz, appelée "recrutement", serait principalement contrôlée par une augmentation de la température (Wiedner et al., 2007) et de la lumière (Karlsson-Elfgren et al., 2004), et

par des changements dans la disponibilité en nutriments (Brookes et al., 1999; Thompson et al., 2009) et en oxygène (Chauvat et al., 1982). Cependant, cela peut aussi être la conséquence d'un mécanisme passif lié à la resuspension des sédiments fins par l'intermédiaire de l'action du vent et des vagues (Rengefors et al., 2004; Verspagen et al., 2004).

1.4 **Approche scientifique de la thèse**

L'objectif général de la thèse est d'évaluer la structure et la dynamique des communautés cyanobactériennes d'un réservoir d'eau douce en milieu tempéré nordique, en relation avec les variables limnologiques. A cette fin, le lac Saint-Charles, à Québec, a été choisi comme site d'étude, puisque bien représentatif de ce type de milieu. Ainsi, la structure de la communauté cyanobactérienne a été appréhendée à deux niveaux: (i) dans la colonne d'eau et (ii) à la surface des sédiments. L'influence des variables limnologiques locales a été étudiée à ces deux niveaux, mais également les variables à l'échelle du bassin-versant telles que la météorologie et l'hydrologie. Les chapitres 2, 3 et 4 ont été déclinés en un à deux objectifs spécifiques associés à des hypothèses de recherche:

Chapitre 2 : Dynamique limnologique d'un réservoir d'eau potable sujet à des floraisons de cyanobactéries.

- **Hypothèse 2.1:** Les indices trophiques tels que la concentration en chlorophylle *a* élevée, la concentration en phosphore total élevée et la transparence de l'eau faible concordent avec l'apparition de cyanobactéries proliférantes telles que *Microcystis aeruginosa* et *Anabaena flos-aquae*.
- **Objectif spécifique 2.1:** Définir la variabilité spatiale et temporelle des variables limnologiques d'un réservoir tempéré nordique, en accordant une attention particulière aux variables qui pourraient influencer de façon significative la croissance et la prolifération des cyanobactéries (température, stratification et nutriments).

- **Démarche scientifique:** La dynamique limnologique du lac Saint-Charles a été définie à partir d'une collecte de variables physiques (température, pH, conductivité spécifique, transparence, concentration en oxygène dissous), chimiques (azote total, phosphore total, nitrates, phosphore soluble réactif) et biologiques (concentration en chlorophylle *a*, composition phytoplanctonique) pendant 5 années consécutives (2007-2011) et à travers 8 stations. Les interactions entre ces variables ont été mises en évidence à l'aide d'analyses statistiques multivariées. Cette analyse complète, ainsi que l'utilisation d'échelles de référence a également permis de définir le statut trophique du lac Saint-Charles.

Chapitre 3 : Variabilité extrême des proliférations de cyanobactéries dans un réservoir d'eau potable.

- **Hypothèse 3.1:** Les cyanobactéries potentiellement proliférantes *Microcystis aeruginosa* et/ou *Anabaena flos-aquae* apparaissent chaque année à la fin de l'été dans la colonne d'eau.
- **Objectif spécifique 3.1:** Définir la variabilité spatiale et temporelle des cyanobactéries potentiellement proliférantes dans un réservoir tempéré nordique sujet à des efflorescences nocives.
- **Démarche scientifique:** Les variations de biovolume et de composition spécifique des cyanobactéries au cours de la période de stratification estivale ont été suivies pendant 5 années consécutives (2007-2011) au lac saint-Charles par l'intermédiaire d'analyses microscopiques. Ce suivi s'est effectué de façon plus détaillée en 2009 et 2010 pour analyser la variabilité spatiale horizontale et verticale (échantillons de surface et échantillons de profondeur intégrée).

- **Hypothèse 3.2:** *Microcystis aeruginosa* et *Anabaena flos-aquae* sont contrôlées majoritairement par la température de l'eau, la stratification de la colonne d'eau et le rapport N/P.
- **Objectif spécifique 3.2:** Identifier les facteurs de contrôle de la croissance et de la prolifération de *Microcystis aeruginosa* et *Anabaena flos-aquae*.
- **Démarche scientifique:** Les variables limnologiques mesurées au chapitre 1 ont été utilisés pour cette question. Certaines variables ont été transformées en indices : degrés-jours pour la chaleur accumulée, indice de Schmidt pour la stabilité de la stratification thermique. De plus, des données d'hydrologie (niveau d'eau dans le lac, temps de résidence de l'eau) et de météorologie (température de l'air, volume des précipitations) ont été obtenues pour les 5 années. Des mesures de corrélation entre toutes ces variables et les données de biovolume des cyanobactéries dominantes ont permis par la suite d'évaluer l'existence de facteurs de contrôle spécifiques.

Chapitre 4 : Détection des cyanobactéries en dormance dans les sédiments d'un réservoir d'eau potable de type mésotrophe.

- **Hypothèse 4.1:** Les caractéristiques sédimentaires d'un réservoir tel que le lac Saint-Charles sont variables entre les zones littorales et les zones pélagiques ; les zones littorales présentent de meilleures conditions potentielles pour le recrutement de cellules en dormance.
- **Objectif spécifique 4.1:** Définir les caractéristiques sédimentaires et le potentiel d'habitat benthique et de recrutement d'un réservoir à écoulement rapide situé en zone tempérée nordique.
- **Démarche scientifique:** Afin de décrire au mieux l'habitat benthique du lac Saint-Charles, des observations telles que la profondeur de la colonne d'eau et le pourcentage de recouvrement des macrophytes au cours de l'été ont été effectuées sur le terrain. De plus, l'échantillonnage de carottes de sédiments a permis d'analyser la granulométrie, la concentration en matière organique et le taux de sédimentation au lac Saint-Charles. Des zones préférentielles de

dormance et/ou de recrutement ont été déterminées en tenant compte de ces caractéristiques mais aussi des caractéristiques limnologiques telles que la pénétration de la lumière, le potentiel de resuspension, la température maximale au fond de la colonne d'eau et le potentiel d'hypoxie.

- **Hypothèse 4.2 :** Les sédiments du lac Saint-Charles contiennent une réserve viable de cellules phytoplanctoniques en dormance, incluant des populations qui ont le potentiel d'initier la prolifération d'*Anabaena flos-aquae* et *Microcystis aeruginosa*
- **Objectif spécifique 4.2:** Quantifier et identifier des populations de phytoplancton en dormance dans les sédiments d'un réservoir tempéré nordique, en portant une attention particulière sur les cyanobactéries benthiques hivernantes susceptibles de servir d'inoculum pour les proliférations dans la colonne d'eau.
- **Démarche scientifique:** Afin d'examiner cette abondance, 5 méthodes de détection des cyanobactéries benthiques ont été comparées. La première méthode s'est déroulée *in situ*, en utilisant un spectrofluorimètre submersible spécifique à la phycocyanine. L'émission de fluorescence à la surface des sédiments a été mesurée selon un quadrillage serré et ce, à 4 dates pendant l'été 2010. Ces résultats ont ensuite permis de construire une carte d'interpolation de la concentration en phycocyanine à la surface des sédiments du lac Saint-Charles. Les autres méthodes ont été appliquées en laboratoire, sur les sédiments récoltés au carottier. La microscopie à épifluorescence, la détection de pigments spécifiques par chromatographie HPLC ainsi que la mise en culture en milieu ambiant et en incubateurs ont ainsi été testées.

1.5 Description du site d'étude

Le lac Saint-Charles est un réservoir d'eau potable alimentant près de 300 000 résidents de la ville de Québec. Il est situé à la latitude 46°54'N, longitude 71°22'W, et à une altitude de 150 m au dessus du niveau de la mer. Le lac fait partie de l'arrondissement de la Haute-Saint-Charles dans l'agglomération de la Ville de Québec, et de la municipalité des cantons unis de Stoneham-et-Tewkesbury. C'est au début du XX^e siècle que l'on entreprend des travaux visant à faire du lac un réservoir d'eau potable. Un barrage est érigé en 1934 afin d'augmenter le volume d'eau et d'assurer ainsi un débit régulier à l'extrémité sud du lac. En 1950, le barrage a été rehaussé et l'eau a submergé une partie des terres basses, modifiant l'hydrologie naturelle du lac (Tremblay et al., 2001).

Le lac a une superficie totale de 3,6 km², un volume total de 14,8x10⁶ m³ et est composé de deux sous-bassins qui diffèrent fortement en morphométrie. Le bassin nord est de forme conique avec une profondeur maximale de 17,5 m et contient 70% du volume total du lac. Le bassin sud présente quand à lui un fond plat et a une profondeur maximale de 6 m.

Du point de vue géologique, le lac Saint-Charles est un lac de fond de vallée localisé sur des dépôts glacio-marins (limon et sable) formés durant et suivant le retrait de la mer de Champlain il y a environ 12 000 ans (Gérardin & Lachance, 1997). Les collines environnantes sont composées de granites et de gneiss appartenant au socle Grenvillien du Bouclier Canadien et couvertes de forêts à dominance de feuillus de type Frêne rouge, Peuplier baumier, Peuplier-faux tremble, Érable rouge et Bouleau jaune (Gérardin & Lachance, 1997). Selon la classification de Litynski (1988), la région connaît un climat tempéré froid sub-humide avec des précipitations annuelles autour de 1300 mm et une durée de croissance de la végétation estimée à environ 165 jours (Environnement Canada, 2012; Gérardin & McKenney, 2001).

La population humaine résidentielle dans le bassin versant a connu une croissance soutenue depuis le début des années 1970 (population de 74 070 en 2006), les zones

urbaines et routes constituant 14% de la superficie totale du bassin versant, tandis que les zones forestières couvrent 78,5% (APEL, 2009).

Le bassin versant du lac s'étend sur 169 km² et fait partie du bassin versant de la rivière Saint-Charles (Fig 1.3.) qui se draine dans le fleuve Saint-Laurent à la hauteur de la ville de Québec. Les eaux usées du territoire sont traitées par des installations sanitaires individuelles ou par l'une des deux stations d'épuration; l'une étant située dans la Ville de Lac-Delage et l'autre dans la municipalité des cantons unis de Stoneham-et-Tewkesbury. Les deux stations d'épuration déversent leurs eaux traitées dans les deux principaux affluents du lac Saint-Charles : la rivière des Hurons (drainant 80% du bassin versant) et l'effluent du Lac Delage (drainant 3% du bassin versant). Les normes de rejets de phosphore total et de coliformes fécaux sont respectées dans les deux stations d'épuration et la qualité bactériologique et physico-chimique de l'eau des principales rivières du bassin versant est considérée "satisfaisante à bonne" (APEL, 2009). L'unique effluent du lac est la rivière Saint-Charles dont le débit moyen annuel mesuré 9 km en aval du lac est de 8,5 m³ s⁻¹ (Gaborit et al., 2010).

Une étude paléolimnologique et limnologique a été menée en 1997 et a indiqué que le lac se situait au stade mésotrophe de son évolution trophique mais qu'il n'y avait pas d'indication d'accélération de l'eutrophisation due aux activités anthropiques depuis 1950 (Tremblay et al., 2001). Cependant, près d'une décennie plus tard (2006 et 2007), des proliférations importantes de cyanobactéries ont été observées en fin d'été et début d'automne sur le lac Saint-Charles avec une dominance des genres *Microcystis* et *Anabaena* (APEL, 2009; Bourget, 2011; Warren, 2011). En effet, la concentration de cyanobactéries a atteint 2x10⁶ cellules de *Microcystis aeruginosa* par mL dans une baie du bassin nord le 17 août 2007. De plus, la concentration en microcystine-LR (6,2 µg L⁻¹) atteignait plus de quatre fois le critère de qualité pour l'eau potable proposé par Santé Canada (Bourget, 2011). La surveillance attentive des conditions trophiques du lac et le développement d'un plan de gestion solide pour la qualité de l'eau sont donc des enjeux cruciaux pour la ville.

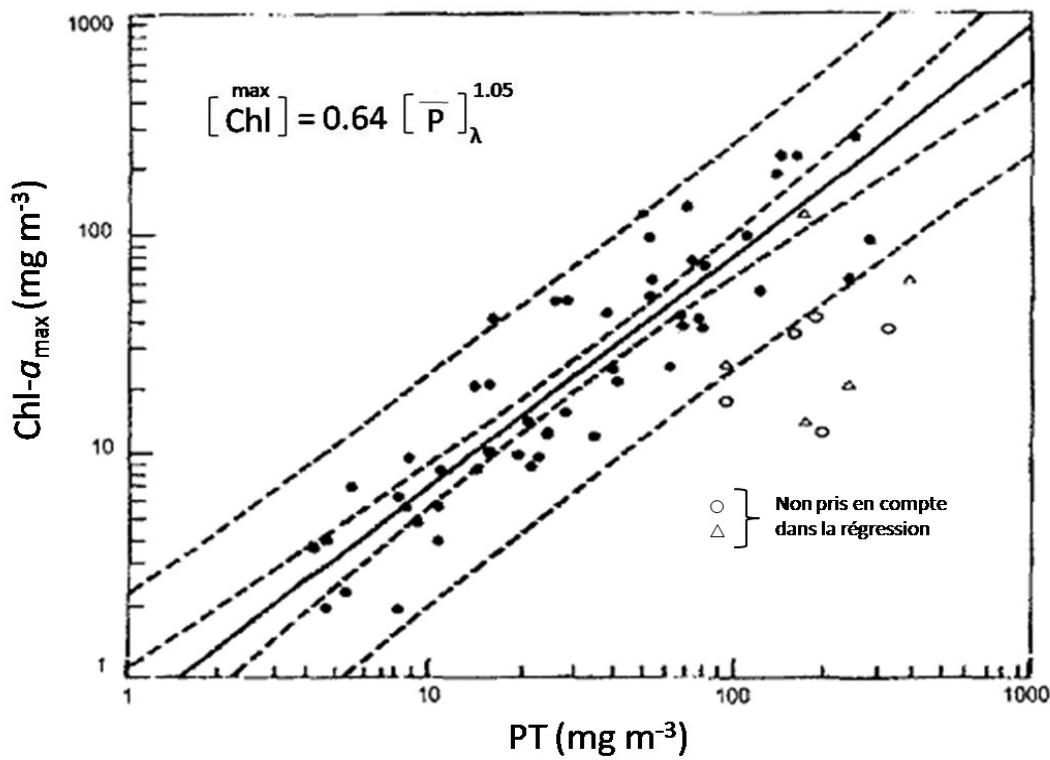


Figure 1.1. Modèle de l'Organisation de Coopération et de Développement Économiques (OCDE) de l'eutrophisation des lacs proposé par Vollenweider en 1968 (d'après Capblancq & Décamps, 2002).

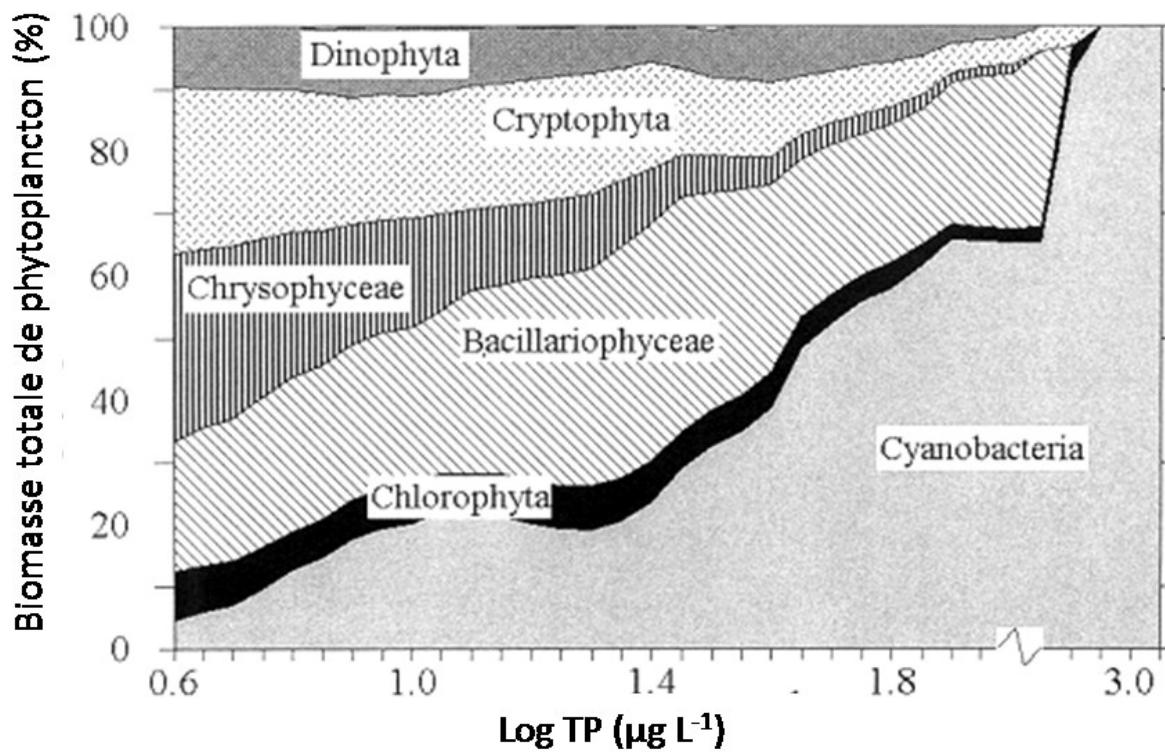


Figure 1.2. Contribution relative (%) des différents groupes taxonomiques par rapport à la biomasse phytoplanctonique totale, en fonction de la concentration de phosphore total (sur 91 lacs au Canada; d'après Watson et al., 1997).

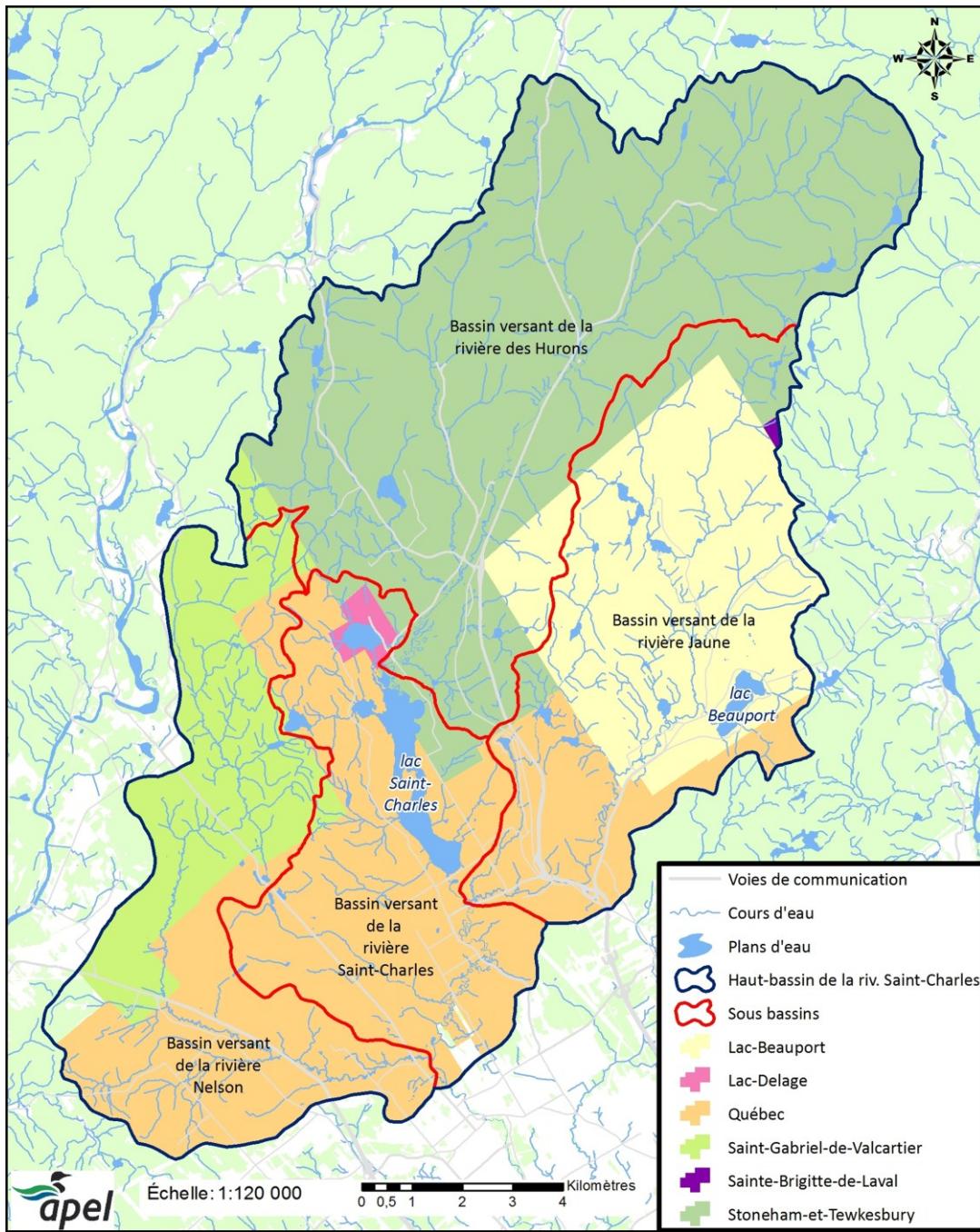


Figure 1.3. Carte du bassin-versant de la Haute Saint-Charles (Magnan, 2011).

Chapitre 2. Limnological dynamics of a reservoir subject to harmful cyanobacterial blooms

Résumé

Les cyanobactéries formant des floraisons sont largement reconnues comme étant contrôlées majoritairement par des conditions particulières de lumière, température et disponibilité en nutriments. Cependant, dans le cas des réservoirs à faible temps de résidence, il peut y avoir des contrôles supplémentaires imposés par le régime d'écoulement longitudinal. Le lac Saint-Charles est une retenue d'eau douce de vallée fluviatile et une importante source d'eau potable pour la ville de Québec (Canada). Des efflorescences de cyanobactéries nocives ont été observées dans ce lac en 2006 et ont suscité des inquiétudes quant à la détérioration de la qualité de l'eau. La présente étude a été menée pendant 5 étés consécutifs (2007-2011), à 8 sites répartis à travers le lac, afin d'évaluer le potentiel d'habitat pour les cyanobactéries et étudier les conditions limnologiques associées à leur croissance et à leur prolifération. Au cours de la stratification, les conditions s'avèrent être oligo-mésotrophes à mésotrophes avancées, avec des moyennes de concentrations en chlorophylle *a* de $5.1 (\pm 1.9) \mu\text{g L}^{-1}$, et en phosphore total de $9.9 (\pm 2.8) \mu\text{g L}^{-1}$. Le lac a également montré plusieurs caractéristiques d'eaux plus riches, incluant la présence de taxa typiques d'eaux eutrophes (*Microcystis aeruginosa*, *Anabaena flos-aquae* et *Dinobryon divergens*), des périodes de déficit en oxygène hypolimnétique, et une profondeur de Secchi toujours faible (2.6 ± 0.2 m). Toutefois, les cyanobactéries formant des efflorescences ont été observées de façon épisodique, l'anoxie a été limitée spatialement et des analyses précédentes ont indiqué que la profondeur de Secchi est contrôlée davantage par la matière organique dissoute colorée plutôt que par la chlorophylle *a*. Ces résultats mettent en évidence la nature dynamique des réservoirs à écoulement rapide, donnant lieu à d'importantes fluctuations saisonnières et interannuelles dans le potentiel de prolifération de cyanobactéries.

Abstract

Bloom-forming cyanobacteria are widely recognized as being mainly controlled by specific conditions of light, temperature and nutrient availability, but in high through-flow reservoirs there may be additional controls imposed by the longitudinal flow regime. Lake St. Charles is a dammed river valley reservoir that provides drinking water for Québec City, Canada. A toxic cyanobacterial bloom was first observed in this lake in 2006 and raised concerns about its deteriorating water quality. The present study was undertaken during 5 consecutive summers (2007-2011) at 8 sites distributed across the lake in order to assess its suitability as a habitat for cyanobacteria, and the limnological conditions associated with the growth and proliferation of bloom-forming taxa. During stratification, trophic conditions were oligo-mesotrophic to advanced mesotrophic, with summer average chlorophyll *a* concentrations of $5.1 (\pm 1.9) \mu\text{g L}^{-1}$, and total phosphorus concentrations of $9.9 (\pm 2.8) \mu\text{g L}^{-1}$. Lake St. Charles also showed several features of more enriched waters, including the presence of eutrophic bloom-forming phytoplankton taxa (*Microcystis aeruginosa*, *Anabaena flos-aquae* and *Dinobryon divergens*), periods of hypolimnetic oxygen depletion and anoxia, and a persistently low Secchi depth (2.6 ± 0.2 m). However, the bloom-forming cyanobacteria occurred episodically, the anoxia was limited in spatial extent, and previous analyses indicated that Secchi depth was controlled by colored dissolved organic matter rather than chlorophyll *a*. The results underscore the limnologically dynamic nature of this reservoir system, giving rise to large seasonal and interannual fluctuations in its suitability for bloom-forming cyanobacteria to grow and dominate the phytoplankton.

2.1 Introduction

The impoundment of water to create reservoirs has accelerated rapidly over the last few decades to keep pace with the growing human population needs for drinking water, agricultural and industrial supplies, and hydropower (Downing et al., 2006). This class of aquatic ecosystems has a number of distinctive limnological properties, including a high ratio of drainage area to lake surface area and the potential for large impacts of anthropogenic activities in the watershed on reservoir hydrology and water quality. One set of impacts of particular concern is eutrophication (Smith et al., 1999) and the development of noxious cyanobacterial blooms (e.g. Dzialowski et al., 2011) due to high nutrient loading from residential and agricultural development.

The proliferation of bloom-forming cyanobacteria in lakes and reservoirs has a variety of negative effects on these aquatic ecosystems, and may greatly diminish their capacity to provide ecosystem services. By forming unpleasant surface scums, blooms of cyanobacteria can lead to the degradation of the aesthetic and recreational value of some water bodies. The collapse and decomposition of blooms may cause the deoxygenation of the water column, and the death of fish and other animals (Oliver & Ganf, 2000; Paerl et al., 2001). Some of the most common bloom-forming taxa synthesize cyanotoxins that may have harmful effects following their ingestion or skin contact (Chorus et al., 2000; Cox et al., 2005; Ernst et al., 2005), and are therefore of major human health concern. Harmful cyanobacteria blooms can significantly increase the costs of water treatment to remove the large phytoplankton biomass and the associated toxins and taste compounds (Jüttner & Watson, 2007; Steffenson, 2008).

Remediation of the water quality problems associated with cyanobacteria requires an understanding of the mechanisms favoring dominance of bloom-forming taxa in freshwater ecosystems. Many factors have been hypothesized to play a role, including high temperatures (Paerl & Huisman, 2008; Reynolds, 2006; Vincent, 2009a), low CO₂ concentrations (Shapiro, 1990), elevated nitrogen and phosphorus inputs (Downing et al., 2001; Wu et al., 2010), stable thermal stratification (Oliver & Ganf, 2000; Visser

et al., 2005), benthic ‘seedbanks’ of resting stages (Barberio & Welch, 1992; Verspagen et al., 2005) and trace element availability (Xing et al., 2008). Bloom-forming cyanobacteria are most frequently found in nutrient-rich waters, and most consistently occur under high total phosphorus concentrations (Dzialowski et al., 2011; and references therein). The control of nutrient loading has therefore become the most widely adopted and effective way of reducing the risk of cyanobacterial blooms.

Bloom-forming cyanobacteria have been increasingly reported in the province of Québec, Canada, over the last decade, and have generated widespread public concern given the importance of lakes and reservoirs as social and economic resources for the province. One water body that has attracted particular attention is Lake St. Charles, a municipal reservoir and the water source for 285,000 residents in Québec City. A previous study in 1997 using a combination of limnological and paleolimnological methods indicated that this lake had a mesotrophic nutrient status, and the authors warned that additional enrichment could cause more serious degradation of the reservoir and the onset of harmful algal blooms such as cyanobacteria (Tremblay et al., 2001). However this study received little attention until the observed appearance of a toxic cyanobacterial bloom in 2006, almost a decade later. In August 2007, *Microcystis aeruginosa* developed a scum and was recorded up to a maximum concentration of 2×10^6 cells mL⁻¹ in an embayment of the lake (Echo Bay), and microcystin-LR was detected up to 6.2 µg L⁻¹, more than four times higher than the safety limit for drinking water proposed by Health Canada (Bourget, 2011; CEHQ, 2007). The appearance of these blooms raised questions about the sustainable water quality of Lake St. Charles and led to intense discussions and debate about the control of nutrient sources from the watershed.

The control of cyanobacteria blooms in Lake St. Charles and similarly affected reservoirs requires an improved understanding of the limnological properties of these water bodies. Such information for Lake St. Charles is scarce, and has been mostly limited to short term, localized observations. To broaden this understanding, the

present study aimed to better define the spatial and temporal scales of variability in the limnology of Lake St. Charles by way of detailed measurements at multiple sites over 5 consecutive summers. Particular attention was given to the occurrence of colonial cyanobacteria in the net plankton, and the temperature, stratification and nutrient regimes that could potentially influence their growth and proliferation in this lake.

2.2 Material and methods

2.2.1. Study site

Lake St. Charles is a reservoir located 21 km north of Québec City at latitude $46^{\circ} 54' N$, longitude $71^{\circ} 22' W$, and an altitude of 150 m above sea level. It has a total area of 3.6 km^2 and a total volume of $14.8 \times 10^6 m^3$, and is composed of two sub-basins that differ in morphometry (Fig. 2.1). The north basin is cone-shaped with a maximum depth of 17.5 m and 70% of the total lake volume, while the south basin has a flatter bottom with a maximum depth of 6 m (Fig. 2.1 and 2.2). The residence time of water in the epilimnion is relatively short and estimated in the range 30-100 days during the ice-free period (Rolland et al., 2013; chapter 3 of this thesis). The watershed of the lake extends over 169 km^2 (including the lake surface) and the lake basin is underlain by glacio-marine deposits; the surrounding mountains are composed of granite and gneiss (Canadian Shield) covered by boreal forest, while the valley is composed of shale and sandstone (Gérardin & Lachance, 1997). The area experiences a north temperate, sub-humid climate, with annual precipitation around 1300 mm. The mean annual flow measured at the gauging station of the single effluent of the lake, the St. Charles River, is $8.5 m^3 s^{-1}$ (Gaborit et al., 2010). The residential population in the watershed has experienced sustained growth since the early 1970s (population of 74,070 in 2006), and the urban areas account for 14% of the total watershed area, while forest covers 78.5% and the remaining 7.5% are agricultural, other aquatic ecosystems and wetlands (APEL, 2009).

2.2.2. Sampling

Sampling was conducted each summer over a 5-year period from 2007 to 2011. Eight sampling stations (Fig. 2.1) covering several bays and the open lake were visited 2-4 times per month, from June to October. One additional sampling site (Hur; Fig 2.1) located downstream of the principal inflow (the Hurons River) was selected for additional nutrient analyses.

2.2.3. Physical and meteorological variables

Temperature, pH, specific conductivity, and dissolved oxygen concentration were measured throughout the water column using a submersible probe (YSI6600V2, YSI Incorporated) at all sampling sites. The apparent redox potential (Eh) was also measured by using another YSI 6600V2 probe in 2011. Transparency measurements were made with a 20 cm diameter Secchi disk, and the mean value of three measurements was recorded at each site. A thermistor chain (Onset Stow Away Tidbit Underwater Data Logger, $\pm 0.2^{\circ}\text{C}$) was installed in the deepest part of the lake to obtain continuous measurements of water temperature down the water column over the entire sampling periods (every 15 min). The thermistors were set at 0.5, 4.5, 10.5 and 15.5 m in 2007 and 2008 and at 0.5, 1.5, 2.5, 3.5, 4.5, 5.5, 6.5, 8.5, 10.5 and 16.5 m in 2009, 2010 and 2011.

