Université de Montréal

Écologie et implications trophiques de la cyanobactérie *Lyngbya wollei* dans le fleuve Saint-Laurent

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Résumé

Les proliférations nuisibles de la cyanobactérie filamenteuse benthique *Lyngbya wollei* qui forme des tapis déposés sur les sédiments ont augmenté en fréquence au cours des 30 dernières années dans les rivières, lacs et sources de l'Amérique du Nord. *Lyngbya wollei* produit des neurotoxines et des composés organiques volatils (géosmin, 2-méthylisobornéol) qui ont des répercussions sur la santé publique de même que des impacts d'ordre socioéconomiques. Cette cyanobactérie est considérée comme un habitat et une source de nourriture de piètre qualité pour les invertébrés en raison de sa gaine robuste et de sa production de toxines.

Les proliférations de *L. wollei* ont été observées pour la première fois en 2005 dans le fleuve Saint-Laurent (SLR; Québec, Canada). Nous avons jugé important de déterminer sa distribution sur un tronçon de 250 km afin d'élaborer des modèles prédictifs de sa présence et biomasse en se basant sur les caractéristiques chimiques et physiques de l'eau. *Lyngbya wollei* était généralement observé en aval de la confluence de petits tributaires qui irriguent des terres agricoles. L'écoulement d'eaux enrichies à travers la végétation submergée se traduisait par une diminution de la concentration d'azote inorganique dissous (DIN), alors que les concentrations de carbone organique dissous (DOC) et de phosphore total dissous (TDP) demeuraient élevées, produisant un faible rapport DIN :TDP. Selon nos modèles, DOC (effet positif), TP (effet négatif) et DIN :TDP (effet négatif) sont les variables les plus importantes pour expliquer la répartition de cette cyanobactérie. La probabilité que *L. wollei* soit présent dans le SLR a été prédite avec exactitude dans 72 % à 92 % des cas pour un ensemble de données indépendantes.

Nous avons ensuite examiné si les conditions hydrodynamiques, c'est-à-dire le courant généré par les vagues et l'écoulement du fleuve, contrôlent les variations spatiales et temporelles de biomasse de *L. wollei* dans un grand système fluvial. Nous avons mesuré la biomasse de *L. wollei* ainsi que les variables chimiques, physiques et météorologiques durant trois ans à 10 sites le long d'un gradient d'exposition au courant et au vent dans un grand (148 km^2) lac fluvial du SLR. L'exposition aux vagues et la vitesse du courant contrôlaient les variations de biomasses spatiales et temporelles. La biomasse augmentait de mai à novembre

et persistait durant l'hiver. Les variations interannuelles étaient contrôlées par l'écoulement de la rivière (niveau d'eau) avec la crue printanière qui délogeait les tapis de l'année précédente. Les baisses du niveau d'eau et l'augmentation de l'intensité des tempêtes anticipées par les scénarios de changements climatiques pourraient accroître la superficie colonisée par *L. wollei* de même que son accumulation sur les berges.

Par la suite, nous avons évalué l'importance relative de *L. wollei* par rapport aux macrophytes et aux épiphytes. Nous avons examiné l'influence structurante de l'échelle spatiale sur les variables environnementales et la biomasse de ces producteurs primaires (PP) benthiques. Nous avons testé si leur biomasse reflétait la nature des agrégats d'habitat basées sur l'écogéomorphologie ou plutôt le continuum fluvial. Pour répondre à ces deux questions, nous avons utilisé un design à 3 échelles spatiales dans le SLR: 1) le long d'un tronçon de 250 km, 2) entre les lacs fluviaux localisés dans ce tronçon, 3) à l'intérieur de chaque lac fluvial. Les facteurs environnementaux (conductivité et TP) et la structure spatiale expliquent 59% de la variation de biomasse des trois PP benthiques. Spécifiquement, les variations de biomasses étaient le mieux expliquées par la conductivité (+) pour les macrophytes, par le ratio DIN:TDP (+) et le coefficient d'extinction lumineuse (+) pour les épiphytes et par le DOC (+) et le NH_4^+ (-) pour *L. wollei.* La structure spatiale à l'intérieur des lacs fluviaux était la plus importante composante spatiale pour tous les PP benthiques, suggérant que les effets locaux tels que l'enrichissement par les tributaire plutôt que les gradients amont-aval déterminent la biomasse de PP benthiques. Donc, la dynamique des agrégats d'habitat représente un cadre général adéquat pour expliquer les variations spatiales et la grande variété de conditions environnementales supportant des organismes aquatiques dans les grands fleuves.

Enfin, nous avons étudié le rôle écologique des tapis de *L. wollei* dans les écosystèmes aquatiques, en particulier comme source de nourriture et refuge pour l'amphipode *Gammarus fasciatus*. Nous avons offert aux amphipodes un choix entre des tapis de *L. wollei* et soit des chlorophytes filamenteuses ou un tapis artificiel de laine acrylique lors d'expériences en laboratoire. Nous avons aussi reconstitué la diète *in situ* des amphipodes à l'aide du *mixing model* ($d^{13}C$ et $\delta^{15}N$). *Gammarus fasciatus* choisissait le substrat offrant le meilleur refuge face à la lumière (Acrylique>*Lyngbya*=*Rhizoclonium*>*Spirogyra*). La présence de saxitoxines, la composition élémentaire des tissus et l'abondance des épiphytes n'ont eu aucun effet sur le

choix de substrat. *Lyngbya wollei* et ses épiphytes constituaient 36 et 24 % de l'alimentation *in situ* de *G. fasciatus* alors que les chlorophytes, les macrophytes et les épiphytes associées représentaient une fraction moins importante de son alimentation. Les tapis de cyanobactéries benthiques devraient être considérés comme un bon refuge et une source de nourriture pour les petits invertébrés omnivores tels que les amphipodes.

Mots-clés : tapis de cyanobactérie, *Lyngbya wollei*, macrophytes, épiphytes, fleuve Saint-Laurent, écologie fluviale, nutriments, carbone organique dissous, hydrologie, amphipodes gammarides, chaîne alimentaire, sélection d'habitats, paradigmes fluviaux.

Abstract

Harmful proliferations of the filamentous cyanobacterium *L. wollei* forming conspicuous benthic mats on the bottom sediment have been reported with increasing frequency in the last 30 years in rivers, lakes, and springs in North America. It is a known producer of neurotoxins and volatile organic compounds (geosmin, 2-methylisoborneol) thus exerting socioeconomic and public health impacts. *Lyngbya wollei* is also considered a poor nutritional source for invertebrates because of its robust sheath and toxin production.

Proliferation of *L. wollei* in St. Lawrence River (SLR; Quebec, Canada) was first noticed in 2005. We deemed important to determine its distribution over a 250 km stretch of the SLR to elaborate predictive models of its presence and biomass based on chemical and physical characteristics. *Lyngbya wollei* was generally found downstream of the inflow tributaries draining farmlands. As enriched waters flowed slowly through submerged vegetation, dissolved inorganic nitrogen (DIN) concentration dropped but dissolved organic carbon (DOC) and total dissolved phosphorus (TDP) remained high, leading to a low DIN:TDP ratio. Models identified DOC (positive effect), TP (negative effect), and DIN:TDP (negative effect) as the most important variables explaining *L. wollei* distribution. The risk of *L. wollei* occurrence in the SLR was correctly forecasted in 72%-92% of all cases with an independent data set.

We then examined if hydrodynamic conditions, namely currents generated by waves and river flow, control spatial and temporal variations of *L. wollei* biomass in a large river system. We measured *L. wollei* biomass together with meteorological, physical, and chemical variables over three years at 10 sites along a gradient of exposure to current and wind in a large (148 km^2) fluvial lake of SLR. Wave exposure and current velocity controlled spatial and temporal biomass variations. Biomass increased from May to November and persisted during winter. Interannual variations were primarily controlled by river flow (water level) with spring discharge dislodging mats from the previous year. As anticipated under climate change scenarios, drops in water level and rising storm intensity may lead to an increase in the areas colonized by *L. wollei*, together with more frequent episodes of mat disruption and beach fouling.

Additionally, we evaluated the relative importance of *L. wollei* with respect to macrophytes and epiphytes. We assessed the influence of the spatial scale in structuring environmental variables and biomass of these benthic primary producers (PP). We also test to which extent their biomass reflected the nature of patches based on ecogeomorphology or the river continuum. To address these two questions, we used a nested design at 3 spatial scales within the SLR: 1) along a 250-km-long upstream-downstream river stretch, 2) among three fluvial lakes located within that river stretch and 3) within each fluvial lake. Environmental factors (conductivity and TP) and spatial structure together explained 59% of the variability in biomass of all three benthic PP. Spatial variability of biomass was best explained by conductivity (+) for macrophytes, DIN:TDP ratio (+) and water extinction coefficient (+) for epiphytes and DOC (+) and NH_4^+ (-) for *L. wollei* mats. Within-lake structure was the most important spatial component for all benthic PP, suggesting that local effects, such as enrichment by the inflow of tributaries, rather than upstream-downstream gradients, determined the biomass and composition of benthic PP. Therefore patch dynamics represents a general framework which adequately covers the spatial variability and wide variety of environmental conditions experienced by aquatic organisms found in large rivers.

Finally, we investigated the ecological role of *L. wollei* mats in aquatic ecosystems, especially as a food source and shelter for the amphipod *Gammarus fasciatus*. We offered amphipods a choice between mats of *L. wollei* and either chlorophytes or an artificial mat made of acrylic wool in laboratory experiment. Moreover, we reconstructed *in situ* amphipod diet using mixing model ($\delta^{13}C$ and $\delta^{15}N$). *Gammarus fasciatus* selected the substratum offering the best light refuge (Acrylic > *Lyngbya* = *Rhizoclonium* > *Spirogyra*). Presence of saxitoxins, tissue elemental composition and epiphyte abundance had no significant effect on substratum choice. *Lyngbya wollei* and its epiphytes constituted 36 and 24% of the *in situ* diet of *G. fasciatus* whereas chlorophytes, macrophytes and associated epiphytes represented a less important fraction of its diet. Benthic cyanobacterial mats should be considered a good shelter and food source for small omnivorous invertebrates such as amphipods.

Keywords : *Lyngbya wollei* cyanobacterial mats, macrophytes, epiphytes, St. Lawrence River, river ecology, nutrients, dissolved organic carbon, hydrology, gammarid amphipods, food web, habitat selection, river paradigm.

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δ^{13}C: Ratio isotopique du carbone

δ^{15}N: Ratio isotopique de l'azote

ANOVA : Analyse de variance

BIC : Critère d'information bayésien

BIC-1 : Meilleur modèle unique

BMA : Moyenne bayésienne des modèles

BMA-Opt : Modèle optimal basé sur la moyenne bayésienne des modèles

BMA-Pars : Modèle parsimonieux basé sur la moyenne bayésienne des modèles

CART : Arbre de classification et de regression

Coeff : Coefficient

DIN : Azote inorganique dissous

DM : Masse sèche

DOC : Carbone organique dissous

E : composante environnementale

F : Fetch effectif

FPZ : Zone de processus fonctionnel

GLS : *Generalized least squares*

H : Hauteur des vagues

HAB : Floraison d'eau néfaste

Iz : Intensité lumineuse à une profondeur donnée

I0 : Intensité lumineuse à la surface

k : Coefficient d'extinction lumineuse

L : Distance entre les vagues

LB ou LP : Fraction de la lumière incidente atteignant le fond

log10 : Logarithme en base 10

LSF : Lac Saint-François

LSL : Lac Saint-Louis

LSP : Lac Saint-Pierre

MC : Expériences à choix multiplesxvii

MEM : Carte des eigenvecteurs de Moran

MIB : Méthylisobornéol

N : Effectif

NA : Non disponible

p : probabilité

P : Fréquence de la direction du vent

PAR : Radiations photosyntétiquement actives

PCA : Analyse en composantes principales

PEP : Probabilité postérieure

PP : Producteur primaire

R : Coefficient de corrélation

R2 : Coefficient de détermination

R2adj : Coefficient de détermination ajusté

RCC : Concept du continuum des rivières

RDA : Analyse de redondance

REI : Indice d'exposition relatif

RMA : *Ranged major axis*

S : Composante spatiale

SD : Écart-type

SDC : Concept des discontinuités en série

SE : Erreur standard

SI : Analyse d'isotopes stables

SLR : Fleuve Saint-Laurent

SM : Matière en suspension

T : Période des vagues

T : Composante temporelle

TDP : Phosphore total dissous

TN : Azote total

TP : Phosphore total

U*d* : Vitesse du courant à une profondeur donnée

V : Vitesse moyenne journalière du ventxviii

WM : Masse humide

X*i* : Angle du fetch direct

Y*i* : Fetch direct

z : Profondeur

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1. Introduction générale

1.1 Les cyanobactéries

Les cyanobactéries, communément appelées algues bleu-vert, sont des bactéries à Gram négatif, autotrophes, faisant de la photosynthèse oxydative. Elles sont apparues il y a environ 3.5 milliards d'années et sont, en grande partie, responsables de l'oxygénation de l'atmosphère terrestre (Schopf 2002). Par leur contribution à la formation des stromatolithes et du traversin, elles seraient à l'origine de la majorité des dépositions de calcaires sur la Terre (Pentecost 1991). Leur endosymbiose par un hôte non photosynthétique est à l'origine du chloroplaste des cellules eucaryotes (Delwiche and Palmer 1997). Elles occupent presque tous les environnements illuminés terrestres ou aquatiques, y compris certains environnements extrêmes tels les eaux hypersalines, les sources thermales, les déserts et les régions polaires (Seckbach 2007).

Parmi les procaryotes, les cyanobactéries forment le groupe le plus distinct morphologiquement. Bien que leur classification taxonomique soit principalement basée sur des critères morphologiques, l'inclusion de critères moléculaires et écologiques est déjà entamée (Komarek 2006). Les cyanobactéries forment un groupe monophylétique composé d'approximativement 2000 espèces réparties en 150 genres qui peuvent être divisées en 5 groupes (Castenholz 2001). Les deux premiers groupes, constitués des cyanobactéries unicellulaires, sont différenciés par le mode de division cellulaire: les membres du groupe I se reproduise par fission binaire et ceux du groupe II par fission multiple. Les cyanobactéries filamenteuses forment les groupes III, IV, et V. Le groupe III, formé des Oscillatoriales, renferme les cyanobactéries formant des filaments simples non-ramifiés et sans cellules spécialisées. Les organismes des groupes IV et V possèdent des cellules spécialisées et ont tous le potentiel de fixer l'azote atmosphérique. On différencie le groupe IV du groupe V par la présence de vraies ramifications chez les cyanobactéries du groupe IV (Castenholz 2001).

1.2 Les problématiques associées aux cyanobactéries: causes et conséquences

Lorsque les conditions sont favorables, la croissance excessive des cyanobactéries, connue sous le nom de floraison d'eau, peut induire une coloration à la surface ou en profondeur dans les plans d'eau. L'augmentation en fréquence et en sévérité des épisodes de floraisons d'eau à travers le monde a été associée à l'eutrophisation d'origine anthropique, qui va sans cesse en augmentant (Hallegraeff 1993, Paerl 1996). En effet, de façon générale, les floraisons de cyanobactéries augmentent avec la concentration en nutriments (Heisler et al. 2008). La dominance des cyanobactéries augmente rapidement lorsque les concentrations en phosphore (P) total passent de 30 à 100 $\mu g\ L^{-1}$ (Downing et al. 2001), mais l'excès d'azote (N) est également problématique (Havens 2008). La relation positive entre les concentrations de nutriments et les biomasses de cyanobactéries a été montrée dans les lacs, rivières et eaux côtières (Paerl 1988). Les floraisons de cyanobactéries sont également associées à un pH élevé et une température élevée (>20 °C). Généralement, une faible concentration de CO_2 dissous favorise la dominance des cyanobactéries (Dokulil and Teubner 2000, Paerl and Huisman 2009) cependant des concentrations élevée de CO_2 augmentent le rythme de divisions cellulaires chez certaines espèces (Hein and SandJensen 1997, Barcelos e Ramos et al. 2007). Leur dominance a aussi été associée, dans certains cas, à leur faible besoin en lumière, leur migration verticale dans la colonne d'eau, leur grande résistance au broutage et à leur production de composés allopathiques (Dokulil and Teubner 2000). La présence de conditions hydrologiques stables et calmes est nécessaires à l'établissement et au maintien des floraisons de cyanobactéries (Havens 2008). En effet, dans la majorité des cas, la dominance par des espèces planctoniques est associée à la stabilité de la colonne d'eau dans les lacs, alors que les rivières, ayant souvent un temps de résidence plus court, sont plutôt colonisées par des espèces filamenteuses (Paerl 2008).

Les floraisons de cyanobactéries causent des problèmes écologiques, de santé publique et entraînent d'importantes pertes économiques. D'abord, les floraisons planctoniques augmentent la turbidité de l'eau limitant la croissance des producteurs primaires benthiques telles que les macrophytes, les épiphytes et le métaphyton, ce qui se traduit par d'importants changements dans la composition en espèces des communautés aquatiques (Paerl et al. 2001). Elles peuvent aussi causer des zones hypoxiques en eaux profondes lorsque leur décomposition par les bactéries hétérotrophes épuise l'oxygène dissous disponible menant à la mort d'invertébrés et de poissons (Paerl et al. 2011). Certaines cyanobactéries produisent des composés organiques volatils non-toxiques (i.e géosmine et 2-méthylisobornéol) donnant à l'eau un goût et une odeur de vase (Watson 2003). Les floraisons de cyanobactéries nuisent aux activités récréatives et augmentent les coûts de traitement de l'eau potable, ce qui engendre des coûts annuels d'au moins 2 milliards de dollars aux États-Unis seulement (Dodds et al. 2009). Les floraisons de cyanobactéries sont également reconnues pour leur production de toxines (Quiblier et al. 2013, Zanchett and Oliveira 2013). En effet, quarante-deux espèces (22 genres) de cyanobactéries produisent des toxines, qui peuvent affecter le foie, le système nerveux ou irriter la peau (Hudnell 2008). Les floraisons toxiques des espèces planctoniques telles qu'*Aphanizomenon, Anabaena, Microcystis* et *Cylindrospermopsis* sont beaucoup étudiées en raison du risque lié à la contamination de l'eau potable (Chorus and Bartram 1999). Cependant, les cyanobactéries filamenteuses benthiques telles que *Lyngbya* et *Oscillatoria* produisent aussi des toxines (Carmichael et al. 1997, Onodera et al. 1997, Osborne et al. 2001, Seifert et al. 2007) et ont également d'importantes répercussions sur l'environnement (Watkinson et al. 2005, Bishop et al. 2006, Hudon et al. 2012), quoique peu d'études aient été consacrées aux espèces proliférant en eau douce. Dans ce contexte, une brève revue de littérature concernant l'écologie et les problématiques associées à la cyanobactérie benthique *Lyngbya wollei* semble de mise.

1.3 Morphologie et taxonomie de la cyanobactérie benthique *Lyngbya wollei*

Au cours des 30 dernières années, plusieurs floraisons de la cyanobactérie filamenteuse benthique, productrice de toxines, *Lyngbya wollei* (Farlow ex Gomont, Speziale et Dyck) ont été reportées en Amérique du Nord (Speziale et al. 1991, Vis et al. 2008, Bridgeman and Penamon 2010). *Lyngbya wollei* fait partie de la famille des Oscillatoriaceae et ne possède donc pas de cellules spécialisées; les trichomes unisériés sont constitués d'un empilement de cellules discoïdes de 24-65 µm de diamètre. Le trichome est entouré d'une large gaine hyaline et lamellée, constitué de polysaccharides, pouvant atteindre 12 μm d'épaisseur (Fig. 1.1A) (Speziale and Dyck 1992). Les filaments n'ont pas de longueur déterminée et sont souvent spiralés. *Lyngbya wollei* forme parfois de fausses ramifications responsables de l'historique chaotique de sa taxonomie (Hudon et al. 2014). En effet, cette espèce était à la fois désignée sous le nom de *Plectonema wollei* (Farlow 1877) et de *Lyngbya wollei* (Wolle 1887) de la fin des années 1800 à 1991. Cependant, une analyse exhaustive des données morphologiques antérieures a mené à la désignation de ce taxon sous le nom de *L. wollei* (Speziale and Dyck 1992). Toutefois, des analyses de phylogénie moléculaire réalisées sur des échantillons provenant du sud-est des États-Unis montrent que ce taxon est constitué d'au moins 2 espèces regroupées en trois sous-groupes (Joyner et al. 2008). Le sous-groupe 3, identifié au nord-ouest de la Floride, auquel appartiennent également des spécimens du lac Érié (J. Joyner, Institute of Marine Sciences, communication personnelle, cité par Bridgeman et Penamon 2010), du lac Ontario, de deux lacs au Manitoba, d'un réservoir en Alabama et du fleuve Saint-Laurent (R. Thacker, University of Alabama, communication personnelle, citée par Hudon et al. 2014) semble le plus géographiquement répandu.

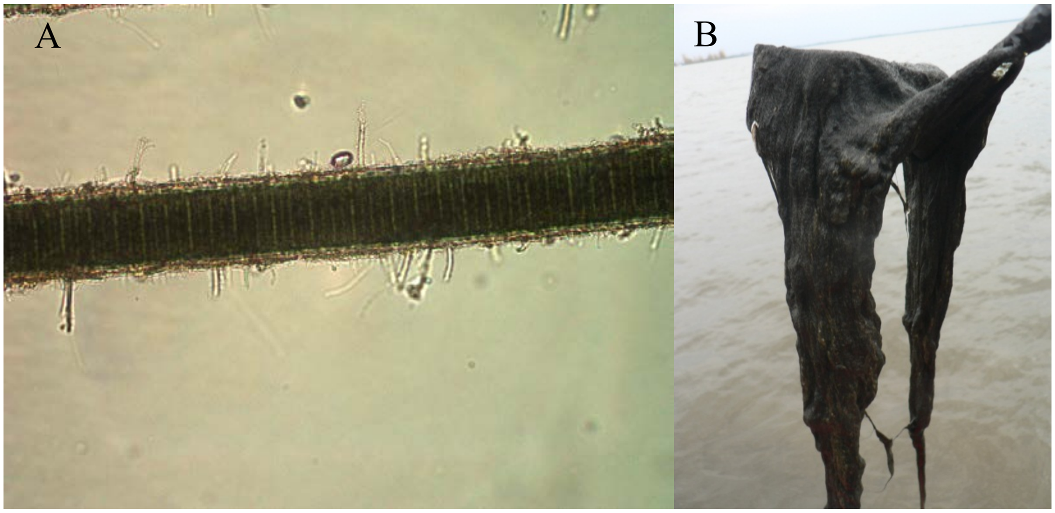

Figure 1.1 A) Filament de *L. wollei* composé du trichome et de l'épaisse gaine recouverte d'épiphytes. B) Tapis de *L. wollei* récolté à l'aide d'un râteau à double tête.

1.4 Distribution et historique des proliférations

Lyngbya wollei est répandu dans le sud-est des États-Unis, notamment en Floride (Phlips et al. 1992, Cowell and Silver Botts 1994, Cowell and Dawes 2004, Stevenson et al. 2007), en Géorgie (Beer et al. 1986), en Caroline du Sud (Speziale et al. 1991), en Alabama et au Tennessee (Doyle and Smart 1998). Plus au nord, on le retrouve dans deux lacs peu profond du Manitoba (Macbeth 2004), au lac Érié près de la rivière Maumee (Bridgeman and Penamon 2010), au lac Saint Clair près de Detroit (Vijayavel et al. 2013) et dans le fleuve Saint-Laurent au lac Saint-Pierre (Vis et al. 2008). Sa distribution semble relativement limitée au continent nord-américain, alors qu'une seule mention dans la littérature scientifique provient du Queensland en Australie (Seifert et al. 2007).

La présence de *L. wollei* en Amérique Nord est documentée depuis la fin du 19e siècle, alors qu'il fut identifié dans des étangs du Massachusetts (Farlow 1877) et du New Jersey (Wolle 1887). Dans le système Saint-Laurent-Grands Lacs*,* la présence de *L. wollei*, identifié sous le nom de *P. wollei*, *L. aestuarii*, ou *L. majuscula*, a été notée dès 1915 (Miller 1915), puis dans les années 30 et 40 (Taft 1942, Poulin et al. 1994) et dans les années 70 (Alaerts-Smeesters and Magnin 1974).

1.5 Morphologie des tapis

Les filaments de *L. wollei* croissent librement sur les sédiments et se retrouvent entremêlés aux plantes vasculaires lorsqu'ils sont peu abondants (Hudon et al. 2014). Au fur et à mesure que la biomasse augmente, les filaments forment un tapis déposé sur les sédiments, devenant de plus en plus épais et pouvant parfois atteindre plus de 30 cm (Fig. 1.1B) (Speziale et al. 1991). Ce tapis, persistant toute l'année dans le sud-est des États-Unis, peut parfois remonter à la surface en période d'intense photosynthèse, soulevé par l'accumulation de nombreuses bulles de gaz produites (Speziale et al. 1991). Par la suite les tapis peuvent être rejetés sur la berge sous la force du vent et des vagues. Ces derniers auraient un rôle important dans la dispersion de l'organisme (Beer et al. 1986).

1.6 Contrôle environnemental

Les facteurs environnementaux contrôlant la distribution et l'abondance de *L. wollei* sont peu connus et encore débattus probablement en raison de la vaste gamme d'environnements colonisés par cette espèce (Hudon et al. 2014).

1.6.1 Nutriments

Les nutriments, l'azote (N) et le phosphore (P), ainsi que la matière organique dissoute favorisent la croissance des cyanobactéries (Paerl and Otten 2013). Leur concentration et leur ratio influencent la composition spécifique, l'importance et la durée des épisodes de floraison (Dokulil and Teubner 2000). Cependant, dans le cas de *L. wollei*, le rôle du N et du P n'est pas clair, puisqu'on retrouve l'espèce dans des écosystèmes présentant une très large gamme de valeurs: de 0 à 25800 µg L^{-1} pour le NO_3^- (Baker 1994 cité dans Yin et al. 1997) et de 24 à 282 µg L^{-1} pour le P total (Cowell and Silver Botts 1994). La large gamme de concentration de nutriments permettant la croissance de *L. wollei* explique l'absence de corrélation entre les nutriments et son abondance, selon une étude de 50 sources de Floride (Stevenson et al. 2007) et une autre portant sur 15 sites de la King Bay (Cowell and Silver Botts 1994). Le long d'un transect de 15 km du le fleuve Saint-Laurent, le ratio N:P semblait moduler la distribution de *Lyngbya wollei* (Vis et al. 2008). La chute des concentrations de NO_2^--NO_3^- et le maintien des teneurs en P total s'est traduit par le passage d'une dominance par les chlorophytes vers une dominance de *Lyngbya* (Vis et al. 2008).