2.2.4. Biological variables

Surface samples and integrated water column samples were obtained with a 5-m long flexible plastic tube, transferred into brown plastic bottles, and stored in cold, dark conditions until further processing. Subsamples of 100 to 1000 ml, depending on the seston concentration, were filtered under low light onto Whatman GF/F (nominal pore size of 0.7 μm) within 5h of sampling to minimize the degradation of pigments. The filters were stored at -80°C until extraction of pigments in ethanol at 70°C , and the chlorophyll a concentration (Chl-a) was determined by fluorescence measurements before and after acidification (Nusch, 1980) using a Varian Cary

Eclipse spectrofluorometer (Varian Inc., Canada). Phytoplankton samples including cyanobacteria were collected with a plankton net (Birge net, 60 µm) drawn through the upper 4 m of the water column at each site, and these were examined under an inverted microscope (Axiovert 200, Zeiss) within 3h of sampling to determine the taxonomic composition of large-cell and colonial phytoplankton, including bloom-forming cyanobacteria.

2.2.5. Chemical variables

Unfiltered water samples were collected in polyethylene bottles washed with hydrochloric acid (10%) and rinsed 7 times with deionized water, and were preserved in sulfuric acid (0.2% final concentration). These samples were digested with persulphate to determine total nitrogen (TN) and total phosphorus (TP), and analyzed respectively in a Lachat flow injection analyser (QuikChem 8500) and by standard colorimetry using a Genesys 10UV spectrophotometer (Thermo Spectronic). Filtered water samples (0.2 µm pore size) were analyzed for nitrate (NO_3^-) using an ICS 2000 ionic chromatograph (Dionex), and soluble reactive phosphorus (SRP) was measured by a colorimetric method with the Genesys 10UV spectrophotometer.

2.2.6. Statistical analysis

Analyses were performed using XLSTAT 2012 and SIGMASTAT 11.0. Initial Shapiro-Wilk tests indicated that the data for most variables were not normally distributed, and the variances were heteroscedastic. Therefore, the non-parametric Friedman repeated measures ANOVA test was used to determine significant differences. Tukey's multiple comparisons were then made to identify significant differences ($p<0.05$) between groups of dates or sampling sites when the sample sizes were unequal and Dunn's multiple comparisons were made when the sample sizes were equal. Principal components analysis (PCA) on the Spearman rank order correlation matrix was also used to ordinate the ensemble of limnological variables in a reduced space.

2.3 Results

2.3.1. Bloom-forming cyanobacteria in the phytoplankton

A total of 81 taxa of net phytoplankton were identified throughout the course of the 5-year study, representing 9 divisions (Table 2.1). For the total species list, Chlorophyta contributed the largest number of taxa (33.3%), followed by Cyanobacteria (28.4%), Bacillariophyta (22.2%) and phytoflagellates (13.6%). In 2007 and 2008, the bloom-forming cyanobacterium *Microcystis aeruginosa* dominated in abundance during August and September. In 2009, bloom-forming cyanobacteria were in low abundance, while colonial picocyanobacteria (*Aphanocapsa* sp.) and Chrysophyceace (*Dinobryon divergens*) rose to prominence. In 2010, the bloom-forming cyanobacterium *Anabaena flos-aquae* dominated the water column throughout the summer. In 2011, there was no clear pattern of dominance but rather an assemblage of 3 to 4 species that were found in co-abundance between June and August: *Dinobryon divergens*, *Aphanocapsa* sp., *Anabaena flos-aquae*, and the diatom *Aulacoseira ambigua*.

2.3.2. Chlorophyll *a*

The summer average of surface Chl-*a* concentration was $5.1 \pm 1.9 \text{ } \mu\text{g L}^{-1}$, with significant variation ($p < 0.001$) among years (Table 2.2) but not between sampling sites. Chl-*a* concentrations were respectively 34 and 49% higher in 2007 and 2008 and 20, 36 and 26% lower in 2009, 2010 and 2011 relative to the 5-year average. Surface samples were compared to the 5 m-integrated samples in 2010 at stations N3, N4 and S4 (Fig. 2.3). At the deepest site N3, the differences between the surface and integrated samples were not significant. However, the 5 m-integrated samples tended to show slightly higher Chl-*a* concentrations than those taken at the water surface. The Chl-*a* maximum was not at the surface but deeper in the water column, except on 6 and 9 August 2010. At N4, there was a statistically significant difference between surface and integrated samples ($p = 0.02$), and the pattern differed from that at N3. The Chl-*a* concentration was three times greater in surface samples ($8.5 \text{ } \mu\text{g L}^{-1}$) than

in 5 m-integrated samples ($2.9 \mu\text{g L}^{-1}$) on 5 July 2010, which was the period of an *Anabaena flos-aquae* bloom ($12,456 \text{ cells mL}^{-1}$ at N4). A similar pattern was also observed on 12 July and 9 August 2010. Conversely, the Chl- α concentration was higher in integrated samples on 19 July and 17, 23 and 30 August. At S4, there was no statistically significant difference between surface and integrated samples.

2.3.3. Temperature and stratification regimes

The average surface temperature ($18.5 \pm 4.1^\circ\text{C}$) between 1 June and 15 October was significantly ($p<0.001$) higher in 2008, 2009 and 2010 relative to 2007 and 2011 (Table 2.2). When considering only the warmer months (July and August), the average surface temperature was significantly ($p<0.001$) higher in 2010 ($21.3 \pm 2.0^\circ\text{C}$) relative to the other years. There were also differences in the timing of lake water heating and cooling: maximum surface temperatures were recorded on 13 July in 2010 and 19 July in 2011, but not until 31 July in 2007, 18 August in 2009 and 3 September in 2008 (Table 2.2). There was no significant variation in surface temperature on each date of sampling among sites: the among-site SD values for each year between June and October were 0.6-1.1°C in 2007, 0.4-0.9°C in 2008, 0.2-0.8°C in 2009, 0.2-1.1°C in 2010 and 0.4-1.0°C in 2011.

The north basin of Lake St. Charles followed the stratification and mixing cycle of a typical dimictic lake, and was strongly stratified throughout summer each year. However, there were interannual differences in the timing and strength of stratification. The north basin became thermally stratified in late May/early June in 2010 and in mid-June in the other years, persisting until mixing, which began between mid-October to early November depending on the year (Fig. 2.4). Mean thermocline depth ($3.0 \pm 1.6 \text{ m}$) was deeper in 2007, 2008 and 2010, and shallower in 2009 and 2011. Stratification was also present in the south basin but less persistent due to a shallower mean depth (5.2 m).

2.3.4. Transparency

The average water column transparency as estimated by Secchi disc was generally low (2.6 ± 0.4 m), with only small differences among stations and years (Table 2.2). The average transparency was however significantly lower ($p<0.001$) in 2011 (21% less than the overall 5-year mean).

2.3.5. Dissolved oxygen

Dissolved oxygen concentrations were near saturation throughout the water column at the beginning of the summer but decreased gradually in the deeper waters during the stratification period, from June to September (Fig. 2.5). There was a severe oxygen deficiency in the deepest portions of the lake in late summer/early fall during each of the five years of sampling, with hypoxic and sometimes near-anoxic conditions. The minimum oxygen saturation values at 15 m were: 0.6% on 10 October 2007, 2.2% on 19 September 2008, 5.2% on 16 September 2009, 0.6% on 14 September 2010, and 0.5% on 19 September 2011. In the shallower south basin and near-shore sites, the water column was well oxygenated from the surface to the bottom (5 m). The apparent redox potential (Eh) measured at bottom of N3 (16.5 m) in 2011 was -75 mV on 24 August, -240 mV on 8 September, -152 mV on 19 September, and -149 mV on 4 October.

2.3.6. Conductivity and pH

The average specific conductivity (surface to bottom, all sampling sites) of Lake St. Charles (Table 2.2) indicated a low ionic content ($77.2 \pm 17.4 \mu\text{S cm}^{-1}$). The values were significantly higher ($p<0.001$) in 2010 relative to the other years, but there was no significant difference among sites, except at N1 where the conductivity was highly variable with time ($CV = 25\%$). The pH values showed near neutral conditions throughout the 5 years, with little variation among sites, depths or dates. The overall average pH in Lake St. Charles was 7.5 ± 0.4 .

2.3.7. Nutrients

The summer average TP concentration was higher in 2011 (+21%) and lower in 2009 (-32%) relative to the 5-year mean ($9.9 \pm 2.8 \mu\text{g L}^{-1}$; Table 2.2). The spatial and temporal distribution of phosphorus was studied in detail in 2007 and 2008, and these observations showed that surface TP exceeded $15 \mu\text{g L}^{-1}$ on several dates and sampling sites in 2007, but in particular at the site close to the Hurons River entry to the lake (Hur; Fig. 2.6). Highest TP concentrations were recorded in the bottom of the deep part of the lake (N3): $27 \mu\text{g L}^{-1}$ and $36 \mu\text{g L}^{-1}$ on 26 September 2007 and 10 October 2007. High bottom concentrations were also recorded during early autumn in 2008 (maximum of $20 \mu\text{g L}^{-1}$ on 14 October). The differences between bottom and surface TP were not significant for the other dates, except on 26 June and 4 August 2008 when TP was higher at surface. Average concentrations of surface SRP were below or just above the detection limit ($0.5 \mu\text{g L}^{-1}$) each year (Table 2.2). Differences between bottom and surface SRP at N3 in 2007 and 2008 were not significant except on 7 July 2007 ($p=0.021$; concentration 3x higher at bottom compared to surface). The average TN concentration was higher in 2008 (+30%) and lower in 2009 (-46%) and 2010 (-32%) relative to the 5-year average ($398 \pm 167 \mu\text{g L}^{-1}$). The mean TN:TP ratio by weight varied from 30 (2011) to 57 (2008). Concentrations of NO_3^- were in the range $20\text{--}200 \mu\text{g N L}^{-1}$, and the summer average was higher in 2008 and 2011 and lower in 2009 (Table 2.2).

2.3.8. Principal Components Analysis

Principal components analysis was applied to the overall limnological data set for all the sampling sites and dates. The first two axes of the PCA accounted for 40% of total variance (Fig. 2.7). Within the sampling dates plot, Axis 1 shows a separation between 2011 (bottom) and the other years (top), and Axis 2 shows a separation between years 2007+2010 (left) and years 2008+2009 (right). No spatial pattern was evident from the sampling sites plot (not shown). Within the variables plot, Axis 1 was especially associated with conductivity, TN, SRP and NO_3^- . Thus, the 2007/2010 group was characterized by waters of higher conductivity and the 2008/2009 group was

associated with higher nutrient concentrations (TN, SRP, NO₃⁻). Axis 2 was especially associated to temperature, pH, O₂, Secchi depth and TP. Thus, 2011 was characterized by higher phosphorus concentrations but lower temperature, oxygen saturation and transparency than in the other years.

2.3.9. Correlation analysis

The contingency table of correlations indicated significant relationships among several key variables (Table 2.3). Chl-a was strongly and positively correlated with temperature, conductivity, O₂ saturation, and pH, and negatively correlated with Secchi depth. Temperature, O₂ saturation and pH were positively inter-correlated, but negatively correlated with TN. Secchi depth was positively correlated with conductivity and pH, and negatively with TN and SRP.

2.4 Discussion

2.4.1. Bloom-forming cyanobacteria and total phytoplankton biomass

Our net phytoplankton analyses showed that although the algal assemblage of the epilimnion of Lake St. Charles was highly variable in species composition among the 5 years of sampling, cyanobacteria were often present and in some years bloom-forming taxa dominated the phytoplankton. The most common cyanobacteria were the colonial species *Anabaena flos-aquae*, *Microcystis aeruginosa*, *Woronichinia naegeliana*, *Aphanocapsa* and *Aphanothecace* spp. The latter two genera are more typical of mesotrophic waters, while the former three are characteristic of eutrophic conditions (Cronberg & Annadotter, 2006; Wehr & Sheath, 2003). Both *M. aeruginosa* and *A. flos-aquae* are well known to be potentially toxicogenic (Chorus & Bartram, 1999), and *W. naegeliana* is also known to produce toxins (Cronberg et al., 1999). *Aphanocapsa/Aphanothecace* spp. are generally considered non-toxicogenic, although an evaluation of cyanobacterial abundance and toxicity in 22 lakes in southern Quebec found that *Aphanocapsa* was sometimes associated with toxicity (Giani et al., 2005). Several other taxa that were often observed in Lake St. Charles, such as *Pediastrum* sp.,

Scenedesmus sp., *Asterionella formosa*, *Aulacoseira ambigua* and the chrysophyte *Dinobryon divergens*, are similarly common in eutrophic waters. The diatom *Tabellaria flocculosa* was abundant during spring and autumn, and is known to be common in mesotrophic waters (Van Dam et al., 1994). Many of these taxa, such as the fast-sinking colonial diatoms, would be outcompeted by the gas vacuolate cyanobacterial species once stratification is established in summer (Kalff, 2002).

The total phytoplankton analysis suggests that the environmental conditions of Lake St. Charles are conducive to bloom-forming cyanobacteria, but only intermittently during summer, and not in all years. Although the periodic abundance of cyanobacteria taxa implies that this reservoir has entered a eutrophic status of nutrient enrichment, the phytoplankton biomass analyses based on Chl-*a* concentrations imply mesotrophic conditions. The overall mean Chl-*a* value of 5 µg L⁻¹ was below the usual thresholds for eutrophy: for example 8 µg L⁻¹ for the Organisation de Coopération et de Développement Économiques criteria (OCDE; 1982) and the province of Quebec criteria (MDDEP, 2007).

Mean Chl-*a* concentrations at the water surface varied greatly among years, with values in 2010 and 2011 that were half those in 2007 and 2008. This indicates that there were large year-to-year differences in the limnological conditions for phytoplankton growth and loss processes. Some of this variability may also reflect changes in the vertical distribution of algal biomass. At stations N3 and N4, the 5-m integrated samples often had significantly higher concentrations than the surface samples, indicating that deeper populations might have been incompletely sampled. A previous study based on phycocyanin fluorescence profiles in the water column showed that the maximum biomass of cyanobacteria was most often localized between 0 and 6 m, but a large hypolimnetic population was detected in late September early October 2007 (Warren, 2011). It will be necessary to consider the vertical variability in the phytoplankton in future sampling and monitoring of Lake St Charles and similar reservoirs.

The spatial variability in Chl-*a* biomass was minor relative to that observed in many small lakes elsewhere (Kalff, 2002), and there were rarely significant differences among the 8 sampling stations. This homogeneous distribution may be linked to the fluvial behavior of Lake St. Charles, which may lead to dilution and rapid flushing of the epilimnetic population throughout the lake to the outlet. However, near-shore accumulations of bloom-forming cyanobacteria were sometimes observed, and were associated with the floating of buoyant colonies and their wind-driven accumulation at the shore. For example, in September 2007, a localized accumulation of *Microcystis aeruginosa* was observed in Echo Bay, with a measured Chl-*a* concentration at the surface of 300 µg L⁻¹ (Bourget, 2011). These near-shore accumulations of noxious cyanobacteria are well known from other lakes, and may subsequently provide an inoculum into the offshore waters (Ishikawa et al., 2002).

2.4.2. Temperature and stratification

Bloom-forming cyanobacteria are favored by elevated water temperatures through two mechanisms (Paerl & Huisman, 2008; Vincent, 2009a): direct effects on their cellular metabolism and growth rates (including synthesis of gas vesicles and carbohydrate production; Šejnohová & Maršálek, 2012), and through the heating of the water column that results in stronger stratification, thereby favoring buoyant species (e.g. Johnk et al., 2008). Bloom-formers have an exceptionally high Q₁₀ value for growth and a warm temperature optimum for maximum photosynthesis (in the range 20-27°C depending on the taxon; Johnk et al., 2008; Robarts & Zohary, 1987; Varis, 1993) compared with most diatoms and chlorophytes. This threshold temperature range was achieved each summer from late May to late June in Lake St. Charles, with maximum surface water temperatures in the range 22-27°C. Moreover, the north basin remained stratified each summer for approximately 4 months (early June to early October). This reduced vertical turbulent mixing and prolonged water column stability could potentially shift the competitive balance in favor of buoyant cyanobacteria. By contrast, the major polymictic behavior of the south basin would

offer better conditions for filamentous species that prefer mixing conditions such as *Limnothrix* sp. (Dokulil & Teubner, 2000).

2.4.3. Nutrient regime

The proliferation of cyanobacteria typically occurs under conditions of high total phosphorus concentrations, with a reported threshold of $20\text{-}30 \mu\text{g TP L}^{-1}$ for the onset of blooms (Downing et al., 2001; Jacquet et al., 2005; Šejnohová & Maršálek, 2012). The summer average TP measured in Lake St. Charles surface water was always well below this threshold, with average TP and also TN concentrations that would place the lake in the mesotrophic (2011) or even oligotrophic (all other summers) category (Nürnberg, 2001). Biologically available phosphorus (Soluble Reactive Phosphorus; SRP) was always close to or below the detection limit ($0.5 \mu\text{g L}^{-1}$) throughout the study. Although bloom-forming cyanobacteria are less common in low phosphorus waters, there are similar accounts of blooms in mesotrophic and even oligotrophic lakes (Carey et al., 2008; Leblanc, et al., 2008).

Intermittent external supply of phosphorus may contribute to the growth of cyanobacterial blooms in Lake St. Charles. For example in 2007, TP concentrations were $>20 \mu\text{g L}^{-1}$ on several dates immediately just downstream of the inflow of the Hurons River into the lake. This inflow is known to transport large amounts of phosphorus during peak flow conditions. For example, an extreme value of $284 \mu\text{g TP L}^{-1}$ was recorded in the river during a flood (APEL, 2009), and a modeling analysis concluded that the four most intense flood events in this river in 2008 transported 46% of the total summer input (Bourget, 2011). The Hurons River watershed is characterized by steep slopes and soils with low infiltration capacity, and it experiences a climate marked by high precipitation events (Roche, 2010). These conditions likely promote high watershed reactivity to rainfall events, and high but episodic nutrient loading into the lake, which could have been missed with the sampling frequency used in the present study. Bloom-forming cyanobacteria are known to have a large capacity for luxury P uptake and storage (Jacobson & Halmann, 1982), which would allow them to benefit from such intermittent nutrient supply.

Another intermittent source of phosphorus to be considered is the entrainment of nutrient-rich bottom waters into the epilimnion by water column mixing during storm events , or by wind-induced boundary mixing near the shoreline (McIntyre & Jellison, 2001; Zhu et al., 2005). The surface waters of the lake were almost always supersaturated in oxygen during the stratified period, while the bottom waters of the north basin were hypoxic and often near anoxic in late summer each year. Bottom water anoxia is often accompanied by phosphorus release from the sediments (Kalff, 2002), but SRP concentrations in the hypolimnion of Lake St. Charles were mostly near the detection limit ($0.5 \mu\text{g L}^{-1}$), and internal nutrient loading appears to be low in this lake. Similarly, Prairie et al., (2001) found no relationship between phosphorus release and hypolimnetic oxygen depletion in a series of Quebec Province lakes, implying the importance of other factors. For example, reducing conditions alone may not be sufficient for the conversion of Fe(III) to Fe(II) and the consequent loading of soluble PO_4^{3-} , because the aggregates are stabilized by a coating of organic matter, or because iron-reducing bacteria are not sufficiently active (Lovley, 1991).

The importance of nitrogen supply for bloom-forming cyanobacteria and the production of their N-rich cellular toxins is still a subject of ongoing discussion (Chen et al., 2003 ; Downing et al., 2005). Nitrate was generally well above detection limits in Lake St. Charles throughout the study, which implies that the N limitation is rare in this lake, but perhaps possible during short episodes at some locations; e.g. $< 5 \mu\text{g N L}^{-1}$ on 12 September at N3. However, it seems unlikely that it would be a factor limiting the growth of taxa such as *Microcystis* and *Aphanocapsa/Aphanothecae* or favoring dominance by N_2 -fixing species. There was no consistent relationship between nitrogen concentrations and cyanobacterial taxa: the average concentrations of TN and NO_3^- were higher in 2008, the year of *Microcystis* dominance. However, the N_2 -fixing species *Anabaena flos-aquae* dominated the water body in 2010 despite higher concentrations of NO_3^- than in 2007, 2009 and 2011.

Low N:P ratios have often been invoked as a factor leading towards cyanobacterial dominance (Hyenstrad et al., 1998; and references therein). Conversely high N:P

ratios (20-50:1 by mass) seem conducive to the development of communities dominated by green algae (Bulgakov & Levich, 1999) or diatoms (McCarthy et al., 2009). However, these relationships are not observed consistently (Pick & Lean, 1987). An analysis of data from 99 lakes in the temperate zone showed that the risk of cyanobacterial blooms was more strongly correlated with variations in TP or TN than with the ratio of N:P (Downing et al., 2001). The average N:P ratios in Lake St. Charles were in the range 10-90:1, suggesting periods of strong P relative to N limitation (e.g., summer 2008), but with other periods of lower ratios (e.g., summer 2011) suggesting periods of N limitation.

2.4.4. Light regime

Cyanobacteria are tolerant of a broad range of conditions, from bright exposure to sunlight in surface blooms (Vincent & Quesada, 1993) to limiting irradiance conditions deeper in the water column (Oliver et al., 2012; and references therein). Bloom-forming cyanobacteria are more tolerant of dim light conditions than other phytoplankton groups because of their specialized pigments (Grossman et al., 2001), their potential motility through the water column as a result of buoyancy regulation (Oliver & Ganf, 2000), and their simple prokaryotic structure that decreases their cellular light demand (Istvánovics, 2009). The Secchi depth measurements in Lake St. Charles indicate a persistently low transparency that would favor such strategies.

The Secchi disc observations would place the trophic status of the lake in the advanced mesotrophic (2007, 2009 and 2010) or eutrophic (2008, 2011) categories. However, previous studies on the lake have shown that this high attenuation of photosynthetically active radiation (PAR) is largely due to coloured dissolved organic matter (CDOM), not phytoplankton (Watanabe, 2011). The lower transparency in 2011 is likely due to increased catchment runoff, given the high precipitation and flood events at the beginning of 2011 (Environnement Canada, 2012). The attenuating effect of CDOM results in an underwater PAR regime that is red-shifted down the euphotic zone, with 580 nm as the most penetrating wavelength (Watanabe, 2011). The spectral absorption characteristics of cyanobacteria (Stomp et al., 2007) would

make them particularly well suited to these orange underwater light conditions in Lake St. Charles.

2.4.5. Conductivity and pH

Eutrophic lakes in which bloom-forming cyanobacteria proliferate are often environments with solute concentrations that are elevated relative to oligotrophic waters (Dodds & Whiles, 2010). For example, in Lake Taihu (China), which is continuously affected by blooms of *Microcystis aeruginosa*, conductivities are in the range 400-1000 $\mu\text{S cm}^{-1}$ (Tao et al., 2012). In Lake St. Augustin, a highly eutrophic water body in the Quebec City region with prolonged noxious blooms of cyanobacteria each year, the conductivity is around 700 $\mu\text{S cm}^{-1}$ (Bouchard Valentine, 2004). In Lake St. Charles, solute concentrations did not seem to be a factor particularly favoring bloom formers. The average specific conductivity of Lake St. Charles was low (overall mean of 77 $\mu\text{S cm}^{-1}$) compared to these eutrophic waters, and relative to mean values for lakes with small drainage basins in the northern hemisphere (Jones & Bachmann, 1978), reflecting the large contribution of waters flowing over weakly mineralized soils. The ionic strength of Lake St. Charles surface waters increased substantially in 2010 to around 100 $\mu\text{S cm}^{-1}$, likely due to the decreased precipitation and increased evaporation during that summer (Environnement Canada, 2012), and an increased contribution of waters flowing over bedrock (gneiss).

Bloom-forming taxa are known to have more efficient inorganic carbon-concentrating mechanisms relative to many eukaryotic phytoplankton taxa (Price et al., 2008), and therefore have a competitive advantage under the low pCO_2 regime associated with alkaline conditions (Shapiro, 1990). However, Lake St. Charles had a relatively stable pH around neutrality (7.5), which would not give such an advantage to bloom-formers.

2.4.6. Interannual variability

The multivariate analysis showed that there was a marked separation of the sampling years into 3 groups. The summers of 2007 and 2010 were characterized by waters of higher conductivity, during which the phytoplankton assemblage was strongly dominated by cyanobacteria: *Microcystis aeruginosa* in 2007 and *Anabaena flos-aquae* in 2010. The summers of 2008 and 2009 were associated with higher nutrient concentrations (TN, SRP, NO₃⁻) and the phytoplankton was dominated by the non N₂-fixing cyanobacteria *Microcystis aeruginosa* or *Aphanocapsa/Aphanothece*, respectively. Summer 2011 was characterized by higher phosphorus concentrations but lower temperature, oxygen saturation, pH and transparency than in the other years, and there was no proliferation of bloom-forming cyanobacteria. These multivariate results should be interpreted with caution given the strong correlations among many variables; however, they underscore the striking interannual variability in the limnological properties of Lake St. Charles, which in turn may induce shifts in phytoplankton community structure and cyanobacterial dominance.

2.5 Conclusion

The bloom-forming cyanobacteria *Microcystis aeruginosa* and *Anabaena flos-aquae* were conspicuously present in Lake St. Charles on many dates of sampling during the 5-year study period. However, these noxious species did not rise to dominance every summer, and in some years they gave way to other colonial cyanobacteria such as *Woronichinia naegeliana* and *Aphanocapsa/Aphanothece* sp., or to motile phytoplankton taxa such as *Dinobryon divergens*. The general conditions of dim water column irradiance with a red-shifted spectral composition would tend to favor cyanobacteria because of their specialized pigments. The pH and conductivity would not especially favor cyanobacteria relative to other groups. TN concentrations were globally not limiting, and the average concentrations of TP and bioavailable phosphorus were apparently not sufficient to allow the persistent dominance of bloom-forming cyanobacteria. However, the mean concentrations may mask some

episodic nutrient inputs favoring intermittent growth of bloom-formers. Warmer summers with longer thermal stratification and warmer surface temperature would probably induce a phytoplankton succession from diatoms and green algae in spring to *M. aeruginosa* and *A. flos-aquae* in summer.

This study has shown that Lake St. Charles has a strong interannual variability in its limnological properties. This variability is likely to be a feature of other high through-flow reservoirs, and could potentially be induced by small year-to-year differences in climate forcing and potential upstream factors. The resultant limnological conditions represent a dynamic equilibrium that may be pushed one way or another, depending on the year, to provide favorable or unfavorable conditions for the proliferation of bloom-forming cyanobacteria.

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Table 2.1. Phytoplankton taxa recorded in Lake St. Charles for the ensemble of sampling dates, from 2007 to 2011.

CYANOBACTERIA	Potentially toxic (Cronberg & Annadotter, 2006)	CHLOROPHYTA
		Chlorophyceae
		<i>Ankistrodesmus</i> sp. <i>Asterococcus</i> sp. <i>Botryococcus</i> sp. <i>Chlamydomonas</i> sp. <i>Chlorella</i> sp. <i>Chodatella quadrisetata</i> <i>Cladotrichum</i> sp. <i>Coelastrum</i> sp. <i>Cosmarium</i> sp. <i>Crucigenia</i> sp. <i>Dictyosphaerium</i> sp. <i>Eudorina elegans</i> <i>Gloeococcus</i> sp. <i>Golenkinia radiata</i> <i>Hyalotheca</i> <i>Micractinium</i> sp. <i>Micrasterias</i> sp. <i>Oocystis</i> sp. <i>Pediastrum</i> sp. <i>Quadrigula closterioides</i> <i>Scenedesmus</i> sp. <i>Schroederia</i> sp. <i>Staurastrum</i> sp. <i>Stauromedes</i> sp. <i>Tetraedron caudatum</i> <i>Volvox</i> sp. <i>Xanthidium</i> sp.
	Not considered toxic	
	<i>Aphanocapsa delicatissima</i> <i>Aphanocapsa cf. elachista</i> <i>Aphanocapsa cf. incerta</i> <i>Aphanothecace cf. clathrata</i> <i>Chroococcus limneticus</i> <i>Geitlerinema cf. splendidum</i> <i>Gomphosphaeria</i> sp. <i>Merismopedia punctata</i> <i>Oscillatoria cf. limosa</i> <i>Planktolyngbya limnetica</i> <i>Pseudanabaena limnetica</i> <i>Radiocystis</i> sp. <i>Raphidiopsis</i> sp. <i>Snowella</i> sp. <i>Woronichinia naegeliana</i>	
BACILLARIOPHYTA		
	Coscinodiscophyceae	
		<i>Aulacoseira ambigua</i> <i>Cyclotella</i> sp. <i>Melosira varians</i> <i>Stephanodiscus</i> sp.
	Fragilariphycaceae	
		<i>Asterionella formosa</i> <i>Diatoma anceps</i> <i>Fragilaria crotonensis</i> <i>Tabellaria flocculosa</i>
	Bacillariophyceae	
		<i>Amphora</i> sp. <i>Caloneis</i> sp. <i>Cocconeis</i> sp. <i>Cymbella</i> sp. <i>Eunotia</i> sp. <i>Gomphonema</i> sp. <i>Gyrosigma</i> sp. <i>Navicula</i> sp. <i>Nitzschia</i> sp. <i>Stauroneis</i> sp.
		PHYTOFLAGELLATES
		Chrysophyceae
		<i>Dinobryon divergens</i> <i>Mallomonas</i> sp. <i>Ochromonas</i> sp. <i>Synura</i> sp. <i>Trachelomonas</i> sp. <i>Uroglena</i> sp.
		Cryptophyceae
		<i>Cryptomonas</i> sp. <i>Dinophyceae</i> <i>Ceratium hirundinella</i> <i>Gymnodinium</i> sp. <i>Peridinium</i> sp.
		Euglenophyceae
		<i>Euglena</i> sp. <i>Phacus</i> sp.

Table 2.2 Mean (\pm SD) values for limnological variables measured in Lake St. Charles during the 5 summer periods (1 June to 30 September, 2007 to 2011).

Variables	Years									
	2007		2008		2009		2010		2011	
		N		N		N		N		N
Surface mean temperature (°C)	17.8 \pm 4.9	79	18.4 \pm 3.8	86	18.0 \pm 4.9	81	22.7 \pm 5.0	88	17.9 \pm 3.9	38
Surface max temperature (°C)	24.5	79	22.4	86	26.0	81	26.9	88	24.7	38
Mean depth of thermocline (m)	3.9 \pm 1.8	13	3.0 \pm 1.7	10	2.4 \pm 1.6	12	3.7 \pm 1.8	8	2.4 \pm 1.0	16
Secchi depth (m)	2.7 \pm 0.4	96	2.4 \pm 0.4	96	2.7 \pm 0.4	40	2.8 \pm 0.4	45	2.1 \pm 0.5	25
pH	7.6 \pm 0.3	124	7.3 \pm 0.2	129	7.6 \pm 0.3	57	7.7 \pm 0.4	69	7.0 \pm 0.3	192
Specific conductivity ($\mu\text{S cm}^{-1}$)	75.3 \pm 5.8	124	64.6 \pm 13.2	129	68.0 \pm 6.8	57	101.2 \pm 12.9	69	72.7 \pm 13.7	192
TP ($\mu\text{g L}^{-1}$)	10.3 \pm 2.8	96	9.6 \pm 2.6	96	6.7 \pm 1.4	7	7.9 \pm 2.8	7	12.0 \pm 2.8	12
TN ($\mu\text{g L}^{-1}$)	342 \pm 99	96	516 \pm 182	96	217 \pm 53	7	271 \pm 74	7	325 \pm 117	18
TN/TP	37.2 \pm 14.1	96	56.6 \pm 28.1	96	34.7 \pm 15.0	7	39.3 \pm 11.0	7	29.9 \pm 19.5	7
SRP ($\mu\text{g L}^{-1}$)	0.33 \pm 0.21	43	0.82 \pm 0.83	66	-	-	0.70 \pm 0.6	7	0.87 \pm 0.59	11
NO ₃ ⁻ ($\mu\text{g N L}^{-1}$)	91 \pm 27	48	178 \pm 30	48	87 \pm 66	7	145 \pm 87	7	125 \pm 31	7
Chl- <i>a</i> ($\mu\text{g L}^{-1}$)	6.7 \pm 2.8	54	7.5 \pm 3.1	78	4.0 \pm 1.1	65	3.2 \pm 0.9	86	3.7 \pm 1.8	12

Table 2.3. Spearman correlations among the limnological variables measured over the 5 summers in Lake St. Charles, from 2007 to 2011.

Variables	1	2	3	4	5	6	7	8	9	10
1. Temperature (°C)	-	-0.06	0.55**	0.65**	0.13	0.04	-0.27**	-0.01	0.13	0.63**
2. Specific conductivity ($\mu\text{S cm}^{-1}$)		-	-0.21*	-0.08	0.33**	0.21*	0.43**	-0.15*	0.46**	0.43**
3. Dissolved oxygen saturation (%)			-	0.81**	-0.02	-0.26**	-0.45**	-0.01	0.11	0.58**
4. pH				-	0.44**	-0.11*	-0.42**	-0.06	0.17*	0.57**
5. Secchi depth (m)					-	-0.26**	-0.16	-0.24*	0.25*	-0.46**
6. TP ($\mu\text{g L}^{-1}$)						-	-0.02	-0.04	0.11	0.30**
7. TN (mg L^{-1})							-	-0.02	-0.02	0.03
8. NO_3^- ($\mu\text{g N L}^{-1}$)								-	-0.09	0.02
9. SRP ($\mu\text{g L}^{-1}$)									-	0.01
10. Chl- α ($\mu\text{g L}^{-1}$)										-

* p < 0.05 ** p < 0.001

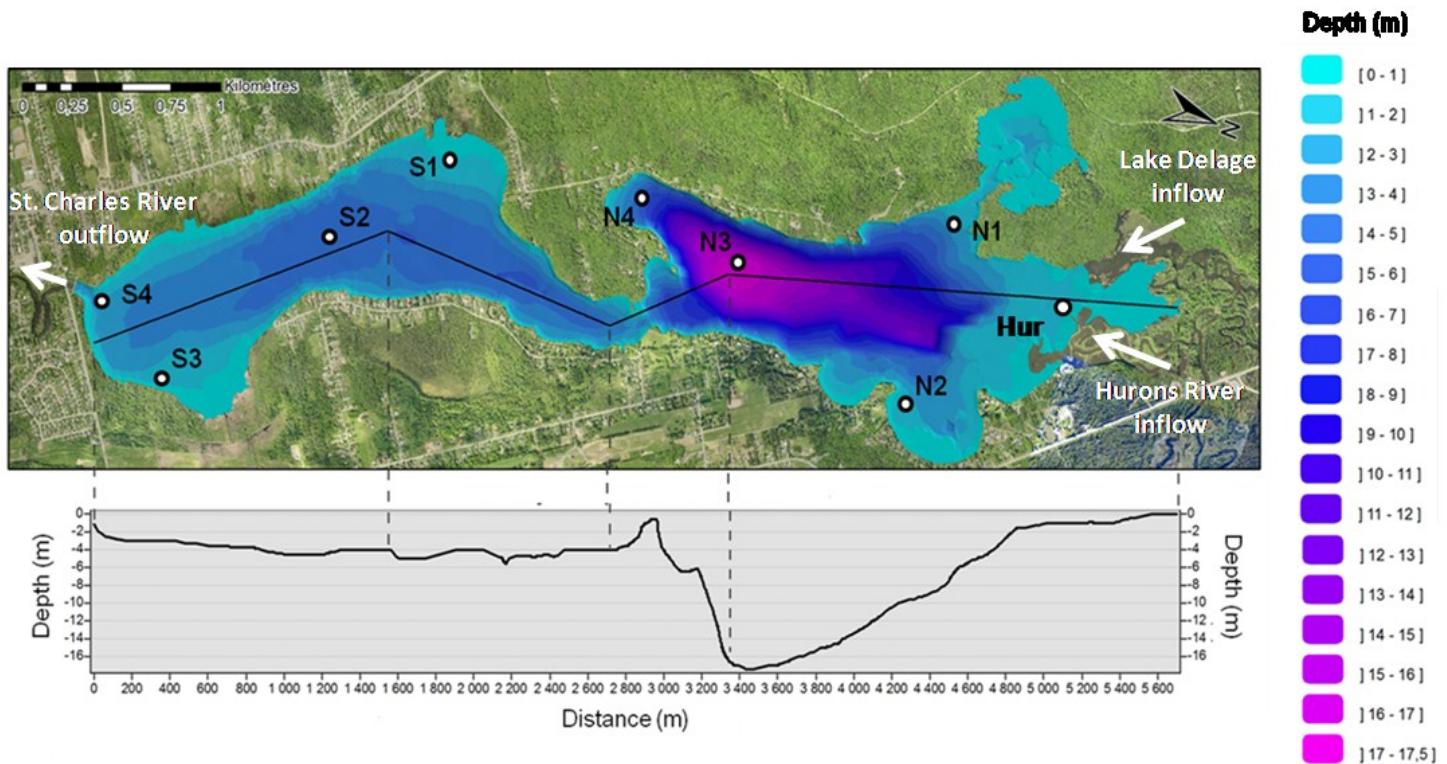


Figure 2.1. Bathymetric map and profile of Lake St. Charles with sampling stations. North basin: Talbot Bay (N1), Des Aigles Pêcheurs Bay (N2), deepest point of the lake (N3), Echo Bay (N4). South basin: Des Milans Bay (S1), middle of the south basin (S2), beach (S3), dam (S4); and Hurons River inflow (HUR). Modified from Sirois (2012).

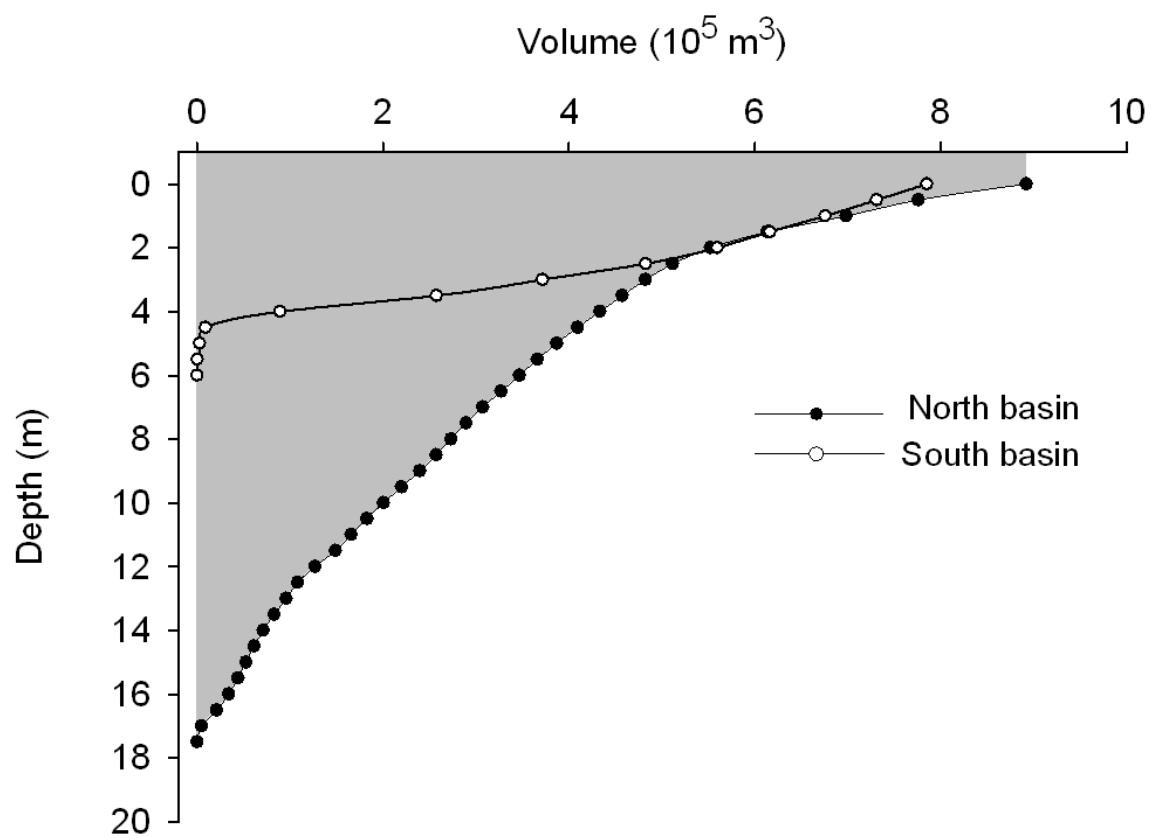


Figure 2.2. Hypsographic curves for the north and south basins of Lake St. Charles.

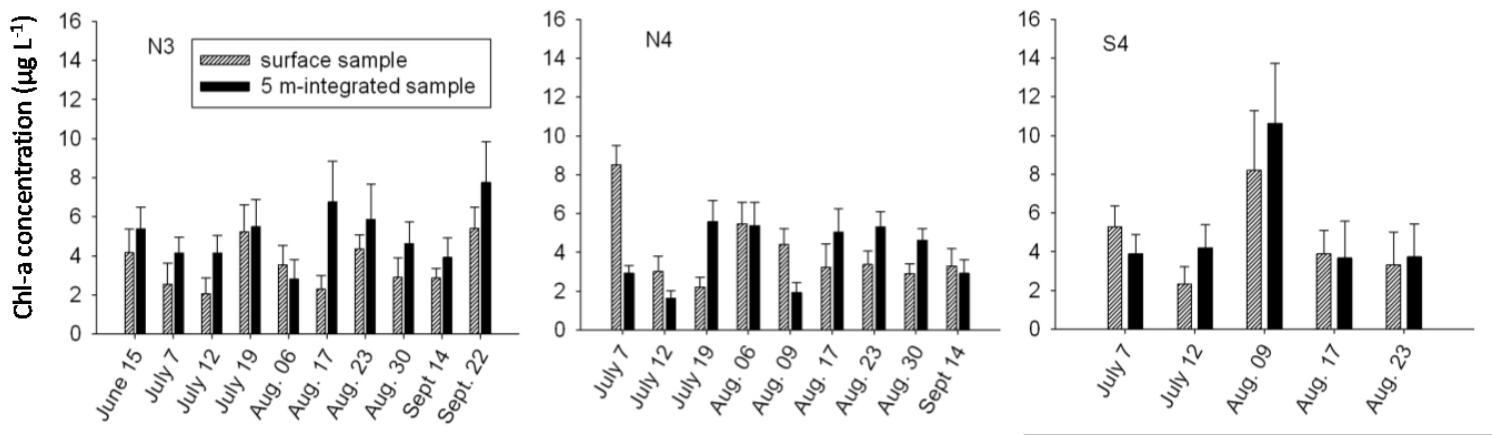


Figure 2.3. Chlorophyll *a* concentrations at N3, N4 and S1 in 2010 in surface and 5 m-integrated samples.

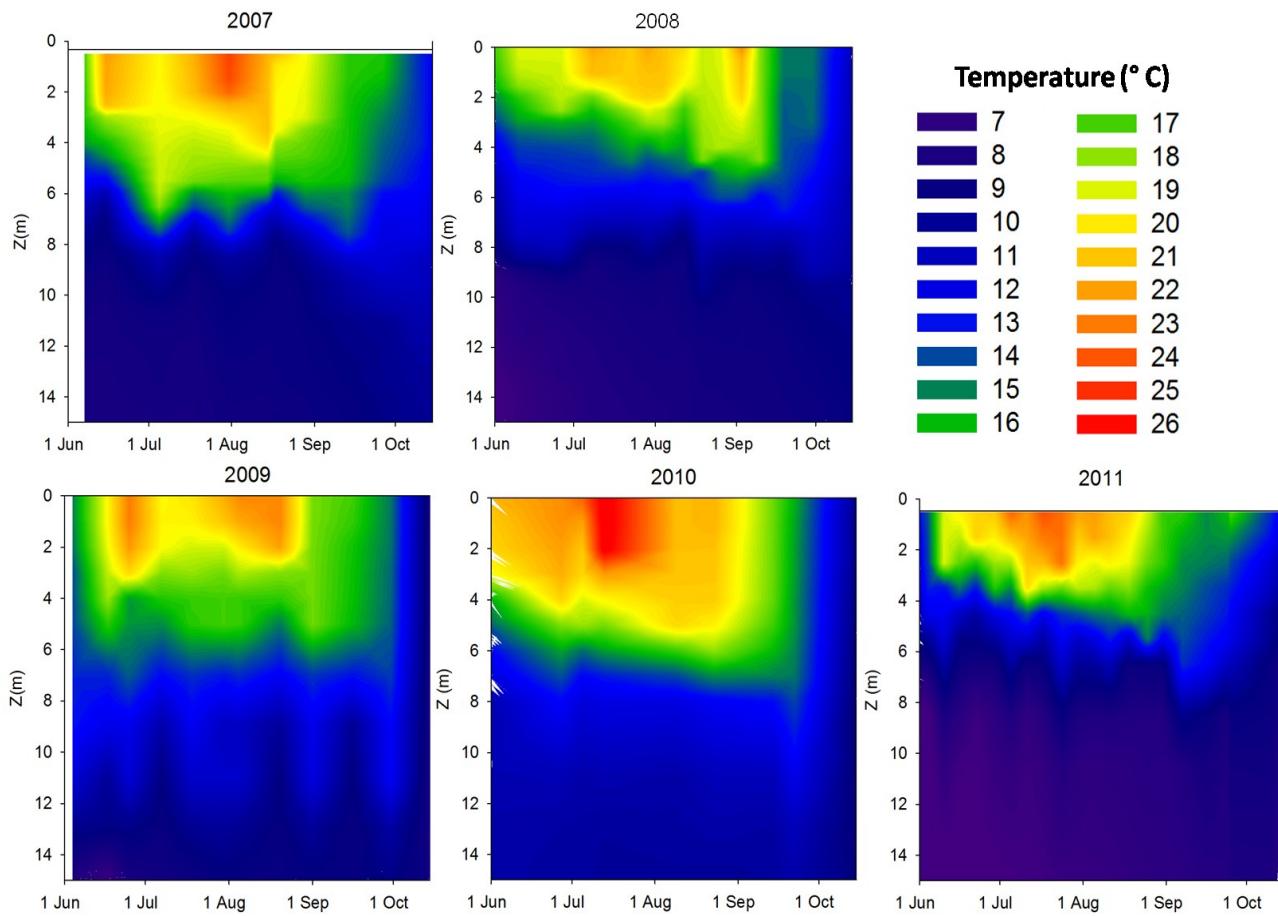


Figure 2.4. Changes in water temperature ($^{\circ}$ C) over depth and time at station N3 during each summer, from 2007 to 2011.

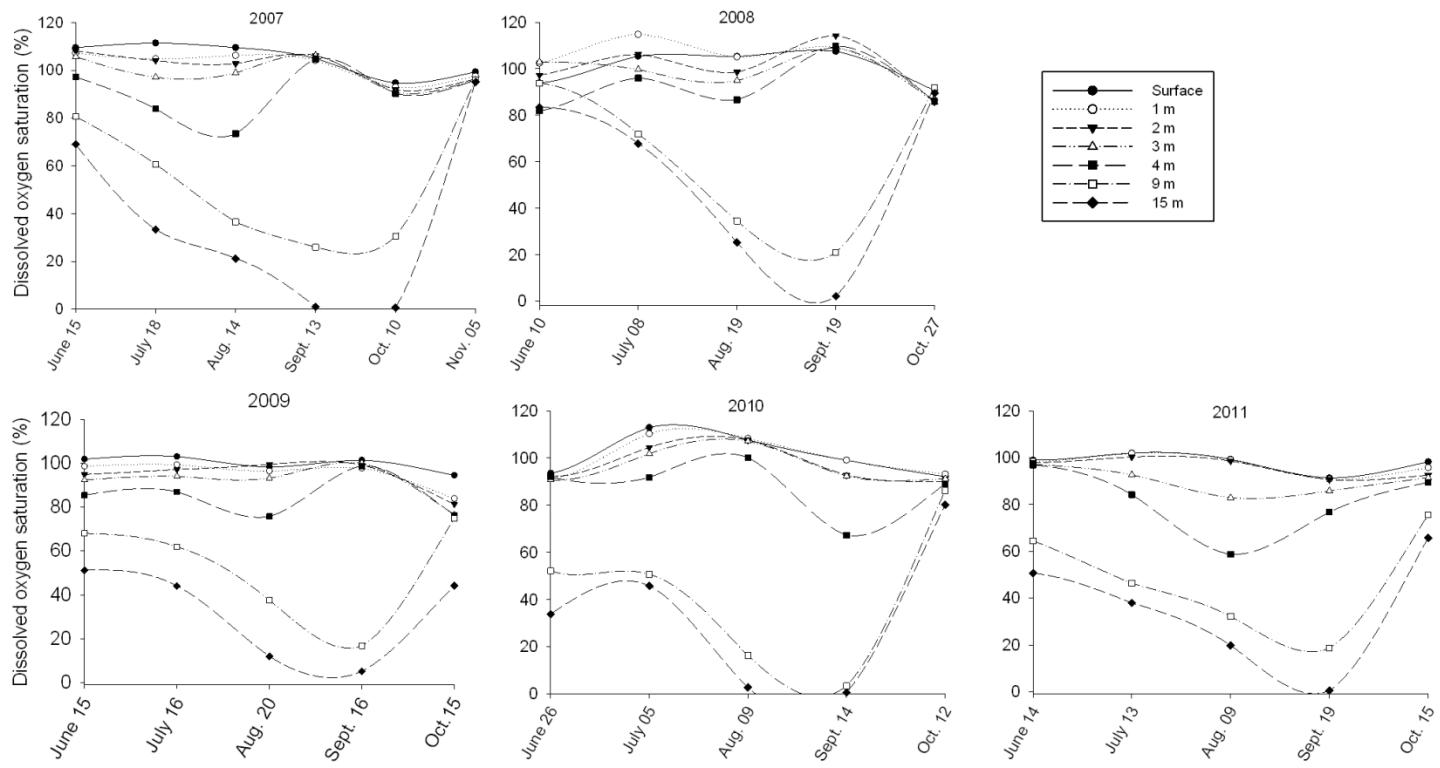


Figure 2.5. Dissolved oxygen saturation (%) over depth and time at station N3 during each summer from 2007 to 2011.

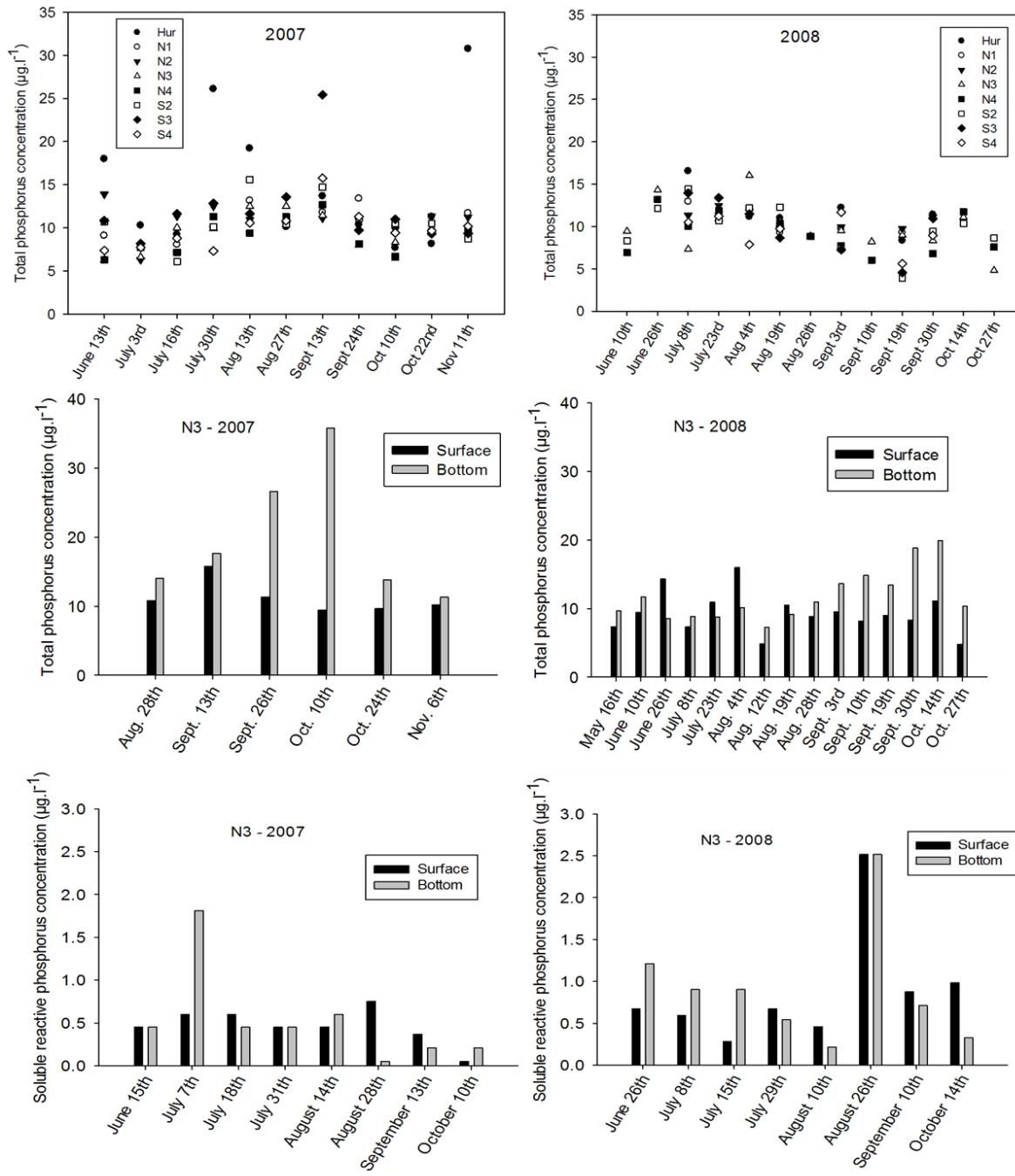


Figure 2.6. Phosphorus concentrations ($\mu\text{g L}^{-1}$) in Lake St. Charles in 2007 and 2008. The top panels show the spatial and seasonal variations in TP at all stations; the middle panels show the variation in TP between surface and deep waters at N3; and the bottom panels show the variation in SRP between surface and deep waters at N3.

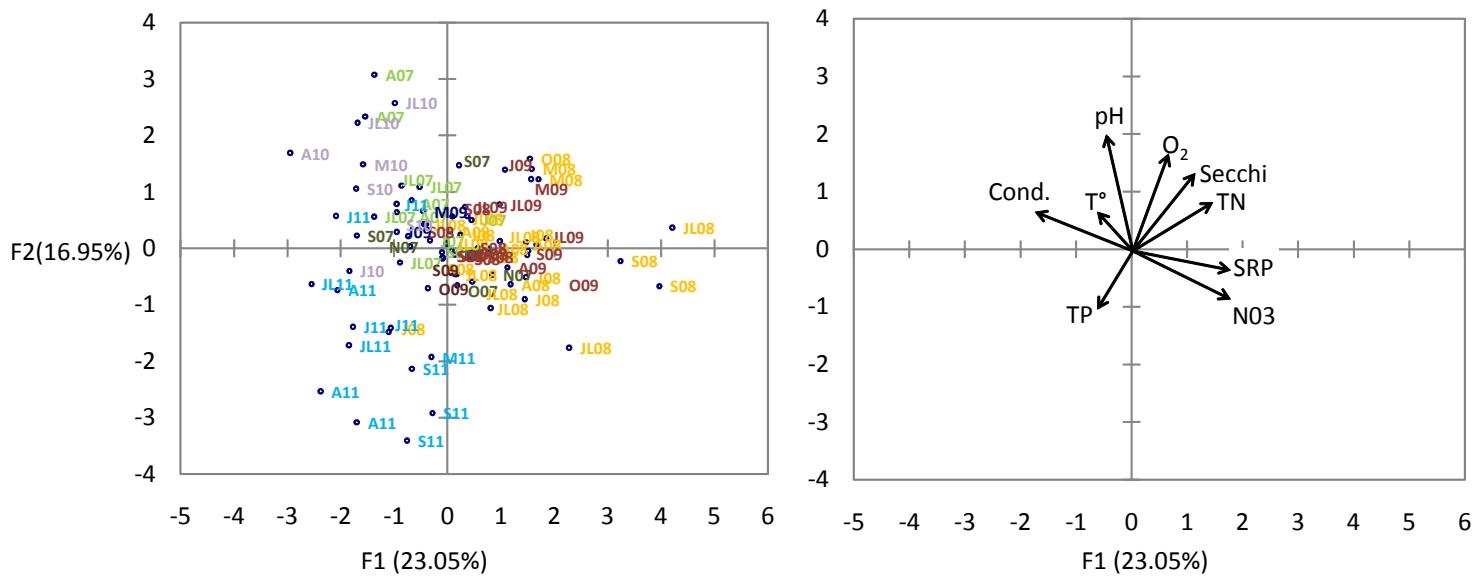


Figure 2.7. Principal components analysis (PCA) of the limnological variables among the 8 sampling sites and 5 years. Left: plot of the sampling dates. M, May; J, June; JL, July; A, August; S, September; O, October; 07, 2007; 08, 2008; 09, 2009; 10, 2010; 11, 2011. Right: plot of limnological variables, where Cond. is the specific conductivity ($\mu\text{S cm}^{-1}$), O_2 , dissolved oxygen saturation (%), Secchi, secchi depth (m), TN, total nitrogen concentration (mg L^{-1}), TP, total phosphorus concentration ($\mu\text{g L}^{-1}$), SRP, soluble reactive phosphorus concentration ($\mu\text{g L}^{-1}$), and NO₃, concentration of NO₃⁻ ($\mu\text{g N L}^{-1}$).

Chapitre 3. Extreme variability of cyanobacterial blooms in an urban drinking water supply

Résumé

Dans un contexte d'eutrophisation, la gestion appropriée des ressources en eau potable nécessite une meilleure compréhension des facteurs de contrôle des efflorescences de cyanobactéries nocives. Depuis 2006 le lac Saint-Charles, un important réservoir en eau potable de la ville de Québec, Canada, est régulièrement sujet à ces efflorescences. L'objectif de cette étude était de définir les variations temporelles et spatiales de la structure de la communauté de cyanobactéries du lac Saint-Charles et d'examiner l'hypothèse que la dynamique des cyanobactéries est principalement contrôlée par le régime thermique, la stabilité de la stratification et le ratio azote/phosphore. Des données biologiques (biovolume et composition spécifique des cyanobactéries), physiques et chimiques (température, oxygène, conductivité, le pH et les formes de l'azote et du phosphore), météorologiques (précipitations, température) et hydrologiques (niveau d'eau, le débit d'eau) ont été obtenues pendant 5 étés consécutifs (2007-2011). Le bassin nord montre des concentrations de cyanobactéries systématiquement plus élevées qu'au bassin sud, et des variations interannuelles extrêmes de la biomasse totale et de la composition spécifique ont été mises en évidence. Les taxons dominants étaient *Microcystis aeruginosa* (2007 et 2008), *Aphanocapsa* sp. / *Aphanothece* sp. (2009) et *Anabaena flos-aquae* (2010 et 2011). Une analyse de corrélation indique l'existence de contrôles environnementaux contrastés sur les différents taxons de cyanobactéries efflorescentes : la température de surface, la stabilité de la colonne d'eau et le temps de séjour de l'eau exerçant un contrôle prépondérant sur la biomasse d'*Anabaena flos-aquae* dans le lac Saint-Charles. *Microcystis aeruginosa* était fortement corrélé avec le phosphore et l'azote total et, dans une moindre mesure, avec l'accumulation de chaleur et le volume des précipitations.

Abstract

Noxious cyanobacterial blooms are of increasing global concern in drinking water supplies, and their prediction and management requires an improved understanding of their controlling factors. In Lake St. Charles, the drinking water supply for Quebec City, Canada, harmful cyanobacterial blooms were first recorded in autumn 2006. Our aims were to define the temporal and spatial variations in the cyanobacterial community structure of Lake St. Charles and to address the hypothesis that interannual variability in cyanobacterial biomass and species composition were mainly controlled by nutrients, temperature and water column stratification. We measured cyanobacterial biomass, species composition, physical and chemical variables (temperature, oxygen, conductivity, pH and forms of nitrogen and phosphorus) in the lake, and obtained meteorological (precipitation, temperature) and hydrological data (water level, water flow) for 5 consecutive summers (2007-2011). The north basin had consistently higher concentrations of bloom-forming cyanobacteria than the south basin, and there were striking variations within and among years in total biomass and species composition. The dominants were *Microcystis aeruginosa* (2007 and 2008), *Aphanocapsa* sp./*Aphanothecace* sp. (2009) and *Anabaena flos-aquae* (2010 and 2011). Correlation analysis underscores the contrasting environmental controls on different taxa of colonial cyanobacteria; surface temperature, water column stability and water residence time may exert primary controls on the biomass of *Anabaena flos-aquae* in Lake St. Charles. *Microcystis aeruginosa* was highly correlated with total phosphorus and total nitrogen and to a lesser extent with heat accumulation and volume of precipitation.

3.1 Introduction

Cyanobacterial blooms have a wide range of impacts on aquatic ecosystems including shading of macrophyte communities, inhibition of zooplankton grazing, altered competitive interactions among phytoplankton and lethal impacts on fish and invertebrates caused by hypoxia (Havens, 2008; Oliver et al., 2012; Vincent, 2009a). The development of cyanobacterial blooms in drinking water supplies is of special concern given the ability of many cyanobacterial species to produce toxic compounds that are hazardous to animal and human health (Carmichael, 1992; Codd, 2000), to produce taste and odour compounds (Izaguirre & Taylor, 2004; Watson, 2003), and to cause filter clogging as a result of the high concentrations of biomass (Falconer, 1999). The occurrence of cyanobacteria blooms may therefore greatly increase the running costs for water treatment plants, as well as affect the confidence that residents place in their drinking water supplies.

One of the challenges for water quality management of drinking water supplies is predicting the occurrence of blooms given the temporal variability of cyanobacteria and other phytoplankton. There is consensus that the typical phytoplankton succession often shows a pattern of greatest cyanobacteria abundance towards the summer when temperatures and water column stratification are maximal (e.g. De Figueiredo et al., 2006; Dokulil & Teubner, 2000; Latour et al., 2004). Although this pattern is often observed in dimictic lakes, it can be substantially modified by eutrophication, climate change and other factors. Predictive models for cyanobacteria abundance usually focus on total phosphorus and total nitrogen (Håkanson et al., 2007) but nitrogen to phosphorus ratios (N/P) have also been identified as a key factor for cyanobacteria dominance in some studies (Bulgakov & Levich, 1999; Oliver et al., 2012; and references therein; Smith & Bennet, 1999).