Les études en laboratoire sur la croissance de *L. wollei* en présence de différentes concentrations de nutriments présentent aussi des résultats variables. En effet, un enrichissement en N sous forme de NO_3^- ou de NH_4^+ pouvait soit augmenter la croissance de *L. wollei* (Cowell and Dawes 2004, Stevenson et al. 2007) ou n'avoir aucun effet, voire induire une légère réponse négative (Cowell and Silver Botts 1994, Yin et al. 1997). Le seuil de saturation de croissance en laboratoire variait de 28 à 1500 µg L^{-1} pour le NO_3^- et de 110 à 821 µg L^{-1} dans le cas du phosphate (Cowell and Dawes 2004, Stevenson et al. 2007). Une étude de la composition stœchiométrique (C, N, P) des filaments prélevés dans des sources de Floride suggérait une limitation en P (Stevenson et al. 2007).

1.6.2 pH et ions dissous

Lyngbya wollei aurait une croissance optimale en condition alcaline à un pH de 8, mais pourrait survivre à des valeurs variant de 5 à 9 lors d'expérience en laboratoire (Cowell and Silver Botts 1994). Cette espèce d'eau douce croîtrait mieux à une salinité de 0 PSU (Cowell and Silver Botts 1994) ce qui la distingue des espèces marines morphologiquement similaires *L. majuscula* et *L. aestuarii. Lyngbya wollei* présenterait une croissance optimale dans des eaux ayant une conductivité entre 100 et 1000 µS cm^{-1} alors que son développement commençait à chuter à des valeurs ≥3000 µS cm^{-1} (Pinowska et al. 2007).

En laboratoire, un ajout de Ca^{2+} a stimulé la croissance de *L. wollei* (Cowell and Silver Botts 1994) et pourrait améliorer sa tolérance à un haut ratio N:P (Turner 1990) en augmentant son acquisition de phosphore (Whitton 1967). Lorsque les concentrations de calcium sont faibles comme dans le lac Whiteshell au Manitoba (Macbeth 2004), le bore pourrait le remplacer pour maintenir la croissance chez les cyanobactéries (Bonilla et al. 1995).

Le Fe est un élément nécessaire aux cyanobactéries, particulièrement à celles fixant l'azote atmosphérique puisqu'il est requis pour le fonctionnement de la nitrogénase (Paerl 1990). En laboratoire, la croissance de *L. wollei* a été stimulée par l'ajout de Fe au milieu de croissance jusqu'à 600 µg Fe L^{-1}, valeur à partir de laquelle la biomasse produite était moindre (Pinowska et al. 2007).

1.6.3 Température et lumière

Lors d'expériences en laboratoire, une température de 26°C a maximisé la production de biomasse de *Lyngbya wollei,* alors qu'elle diminuait lorsque la température était de10°C (Yin et al. 1997). Les grandes biomasses dans le sud-est des États-Unis ont généralement été enregistrées à des températures entre 18 à 22°C (Speziale et al. 1991, Joyner et al. 2008).

Lyngbya wollei absorbe dans le PAR (photosynthetic active radiation, 400-700 nm) grâce à ses trois types de pigments, la chlorophylle, les phycobilines et les caroténoïdes (Speziale et al. 1991). En laboratoire, les biomasses étaient maximisées à des intensités lumineuses entre 22 et 50 µmol m^{-2} sec^{-1} (Yin et al. 1997, Pinowska et al. 2007). *In situ*, les tapis de *L. wollei* sont adaptés à de faibles intensités lumineuses avec un point de compensation lumineuse variant de 31-216 µmol m^{-2} sec^{-1}, lui permettant de survivre et de se développer dans des milieux où l'on retrouve moins de 0.1 % de l'intensité lumineuse incidente à une profondeur de 2 m (Speziale et al. 1991). Cette adaptation à de faibles luminosités est conséquente avec l'atténuation lumineuse produite par les tapis flottants. Il a été montré dans le sud-est des États-Unis, que la lumière pénétrant 10 centimètres sous un tapis flottant était réduite à <2 % de la lumière incidente (Speziale et al. 1991). Cependant, les fortes biomasses de métaphyton, dominées par *L. wollei* dans les sources de Floride, sont retrouvées à des quantités de lumière >10 % (Hoyer et al. 2004). Dans le lac Érié, les biomasses maximales de *L. wollei* (~10 fois plus faible que les biomasses mesurées dans les sources de Floride) ont été retrouvées dans le panache turbide (0.05-4% du PAR incident) de la rivière Maumee à des profondeurs variant de 1.6 à 3.5 m (Bridgeman and Penamon 2010).

1.6.4 Conditions hydrologiques et météorologiques

L'influence du débit, du temps de résidence ainsi que de la vitesse du courant sur la croissance et l'accumulation de biomasse de la végétation aquatique submergée est connue de longue date (Butcher 1927). Une baisse de débit au cours des 10 dernières années a été évoquée pour expliquer l'augmentation de couverture par le métaphyton (*L. wollei* et *Vaucheria* sp.) dans les sources de Floride (King 2014). En effet, la couverture de métaphyton dans cet écosystème devient limitée lorsque la vitesse du courant est plus grande que 22-25 cm s^{-1} (Hoyer et al. 2004, King 2014). *Lyngbya majuscula* était l'espèce dominante seulement dans les zones ayant un long temps de résidence (8-24 jours comparativement à 4-12 jours) d'un lagon eutrophe au sud de Taiwan (Lin and Hung 2004), suggérant que l'accumulation de biomasse était régulée par ce facteur.

Les vents de grande vélocité peuvent déloger les tapis de filaments en eau peu profonde et les amener à la berge. En effet, après un épisode de 6 jours de forts vents (moyenne de 23 km h^{-1}) en 2006, une bande de 100 m sur la rive du lac Erie a reçu ~200 tonnes (masse humide) de *L. wollei* (Bridgeman and Penamon 2010).

1.7 Physiologie des tapis *L. wollei*

À l'intérieur des tapis de *L. wollei*, de forts gradients physiques (luminosité) et chimiques (pH, O_2 dissous, nutriments et microéléments) se développent entre l'interface eau-tapis et les sédiments (Stevenson et al. 2007). La luminosité, la concentration d'O_2 dissous et de NO_3^- diminuent entre la surface du tapis et les sédiments, alors que le NH_4^+ et le TP suivent la tendance inverse (Stevenson et al. 2007). Seulement une faible proportion (1-5 %) de la lumière incidente semble pénétrer les tapis de *L. wollei* (Doyle and Smart 1998). Pourtant, des filaments sont retrouvés dans les sédiments sous les tapis et semblent survivre de manière hétérotrophe dans l'obscurité quasi totale (Doyle and Smart 1998). Ces conditions de faible intensité lumineuse et d'O_2 dans les tapis permettent, malgré l'absence d'hétérocystes chez *L. wollei*, la fixation de l'azote atmosphérique (Phlips et al. 1992). Ce phénomène serait expliqué par la présence de microzones anoxiques ou par la présence d'autres organismes diazotrophes dans le tapis de filaments (Tall 2012). Les forts gradients à l'intérieur des tapis de *L. wollei* favorisent également le recyclage interne des nutriments et microéléments, incluant le Fe dans les zones anoxiques (Stevenson et al. 2007).

1.8 Toxines et composés organiques volatils

Plusieurs toxines et composés organiques volatils ont été retrouvés dans les tapis de *L. wollei* dans différents environnements. Trois neurotoxines, de type saxitoxine, ont été découvertes jusqu'à présent: la décarbamoylsaxitoxine, la décarbamoylgonyautoxine 1 et 2 et la *Lyngbya wollei* toxine (LWTX 1-6) retrouvées dans un réservoir et une rivière de l'Alabama (Carmichael et al. 1997, Onodera et al. 1997) ainsi que dans deux sources de Floride (Foss et al. 2012). La LWTX 1 et 6 ont également été identifiées dans les tapis de *L. wollei* du fleuve Saint-Laurent (Lajeunesse et al. 2012). Les saxitoxines produites sont 9 à 50 fois moins toxiques, en termes de taux de mortalité mesurée chez la souris, que d'autres saxitoxines plus communes (Foss et al. 2012). Une seule hépatotoxine, la cylindrospermopsine a été retrouvée, pour le moment, dans du *L. wollei* provenant de deux rivières en Australie (Seifert et al. 2007). Aucune dermatotoxine n'est officiellement documentée, bien que l'espèce marine *L. majuscula* produise l'aplysiatoxine et la débromoaplysiatoxine (Carmichael et al. 1997, Osborne et al. 2001) et que certaines floraisons de *Lyngbya* sp. dans des sources et sur la côte de la Floride puissent produire de la lyngbyatoxine-A et de la débromoaplysiatoxine (Burns 2008). *Lyngbya wollei* retrouvé dans le fleuve Saint-Laurent peut produire de la géosmine et du 2-méthylisobornéol (S. Watson, Environnement Canada, communication personnelle, citée par Hudon et al. 2014), deux composés organiques volatils non toxiques donnant un goût et une odeur de vase à l'eau potable (Tabachek and Yurkowski 1976).

1.9 Compétition avec les autres producteurs primaires

La biomasse de *L. wollei* semble avoir une relation inverse avec l'abondance des macrophytes et des chlorophytes filamenteuses (Hudon et al. 2014). Dans le sud-est des États-Unis, la présence simultanée de *L. wollei* et de la macrophyte *Hydrilla verticilla* était rare (Beer et al. 1986, Cowell and Silver Botts 1994). Similairement, la biomasse de la macrophyte *Vallisneria americana*, une espèce dominante dans le fleuve Saint-Laurent, était réduite d'un facteur 4 dans les zones où *L. wollei* était abondant (12-26 g DM m^{-2}) (Hudon et al. 2012). Le remplacement des chlorophytes filamenteuses par un tapis de *L. wollei* a été observé au lac Érié (baie de Maumee) (Bridgeman and Penamon 2010) et dans le fleuve Saint-Laurent (Vis et al. 2008). Les facteurs expliquant cette ségrégation des tapis de *L. wollei* des autres groupes de végétaux pourraient résider dans l'acidification créée par le relargage de CO_2 et d'ions H^+ par les racines des macrophytes (Doyle and Smart 1998) ou la plasticité métabolique de *L. wollei* lui permettant de survivre dans des conditions peu favorables aux compétiteurs avec peu de nutriments, de lumière et d'O_2 (Hudon et al. 2014).

1.10 Rôle des tapis de *L. wollei* dans la chaîne trophique

Malgré l'importante communauté d'algues épiphytes, de la microfaune et des macroinvertébrés qu'ils supportent, le rôle des tapis benthiques de *L. wollei* en tant qu'habitat et source de nourriture est assez peu connu (Hudon et al. 2014). Les zones dominées par les tapis de *L. wollei* sont associées à une dégradation de l'habitat puisqu'elles supportent une plus faible biomasse de plantes, d'invertébrés et de gros poissons. On dénote aussi une faible richesse spécifique de l'ichtyofaune comparativement aux zones dominées par les macrophytes au lac Saint-Pierre, un grand lac fluvial du fleuve Saint-Laurent (Hudon et al. 2012).

Les amphipodes, *Hyallela azteca* dans le sud-est des États-Unis (Camacho and Thacker 2006) et *Gammarus fasciatus* (Tourville Poirier et al. 2010) dans le fleuve Saint-Laurent, sont les macroinvertébrés les plus abondants de ces tapis. Dans le fleuve Saint-Laurent, les chironomides étaient plus abondants dans ces tapis que dans les macrophytes et les chlorophytes filamenteuses, alors que les gastéropodes étaient retrouvés en présence réduite (2-18 fois moins) dans les tapis de cyanobactéries (Tourville Poirier et al. 2010). Les gastéropodes ayant un choix de substrat entre des tapis de *L. wollei*, des chlorophytes filamenteuses et des macrophytes préféraient ces dernières sans toutefois éviter les cyanobactéries (Visconti et al. 2014) Lors d'autres expériences de laboratoire, la survie de *H. azteca* face au crapet arlequin, un prédateur d'invertébrés benthiques, était plus élevée dans les tapis de *L. wollei* que dans les masses de filaments de la chlorophyte *Rhizoclonium hieroglyphicum,* suggérant que les matelas de *L. wollei* représente un refuge potentiel contre la prédation (Camacho and Thacker 2013).

Les tapis de *L. wollei* semblent une source de nourriture négligeable pour les poissons herbivores comme la carpe amour (*Ctenopharyngodon idella*) (Dyck 1994, cité par Doyle et Smart 1995). Des analyses isotopiques (δ^{13}C et δ^{15}N) réalisées dans le fleuve Saint-Laurent suggèrent que *L. wollei* ferait partie de la diète de *Gammarus fasciatus* (Hudon et al. 2012). Cependant lors d'expériences sur les préférences alimentaires, *Hyallela* a sélectionné la chlorophycée filamenteuse *Rhizoclonium* plus souvent que *L. wollei* (Camacho and Thacker 2006). Les amphipodes évitaient la gaine de polysaccharides de *L. wollei* qui agirait comme une défense morphologique, alors que des extraits de saxitoxines stimulaient la consommation de *Hyallela* (Camacho and Thacker 2006). Des individus de *G. fasciatus* retrouvés dans des tapis de *L. wollei* du fleuve Saint-Laurent présentaient des signes de stress physiologiques suggérant ainsi une certaine toxicité pour ces derniers (Gelinas et al. 2013).

1.11. Site d’étude

Le fleuve Saint-Laurent (SLR) avec un débit annuel moyen à Québec ~12000 m^3 s^{-1} et un bassin versant d'une superficie >1 000 000 km^2 est l'un des plus grands fleuves d’Amérique du Nord. Sa portion fluviale en eau douce s'étend sur près de 600 km: de l'embouchure du lac Ontario jusqu’à Trois-Rivières. Le SLR a également été modifié par l'humain le long de son parcours avec le dragage et la canalisation pour le trafic maritime, la création d'îles et l'approfondissement du port de Montréal. Mais, sa modification la plus importante demeure la régularisation de son débit par le barrage hydroélectrique Moses-Saunders localisé 165 km en aval du lac Ontario, pour répondre aux demandes de la production en hydroélectricité et de la navigation dans la Voie Maritime. Dans ce contexte, la prolifération de *L. wollei* représente un stress supplémentaire sur l'écosystème du fleuve du Saint-Laurent et pose des risques à la santé publique.

Notre zone d'étude se situe entre le barrage Moses-Saunders et Trois-Rivières; un tronçon de 250 km où se succèdent trois lacs fluviaux du SLR, les lacs Saint-François (LSF), Saint-Louis (LSL) et Saint- Pierre (LSP). Ces trois lacs fluviaux sont larges (>5 km), peu profonds (profondeur moyenne <5 m) et s'écoulent lentement (<0.4 m s^{-1} à l'extérieur du chenal de navigation). Ils sont joints par des corridors plus étroits (<4 km) où la vitesse du courant est plus grande.

Le lac Saint-François (235 km^2) débute juste en aval du barrage Moses-Saunders et son eau provenant du lac Ontario est claire (Secchi >5 m), avec peu de carbone organique dissous (~2.6 mg L^{-1}), une faible concentration en phosphore total (~14 µg L^{-1}) et une forte conductivité (étendue de 226-350 µS cm^{-1}). Il est délimité en aval par le barrage hydroélectrique de Beauharnois, ce qui stabilise largement son débit (~7500 m^3 s^{-1}) et les variations annuelles de son niveau d'eau (<0.2 m). Le bassin versant du LSF est composé de zones rurales modérément peuplées (100-500 hab. km^{-2}) et est desservi par de petits tributaires. Lac Saint-Louis (140 km^2), débutant en aval du barrage de Beauharnois, est situé dans une zone densément peuplée (>500 hab. km^{-2}) incluant la ville de Montréal. À cet endroit, le SLR a un débit moyen ~9500 m^3 s^{-1} et ses variations annuelles de niveau (0.5-1.4 m) sont modulées de façon saisonnière par l'écoulement partiel de la rivière des Outaouais (débit moyen ~1800 m^3 s^{-1}), son plus important tributaire. L'eau de la rivière des Outaouais est brune, possède une faible transparence (Secchi 1-5 m), une faible conductivité (~81 µS cm^{-1}) et est enrichie en phosphore (~34 µg L^{-1}) ainsi qu'en en DOC (~6.1 mg L^{-1}). Le lac Saint-Pierre est le dernier et le plus grand (402 km^2) des lacs fluviaux. Il est situé ~90 km en aval du LSL et son débit de 10 500 m^3 s^{-1} inclut plusieurs tributaires additionnels. Les apports de l'Outaouais ainsi que des rivières Richelieu, Yamaska et Saint-François (débit moyen de 434, 86 et 168 $m^3 s^{-1}$, respectivement) contribuent aux importantes variations annuelles de niveau d'eau (1.31 à 2.26 m) de ce lac fluvial et à sa faible transparence (Secchi 0.1-3 m). Le bassin versant du LSP est majoritairement agricole avec une faible densité de population (10 à 25 hab. km^{-2}).

1.12. Structure et objectifs de la thèse

Cette étude a pour objectif général d'identifier les facteurs chimiques et physiques contrôlant la distribution et la biomasse des tapis de *L. wollei* dans le fleuve Saint-Laurent, et de déterminer leur rôle dans la chaîne trophique. Cette thèse de doctorat est organisée en six chapitres, ce premier chapitre dressait un état des connaissances actuelles concernant les tapis de *L. wollei*, les quatre chapitres suivants se présentent sous la forme d'articles scientifiques et développent chacun un objectif de recherche différent. Le dernier chapitre de la thèse consiste en une synthèse des résultats les plus importants et présente son apport à l'avancement des connaissances dans le domaine scientifique ainsi que les perspectives ouvertes par les résultats obtenus.

Le premier objectif de recherche était d'établir la distribution de *L. wollei* dans un tronçon de 250 km du fleuve Saint-Laurent afin d'élaborer des modèles prédictifs de sa présence et sa biomasse en utilisant les variables chimiques et physiques de l'eau. En effet, suite à la découverte de proliférations de *L. wollei* dans le lac fluvial Saint-Pierre, plus précisément dans le panache de la rivière Yamaska et Richelieu (Vis et al. 2008), il devenait impératif de déterminer la répartition de *L. wollei* dans l'ensemble du tronçon fluvial afin de connaître l'ampleur du problème. Nous avons émis l'hypothèse que les zones littorales calmes du fleuve St-Laurent situées en aval de tributaires riches en nutriments et en matières organiques supporteront des tapis de *L. wollei.* Afin de tester cette hypothèse, nous avons échantillonné en amont, à l'embouchure et en aval de 33 tributaires sur un tronçon de 250 km du fleuve Saint-Laurent. Les données recueillies permettront d'élaborer des modèles prédictifs afin d'identifier les risques de proliférations futures et d'établir de potentielles actions de gestion.

Le second objectif de recherche était d'évaluer l'hypothèse selon laquelle les facteurs physiques, tels que le courant, le vent, les vagues et le débit du fleuve Saint-Laurent, contrôlent la biomasse de *L. wollei*, autant sur une base temporelle (annuelle, saisonnière) que spatiale. En effet, suite à des épisodes de forts vents ou à la crue printanière, des accumulations de >30 cm de *L. wollei* ont été reportées sur les berges à divers endroits. Pour tester cette hypothèse, nous avons suivi les variations temporelles (2009-2011) de la biomasse de *L. wollei* ainsi que les variables physiques, chimiques et météorologiques, à 10 sites le long d'un gradient d'exposition au courant et aux vagues dans le lac Saint-Louis (fleuve Saint-Laurent). Dans le contexte des changements climatiques, le contrôle de la biomasse par les facteurs physiques pourrait avoir des répercussions importantes sur la prolifération de *L. wollei*, favorisant l'accumulation de masses de cyanobactéries nauséabondes sur les rives de l'île de Montréal.

Le troisième objectif de recherche était de déterminer l'influence de l'échelle spatiale sur le contrôle de la biomasse des producteurs primaires (PP) benthiques (*Lyngbya wollei,* macrophytes et épiphytes) par les variables environnementales et les répercussions que cela entraîne sur notre interprétation des modèles théoriques fluviaux. Les variables environnementales expliquant la biomasse des PP benthiques dépendent de l'échelle spatiale d'observation. Une approche multi-échelle pourrait permettre une compréhension plus globale du contrôle de la biomasse des communautés de PP benthiques par les facteurs environnementaux en isolant leur influence à différentes échelles (échelle du fleuve, échelle inter lacs fluviaux, échelle intra lac fluviaux). Cette étude nous permettra également de tester si les patrons observés dans les communautés biotiques des grands fleuves sont régis par les gradients environnementaux de l'amont vers l'aval (*river continuum concept*, RCC) (Vannote et al. 1980) ou s'ils dépendent plutôt des caractéristiques spécifiques d'un agrégat d'habitat au sein d'une large mosaïque formée de plusieurs de ces agrégats arrangés discrètement (Thorp et al. 2006). Ultimement, une meilleure compréhension de l'échelle d'action des facteurs environnementaux et contrôlant les biomasses de PP benthiques des patrons globaux du fonctionnement des écosystèmes fluviaux pourrait permettre d'adapter les mesures de gestion à l'échelle où elles auront un plus grand impact.

Le dernier objectif de recherche était d'évaluer le rôle écologique des tapis de *L. wollei* dans l'écosystème aquatique en tant que nourriture et refuge pour l'amphipode *Gammarus fasciatus*. Bien que cet amphipode omnivore soit très abondant (25 mg g^{-1} DM de *L. wollei*) dans les tapis de cyanobactérie, la cause de cette association reste nébuleuse. En effet, *L. wollei* est considéré comme une mauvaise source de nourriture en raison de sa gaine robuste (Camacho and Thacker 2006) et semble un habitat peu propice en raison de sa production de saxitoxines (Carmichael et al. 1997). Nous posons cependant l'hypothèse que les tapis de *L. wollei* sont un refuge efficace contre les prédateurs puisque leur architecture favoriserait le camouflage des amphipodes et que ces derniers tirent profit de la consommation du *L. wollei* des algues et de la microfaune associée qui se trouvent à l'intérieur des tapis.

2. Predicting the risk of proliferation of the benthic cyanobacterium *Lyngbya wollei* in the St. Lawrence River

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2.1 Abstract

Lyngbya wollei is a toxin-producing cyanobacterium, forming mats of filaments that proliferate in rivers, lakes, and springs in North America. We determined its distribution over a 250 km stretch of the St. Lawrence River (SLR; Quebec, Canada) to elaborate predictive models of its presence and biomass based on chemical and physical characteristics. A 2008 survey revealed *L. wollei* was generally found downstream of the inflow of small tributaries draining farmlands. As enriched waters flowed slowly through dense submerged vegetation, dissolved inorganic nitrogen (DIN) concentration dropped but dissolved organic carbon (DOC) and total dissolved phosphorus (TDP) remained high, leading to a low DIN:TDP ratio. Models identified DOC (positive effect), TP (negative effect), and DIN:TDP (negative effect) as the most important variables explaining *L. wollei* distribution. The risk of *L. wollei* occurrence in the SLR was correctly forecasted in 72%-92% of all cases with an independent data set. Proliferation of *L. wollei*, a potentially heterotrophic, diazotrophic cyanobacterium, is favoured by organic enrichment and imbalance of DIN:TDP ratio. Its dominance coincided with low macrophyte biomass, yielding a simplified, less productive ecosystem.

2.2 Introduction

The increased occurrence of harmful algal blooms (HABs) worldwide, due mainly to human activity, has important repercussions on the aquatic ecosystems (Hallegraeff 1993; Carpenter et al. 1998) through proliferations of potentially toxic species and episodic hypoxia (Heisler et al. 2008). The filamentous cyanobacterium *Lyngbya wollei* (Farlow ex Gomont) comb. nov. forms dark green to black benthic mats on the bottom of rivers and lakes. Benthic mats often remain inconspicuous until they reach sufficient biomass to trap gas bubbles and float to the surface, where winds can push them ashore (Speziale et al. 1991). In addition to the impairment of recreational water uses, *L. wollei* produces saxitoxins (Carmichael et al. 1997; Lajeunesse et al. 2012), as well as volatile organic compounds (geosmin, MIB), which are responsible for a musty taste and odor in water (Schrader and Blevins 1993; Watson et al. 2003). *Lyngbya wollei* is a poor food resource owing to its production of toxins (Lajeunesse et al. 2012) and thick sheath that reduces herbivory (Camacho and Thacker 2006). Wetlands dominated by *L. wollei* supported less biomass of invertebrates and large fish, lower fish species richness, and slower-growing juvenile perch than macrophytes-dominated wetlands (Hudon et al. 2012).

Proliferations of *L. wollei* have been reported with increasing frequency in the last 30 years in rivers, lakes, reservoirs, and springs in southeastern USA (Speziale et al. 1991; Cowell and Botts 1994; Stevenson et al. 2007). Recently, *L. wollei* has been observed also at higher latitudes in two Manitoba lakes (Macbeth 2004), in the Great Lakes (Bridgeman and Penamon 2010), and in the St. Lawrence River (Vis et al. 2008). *Lyngbya wollei* is morphologically similar to the brackish water *Lyngbya aestuarii* and the saltwater species *Lyngbya majuscula*; the latter produces dermatotoxins and deleterious proliferations in Australian coastal waters (Albert et al. 2005; Watkinson et al. 2005). In the freshwater portion of the SLR, *L. aestuarii* and *L. majuscula* (now both identified as *L. wollei*) have been identified as early as 1915 (Miller 1915), again in 1932 (Poulin et al. 1994), and in the 1970s (Alaerts-Smeesters and Magnin 1974), although proliferation has only been noted since the mid 1990s in Lake Saint-Louis (C. Hudon, personal observations) and since 2005 in Lake Saint-Pierre (Vis et al. 2008).

Given the wide geographical range of *L. wollei* and its potential for noxious environmental effects, it was deemed important to assess its environmental niche so as to predict its potential proliferation. To this end, we determined environmental variables and the distribution of *L. wollei* over a 250 km stretch of the SLR in late summer 2008 as the baseline data to elaborate a predictive model of its abundance. Sampling focussed on areas located upstream, within, and downstream of the inflow of nutrient-rich tributaries draining into the SLR, which markedly degrade water quality along the shoreline (Hudon and Carignan 2008). The predictions of the models derived from the 2008 river-wide survey were then validated using 2006-2007 data for two fluvial lakes of the SLR where *L. wollei* commonly occurred. This study aimed at assessing the areas at risk of future proliferation to identify potential management actions.

2.3 Materials and methods

2.3.1 Study area

The study area covers a 250 km stretch of the SLR (mean 2008 discharge at Cornwall: 7338 m^3 s^{-1}, Environment Canada 2012) between the cities of Cornwall (Ontario) and Trois-Rivières (Quebec), including the lower part of the Ottawa River, the largest SLR tributary (mean 2008 discharge: 2340 m^3 s^{-1}, Hydro-Québec 2012) (Fig. 2.1). Sampling was concentrated along the shoreline, in shallow waters (<2.5 m deep) potentially colonized by submerged aquatic vegetation (Hudon et al. 2000). Assemblages of vascular macrophytes in the SLR are dominated by *Vallisneria americana*, *Heteranthera dubia*, *Myriophyllum* spp., and *Elodea canadensis*. Sampling sites were systematically selected in areas located upstream, within, and downstream of the inflow of tributaries draining into the SLR.