An additional challenge for cyanobacterial monitoring in lakes and reservoirs is their potentially large spatial variability, both through the water column and over horizontal space, due to diverse ecological strategies (Carey et al., 2012). Spatial

variation in environmental conditions will interact with physiological variation in cyanobacteria to create differences in the dominant taxa among areas. For example; sampling protocols for bloom monitoring assume that the vertical distribution of cyanobacteria, like other groups of phytoplankton, is uniform throughout the mixed layer. However, some taxa of cyanobacteria such as *Microcystis aeruginosa* and *Anabaena flos-aquae* are able to regulate their buoyancy during thermal stratification (reviewed in Oliver et al., 2012). Cyanobacteria can be distributed horizontally in a patchy way due to the wind-driven accumulation of these surface blooms, or by spatial variations in growth and loss processes (e.g. Ishikawa et al., 2002).

Despite these potential spatial and temporal variations, many temperate lakes show an interannual regularity in the species composition and abundance of their phytoplankton communities (Kalff, 2002; Talling, 1993). This appears often to be the case for cyanobacteria, where the same genus or even species dominates each summer; for example, *Microcystis* in Lake Taihu, China (Chen et al., 2003) and Lake Grangent, France (Latour et al., 2004), and *Anabaena* in Fort Whyte Lakes, Canada (Dupuis & Hann, 2009) and Lake Rotongaio, New Zealand (Vincent, 1989). However, reservoir systems may deviate from this lake pattern given their short hydraulic residence times and more fluvial character. For example, in the Murray Darling River ecosystem, Australia, cyanobacteria proliferations have been linked to low discharge periods (Bormans et al., 1997).

In southern Quebec, Canada, cyanobacterial bloom events have been of increasing concern over the last decade. More than 150 lakes were observed to contain substantial bloom-forming cyanobacteria in 2007, with implications for the sustained provision of ecosystem services from these waterbodies (Boissonneault et al., 2007; Laurion et al., 2009). One of these lakes, Lake St. Charles, is the drinking water supply for 285,000 residents in Québec City, where cyanobacterial blooms were first reported in autumn 2006 (APEL, 2009). Since that time, the proliferation of harmful cyanobacteria such as *Microcystis aeruginosa* and *Anabaena flos-aquae* has become more pronounced in this lake, appearing earlier in the summer and persisting for a

longer period (Bourget, 2011; Warren, 2011). A surface scum detected in August 2007 near the shoreline of Echo Bay had *M. aeruginosa* concentrations reaching 2 million cells mL⁻¹ and 6.2 µgL⁻¹ of microcystin-LR, more than four times higher than Health Canada criteria for drinking water quality (Bourget, 2011; CEHQ, 2007).

Our aims in the present study were: (i) to define the spatial and temporal variations in bloom-forming cyanobacteria in Lake St. Charles as a case study of changing phytoplankton community structure in a north temperate reservoir; and (ii) to address the hypothesis that cyanobacterial biomass and species composition are controlled by temperature, stratification conditions and N/P ratios. We undertook a 5-year study of the lake, measuring phytoplankton as well as physical and chemical variables. This provided a detailed multiyear data set for assessing the extent and causes of interannual and spatial variability.

3.2 Methods

3.2.1. Site description

Lake St. Charles is located 21 km north of Québec City at latitude 46° 54' N, longitude 71° 22' W and it covers a total area of 3.6 km² with a total volume of 14.8 x10⁶ m³. The lake is composed of two sub-basins that differ in morphometry: the north basin is conical and reaches a maximum depth of 17.5 m, and the south basin has a maximum depth of 6 m (Fig. 3.1). The watershed of Lake St. Charles extends over an area of 169 km². The mountains around the lake are composed of granite and gneiss covered by boreal forest, while the valley is overlain by fine glacio-marine sediments (Gérardin & Lachance, 1997). The watershed of Lake St. Charles is subject to a temperate sub-humid climate, with an annual rainfall around 1300 mm. The principal inflow to Lake St. Charles is the Hurons River, which drains 80% of the watershed and the single outflow is the St. Charles River. The mean annual discharge measured at the gauging station of the St. Charles River, 9 km downstream of the lake, is 8.5 m³ s⁻¹ (Gaborit et al., 2010). The trophic status of Lake St. Charles is considered to be oligo-mesotrophic to mesotrophic depending on trophic indicators (Rolland et al., 2013; chapter 2 of this

thesis). Eight principal sampling stations were selected, covering several bays as well as the open waters of the lake (Fig. 3.1). In 2009, triplicate samples were taken at each station to assess the within-station variability. The sampling was undertaken once or twice per month throughout the summer, between May and October.

3.2.2. Physical, hydrological and meteorological variables

A thermistor chain (Onset Tidbit TBI32, resolution 0.2°C) was installed in the deepest part of the lake (N3; 17.5 m) to obtain continuous measurements of water temperature down the water column over the entire sampling periods. These data were then used to calculate two indices. Firstly, the temperature values were converted to density and water column stability was estimated by the Schmidt stability index (S , g cm⁻¹), calculated as:

$$S = A^{-1} \sum (z - z^*) (\rho_z - \rho^*) A_z \Delta_z$$

$$\rho^* = V^{-1} \sum (V_z \cdot \rho_z)$$

where A_z is the lake area (m²), ρ_z is the density (g cm⁻³) at depth z (m), z^* represents the depth where the mean density ρ^* is found, and V is the volume of water (m³). Depth intervals (Δ_z) of 1 m were used for the calculations. Secondly, as a measure of favorable conditions for cyanobacterial production, cumulative degree-days (°C day) were calculated by summing the recorded degrees (C°) each day above 20°C, a value that has been considered a threshold for cyanobacterial growth (Dupuis & Hann, 2009).

Meteorological data were obtained from the weather station at Québec City Airport, located 14 km west of the lake (Environnement Canada, 2012). Water level (WL, m) of Lake St. Charles was measured near the dam at the outflow of the lake. The average water residence time (WRT, days) for each summer was obtained from the lake volume (V_L , m³) and the average summer water outflow (Q , m³ s⁻¹) as V_L/Q . The lake volume was calculated for each day from the water level and the hypsographic curve of the lake (Rolland et al., 2013; chapter 2 of this thesis). The average summer water

outflow was estimated by using the outflow measured each day at the gauging station of the River St. Charles (Centre d'Expertise Hydrique du Québec). This station is 9 km below the outlet of the lake, and the values were corrected for other watersheds discharging into the river between the lake outlet and the gauging station, as well as for the drinking water intake, also located upstream of the station.

3.2.3. Biological variables

Integrated water column samples were collected with a 30 mm diameter plastic tube that extended from the surface to 2 m depth, and these were immediately transferred in the field into brown plastic bottles. The sampling was always done early in the morning in the north basin and early in the morning the day after in the south basin. The 2 m integrated sample therefore always included more than 80% of the euphotic zone. A volume of 250 mL was filtered under low light onto Whatman GF/F filters (nominal pore size of 0.7 µm), immediately after sampling to minimize the degradation of pigments. The filters were stored at -80°C until extraction of pigments in boiling ethanol (65°C), and the chlorophyll *a* concentration (Chl-*a*) was determined by fluorometry (Varian Cary Eclipse spectrofluorometer, Varian Inc., Canada) before and after acidification (Nusch, 1980). Another 250 mL was transferred into polyethylene bottles, fixed with Lugol's iodine (5% final concentration) and stored in the dark at 4°C. These samples were then used for the enumeration of cyanobacteria. The sedimentation method (Utermöhl, 1958) was used to concentrate samples before enumeration using an inverted microscope (Zeiss Axiovert 200), and biovolume (BV, mm³ L-1) was calculated from the cell counts and size measurements. Enumeration was done at two sites in 2007 and 2008 (N3 and N4), the eight sites in 2009 and four sites in 2010 and 2011 (N3, N4, S2 and S4).

3.2.4. Chemical variables

For chemical analysis, unfiltered water samples were collected in polyethylene bottles previously washed with hydrochloric acid (10%) and rinsed 7 times with deionized water. These samples were preserved in sulfuric acid (0.2% final concentration), and

later digested with persulphate to determine total nitrogen (TN) and total phosphorus (TP), respectively with Lachat flow injection analyser and Genesys 10UV spectrophotometer (Thermo Spectronic) using standard techniques. Filtered water samples (0.2 µm filter) were analyzed for nitrate (NO_3^-) using a Dionex ICS 2000 ionic chromatograph, and for soluble reactive phosphorus (SRP) by a colorimetric method using the above spectrophotometer.

3.2.5. Statistical analysis

Analysis was performed using SIGMASTAT (version 11.0), and initial Shapiro-Wilk tests indicated that the data for most variables were not normally distributed. Mann-Whitney non-parametric rank sum tests were performed to test differences between two independent observations. Kruskal-Wallis ANOVA on rank tests was used to compare more than two independent observations, and then all pairwise multiple comparisons were made using Dunn's method to identify significant differences ($p<0.05$) between groups. Spearman rank order correlation analysis was conducted on the entire dataset. Given the spatial correlation among environmental variables, the variance heteroscedasticity and some gap in the dataset, it was considered inappropriate to apply multivariate analysis (Legendre & Legendre, 2012).

3.3 Results

3.3.1. Meteorological conditions

Summer temperatures for the period from May to October during the 5 years of study (Table 3.1) were within the climate range for the period 1971 to 2000, which was 13.9 (± 1.2) °C (Environnement Canada, 2012). However, 2010 was characterized by more frequent periods of high warm temperatures, particularly in July, August and September. Rainfall between May and October was significantly higher in 2007, 2008 and 2011, and significantly lower in 2010 than the average conditions from 1971 to 2000 (689 mm of total precipitation, with 85 rainy days; Environnement Canada, 2012). The total amount of precipitation between May and October was higher by

14% in 2007, 21% in 2008 and 11% in 2011 compared to this average. The variation of water level was moderate during the 2007 and 2009 summers (respectively 30 cm and 70 cm of variation between min and max; Table 3.1). Water level was high throughout the 2008 summer, with a maximum value that exceeded the dam threshold. The Quebec Province experienced severe flooding at the beginning of summer 2011, including in the Lake St. Charles watershed, and the water level of the lake rose to the full height of the dam on 4 May. This is also the year of shortest hydraulic residence time during the study period (19% below the 5-year mean value of 72 (± 13) days). In contrast, summer 2010 was a much drier season: the volume of precipitation was 15% less than the average from 1971 to 2000, the water level fell to a minimum of 1.95m on 6 September, and the residence time that year was 28% longer than the 5-year mean value. There was a close inverse correlation between water level and the lake water residence time ($r = -0.92$, $p < 0.001$).

3.3.2. Water temperature and stratification

A maximum of 210 °C-days was recorded in early September 2010 (Fig. 3.2). In 2008, the heat accumulation in the lake was much smaller, with a maximum of only 50 °C-days by early September. The accumulation of heat was intermediate in 2007, 2009 and 2011 (respectively 100, 92 and 113 °C-days), with the maximum cumulative value reached by the middle of August.

The Schmidt stability index (S ; Fig. 3.3) did not vary significantly between 2007 and 2009 but was significantly different in 2008, 2010 and 2011 ($p=0.021$). The variability of S , as indicated by the standard deviation of average seasonal values, was intermediate in 2007 (190 g cm^{-1}), lower in 2008 and 2009 (respectively 153 and 160 g cm^{-1}) and higher in 2010 and 2011 (respectively 233 and 239 g cm^{-1}). Years 2007, 2008 and 2009 showed two periods of maximal stability: during the first part of summer (mid-June 2007, mid-July 2008 and end of June 2009) and during the second part of summer (early August 2007, early September 2008 and mid-August 2009). These periods of maximal stability varied in amplitude and duration. In 2010, there were two periods of maximal stability restricted to the first part of the summer (early

June and mid-July), while in 2011 there were three brief periods of maximal stability during the first part of the summer (mid-June, mid-July and early August).

3.3.3. Nutrient concentrations

Average total phosphorus concentrations (TP) in the surface waters of Lake St. Charles (Table 3.2) were significantly higher in 2011 (by 29%) and lower in 2009 (by 30%) by comparison with the 5-year mean ($9.5 \mu\text{g L}^{-1}$). Average total nitrogen concentrations (TN) were significantly lower in 2009, 2010 and 2011 (respectively by 40.7, 23.8, and 9.6%) relative to the mean for the 5 years (0.35 mg L^{-1}). As a result, there was a large range in TN:TP from 26 to 39. These values place Lake St. Charles in an oligotrophic to near mesotrophic state (Kalff, 2002). Concentrations of surface SRP were near or below the detection limit ($0.5 \mu\text{g L}^{-1}$) each year. Surface NO_3^- -N concentrations were generally in the range $50 - 150 \mu\text{g L}^{-1}$, with values in 2008 and 2011 that were higher than the overall mean (by 10% and 28% respectively).

3.3.4. Spatial variation of the cyanobacterial communities

There was a significant ($p < 0.05$) but not close correlation ($r = 0.47$) between the total biovolume of cyanobacteria and Chl- a concentration. The former varied to a much greater extent among stations and among years: the overall coefficient of variation for cyanobacterial biovolume was 173%, while that for Chl- a was 44%. This greater variability was also apparent from the analysis of triplicate samples at each station in 2009 (Fig. 3.4). The coefficient of variation of total cyanobacterial concentrations among triplicates ranged from 3.2% to 74%, with most coefficients below 15%. The maximum within-site variation was recorded in June (CV for triplicates of 26% at N3, 36% at N4, 74% at S1, and 64% at S2) but occurred at low cell concentrations (respectively 5393, 5336, 2728 and 2712 cells mL^{-1}).

The spatial heterogeneity of cyanobacterial communities in Lake St. Charles was closely examined in 2009 (Fig. 3.5). Total cyanobacterial biovolume showed no significant difference among the 8 sampling stations (mean \pm SD of $0.251 \pm 0.018 \text{ mm}^3$

L^{-1} ; $p=0.900$). However, the community structure was clearly different between the north and south basins. *Anabaena flos-aquae* accounted for 5.6% (N3) to 13.0% (N1) of the total biovolume of cyanobacteria in the north basin, but appeared only sporadically in the south basin (less than 0.5%). In contrast, *Aphanothece* sp. accounted for less than 0.5% of total biovolume in the north basin, but up to 33.6% (S4) to 40.1% (S2) of total biovolume in the south basin. *Aphanocapsa* sp. appeared in similar concentrations among all sampling sites, but it accounted for a consistently low proportion of the total biovolume (2.4 to 4.1%). *Aphanothece* and *Aphanocapsa* cells were very small compared to other taxa (around 1% of the *Anabaena flos-aquae* cell volume) resulting in a low biovolume contribution despite relatively high cell concentrations. *Microcystis aeruginosa* appeared only sporadically at all stations (<0.5%), except in S4 where there was a slightly higher accumulation (3.1%). *Woronichinia* sp. was always dominant in the north basin (78.9 to 86.9%) while *Snowella* sp. was dominant in the south basin (39.7 to 44.1%). These latter two taxa have large cells (200% of the *Anabaena flos-aquae* cell volume), and were therefore disproportionately important in cell biovolume relative to their total cell concentrations.

In 2010, the horizontal distribution pattern of cyanobacteria (Fig. 3.5) was strikingly different when compared to 2009. Maximum concentrations were observed in the middle of north basin (N3; $0.360 \pm 0.011 \text{ mm}^3 \text{ L}^{-1}$) while the minimum was observed at the outflow near the dam (S4; $0.140 \pm 0.010 \text{ mm}^3 \text{ L}^{-1}$), but the overall statistical analysis showed no significant differences among sites ($p>0.5$). Community structure was less variable across the lake than in 2009, with *Anabaena flos-aquae* comprising the greater part of total biovolume at all sites (60.9% in S4 to 89.7% in S2). For *Microcystis aeruginosa*, there was a south/north difference with an order of magnitude greater biovolume in the north basin (around $0.04 \text{ mm}^3 \text{ L}^{-1}$ at N3 and N4) relative to the south basin (0.004 and $0.009 \text{ mm}^3 \text{ L}^{-1}$ for S3 and S4, respectively). *Aphanizomenon* sp. was in higher concentration at S4 ($0.02 \text{ mm}^3 \text{ L}^{-1}$) than in other stations. There was no significant difference among all stations for the other taxa, which appeared sporadically and contributed globally less than $0.03 \text{ mm}^3 \text{ L}^{-1}$.

3.3.5. Temporal variation of the cyanobacterial communities

Cyanobacteria were present at all sampling dates and all sites, but their abundance ranged over more than two orders of magnitude, from a minimum of $0.01 \text{ mm}^3 \text{ L}^{-1}$ on 27 September 2011 to a maximum of $3.90 \text{ mm}^3 \text{ L}^{-1}$ on 17 August 2007. There were large differences in the median values of cyanobacterial biovolume among the 5 summers of sampling (Fig. 3.6; $p = 0.031$). Biovolume was highly variable both over the summer season and interannually. Furthermore, the timing of peak cyanobacterial biomass differed among years: August 2007, September 2008, September 2009, July 2010 and August 2011.

Microcystis aeruginosa was the dominant phytoplankton in August 2007, but this dominance did not occur throughout the entire summer (Fig. 3.6). July communities were dominated by *Aphanocapsa* sp., while in September *Aphanothece* sp. and *M. aeruginosa* co-dominated. In summer 2008, there was a slight increase of the cyanobacteria biovolume at the end of the summer, with a co-dominance of *M. aeruginosa* and *Aphanocapsa* sp. in September. Bloom-forming cyanobacteria were scarce in 2009. Throughout the summer, the water column was dominated by *Woronichinia* sp. but its concentration remained low. *Aphanothece* sp. biovolume was negligible in 2009, but this taxon was often dominant in terms of cell concentrations, with averages of $22\,416 \text{ cells mL}^{-1}$ in July, $14\,303 \text{ cells mL}^{-1}$ in August and $11\,898 \text{ cells mL}^{-1}$ in September. In 2010, *Anabaena flos-aquae* strongly dominated from June to September. *Aphanizomenon* sp. appeared in August 2010 in low concentrations, but was absent during the other summers. In 2011, the total biovolume of cyanobacteria remained low throughout the summer, with dominance of the assemblage by *Anabaena flos-aquae*.

3.3.6. Correlations between biotic and abiotic variables

For the entire 5 years of seasonal and spatial data, there were significant correlations between the abundance of specific cyanobacterial taxa and certain environmental variables (Table 3). The biovolume of *Anabaena flos-aquae* (BV_{Anab}) was positively

correlated with surface water temperature, Schmidt stability index, average water residence time over the previous 15 days, and total precipitation over the previous 3 days, while it was negatively correlated with the average water level over the previous 15 days. The biovolume of *Microcystis aeruginosa* (BV_{Micro}) was positively correlated with the cumulative degree-days, total phosphorus, total nitrogen, and total precipitation over the previous 3 days. The biovolume of *Aphanocapsa/Aphanothecace* spp. (BV_{Aphano}) was positively correlated only with total nitrogen, while the biovolume of other non-dominant cyanobacteria (BV_{others}) was positively correlated with the total precipitation over the previous 3 days. Chl-*a* was positively correlated with precipitation and total nitrogen, and negatively with the Schmidt stability index.

3.4 Discussion

3.4.1. Spatial and temporal variability

The community of cyanobacteria in Lake St. Charles was characterized by a pronounced heterogeneity across the lake in terms of both biomass and structure. We observed marked differences in species composition between the north and south basins in 2009 (Fig. 3.5). That summer, there were large concentrations of *Anabaena flos-aquae* in the north basin while negligible concentrations occurred in the south basin. The population of the north basin was relatively homogeneous, with little variation among sites. This *A. flos-aquae* population would seem to have its origin within or upstream of the north basin, and may be retained within this sector of the lake by recirculation processes.

The spatial pattern of cyanobacteria differed markedly in 2010. We observed a significant difference in total biovolume between the north and south basins but the community structures were similar. *A. flos-aquae* biovolume was higher in the north basin and particularly at N3, which is at the middle of this basin where depth is maximal (17.5 m). This was unexpected given that this sampling site should not be subject to wind accumulation effects. At N4, there was also a high biovolume of *A. flos-aquae* but less than at N3; this site was located in a steep-sided 8 m-deep bay (Echo

bay), in which near shore cyanobacterial accumulations have been observed. Cyanobacterial populations may develop in the near shore N4 area, with subsequent transport to the center of the lake by surface water flow or a recirculation gyre. Such hydrodynamic effects have been observed in a much larger waterbody, Lake Biwa, Japan, where cyanobacterial blooms developed under low nutrient conditions in the center of the lake, after advection of the source populations from near shore, nutrient replete environments (Ishikawa et al., 2002).

We observed extreme interannual variations not only in cyanobacterial biovolume, but also in species composition (Fig. 3.6). The 2007 summer was characterized by high biomass of *M. aeruginosa*, 2008 by relatively low biomass of *M. aeruginosa* but high biomass of *Aphanocapsa* sp., 2009 by high biomass of *Aphanothece* sp., 2010 by high biomass of *A. flos-aquae*, and 2011 by low biomass of *A. flos-aquae*. This variability in dominance suggests a similarly high variability in environmental conditions from one year to another, and strong ecological sensitivity to these variations.

3.4.2. Factors controlling the temporal variation

Water temperature

An increase in the abundance of cyanobacteria is often associated with high temperatures because of their higher growth optimum relative to other groups of phytoplankton (Paerl & Huisman, 2008; and references therein). The maximum growth rates of most cyanobacteria are achieved at temperatures above 25°C (Robarts & Zohary, 1987), and even cold-tolerant cyanobacterial genotypes growing in polar and alpine environments often show warm temperature optima (Vincent & Quesada, 2012).

There was a positive relationship between the total biovolume of *A. flos-aquae* and water temperature (Table 3.3), while *M. aeruginosa* was correlated with cumulative °C-days, a measure of thermal growth conditions. This and the other correlative relationships must be interpreted with caution given that the data cannot be

considered spatially independent (Legendre & Legendre, 2012). The responsiveness of *Microcystis* to warm temperatures has been reported in several studies; for example, Johnston and Jacoby (2003) observed that *Microcystis* blooms in a mesotrophic lake were associated with temperatures above 22°C. The study of Wu et al. (2010) showed different responses of *M. aeruginosa* and *A. flos-aquae*, with the former growing faster than the latter at 20°C and 25°C, but growing very slowly at 15°C. These observations implied that *A. flos-aquae* would occur in early spring when the water temperature is lower, and *M. aeruginosa* in mid-to late summer when the epilimnion has sufficiently warmed. In Lake St. Charles, the peak population of *M. aeruginosa* was indeed observed in mid-August 2007, corresponding to the time of cumulative warm growing conditions for that summer (about 100 °C-days; Fig. 3.2). Conversely, the peak population of *A. flos-aquae* was observed in early July 2010, which corresponded to a lower cumulative warmth (about 50°C-days) but a higher water surface temperature compared to August. However, summer 2010 was a particularly warm summer ($23.2 \pm 2.7^\circ\text{C}$ between 1st July and 30th August) with an elevated cumulative number of °C-days (210°C-days). *A. flos-aquae* persisted throughout that summer, yet *M. aeruginosa* never rose to dominance, implying the influence of other environmental conditions on its net growth and abundance.

Water column structure

Another factor influencing the prevalence of cyanobacteria is water column stability (Paerl & Huisman, 2008; Taranu et al., 2012). Gas vacuoles produced by some cyanobacteria such as *A. flos-aquae* and *M. aeruginosa* allow a competitive advantage for light over other non-buoyant phytoplankton under conditions of low mixing intensity (Dokulil & Teubner, 2000; Reynolds & Walsby, 1975; Visser et al., 2005). For example, *Microcystis*, *Aphanizomenon* and *Anabaena* have been observed to achieve their highest biomass when the duration of stratified conditions exceeded 3 weeks (Šejnohová & Maršálek, 2012).

The water column stability in Lake St. Charles was significantly variable among years (Fig. 3.3) but only *A. flos-aquae* correlated with the Schmidt stability index (Table 3.3).

Thermal stratification in the lake started earlier in 2010 than in the other summers and was well established by early June (Fig. 3.3). This situation appeared to favor the N-fixing cyanobacteria *A. flos-aquae*, which dominated throughout the summer. N limitation can affect gas vesicle activation by restricting the production of essential proteins resulting in a loss of buoyancy (Chu et al., 2007; Whitton, 2012; and references therein). During warm and dry summers such as 2010, the thermal stratification was strong and the epilimnion would have received only low inputs of N. The ability of *Anabaena* sp. to fix atmospheric N₂ would provide a competitive advantage against other species, while N limitation under such conditions would negatively impact the buoyancy capacity of non N₂-fixing cyanobacteria such as *M. aeruginosa*. Under calm and turbid conditions, the flotation rate of *Anabaena circinalis* can be high due to trichome aggregation, while turbulent mixing may cause lower flotation rates by preventing trichome aggregation (McCausland et al., 2005). Irradiance is strongly attenuated with depth in Lake St. Charles, and *A. flos-aquae* may require a high degree of water column stability to dominate. Periods of short intermittent stability have been shown to result in a significant increase in growth of this species (McCausland et al., 2005), and a similar alternation of stratification and mixing may favor this taxon in Lake St. Charles.

As described by Stoke's Law, colony size has a strong influence on the flotation rates of colonial cyanobacteria (Oliver et al., 2012). *M. aeruginosa* colonies smaller than 20 µm in diameter have shown a low migration capacity, while colonies around 1600 µm have been estimated to migrate 10 m vertically over a period of hours (Cronberg & Annadotter, 2006). Large colonies tend to show little diurnal repositioning and are less affected by wind-induced mixing than small colonies and are thus mainly concentrated in the surface layer (Wu & Kong, 2009). *M. aeruginosa* colonies in Lake St. Charles were generally large, and thus may have been less affected by intermittent decreases in water column stability. This would potentially explain the lack of correlation between *M. aeruginosa* biovolume and the Schmidt stability index.

Nitrogen and phosphorus

Phosphorus has been identified as a major factor controlling cyanobacterial population size (Downing et al., 2001; Salmaso, 2002; Zhang & Prepas, 1996), and the increased enrichment of lakes by phosphorus leading to eutrophic conditions is often accompanied by the development of cyanobacterial dominance and blooms. N:P ratios have also been identified as a key factor for species composition in some studies (McQueen & Lean, 1987; Oliver et al., 2012; and references therein; Smith & Bennet, 1999), while many other studies have found little relationship to this variable (Downing et al., 2001; McCarthy et al., 2009; Pick & Lean, 1987; Xie et al., 2003).

Our nutrient analyses indicate that nitrogen limitation is likely to be rare in Lake St. Charles (Table 3.2). However, significant correlations with TN suggest that nitrogen may be a controlling factor of *Aphanocapsa/Aphanothece* spp. and Chl-a, and may also play a role in the dominance of *M. aeruginosa* (Table 3.3), but to a lesser extent. Although nitrogen demands may be met by N₂-fixation by diazotrophic species, this process is more energetically costly than the assimilation of other forms of nitrogen such as ammonium or nitrate (Rabouille et al., 2006). Thus, *A. flos-aquae* could be outcompeted by *M. aeruginosa* during periods of adequate nitrogen supply.

Our results suggest that in general P is limiting compared to N in Lake St. Charles. The threshold of phosphorus generally mentioned in the literature to induce dominance of cyanobacteria is 20-30 µg L⁻¹ (Downing et al., 2001; Jacquet et al., 2005). Although the average TP measured in Lake St. Charles never reached this threshold (Table 3.2), there may be episodes of enhanced internal and external supply of bio-available phosphorus, not captured by our lake sampling location or frequency, which may allow cyanobacteria to proliferate. An extreme value of 284 µg L⁻¹ of TP was recorded in the major inflow to Lake St. Charles, the Hurons River, during flood conditions (Bourget, 2011). Furthermore, the modeling of phosphorus inputs by the Hurons River to the lake in 2008 revealed that the four most intense floods transported 46% of the summer inputs over short periods of time that totalled only 8 days (Bourget, 2011). In addition, hypolimnetic oxygen depletion in late summer at station N3 was

observed every year (D. Rolland; chapter 2 of this thesis) and could potentially result in phosphorus release from sediments. A previous study in Lake St. Charles (Lavoie & Auclair, 2012) showed that the potential of internal loading from the deeper sites (N3, N4) was lower than from shallower sites. These potential sources of phosphorus enrichment are mainly located in the north basin, and could be an additional explanation for the greater success of cyanobacteria in this part of the lake.

The abundance of *M. aeruginosa* correlated with TP concentrations (Table 3.3), consistent with previous observations in the literature (e.g. Reynolds et al., 1981). *Microcystis* is able to increase its P uptake capacity in waters with a fluctuating P-supply (Šejnohová & Maršálek, 2012), as may be the case in Lake St. Charles. There is evidence in literature that increases in temperature and P concentration yield the highest growth rate for toxic *Microcystis* cells suggesting that future eutrophication and climatic warming may synergistically promote the growth of toxic, rather than non-toxic, populations of *Microcystis*, leading to blooms with higher microcystin content (Davis et al., 2009).

Non N₂-fixing species of cyanobacteria such as *M. aeruginosa* are often the dominant contributors to summer phytoplankton in lakes with TN:TP ratios much higher than the optimum ratio of 16:1 (Dokulil & Teubner, 2000). In Lake St. Charles, average TN:TP ratios were always higher than this threshold value (36 in 2007, 39 in 2008, 31 in 2009, 35 in 2010 and 26 in 2011), yet *M. aeruginosa* was only dominant in 2007 and 2008 and the potentially N₂-fixing *A. flos-aquae* dominated in 2010 and 2011 (Fig. 3.6). This is consistent with Dolman et al. (2012) who showed that the distribution of N₂-fixing taxa did not always differ from other cyanobacterial taxa in relatively N or P rich lakes. Furthermore, there was no statistical relationship between the biovolume of the two taxa and the TN:TP ratio in Lake St. Charles. This absence of relationship with TN:TP is consistent with the analyses by Downing et al. (2001) and Håkanson et al. (2007) from respectively 99 and 500 lakes throughout the world. Overall, our results imply that N and P supply, but not the fluctuations in TN:TP, may affect the shift in dominance between *A. flos-aquae* and *M. aeruginosa* in Lake St. Charles. There

were striking differences among species in their correlations with limnological variables (Table 3.3), indicating marked differences among taxa in their ecological preferences and in their responses to environmental changes.

Hydrology

The fluvial character of Lake St. Charles and other reservoirs could potentially exert a wide range of effects on their phytoplankton biomass and species composition and in contrasting ways. The inflow of high volumes of water during rain events can lead to a reduction of algal biomass due to high flushing rates and increased turbidity (Reichwaldt & Ghadouani, 2012). Nutrients are transported from the drainage basin to the lake during such events but less intense rainfall may increase cyanobacterial biomass through nutrient enrichment if the storm does not lead to de-stratification (Reichwaldt & Ghadouani, 2012).

The biovolume of *M. aeruginosa* in Lake St. Charles was positively correlated with the volume of precipitation (Table 3.3) and may be linked to the input of nutrients such as N and P. However, this correlation was relatively weak and may operate only during less intense rainfalls. *A. flos-aquae* biovolume was positively correlated both with the volume of precipitation and the water residence time (Table 3.3). Such results suggest a sensitive equilibrium between conditions favoring its dominance: input of nutrients, water column stability and low flushing rate. Moreover, the positive correlation with rainfall but no correlation with N and P suggest that other components not measured during this study may influence the biomass of *A. flos-aquae*. For example, iron is an essential micronutrient for cyanobacterial growth because it is necessary for the synthesis and activities of key enzymes involved in photosynthesis, electron transport and energy transfer (Oliver et al., 2012), and in some studies has been shown to stimulate N₂-fixing cyanobacteria (Wurtsbaugh, 1988; Wurtsbaugh & Horne, 1983).

Waterbodies with a water residence time of less than 2 years experience the greatest interannual and seasonal variation in flushing rate caused by variations in runoff and their high catchment area to lake volume ratios (Kalff, 2002). Field observations in

temperate reservoirs elsewhere have indicated that the effect of flushing rate on the summer composition of phytoplankton communities becomes evident when the water residence time declines below 60-100 days (Kimmel et al., 1990; Soballe & Threlkeld, 1985). Similarly, the short residence time of Lake St-Charles (30-100 days) may result in enhanced sensitivity to year-to-year fluctuations in hydrology, stratification and nutrient loading. The extreme interannual variability in phytoplankton biomass and species composition observed here may prove to be a general feature of many high through-flow reservoirs, and it implies the need for vigilant environmental monitoring of such lakes to detect the onset of large fluctuations in drinking water quality each year.

3.5 Conclusion

We defined the spatial and temporal variations of bloom-forming cyanobacteria in a north temperate reservoir, subject to short water residence time and P limitation. Despite these latter conditions, the noxious taxa *Anabaena flos-aquae* and *Microcystis aeruginosa* were able to dominate some years, mostly in the north basin. Each year of sampling showed some striking differences relative to other years in terms of the total biomass and structure of the cyanobacterial community, with dominance by a single species that also varied among years. Our results indicated that temperature plays a key role in controlling bloom-forming cyanobacteria, and that the time of onset of warming, the maximum water temperature, and the rate of accumulated heat, seems to affect the shift between *Anabaena* and *Microcystis*. Stratification of the water column favored bloom formers but *M. aeruginosa* seemed more competitive than *A. flos-aquae* under less stable conditions. Our results also imply that TN and TP supply, but not the fluctuations in TN:TP, may affect the shift in dominance between *A. flos-aquae* and *M. aeruginosa*.

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Table 3.1. Meteorological data for the 184 days period of sampling (May 1st to October 31th) from the Québec City Airport weather station (Environment Canada). Also given are the water levels relative to a reference datum at the dam across the lake outflow, and estimates of hydraulic residence time in the lake (mean ± SD).

Variables	Year				
	2007	2008	2009	2010	2011
Mean temperature ± SD (°C)	14.8 ± 4.8	14.3 ± 5.2	13.7 ± 5.7	15.2 ± 6.1	15.2 ± 5.2
Maximum extreme temperature (°C)	31.8 (2 Aug.)	30.3 (2 Sept.)	30.5 (17 Aug.)	33.4 (7 July)	31.2 (22 July)
Days of daily mean temperature > 20°C	22/184	17/184	25/184	45/184	35/184
Days of daily mean temperature > 25°C	0/184	0/184	1/184	7/184	0/184
Total rainfall (mm)	783	831	696	585	764
Maximum daily rainfall (mm)	60.8 (20 July)	52.6 (14 Sept.)	45.4 (29 July)	32.6 (8 Sept.)	52.0 (28 Aug.)
Total number of rainy days	82	96	88	90	96
Minimum water level (m)	2.49	2.53	2.10	1.95	2.19
Maximum water level (m)	2.78	3.39 (threshold)	2.81	2.99	3.39 (threshold)
Average residence time (days)	66 ± 18	65 ± 21	77 ± 16	91 ± 14	58 ± 15

Table 3.2. Nutrient and chlorophyll *a* concentrations in the surface waters of Lake St. Charles. Values are summer means \pm SD, with the number of samples given in parentheses.

Variables	Year									
	2007		2008		2009		2010		2011	
TP ($\mu\text{g L}^{-1}$)	9.6 \pm 2.3	(96)	9.4 \pm 2.9	(96)	6.7 \pm 1.3*	(7)	7.8 \pm 1.4*	(7)	12.3 \pm 2.9	(12)
TN ($\mu\text{g L}^{-1}$)	341 \pm 71	(96)	375 \pm 117	(96)	211 \pm 51*	(7)	270 \pm 82*	(7)	320 \pm 121	(18)
TN/TP	36 \pm 14	(96)	39 \pm 11	(96)	31 \pm 15	(7)	35 \pm 11	(7)	26 \pm 19	(12)
SRP ($\mu\text{g L}^{-1}$)	0.33 \pm 0.21	(43)	0.82 \pm 0.83	(66)	-		-		0.93 \pm 0.56	(11)
NO ₃ -N ($\mu\text{g L}^{-1}$)	94 \pm 27	(48)	129 \pm 33	(48)	85 \pm 57*	(7)	110 \pm 80*	(7)	150 \pm 103	(7)
Chl- <i>a</i> ($\mu\text{g L}^{-1}$)	6.5 \pm 2.8	(54)	7.5 \pm 3.1	(78)	4.0 \pm 1.1	(65)	3.2 \pm 1.0	(86)	3.7 \pm 1.8	(12)

*Provided by MDDEP (2011)

Table 3.3. Spearman rank correlations between biotic and abiotic variables of surface water. Biotic variables: biovolume of total cyanobacteria (BV_{TOT} , $\text{mm}^3 \text{ L}^{-1}$), *Anabaena flos-aquae* (BV_{Anab} , $\text{mm}^3 \text{ l}^{-1}$), *Microcystis aeruginosa* (BV_{Micro} , $\text{mm}^3 \text{ L}^{-1}$), *Aphanocapsa/Aphanothecace* sp. (BV_{Aphano} , $\text{mm}^3 \text{ L}^{-1}$) and of others groups of cyanobacteria (BV_{others} , $\text{mm}^3 \text{ L}^{-1}$), concentration of chlorophyll *a* (Chl-*a*, $\mu\text{g L}^{-1}$). Abiotic variables: water temperature (T° , $^\circ\text{C}$), degree-days (DD, $^\circ\text{C}\text{-days}$), Schmidt stability index (S , g cm^{-1}), average water residence time for last 15 days (WRT_{15} , days), average water level for last 15 days (WL_{15} , m), total precipitation for the last 3 days (PPT, mm), total phosphorus concentration (TP, $\mu\text{g L}^{-1}$), total nitrogen concentration (TN, mg L^{-1}), ratio of total nitrogen on total phosphorus (TN/TP).

Biotic variables	Abiotic variables								
	T° ¹	DD ¹	S ¹	WRT_{15} ¹	WL_{15} ¹	PPT ¹	TP ²	TN ²	TN/TP ²
BV_{TOT}	0.18	0.02	0.19	0.33**	-0.26*	0.20*	0.59*	0.64*	-0.68*
BV_{Anab}	0.48**	0.02	0.33**	0.30**	-0.26*	0.27*	0.44	0.30	-0.45
BV_{Micro}	0.16	0.25*	-0.09	0.12	-0.14	0.22*	0.70*	0.60*	-0.27
BV_{Aphano}	0.13	-0.10	0.09	0.05	0.01	0.13	0.19	0.58*	-0.32
BV_{others}	0.01	0.09	0.07	0.09	-0.08	0.19*	0.43	0.27	-0.54
Chl- <i>a</i>	-0.06	0.10	-0.25*	0.01	0.01	0.20*	0.48	0.61*	-0.40

* $p < 0.05$, ** $p < 0.001$

¹N = 88, ²N = 21

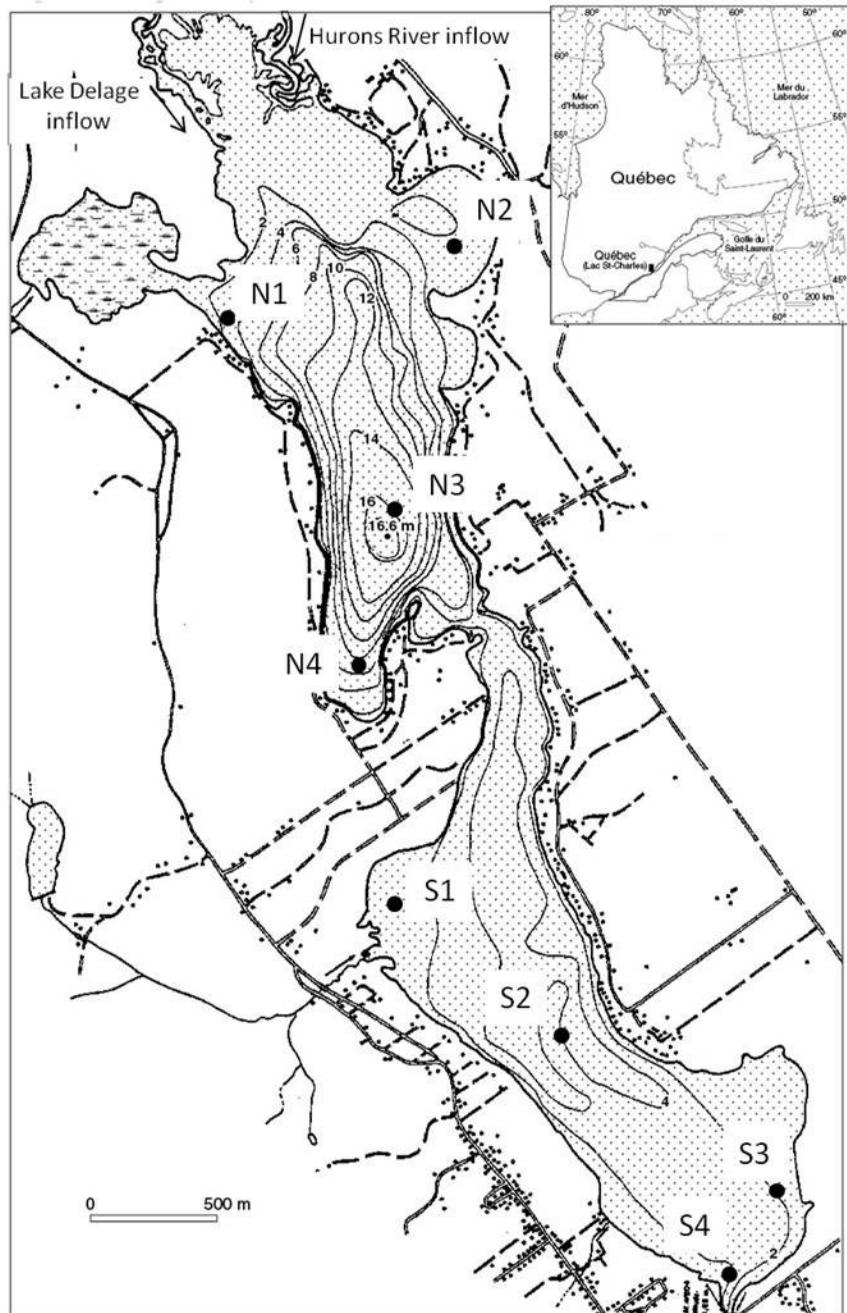


Figure 3.1. Map of the Lake St. Charles and location of the sampling sites. Northern basin: Talbot bay (N1), Aigles Pêcheurs bay (N2), deepest point of the lake (N3), Echo bay (N4). Southern basin: Milans bay (S1), middle of the southern basin (S2), beach (S3), dam (S4).

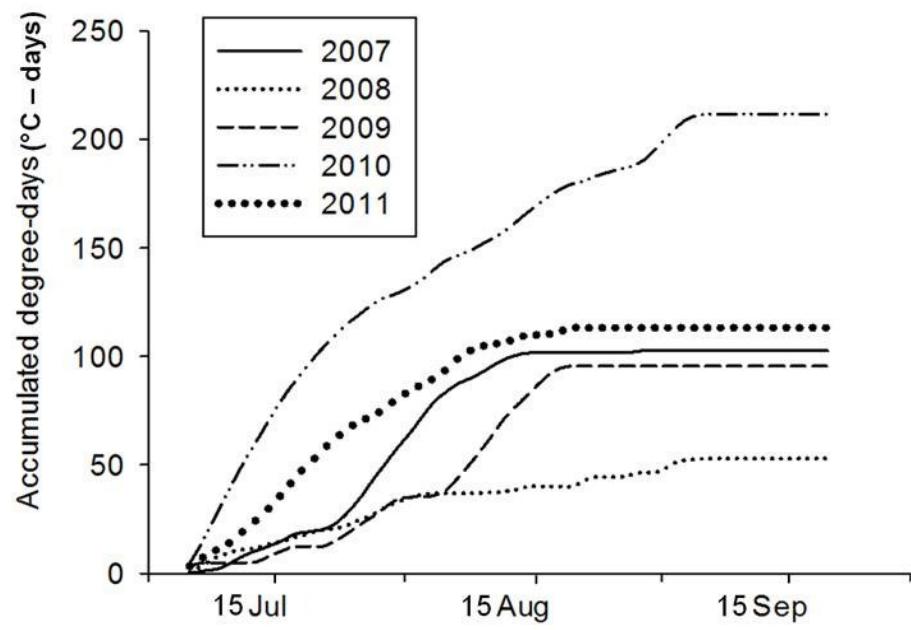


Figure 3.2. Cumulative degree-days during 5 consecutive summers (2007 – 2011) at site N3 (station codes given in Fig. 3.1 legend).

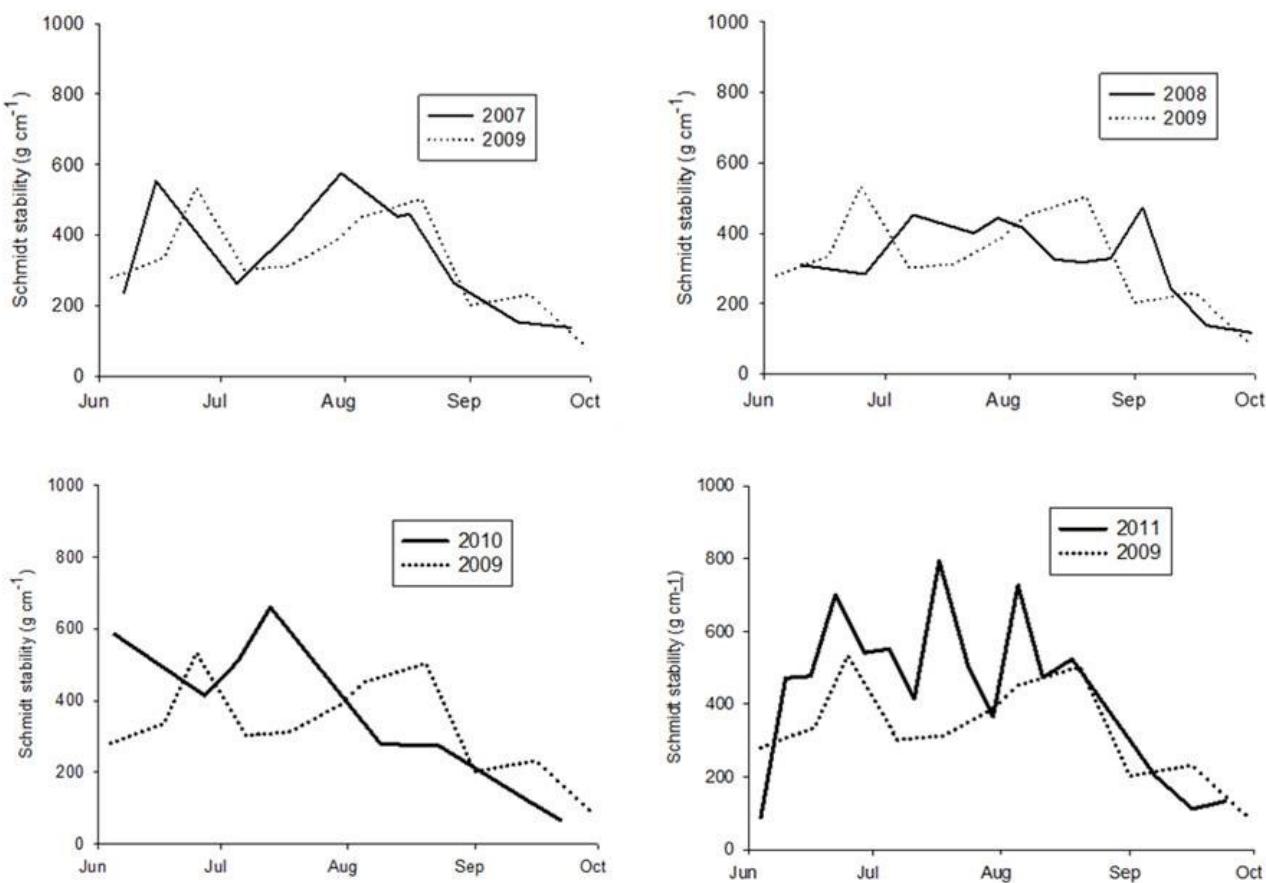


Figure 3.3. Pairwise comparisons of the Schmidt stability index of the water column during 5 consecutive summers (2007 – 2011) at site N3 (station codes given in Fig. 3.1 legend). Year 2009 is used as a comparison because it was less subject to cyanobacterial blooms.

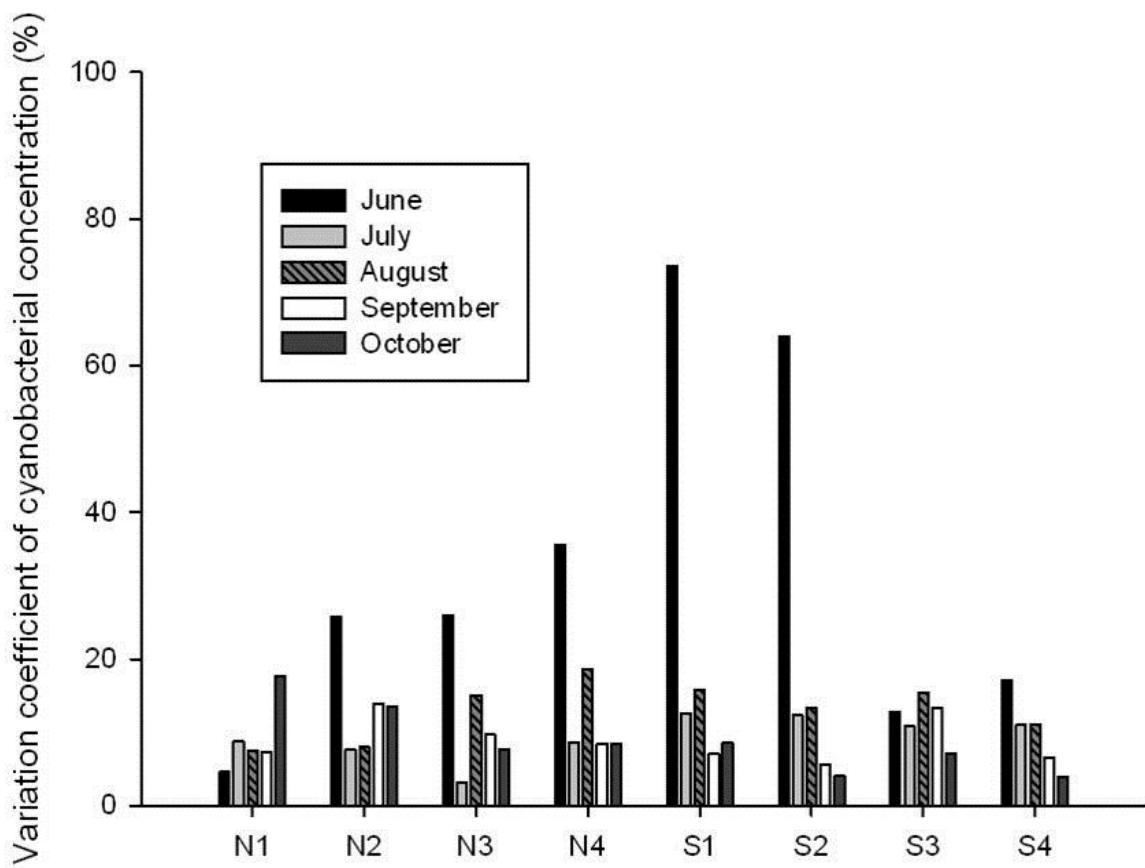


Figure 3.4. Coefficient of variation (%) of cyanobacterial concentrations among each set of triplicate samples at each station in summer 2009.

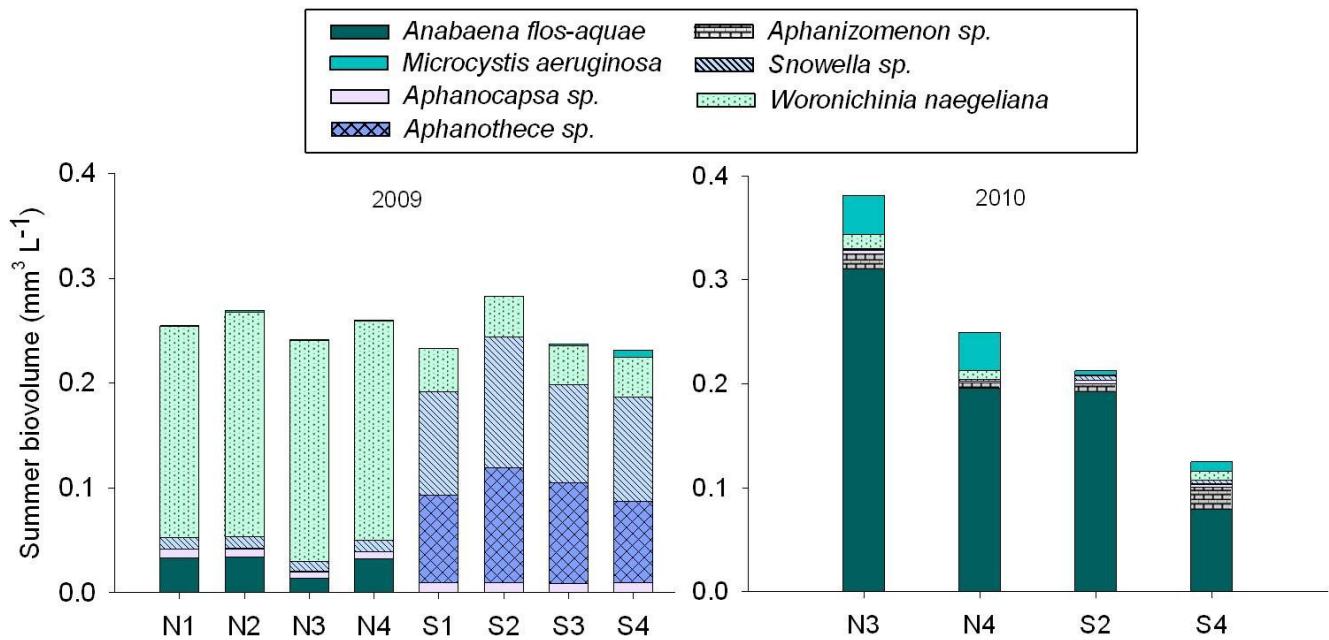


Figure 3.5. Total biovolume and specific composition of cyanobacteria during summers 2009 and 2010. The values are averages for 10 (2009) and 13 (2010) sampling dates.

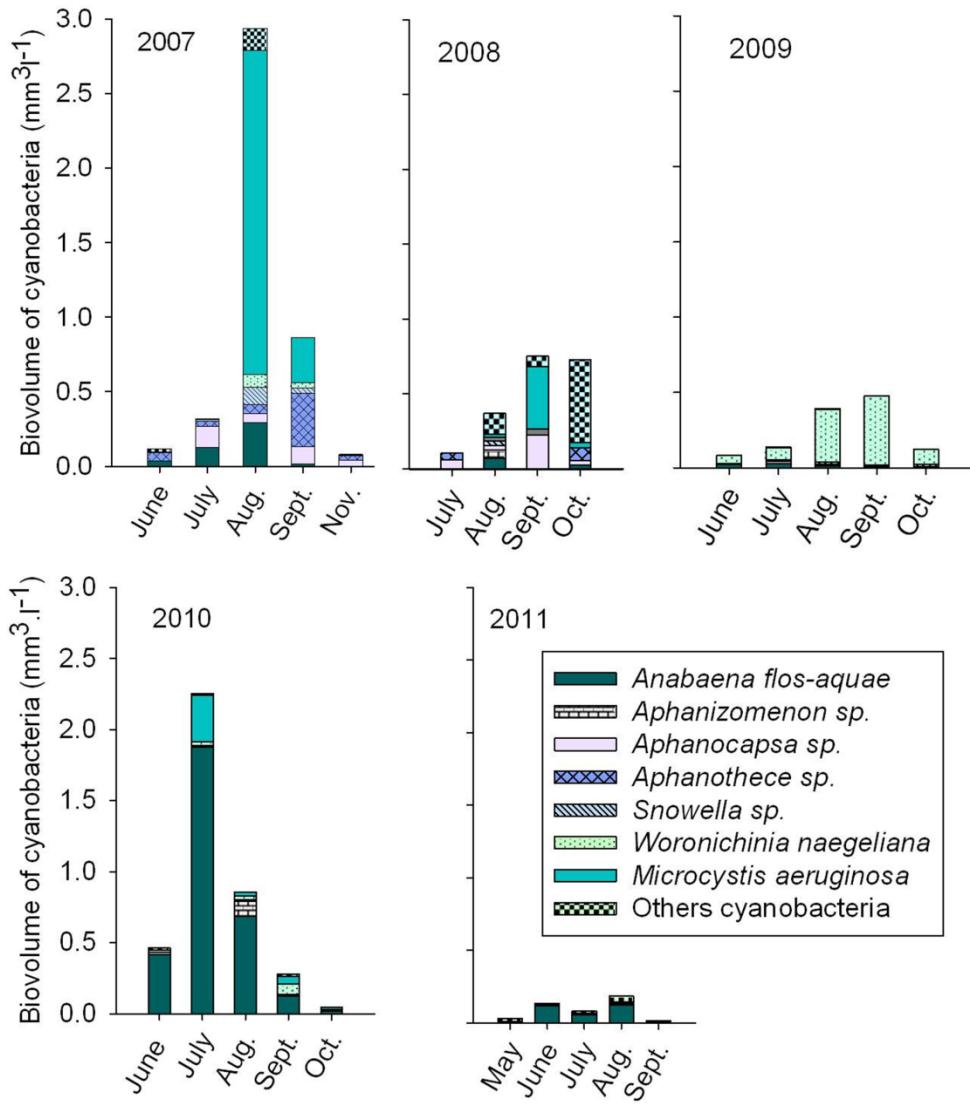


Figure 3.6. Seasonal and interannual variations in total biovolume and the specific composition of cyanobacteria in Lake St. Charles.

Chapitre 4. Phytoplankton seed banks in lake sediments: application of five methods to detect cyanobacterial resting stages in a drinking water reservoir

Résumé

Des efflorescences nocives de cyanobactéries ont été observées depuis l'automne 2006 dans le lac Saint-Charles, une importante source d'approvisionnement en eau potable pour la ville de Québec, Canada. Ces efflorescences se sont avérées inattendues du fait des faibles concentrations de phosphore total mesurées dans le lac (moyenne estivale $<15 \mu\text{g L}^{-1}$). Les objectifs de la présente étude étaient de décrire les caractéristiques sédimentaires du lac Saint-Charles et de détecter la présence éventuelle de populations dormantes de *Microcystis* et/ou *Anabaena* constituant un inoculum pour la prolifération de cyanobactéries dans la colonne d'eau. Diverses techniques ont été appliquées pour détecter ces populations ; la cartographie *in situ* de la phycocyanine fluoresçant à la surface des sédiments, l'observation au microscope à épifluorescence, l'analyse des pigments par chromatographie HPLC et l'incubation de sédiments superficiels en conditions ambiantes, puis contrôlées. Ces analyses ont révélées une dominance de diatomées, dinoflagellés et chrysophytes à la surface des sédiments et la présence de cyanobactéries filamenteuses benthiques. Cependant, aucune cellule dormante d'*Anabaena* et *Microcystis* n'a été détectée. Même si les sédiments en zones peu profondes reçoivent un éclairement suffisant et se situent dans des eaux suffisamment réchauffées pour favoriser le recrutement des cyanobactéries au printemps, leur exposition à la resuspension, associée au court temps de résidence hydraulique du lac semble empêcher l'accumulation de populations benthiques. Ces résultats impliquent que l'inoculum des efflorescences provient d'une autre source que les sédiments, comme par exemple les affluents ou une population holoplanctonique persistante dans la colonne d'eau.

Abstract

Cyanobacterial blooms have been reported since autumn 2006 in Lake St. Charles, a major drinking water supply for Quebec City, Canada. These blooms were unexpected given the low concentrations of total phosphorus in the lake (summer average $< 15 \mu\text{g P L}^{-1}$). The objectives of the present study were to describe the sediment characteristics of Lake St. Charles, determine the presence and composition of phytoplankton overwintering in the sediments, and to test the hypothesis that these populations include an inoculum for the proliferation of *Anabaena* and *Microcystis*. Diverse techniques were applied; *in situ* phycocyanin mapping, observations of surficial sediments by epifluorescence microscopy, pigment analysis by HPLC chromatography, and culture of sediment samples under ambient and controlled conditions. These analyses revealed an abundance of phytoplankton in the sediments, notably diatoms, dinoflagellates, chrysophytes and chlorophytes. Growth of benthic filamentous cyanobacteria was induced from the sediments; but dormant cells of bloom-forming genera such as *Anabaena* and *Microcystis* were not detected. The sediments of the shallow areas of the lake received adequate irradiance and were in sufficiently warm waters to favor cyanobacterial recruitment in spring, but their exposure to wind-induced mixing combined with the short residence time of the lake may have precluded the build-up of benthic populations. The ensemble of data implies that cyanobacteria blooms were inoculated from sources other than the sediments, possibly from inflowing waters or from a holoplanktonic population persisting in the water column throughout the year..

4.1 Introduction

Harmful cyanobacterial blooms are an increasing problem for lake and reservoir management (e.g. Dzialowski et al., 2011; Watson et al., 2008; Winter et al., 2011), and their detection, mitigation and control require an improved understanding of the ecological characteristics of bloom-forming species. Here we focus on one specific feature of the cyanobacterial life cycle, the overwintering of resting stages in lake sediments, and their potential recruitment into the water column as the inoculum for noxious blooms.

The alternation of benthic-planktonic stages in phytoplankton in general and cyanobacteria specifically is an adaptive strategy that may allow bloom-forming species to survive harsh conditions during winter such as cold temperatures, ice-cover and low irradiance (Barberio & Welch, 1992; Head et al., 1999b; Karlsson-Elfgren & Brunberg, 2004). When environmental conditions are optimal, resting stages contained in the surface layer of sediments may return to a more intense metabolic activity, differentiate and then emerge in the water column. In the Nostocales, taxa such as *Anabaena flos-aquae* produce overwintering akinetes, which then germinate as gas-vacuolate vegetative cells that rise up into the overlying water (Kaplan-Levy et al., 2010). In the genus *Microcystis*, the dormant stage occurs as modified vegetative cells that remain in the sediments throughout winter, and then develop gas vacuoles and enter the water column during the subsequent growing season (Brunberg & Bostrom, 1992; Reynolds et al., 1981). These benthic colonies of cyanobacteria thus retain their viability throughout winter and constitute the inoculum for the next year of growth in the phytoplankton (Holland & Walsby, 2008; Latour et al., 2004; Reynolds et al., 1981).