2.3.2 Sampling

Sampling to describe the biomass of *L. wollei* and the river environmental characteristics was carried out during the period of maximum macrophyte biomass (19 August-18 September 2008; Vis et al. 2006). At each site, we measured water depth (z, m), water temperature (°C), dissolved oxygen (%), pH, conductivity (µS cm^{-1}) (YSI 600 XLM), and light extinction coefficient (k, m^{-1}) (LI-COR LI-190SA air and underwater LI-193SA

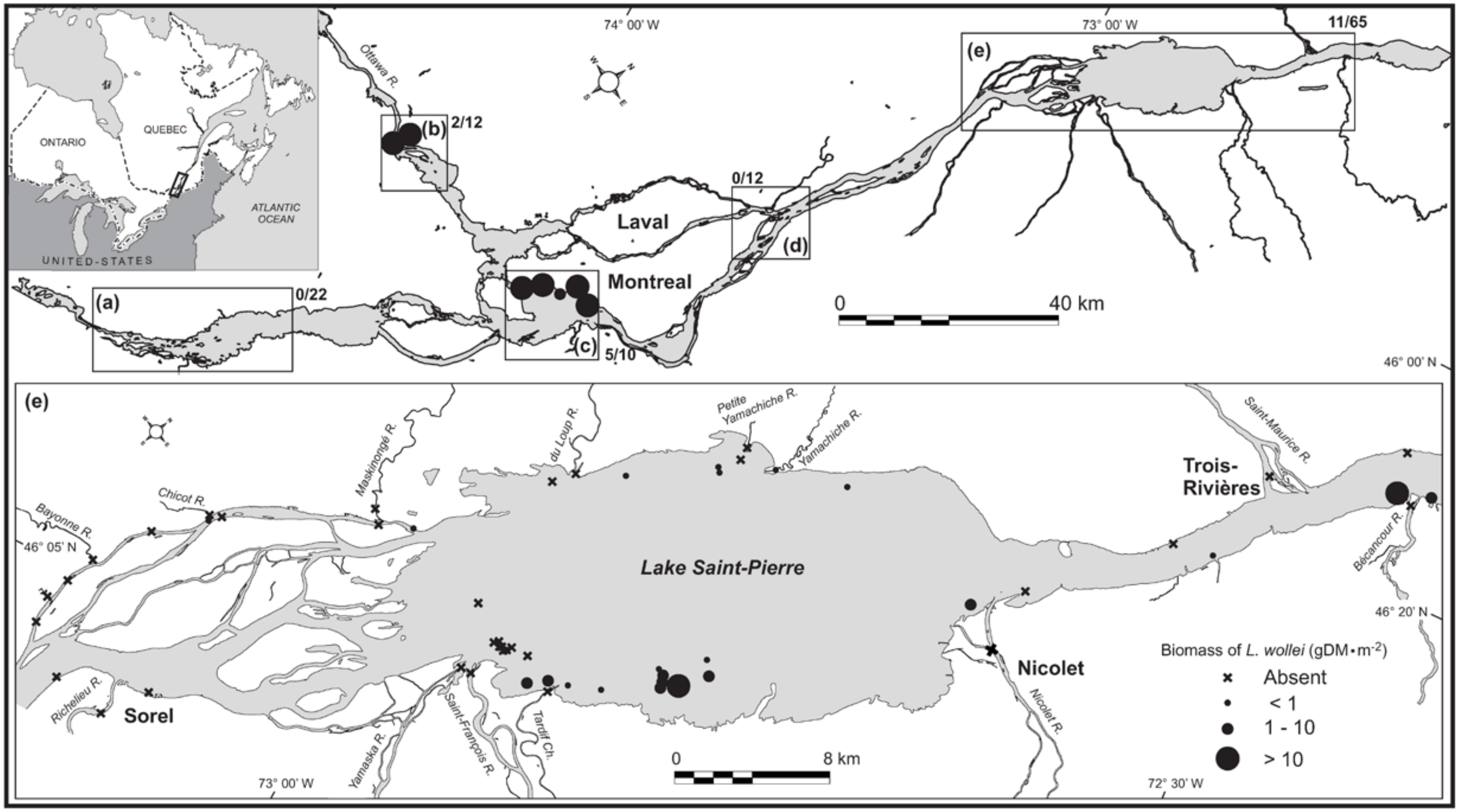

Figure 2.1 Map of the study area showing, for each major sampling regions, the location and number of sites where *Lyngbya wollei* occurred (>1 g DM·m^{-2}) over the total number of sites sampled. Regions refer to (a) Lake Saint-François (0 observation out of 22 sites); (b) the Ottawa River and Lake des Deux-Montagnes (2 observations out of 10 sites); (c) Lake Saint-Louis (5 observations out of 10 sites); (d) Montréal (0 observation out of 12 sites), and (e) Lake Saint-Pierre (11 observations out of 65 sites). Symbols represent classes of *L. wollei* biomass (g DM·m^{-2}) found at each site; for the sake of clarity, location of sites at which no *L. wollei* was found are only shown for the Lake Saint-Pierre region (lower panel).

spherical sensors). The fraction of incident light reaching the bottom (LB) was calculated using the Beer-Lambert law ($I_z/I_0 = e^{-kz}$). At each site, water samples were collected just below the surface; unfiltered subsamples were used for analyses of suspended matter (SM; American Public Health Association 1995), total phosphorus (TP), and total nitrogen (TN) (Environment Canada 2005). Filtered water (Whatman GF/C) was analyzed for total dissolved phosphorus (TDP), NO_2^--NO_3^-, NH_4^+, dissolved organic carbon (DOC), and color (Pt/Co method) (Environment Canada 2005). TP and TDP were determined by acid digestion followed by colorimetry with ammonium molybdate. TN was analyzed after persulfate digestion with a LACHAT Continuous Flow Quick-Chem 8000. NO_2^--NO_3^- was measured by reducing nitrate to nitrite in a cadmium column prior to colorimetry; NH_4^+ was analyzed by colorimetry after the addition of sodium nitroprusside and phenate sodium. DOC was oxidized to carbon dioxide by the addition of persulfate prior to infrared detection (Shimadzu TOC-5000; Environment Canada 2005). Dissolved inorganic nitrogen (DIN) was calculated as the sum of NO_2^--NO_3^- and NH_4^+ concentrations. The biomass of *L. wollei*, either on the bottom or entangled in vascular plants, was estimated semiquantitatively using a double-headed rake (35 cm wide) dragged over a length of 1 m (Yin et al. 2000). Biomass was averaged from collections made in front and on both sides of the boat. Filamentous cyanobacteria collected simultaneously with vascular macrophytes were brought back to the laboratory for cleaning, sorting, identification, and measurement of wet mass (WM) and conversion to dry mass (DM) using previously established conversion factors (Hudon et al. 2012).

2.3.3 Statistical analyses

2.3.3.1 Environmental characteristics

Physical and chemical variables of sites characterized by different biomass of *L. wollei* were compared using Kruskal-Wallis nonparametric analysis of variance (ANOVA; package stats; R Development Core Team 2011) followed by multiple comparisons of medians (package pgirmess; Giraudoux 2011) in the R statistical program (R Development Core Team 2011). Environmental variability among sites was examined by principal component analysis (PCA) using the FactoMineR package (Husson et al. 2009) in the R statistical program (R Development Core Team 2011). All variables were scaled to unit variance to allow comparison of factors with different scales (Legendre and Legendre 1998). Only the most biologically relevant of mathematically related factors were kept for analysis. Depth and light extinction coefficient (k) were excluded in favor of light fraction reaching the bottom (LB). DIN was excluded because it was highly correlated to NO_2^--NO_3^- and NH_4^+, from which it was calculated. Similarly, TDP exclusion was justified because it represents a fraction of total phosphorus, to which it was well correlated. PCA revealed six outlier sites with respect to environmental variables, five of which were located at the mouth of small, heavily enriched tributaries (Petite Yamachiche, Gray Creek, aux Pins, Chicot, Chaloupe, and Nicolet rivers); none of these sites supported vegetation and thus they were removed from subsequent analyses.

2.3.3.2 Modeling the presence-absence of *L. wollei*

Data from the 2008 large-scale survey were used to develop presence-absence models, which were then assessed and compared against previous observations (2006-2007). A minimum biomass value of 1 g $DM \cdot m^{-2}$ was set as the threshold of *L. wollei* presence. Bayesian model averaging (BMA) of logistic regression models was used to predict the occurrence of *L. wollei* from environmental variables using the BMA package (Raftery et al. 2011) in the R statistical program (R Development Core Team 2011). In BMA, the predictions are weighted averages of the individual predictions from several models, with weights proportional to the posterior probability representing the relative strength of evidence in favor of each model (Raftery 1995; Wintle et al. 2003). The BMA procedure assumes that all models under consideration partially explain the data, but only a certain number of them, chosen on the basis of the Bayes information criterion (BIC), are combined to improve the overall predictive power of the final model (Hoeting et al. 1999).

We then simplified our BMA-optimal model (BMA-Opt) using two simplification strategies: (i) obtaining an averaged parsimonious model (BMA-Pars) by tightening the BIC in BMA so that fewer models involving fewer predictors were averaged, and (ii) adopting the single best model (BIC-1) of a given size proposed by best subset selection.

2.3.3.3 Modeling the biomass of *L. wollei*

Predicting cyanobacterial biomass ($\log_{10}$ g DM·m^{-2}) was attempted from the same set of environmental variables, using a regression tree analysis (CART) (De'ath and Fabricius 2000; De'ath 2002) implemented with R statistical program (R Development Core Team 2011) and the package rpart (Therneau and Atkinson 2010). The optimal size of the regression tree, minimizing the predicted mean square error (on the logarithmic scale), was determined by cross-validation (Breiman et al. 1984).

2.3.3.4 Validation of models

To validate the model established with data from the 2008 survey, we used a data set collected using the same field and laboratory methods in 2006-2007 (Table 2.1). The three years coincided with sharply different water level conditions during sampling, which were highest in 2008 (4.94 m above sea level (asl), Department of Fisheries and Oceans Canada 2009), lowest in 2007 (3.77 m asl), and intermediate in 2006 (4.46 m asl) (Table 2.1). Validation data included *L. wollei* biomass and environmental variables for 184 sample points from sites located in fluvial lakes Saint-Pierre and Saint-Louis (Fig. 2.1). This independent set was used to assess the predictive performances of the three logistic models (BMA-Opt, BMA-Pars, and BIC-1) and of the biomass model (CART). Models were assessed for their accuracy, sensitivity, and specificity. Accuracy is the proportion of samples where presence or absence of *L. wollei* was correctly predicted. Sensitivity is the proportion of correct predictions of *L. wollei* presence. Specificity is the proportion of correct predictions of *L. wollei* absence.

2.4 Results

2.4.1 Environmental characteristics coinciding with *L. wollei* occurrence

Physical and chemical variables covered a wide range of values across the study area (Table 2.2). In 2008, *L. wollei* was observed at 37 of the 113 sites, but was >1 g DM·m^{-2} at 18 sites (Fig. 2.1). The highest biomass was observed along the north shore of Lake Saint-Louis (Fig. 2.1c) and along the south shore of Lake Saint-Pierre (Fig. 2.1e), reaching a maximum of 46 g DM·m^{-2}. *Lyngbya wollei* was generally found downstream of the inflow of tributaries, in plumes flowing along the SLR shoreline. It is noteworthy that *L. wollei* was never encountered in the water originating from Lake Ontario or within the mouth of tributaries. Sites where *L. wollei* occurred were characterized by high DOC, low concentrations of all forms of nitrogen and phosphorus, and a low DIN:TDP ratio (Table 2.2). Moreover, macrophyte biomass was significantly reduced where *L. wollei* occurred (Table 2.2).

We explored the relationships between the different physical and chemical variables with PCA. The first two principal components captured 65.3% of the total variance in the data set (Fig. 2.2 top panel). Concentrations of all nitrogen and phosphorus forms were grouped together along the first axis (44.5%) and were closely associated with suspended matter. Nutrients appeared rather poorly related with physical variables. Conductivity and the proportion of incident light reaching the bottom were negatively related with color and DOC, reflecting the contrasting optical properties of water masses originating from Lake Ontario (high conductivity, clear waters) and the tributaries (low conductivity, brown waters). In the PCA (Fig 2.2 bottom panel), sites tended to cluster by region and water masses. Lake Saint-François was associated with high water clarity and conductivity while sites in LSP and in Montreal region were more related to nutrients and DOC. Sites of Lake Saint-Louis were split in two groups based on their location in water masses originating either from Lake Ontario or Ottawa River.

Table 2.1 Summary of data sets used for model elaboration and validation. Daily water level (metres above sea level, recorded at Sorel-gauging station No. 15930, 02OJ022) was averaged over the sampling period.

Year	Use	N	Region	Sampling period	Daily level Mean (Range)
2006	Validation	96	Lake Saint-Pierre	26 July-10 Oct.	4.46 (4.13-4.96)
2007	Validation	22	Lake Saint-Louis	30 Aug.-10 Oct.	3.77 (3.56-4.04)
		66	Lake Saint-Pierre	28 Aug.-4 Oct.	
2008	Modeling	113	Cornwall to Becancour	29 July-29 Sept.	4.94 (4.24-5.76)

2.4.2 Modeling the presence-absence of *L. wollei*

Out of the 1024 possible logistic models generated by combining the 10 variables ($2^{10} = 1024$), 34 models passed our BIC-based criterion for the BMA-Opt, the five best of which accounted for a posterior probability of 0.5. By tightening the BIC-based criterion for model selection, we obtained the BMA-Pars model that included only four models and four variables (Fig. 2.3). For both BMA-Opt and BMA-Pars, DOC was the most important variable with a strong positive effect (posterior effect probability of 88% and 100%, respectively). Occurrence of *L. wollei* coincided with low TP concentration, which exerted a strong mathematical effect on the relationship, as shown by posterior effect probabilities of 86% and 84%, for BMA-Opt and BMA-Pars, respectively (Table 2.3). DIN:TDP and NO_2^--NO_3^- also exhibited low values where *L. wollei* occurred, yet exerted a lesser mathematical weight (posterior effect probabilities <50%). No other variable showed any important effect with posterior effect probability <30% (Table 2.3). Similarly, the BIC-1 logistical model comprised DOC, TP, and DIN:TDP, which exhibited significant coefficients (Table 2.3).

2.4.3 Modeling the biomass of *L. wollei*

Lyngbya wollei biomass (log-transformed) was modeled using a regression tree analysis (CART) on the physical and chemical variables (Fig. 2.4). The biomass was most efficiently split in two categories by the DIN:TDP ratio (by weight) at a threshold of 12.5. *Lyngbya wollei* was absent at 50 of the 55 sites where DIN:TDP ≥12.5. The remaining 58 sites were again divided in two subgroups by a DOC threshold of 6.8 mg $C \cdot L^{-1}$. Again, *L. wollei* was absent from 25 out of 32 sites where DOC was <6.8 mg $C \cdot L^{-1}$. In contrast, the remaining 26 sites supported the highest *L. wollei* biomass (up to 26.3 g $DM \cdot m^{-2}$). This regression tree model explained 31.2% of *L. wollei* biomass variation.

Because two of the three branches of the regression tree exhibited zero median biomass (Fig. 2.4), the CART model behaved in this instance as a presence-absence model and could thus be compared with the three logistic models in the subsequent validation.

Table 2.1 Summary (median and range) of the physical and chemical characteristics at St. Lawrence River sites where different classes of *L. wollei* biomass (g DM m^{-2}) were observed in 2006-2007-2008 (N=297). For each variable, the probability (p) of significant difference between classes of abundance is indicated; abundance groups for which means differ significantly ($p < 0.05$) are identified by different letters (Kruskal-Wallis non parametric ANOVA followed by multiple comparisons of medians). Macrophyte biomass mostly comprised *Vallisneria americana*, *Heteranthera dubia*, *Myriophyllum* spp. and *Elodea canadensis.* (†) Although the probability of the test was significant, the multiple comparisons of medians did not identify different groups of biomass.

	Groups of biomass of *Lyngbya wollei*				
Variables (units)	**Absent**	**<1 g DM m^{-2}**	**1-10 DM m^{-2}**	**>10 DM m^{-2}**	**p**
	N=151	**N=66**	**N=52**	**N=28**	
Depth (cm)	120 (18-380)	121 (33-247)	121 (30-261)	128 (58-225)	0.484
Water Temperature (°C)	20.2 (N=148) (10.0-28.8)	21.7 (N=64) (16.3-24.3)	21.4 (9.7-24.9)	21.3 (N=27) (9.4-24.1)	0.143
Dissolved Oxygen (%)	93.8 (N=104) (25.0-176.0)	96.0 (N=33) (76.4-124.0)	94.2 (N=32) (31.0-111.9)	93.7 (N=16) (29.0-117.9)	0.639
Conductivity (µS cm^{-1})	173 (23-363)	155 (69-278)	155 (70-237)	151 (64-232)	0.056
Light Extinction Coefficient (m^{-1})	2.02^a (0.35-10.48)	1.70^a (0.00-4.13)	2.04^a (0.53-3.28)	1.60^a (0.59-2.63)	0.033 †
Light on the Bottom (% of incident light)	14 (0-80)	16 (0-100)	10 (0-71)	10 (1-55)	0.404
pH	8.4 (N=104) (7.3-9.4)	8.2 (N=33) (7.4-9.1)	8.5 (N=32) (7.4-9.1)	8.6 (N=16) (7.0-9.2)	0.477

Variables (units)	**Groups of biomass of *Lyngbya wollei***				
	Absent	**<1 g DM m^{-2}**	**1-10 DM m^{-2}**	**>10 DM m^{-2}**	**p**
	N=151	**N=66**	**N=52**	**N=28**	
Color (Pt/Co)	36 (2-125)	36 (5-79)	38 (13-75)	41 (16-57)	0.561
Suspended Matter (mg L^{-1})	6^{a} (1-221)	3^{ab} (2-60)	5^{ab} (1-37)	3^{b} (1-25)	0.009
NH_4 (µg N L^{-1})	14^{a} (0-268)	10^{ab} (0-87)	6^{b} (0-69)	8^{b} (2-26)	<0.001
TN (µg N L^{-1})	563^{a} (287-1453)	476^{ab} (300-2111)	474^{ab} (270-1385)	453^{b} (269-1000)	0.003
NO_2-NO_3 (µg N L^{-1})	140^{a} (0-650)	80^{ab} (0-1010)	13^{b} (0-370)	25^{b} (0-310)	<0.001
DIN (µg N L^{-1})	163^{a} (0-898)	93^{ab} (0-1046)	25^{b} (0-388)	40^{b} (2-319)	<0.001
TDP (µg P L^{-1})	18^{a} (5-58)	19^{a} (6-40)	16^{a} (8-34)	14^{b} (7-18)	<0.001
TP (µg P L^{-1})	31^{a} (7-326)	29^{a} (10-107)	26^{ab} (14-86)	20^{b} (9-86)	0.002
DIN:TDP	10^{a} (0-46)	5^{b} (0-27)	2^{b} (0-31)	3^{b} (0-29)	<0.001
DOC (mg L^{-1})	5.9^{ab} (2.2-10.9)	5.6^{a} (2.2-12.0)	6.5^{b} (3.1-12.0)	6.8^{b} (3.2-8.6)	0.003
Macrophyte biomass (g DM m^{-2})	43.7^{a} (0-83.3)	28.6^{ab} (0.0-258.8)	19.8^{ab} (0.7-191-7)	14.6^{b} (0-93.1)	0.003

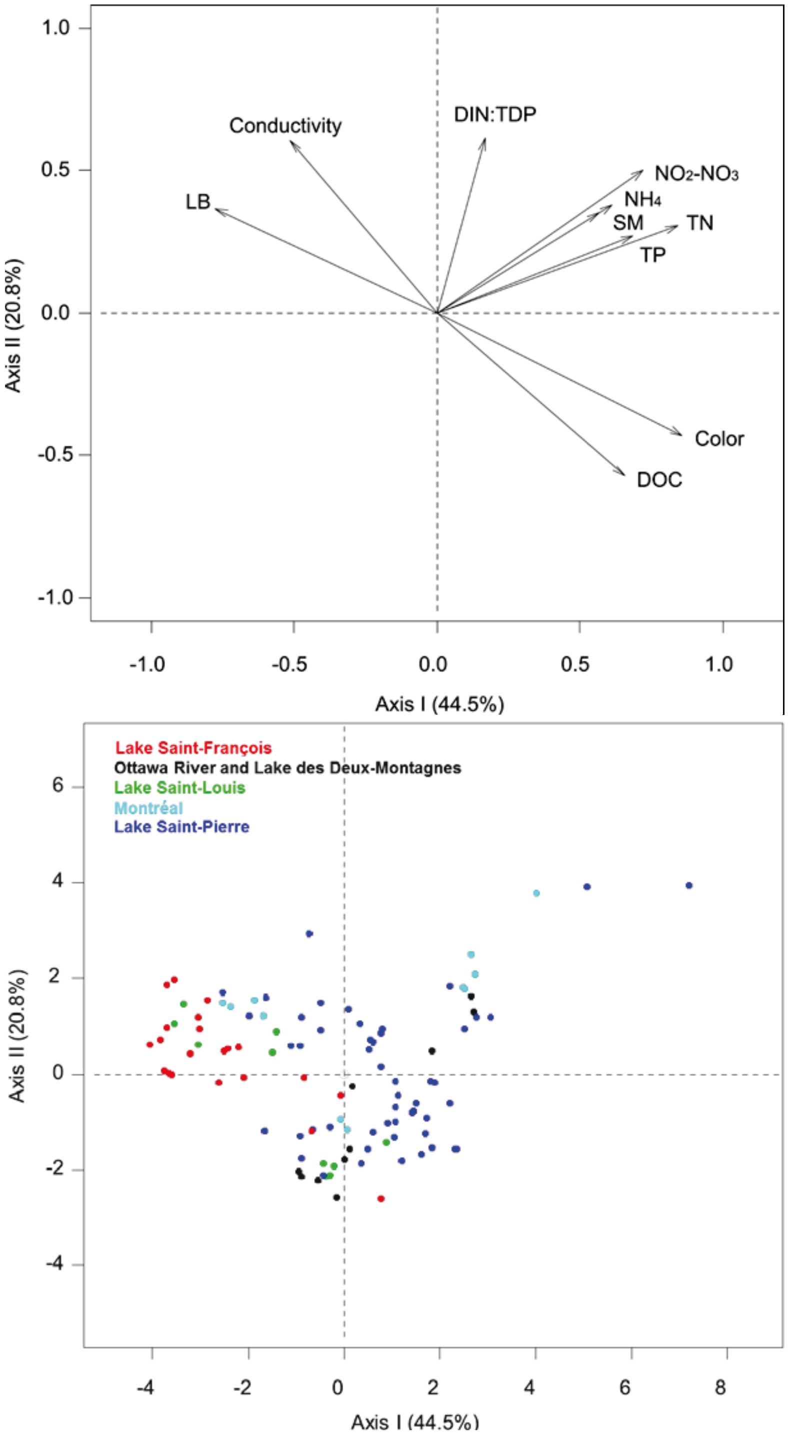

Figure 2.1 Biplot of the principal component analysis (PCA) based on correlations. Arrows represent environmental variables (top panel) and dots represent sites (bottom panel). The axes represent 65% of the data variance. SM refers to the concentration of suspended particulate matter and LB to the fraction of incident light reaching the bottom.

2.4.4 Validation of models' performance

Validation of the predictions of the BMA-Opt, BMA-Pars, BIC-1 logistic models, and CART model against the independent data sets collected in 2006 and 2007 showed that the predictions of all four models were about 70% accurate (Table 2.4). Presence was best predicted (53% sensitivity) by the CART model, whereas absence was predicted with the highest level of specificity by BMA-Opt (92%).

2.5 Discussion

2.5.1 Abiotic conditions

Our study identified simple, coherent models predicting the occurrence of *L. wollei* with a high level of reliability, from a subset of 2-4 environmental variables. DOC was constantly identified as a highly significant variable by the three logistic and CART models. In our data set, DOC was negatively related (see PCA) with percent light on the bottom and positively with color, indicating its relation with the light regime. The capacity of *L. wollei* to grow at low light intensities (<50 µmol m^{-2} s^{-1}), potentially limiting for other aquatic vegetation, has been observed in both field (Speziale et al. 1991; Bridgeman and Penamon 2010) and laboratory studies (Yin et al. 1997; Pinowska et al. 2007).

The positive relationship of DOC with the occurrence of *L. wollei* may further indicate the reliance of this cyanobacterium on organic C inputs from the watershed, which is further supported by its common occurrence in the plume of tributaries. High DOC concentration and low ambient light from high colour and turbidity are conducive to heterotrophic growth using various organic substrates, an increasingly reported ability for harmful algae (Burkholder et al. 2008). Such alternate energetic pathway was previously suggested for *L. wollei*, since filaments buried in organic sediments remained alive despite complete darkness (Doyle and Smart 1998). The occurrence of *L. wollei* in the SLR at <5% of incident light on the bottom (this study), as well as in complete darkness under winter ice cover (D. Lévesque and C. Hudon, unpublished observations), support this hypothesis.

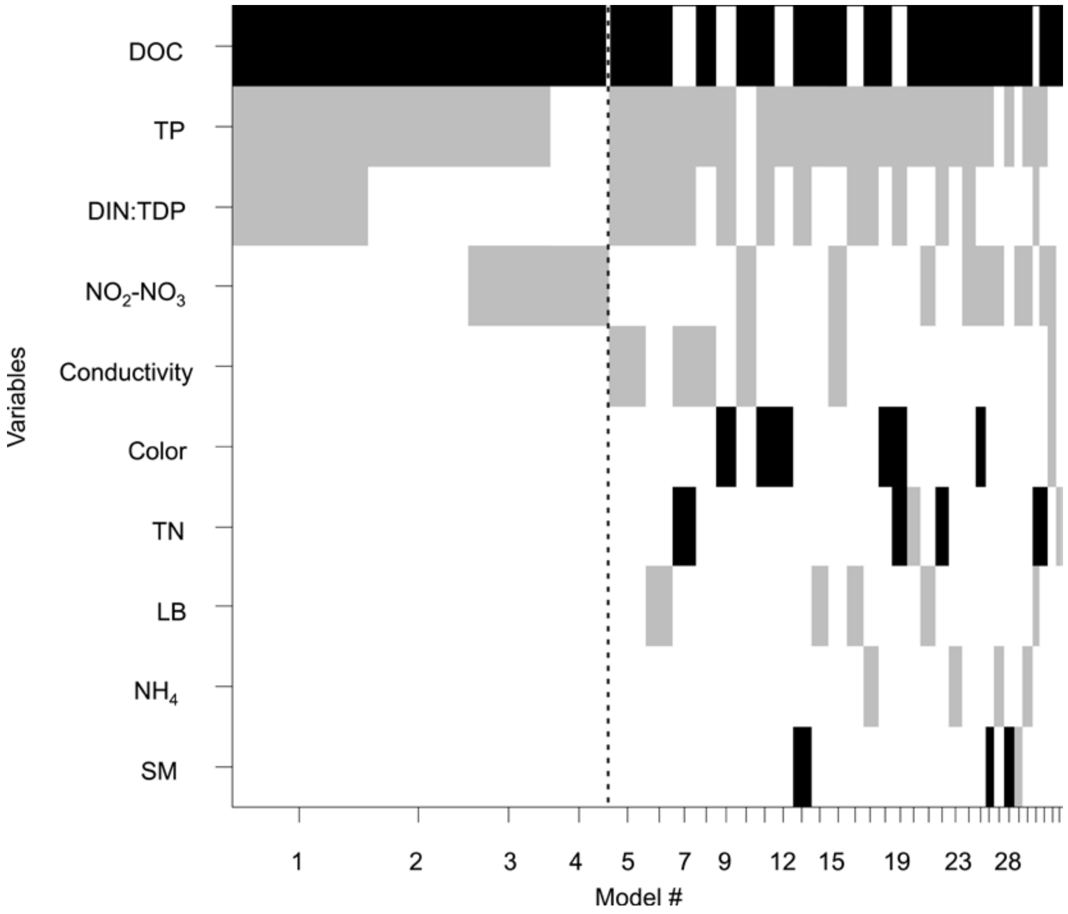

Figure 2.2 Logistic models summarized by Bayesian model averaging (BMA) to form the BMA-optimal model. The vertical dashed line delimits the BMA-parsimonious model (left) from the BMA-optimal model (whole). Logistic models chosen using a Bayes information criterion (BIC)-based criterion are ordered from left to right by decreasing posterior model probability. Bar width is proportional to posterior model probability. Variables are ordered from top to bottom by posterior effect probability. Black bars indicate a positive effect of the covariates on the occurrence of *Lyngbya wollei* and grey bars indicate a negative effect. The five best models account for half of the posterior probability. SM refers to the concentration of suspended particulate matter and LB to the fraction of incident light reaching the bottom.