Recruitment of benthic inocula is thought to be an active process that is triggered in the sediments by increased temperature (Wiedner et al., 2007) and light (Karlsson-Elfgren et al., 2004), and by changes in nutrients (Brookes et al., 1999; Thompson et al., 2009) and oxygen concentrations (Chauvat et al., 1982). However, it may also be

due to a passive mechanism, with the resuspension of fine sediments by wind, and the subsequent activation of resting stages once they are entrained into the water column (Rengefors et al., 2004; Verspagen et al., 2004). These two disparate mechanisms of recruitment imply that there may be local differences in the resting stage pool and in the recruitment rate between shallow and deep areas. The highest concentrations of benthic forms of cyanobacterial colonies are often found in the deeper parts of lakes (Tsujimura et al., 2000; Verspagen et al. 2005), and may result from settlement in shallow areas near the shore after wind-blown accumulation, followed by resuspension by the wind and transport to deeper offshore areas where sinking colonies can no longer be mixed back into the pelagic zone (Latour et al., 2004; Verspagen et al., 2005). The survival of cyanobacteria in deepwater sediments may depend on environmental conditions such as oxygen concentration, irradiance and nutrient content of the sediments (Brunberg, 1993; Reynolds et al., 1981; Verspagen et al., 2005) or presence of macrophytes (Hilt & Gross, 2008; Jasser 1995). Other studies have indicated that littoral and deep areas of lakes can have a similar potential seed bank, and during optimal conservation conditions; there should be no spatial differences in the concentration of cyanobacteria in their benthic phase (Brunberg & Blomqvist, 2002; Rengefors et al., 2004). However, shallower sediments are typically warmer, better illuminated and more subject to wind-induced resuspension, and therefore the recruitment rate from inshore sites is likely to be much higher than from deeper offshore sediments (Brunberg & Blomqvist, 2002; Verspagen et al., 2005).

The present study addresses the spatial distribution of cyanobacteria in the sediments of Lake St. Charles, a major water supply for Québec City, Canada. Noxious blooms of *Microcystis aeruginosa* and *Anabaena flos-aquae* have been observed in this reservoir since 2006 (APEL, 2009) and their occurrence has created major concern about drinking water quality and the best strategies for environmental management of this important resource. Our aim was to evaluate the hypothesis that the sediments of Lake St. Charles contain an inoculum of cells that seeds the proliferation of *Anabaena flos-aquae* and *Microcystis aeruginosa* in the water column each year. We first undertook a detailed analysis of the sediment characteristics of this reservoir

(macrophyte cover, particle size, organic matter content, pore water phosphorus and sedimentation rate), and of the limnological conditions at the sediment surface in a way to evaluate the potential habitat for cyanobacteria. We then examined by way of five separate methods, the presence and composition of phytoplankton in the lake sediments, with particular attention to cyanobacteria that could potentially act as an overwintering inoculum for bloom development. Specifically, the methods tested were: (i) *in situ* detection by using a submersible fluorescence probe specific to cyanobacterial pigments; (ii) analysis of sediment samples by epifluorescence microscopy; (iii) sediment pigment analysis by HPLC chromatography; (iv) sediment incubations at ambient room temperature and irradiance; and (v) sediment core incubations under controlled laboratory conditions of temperature, light and nutrients.

4.2 Methods

4.2.1. Site description

Lake St. Charles ($46^{\circ} 54' N$, $71^{\circ} 22' W$) is located 20 km north of Québec City, Canada. It has a surface area of 3.6 km^2 and a total water volume of $14.8 \times 10^6 \text{ m}^3$, and is composed of two basins that differ in morphometry: the north basin is conical and reaches a maximum depth of 17.5 m, and the south basin has a maximum depth of 6 m (Fig. 4.1). The watershed of Lake St. Charles extends over an area of 169 km^2 and the hydraulic residence time for summertime is in the range 30-100 days (Rolland et al., 2013; chapter 3 of this thesis). The lake overlies glacio-marine deposits and the surrounding mountains are composed of granite and gneiss (Gérardin & Lachance, 1997). Lake St. Charles experiences a temperate sub-humid climate, with an annual rainfall around 1300 mm. It is covered with ice during 5 months of the year, from early December to the end of April. The trophic status of Lake St. Charles is considered to be oligo-mesotrophic to mesotrophic (Rolland et al., 2013; chapter 2 of this thesis). Eight sampling sites were selected, covering several bays as well as the open waters of the lake (Fig. 4.1). The sampling was conducted in 2009 and 2010, from immediately after the lake became ice-free in May, to the onset of mixing in October.

4.2.2. Limnological variables

Temperature, pH, specific conductivity, and dissolved oxygen were measured throughout the water column with a submersible probe (YSI 6600V2, YSI Inc.), at all sampling sites and sampling dates. Transparency measurements were made with a 20 cm diameter Secchi disk. A chain of 10 thermistors (Onset Tidbit TBI32; resolution of $\pm 0.2^{\circ}\text{C}$) was installed at site N3 (17.5 m) to obtain continuous measurements of water temperature down the water column over the entire sampling period each year.

4.2.3. Sediment analysis

Core extraction

Sediment cores were collected using a 75 mm diameter Kajac-Brinkhurst gravity corer (Aquatic Research Instruments) at 8 sites throughout the lake (Fig. 4.1). Triplicate samples were taken at each site in 2009, and single cores were obtained per site in 2010. Three additional cores were obtained at site N4 on January 2010 when the lake was covered by ice. The cores were covered with an opaque bag immediately after sampling to avoid prolonged exposure to light, and were conserved in a vertical position at 4°C during 24 h. In the laboratory, the cores were sub-sampled in dim light using an extractor for expelling thin layers of sediment. The two uppermost 1-cm layers of sediment and 20 mL of the overlying water were kept for further analysis. A subsample was conserved at 4°C for microscopy analyses, and another was kept at -80°C for HPLC analysis and particle-size analysis.

Particle-size analysis

The particle-size of the top 1 cm-layer of sediment was determined for each core sample at the Institut des Sciences de la Mer de Rimouski. The samples were first deflocculated by the addition of sodium hexametaphosphate and mixed during 3 h on a shaking table. The sediment was then passed through a 2 mm sieve and the fraction smaller than 2 mm was analyzed with a particle size analyzer by laser diffraction LS13320 (Beckman Coulter). The results were analyzed using Gradistat v.4 (Blott and

Pye 2001). This analysis would then bring some indication about the resuspension potential at the sampled sites.

Organic matter content

The organic matter content was determined by loss-on-ignition. A known mass of dry sediment was placed in the oven at 375°C during 16 h and the resulting mass difference corresponded to the total organic material (Bell, 1964). The content was expressed in % dry weight of sediment..

Macrophyte cover

Percentage macrophyte cover was estimated visually or by a submersible camera deployed from the boat at each sampling site and date. The estimates were made at the middle of each square of a grid (Fig. 4.1) that was georeferenced with a GPS (Garmin Inc.).

Radio-isotopic datation

One core was collected at N3 and N4 to determine the sedimentation rate in the north basin of Lake St. Charles. The ^{137}Cs and ^{210}Pb dating techniques were used to date the most recent sediments, and several layers were selected in each core to determine the age of the sediments with depth. Each layer was sub-sampled, transferred in sealed bags and processed according to the method of Eakins and Morrison (1978). Analyses of ^{210}Pb and ^{137}Cs activity were performed using a High Purity Germanium radiation detector in the Laboratoire Radiochronologique du Centre d'Études Nordiques (Université Laval, Quebec City). ^{137}Cs activity was used to detect a reference date (1963) and, after a logarithmic transformation of the ^{210}Pb activity, the calendar age of each layer was estimated using the Constant Rate of Supply Model method (Appleby, 2001). This model corresponds to a constant flux of atmospheric ^{210}Pb but considers a variable sedimentation rate. Sedimentation rates were then calculated using algorithms described by Sorgente et al. (1999) and transformed from g/cm²/y to mm/y by using the dry bulk density of each layer (g/cm³).

Phosphorus in pore water

The sediment pore water was sampled at 5 littoral zones (N2, N4, S1, S3, S4) from the shore using mini-piezometers (1 m long metallic tubes with 1.5 cm internal diameter) that were inserted 20 cm into the sediment. The mini-piezometers were perforated over the bottom 20 cm in order to allow the penetration of pore water. The water was pumped from inside the piezometers using a syringe and tube, and transferred into a plastic sampling bottle. Soluble reactive phosphorus (SRP) concentrations were determined on water that passed through a 0.45 µm membrane filter. The samples were stored at 4°C until analysis, e.g. no more than 48h after the sampling. SRP was analyzed by a colorimetric assay using ammonium molybdate and a Genesys 10UV spectrophotometer (Thermo Spectronic, Waltham, USA). The absorbance measure was performed at 885 nm in a 10 cm quartz cell and the detection limit was 0.4 µg P L⁻¹.

4.2.4. Detection of phytoplankton in the sediments

Phycocyanin fluorescence mapping

The presence and distribution of the cyanobacterial pigment phycocyanin over the sediment surface of Lake St. Charles were assessed over the period May to September 2010 using a submersible phycocyanin fluorometer (TriOS microFlu-blue). This instrument has an excitation peak at 620 nm and detects the emission of fluorescence between 650 and 660 nm, and the results are expressed in terms of µg phycocyanin (PC)L⁻¹. The measurements of PC concentration at the sediment surface were performed in each square of the grid previously described. The probe was mounted in a tripod that allowed it to be carefully placed at a constant distance (5 cm) from the lake bottom (Brient et al., 2008). The manufacturer's calibration was used but was first validated in laboratory. A concentration of PC, made up using a commercial extract of C-phycocyanin, was determined from the equation of Patel et al. (2005):

$$PC \text{ (mg mL}^{-1}\text{)} = [A615 - 0.474 (A652)]/5.34$$

where A615 nm and A652 nm are, respectively, maximum absorption of phycocyanin and allophycocyanin. The linearity of the probe signal was tested with the commercial extract over the range 0 to 100 mg L⁻¹ phycocyanin, yielding a R value of 0.946. This linearity was then tested using monospecific cultures of picocyanobacteria *Synechococcus* sp. and filamentous taxa *Anabaena flos-aquae*. The results showed a linear probe signal response with R= 0.985 for *Synechococcus* sp., with an estimated number of 4050 cells mL⁻¹ by fluorescence unit, while *Anabaena flos-aquae* yields R= 0.987 with 550 cells mL⁻¹ by fluorescence unit..

The effect of macrophytes was analyzed by comparing the fluorescence measured by the TriOS probe and the *in vitro* fluorescence measured in a Cary Eclipse (Varian) spectrofluorometer. Samples of macrophytes were collected on 20 July at N1 and N2. Each sample was transferred to a polyethylene bag and transported in a cooler to the laboratory. On the same day, epiphytic microalgae were collected by gently scraping the macrophyte leaves with a metallic spatula into filtered lake water. The macrophytes were divided into small pieces and rinsed with filtered Lake St. Charles water. Spectrofluorometer cells were then filled with a sample of macrophyte tissue, epiphytic microalgae diluted in filtered lake water or *Anabaena flos-aquae* culture diluted in filtered lake water. The fluorescence emission spectrum between 640 and 700 nm was analyzed for each sample at an excitation wavelength of 620 nm. The values were compared to measurements on a blank sample of filtered lake water.

*Epi*fluorescence microscopy

For microscopic analysis of benthic populations, 1 cm³ of sediment was inserted into a glass tube and the same volume of distilled water was added. The sample was agitated, large sand and silt particles were allowed to sediment, and then the supernatant was removed. This washing was repeated 3 times, and then the supernatant was observed under an inverted fluorescence microscope (Zeiss Axiovert 100). The water overlying the sediment cores was also observed by microscopy. Either random 30 fields of view or a minimum of 100 individuals of the most abundant species were counted, and expressed on a semi-quantitative scale. Some

preliminary tests of this method were done using monospecific cultures of *Synechococcus* sp. A known density of *Synechococcus* sp. was inserted in a glass tube containing sediments and the same protocol was followed. This experiment was replicated 3 times. After counting, the difference of cells density was around 5% of underestimation.

Pigment analysis by high performance liquid chromatography (HPLC)

The frozen sediment samples were freeze-dried for 48 h and then stored frozen at -20°C. A dried subsample was weighed and transferred to a tube containing acetone (95%) and an aqueous solution of Sudan II (130 mg L⁻¹). The samples were sonicated and stored for 23h in the dark at -20°C. After extraction, the tubes were centrifuged at 4°C and 4150 rpm for 15 min. The supernatant was then filtered (PTFE, 0.2 µm) and analyzed in a Thermo Scientific Accela 600 HPLC using the protocol of Zapata et al. (2000). Chlorophylls were detected by fluorescence (excitation, 440 nm; emission, 650 nm), and carotenoids were detected by photodiode array (PDA) spectroscopy (350–750 nm) with a slit width of 2 nm. Absorbance chromatograms from the PDA were obtained at 450 nm.

Culture experiment

Surficial sediment samples were collected from Lake St. Charles by sediment coring on 15 June and 16 September 2009 at deep (N3; 7 m and N4; 17.5 m) and shallow sites (S1; 1 m and S4; 1.2 m). Subsamples were transferred aseptically into sterilized glass flasks containing BG11 medium (SIGMA; Allen & Stanier, 1968). The flasks were closed with a sterilized gauze stopper incubated at room temperature (20°C) and ambient light. At 1-2 week intervals, subsamples from the flask were observed under the inverted fluorescence microscope to determine the presence and growth of algae and cyanobacteria.

Microcosm experiment

Additional sediment cores (24) were collected on 25 October 2010 at N4, which is a site where cyanobacterial blooms often occurred since 2006. These cores and their overlying water column were maintained in their sampling tubes and installed in 4 programmable incubators (Sanyo -MIR445) of the Laboratoire Regional des Sciences Aquatiques de l'Université Laval (Québec City) during 35 days. The cores were initially incubated under simulated winter conditions: initially at 10°C for 2 weeks under an irradiance of 150 $\mu\text{mol photons}^{-1} \text{ m}^{-2} \text{ s}^{-1}$, and an irradiance cycle of 12h light /12h dark, and then at 4°C, in the dark for 2 weeks. Two controlling factors for resting stages recruitment were then tested: temperature and phosphorus enrichment. Each incubator was set to a different temperature and had 6 cores: 3 control replicates and 3 replicates with addition of phosphorus. The temperature was gradually increased by 5°C every 5 days to final temperatures of 15, 20, 25, and 30°C. The phosphorus enrichment of K_2PO_4 (final concentration of 10 $\mu\text{g P L}^{-1}$) was added to 3 cores in each incubator when the final temperature was reached, and phosphorus levels were maintained thereafter by the same enrichment every 5 days. The light regime was maintained at 150 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ and 12h light/12h dark, and bubblers were installed at the surface of the water column in each core to allow oxygenation and circulation of the overlying water. Phycocyanin fluorescence was measured each 5 days in the overlying water throughout the experiment using the TriOS probe, and 100 mL of surface water were collected using a syringe and transferred into a plastic bottle containing Lugol's iodine (final concentration 5 %) for microscopy. Cyanobacteria cells in these samples were then enumerated under the inverted fluorescence microscope (Zeiss Axiovert 100). The subsample of water was replaced by an equal volume of Lake St. Charles filtered water with or without phosphorus enrichment according to the treatment.

Statistical analysis

The non-parametric Friedman repeated measures ANOVA procedure was applied to test the differences in phycocyanin concentration and granulometry between dates

and sampling sites. When the ANOVA results showed significant differences ($p < 0.05$), Dunn's or Tukey's multiple comparison tests were applied to compare treatments. All statistical analyses were performed with the software SIGMASTAT 11.0 (Systat Software). Phycocyanin fluorescence results for the mapping analysis were previously interpolated by using the Inverse Distance Weighting method, and plotted with ArcGIS (Environmental Systems Research Institute, Inc.).

4.3 Results

4.3.1. Temperature, oxygen and irradiance at the sediment surface

Lake St. Charles was free of ice by 1 May in 2009 and by 13 April in 2010. For the summer period, the average water temperature near the sediment surface was $16.3 \pm 5.0^\circ\text{C}$ in 2009 and $17.9 \pm 6.3^\circ\text{C}$ in 2010. The temperature at 16.5 m, over the deepest sediments, was always $\leq 9.5^\circ\text{C}$ during summer 2009 and $\leq 11.2^\circ\text{C}$ during summer 2010 (Fig. 4.2). At the beginning of the ice-free season in 2009, the temperature was less than 14°C , a temperature threshold for recruitment of Nostocales and *Microcystis* that is often given in the literature (Kaplan-Levy et al., 2010, Šejnohová & Maršálek, 2012). This limit was exceeded on 5 June down to 4.5 m depth. The temperature was always $\leq 14^\circ\text{C}$ below 6 m in 2009. At the beginning of the ice-free season in 2010, the temperature was already 2 or 3°C higher than the 14°C limit down to 3 m, and was exceeded on 16 June down to 8.5 m.

The water column of Lake St. Charles during summer was well oxygenated down to 4 m, with a minimum dissolved oxygen saturation of 76 % on 20 August 2009 and 67 % on 14 September 2010. However, there was a strong deficit in dissolved oxygen near the sediments at the deepest site (N3) for 2 to 4 weeks, with a minimum saturation of only 5.2 % on 16 September 2009 and 0.6 % on 9 August 2010 (Fig. 4.3).

The Secchi disk transparency of the water column of Lake St. Charles was low throughout summer, averaging 2.7 ± 0.3 m in 2009 and 2.6 ± 0.2 m in 2010. These results imply that the euphotic depth would extend to the lake bottom at the shallow

inshore sites for all of the ice-free period, while the sediments at the deeper sites were well below the euphotic zone.

4.3.2. Sediment properties and macrophyte distribution

Sediment particles sizes and chemistry

The bottom substrate of Lake St. Charles was dominated by pale beige colored fine sediments, particularly on the western shore of the lake and in the middle of each basin (Table 4.1). The proportion of silt appeared to be higher than sand at sites N1, N3, N4, S1, S2; however these differences were not significant. The eastern bays (N2, S3) and the area just in front of the dam (S4) were dominated by sand. Clays represented mostly less than 2% of the total sediments. The percentage of organic matter by weight was quite low ($8.8 \pm 1.4\%$) and significantly higher in N1 and lower in N2 and S4 ($p=0.0013$) but differences were not significant between June and September ($CV=6\%$). Sediment pore waters were analyzed for soluble reactive phosphorus at 5 littoral sites (Table 4.1). Concentrations were low at most of the sites and not significantly different, with the exception of Aigles Pêcheurs Bay (N2) where values were an order of magnitude higher.

Macrophyte cover

Macrophytes were heterogeneously distributed across Lake St. Charles and appeared to be more favored in shallow areas that had a large proportion of fine sediment (Table 4.1). Macrophytes were completely absent from the deeper sites (N3, N4 and S2) throughout summer. The visually most abundant species was *Myriophyllum spicatum* that occurred throughout the lake, and the stands were particularly dense at site S1. Other species that were recorded at the time of sampling were: *Brasenia schreberi*, *Eleocharis palustris*, *Nuphar variegatum*, *Pontederia cordata*, *Potamogeton* sp., *Sparganium eurycarpum*, *Sparganium fluctuans*, *Typha* sp. and *Utricularia vulgaris*.

Sedimentation rate

The sediment cores of Lake St. Charles showed equilibrium dates of 1903 ± 17 years at 21.5 cm core depth for site N3, and 1891 ± 26 years for 19 cm core depth at site N4. These give net average sediment accumulation rates of 2.0 (N3) and 1.6 (N4) mm per year, respectively. The sedimentation rate in the north basin showed high variations with ages. The sedimentation rates at deepwater site N3 showed evidence of greatly increased net values since the 1900s: from 0.1 mm y^{-1} in 1903 to peaks of 2.4 mm y^{-1} in 1967 and 3.0 mm y^{-1} in 1998 (Fig. 4.4). The sedimentation rate then appeared to increase gradually over the last 10 years to a maximum of 7.8 mm y^{-1} in 2007, probably due to construction work on a highway (R-175) located near the Hurons River, the principal inflow of Lake St. Charles, from 1994 until today. Sedimentation rates at N4 also showed an increase since the 1900s, but to a lesser extent. The maximum sedimentation rate of 4.9 mm y^{-1} in 2007 was about one half of the maximum at N3.

4.3.3. Benthic phytoplankton stocks

Fluorescence mapping

In situ measurements with the TriOS microFlu-Blue fluorescence probe gave values above detection at most sites. The data were not normally distributed and ranged from 0.6 $\mu\text{g PC L}^{-1}$ (N3 on 16 September) to 130.6 $\mu\text{g PC L}^{-1}$ (S1 on 15 July; Fig. 4.5). There were significant differences among the median values for the 4 sampling dates and 8 sampling locations ($p < 0.001$ and $p = 0.032$, respectively). During early summer (15 May), the PC values were higher at N1 and S1 than at N3 and N4, and during mid-summer (15 July) were higher at N1 and N2 than at all other sampling sites. At the end of summer (16 September), PC values were significantly higher at N1, N2 and S1, and during early fall (14 September) were higher at N1, N2, S1 and S4.

Epifluorescence microscopy

Examination of sediment samples from each site in 2009 and 2010 (summer and winter) by fluorescence microscopy revealed the presence of many algal species with intact fluorescing plastids, but there was no evidence of bloom-forming cyanobacteria as either vegetative cells or akinetes. All samples contained several diatom genera in high abundance, notably *Aulacoseira*, *Fragilaria*, *Asterionella*, *Tabellaria*, *Gomphonema*, *Navicula* and *Cyclotella*. The samples also contained representatives of the Euglenophyceae (*Euglena*, *Trachelomonas*) and Chlorophyceae (*Ankistrodesmus*, *Pediastrum*, *Scenedesmus*, *Coelastrum*, *Chlorococcum*), as well as oscillatorian cyanobacteria (*Oscillatoria*, *Arthospira*) and high concentrations of unidentified picoeukaryotic cells. Germinating akinetes of *Anabaena flos-aquae* were twice observed in water samples, but in sparse concentrations: in the overlying water of a sediment sample taken on 10 October 2010 at N4, and in a surface water sample taken on 10 June 2010 at N4 (Fig. 4.6).

Culture at ambient temperature in BG11

After 10 weeks incubation of Lake St. Charles sediment at room temperature, the N3 and N4 cultures showed a dominance of filamentous cyanobacteria (*Cylindrospermum majus*, *Oscillatoria* sp.) and the presence of Chroococcalean cyanobacteria, notably the genera *Chroococcus* and *Gomphosphaeria* sp. (Table 4.2; Fig. 4.7). Diatoms and chlorophytes were also well represented in the cultures. The incubations of September-sediment samples from N3 and N4 gave similar results but with a smaller proportion of Chroococcales. The June S1 and S4 samples produced only a low growth of Chroococcales and some filaments of *Oscillatoria* sp. However, the September S1 and S4 samples produced substantial growth of *Oscillatoria* sp., diatoms and Chlorophyceae. No bloom-forming taxa such as *Anabaena flos-aquae* or *Microcystis aeruginosa* were observed.

Cultures under controlled light, nutrient and temperature conditions

The microcosm experiment in the environmental chambers yielded similar results to those at room temperature. PC fluorescence as measured by the TriOS fluorescence probe was below or near the detection limit throughout the experiment, and no bloom-forming cyanobacteria such as *Anabaena flos-aquae* or *Microcystis aeruginosa* were observed. The 20, 25 and 30°C microcosms enriched with phosphorus additions showed substantial growth of coccoid chlorophytes, to maximum concentrations of 4.6, 6.6, and 4.4×10^3 cells mL⁻¹ (respectively) by the end of the experiment (35 days). The walls of the microcosms incubated under 30°C were colonized by attached filamentous cyanobacteria (*Oscillatoria* sp.), in treatments both with and without phosphorus additions.

Pigment analysis of the surficial sediments

The algal pigment assemblage in sediments of Lake St. Charles was composed of a combination of pigments that implied a diverse phytoplankton community containing Chlorophyceae (chl-*b*, lutein, neoxanthin and violaxanthin), Cryptophyceae (alloxanthin), Diatomophyceae and Dinophyceae (fucoxanthin, diadinoxanthin, diatoxanthin), Prymnesiophyceae (19'-Hex-fucoxanthin), and Cyanobacteria (Zeaxanthin, canthaxanthin), with many other degraded unidentified carotenoids with a lutein-like absorption spectrum. The spatial pattern was studied in detail during July 2010 and showed highest total pigment abundance at S2 (182 µg g⁻¹), S4 (187 µg g⁻¹) and N2 (184 µg g⁻¹), and lowest abundance at S3 (55 µg g⁻¹; Table 4.3). The dominant pigments (per unit Chl-*a*) were fucoxanthin, diadinoxanthin, diatoxanthin and 19'-Hex-fucoxanthin, indicating the importance of the red algal lineage in the phytoplankton (Roy et al., 2011). Photoprotective carotenoids were in low proportion, including the cyanobacterial pigments canthaxanthin (maximum of 0.6 %). The ratios of photoprotective to photosynthetic pigments were low (0.11 ± 0.07) due to the high Chl-*a* and fucoxanthin contributions to the total pigment budget.

In vivo fluorescence tests

The spectrofluorescence emission spectrum of all macrophyte samples (*Myriophyllum spicatum*, *Potamogeton* sp., *Utricularia* sp.) with excitation at 620 nm showed a maximum around 680 nm, corresponding to the peak in Chl-a fluorescence (Fig. 4.8). The emission spectrum differed for *Anabaena flos-aquae*, which showed a typical maximum peak around 650 nm corresponding to C-phycocyanin. Epiphytic microalgae that were collected from the macrophytes on the same date showed maximal emission from 640 to 675 nm. Analysis of this epiphytic material by epifluorescence microscopy revealed the presence of abundant coccoid cells < 3 µm in diameter, either solitary or forming microcolonies. The cells emitted a red-orange light when observed under a green excitation filter, indicating that they were picocyanobacteria.

4.4 Discussion

4.4.1. Benthic microalgal assemblages

Our analyses of the sediments of Lake St. Charles showed that they contained diverse algal taxa that could potentially act as a seed-bank for recruitment into the overlying phytoplankton. As in many dimictic lakes of the north temperate zone (e.g. Hausmann & Pienitz, 2009), diatoms dominated the benthic assemblages throughout sampling in both 2009 and 2010. The most common taxa were the pennate diatoms *Fragilaria*, *Asterionella* and *Tabellaria*, which are genera that are known to thrive in the phytoplankton of eutrophic lakes and reservoirs (Hoagland & Peterson, 1990; Wehr & Sheath, 2003). The HPLC pigment signatures of surficial sediments were characteristic of a community dominated by diatoms and, to a lesser extent, by Dinophyceae and Chrysophyceae (Roy et al., 2011). These two latter groups are well known for their ability to produce benthic resting stages (Wehr & Sheath, 2003), and according to our previous work (Rolland et al, 2013; chapter 2 of this thesis), these algal phyla were well represented in the phytoplankton (e.g., *Ceratium hirundinella* and *Dinobryon divergens*). The HPLC sediment analyses also indicated the presence of cyanobacteria,

but these pigments were in trace concentrations, at or near the detection limit. Consistent with these results, some cyanobacteria were observed under the microscope, specifically benthic filamentous taxa such as *Cylindrospermum majus* and *Oscillatoria* sp., and the small-celled taxa *Aphanocapsa* sp., *Chroococcus* sp. and *Merismopedia* sp. The bloom-forming species *Woronichinia naegeliana* was observed, yet only a few colonies after growth in the nutrient media. *Woronichinia* is known to be able to differentiate into resting cells that remain dormant in sediments, and its recruitment from sediments into the water column has been observed in Lake Guelph, Canada (Trimbee & Harris, 1984) and Esthwaite Water, United Kingdom (Head et al., 1999a).

4.4.2. Comparison and limits of the detection methods

The sediments of lakes with periodically large populations of planktonic cyanobacteria often contain high concentrations of resting cells that may provide an inoculum for the subsequent development of pelagic populations (e.g. Brunberg & Blomqvist ,2003; Latour et al., 2007; Verspagen et al., 2004). The results of application of five separate methods at many sites throughout the lake imply that, contrary to our hypothesis, this is not the case for Lake St. Charles. The various analyses utilized, from direct microscopic observation to HPLC pigment analysis and laboratory enrichment cultures, provided a consistent picture, and indicated that such resting stages - if present - were in low concentrations or below detection. This apparent absence of bloom-forming cyanobacteria contrasted with the abundance of other phytoplankton groups in the sediments, notably diatoms, dinoflagellates, chrysophytes and chlorophytes that were detected by light microscopy and/or HPLC analysis.

Some limitations of the present sampling and analytical methods must be considered to assess whether a sediment population of cyanobacterial resting cells could have in some way been undersampled or erroneously not detected. The cells may have been transported deeper than 2 cm in the sediments during the core collection or by faunal mixing processes (Kalff, 2002). However, this would also have been the case for the other phytoplanktonic groups and the presence of many other cell types and pigments

in the surficial sediments suggests that a surface population would still be detectable. It is possible that sampling was too late, after cell recruitment from the sediments into the water column. However, there was no evidence of cyanobacterial resting cells in cores sampled in winter at site N4, which is a site where concentrated blooms have been observed.

We applied a microscopy method that has been previously used by many authors (e.g. Brunberg & Blomqvist, 2002; Latour et al., 2007; Tsujimura & Okubo, 2003,), and our preliminary tests using *Synechococcus* cells mixed into sediments showed that these test populations could be readily detected. However, cyanobacteria such as *Microcystis* colonies may aggregate with suspended particles (Oliver et al., 1985; Verspagen et al., 2005), thus some colonies could have been lost during the treatment of samples prior to their observation by microscopy.

Cyanobacteria, including Chroococcales (*Woronichinia naegeliana*) as well as filamentous benthic forms, grew in the enrichment incubations, but neither *Microcystis* nor *Anabaena* were detected implying an absence of source population. It is possible that the latter two genera are patchy in the lake and were not sampled, that they were present but in concentrations that were too low to grow to detectable populations during incubation, or that they were not favored by some incubation conditions (e.g. intensity or quality of light, macronutrients and trace elements availability, mixing regime). However, since we sampled at many locations inshore and offshore, and incubated under a wide range of conditions, this uncertainty is unlikely to play a significant role.

A differential loss of pigments may have contributed to an underrepresentation by cyanobacteria. However, in comparison with diatom marker pigments, the cyanobacterial signature pigments zeaxanthin and canthaxanthin are chemically very stable with zeaxanthin being well preserved even in aerobic environments (Bianchi et al., 2000; Buchaca & Catalan 2007; Reuss & Conley, 2005) but they were little detected in the present study.

There was some contradiction between the results obtained with the TriOS probe and the other methods, especially during July 2010. However, this is likely due to the influence of macrophytes on the TriOS measurements. Our laboratory experiments with the TriOS probe showed that macrophytes themselves do not emit significant fluorescence signals that could be detected by this instrument, but our analyses of sampled macrophytes from Lake St. Charles by spectrofluorometry implied an influence of the abundant picocyanobacteria that were growing on the macrophytes as epiphytes. Therefore, phycocyanin mapping at the sediment surface must be applied with caution in areas containing abundant macrophytes.

4.4.3. Environmental conditions at the sediment surface

Lakes with a large surface area of sediments in warm shallow waters and receiving adequate irradiance at the sediment surface will provide the most favorable environment for benthic populations to develop and migrate into the overlying water column (Head et al., 1999a). Considering its morphometry, with a large (80%) proportion of shallow and warm areas and a euphotic zone around 4.5 m (Watanabe, 2011), Lake St. Charles would fit into this category. Conversely, sediments at N3 in the deep north basin receive low levels of irradiance and are subject to low temperatures and periods of hypoxia along the year, thus representing a poor environment for the benthic taxa growth and recruitment of resting cells. Shallow areas (up to 4 m deep) are also more exposed to wind-induced mixing and thus provide the conditions for the resting stages to relocate from the sediment into the warmer water column and photic zone in late spring. However, this resuspension combined with the very short residence time of water in Lake St. Charles (30-100 days; Rolland et al., 2013; chapter 3 of this thesis) and high flow during spring flood may also cause the flushing of bottom sediments, and therefore a loss of benthic phytoplankton stocks. Incubation experiments in BG11 medium showed that sediment samples from shallow sites in the south basin (S1 and S4) had significantly less phytoplanktonic cells than sediments sampled taken in the deep north basin (N3 and N4). Conditions permitting the benthic

accumulation of cells are often interrupted by physical disturbances such as currents and turbulent mixing in the shallower part of a lake (Scott & Marcarelli, 2012).