Table 2.2 Variables identified by the optimal BMA (BMA-Opt), parsimonious BMA (BMA-Pars) and best subset (BIC-1) logistic regression as predictors of *L. wollei* occurrence in the SLR. For each model, the coefficient (Coeff), standard deviation (SD) and significance are given for each variable. For BMA, posterior effect probability (PEP) of each variable refers to the sum of probabilities observed in the different models. Probability (p) is given for the BIC-1 Logistic Regression.

	BMA-Opt			BMA-Pars			BIC-1 Logistic Regression		
	Coeff	SD	PEP (%)	Coeff	SD	PEP (%)	Coeff	SD	p
Intercept	-1.505	1.891	100	-2.209	1.329	100	-1.107	1.087	0.309
DOC	0.463	0.239	88	0.534	0.157	100	0.525	0.153	0.001
TP	-0.078	0.048	86	-0.072	0.046	84	-0.094	0.036	0.009
DIN:TDP	-0.059	0.082	43	-0.043	0.068	36	-0.121	0.060	0.043
NO_2^--NO_3^-	-0.002	0.004	32	-0.003	0.004	37			
Conductivity	-0.001	0.004	15						
Color	0.004	0.018	12						
% Light on Bottom	-0.004	0.017	10						
TN	0.0003	0.002	11						
Suspended Matter	0.002	0.025	6						
NH_4^+	-0.001	0.008	6						

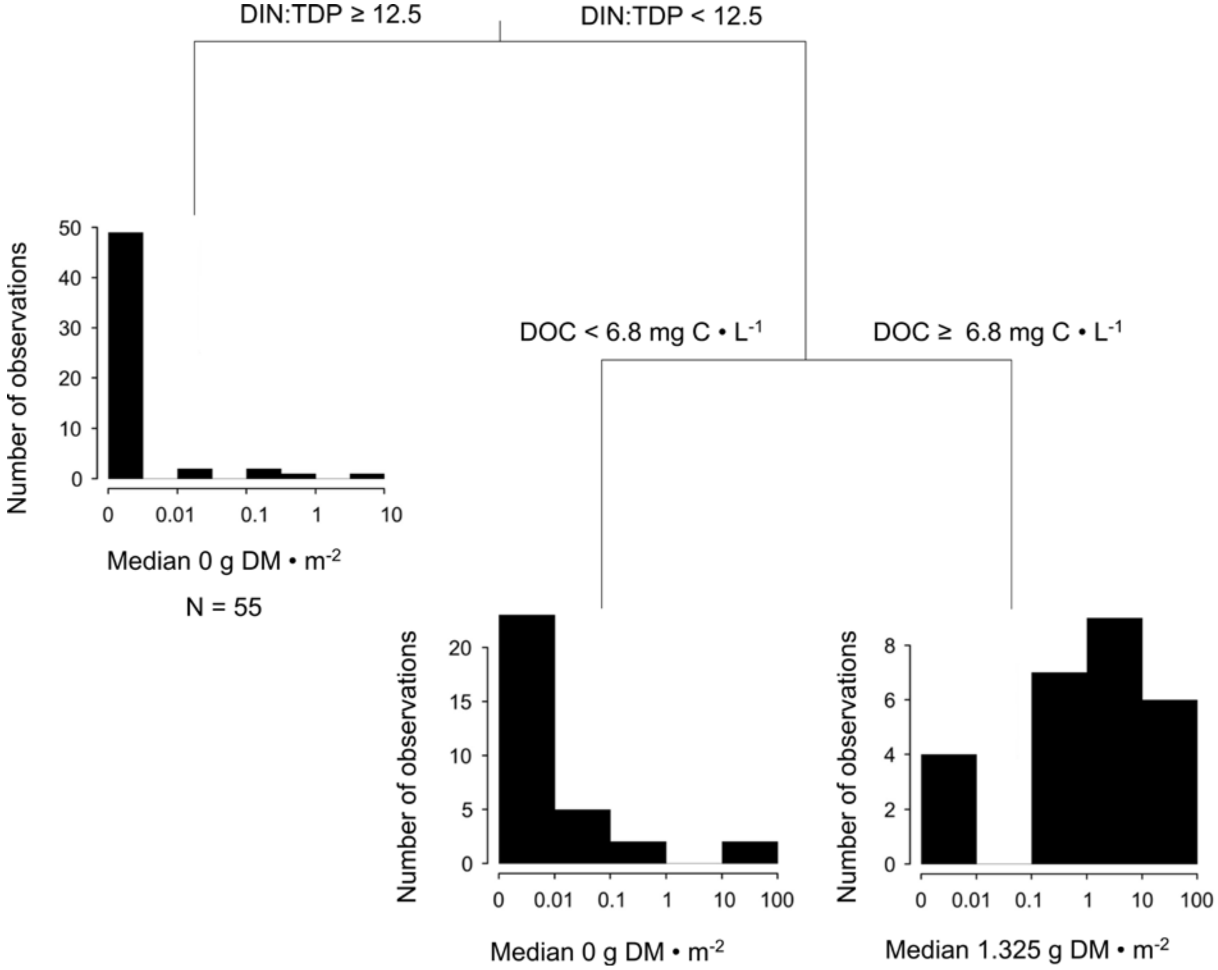

Figure 2.3 Results of the regression tree (CART) model predicting the biomass of *Lyngbya wollei*, using critical thresholds for the DIN:TDP ratio and DOC concentration defining three groups of biomass (histograms). The three-leaf tree is formed by two splits; the first based on DIN:TDP ratio (≥12.5 and <12.5) and then, for low DIN:TDP ratio, a second split based on DOC (<6.8 mg $C{\cdot}L^{-1}$ and ≥6.8 mg $C{\cdot}L^{-1}$). Most observations of *L. wollei* occurrence are found in the right branch of the regression tree. For each branch, median biomass (g $DM{\cdot}m^{-2}$), number of observations (N), and a histogram of the observed distribution of *L. wollei* biomass ($\log_{10}$) are shown.

Table 2.4 Performance of the optimal BMA (BMA-Opt), parsimonious BMA (BMA-Pars), best subset (BIC-1) logistic regression and CART (regression tree) established on a river-scale survey in 2008 on a validation data set comprising 184 samples collected in SLR in 2006-2007.

Measurement	Definition	BMA-Opt	BMA-Pars	BIC-1 Logistic Regression	CART
Accuracy	Prediction of presence and absence	0.72	0.71	0.68	0.67
Sensitivity	Success in presence prediction	0.32	0.32	0.39	0.53
Specificity	Success in absence prediction	0.92	0.91	0.84	0.72

High DOC originating from terrestrial runoff has also been shown to coincide with proliferation of *L. majuscula* in marine coastal waters of Queensland (Albert et al. 2005). The inflow of iron and other chelating substances associated to organic matter from soil inputs were shown to stimulate growth of *L. majuscula* (Watkinson et al. 2005), Although concentration of total iron is high in the SLR (C. Hudon, unpublished data) as in many freshwater bodies, bioavailable iron may nevertheless be low due to binding by organic matter (Hassler et al. 2009). Both *L. majuscula* and *L. wollei* form benthic mats, in which only the superficial layer of filaments is exposed to light and oxygen, with steep geochemical gradients of pH, iron, and nutrients leading to dark, anoxic conditions next to the sediment (Paerl and Yannarell 2010). These conditions may allow for both photochemical iron reduction at mat surface (Fujii et al. 2010) and (or) internal recycling of elements within it (Stevenson et al. 2007). Production of superoxides by *L. majuscula* under light conditions was shown to increase iron availability to the organism (Rose et al. 2005).

Our models also identified low concentrations of nitrogen, phosphorus, and their ratio in the overlaying waters as predictors of the occurrence of *L. wollei*. This finding may seem counterintuitive because of the well-accepted paradigm associating the proliferation of harmful algae with eutrophication (Heisler et al. 2008), yet highlights the complexity of the processes taking place within cyanobacterial mats. For example, phosphorus concentrations within mats could be considerably higher than in the overlaying water owing to internal nutrient recycling, remineralisation, release from anoxic sediment, or groundwater transport (Stevenson et al. 2007). Cyanobacterial mats of *L. aestuarii* were shown to simultaneously carry out oxygenic photosynthesis and atmospheric nitrogen fixation (Paerl et al. 1991). In addition, both nitrogen fixation and denitrification processes were documented for *L. wollei* in Lake Okeechobee (Phlips et al. 1991) and confirmed in the SLR (L. Tall and R. Maranger, Université de Montréal, Montréal, Quebec, personal communication 2011).

Lyngbya wollei proliferation in Florida springs have been linked with increased nitrate concentration (from <0.1 mg $N \cdot L^{-1}$ up to 7.5 mg $N \cdot L^{-1}$) over the last 60 years, although weakly supported by empirical evidence over a gradient of differently enriched springs (Stevenson et al. 2007). Our models clearly indicate a negative correlation between phosphorus (TP and TDP) and nitrogen (DIN) concentrations and *L. wollei*. Measurable amounts of *L. wollei* were found at low median TP (<26 μg P·L^{-1}), TDP (<16 μg P·L^{-1}), and DIN (<40 μg N·L^{-1}) in overlaying waters, which could be considerably lower compare to values in sediments below benthic mat (median TDP of 452 μg P·L^{-1} and median DIN of 1080 μg N·L^{-1} at 2 sites) (Hudon, unpublished data)

Strong nitrogen limitation is indicated by the low DIN: TDP ratios (≤12.5 by weight or ≤5.4 molar) in water overlaying *L. wollei* in the SLR, well below the Redfield ratio (16 molar). Similarly low DIN:TDP ratios were shown to sustain the diazotrophic epiphytic cyanobacterium *Gloeotrichia pisum* in the SLR (Hudon et al. 2009) as well as planktonic cyanobacteria in a Boreal Shield lake (Schindler et al. 2008). Alternative metabolic pathways such as heterotrophic growth under low light intensity, diazotrophy under low N:P ratio, and establishment of favorable conditions within the filamentous mat are all strategies invoked to explain the proliferation of harmful algae, when environmental conditions are not suitable for competitors (Stal 1995; Burkholder et al. 2008; Severin and Stal 2008).

2.5.2 Interaction with other primary producers and grazers

Besides physical and chemical variables, the proliferation of *L. wollei* could be affected by biotic interactions. In this study, we observed a significant twofold reduction in vascular macrophyte biomass in the presence of *L. wollei*. The switch in dominance between *L. wollei* and other primary producers was previously reported in several other studies in Florida springs (Stevenson et al. 2007), Lake Erie (Bridgeman and Penamon 2010), Manitoba lakes (Macbeth 2004), and SLR (Vis et al. 2008). *Lyngbya wollei* appears to proliferate only when native primary producers are curtailed by unfavorable light or nutrient conditions or physically removed (Evans et al. 2007). In contrast, experimental re-establishment of native emergent or floating-leaved plants appeared to minimize the proliferation of *L. wollei* in Guntersville Reservoir, Tennessee (Doyle and Smart 1998). Cyanophages have also been invoked as a cause of disappearance of bloom for *L. majuscula* in Moreton Bay, Australia (Hewson et al. 2001). Reduced grazing was also invoked as a possible mechanism explaining excessive cyanobacterial mat growth. This hypothesis was prompted by the negative correlation between filamentous mat cover in Florida springs and reduced grazer abundance by hypoxia in inflowing spring water (Heffernan et al. 2010). In the SLR, grazer biomass was indeed severely reduced in areas where *L. wollei* dominated (Tourville Poirier et al. 2010), but continuous monitoring of daily O_2 concentrations in overlaying waters demonstrated that sites dominated by *L. wollei* were never hypoxic (C. Hudon, unpublished data). In the SLR, low grazer abundance appeared related to reduced food and habitat availability, through the decline in epiphyte and macrophyte biomass.

2.5.3 Management implications

The overall risk of *L. wollei* occurrence was successfully forecasted in the SLR as different models correctly predicted its absence in 72%-92% of cases. Areas most at risk of proliferation were always located downstream of nutrient and DOC-rich tributaries, and were characterized by low to moderate flow (slow but steady current), low ambient light intensity, and low DIN:TDP ratios. The high performance of models elaborated in the present study is particularly impressive in view of the high variability of water quality in a large river (Hudon and Carignan 2008). Despite vastly different hydrological conditions between years (mean summer water levels in 2006, 2007, and 2008 equalled 4.46, 3.77, and 4.94 m asl, respectively), models established with 2008 observations fitted very well with 2006 and 2007 data.

Furthermore, the critical concentrations of DOC, TP, and DIN:TDP ratio identified by our models point out the operational water quality thresholds that should guide the interventions of water managers. Mean instantaneous nutrient concentrations measured in 2008 at the mouth of tributaries (N=33) compared with fluvial sites devoid of *L. wollei* (N=53) revealed slightly higher tributary concentrations of DOC (6.0±2.2 mg $C \cdot L^{-1}$ and 5.3±2.5 mg $C \cdot L^{-1}$, respectively) but substantially elevated TP (58±52 µg $P \cdot L^{-1}$ and 31±15 µg $P \cdot L^{-1}$, respectively) and NO_2-NO_3 (439±787 and 192±114 µg $N \cdot L^{-1}$, respectively), yielding equally high DIN:TDP ratio (16±14 and 13±6, respectively). These results suggest that a sharp reduction of TP concentration from tributaries will likely reduce cyanobacterial proliferation in the SLR by increasing DIN:TDP ratio. However, application of the current target TP concentration of 30 µg $P \cdot L^{-1}$ for running waters (MDDEP 2012) may not yield the desired reduction in *L. wollei* biomass since its highest biomass was recorded at 20 µg $P \cdot L^{-1}$. For SLR fluvial lakes, the 10 µg $P \cdot L^{-1}$ guideline for lakes and standing water bodies would therefore be more appropriate. However, beyond a specific TP concentration target, our observations argue in favor of an overall reduction of particulate and dissolved nutrient runoff from the watershed, through the implementation of best management practices for agriculture.

In comparison with presence-absence models, biomass of *L. wollei* was more difficult to predict, as only 31% of the variation among sites was explained (CART model). This relatively low success is not surprising in view of the notoriously high variability of benthic vegetation biomass (Morin and Cattaneo 1992), in conjunction with the fact that biomass accumulation and reduction are determined by largely different processes. Accumulation results from a slow, but steady growth under stable environmental conditions. In contrast, biomass reduction is a rapid, dramatic process, following mechanical mat disruption, either when gas bubbles trapped within the filament matrix lift the mat away from the bottom or during episodes of high discharge, strong winds, or waves (C. Hudon and A. Cattaneo, unpublished data).

The maximum *L. wollei* biomass observed in the SLR (27-46 g DM·m^{-2}) was in the same order of magnitude as that observed in western Lake Erie in 2008 (75 g DM·m^{-2} ±45; Bridgeman and Penamon 2010), but an order of magnitude lower than values reported for the southeastern USA (6.6 kg·m^{-2} WM, Speziale et al. 1991; 1 kg DM·m^{-2}, Cowell and Botts 1994). In both SLR and Lake Erie (Bridgeman and Penamon 2010), strong winds and winter conditions result in periodic disruption of mats that are thrown ashore, thus resetting the system, whereas physical conditions in southeastern US reservoirs and springs are likely less variable, allowing important biomass accumulation. Suitably warm conditions for optimal growth of *L. wollei* (about 26°C, Yin et al. 1997) occur only in July and August in the SLR (Hudon et al. 2010), although measured and projected temperature rise under global warming scenarios will likely increase the risk of *L. wollei* proliferation (O'Neil et al. 2012).

The proliferation of *L. wollei* under a wide range of geographically disconnected locations throughout North America further suggests that this species could be a very efficient invader of environmentally unbalanced environments. *Lyngbya wollei* often coincides with large scale ecosystem degradation (Hudon et al. 2012). Impacts on humans are both direct, since floating mats near the surface disrupt recreational activities, and indirect, through the increased costs of drinking water production and beach maintenance to clear massive, unsightly and malodorous accumulations.

Our study shows that harmful algal proliferations are not necessarily linked with elevated nutrients but, at the same time, it highlights the major influence of agricultural tributary inputs on large river ecosystems. This apparent paradox stems from the complex interactions of biotic and abiotic components taking place when tributaries bring in DOC and nutrients through a densely vegetated littoral zone. The slow passage of enriched waters through a macrophyte bed results in intense bacterial processing of carbon and nutrients. DOC partly increases through macrophytes release (Lapierre and Frenette 2009), DIN is severely depleted through denitrification and assimilation (Saunders and Kalff 2001), while phosphorus is only slightly reduced because it is in part recycled (Rooney and Kalff 2003). This organic enrichment and nutrient imbalance favor potentially heterotrophic, diazotrophic cyanobacteria, ultimately leading to a simplified, less productive ecosystem, with repercussions across the entire food chain (Hudon et al. 2012). The outcome of eutrophication and oligotrophication thus appears as a complex process, where perturbations and their effects are spatially or temporally disconnected (Carpenter and Kinne 2003; Duarte et al. 2009). Our findings stress the need to manage the excessive input of runoff from agricultural watersheds, whose harmful effects on the aquatic ecosystems materialize several kilometres downstream of the pollution source.

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3. Wave exposure and current regulate biomass accumulation of the benthic cyanobacterium *Lyngbya wollei* in a large fluvial lake

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3.1 Abstract

Harmful proliferations of the mat-forming cyanobacterium *Lyngbya wollei* are increasingly reported in North American lakes, springs, and reservoirs. We examined the hypothesis that hydrodynamic conditions, namely currents generated by waves and river flow, control spatial and temporal variations of *L. wollei* biomass in a large river system. For this, we measured *L. wollei* biomass together with meteorological, physical, and chemical variables over three years (2009-2011) at 10 sites along a gradient of exposure to current and wind in Lake Saint-Louis, a large (148 km^2) fluvial lake of St. Lawrence River. Where water chemistry was conducive to *L. wollei* growth, wave exposure and current velocity controlled spatial and temporal biomass variations. Biomass increased from May to November and persisted during winter. Interannual variations were primarily controlled by river flow (water level) with high spring discharge dislodging mats from the previous growing season. Under climate change scenarios, anticipated drops in water level and rising storm intensity may lead to an increase in the areas colonized by *L. wollei*, together with more frequent episodes of mat disruption, water use impairment, and beach fouling.

3.2 Introduction

In the past three decades, proliferations of the benthic filamentous cyanobacterium *Lyngbya wollei* (Farlow ex Gomont) Speziale and Dyck have been increasingly reported in lakes, springs, and rivers of North America (Speziale and Dyck 1992, Stevenson et al. 2007). *Lyngbya wollei* forms mats lying on bottom sediments. These mats may be brought to the surface by trapped gas bubbles and washed ashore by wind, consequently degrading shoreline aesthetic and recreational value (Speziale and Dyck 1992). *Lyngbya wollei* releases volatile organic compounds (i.e. geosmin and 2-Methylisoborneol), which give drinking water a muddy taste and odour (Watson 2003). In addition, *L. wollei* produces saxitoxins (Carmichael et al. 1997, Lajeunesse et al. 2012) and cylindrospermopsin (Seifert et al. 2007) that have potential implications for human and ecosystem health. The trophic implications of *L. wollei* in ecosystems are still unclear. On one hand the cyanobacteria is considered a poor food source for the small amphipods *Hyalella azteca* because of its robust sheath and toxin production (Camacho and Thacker 2006), but on the other hand mats of *L. wollei* seems to constitute an efficient refuge and an important part of the diet of the more robust amphipod *Gammarus fasciatus* (Levesque et al. 2015 in press). Additionally, three out of four gastropods that were offered a choice between *L. wollei* and filamentous chlorophytes were either indifferent or attracted to the cyanobacterium (Visconti et al. 2014). In a wetland-dominated fluvial lake, the zone covered by *L. wollei* supported less invertebrate biomass and had poorer perch recruitment than the zone dominated by macrophytes (Tourville Poirier et al. 2010, Hudon et al. 2012). Proliferations of *L. wollei* are common in the southern United States (Speziale and Dyck 1992, Carmichael et al. 1997) but are also observed in Manitoba (Macbeth 2004), in the Great Lakes (Bridgeman and Penamon 2010), and in the St. Lawrence River (Vis et al. 2008).

The chemical variables controlling *L. wollei* biomass are still debated. In the laboratory, *L. wollei* growth was stimulated by nitrate (NO_3^-) and phosphate (PO_4^-) addition with growth saturation threshold values ranging from 28 to 1500 µg nitrogen N L^{-1} and from 110 to 821 µg phosphorus P L^{-1}, respectively (Cowell and Dawes 2004, Stevenson et al. 2007). This wide range in growth saturation threshold resulted in the absence of relationship between *L. wollei* proliferation and N and P concentration in overlaying waters over a gradient of differently enriched springs in Florida (Stevenson et al. 2007). *Lyngbya majuscula*, a marine taxon morphologically similar to *L. wollei*, was limited by both N and P in coastal Florida (Paerl et al. 2008) and its growth was stimulated, both in laboratory and *in situ*, by organically chelated iron and phosphorus from soil runoff (Albert et al. 2005, Ahern et al. 2007). Over a 250-km stretch of the St. Lawrence River, the presence of *L. wollei* was associated with high concentration of dissolved organic carbon (DOC) and with low ratios of dissolved inorganic nitrogen: total dissolved phosphorus (DIN:TDP) in water originating from nutrient rich tributaries flowing through dense vegetation beds (Levesque et al. 2012). Although DOC concentrations and DIN:TDP ratio were excellent predictors of *L. wollei* occurrence (67-72% of success in predicting presence/absence) these chemical variables only explained 31% of biomass variations (Levesque et al. 2012).

The fluvial lakes of the St. Lawrence River represent large (up to 12 km wide), shallow (average depth <5 m) areas over which wind can exert a strong effect along main fetch direction (Lepage et al. 2000). Near-bed water movements are thus influenced by the combined effects of wind-induced waves and unidirectional river flow, which is discharge-related. Hydrodynamic forces generated by river flow or wave action scour the bottom and affect benthic vegetation (Keddy 1982, Duarte and Kalff 1986, Stevenson et al. 1996). Cyanobacterial mats that are not attached to the bottom should be particularly affected by these forces, as observed for *Oscillatoria* mats off coastal Guam (Thacker and Paul 2001). Mat disruption by wave action generated by prolonged strong wind (>24 km h^{-1} over at least 1 d) led to large accumulations (>30 cm deep) of *L. wollei* on the shores of southwestern Lake Erie (Bridgeman and Penamon 2010). Storm events commonly result in similar accumulations on the shores of Lake Saint-Louis, a fluvial lake of the St. Lawrence River (personal observation).

These observations led us to hypothesize that, under suitable chemical conditions for *L. wollei* presence, mat disruption by wind and currents would modulate biomass accumulation. Spatially, we predicted that sites exposed to a large fetch, high winds and strong current would support less biomass than sheltered sites. Temporally, we expected that drops in *L. wollei* biomass would coincide with periods of high wind and/or high discharge rather than a seasonal decline in its condition. To test these hypotheses, we conducted a 3-year survey of *L. wollei* biomass and condition (as nutrient tissue content) at several sites located along a gradient of exposure to wind, waves and current in an embayment of the St. Lawrence River where previous surveys consistently showed the occurrence of this cyanobacterium (Levesque et al. 2012). These results should increase our understanding and management of future benthic cyanobacteria proliferations with regard to climate change because the anticipated rise in frequency of intense storm events would likely increase cyanobacterial mat dislodgement leading to water use impairment and beach fouling.

3.3 Material and Methods

3.3.1 Study area

The study was carried out in Lake Saint-Louis, a shallow (mean depth ~3 m), slow flowing (<40 cm s^{-1} outside the central navigational channel) enlargement (148 km^2) of the St. Lawrence River at its confluence with the Ottawa River, located upstream of the city of Montreal, Quebec (Fig. 3.1). Mean annual (2000-2011) St. Lawrence River discharge at the Lake Saint-Louis outlet equals 8100±1100 m^3 s^{-1}. Seasonal variations of flow regime in Lake Saint-Louis are determined primarily by the discharge of the Ottawa River (mean±SD annual 2000-2011 discharge = 1900±960 m^3 s^{-1}) since the outflow of Lake Ontario is regulated by the Moses-Saunders dam located upstream of Lake Saint-Louis (Carpentier 2003). In Lake Saint-Louis, waters from the main stem of the St. Lawrence River and from the Ottawa River flow side by side and form two water masses with distinct chemical properties. The so called "green" transparent waters that prevail along the south shore and the central part of Lake Saint-Louis originate from Lake Ontario and are characterized by high conductivity (range 226-350 µS cm^{-1}), low DOC (~2.6 mg L^{-1}) and low TP (~14 µg L^{-1}) concentrations. In contrast, the brown waters originating from the Ottawa River flowing along Lake Saint-Louis north shore exhibit low conductivity (~81 µS cm^{-1}), high DOC (~6.1 mg L^{-1}), and high TP (~34 µg L^{-1}) concentrations (Hudon and Carignan 2008). Assemblages of submerged vascular macrophytes in the St. Lawrence River are dominated by *Vallisneria americana*, *Heteranthera dubia*, *Potamogeton* spp., and *Chara* spp. (Vis et al. 2003).

In preliminary surveys we conducted in 2007 (unpublished data) and 2008 (Levesque et al. 2012), high biomass (≥60 g DM m^{-2}) of *L. wollei* was exclusively found along the north shore of Lake Saint-Louis, in waters originating from the Ottawa River (Fig. 3.1). This observation prompted the present small scale survey, focusing on 10 sites positioned along a transect perpendicular to the St. Lawrence River flow. Eight sites were located in the water mass originating from the Ottawa River (A to H) where *L. wollei* was commonly observed. Two additional sites (J-K) were located in waters originating from Lake Ontario, in which *L. wollei* was not found (Fig. 3.1). The transect extended from a small protected embayment towards the center of Lake Saint-Louis, yielding a gradient of increasing current velocity and wave action. The presence of the heavily urbanized St. James stream, draining storm sewers with high total phosphorus (median 40 µg P L^{-1}), medium NH_4^+ (median 20 µg N L^{-1}), and high Ca_2^+ (median 113 mg L^{-1}) (Ville de Montreal 2013; data for 2009-2011), modified the water chemistry at sites closest to shore. All sites but one were positioned on the same isobath (2 m) resulting in identical depth variations with water level fluctuations. The site closest to shore (site A) was about 1.3 m shallower than the other sites. Over the three years of the study, Lake Saint-Louis water level varied by 1.5 m, owing to seasonal variations in river discharge.

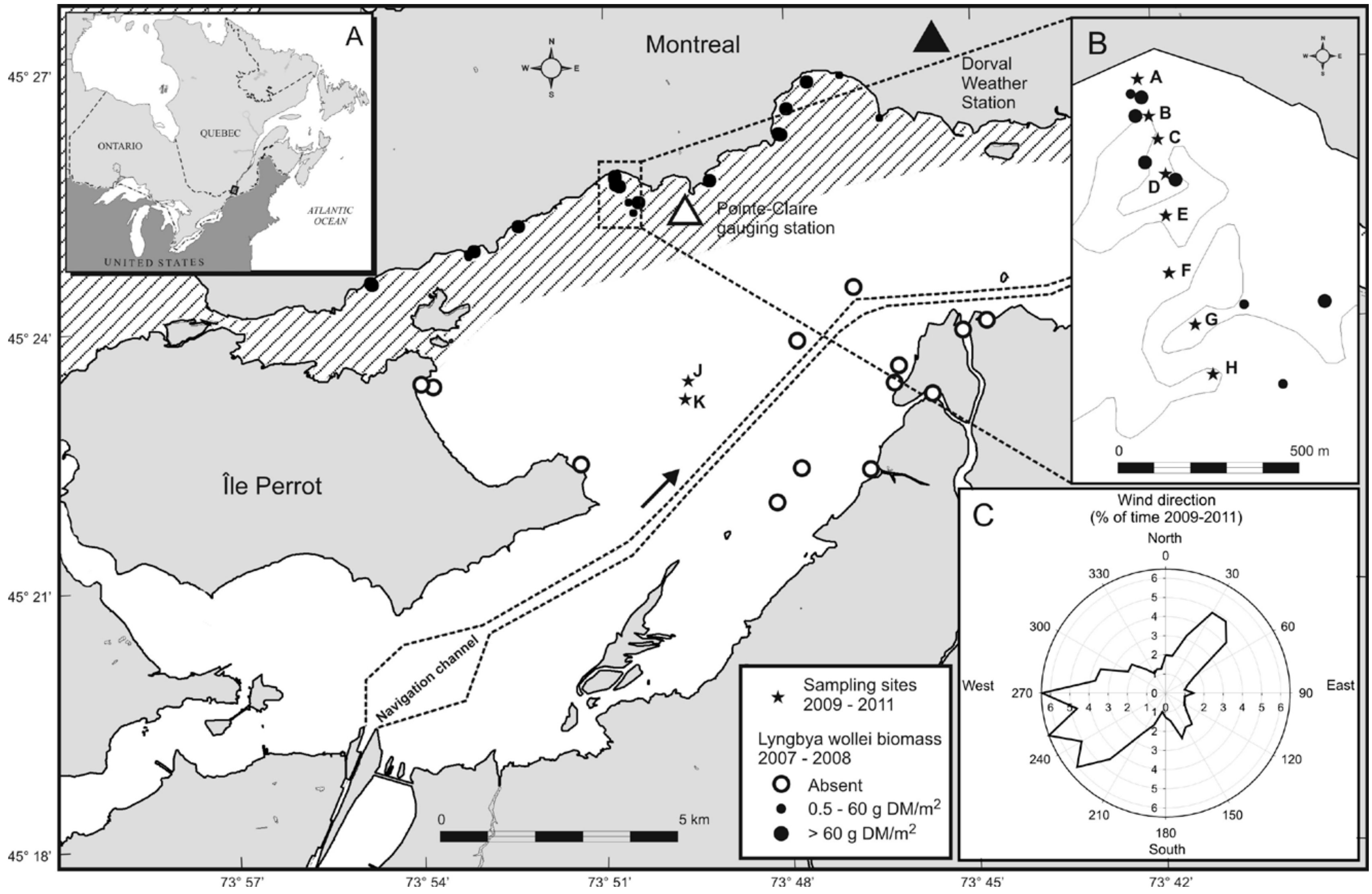
A
ONTARIO
QUEBEC
ATLANTIC OCEAN
UNITED STATES
Montreal
Dorval Weather Station
Pointe-Claire gauging station
Île Perrot
J
K
Navigation channel
0
5 km
Sampling sites 2009 - 2011
Lyngbya wollei biomass 2007 - 2008
Absent
0.5 - 60 g DM/m²
> 60 g DM/m²
B
A
B
C
D
E
F
G
H
0
500 m
C
Wind direction (% of time 2009-2011)
North
South
East
West
0
30
60
90
120
150
180
210
240
270
300
330
45° 27'
45° 24'
45° 21'
45° 18'
73° 57'
73° 54'
73° 51'
73° 48'
73° 45'
73° 42'

Figure 3.1 Map of Lake Saint-Louis (QC, Canada, inset A) showing location of the 10 sampling sites (stars) and areas under the influence of water masses originating from the Ottawa River (hatched) and Lake Ontario (white); the arrow next to the navigation channel (dashed lines) indicates flow direction. Distribution of *L. wollei* biomass sampled in 2007-2008 surveys is shown, contrasting sites with abundant (large full circles), scarce (small full circles) and no biomass (open circles). Location of individual sites (A-H, stars) with respect to the 2 m isobath is shown (Inset B). Frequency distribution of hourly wind directions (% of hourly data) at Dorval weather station (full triangle) and location of Pointe-Claire gauging station (open triangle) are indicated.

3.3.2 Sampling

Physical and chemical characteristics of water and biomass of *L. wollei* were sampled on 21 occasions between April 2009 and October 2011, including once in March 2010 under the ice. At each site, we measured water depth (z, m), water temperature (°C), dissolved oxygen (%), pH, conductivity (µS cm^{-1}) (YSI 600 XLM, YSI, Yellow Springs, Ohio), and light extinction coefficient (k, m^{-1}) (LI-COR LI-190SA air and underwater LI-193SA spherical sensors, LI-COR Biosciences, Lincoln, Nebraska). Light penetration (LP) corresponding to the fraction of incident light (I_0) reaching the bottom (I_z) was calculated using the Beer-Lambert law ($LP=I_z/I_0=e^{-kz}$). Current velocity and direction were determined from the movement of a Lagrangian drifter deployed at each site. The drifter, based on the model described by Johnson et al. (2003), consisted of a near-surface, vertical, neutrally buoyant, sealed plastic tube (50 cm high by 12 cm diameter) attached to a weighted bucket to integrate water movements in the upper 1.5 m of the water column while reducing the effect of wind-induced movement of the surface layer. The drifter was equipped with a GPS receiver and a data logger, which recorded drifter position every 30 s, allowing calculation of current velocity and direction. Current velocity estimates by such drifters were closely correlated with those obtained with an acoustic Doppler velocimeter (R=0.95; Schmidt et al. 2003). Current measurements at shallow site A were not possible under low level conditions, thus preventing inclusion of that site in statistical analyses. Current measurements were used to contrast hydrological characteristics among sites in the spatial analysis.

At each site, water samples were collected 10 cm above the bottom using an electric pump. Unfiltered subsamples were used for analyses of suspended matter (SM), total phosphorus (TP), and total nitrogen (TN) and filtered water (Whatman GF/C, General Electric Healthcare Life Sciences, Piscataway, New Jersey) was analyzed for total dissolved phosphorus (TDP), NO_2^--NO_3^-, NH_4^+, total dissolved nitrogen (TDN), dissolved organic carbon (DOC), dissolved Ca, and color (Pt/Co method) using standard methods (Environment Canada 2011). Dissolved inorganic nitrogen (DIN) was calculated as the sum of NO_2^--NO_3^- and NH_4^+ concentrations.

Sediment particle size was measured once at each site in the study period (31 August 2009). Divers collected five replicates shallow sediment cores (8 cm diameter) at each site. The top 7 cm of sediment were kept for analysis, freeze-dried, and sieved to separate the different size fractions (Environment Canada 2011).

The biomass of *L. wollei*, either on the bottom or entangled in vascular plants, was estimated using a 35 cm wide double-headed rake (Annexe 1A) dragged over a distance of about 1 m on the bottom. Before pulling off the rake from the bottom, it was flipped 180° to minimize vegetation loss (Yin et al. 2000). Biomass was averaged from 3-5 rake samples collected around the boat. Biomass estimates from rake samples were calibrated by building a regression model with paired values representing simultaneous complete removal of plants in contiguous quadrats by divers at the same sites, as suggested by Kenow et al. (2007). This calibration was done at 25 St. Lawrence River sites (mean of 2-11 pairs per site) over a wide range of depth (0.75-3 m) and biomass (0-1600 g WM m^{-2}). The measurements obtained with the two methods were closely correlated ($R^2adj=0.95$, $p<0.001$) and the slope was not significantly different from 1 (Annexe 1B). Filamentous cyanobacteria and vascular macrophytes that were collected simultaneously were brought back to the laboratory, where they were rinsed with running water to eliminate sediments, debris and invertebrates. Fresh vegetation was sorted, identified, weighed and converted to dry mass (DM) using previously established conversion factors (Hudon unpublished data).

3.3.3 Condition of *L. wollei*

Carbon, nitrogen and phosphorus tissue content (as % of dry mass) was analysed in subsamples collected at sites B and C to characterize temporal variations of *L. wollei* condition. Carbon and N tissue content were determined using an elemental analyser (vario MACRO cube CHNS, Elementar, Germany; Environment Canada 2011). Phosphorus content was measured after autoclaving ~5 mg of powdered sample suspended in 50 mL of water with 0.5 g of potassium persulfate for 45 min at 120°C (Stainton et al. 1977).

Lyngbya wollei condition was characterized by quantifying the fraction of filaments filled with cells relative to empty sheath (Agrawal and Gupta 2009). This analysis was done on samples preserved in Lugol's solution, which were collected at each sampling date at site

C. For each sample, subsamples of filaments were mounted on five slides and observed at 100X magnification. On each slide, three fields containing 5-10 filaments were photographed to assess percent fullness of filaments (N=15 values per date) using an image analysis software (Image-Pro Plus, Media Cybernetics, Rockville, Maryland).

3.3.4 Climatic and hydrological variables

Daily water levels at Pointe-Claire (gauging station 02OA039, Fig. 3.1; Environment Canada 2012a), St. Lawrence River discharge measured at LaSalle (outlet of Lake Saint-Louis), and climatic information (hourly wind velocity and direction) monitored at Montreal International Airport (Fig. 3.1; Environment Canada 2012b) were used for the analyses. Prevailing wind in Lake Saint-Louis are from the west to southwest (225° to 270°; Fig. 3.1). The transect was located in a south-facing embayment with the longest fetch (13.2 km) along the two southern quadrants (90° to 270°). Winds from those quadrants were used to assess cumulative hours of high winds (>24 km h^{-1}) for each month without ice cover. Wind speed >24 km h^{-1} was selected because it corresponds to exceedance wind level (15% of highest wind speed recorded in the study area), which is an efficient predictor of wave exposure effects on aquatic vegetation (Keddy 1982). Data on the duration of ice cover in Lake Saint-Louis were obtained from Environment Canada (2012c).

Relative exposure index (REI)

We used a measure of wave exposure (REI) developed by Keddy (1982) based on wind velocity and direction and fetch to quantify within-lake gradients of wave energy. REI was calculated for each site using the formula:

$$\mathrm{REI} = \sum_{i=1}^{16} (\mathrm{V P}_i \mathrm{F}_i) \qquad \text{(Eq. 1)}$$

where i is the i^{th} compass bearing, V the mean daily wind velocity in m/s, P_i the wind direction frequency (%), and F_i the effective fetch (m). Effective fetch, defined as the distance between a site and the nearest wave-blocking obstacle along a given compass bearing (US Army Corps of Engineers 1984), was calculated at each site using the equation:

$$\mathrm{F}i = \sum_{n=1}^{5} \mathrm{Y_n} \cos \mathrm{X}_i \qquad \text{(Eq. 2)}$$

where Y_n is the length of the radiating lines (direct fetch), and X_i the angle of departure from the i^{th} compass heading (i = 16) (i.e. 1 to 16 from headings in 22.5° increments).

Wave-induced current

Because REI provides information on wave exposure but does not account for the effect of water depth on near-bed currents, we used equations developed by the US Army Corps of Engineers (1984). Velocities induced by wave action at the sediment surface were calculated for the range of conditions present in this study. Velocity at sediment surface (U_d) was calculated as:

$$U_d = \frac{\pi H}{\sinh\left(\frac{2\pi d}{L}\right) T} \qquad \text{(Eq. 3)}$$

where d (m) is water depth, H (m) is wave height, T (s) is wave period, and L (m) is wave length. Wave height, period, and length were calculated based on wind direction, water depth, and fetch data (see Annexe 2 for detailed calculations).

3.3.5 Statistical analyses

The analysis of spatial biomass variation along the transect considered only data from June-Oct 2009-2011 This period corresponded to the growing season with water temperature >15°C and excluded ice cover, spring discharge, and spring and fall strong wind events. Sites J and K, situated in water originating from Lake Ontario, were excluded because water chemistry of this water mass was not conducive to *L. wollei* growth, as previously observed (Fig. 3.1; Levesque et al. 2012).

Physical and chemical variables were compared among sites using Kruskal-Wallis nonparametric analysis of variance followed by multiple comparisons of medians. Overall environmental variability among sites from June to September 2009-2011 was examined by principal component analysis (PCA). All variables were scaled to unit variance to allow comparison of factors with different scales (Legendre and Legendre 2012). The data set for the spatial biomass variation analysis included 14 dates and 108 data points after exclusion of 4 points, which were identified as outliers in a preliminary PCA analysis of environmental data.

Lyngbya wollei biomass ($\log_{10}$ transformed) variation was explained by multiple regressions decomposing the effects of environmental (E), spatial (S), and temporal (T) components (Borcard et al. 1992). The environmental model (E) was built by applying the forward selection procedure of Blanchet et al. (2008) to the environmental variables (REI, current velocity, water chemistry and physical characteristics). The spatial model (S) was based on the distance of each site from the north shore, given that the transect was perpendicular to the shore. The temporal model (T) consisted of a matrix of 13 dummy variables representing the 14 sampling dates.

Temporal variation of *L. wollei* biomass was investigated at sites where biomass was maximal (B and C) to examine the impact of the hydrological regime and wind events. We divided the year into 4 seasons based on climatic and hydrologic events. Spring (April to May) corresponded to the period where ice cover disappeared and discharge was maximal. Summer (June to September) represented the growing period when water temperature was >15°C. Fall extended from October until ice cover formation in December. Winter corresponded to months of ice cover (January to March). A multiple regression analysis of *L. wollei* biomass (Log_{10} transformed mean biomass recorded at sites B and C) was performed on a dataset of 21 dates. We excluded June 7th 2011 because of its excessive leverage (estimated by Cook's distance) as determined in a preliminary multiple regression analysis (Maindonald and Braun 2010). Variables were selected using a double stop criterion procedure (Blanchet et al. 2008) on hydrological (mean water level and mean discharge), meteorological (maximum daily wind speed) and environmental (water temperature, conductivity, light penetration, DIN, TP, DOC, dissolved Ca) variables. Hydrological and meteorological variables were averaged over 15 d prior to sampling because this was the time interval between two consecutive samples and constituted a relevant time scale for their effects on mat biomass. We selected discharge over current velocity in this analysis as a more pertinent hydrological variable susceptible to control biomass of *L. wollei*. All statistical analyses were performed in R statistical software (version 3.0.1; R Project for Statistical Computing, Vienna, Austria)

3.4 Results

3.4.1 Environmental conditions and *L. wollei* biomass

Sites located at increasing distance from the shore were exposed to steadily increasing current velocity and relative wave exposure (REI), which were highly correlated with each other (R=0.97, N=10) and to distance from shore (R=0.85 and 0.90, N=10, respectively; Fig. 3.2A). Sites located close to shore (A-H) exhibited smaller sediment particle size (mean diameter ≤0.08 mm) and a more heterogeneous sediment composition (≤60% sand) than sites located near the navigation channel (J-K), where sand prevailed (>90%; Fig. 3.2B).

All sites had a similar range of pH (median 8.13, range 7.7-9.2), DO (median 9.0, range 7.2-12.3 mg L^{-1}), and temperature (median 20; range 15-26°C). Sites influenced by the water mass from Lake Ontario (sites J and K) exhibited lower DOC and higher conductivity, Ca concentration, and DIN:TDP ratio than sites located in water originating from the Ottawa River (A to H) (Table 3.1, Fig. 3.2C, D). All chemical variables were similar among sites B-H with the exception of NH_4^+ concentration, which were higher at sites D-H (Table 3.1). In contrast, site A, located 50 m from shore and just downstream of the heavily urbanized St. James stream, had higher values of conductivity (~240 µS cm^{-1}) and calcium (~24 mg L^{-1}) than other sites influenced by the Ottawa River. This site was also ~130 cm shallower than sites B-H resulting in higher light penetration (10% of incident light) than in the other sites (1%) influenced by the brown water of the Ottawa River (Fig. 3.2E).

Lyngbya wollei was exclusively found at sites located in water originating from the Ottawa River (A to H) and was never observed in areas under the influence of Lake Ontario waters (J and K). Substantial *L. wollei* biomass was only recorded at sites B and C, located 100-250 m from shore (Table 3.1). Small *L. wollei* biomass (<25 g DM m^{-2}) was constantly found at nearshore site A, while it was completely or virtually absent (<10 g DM m^{-2}) at sites D to H. Conversely, submerged vascular plants were abundant at sites J-K and at site A, but completely absent at sites B-H (Table 3.1).

Table 3.1 Chemical and physical water characteristics (median followed by range in parentheses) measured at 10 sites in Lake Saint-Louis, during June-September 2009-2011

		Site A		Sites B and C		Sites D-H		Sites J and K
		N=12		N=27		N=69		N=25
Light penetration (%)	10	(4-40)^{a}	1	(0-13)^{b}	1	(0-9)^{b}	18	(0-53)^{a}
Conductivity (μS cm^{-1})	242	(78-510)^{a}	167	(84-520)^{ab}	123	(71-261)^{b}	274	(176-307)^{a}
TP (μg P L^{-1})	25	(16-66)^{ab}	40	(12-88)^{a}	24	(13-101)^{ab}	20	(12-51)^{b}
TDP (μg P L^{-1})	12	(8-20)^{a}	12	(7-17)^{a}	13	(7-19)^{a}	8	(6-12)^{b}
TN (μg N L^{-1})	501	(310-810)^{a}	525	(320-790)^{a}	494	(343-625)^{a}	490	(372-740)^{a}
DIN (μg N L^{-1})	174	(15-400)^{a}	137	(67-538)^{a}	181	(89-326)^{a}	180	(128-309)^{a}
NH_4^+ (μg N L^{-1})	14	(4-60)^{a}	13	(7-50)^{a}	20	(6-40)^{b}	11	(2-21)^{a}
DIN:TDP (mass ratio)	13	(2-38)^{a}	12	(6-54)^{a}	14	(9-36)^{a}	22	(13-52)^{b}
DOC (mg C L^{-1})	5.2	(3.9-6.3)^{a}	4.8	(3.3-6.2)^{a}	5.0	(2.9-6.5)^{a}	2.6	(2.2-2.9)^{b}
Dissolved Ca (mg Ca L^{-1})	24	(10-46)^{ab}	18	(10-46)^{bc}	14	(8-32)^{c}	32	(29-33)^{a}
Current velocity (cm s^{-1})	8.8	(4.4-11.7) N=4	11.6	(2.4-25.3)^{a} N=21	22.9	(2.5-48.8)^{b} N=61	50.8	(26.6-77.9)^{c} N=22
L. wollei biomass (g DM m^{-2})	1.58	(0.2-24.9)$_{b}$	38.9	(0.0-108.7)^{ab}	0.0	(0.0-7.4)^{c}	0.0	(0.0-0.0)^{d}

Vascular plant biomass (g DM m^{-2})	1.6	$(0.0\text{-}4.3)^{a}$	0.0	$(0.0\text{-}0.0)^{b}$	0.0	$(0.0\text{-}0.3)^{b}$	2.7	$(0.0\text{-}34.2)^{a}$

Note. - Sites were grouped keeping into account water mass, presence/absence of *L. wollei* and shallow depth of site A. For each variable, different letters identify sites for which medians differ significantly ($p<0.05$; Kruskal-Wallis nonparametric analysis of variance followed by multiple comparisons of medians). Current velocities at site A were excluded from the comparisons because of the small N.

The relationships between the different physical and chemical variables of sites located in water originating from the Ottawa River (A-H) were explored with PCA. The first two principal components explained 55.9% of the total variance in the data set (Fig. 3.3). Concentrations of phosphorus (TP and TDP), depth, DOC, and color were grouped together on one side of the first axis (30.0%), in opposition with pH, dissolved Ca, conductivity, and light penetration. All forms of nitrogen were grouped along the second axis (25.9%).

3.4.2 Spatial variations of *L. wollei* biomass

For sites located in water originating from the Ottawa River (B-H), the combined influence of environmental conditions, spatial and temporal structure explained 75.8% (R_2adj.) of *L. wollei* biomass variation over the 2009-2011 growth seasons (June-Sept.) (Fig. 3.4). Environmental and spatial variables together explained the largest proportion of total variance of *L. wollei* biomass through the strong negative effect of REI and current velocity, which markedly increased with distance away from the shoreline. Since REI, current and distance were strongly correlated to each other, most of the explanatory power resided in their intersection (59.3%) rather than in spatial (3.6%) or environmental (3.2%) component on their own (Fig. 3.4). Ammonium concentration was negatively correlated with *L. wollei* biomass but contributed only marginally (2%) to the overall model. Temporal variables (i.e. sampling date between June and September) only explained 3.5% of total variance in *L. wollei* biomass (Figure 3.4).

To explain the paucity of *L. wollei* at the most sheltered, nearshore site A relative to sites B-C, we investigated the potential near-bed current velocities that would be generated under different combinations of water depth, fetch, and wind speed observed during our study (Table 3.2). Effective fetch at sites B-C ranged between 0.2-7.9 km, equalling 4.6 km under dominant southwesterly winds. Potentially scouring near-bed current speed close to 25 km h^{-1} were reached under rare occasions (0.5% of time; wind speed ≥43 km h^{-1}) at sites B-C but were encountered more often (2% of time; wind speed ≥35 km h^{-1}) at shallow site A.

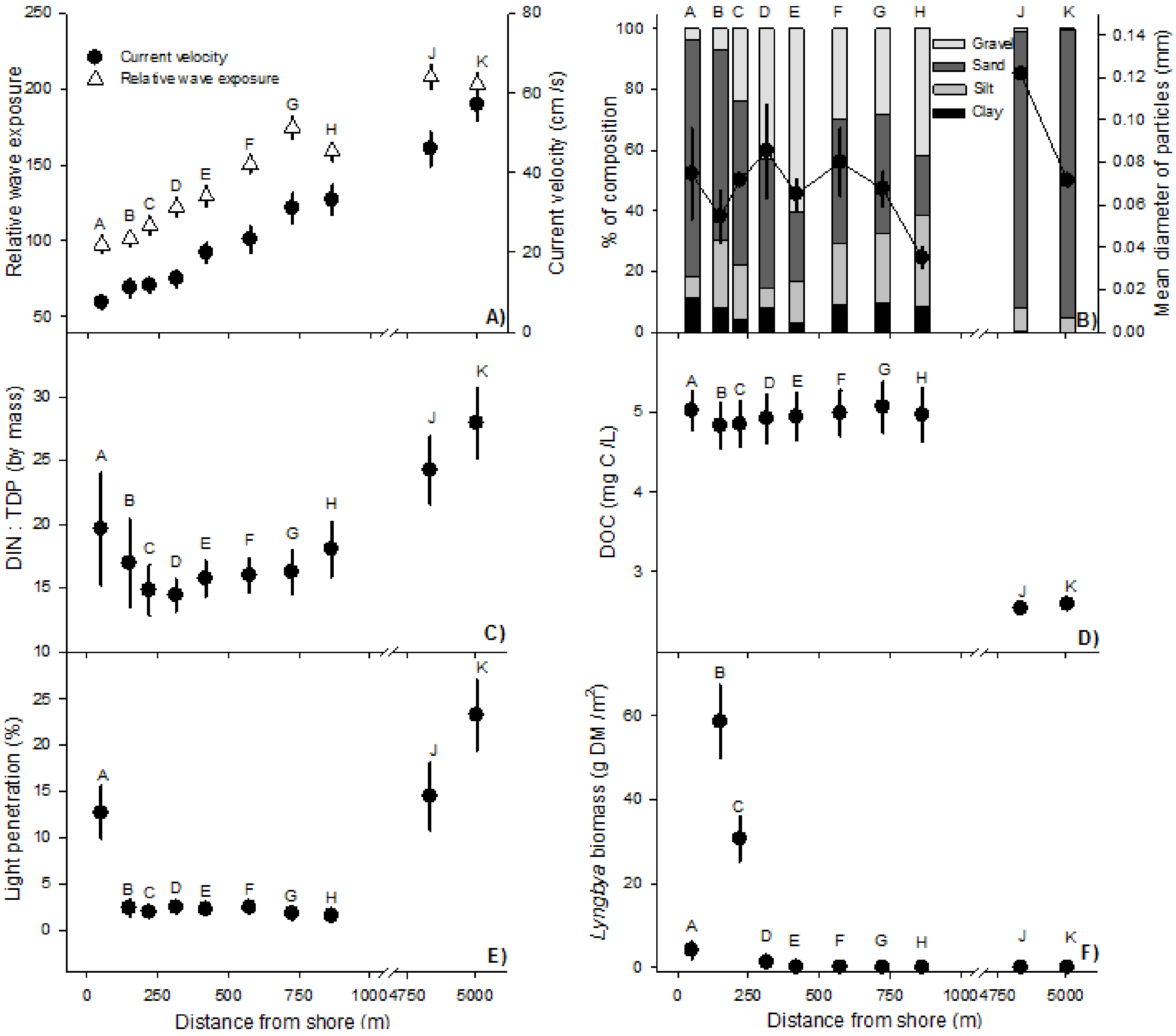

Figure 3.2 Spatial changes in physical, chemical and biological variables recorded along a transect of 10 sites in Lake Saint-Louis, Quebec. Values are mean ±1 SE calculated for samples taken between June and September 2009-2011. A) Current velocity (N=4-13; full circles), and relative wave exposure (REI; N=15; open circles), B) Sediments mean size (full circles ±1 SE, N=5, right Y-axis) and proportion of gravel (>1000 µm; pale gray), sand (63-1000 µm; dark gray), silt (3.9-63 µm; medium gray) and clay including colloids (<3.9 µm; black, stacked bars, N=5, left Y-axis). C) Mass ratio between dissolved inorganic nitrogen and total dissolved phosphorus water concentration (N=11-14 per site), D) Dissolved organic carbon (N=11-14 per site), E) Light penetration (N=11-14 per site), and F) *Lyngbya wollei* biomass (N=11-14 per site).