A previous study showed that SRP concentrations in the hypolimnion of the deepest area of Lake St. Charles were mostly near the detection limit ($0.5 \mu\text{g L}^{-1}$; Rolland et al., 2013; chapter 2 of this thesis) implying a low bioavailability of P coming from sediments that would support cyanobacteria growth and recruitment. However, fluorescence of PC was greatest at site N2, where the higher pore water SRP values ($48 \mu\text{g L}^{-1}$) implied richer nutrient conditions perhaps favoring macrophytes and coating by epiphytes. However, this SRP pore water concentration remains still very low compared to shallow eutrophic lakes (e.g. Lake Finjasjön in Sweden: $2000 \mu\text{g L}^{-1}$, Eckerot & Pettersson, 1993).

The recent (2008) sedimentation rate in the deeper parts of the lake ($5\text{-}8 \text{ mm y}^{-1}$) was high relative to many mesotrophic lakes elsewhere, for example 0.3 mm/y in Lake Nairne, Canada (Roy, 2012). The net average accumulation rate from 1900 to 2008 was near 2 mm y^{-1} like in the hypereutrophic Lake St. Augustin, Canada (Pienitz et al., 2006). However, considering the low proportion of organic matter at the sediment surface (< 10 %), these high net rates may in part be a result of the settling of mineral particles coming from the Hurons River, the principal inflow of Lake St. Charles, and may be amplified by an increase of erosion in the watershed (APEL, 2012) as well as “sediment focusing” (Blais & Kalff, 1995) into the deeper waters of the lake. This last hypothesis suggests that shallower sites are erosion and transportation zones that would be less subject to sedimentation, but more subject to resuspension (Blais & Kalff, 1995).

4.4.4. Origin of the cyanobacteria in Lake St. Charles

Recruitment of cells from lake sediments has often been identified as a major contributor to cyanobacterial blooms, but to an extent that varies greatly among studies. For example, in Lake Green, USA, 8% of the benthic *Aphanizomenon flos-aquae* filaments were recruited (Barbiero & Kann, 1994). In Lake Erken, Sweden, around

50% of benthic *Gloeotrichia echinulata* inoculated the epilimnetic population (Forsell & Pettersson, 1995), while in Lake Limmaren, Sweden, sediment recruitment contributed up to 50 % of the epilimnetic colonies of *Microcystis* in shallow areas and 8 % in deeper areas (Brunberg & Blomqvist, 2003). However in other lake studies, sediment recruitment contributed only a minor or negligible fraction of the bloom inoculum. For example, in Lake Esthwaite, recruitment was not a significant source of biomass for the planktonic populations of five species of cyanobacteria (Head et al., 1999a), and in Lake Mendota no benthic recruitment of *Aphanizomenon* was recorded during the stratification period (Hansson et al., 1994). Lake St. Charles would appear to fall into this latter category, with the ensemble of data implying that its cyanobacterial blooms were inoculated from sources other than the sediments.

Terrestrial inputs of microbiota from river runoff can be substantial and could potentially be a contributing inoculum for cyanobacteria blooms (Caporaso et al., 2012). Most of the water entering Lake St. Charles comes from the Hurons River, which drains 80 % of the watershed. However, the residence time in this river is likely to be short (mean summer discharge of $2.5 \text{ m}^3 \text{ s}^{-1}$; CEHQ, 2012), with insufficient time for the development of a substantial bloom-formers inoculum (at a flow rate of 1 m s^{-1} , the residence time in the river over its 3 km length would be only 50 min). Furthermore, measurements of cyanobacterial cell concentrations in the Hurons River at 3 sampling times in autumn 2012 (20 September, 1 and 17 October; APEL, January 2013, unpubl.) showed no presence of bloom-forming taxa. Cyanobacterial density was low in this river throughout summer (maximum of $1.7 \times 10^3 \text{ cells mL}^{-1}$) and always dominated by *Chroococcus* sp. or colonial picocyanobacteria such as *Merismopedia* sp., and *Aphanocapsa* sp. A second inflow enters Lake St. Charles from Lake Delage, but with a discharge that is on average < 5% of the Hurons River (Bourget, 2011). Periodic sampling of this inflow in summer 2012 (11 and 17 July, 7 and 15 August, 9 and 20 September, 1 and 17 October; APEL, January 2012, unpubl.) showed the episodic presence of *Microcystis aeruginosa*, but at low concentrations (up to $4 \times 10^3 \text{ cells mL}^{-1}$) and not until the autumn (September and October). However,

this observation could vary from year to year thus this hypothesis should not be neglected.

Another possibility for the inoculum of blooms in Lake St. Charles is that the cyanobacteria are holoplanktonic; i.e., resting cyanobacterial cells persist in the water column throughout winter, and these provide the starting population for a subsequent bloom. These pelagic populations would already be positioned in the water column to take immediate advantage of improved conditions early during the growing season. Oliver & Ganf (2000) estimated that the probability of blooms developing is very low in lakes where the water residence time is under 10 days and the inoculum concentration is less than 15 cells mL⁻¹. The residence time for Lake St. Charles is > 10 days, and at concentrations below the detection limits of light microscopy, overwintering communities could still represent a substantial total biomass for inoculating the next season's growth. For example, we observed no *Microcystis* sp. or *Anabaena* sp. cells in May, but our detection limit of around 50 *Microcystis* cells mL⁻¹ would be equivalent to a total lake-wide population (to a depth of 4 m) of around 10¹⁵ *Microcystis* cells. Cell concentrations of an order of magnitude lower would not be detectable, yet would still represent a huge residence population to initiate summer growth.

The application of high resolution molecular methods has begun to shed light on the potential importance of low background populations of microbiota as an inoculum for seasonal blooms. Rare microorganisms, referred to in the marine literature as the "rare biosphere" (Sogin et al., 2006) represent a reservoir of genetic diversity that is capable of responding rapidly to environmental change (Lennon & Jones, 2011). In a coastal marine study in the English Channel, high throughput DNA sequencing showed that the observed seasonal differences in microbial community structure, including cyanobacteria, represented changes in the relative abundances of taxa that are always present throughout the year rather than the sudden appearance of new taxa (Caporaso et al., 2012). Similarly, in Lake St. Charles and lakes elsewhere, a 'rare biosphere' of background cyanobacteria could provide the seed bank to initiate

summer blooms. Future applications of molecular microbiological methods to lakes will provide an important test of this intriguing hypothesis.

4.5 Conclusion

Given the low concentrations of total phosphorus in the epilimnetic water (summer average $< 15 \mu\text{g P L}^{-1}$) we expected an inoculum recruitment from sediments to be responsible of the cyanobacteria harmful blooms in lake St. Charles. The application of five detection methods permitted to highlight the presence of a diverse microbial population at the sediment surface. This population was mainly dominated by meroplanktonic diatoms and flagellates that can exhibit resting stages and benthic taxa such as oscillatoriales. However, these observations contrast with the apparent lack of *A. flos-aquae* and *M. aeruginosa* resting cells. The sediments of the shallow areas of the lake received adequate irradiance, were in sufficiently warm waters and exhibited a potential to favor cyanobacterial recruitment in spring, but their exposure to wind-induced mixing combined with the short residence time of the lake may have precluded the build-up of benthic populations. The absence of a large inoculum in sediments implies that a control of external inputs of nutrients may be an effective approach to reduce the occurrence of cyanobacteria harmful blooms.

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Table 4.1. Sediment characteristics at the 8 sampling sites in Lake St. Charles. All values are the means \pm SD for triplicates.

Properties	Sampling sites							
	N1	N2	N3	N4	S1	S2	S3	S4
Mean depth (m)	1.1 \pm 0.5	1.2 \pm 0.5	14.8 \pm 2.4	4.3 \pm 2.0	1.1 \pm 0.4	4.0 \pm 0.4	0.9 \pm 0.8	1.0 \pm 0.7
Sand (%)	37 \pm 7	59 \pm 25	17 \pm 8	31 \pm 7	36 \pm 13	31 \pm 6	55 \pm 6	75 \pm 29
Silt (%)	62 \pm 6	40 \pm 25	80 \pm 8	66 \pm 7	62 \pm 13	67 \pm 6	43 \pm 6	25 \pm 29
Clay (%)	2.0 \pm 0.2	1.4 \pm 0.6	3.5 \pm 0.6	2.8 \pm 0.2	2.0 \pm 0.7	2.4 \pm 0.3	2.4 \pm 0.6	1.1 \pm 0.7
Organic matter (%)	12.8 \pm 2.5	4.4 \pm 1.4	9.9 \pm 2.8	9.0 \pm 4.5	9.8 \pm 2.8	9.1 \pm 2.1	9.1 \pm 5.7	6.0 \pm 2.8
Macrophytes (%)								
15 May 2010	7 \pm 3	10 \pm 0	0	3 \pm 6	37 \pm 12	0	10 \pm 0	7 \pm 6
16 July 2010	83 \pm 12	63 \pm 46	0	17 \pm 12	50 \pm 35	0	62 \pm 7	20 \pm 17
20 August 2010	77 \pm 23	27 \pm 6	0	17 \pm 29	57 \pm 42	0	46 \pm 10	27 \pm 5
Pore water SRP ($\mu\text{g L}^{-1}$)								
23 Sept. 2010	-	44.8 \pm 14.0	-	8.8 \pm 2.8	1.9 \pm 0.8	-	3.5 \pm 1.5	3.7 \pm 0.9
29 June 2011	-	1.9 \pm 1.2	-	5.2 \pm 1.1	2.4 \pm 0.7	-	2.4 \pm 0.7	1.9 \pm 0.9

Table 4.2. Phytoplankton taxa observed at the sediment surface after 128 days of culture in BG11 medium. Sediments were sampled in June and September 2009, at N2, N4, S1 and S4.

Origin of sediments	Phytoplankton taxa									
	Cyanobacteria	<i>Aphanocapsa</i> sp.	<i>Cylindrospermum majus</i>	<i>Chroococcus</i> sp.	<i>Woronichinia naegeliana</i>	<i>Lyngbya bergei</i>	<i>Lyngbya limnetica</i>	<i>Oscillatoria</i> sp.	<i>Merismopedia</i> sp.	Diatomophyceae
15 June 2009										
N3		***	***	*		*	***	p	**	***
N4		***	**	**			*		**	***
S1			*				*			
S4			*				*			
16 September 2009										
N3		***	**			**		**	**	***
N4		***	*			*		**	**	***
S1						**		***	***	***
S4		**		*	**	*	***		**	***

(p) a single observation, (*) 2-5 observations, (**) 5-10 observations, (***) > 10 observations

Table 4.3. Pigment composition of Lake St. Charles surface sediment in July 2010. Ratio of pigment/Chl-*a* concentration.

Pigments (ratio/ Chl- <i>a</i>)		Sampling sites							
		N1	N2	N3	N4	S1	S2	S3	S4
Chlorophylls	Chlorophyll <i>b</i>	0.005	0.036	0.014	0.012	0.039	0.012	0.026	0.022
	Chlorophyll <i>c</i>	nd	nd	nd	nd	nd	nd	nd	nd
Microalgae	Violaxanthin	0.007	0.014	0.008	0.000	0.000	0.000	0.022	0.000
and higher plants	9'-cis-Neoxanthin	0.000	0.010	0.009	0.000	0.008	0.000	0.000	0.000
carotenoids	Lutein	0.000	0.020	0.024	0.002	0.014	0.001	0.000	0.005
	β,β-Carotene	0.000	0.009	0.009	0.001	0.027	0.000	0.000	0.000
Microalgae specific carotenoids	19'-Hex-fucox.	0.015	0.037	0.019	0.047	0.033	0.048	0.012	0.072
	Fucoxanthin	0.282	0.297	0.141	0.238	0.185	0.279	0.538	0.319
	Diadinoxanthin	0.060	0.086	0.058	0.071	0.065	0.074	0.055	0.100
	Diatoxanthin	0.017	0.037	0.146	0.017	0.088	0.008	0.000	0.012
	Alloxanthin	0.002	0.000	0.022	0.002	0.004	0.006	0.000	0.000
	Canthaxanthin	0.003	0.000	0.006	0.003	0.000	0.004	0.000	0.003
Unknown carotenoids	Lutein like	0.027	0.104	0.245	0.098	0.200	0.129	0.031	0.126
Total pigments		0.418	0.649	0.699	0.491	0.664	0.561	0.684	0.658

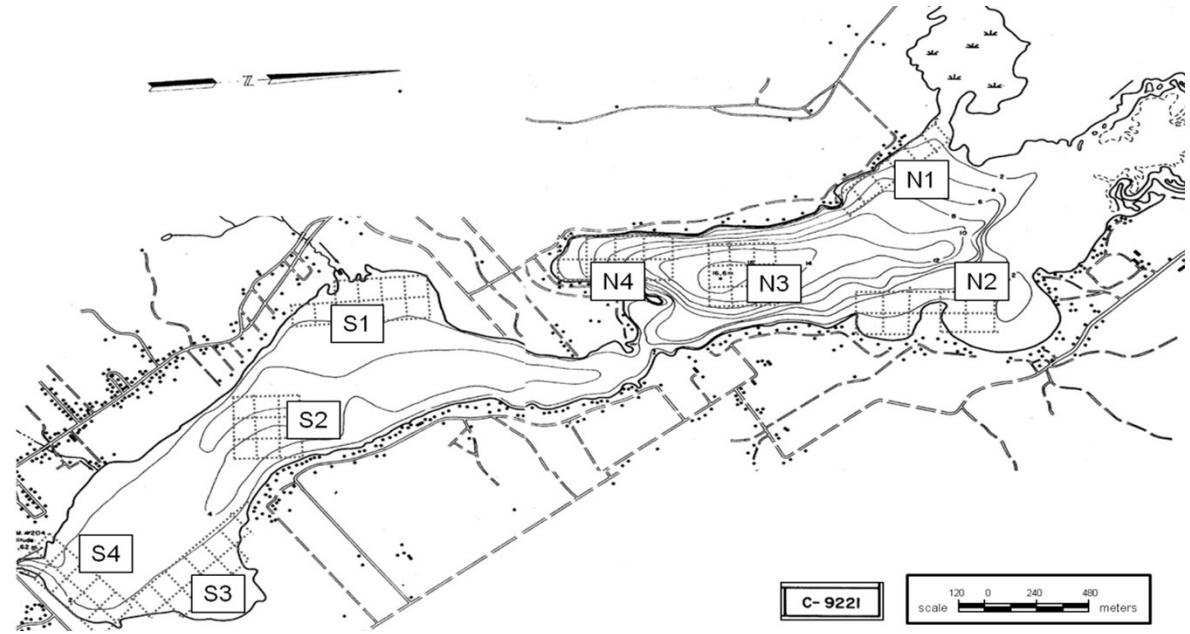


Figure 4.1. Map of Lake St. Charles showing the location of sediment sampling sites and the phycocyanin fluorescence mapping grid. North basin: Talbot Bay (N1), Des Aigles Pêcheurs Bay (N2), deepest point of the lake (N3), Echo Bay (N4). South basin: Des Milans Bay (S1), middle of the south basin (S2), beach (S3), dam (S4).

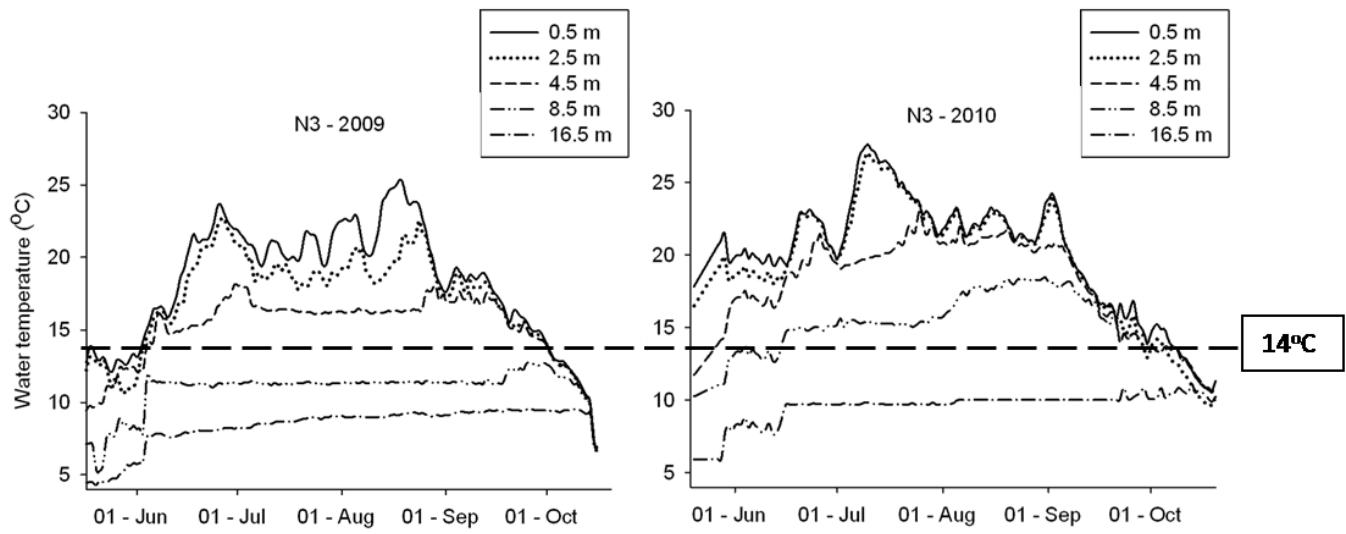


Figure 4.2. Temporal variation in water temperature ($^{\circ}\text{C}$) at different depths at Lake St. Charles station N3 in 2009 and 2010. The straight dashed line represents the 14°C threshold for recruitment.

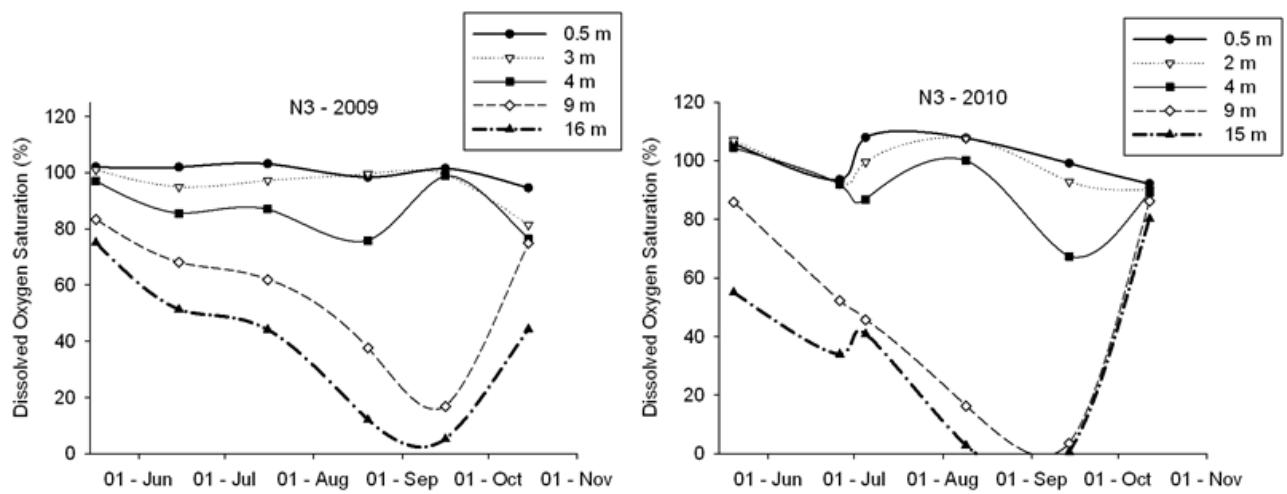


Figure 4.3. Temporal variation of dissolved oxygen concentrations (% saturation) at different depths at station N3 in 2009 and 2010.

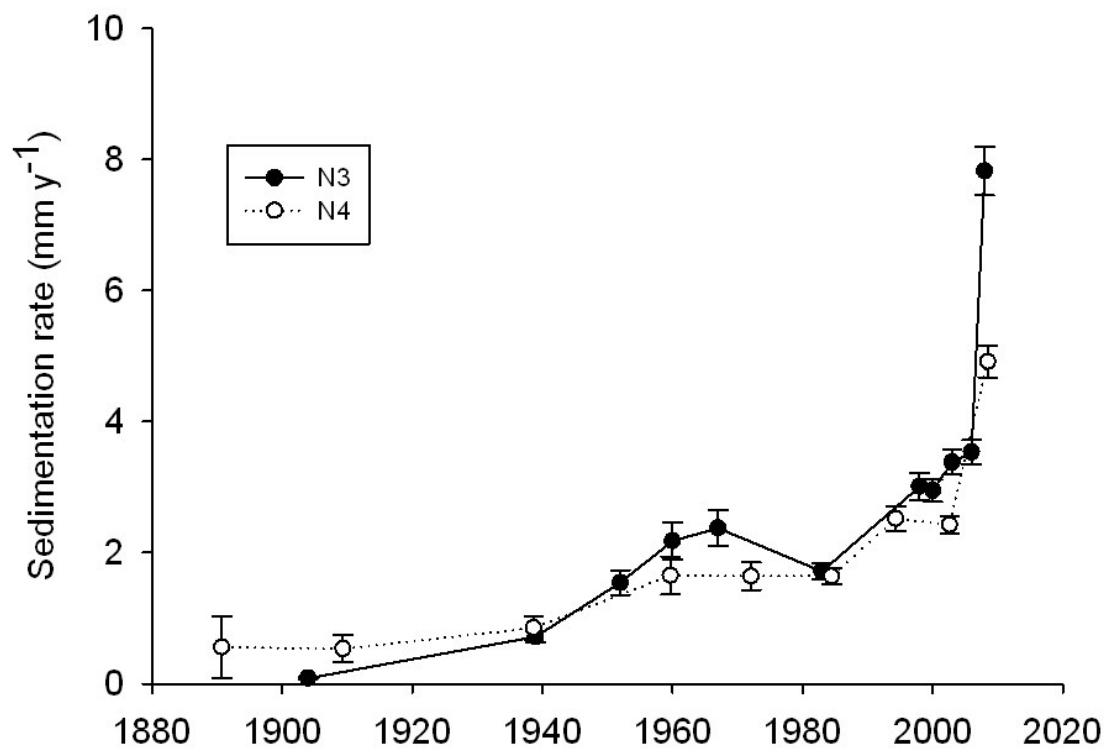


Figure 4.4. Variation of the sedimentation rate \pm calculated error (mm yr^{-1}) at stations N3 and N4, estimated by ^{210}Pb dating.

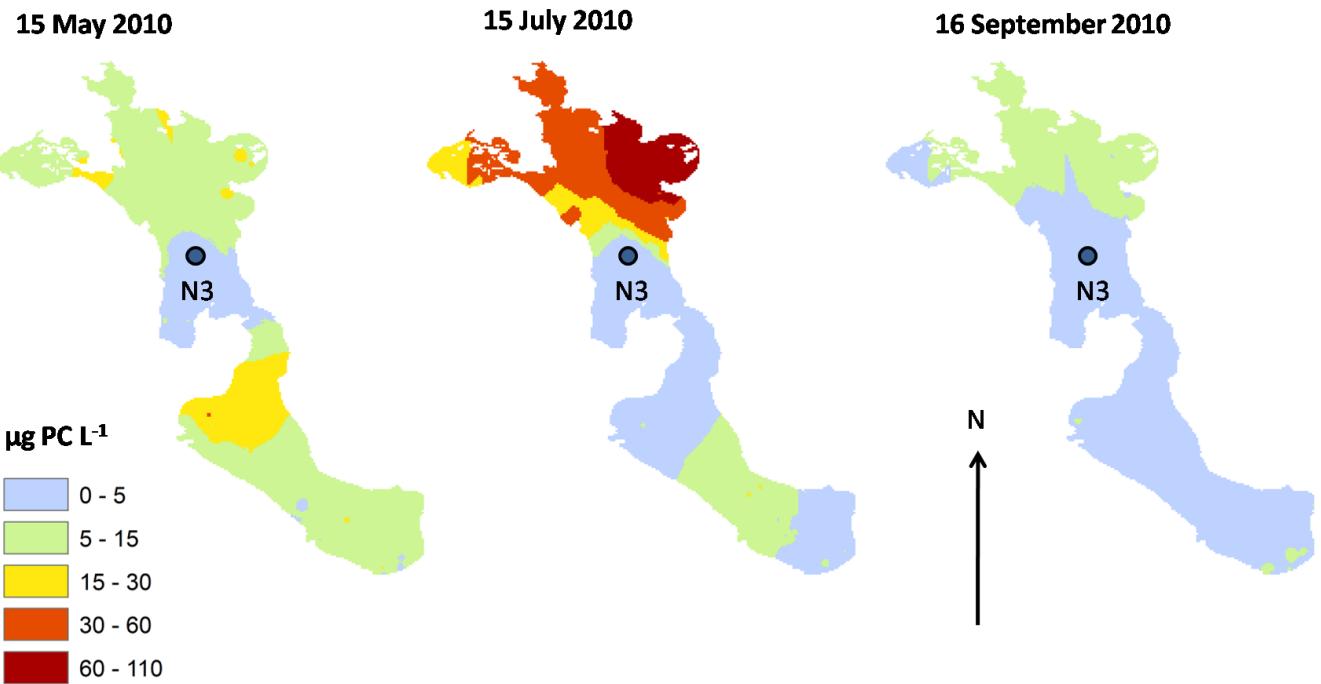


Figure 4.5. Spatial and temporal variations of phycoerythrin fluorescence ($\mu\text{g PC L}^{-1}$) at the sediment surface of Lake St. Charles in 2010.

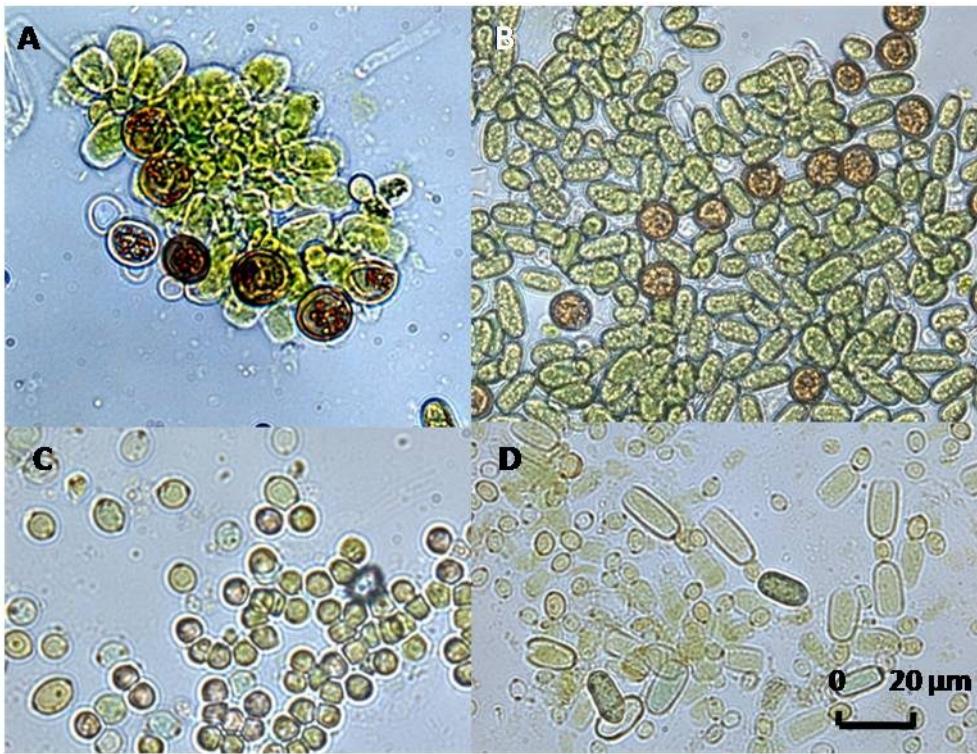


Figure 4.6. Photomicrographs of germination stages of *Anabaena flos-aquae* akinetes observed in surface lake water on 10 June 2010. (A) Opening of the akinete, and vegetative cells emerging from the envelope; (B) Matured akinetes and vegetative cells; (C)-(D) germination of the vegetative cells.

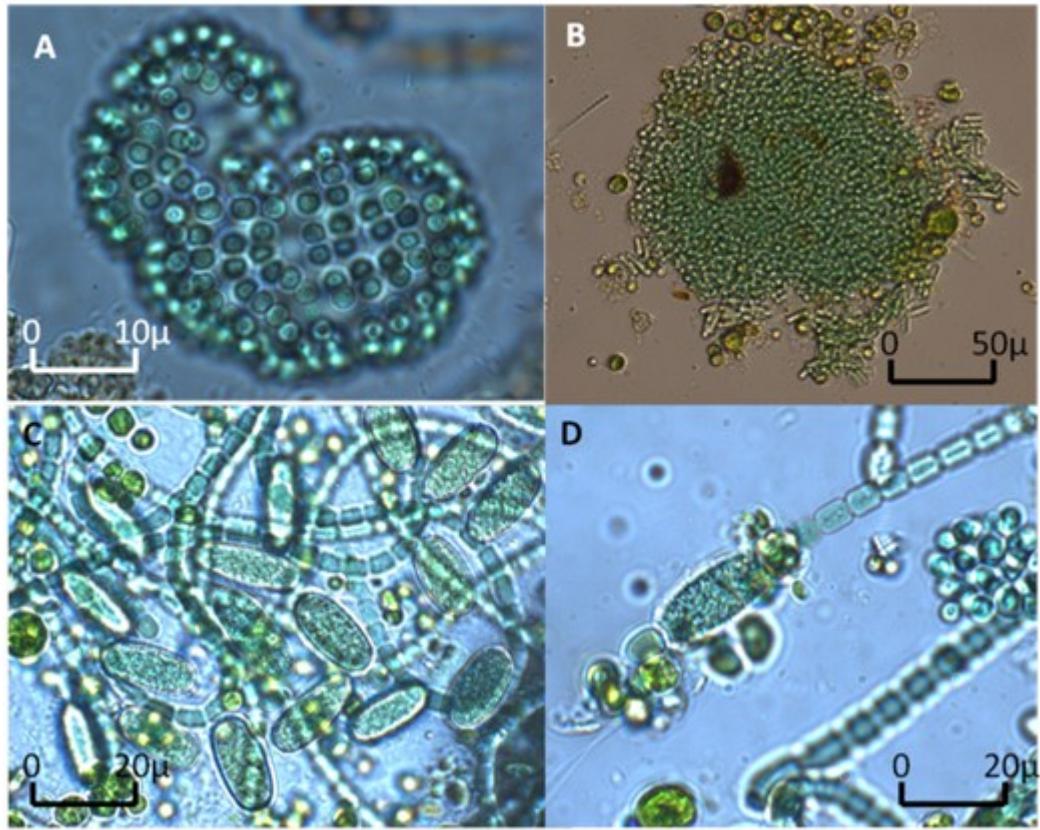


Figure 4.7. Photomicrographs of cyanobacteria observed in samples from the sediment surface of Lake St. Charles during summer 2009 and 2010 (A) *Woronichinia naegeliana*, (B) akinetes of *Cylindrospermum majus* before trichome growth, (C) akinetes of *Cylindrospermum majus* after trichome growth, (D) *Cylindrospermum majus* trichomes.