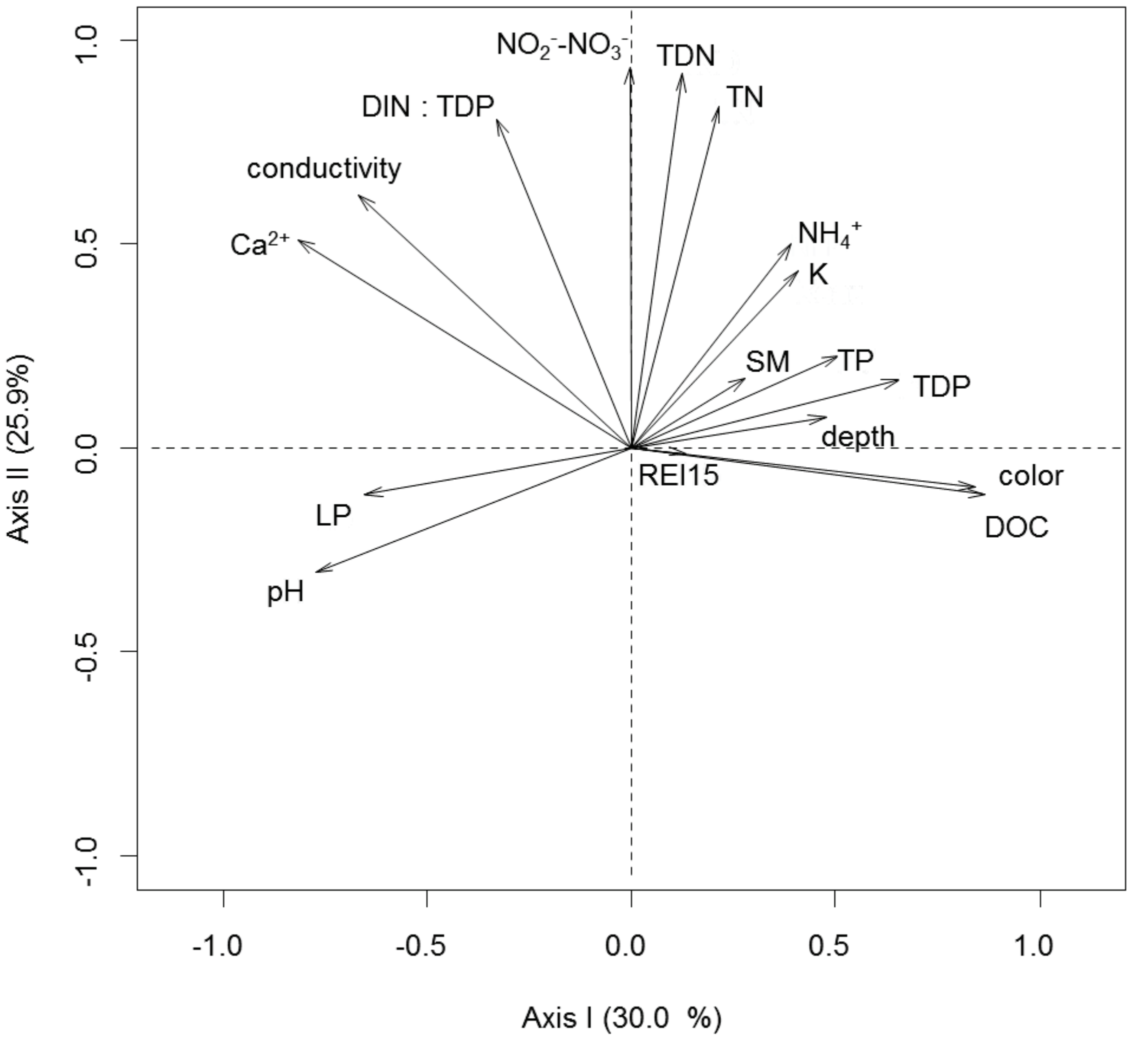

Figure 3.3 Biplot of the principal component analysis (PCA) based on correlations among physical and chemical variables measured from June-September of 2009-2011 (N=108) at sites (A-H). Arrows represent environmental variables (SM=concentration of suspended particulate matter, LP=light penetration, K=water extinction coefficient, Ca=dissolved Ca, and REI15=relative wave exposure in the previous 15 d). The axes represent 57% of the data variance.

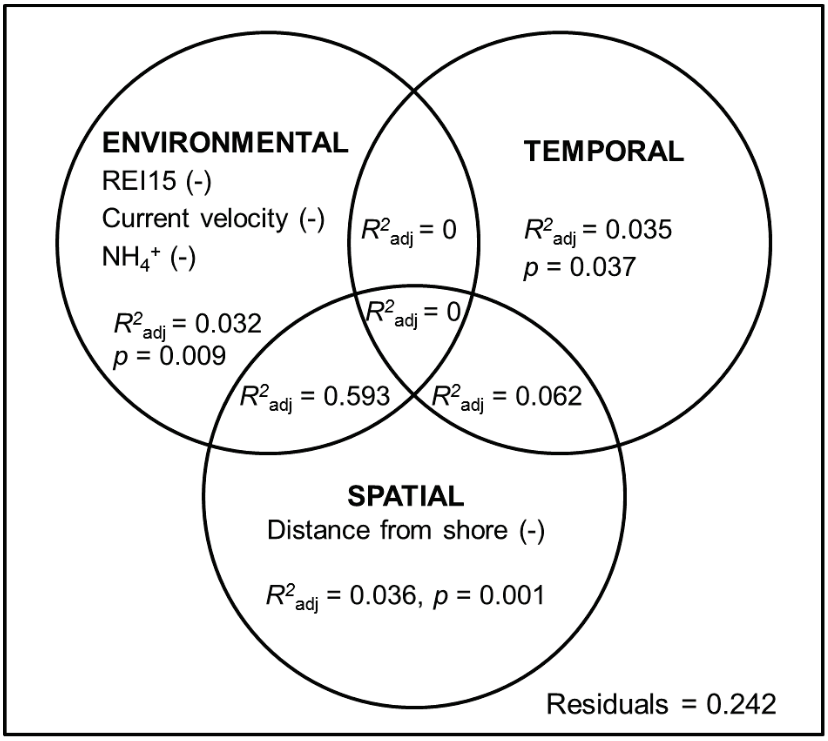

Figure 3.4 Fractions of *Lyngbya wollei* biomass (Log_{10} transformed) variation explained (R^2adj, N=82) by different groups of predictor variables: ENVIRONMENTAL (df=3); SPATIAL (df=1) and TEMPORAL (df=12). REI15 refers to relative wave exposure in the previous 15 d. Probabilities (p) are represented for all testable fractions

Table 3.2 Theoretical near-bed current velocity (cm s^{-1}) generated by waves for different combinations of effective fetch, water depth and increasing wind speeds.

		Near-bed current velocity (cm s^{-1}) generate by wind speed of:			
		13 km h^{-1}	24 km h^{-1}	35 km h^{-1}	43 km h^{-1}
Effective fetch (km)	Water depth (m)	(median)	(15% highest)	(2% highest)	(0.5% highest)
1	0.5	5.5	16.5	**24.8**	**29.7**
	1.5	0.2 (A)	4.6 (A)	13.2 (A)	19.9 (A)
	3.0	<0.1	0.4 (B-K)	2.9 (B-K)	6.5 (B-K)
	4.0	<0.1	0.1	0.9	2.8
5	0.5	10.3	21.3	**28.6**	**33**
	1.5	2.1 (A)	14.2 (A)	**26** (A)	**33.2** (A)
	3.0	0.1 (B-K)	4.8 (B-K)	15.2 (B-K)	23.4 (B-K)
	4.0	<0.1	2.1	9.6	16.9
10	0.5	11.6	22.3	**29.4**	**33.6**
	1.5	3.5 (A)	17.9 (A)	**29.7** (A)	**36.5** (A)
	3.0	0.3 (B-K)	8.4 (B-K)	21.4 (B-K)	**30.3** (B-K)
	4.0	0.1	4.5	15.7	24.7
15	0.5	12.2	22.7	**29.7**	**33.9**
	1.5	4.3	19.7	**31.3**	**37.9**
	3.0	0.5 (J-K)	10.6 (J-K)	24.6 (J-K)	**33.6** (J-K)
	4.0	0.1	6.3	19.3	**28.8**

Note. - Values of near-bed current velocities occurring at each site (A-K) are indicated; values above the critical threshold of 25 cm s^{-1} (Hoyer et al. 2004, Luce et al. 2010) are shown in bold. Grey areas represent fetch under dominant winds for site B-C (see Fig. 3.1). Calculations are based on equation 3.

3.4.3 Temporal variation of physical conditions and of *L. wollei* biomass

The overwhelming effect of spatially-structured hydrodynamic variables prompted us to focus further analyses of temporal variations at the two sites (B and C) with highest *L. wollei* biomass. The study period covered a wide range of hydrological and wind conditions, which were highly contrasted between years (Fig. 3.5). In 2009 and 2011, Lake Saint-Louis water level followed the typical seasonal pattern, with high values in spring dropping to minimum values in summer and fall. In contrast, 2010 lacked a spring freshet and exhibited exceptionally low water levels from May to October. Accordingly, mean annual level was 40 cm higher in 2009 (21.41±0.28 m asl) and 2011 (21.37±0.23 m asl) than in 2010 (20.99±0.23 m asl). Water level was strongly correlated with St. Lawrence River discharge at the outlet of Lake Saint-Louis ($R=0.998$; $p<0.001$; $N=366$).

The year 2011 was the windiest, with 16 d of strong wind (≥43 km/h) compared to 10 d and 12 d in 2009 and 2010, respectively. Maximum wind speeds in the 15 d prior sampling were also higher in 2011 (median=46 km h^{-1}) than in 2009 and 2010 (median=39 km h^{-1} and 40 km h^{-1}, respectively). After the break-up of ice cover, the period of high spring discharge (April and May), coincided with 278 h of high winds (>24 km h^{-1}) in 2009, in comparison with 126 h in 2010 and 178 h in 2011. In summary, 2011 was characterized by windy conditions and high water levels, whereas 2010 exhibited low winds and unusually low water levels; 2009 was somewhat intermediary in both respects.

Over the three years of the study, biomass at sites B and C consistently reached its peak (between 58 and 101 g DM m^{-2}) at the end of the growing season in September. However, major differences in the pattern of biomass accumulation were observed among years (Fig. 3.5). In 2009, high spring water level combined with strong winds resulted in low biomass between April and May, followed by a steady increase throughout the growing season. In March 2010, sampling under ice cover revealed high biomass, which persisted through spring and increased throughout the growing season, under very low discharge and light winds. In April 2011, high water levels in conjunction with strong winds resulted in the almost complete absence of *L. wollei* biomass until July (Fig. 3.5).

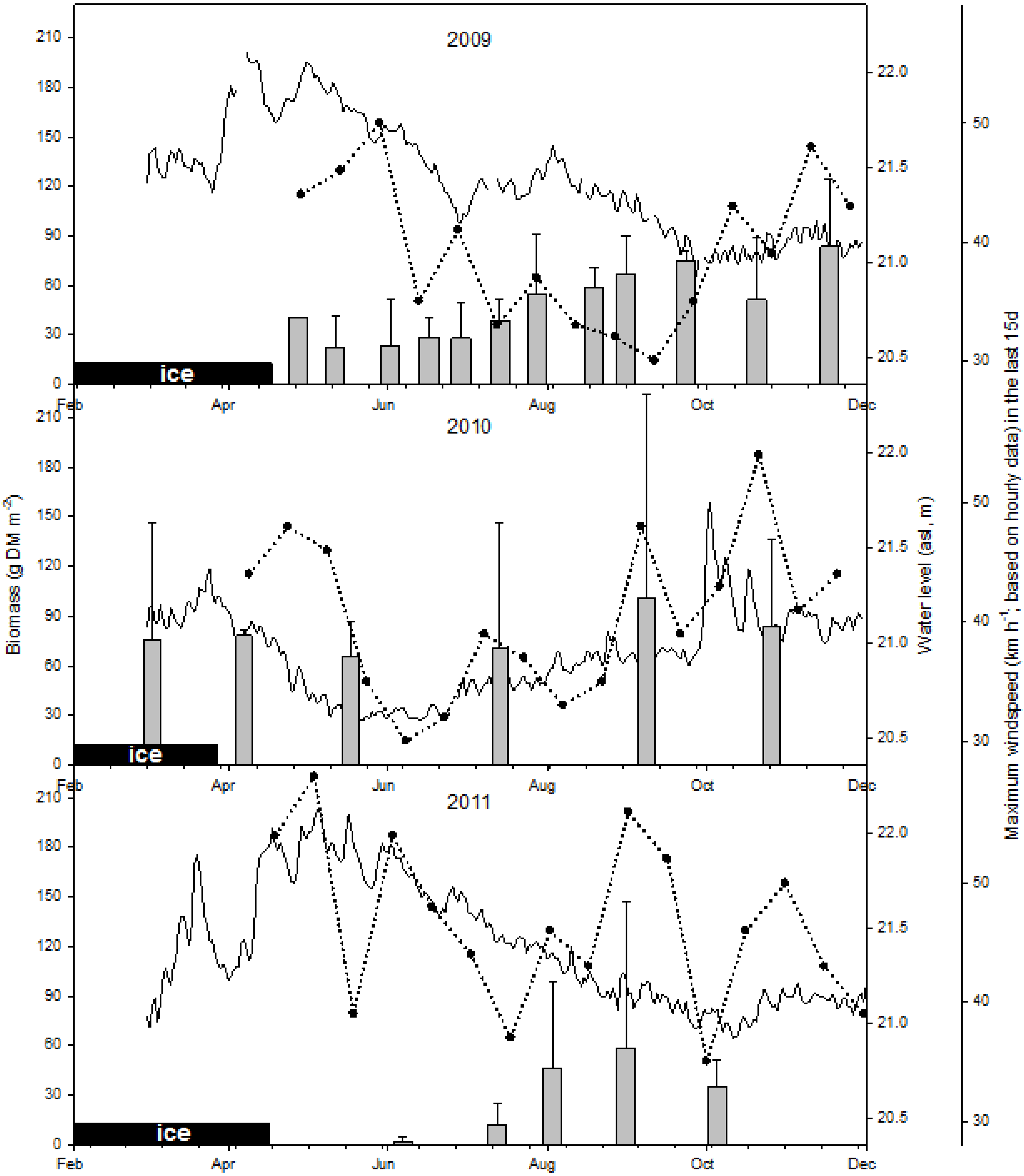

Figure 3.5 Mean biomass of *Lyngbya wollei* (g DM m^{-2}, grey vertical bars±range) at sites B-C (left Y-axis) in 2009-2011. Daily water level at Lake Saint-Louis (m above sea level, full line) and maximum wind speed (hourly based) in the 15 previous d (dotted line and full symbols) are shown (right Y-axes). The ice cover is indicated by a horizontal black bar.

Temporal variation of *L. wollei* (g DM m^{-2}) biomass at sites B and C was best explained by water level averaged over 15 d before sampling (R^2adj.=0.416) and DOC concentration (R^2adj.=0.185) in a linear regression model (Eq. 4) (R^2adj.=0.601, $p<0.0001$, N=20):

$$\text{Log}_{10}\,(\text{Biomass}) = a + b\,(\text{water level 15 d}) + c\,(\text{DOC}) \qquad \text{(Eq. 4)}$$

where the values of estimated parameters (±SE) are:

$a=-1.256\pm0.159$, $b=-0.646\pm0.114$, $c=0.104\pm0.033$.

Despite the large temporal variations in biomass, *L. wollei* condition (C:N, C:P, and N:P tissue ratios) remained fairly constant among seasons (Fig. 3.6A, B, C). Comparison of elemental ratios with thresholds for potential N- or P-limited growth (Hillebrand and Sommer 1999) indicated that *L. wollei* growth in the St. Lawrence River was slightly limited by P. Fraction of filaments filled with cells relative to empty sheath varied during the study from 44 to 73% (Fig. 3.6D).

3.5 Discussion

The present study confirmed earlier findings that *L. wollei* occurred under high DOC concentrations and low DIN:TDP ratios in the St. Lawrence River (Levesque et al. 2012). The eight sites where water chemistry was conducive to *L. wollei* exhibited a wide range of cyanobacterial biomass. Although similar in terms of water quality, these sites were very different hydrodynamically, since they were positioned along a strong gradient of current velocity and wave exposure. In addition, seasonal and interannual differences in water level and wind conditions varied sufficiently along the transect to test our hypotheses that hydrological and climatic conditions modulate the spatial and temporal patterns of *L. wollei* biomass accumulation.

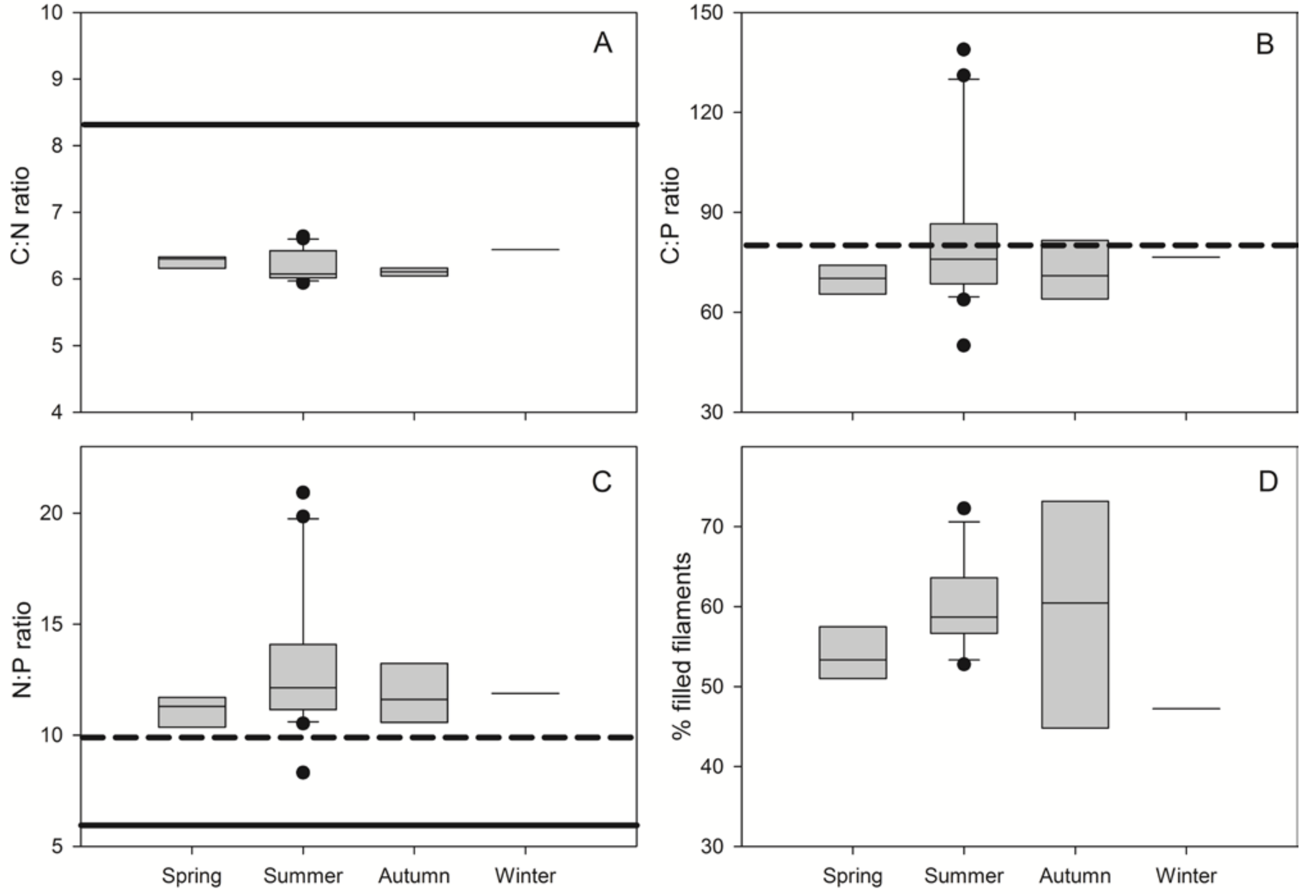

Figure 3.6 Box plots showing the elemental mass ratio of *Lyngbya wollei* filaments: A) carbon to nitrogen, B) carbon to phosphorus C) nitrogen to phosphorus, and D) fraction of filaments filled with cells relative to empty sheath. For A, B, C (Spring N=7, Summer N=22, Fall N=5, Winter N=2); for D (Spring N=5, Summer N=11, Fall N=3, Winter N=1). Horizontal black lines represent the threshold of nitrogen (bold) or phosphorus (dashed) limited growth (Hillebrand and Sommer 2001). Nitrogen-limited growth is expected when C:N > 69.8 and N:P < 5.9 threshold. Phosphorus-limited growth is expected when C:P > 8.6 and N:P > 9.9 thresholds.

3.5.1 Physical variables controlling *L. wollei* biomass

Spatially, we predicted that sites exposed to a large fetch, high winds and strong current would support less biomass than those under sheltered conditions. Due to the morphology of the embayment, the transect we studied exemplified a gradient in fetch and current. As expected from hydrological models (Ji 2008), current increased with increasing distance away from the shore towards the main river channel. Fetch also increased with distance from shore because the dominant winds blow in the same direction as the St. Lawrence River flow. Accordingly, current velocity and REI, an index of wave exposure calculated with fetch and wind direction/speed, accounted for 60.5% of the *L. wollei* biomass variation among sites (B-H). Therefore, both the effect of wave-induced currents and the main river flow explained the biomass pattern (maximum biomass between 150-250 m from shore) along the transect during the growing season. Those results are supported by a preliminary survey in 2006-2007, where biomass (≥60 g DM m^{-2}) was consistently found in the hydrodynamically-favourable stripe located between 75-360 m along the north shore of Lake Saint-Louis (Fig. 3.1). However, the gradient of current and fetch along the study transect did not explain the low biomass of *L. wollei* observed at site A, which was the most sheltered and shallowest site. Shallow depth made this site the most vulnerable to wave action (Table 3.2). In agreement with our results, two studies carried out in western Lake Erie (Bridgeman and Penamon 2010, Panek 2012) reported that *L. wollei* was absent in shallow nearshore areas (<1 m) of Maumee Bay.

Temporally, we expected that periods of high wind and/or high water level and discharge would coincide with low biomass. We indeed recorded major inter-annual differences in *L. wollei* biomass at sites B-C, with high biomass (maximum of 101 g DM m^{-2}) in a year with low discharge (2010) and reduced biomass (maximum of 75 and 58 g DM m^{-2}) over two years with high discharge (2009 and 2011, respectively). Water level in the 15 d prior to sampling, a proxy for river discharge, explained 45% of temporal variation in biomass whereas wind, either as maximum or as cumulative frequency >24 km h^{-1}, was not a significant explanatory factor. Therefore, high discharge presumably associated with an increase in current velocity (Leopold and Maddock 1953) was the strongest driver of interannual biomass variations, likely dislodging mats accumulated on the bottom in the previous growing season.

Lyngbya wollei advection happens when drag exceeds the critical shear stress required to move the mats. Wind-induced bottom velocities on the order of 15-20 cm s^{-1} are needed to resuspend fine sand particles (Heezen and Hollister 1964) and are likely to dislodge unattached mats of *L. wollei*. Current velocity thresholds of 25 cm s^{-1} have been proposed for macroalgae in coastal rivers (Hoyer et al. 2004) and for periphyton in gravel-bed rivers (Luce et al. 2010). Mean current velocity measured in the water column were below this threshold at sites with abundant *L. wollei* biomass. Moreover, near-bed velocities are lower than values measured in the water column. However, these values were averaged over June-September and therefore did not include spring peak discharge. Even if rare (0.5 % of the study period), high winds ($\geq$43 km h^{-1}) from the southern quadrant (90-270°) may generate near-bed current in the 20-33 cm s^{-1} range, which are capable of dislodging *L. wollei* mats. Such short-lived, punctuated, albeit dramatic events are particularly hard to capture, yet are most likely to exert major effects on *L. wollei* biomass. Water current velocity is one of the main factors regulating distribution and biomass of aquatic macrophytes (Barko and Smart 1986, Haslam 2006, Franklin et al. 2008) and long filamentous algae (Biggs et al. 1998) in rivers. Wave exposure was negatively correlated with benthic cyanobacterial abundance in coastal Guam (Thacker and Paul 2001). Conversely, large and persistent *L. wollei* mats have been reported in springs, small sheltered lakes, ponds, and reservoirs of southern USA (Speziale and Dyck 1992, Stevenson et al. 2007).

3.5.2 Chemical controls of *L. wollei* biomass

Our study highlighted other factors in addition to exposure to wind and hydrology. In our temporal analysis, DOC alone explained 18% of *L. wollei* temporal biomass variation once the effect of water level was removed. The labile portion of DOC, composed in part by photosynthesis release, is directly usable by some algae and cyanobacteria as a supplemental source of energy to achieve optimal growth (Burkholder et al. 2008, Tittel et al. 2009) while the non-labile fraction, coming from terrestrial origin, need to be broken by heterotrophic bacteria before being incorporated in the food web (Pace et al 2004). The labile fraction represents a non-negligible potential energy source for *L. wollei* and its associated microorganisms in the St. Lawrence since it varied from 18% in water masses influenced by tributaries to 26% in the Great Lake water mass (Massicotte and Frénette 2011). A relationship between *L. wollei* distribution and high DOC concentrations was previously established in a 250-km long St. Lawrence River survey (Levesque et al. 2012). DOC was also shown to increased algal gross primary production which in turn increased DOC (Wyatt et al. 2012) releases thus partly explaining the correlation between DOC and *L. wollei* biomass. Additionally, DOC strongly influences the bioavailability of metal ions (Paerl 1988, Rose and Waite 2003) including iron which is needed in *L. wollei* growth (Pinowska et al 2007). In our study, DOC was strongly correlated with dissolved iron (R=0.81, N=108) (unpublished data) but we favored the inclusion of DOC over dissolved iron in our regression model given the notorious complexity of measuring the biologically available iron forms (Molot et al. 2010). High DOC originating from tributary runoff in Moreton Bay (Australia) was shown to act as a proxy for iron and positively correlated with *L. majuscula*, a marine counterpart of *L. wollei* (Albert et al. 2005). Here, both iron and DOC concentration were indicative of the influence of the Ottawa River. Conversely, conductivity and calcium concentration were located at the opposite ends of the PCA axis, indicative of the dilution and mixing of the Ottawa River with the more mineralized waters of the St. Lawrence River main stem.

In the spatial analysis, we observed a negative correlation between NH4+ concentration and *L. wollei* biomass, which, however, explained only 2% of variation. This observation agrees with previous findings associating high biomass of this cyanobacterium with low NH_4^+ concentrations (median 6 µg L^{-1}) in the St. Lawrence River (Vis et al. 2008, Levesque et al. 2012), although this relation is not always observed elsewhere (Stevenson et al. 2007, Heffernan et al. 2010).

3.5.3 Interactions with vascular macrophytes

Proliferation of *L. wollei* tends to be inversely related with the abundance of macrophytes (Cowell and Silver Botts 1994, Hudon et al. 2014). Accordingly, we observed vascular macrophytes only at sites in the Lake Ontario water mass (J-K) and at the shallowest site (A) where *L. wollei* was absent or rare, respectively. These sites were the only ones where a high proportion (mean >10%) of incident light reached the bottom favouring vascular macrophytes. All other sites (B-H) received on average only 1% of incident light, which would be limiting for vascular plants but suitable for *L. wollei* given its very low photosynthetic saturation point (150 µmol m^{-2} s^{-1}) and compensation point (20 µmol m^{-2} s^{-1}) (Beer et al. 1986). Occurrence of *L. wollei* at low light (0.05-1% of incident surface light) has been observed also in Lake Erie (Panek 2012). We also collected high biomass of apparently viable *L. wollei* under the ice, coinciding with no wave action, low turbidity and almost complete darkness (0.1% light) near the bottom.

3.5.4 Tissue content and condition of *L. wollei*

Carbon, N, and P content in *L. wollei* filaments were consistent throughout the year without evidence of an effect of the wide range of water temperature, including under ice in winter conditions. Temporal biomass variation of *L. wollei* therefore did not appear to be related to a seasonal decline in its condition. Percentage of filament filled with cells rose from winter to summer but was highly variable in the fall, possibly as a result of mat disturbance by waves leading to a mix of senescent and vigorous filaments (Nozaki et al. 2003). Overall, tissue stoichiometry suggested that ambient water nutrient concentrations were not seriously limiting *L. wollei* growth. The slight P limitation was in agreement with findings in Florida springs (Stevenson et al. 2007). Nitrogen limitation may be less likely due atmospheric N fixation (Phlips et al. 1992, Tall 2012), internal nutrient recycling, acquisition from dissolved organic N sources and release from anoxic sediment (Stevenson et al 2007) .

3.5.5 Abundance of *L. wollei* with regard to climate change

Climate change scenario for St. Lawrence-Great Lakes region forecasts chronically low water levels (Lefaivre 2005) but increased frequency and magnitude of storm events (Solomon et al. 2007). Water level of the St. Lawrence River is expected to drop by 0.2-1.2 m in the Montreal area, increasing the tendency for water flow to concentrate in the excavated central navigational channel (D'Arcy et al. 2005). These physical alterations should increase the extent of marginal areas of low flow velocity, which are potentially colonized by *L. wollei*. If water depth decreases, however, light availability might increase enough to promote the growth of vegetation other than *L. wollei*. Frequent heavy precipitation events may lead to a rise in storm sewer overflow and in flashiness of farmland tributaries (Croley 2003) with consequent pulsed runoff of high loads of DOC and other nutrients that could promote *L. wollei* growth. Intense storm and wind events will likely increase wave actions, which disrupts mats and washes them ashore, especially considering that bottom scouring by waves would be exacerbated under reduced water depth (US Army Corps of Engineers 1984). In summary, we expect an increase in the area colonized by *L. wollei* due to favourable chemical and physical conditions for its growth combined with a decrease of vascular macrophytes due to competition with those cyanobacterial mats. Consequently, we forecast increasingly frequent episodes of mat disruption, leading to an intensification of shoreline accumulation, beach fouling, and impaired domestic and recreational water uses.

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4. Environmental factors structuring benthic primary producers at different spatial scales in the St. Lawrence River (Canada)

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4.1 Abstract

We studied the environmental factors controlling the biomass of submerged aquatic macrophytes, cyanobacterial mats, and epiphyton to examine the influence of the spatial scale in structuring environmental variables and biomass of these benthic primary producers. To address this question, we used a nested design at 3 spatial scales within the St. Lawrence River (SLR): 1) along a 250-km-long upstream-downstream river stretch, 2) among three fluvial lakes located within that river stretch and 3) within each fluvial lake. Environmental factors (conductivity and TP) and spatial structure together explained 59% of the variability in biomass of all three benthic primary producers (PP): spatially-structured environmental variables explained 22% of biomass variations, whereas taken on their own, environmental (7%) and within-lake spatial (15%) factors had a smaller explanatory power. Spatial variability of biomass was best explained by conductivity (+) for macrophytes, DIN:TDP ratio (+) and light extinction coefficient (+) for epiphyton and DOC (+) and NH_4^+ (-) for cyanobacterial mats. Within-lake structure was the most important spatial component for all benthic PP, suggesting that local effects, such as enrichment by the inflow of tributaries, rather than upstream-downstream gradients, determined the biomass and composition of benthic PP. Additionally, our results allows us to discuss to which extent biomass of benthic PP reflected the eco-geomorphological properties of a river patch and the fluvial continuum.

4.2 Introduction

Benthic primary producers (PP), such as submerged aquatic macrophytes and filamentous algae, occasionally cover important portions of the littoral of large rivers, supporting secondary production in addition to being an important habitat and food source for many fish and invertebrates (Jeppesen et al., 1998). Despite their important role in such ecosystems, our understanding of environmental processes controlling the abundance and composition of communities of benthic PP in large rivers is still limited.

Rivers have been described as a gradient of physical conditions (depth, width, velocity, temperature, and turbidity) affecting community patterns and distribution from upstream to downstream by the river continuum concept (RCC) (Vannote et al., 1980). This view of rivers as a longitudinal continuum has been progressively expanded to encompass the spatial and temporal variations of nutrient cycling through organisms and detritus in the resource spiraling concept (Elwood et al., 1983) and spatial discontinuities induced by dams in the serial discontinuity concept (SDC) (Ward and Stanford, 1983). The lateral connectivity and the importance of the annual flood pulse in reconnecting the main channel to its floodplain were elaborated through the flood pulse concept (Junk et al., 1989). Subsequent efforts (Thorp et al., 2006) developed the riverine ecosystem synthesis, following which rivers are a mosaic of large and discrete patches, combining concepts of hierarchical patch dynamics and eco-geomorphology (hydrology, geomorphology, climate and vegetation). Patches are defined by areas characterized by a series of functional attributes such as geology, climate, vegetation, nutrient and organic matter concentrations, discharge and current speed. The riverine ecosystem synthesis hypothesized that river processes were driven by the spatial arrangement of patches rather than by the downstream gradient of the river continuum.

Spatial structure is rarely explicitly taken into account when evoking environmental factors controlling biological communities (Cottenie, 2005), which agglomerates pure environmental control and environmentally-induced spatial variation and does not account for neutral processes (i.e. dispersion) (Legendre and Legendre, 2012). The environmental factors evoked to explain biological communities depend on the spatial scale at which the study was conducted (Forman and Godron, 1986). Some environmental variables show large variation at small spatial scales which create high heterogeneity in biological communities in relatively small areas while others show more variation at large spatial scales giving rise to community variations in large study areas (Borcard et al. 2004). Unfortunatly, only a few studies integrate multiscale spatial and environmental effects together (Capers et al., 2010; Mikulyuk et al., 2011; O'Hare et al., 2012; Alahuhta and Heino, 2013; Gallego et al., 2014) and none of them examined large rivers.

At the landscape scale, the watershed area controls the morphometry and the residence time, discharge and water velocity of rivers, which in turn influence the amount of substrate suitable for the establishment of benthic PP species (Duarte and Kalff, 1986; Morrice et al., 2004; Franklin et al., 2008). Land use and soil type influence pH, conductivity, concentrations and forms of nutrients and organic matter in the water (Barko and Smart, 1986; Capers et al., 2010; Alahuhta and Heino, 2013). At the riverbed scale, nutrient concentrations (Carignan and Kalff, 1980; Jones et al., 2002) and light availability (Barko et al., 1982; Sand Jensen, 1989; Lacoul and Freedman, 2006) determine the composition of benthic PP. In rivers, the importance of filamentous algae tends to increase progressively through their courses until rising water turbidity and depth induce a shift towards phytoplankton (Hilton et al., 2006). At local scales, biotic interactions between benthic PP and grazers may control the dominance of the different groups of vegetation (Lacoul and Freedman, 2006). Competition for light and nutrients between submerged macrophytes, loosely attached algae and epiphyton was also shown to influence community composition (Vadeboncoeur and Steinman, 2002; Hilton et al., 2006; Franklin et al., 2008).

The present study uses three groups of benthic primary producers (submerged aquatic macrophytes, cyanobacterial mats and epiphyton) in the St. Lawrence River (SLR) to examine the relative importance of environmental factors acting at three naturally-nested spatial scales: 1) at the large scale of a 250-km-long fluvial section, 2) at the intermediate scale of three large fluvial lakes located within this stretch and 3) within each lake, by using sites located upstream, at the mouth and downstream of inflowing tributaries. Over its course, the SLR alternately runs through narrow (~2-4 km-wide) cross-sections and three wide (≥10 km) fluvial lakes with numerous tributaries. This large river thus provides us with a longitudinal series of fluvial lakes likely to support patches characterized by different benthic PP assemblages (Thorp et al., 2006). Heterogeneity in this system is created by tributaries draining farmlands, resulting in a degradation of water quality locally at their confluence, regionally along the littoral area of fluvial lakes, and globally along the downstream axis of the SLR (Hudon and Carignan, 2008).

We expected the biomass of the different benthic PP to be regulated both environmentally and spatially at different spatial scales depending on their functional attributes. To test these hypotheses, we examined the response of benthic PP (submerged aquatic macrophytes, cyanobacterial mats and epiphyton) to environmental conditions over a 250-km stretch of SLR in late summer 2008. Sampling was concentrated in a single season, at the maximum of benthic primary producer biomass (end of August, beginning of September), to remove the effects of seasonal successions and hydrological variation. Our results should increase our understanding and management of benthic PP in rivers and allow us to discuss whether they reflected the nature of a patch (Thorp et al., 2006) (table 4.1) or the position along the river continuum.

4.3 Material and Methods

4.3.1 Study area

The study took place across three fluvial lakes of SLR (Lake Saint-François (LSF), Lake Saint-Louis (LSL) and the lower portion of the Ottawa River, and Lake Saint-Pierre (LSP) located in the 250-km-long fluvial section of the SLR between Cornwall and Trois-Rivières (Fig 4.1). The wide (>5 km), shallow (mean depth <5 m), slow flowing (<0.4 m s^{-1} outside the navigation channel) fluvial lakes are joined by narrow (<4 km) corridors where current speed are faster. Lake Saint-Francois (235 km^2) is located ~175 km downstream) conferring LSF a high water clarity (Secchi >5m) and low sedimentation rate (Table 4.1). Lake Saint-Francois is bound by the Moses-Saunders power dam upstream and the Beauharnois power dam downstream, leading to largely stabilized discharge (~7500 m^3 s^{-1}) and water level variations (<0.2 m). The watershed of LSF is composed of rural area, moderately populated (100-500 hab. km^{-2}) and drained only by a few small tributaries. Lake Saint-Louis (140 km^2), located downstream of the Beauharnois dam, is set in a densely populated (>500 hab. km^{-2}) area near the city of Montreal. SLR discharge (~9500 m^3 s^{-1}) and water level (0.5-1.4 m) variations in Lake Saint-Louis are seasonally modulated by the partial inflow of the Ottawa River (discharge ~1838 m^3 s^{-1}), the largest SLR tributary. The Ottawa River waters are brown and enriched in suspended sediments and phosphorus, resulting in low water clarity (Secchi 1-5 m). By Lake Saint-Pierre (402 km^2) ~90 km downstream, the SLR discharge adds up to 10500 m^3 s^{-1}, including 3 additional tributaries (Richelieu, Yamaska and Saint-François; discharge: 434, 86 and 168 m^3 s^{-1}, respectively) contributing to its large water level range (1.31 m to 2.26 m annually), low water clarity (Secchi 0.1-3 m) and high sediment accumulation rate (Table 4.1). The watershed of LSP is rural with a low population density (10-25 hab. km^{-2}). Wetland area vary substantially among our 3 fluvial lakes with 4100 ha for the water stabilized LSF, 950 ha for the heavily urbanized LSL and 18350 ha for LSP presenting a more natural flow and shoreline. The SLR has also been considerably modified by human along its course with the dredging and channelling for ship traffic, creation of islands, and deepening of the Montreal harbour (Carpentier 2003).

4.3.2 Sampling

Sampling was performed in the littoral zone potentially colonized by submerged plant communities where the water depth was <2.5 m (Hudon et al. 2000). Sampling sites were selected in areas upstream, within, and downstream of the inflow of tributaries to the SLR. Sampling to describe the biomass of submerged plant communities and environmental characteristics of SLR was conducted in the period of maximum macrophyte biomass (August 19-September 18, 2008) (Vis et al. 2006). At each site, we measured water depth (z, in m), temperature (°C), dissolved oxygen (%), pH, conductivity (µS cm^{-1}) (YSI 103 600 XLM, Ohio) and the light extinction coefficient (k, in m^{-1}) (LI-COR LI-190SA air and underwater LI-193SA spherical sensor, Nebraska). At each site, water samples were taken just below the surface and unfiltered sub-samples were used for analyses of suspended matter (SM, American Public Health Association 1995), total phosphorus (TP) and total nitrogen (TN) (Environment Canada 2005). Filtered subsamples (Whatman GF/C, GE Healthcare Bio-Sciences AB, Sweden) were analyzed for total dissolved phosphorus (TDP), NO_2^--NO_3^-, NH_4^+, dissolved organic carbon (DOC) and color (Method Pt/Co) (Environment Canada 2005). TP and TDP were determined by acid digestion followed by colorimetry with ammonium

Table 4.1 Comparison of the attributes potentially affecting the abundance, composition and scale of distribution of benthic primary producers in the three fluvial lakes of the St. Lawrence.

Functional attribute	Lake Saint-François (Cornwall to Beauharnois dam)	Lake Saint-Louis (Beauharnois to Lachine Rapids)	Lake Saint-Pierre (Sorel to Trois-Rivières)
St. Lawrence River discharge (m^3 s^{-1})[f]	7500	9500	10500
Total fluvial lake area (km^2)[c]	235	140	402
Annual (1998-2008) Water Level variation (m)[f]	0.09-0.28, largely stabilized	0.53-1.42	1.31-2.26
Major tributaries (Mean annual tributary discharge, m^3 s^{-1}) [a]	None	Ottawa River (1838)	Richelieu, Yamaska, Saint-François rivers (434, 86, 168)
Population density (hab km^{-2})[b]	100-500	>500	10-25
Shoreline use	Rural	Urban	Wetlands
Connectivity with floodplain	Low because of stabilized water level	Low because of heavily urbanized shorelines	High because of high range of level and natural wetlands along the shoreline
Littoral areas (defined as $z < 4.5$ m, km^2) (% of total area)[c]	176 (75%)	100 (71%)	249 (62%)
Total area of wetlands (ha)[d]	4100	950	18350
Mean Depth (m)[c]	5.1	3.4	2.7
Water clarity (Secchi Depth range, m)[e]	5-10	1-5	0.1-3
Sediment accumulation (kg m^{-2} $year^{-1}$)[c]	3.2	6.7	12.1

[a]from Hudon and Carignan (2008); [b]from Répertoire des Municipalités du Québec (1995); [c]from Carignan and Lorrain (2000); [d]from http://www.qc.ec.gc.ca/csl/fich/fich001_002_e.html#overview; [e]from Hudon et al. (2000); [f]from Environment Canada (2012).

molybdate. TN was analyzed after persulfate digestion with a LACHAT Continuous Flow Quick-Chem 8000 ion analyzer (Loveland, Colorado). NO_2^--NO_3^- was measured by reducing nitrate to nitrite in a cadmium column prior to colorimetry; NH_4^+ was analyzed by colorimetry after the addition of sodium nitroprusside and sodium phenate. DOC was oxidized to carbon dioxide by the addition of persulfate prior to infrared detection (Shimadzu TOC-5000; Shimadzu Corporation, Japan) (Environment Canada 2005). Dissolved inorganic nitrogen (DIN) was calculated as the sum of NO_2^--NO_3^- and NH_4^+ concentrations. Distance of the closest upstream sampled tributary was measured (MapInfo Professional v8.5, Pitney Bowes Inc, Connecticut) to represents the punctual effect of tributary over water quality.

Biomasses of benthic PP (macrophytes, cyanobacterial mats and epiphyton) was estimated quantitatively using a double-headed rake dragged over a length of 1 meter on the bottom of the SLR (Yin et al. 2000, Kenow et al. 2007). Biomass was averaged from collections made in front and on both sides of the boat. Macrophytes collected simultaneously with filamentous algae were brought back to the laboratory for cleaning, sorting, identification, and measurement of wet mass (WM) and conversion to dry mass (DM) using previously established conversion factors (Hudon et al. 2012). The algae mats were dominated by the cyanobacterium *Lyngbya wollei* (Levesque et al. 2012). The epiphyton biomass (µg of chla mg^{-1} DM on macrophytes leaves) was estimated by manually dislodging epiphytes of 10 leaves of vascular macrophytes, drying the leaves at 50°C, measuring their dry mass (±0.1 mg) and measuring chlorophyll-a of epiphyton following cold ethanol extraction and spectrometry (Stainton et al. 1977).

4.3.3 Statistical analysis

Environmental variables

Water depth was excluded from the analysis on the basis that the sampled sites were selected to have a depth in the 0.5-2 m. Temperature, dissolved oxygen and pH were excluded because of their high daily variation.

Physical, chemical and biological variables (biomass) of the sites in the littoral zone and at the mouth of tributaries of our three fluvial lakes were compared separately among lakes using Kruskal-Wallis nonparametric analysis of variance (ANOVA; function kruskal.test of package stats) followed by multiple comparisons of medians (function kruskalmc of package pgirmess) (Giraudoux 2011) in the R statistical language (R Development Core Team 2011, Austria). In addition, sites within littoral zone and at the mouth of the tributaries for the same fluvial lake were compared using the Wilcoxon rank sum in the same fashion.

Variability among sites of the littoral zone was explored by principal component analysis (PCA) using the FactoMineR library (Husson et al. 2010) in R. All variables were reduced to unit variance by standardization in order to facilitate the comparison of variables with different scales (Legendre and Legendre 2012).

Benthic PP analysis

We determined the influence of environmental and spatial variables on the benthic primary producer community using redundancy analysis (RDA) and variation partitioning (Borcard et al. 1992, Borcard and Legendre 2002). Vegetation biomass data were transformed using the Hellinger transformation to eliminate the differences of total biomass among sites and reduce the importance of the most abundant vegetation types, as recommended for RDA (Legendre and Gallagher 2001). We also evaluated environmental and spatial control for individual functional groups of benthic PP using multiple regressions on $\log_{10}$ transformed biomass.

Spatial structure was modeled hierarchically at three levels: 1) at the fluvial scale using a linear trend in the x coordinates (longitude) of the sampling sites, 2) at the among-lake scale by using two binary variables to represent the three SLR fluvial lakes, and 3) at the within-lake scale with Moran's eigenvector maps (MEM) (Declerck et al. 2011). MEM produce a group of orthogonal spatial variables from the geographic distances among the sampling sites (Dray et al. 2006). These variables model spatial variation at different scales and can be used as explanatory variables in RDA and regression (Borcard et al. 2011). Forward selection was applied separately to the environmental and MEM variables in order to reduce the number of variables before RDA or regression. Vegetation biomass variation was decomposed (Borcard et al. 1992) between environmental variables, river scale, among-lake and within-lake scales using the varpart function of the vegan package in R (Oksanen et al. 2013).

4.4 Results

4.4.1 Environmental variables

St. Lawrence River waters originating from the Great Lakes changed progressively over their 250-km-long course through LSF, LSL and LSP. As expected, LSF was clear (light extinction coefficient of 0.5 m^{-1}) and showed an increase in water colour (5x), suspended matter (10x) and DOC (2x) (Table 4.2) toward LSP, resulting in a decrease in light penetration (from >50% of incident light reaching the bottom in LSF to <5% in LSP). Water of the SLR became enriched in nutrients, showing a 2.5-fold increase in both dissolved N and P.

Comparison of the water quality between littoral zone and tributaries for each fluvial lake showed that LSF tributaries were significantly more turbid and rich in DOC than the SLR waters, whereas no such difference existed for the two downstream lakes (Table 4.2). Although conductivity was highly variable within the fluvial lakes and among tributaries, it tended to decrease along the longitudinal river axis. Tributaries from LSP exhibited particularly high concentrations of suspended matter, DIN and DIN:TDP ratio as well as the highest range of conductivity values (Table 4.2). Generally, tributaries were located between 1 and 10 km upstream of the sampling sites. This emphasizes the cumulative impact of tributaries on the progressive downstream degradation of water quality of SLR.

We explored the relationship between the physical, chemical and spatial variables of SLR littoral zone along the downstream gradient by PCA. The first two principal components captured 62% of the total variance of the 13 standardized variables (Fig. 4.2). The contrasting optical properties of water masses from LSF (high conductivity, clear waters) and of LSL and LSP (low conductivity, brown waters) was shown by the strong negative relation between conductivity and light penetration with color and DOC along the first PCA axis (49%). In addition, the concentrations of all forms of N and P were grouped together along the first axis and were strongly associated with water optical properties (Colour, DOC, SM). The second axis (13%) was driven by the opposition between DIN: TDP and distance to nearest upstream tributary.

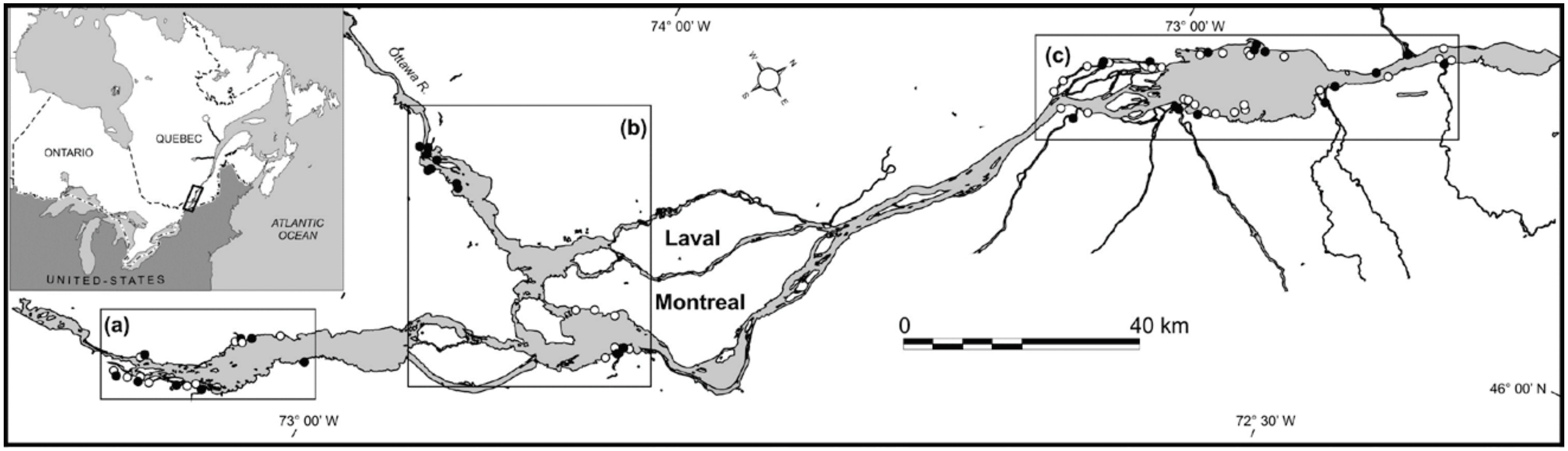

Fig. 4.1 Map of the study area showing, for each major sampling region, the location of littoral sites (open circles) and tributaries (full circle). Regions refer to (a) Lake Saint-François (11 littoral and 9 tributary sites); (b) the Ottawa River and Lake Saint-Louis (6 littoral and 10 tributary sites), and (c) Lake Saint-Pierre (26 littoral and 15 tributary sites).

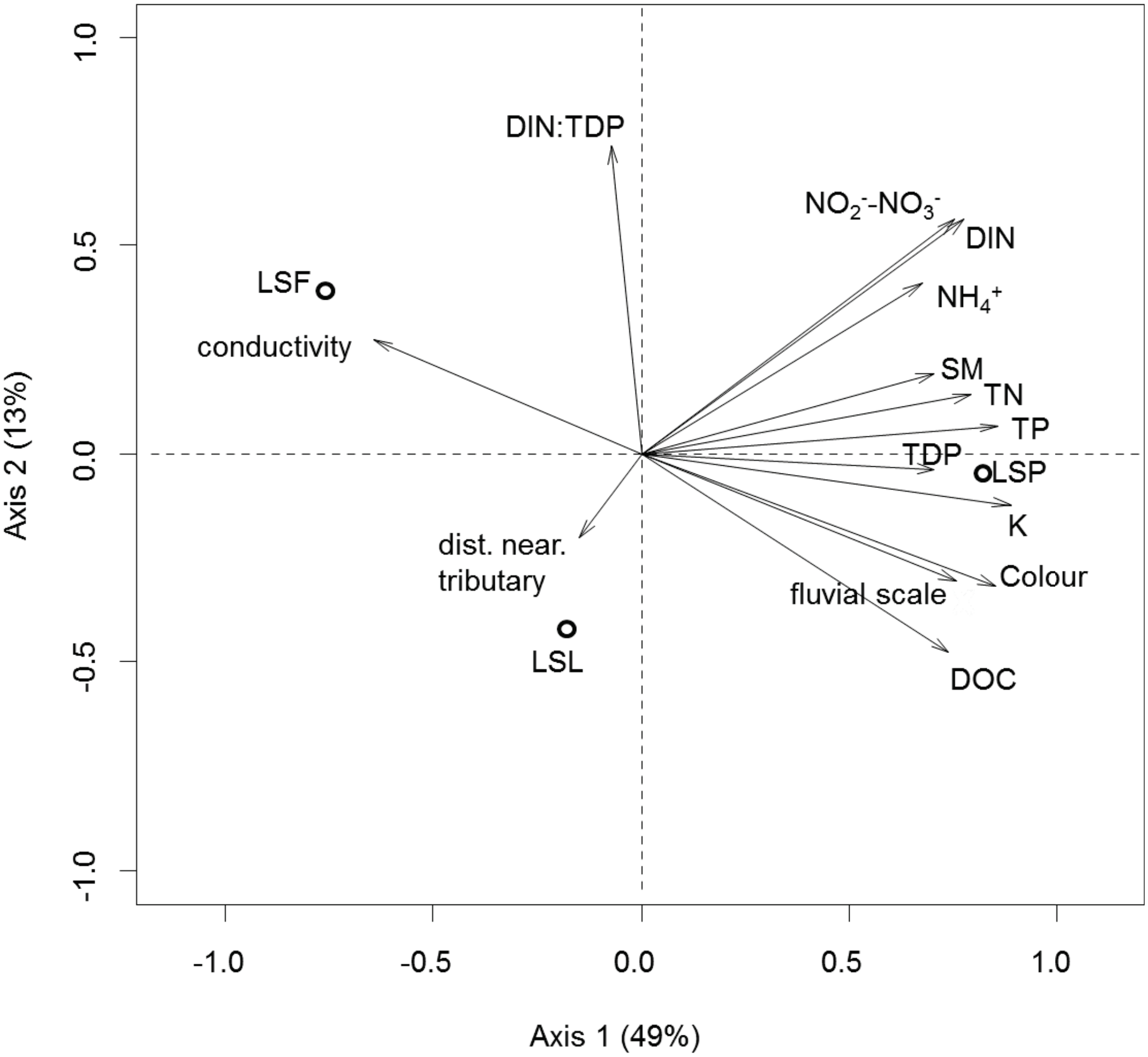

Fig. 4.2 Principal component analysis (PCA) biplot based on correlations among the physical and chemical variables of the littoral sites (N=43) of SLR. Arrows represent environmental variables (SM=concentration of suspended particulate matter, K=light extinction coefficient, dist. near. tributary=distance to the nearest upstream tributary). White circles represent the centroids of the states of the qualitative variable fluvial lake.