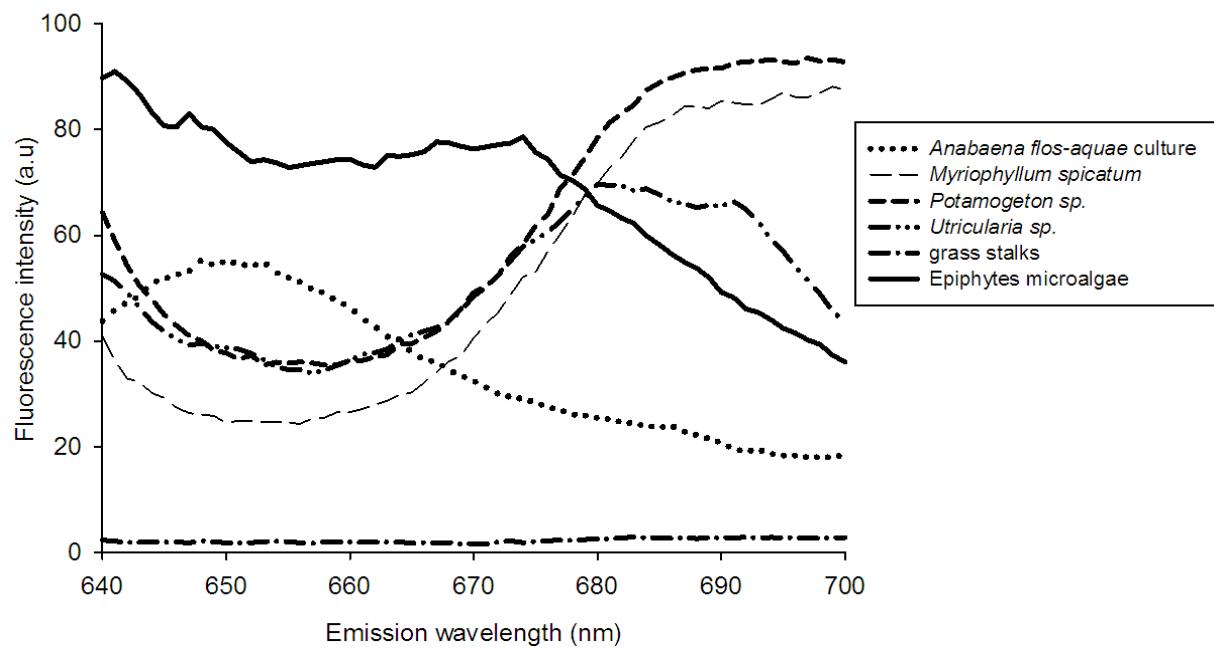


Figure 4.8. Fluorescence emission spectra of macrophyte samples compared to *Anabaena flos-aquae*, with excitation at 620 nm.

Chapitre 5. Conclusion générale

Au terme de ce travail de recherche, il est possible de dresser une synthèse (Fig. 5.1) qui permet de répondre aux trois principales questions abordées au cours de la thèse (5.1) et de poser les jalons de futurs travaux de recherche (5.2). Les réponses apportées à ces questions permettront de formuler des recommandations sur les modes de surveillance, de gestion et de restauration des lacs et réservoirs et de leurs bassins-versants. Cette problématique est d'une importance particulière dans un contexte mondial de risques d'eutrophisation (Kumagai & Vincent, 2003)

5.1 Synthèse de l'étude

Dans la présente étude, l'analyse détaillée de la limnologie du lac Saint-Charles à l'échelle pluriannuelle a permis d'améliorer les connaissances concernant la dynamique spatio-temporelle des cyanobactéries d'eau douce dans un contexte d'eutrophisation. Nos résultats ont mis en évidence la vulnérabilité aux efflorescences de cyanobactéries de cet important réservoir en eau potable. Cependant, la structure de la communauté cyanobactérienne et le biovolume total varient grandement entre les années, mais aussi spatialement, sur un gradient bassin nord-bassin sud. Les proliférations intermittentes de cyanobactéries, et leur relation étroite avec le phosphore total et l'azote total, indiquent un besoin urgent d'identifier et de contrôler les sources externes de nutriments provenant du bassin-versant, en particulier dans le sous-bassin de la rivière des Hurons, qui fournit la majeure partie de l'eau du réservoir. Les proliférations de cyanobactéries au lac Saint-Charles étant majoritairement contrôlées par la température de l'eau et le degré de stratification, cela implique que les changements climatiques globaux auront tendance à faire du lac Saint-Charles une zone encore plus propice à la prolifération. Cependant, le court temps de séjour de l'eau dans le lac, combiné avec l'apparente absence d'une "banque de graines" constituée par des formes dormantes de cyanobactéries dans les sédiments, suggère que ce réservoir pourrait répondre rapidement à une réduction des apports externes en éléments nutritifs. Le lac Saint-Charles est actuellement

parvenu à une étape critique de son évolution, impliquant l'urgence de prendre des décisions quant à la gestion de son environnement afin d'assurer la qualité de la ressource en eau à long terme.

Le chapitre 2 de la thèse a permis d'évaluer l'état d'évolution trophique du lac et sa dynamique limnologique à travers 5 étés consécutifs. Contrairement à l'hypothèse selon laquelle tous les indices concordent vers un même état trophique, les concentrations en chlorophylle *a*, phosphore total et azote total sont caractéristiques d'un état oligotrophe avancé à mésotrophe, alors que l'apparition de cyanobactéries proliférantes telles que *Microcystis aeruginosa* et *Anabaena flos-aquae* et un systématique déficit en oxygène à la fin de l'été au niveau de la fosse indiquent une évolution vers l'état de mésotrophie avancée. La contradiction entre ces indices implique l'existence de contrôles complexes agissant sur la dominance des cyanobactéries, probablement très localisés dans le temps et dans l'espace, donc difficiles à mettre en évidence en se basant exclusivement sur des moyennes. En effet, la variabilité interannuelle des variables limnologiques mesurées au lac Saint-Charles, caractéristique des réservoirs à écoulement rapide, est induite par des variations interannuelles des conditions climatiques telles que l'intensité et la durée de la période de chaleur estivale et le volume des précipitations. Les conditions limnologiques du lac Saint-Charles sont donc caractérisées par un équilibre fragile, à la limite d'un seuil critique (théorie de *alternate stable state*) – telle une balance qui peut basculer dans un sens ou dans un autre selon l'année – et peuvent ainsi fournir des conditions épisodiquement optimales pour la prolifération de cyanobactéries.

Le chapitre 3 de la thèse a permis de définir la variabilité spatiale et temporelle des cyanobactéries proliférantes au lac Saint-Charles et de déterminer les facteurs de contrôle des espèces dominantes. Contrairement à l'hypothèse selon laquelle *M. aeruginosa* et/ou *A. flos-aquae* dominent la colonne d'eau chaque année à la fin de l'été, le biovolume total de cyanobactéries ainsi que les taxons dominants ont été très variables entre les années. Il a été possible de différencier des années "positives", durant lesquelles un seul taxon de cyanobactéries à efflorescence a

largement dominé (*A. flos-aquae* ou *M. aeruginosa*), des années “négatives” durant lesquelles le biovolume total et la biodiversité des cyanobactéries étaient faibles, et des années “neutres” durant lesquelles plusieurs taxons de cyanobactéries dominaient la colonne d'eau mais pour un biovolume total faible. Ce patron de variabilité correspond au patron de variabilité observé au chapitre 2. De plus, les périodes d'efflorescences ne se sont pas limitées à la fin de l'été (août-septembre) mais se sont réparties sur toute la saison à partir de la fin du mois de Juin.

L'hypothèse que *M. aeruginosa* et *A. flos-aquae* sont contrôlées majoritairement par la température de l'eau, la stratification de la colonne d'eau et le rapport N/P n'a été que partiellement appuyée. En effet, les corrélations avec les variables limnologiques se sont avérées très nuancées selon les taxons considérés. Ce résultat reflète les différentes stratégies écologiques employées par les cyanobactéries, liées à leur écophysiologie. Ainsi, la corrélation positive entre d'une part, l'abondance d'*A. flos-aquae* et la température de l'eau et, d'autre part, l'abondance de *M. aeruginosa* et les degrés-jours cumulés, implique que ces deux espèces sont influencées par différentes modalités de la variable température. *A. flos-aquae* serait ainsi plus dépendante de l'intensité de la chaleur et *M. aeruginosa* de sa durée. Du fait de leur potentiel de migration active, ces deux espèces sont physiologiquement favorisées par une stratification thermique stable, mais seule l'espèce *A. flos-aquae* a montré une corrélation significative avec l'indice de stabilité de Schmidt, indiquant un pouvoir de flottabilité moins important que *M. aeruginosa*. Au cours du passé récent (1960-2005), les températures journalières moyennes du sud du Québec ont augmenté de 0,2°C à 0,4°C par décennie (Yagouti et al., 2008), et le nombre de jours avec précipitations de faible intensité ont augmenté (Vincent & Merkis, 2006). Ces conditions, associées à l'urbanisation du bassin versant, ont probablement favorisé la dominance des cyanobactéries jusqu'à un point critique en 2006.

Les résultats de ce chapitre n'ont pas montré de corrélation entre le biovolume des cyanobactéries et le ratio azote/phosphore. Cependant, les concentrations en azote et phosphore total, considérées séparément, jouent un rôle dans le transfert de

dominance entre *A. flos-aquae* et *M. aeruginosa*. La corrélation entre l'azote total et l'abondance de *M. aeruginosa* implique que les espèces capables de fixer le N₂ atmosphérique, telles qu'*A. flos-aquae*, sont supplantées lors des périodes d'approvisionnement suffisant en azote. De même, la corrélation entre le phosphore total et l'abondance de *M. aeruginosa* implique que cette espèce présente un taux d'absorption plus important lorsque les nutriments ne sont pas limitants, mais qu'*A. flos-aquae* a une meilleure capacité de vivre sur ses réserves.

Dans ce chapitre, les variables hydrologiques ont également révélé des corrélations importantes avec l'abondance des cyanobactéries. En effet, le volume des précipitations et le temps de résidence de l'eau ont un effet indirect sur la dominance des différents taxons, en modifiant l'apport en nutriments, les conditions de turbidité et la stratification de la colonne d'eau. Ainsi, à condition que les événements de pluie ne soient pas extrêmes, les précipitations vont avoir tendance à favoriser *M. aeruginosa* par l'apport de nutriments. Au contraire, un temps de résidence hydraulique plus long va avoir tendance à favoriser *A. flos-aquae* par l'augmentation de la stabilité de la colonne d'eau. Du fait du court temps de résidence hydraulique (de l'ordre du mois lors des périodes de hauts débits), le lac Saint-Charles se comporterait donc plus comme une large rivière plutôt qu'un lac à proprement parler. Cela implique que les nutriments dissous ou adsorbés aux sédiments transitent rapidement dans le lac ("flushing"), ce qui laisse un intervalle de temps court pour la multiplication de plusieurs générations de cellules. Ces conditions hydrauliques ont probablement permis jusqu'à maintenant de ralentir le processus d'eutrophisation au lac Saint-Charles, malgré l'accélération de l'urbanisation dans le bassin versant.

Le chapitre 4 a permis de définir les caractéristiques sédimentaires et le potentiel d'habitat benthique du lac Saint-Charles. Il a également examiné le potentiel de "banque de graines" dans les sédiments qui pourrait servir d'inoculum pour les proliférations de cyanobactéries. L'hypothèse selon laquelle les zones littorales présentent les meilleures conditions potentielles pour le recrutement de cellules phytoplanctoniques en dormance n'a été que partiellement appuyée. En effet,

les sédiments en zones peu profondes (moins de 4 m) sont plus favorables à la croissance de microalgues et de cyanobactéries, à la conservation de cellules en dormance et au recrutement de ces cellules, du fait de conditions de lumière et de température plus appropriées. Compte tenu de sa morphométrie, avec 80% de la surface benthique dans des zones peu profondes, le lac Saint-Charles devrait donc être un écosystème favorable à l'installation et à la survie de ces populations à la surface des sédiments. Cependant, ces zones sont aussi potentiellement beaucoup plus exposées à la remise en suspension des sédiments par l'effet du vent ou des vagues. Ce phénomène a le potentiel de favoriser le recrutement de cellules en dormance, mais dans le cas de réservoirs à écoulement rapide, il y a aussi une possibilité de perte de cette "banque de graines" par un effet de "*flushing*". Les expériences d'incubation de sédiments montrent d'ailleurs une biodiversité plus importante de phytoplancton dans les sédiments profonds du bassin nord, peu soumis à la resuspension.

*L'hypothèse selon laquelle les sédiments du lac Saint-Charles contiennent une réserve viable de cellules phytoplanctoniques, incluant des populations qui ont le potentiel d'initier la prolifération d'*A. flos-aquae* et *M. aeruginosa*, n'a été que partiellement soutenue.* En effet, les 5 méthodes de détection utilisées ont permis de mettre en évidence la présence d'une population microbienne diversifiée. Cette population est majoritairement dominée par des taxons qui subissent la sédimentation tels que les diatomées, des taxons pouvant passer par une phase de dormance tels que les dinoflagellés, et des taxons exclusivement benthiques tels que des cyanobactéries de l'ordre des Oscillatoriiales. Ces observations contrastent avec l'apparente absence d'*A. flos-aquae* et *M. aeruginosa*. Cette absence d'un grand inoculum de cellules dans les sédiments, ayant la faculté d'accumuler des réserves de nutriments en conditions limitantes, implique qu'un contrôle des apports externes de nutriments pourrait être une approche efficace pour réduire l'occurrence des efflorescences. Les actions déjà entreprises dans le bassin versant (revégétalisation des berges, diminution des normes de rejet des usines d'épuration, contrôle des eaux de ruissellement) devraient donc être payantes à condition qu'il n'y ait pas de relargage important de phosphore interne (cf. Lavoie & Auclair, 2012).

D'autres hypothèses ont également été formulées pour expliquer l'origine de l'inoculum des proliférations au lac Saint-Charles. Les apports de cellules microbiennes provenant d'affluents peuvent constituer un apport substantiel dans certains cas (Caporaso et al., 2012). Le principal affluent du lac Saint-Charles est la Rivière des Hurons, mais son débit important en fait un écosystème peu favorable à la croissance de cyanobactéries proliférantes, même en considérant les rejets provenant d'une usine de traitement d'eau usée. En revanche, l'effluent du lac Delage, affluent secondaire du lac Saint-Charles, semble constituer une source d'inoculum plus probable du fait d'un débit moyen beaucoup plus lent. Enfin, une autre hypothèse réside dans la possibilité qu'*A. flos aquae* et *M. aeruginosa* seraient holoplanctoniques, c'est-à-dire qu'une partie de cellules viables resterait en suspension dans la colonne d'eau pendant l'hiver et ferait donc partie de ce que l'on appelle la "biosphère rare" (Sogin et al., 2006). Cette hypothèse expliquerait le comportement de balance à l'équilibre fragile mentionné au chapitre 2.

5.2 Perspectives

Les résultats de cette recherche ont révélé la nécessité d'adresser d'autres questions dans le futur. Certaines sont directement reliées au cas du lac Saint-Charles, d'autres se réfèrent à l'écologie des cyanobactéries dans les réservoirs d'eau potable en général.

Plusieurs variables biologiques peuvent jouer un rôle dans la dynamique des cyanobactéries, par le contrôle de leur dominance. Par exemple, le broutage effectué par le zooplancton et le zoobenthos peuvent avoir une influence considérable sur la communauté de microalgues (Reichwaldt & Stibor, 2005) et ainsi favoriser les cyanobactéries, moins "comestibles" en règle générale. L'abondance des cyanobactéries peut aussi être influencée par la présence de cyanophages (Deng & Hayes, 2008). Il serait donc intéressant d'effectuer un suivi de ces populations en parallèle avec celui des cyanobactéries. Par ailleurs, la colonisation des macrophytes étant importante dans le lac Saint-Charles, il serait souhaitable d'étudier également la

dynamique spatio-temporelle des macrophytes sur une échelle de plusieurs années et d'examiner les interactions avec la quantité de nutriments et l'abondance et la composition des cyanobactéries. De plus, on peut se poser la question de la direction d'évolution du lac; vers une dominance des macrophytes ou du phytoplancton, deux situations qui peuvent alterner rapidement (Jeppesen et al., 1990). Le rôle des macro-invertébrés bioturbateurs, comme par exemple les moules présentes dans les sédiments du lac Saint-Charles, devrait aussi être examiné, notamment vis-à-vis de leur implication dans le relargage de nutriments (Cha et al., 2011; Knoll et al., 2008) mais aussi dans l'enfouissement éventuel de cellules déposées à la surface des sédiments (Karlson et al., 2008).

L'hypothèse du rôle potentiel des affluents ayant été suggérée, il serait souhaitable d'envisager d'effectuer un suivi des populations de cyanobactéries au Lac Delage et dans son effluent, et d'évaluer son potentiel d'inoculum pour le lac dès la fonte du couvert de glace. Cet affluent est en effet plus propice à la croissance de cyanobactéries et au transfert de cellules vers le LSC que la Rivière des Hurons du fait de l'existence de zones de méandres au débit très faible. Un échantillonnage et des analyses des nutriments (N et P), de la Chl- α et de la taxonomie ont été effectués à plusieurs points entre le lac Delage et le lac Saint-Charles en 2011 et 2012, et se poursuivent en 2013. Les résultats à disposition ne permettaient pas de répondre à la question lors de la rédaction de la thèse mais la question n'a pas été abandonnée.

La concentration en cyanotoxines n'a pas été mesurée dans cette étude. Les espèces dominantes étant potentiellement toxiques, un suivi des cyanotoxines sur le plan spatio-temporel et une évaluation des conditions limnologiques favorisant leur production est donc indispensable.

Le rôle des éléments traces tels que le fer, le manganèse, et le zinc devrait aussi être étudié car ces micronutriments peuvent fortement influencer la dynamique des cyanobactéries (e.g. Ahn et al., 2011; Wang et al., 2010).

Un échantillonnage plus serré des différentes formes de phosphore et d'azote, à la fois dans le temps et dans l'espace, permettrait de mieux comprendre leur dynamique et de mieux identifier leurs sources, qu'elles soient internes ou externes. Il serait ainsi envisageable de prédire si une diminution des apports externes suffirait à préserver la ressource en eau potable. Une étude précédente de Lavoie & Auclair (2012) au lac Saint-Charles a mis en évidence une relation entre la proportion de matière organique et la capacité des sédiments à adsorber le P. Les zones moins profondes que la fosse (baie Echo et centre du bassin sud), plus riches en matière organique, seraient donc de meilleures source de P biodisponible. En effet, le recyclage de la matière organique dans ces zones pourrait ainsi créer une réserve de SRP. Il est maintenant nécessaire de compléter cette étude en explorant plus en détail les zones littorales du lac.

La composante climatique des variables limnologiques (intensité et durée des températures élevées et volume des précipitations) ayant un rôle important dans la dynamique d'*A. flos aquae* et *M. aeruginosa*, une étude portant sur les changements climatiques récents dans la région et la modélisation de ces changements pour le futur, permettrait de mieux prédire les changements potentiels dans la communauté de cyanobactéries.

Le suivi des courants internes et du patron hydrodynamique à travers le lac, par l'intermédiaire de mesures détaillées des variations de température au sein de la colonne d'eau, pourrait permettre de mieux comprendre la dynamique spatiale du phytoplancton et éventuellement de fournir une explication quant à l'existence du gradient nord-sud. Certains types de courants (recirculations convectives par ex.) impliquent un temps de résidence plus long pour certaines masses d'eau et donc aussi pour les nutriments (Kalff, 2002).

Afin de raffiner la compréhension de la biodiversité microbienne des réservoirs à écoulement rapide et de tester l'hypothèse de la "biosphère rare", des analyses moléculaires sensibles (e.g.. l'analyse du gène pour l'ARN 16S) pourraient être réalisées en hiver et dès la fonte du couvert de glace. Enfin, le caractère extrêmement variable de la distribution des cyanobactéries dans ce type de réservoir devrait

induire une réflexion sur le développement de nouvelles méthodes de détection des efflorescences.

5.3 Mot de la fin

La problématique d'eutrophisation accélérée a connu un second essor dans les années 1990, lorsque des efflorescences de cyanobactéries toxiques sont apparues de plus en plus fréquemment, non seulement dans des pays en développement (e.g. le lac Taihu en Chine; Guo, 2007), mais aussi dans des lacs où l'on pensait l'eutrophisation sous contrôle suite aux opérations de restauration menées dans les années 1970 (e.g. le lac Érié aux États-Unis; Brittain et al., 2000). Les efflorescences de cyanobactéries risquent d'être de plus en plus fréquentes à l'avenir, favorisées par le réchauffement climatique global, non seulement à cause de l'augmentation du taux de croissance des cyanobactéries, mais aussi dues à l'augmentation de la stabilité de la stratification thermique (Paerl & Huisman, 2008; Vincent, 2009b). Les proliférations de cyanobactéries sont particulièrement préoccupantes dans le cas des réservoirs en eau potable comme le lac Saint-Charles. Par conséquent, le travail présenté dans cette thèse met en évidence le besoin urgent d'élaborer des protocoles de surveillance continue de ces eaux et de mettre en œuvre des mesures strictes de contrôle des nutriments dans les bassins versants environnants.

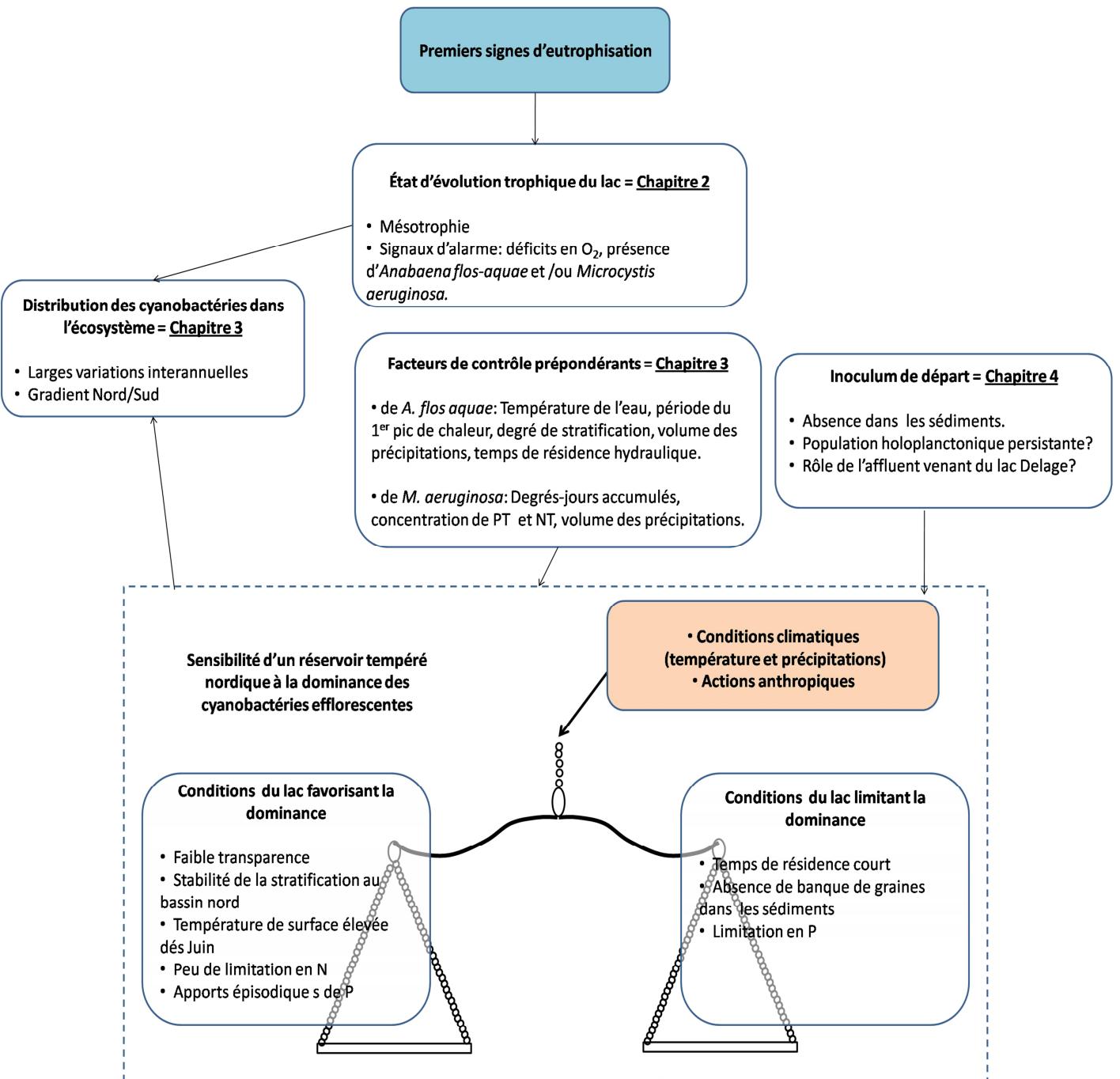


Figure 5.1. Synthèse des résultats clés de la thèse et liens entre les chapitres.

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Annexe : Listes taxonomiques détaillées

	2009				
	Juin	Juillet	Août	Septembre	Octobre
Cyanophycées					
<i>Anabaena flos-aquae</i>	*	*	*	p	p
<i>Anabaena spiroides</i>					
<i>Aphanizomenon cf. gracile</i>					
<i>Aphanizomenon issatschenkoi</i>					
<i>Aphanocapsa sp.</i>	**	*** (D)	*** (D)	**	**
<i>Aphanothece cf. clathrata</i>	*	*	*	*	*
<i>Chroococcus sp.</i>		p			
<i>Coelosphaerium sp.</i>	*	**	**	*	*
<i>Geitlerinema sp.</i>					
<i>Gomphosphaeria sp.</i>	*	*	**	**	*
<i>Limnothrix redekei</i>					
<i>Merismopedia sp.</i>			*	p	
<i>Microcystis aeruginosa</i>	p	p		p	
<i>Oscillatoria sp</i>					
<i>Radiocystis sp</i>					
<i>Raphidiopsis sp.</i>					
<i>Snowella sp</i>					
Chlorophycées					
<i>Chlamydomonas sp.</i>					
<i>Chlorella sp.</i>		*		*	
<i>Cladophora sp</i>					
<i>Coelastrum sp</i>					
<i>Cosmarium sp.</i>	p		p	p	
<i>Crucigenia sp.</i>	p		p	p	
<i>Dictyosphaerium sp.</i>	*			*	**
<i>Gloeococcus sp.</i>		*			
<i>Oocystis sp.</i>	*	*	*	*	*
<i>Micrasterias sp.</i>					

	Suite 2009				
	Juin	JUILLET	Août	Septembre	Octobre
Chlorophycées					
<i>Pediastrum sp.</i>			*	p	p
<i>Scenedesmus sp.</i>		*			
<i>Schroederia sp.</i>					
<i>Sphaerocystis sp.</i>	*	*	*		*
<i>Staurastrum sp.</i>		p	*	***	p
<i>Tribonema sp</i>					
<i>Xanthidium sp.</i>					
Dinophycées					
<i>Ceratium sp.</i>			p	***	*
Diatomées					
<i>Asterionella sp.</i>	(D)	**	*	***	*
<i>Aulacoseira sp.</i>	**	*	*	***	**
<i>Cyclotella sp.</i>		*			
<i>Fragilaria sp.</i>	**			*	
<i>Navicula sp.</i>	*		p	P	
<i>Nitzschia sp.</i>				P	
<i>Synedra sp</i>					
<i>Tabellaria sp.</i>		*	*	***	***
<i>Stephanodiscus sp.</i>	**		p		
Chrysophycées					
<i>Chlamydomonas sp</i>					
<i>Dinobryon sp.</i>	**	**	**	*** (D)	*** (D)
<i>Mallomonas sp.</i>	*	***	*	P	
<i>Ochromonas sp.</i>		***		P	
<i>Synura sp.</i>		**		**	*
<i>Trachelomonas sp.</i>					
<i>Volvox sp</i>					
Euglenophycées					
<i>Euglena sp.</i>	p			*	

	Suite 2009				
	Juin	JUILLET	Août	Septembre	Octobre
Euglenophycées					
<i>Phacus sp</i>					
<i>Uroglena sp.</i>		p			
Cryptophycées					
<i>Cryptomonas sp.</i>		***			
<i>non identifiées</i>					

	Juin	Juillet	Août	Septembre	Octobre
Cyanophycées					
<i>Anabaena flos-aquae</i>	*** (D)	*** (D)	***	*** (D)	*
<i>Anabaena spiroides</i>		*			
<i>Aphanizomenon cf gracile</i>			**		
<i>Aphanizomenon issatschenkoi</i>			*		
<i>Aphanocapsa delicatissima</i>	*	*	*	*	p
<i>Aphanothece cf. clathrata</i>	p	*	*		
<i>Chroococcus sp.</i>			p		
<i>Coelosphaerium sp.</i>					
<i>Geitlerinema sp.</i>			*		
<i>Gomphosphaeria sp.</i>	p			*	
<i>Limnothrix redekei</i>			**		p
<i>Merismopedia sp.</i>	p	*	p		
<i>Microcystis aeruginosa</i>	*	***	**	***	*
<i>Oscillatoria sp</i>		*	*		
<i>Radiocystis sp</i>			p		
<i>Raphidiopsis sp.</i>			p		
<i>Snowella sp</i>	p		**		p
Chlorophycées					
<i>Chlamydomonas sp.</i>	*				
<i>Chlorella sp.</i>					
<i>Closterium sp</i>	p				
<i>Coelastrum sp</i>	p	p			
<i>Cosmaruim sp.</i>	p	p			
<i>Crucigenia sp.</i>	*				p
<i>Dictyosphaerium sp.</i>		p			
<i>Gloeococcus sp.</i>					
<i>Micrasterias sp.</i>					
<i>Oocystis sp.</i>					
<i>Pediastrum sp.</i>	p				
<i>Scenedesmus sp.</i>	p	*			*
<i>Schroederia sp.</i>					
<i>Sphaerocystis sp.</i>	p				

	Suite 2010				
	Juin	Juillet	Août	Septembre	Octobre
Chlorophycées					
<i>Staurastrum sp.</i>	p	*	***		*
<i>Tribonema sp.</i>					
<i>Xanthidium sp.</i>					
Chlorophycées non motiles coccoides	**				
Dinophycées					
<i>Ceratium sp.</i>	**	***	***	*	*
<i>Peridinium sp</i>		*			
Diatomées					
<i>Asterionella sp.</i>	***	**	***		*
<i>Aulacoseira sp.</i>	*	*	**	***	*
<i>Cyclotella sp.</i>	*				*
<i>Fragilaria sp.</i>	p		**		
<i>Navicula sp.</i>	*	p			*
<i>Nitzschia sp.</i>	p	*	**		
<i>Synedra sp</i>	p	p			
<i>Tabellaria sp.</i>	**	**	***	***	

Chrysophycées					
<i>Chlamydomonas sp</i>			**		
<i>Dinobryon sp.</i>	***	**	***	**	***
<i>Mallomonas sp.</i>	p	*			
<i>Ochromonas sp.</i>	*				
<i>Synura sp.</i>			*		
<i>Trachelomonas sp.</i>	p	p			
<i>Volvox sp</i>				*	
Euglenophycées					
<i>Euglena sp.</i>	*	p			
<i>Phacus sp</i>		p			

	Suite 2010				
	Juin	Juillet	Août	Septembre	Octobre
Cryptophycées					
<i>Cryptomonas sp.</i>		*			
<i>non identifiées</i>					

Légende:

p : 1 observation

*: 2 à 5 observations

**5 à 10 observations

*** plus de 10 observations

D: largement dominante