Table 4.2 Median and (range) of the chemical and physical water properties in SLR fluvial lakes and their tributaries.

	LSF		LSL		LSP	
	SLR littoral (N=11)	Tributaries (N=9)	SLR littoral (N=6)	Tributaries (N=10)	SLR littoral (N=26)	Tributaries (N=15)
Conductivity (µS cm^{-1})	261 (23-282)	244 (50-565)	161 (64-253)	124 (67-253)	130 (72-259)	172 (27-597)
Light extinction coef. (m^{-1})	**0.5 (0.4-1.5)a**	**1.2 (0.6-2.0)*a***	1.0 (0.4-2.1)ab	1.8 (0.5-2.3)*ab*	2.1 (0.8-3.5)b	2.4 (1.2-5.1)*b*
Colour (Pt/Co)	**9 (2-16)a**	**21 (6-80)**	36 (6-55)ab	47 (7-59)	46 (9-71)b	47 (11-206)
SM (mg L^{-1})	1 (1-9)a	1 (1-4)*a*	2 (1-5)a	4 (1-12)*a*	11 (2-48)b	18 (2-170)*b*
Total Nitrogen (µg N L^{-1})	435 (315-495)a	508 (370-1085)	440 (370-1000)ab	510 (360-1030)	622 (365-885)b	670 (353-4620)
DIN (µg N L^{-1})	102 (22-183)a	64 (20-246)*a*	123 (104-217)ab	106 (25-643)*a*	241 (26-486)b	262 (88-4577)*b*
NH$_4^+$ (µg N L^{-1})	11 (7-15)a	8 (5-41)*a*	14 (12-37)ab	18 (9-69)*ab*	21 (2-96)b	27 (8-757)*b*
Total Phosphorus (µg P L^{-1})	13 (7-35)a	33 (10-44)	20 (11-56)ab	28 (12-64)	40 (16-68)b	40 (13-138)
TDP (µg P L^{-1})	8 (5-23)a	20 (6-37)	13 (6-48)ab	16 (8-40)	20 (10-34)b	19 (7-67)
DIN: TDP (by mass)	14 (2-24)	3 (1-18)*a*	9 (5-21)	6 (2-23)*ab*	10 (2-18)	15 (5-68)*b*
DOC (mg C L^{-1})	**2.7 (2.3-4.12)*a**	**4.8 (2.9-10.9)**	5.6 (2.4-7.0)ab	7.1 (2.3-7.4)	6.3 (2.8-7.1)b	5.9 (3.4-12.6)

Normal letters show significant differences in the littoral zone among lakes. Italics letters show significant differences in tributaries among lakes. Values in bold show significant differences between littoral zone and tributaries within a fluvial lake. These results of the three different test are based on Kruskal-Wallis nonparametric analysis of variance (ANOVA) followed by multiple comparisons of medians.

4.4.2 Vegetation biomass

Macrophytes composition was dominated by *Vallisneria americana* through the whole study area, with the presence of *Elodea canadensis* in all tributaries and of various other taxa in SLR littoral zone. Macrophytes represented the most abundant vegetation throughout the study area (Table 4.3) and showed a clear decreasing trend along the river continuum (Fig. 4.3). Epiphyton biomass tended to increase downstream in littoral zone, but showed the opposite trend in tributaries (Fig. 4.3). Cyanobacterial mats of *Lyngbya wollei* were absent from LSF and their biomass increased downstream; they were first observed in the Ottawa River and LSL and reached their highest biomass in LSP (Table 4.3 and Fig. 4.3).

4.4.3 Environmental and spatial variables controlling biomass of benthic PP

The combined influence of environmental variables (conductivity and TP) and spatial structure (fluvial, regional and lake scale) explained 59% of the variation in the biomass of the benthic primary producers of the SLR. The first axis (55% of explained variation) contrasted macrophytes, which are found under high conductivity in LSF, and epiphyton which was dominant in the TP-enriched LSP at the downstream end of the fluvial gradient (Fig. 4.4). Nutrients and DOC were grouped together along the first axis and opposed to conductivity (see Annexe 3 for the full model with all environmental variables). The second axis (4% of explained variation) related the biomass of *L. wollei* to the spatial structure of the LSL.

Since environmental conditions, namely conductivity and TP, were spatially structured, most of the explanatory power resided in the intersection (22%; Table 4.4). Environmental variables and within lake scale were important component on their own with, respectively, 7% and 15%, but also together with 5.5%. This was not surprising given the change occurring in water chemistry following the inputs of large and small tributaries along the course on the SLR.

We also investigated specific environmental factors controlling each group of benthic PP and to which spatial scale they responded. Macrophytes biomass was positively related to conductivity (R^2adj.=37%; Table 4.4), which was spatially structured at all scales (R^2adj.=11%), but also important on its own (18%). Biomass variation of epiphyton was best explained by a positive association with the light extinction coefficient and the DIN:TDP ratio (R^2adj.=15%) although it was almost entirely spatially structured, with the most important portion at the within-lake scale (R^2adj.=7%). *Lyngbya wollei* biomass was best explained by DOC with a positive effect and negative effect of NH_4^+ (R^2adj.=32%) which was entirely spatially structured. The spatial structure within lake alone was important for all vegetation groups with 21% of biomass variation explained for both macrophytes and epiphyton and to a lesser extent for *Lyngbya* with 13% of biomass variation.

4.5 Discussion

In this study we compared littoral zone of three fluvial lakes located along a fluvial continuum providing a natural, three-level nested design (fluvial scale, among lakes and within lakes) to understand the environmental control of benthic primary producer biomass. Tributaries of the SLR reflected land use and the geology of their drainage basins as their turbidity (K, SM) and DIN:TDP increased along the longitudinal river axis. We expected that biomass variation of benthic PP would be both environmentally and spatially controlled, which turned out to be the case; that will allow us to revisit the principles underlying the functioning of large rivers at various scales.

Table 4.3 Median biomass and range for each of the three major types of benthic primary producers collected in SLR fluvial lakes and their tributaries.

	LSF		LSL		LSP	
	SLR littoral (N=11)	Tributaries (N=9)	SLR littoral (N=6)	Tributaries (N=10)	SLR littoral (N=26)	Tributaries (N=15)
Dominant macrophytes taxa	*Vallisneria americana, Heteranthera dubia*	*Vallisneria americana, Elodea canadensis*	*Vallisneria americana, Alisma*	*Vallisneria americana, Elodea canadensis*	*Vallisneria americana, Potamogeton richardsonii*	*Vallisneria americana, Elodea canadensis*
Macrophytes biomass (g DM m^{-2})	182 (1-345)a	165 (11-277)*a*	30 (9-75)ab	67 (5-176)*a*	**26 (0-169)b**	**0 (0-30)*b***
Epiphyton biomass (µg of chla mg^{-1} DM of macrophytes)	642 (106-5790)a	1219 (250-4694)*a*	538 (386-1109)a	955 (127-5305)*a*	**1090 (164-7623)a**	**0 (0-2210)*b***
Cyanobacterial mats biomass (g DM m^{-2})	0 (0-0)a	0 (0-0)*a*	2 (0-24)ab	0 (0-16)*a*	**0 (0-46)b**	**0 (0-0)*b***

Normal letters show significant differences in the littoral zone among lakes. Italics letters show significant differences in tributaries among lakes. Values in bold show significant differences between littoral zone and tributaries within a fluvial lake. These results of the three different test are based on Kruskal–Wallis nonparametric analysis of variance (ANOVA) followed by multiple comparisons of medians.

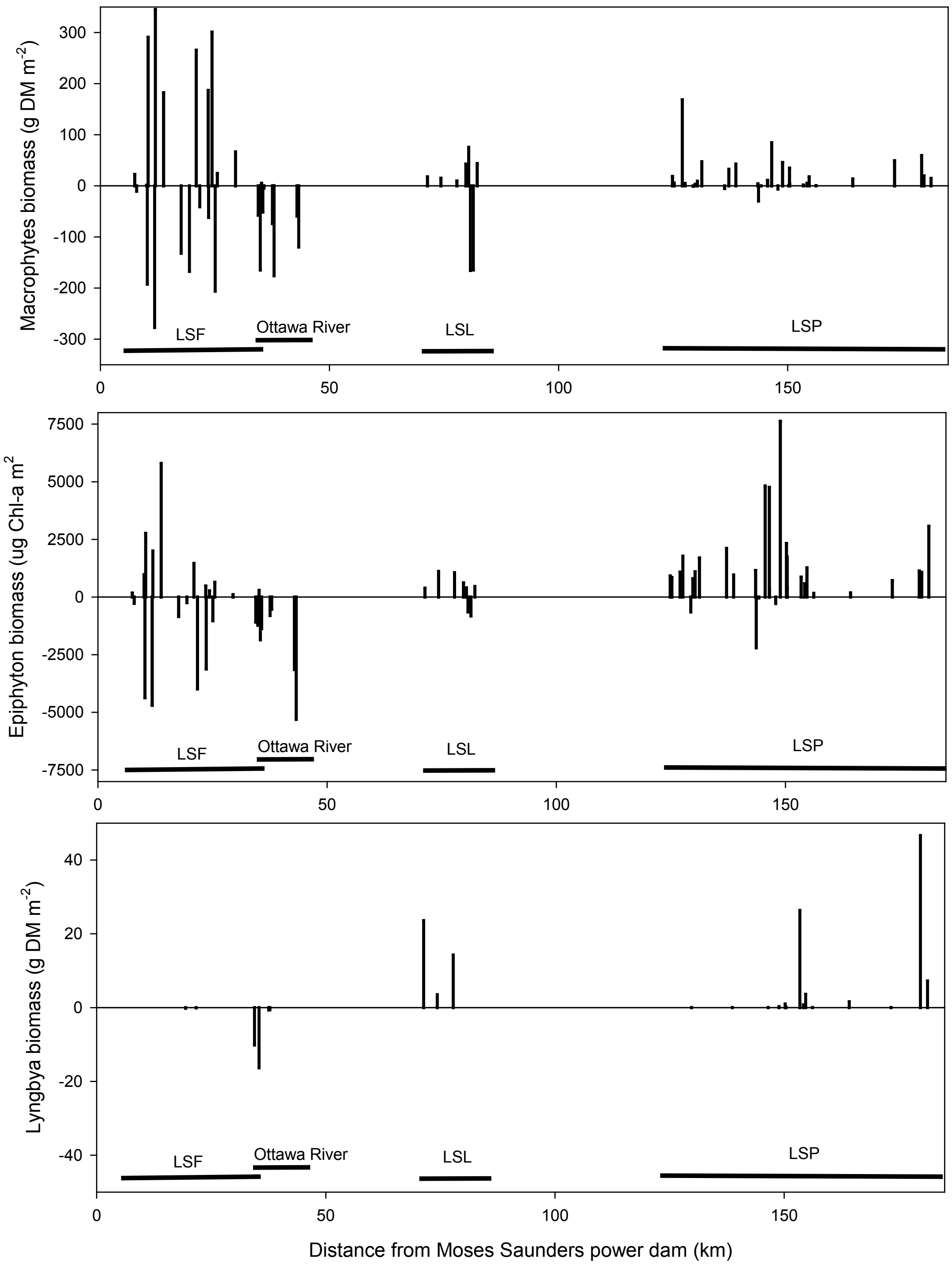

Fig. 4.3 Vertical barplot of the biomass of a) submerged macrophytes, b) epiphyton, and c) cyanobacterial mats against distance from the Moses-Saunders power dam, for each major sampling regions (black horizontal bars). The positive portion of the plot represents biomass in the SLR littoral sites and the negative portion, the biomass in tributaries.

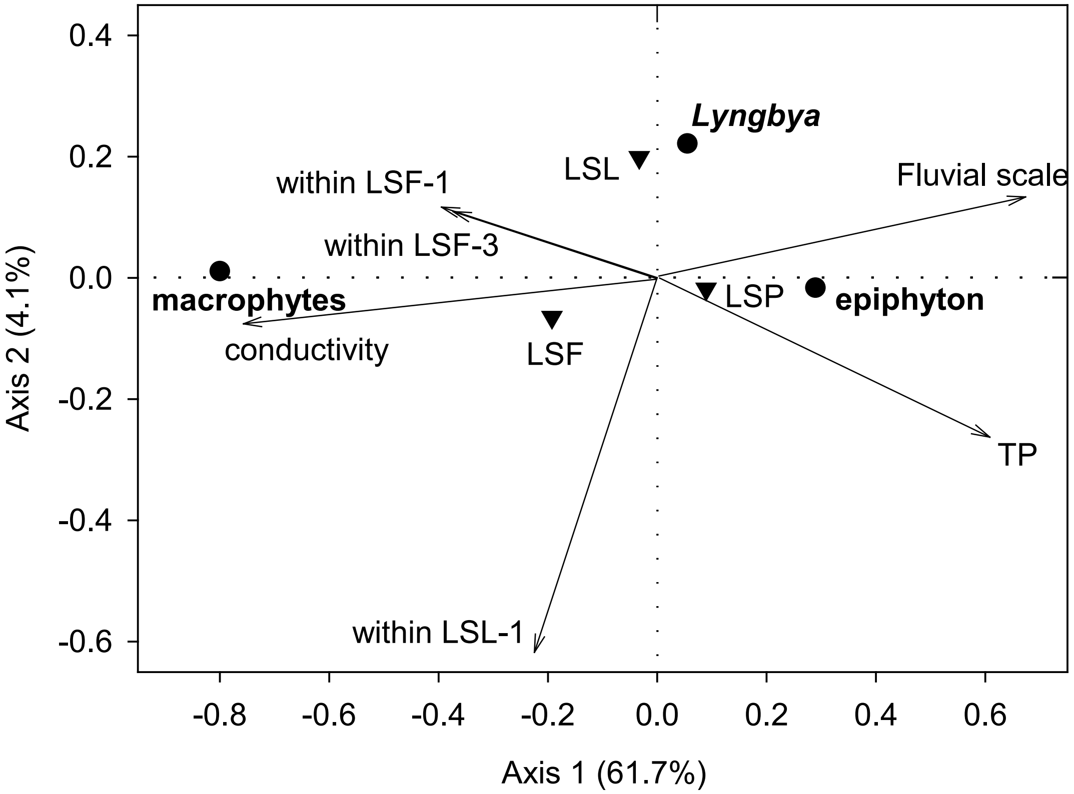

Fig. 4.4 Redundancy analysis (RDA) triplot with scaling type 2. Hellinger transformed biomasses of benthic PP are represented by filled circles. Quantitative environmental and spatial variables selected by forward selection are represented by arrows and centroids of the states of the qualitative variables by filled triangles. The analysis explained 59% of the PP biomass variance.

Table 4.4 Variation partitioning (R^2adj. x 100) of benthic PP community biomass and individual group biomass using environmental factors, fluvial scale, among-lake and within-lake scale variables subsets.

		Benthic PP community	Macrophytes	Epiphyton	Cyanobacterial mats
	Overall model	58.9^{***}	63.7^{***}	36.9^{***}	58.9^{***}
Individual models	Environment	39.7^{***}	36.9^{***}	15.4^{**}	31.8^{***}
	Fluvial scale	26.4^{**}	20.2^{***}	4.0^{NS}	21.3^{**}
	Among-lake scale	30.9^{***}	16.1^{*}	6.6^{NS}	19.0^{**}
	Within-lake scale	48.1^{***}	38.9^{***}	29.1^{**}	58.4^{***}
Pure fractions	Environment	7.0^{*}	17.7^{***}	0.1^{NS}	0.0^{NS}
	Fluvial scale	0.2^{NS}	3.8^{*}	0.0^{NS}	0.0^{NS}
	Among-lake scale	0.1^{NS}	0.7^{*}	0.0^{NS}	0.0^{NS}
	Within-lake scale	14.9^{***}	21.1^{***}	21.3^{**}	12.7^{**}
Fractions explained jointly	Environment∩Fluvial scale	0.0^{NT}	0.0^{NT}	2.0^{NT}	0.1^{NT}
	Environment∩Among-lake	2.3^{NT}	0.0^{NT}	4.3^{NT}	0.1^{NT}
	Environment∩Wihin-lake scale	5.5	3.2	6.8	12.7
	Environment∩Fluvial scale∩Among-lake	0.0	2.3	1.5	0.0
	Environment∩Fluvial scale∩Within-lake	0.4	1.7	0.2	8.0
	Environment∩Among-lake∩Within-lake	2.7	0.7	0.5	6.4
	Fluvial scale∩Among-lake	1.2	0.2	0.0	0.3
	Fluvial scale∩Within-lake	0.0	0.0	0.0	7.4
	Among-lake∩Within-lake	0.0	0.0	0.0	6.7
	Fluvial scale∩Among-lake∩Within-lake	2.4	0.9	0.3	0.0
	Env∩Fluvial scale∩Among-lake∩Within-lake	22.2	11.3	0.0	4.5

Note - * $p < 0.05$, ** $p<0.01$, ***$p < 0.001$, NS not significant. Intersections (fractions explained jointly) are not mathematically testable. Selected environmental factors were: conductivity and TP for the benthic PP community; conductivity for the macrophytes; light extinction coefficient and the DIN:TDP for the epiphyton; DOC and NH_4^+ for cyanobacterial mats.

4.5.1 Factors controlling the biomass of benthic primary producers

Conductivity possesses good integrator capabilities across multiple scales and is often the most important environmental variable controlling macrophytes (Capers et al. 2010, O'Hare et al. 2012, Alahuhta and Heino 2013) and benthic algae (Biggs 1995) in large-scale studies. Indeed, conductivity represents a reliable surrogate to nutrient concentrations because, although they are generally positively correlated, the major ions that conductivity represents are less subject to the influence by biological processes (Biggs, 1988). The apparent decreasing gradient of conductivity in the littoral zone of SLR is likely related to the difference in geology between water coming from the Great Lakes in the interior lowlands (high conductivity) and water coming from the Canadian shield (low conductivity). This decrease in conductivity and increase in TP is also amplified by changes in land use (Biggs 1995) from the rural section in LSF, crossing the heavily urbanized and densely populated section in LSL, toward LSP were land use is dominated by farmland. The association of TP with benthic PP biomass is a reflection of the nutrient acquisition of the different functional groups: epiphyton is dependent upon the water column nutrient concentrations (Vadeboncoeur and Steinman 2002), whereas macrophytes rely more on sediment nutrients via root absorption (Carignan and Kalff 1980, Barko and Smart 1986) and cyanobacterial mats on a combination of the two along with recycling through the mat (Stevenson et al. 1996). Biomass of epiphyton was positively associated with DIN:TPD, reflecting the degradation of the tributaries of SLR along the river continuum. Tributaries bring enriched nutrient concentrations in the littoral zone of SLR, particularly in LSP, where epiphyton is abundant, showing that tributary confluences are key ecological nodes (Thorp et al. 2006). The positive relation between epiphyton biomass and the light extinction coefficient is probably the reflection of the optic water properties of SLR, also controlled by geology. DOC and NH_4^+ were also previously documented as environmental factors explaining the distribution and biomass variation of cyanobacterial mats in SLR (Levesque et al. 2012, Levesque et al. Accepted in Freshwater Science).

Although the importance of direct environmental selection was only important for the benthic PP community and specifically for macrophytes, a large portion of the variation was explained by environmental variables that were structured spatially at all scales studied (fluvial scale, among lakes and within lakes) a common feature in similar studies (Capers et al. 2010, O'Hare et al. 2012, Alahuhta and Heino 2013). The importance of the within-lake scale alone for the whole benthic community and each functional group might be indicative of the importance of autogenic biological processes (e.g. competition, grazing) and that environmental factors act at smaller scale than the one sampled (<10 km) (Legendre and Legendre 2012). In a management perspective, our results indicate that small-scale actions must be undertaken to preserve the integrity of the benthic primary producer community. The small importance of 250-km-long fluvial scale alone showed that benthic PP community are spatially structured at a scale inferior to 250 km and thus that dispersion limitation occurred in microorganisms as well as macrophytes that possessed larger dispersion propagules (Chytry et al. 2012). This dispersion limitation might be associated with different water masses (both chemically and physically) of the St. Lawrence, that do not readily mix owing to rapid downstream advection (Hudon and Carignan 2008, Massicotte and Frenette 2011).

Part of the unexplained variation in our general model could result from the high variation in community organisation, originating from stochastic events disrupting patches of benthic PP (Thorp et al. 2006, Capers et al. 2010). Vulnerability to stochastic hydro-climatic events (drought, drag by ice, strong winds and waves, high spring discharge) increase from the stabilized LSF to the high amplitude LSP, which are also subjected to one major (inflow of Ottawa River into LSL) or multiple minor tributaries (in LSP) (Table 5.1). This stochastic effect could be exemplified by the impact of the extremely low water levels experienced in 2007, which may have amplified the among-lake differences in benthic PP. Since submerged macrophytes usually have shallow buried belowground structures (Wetzel 2001) they are susceptible to water level decline as was shown by the low survival of macrophytes after a 1-year drop in water level in SLR (Hudon 1997). With increasing distance from the Moses-Saunders dam, the rising amplitude of seasonal water level variation would exert a more important impact on benthic PP in LSF than in LSL and LSP. Stochastic events can therefore break the annually repeated succession ruled by seasonal replacements of species and instead allow more importance to dispersion where species colonized a previously disturbed environment to fill empty niches (Thorp et al. 2006).

4.5.2 Revisiting concepts addressing spatial gradients in river systems

As predicted by the RCC (Vannote et al. 1980), littoral zone of the SLR became progressively more turbid, enriched in DOC and in nutrients (N and P, both in dissolved and total concentration) along its course. Overall, benthic PP community biomass decreased along the river continuum (Vannote et al. 1980), driven by a strong decrease of macrophytes, although cyanobacterial mats and epiphyton showed opposite trends. It should nevertheless be pointed out that the decrease in macrophyte biomass did not lead to changes in community composition.

In contrast, predictions of the serial discontinuity concept were verified by the high biomass of macrophytes that we recorded in LSF, downstream of the Moses-Saunders power dam (Ward and Stanford 1983), although water clarity in the upper SLR results from its origin in the Great Lakes rather than the presence of the dam itself. However, wetland areas did not increase downstream as predicted by the serial discontinuity concept extension (Ward and Stanford 1995), as shown by the low wetland area in the heavily urbanized LSL, indicative of the major impact of anthropogenic activities on fluvial landscape despite the increasing range of water level variations and discharge (Table 4.1) with the distance downstream. In summary, the spatial changes across the SLR fluvial lakes are partially consistent with the presence of a fluvial gradient along the SLR longitudinal axis but are best described by an assemblage of heterogeneous patches induced by human activities at small (tributaries) and large (dams) scales (Thorp et al. 2006). Given the major importance of submerged macrophytes as habitat for microfauna and fish that feed on them, water quality of all the tributaries of the St. Lawrence is likely to have a significant cumulative impact on river ecosystems at the fluvial scale. Our study shows that the sum of local effect indirectly have a significant overall repercussion on river ecosystems and, thus, that regional-scale management of small watersheds could improve ecological condition of SLR.

5.6 Acklowledgements

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5. Benthic cyanobacterial mats serve as a refuge and food for the amphipod *Gammarus fasciatus*

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5.1 Abstract

We investigated the ecological role of *Lyngbya wollei* (Farlow ex Gomont, comb. nov.) cyanobacterial mats in aquatic ecosystems, especially as a food source and shelter for the amphipod *Gammarus fasciatus* (Say). For this, we offered amphipods a choice between mats of *L. wollei* and either chlorophytes (*Spirogyra, Rhizoclonium*) or an artificial mat made of acrylic wool in laboratory experiment. Moreover, we reconstructed *in situ* amphipod diet using a dual isotope mixing model ($\delta^{13}C$ and $\delta^{15}N$). *Gammarus fasciatus* consistently selected the substratum offering the best light refuge (Acrylic>*Lyngbya*=*Rhizoclonium*>*Spirogyra*). Neither the presence/absence of saxitoxins, nor the tissue elemental composition and epiphyte abundance exerted any significant effect on substratum choice. *Lyngbya wollei* and its epiphytes constituted 36 and 24%, respectively, of the *in situ* diet of *G. fasciatus* whereas chlorophytes, macrophytes and associated epiphytes represented a less important fraction of its diet. Benthic cyanobacterial mats should be considered a good shelter and food source for small omnivorous invertebrates such as amphipods.

5.2 Introduction

Proliferations of the benthic filamentous mat forming cyanobacterium *Lyngbya wollei* (Farlow ex Gomont, comb. nov.) in North America have been increasingly reported in the last 30 years (Speziale and Dyck 1992, Stevenson et al. 2007, Hudon et al. 2014). Despite the occasionally large biomass reached by these mats (Stevenson et al. 1996), their role as habitat and food source for invertebrates is largely unknown (Hudon et al. 2014). Areas dominated by mats of *L. wollei* are associated to habitat degradation, supporting less biomass of plants, invertebrates, and large fish, lower fish species richness, and slower-growing juvenile perch than macrophyte-dominated wetlands (Hudon et al. 2012). *Lyngbya wollei* is considered a poor food resource owing to its thick sheath that reduces herbivory (Camacho and Thacker 2006). It may also be an unsuitable food choice because production of saxitoxins by *L. wollei*, which have been consistently reported from Florida to the St. Lawrence River (Foss et al. 2012, Lajeunesse et al. 2012). Gammarid amphipods collected at sites where *L. wollei* occurred showed signs of physiological stress (Gelinas et al. 2013), although saxitoxin extract seemed to stimulate consumption by the amphipod *Hyalella azteca* (Saussure) in feeding choice experiment (Camacho and Thacker 2006).

Despite these potentially negative traits, substantial biomass of the amphipod *H. azteca* was found within mats of *L. wollei* in Lake Guntersville (AL, USA; Camacho and Thacker, 2006). Similarly, the gammarid amphipod *Gammarus fasciatus* (Say) was consistently more abundant (25 mg g^{-1} vegetation dry mass) in *L. wollei* mats than in filamentous green algae and macrophytes ($\leq$8 mg g^{-1} vegetation dry mass) in the St. Lawrence River (Tourville Poirier et al. 2010).

The positive association between *L. wollei* and *G. fasciatus* provides an opportunity to investigate the ecological role of cyanobacterial mats in aquatic ecosystems as a refuge and as food for omnivorous invertebrates. Refuge and food are fundamental criteria for habitat selection by animals in general and amphipods in particular (Buschmann 1990, Duffy and Hay 1991, Norderhaug 2004). The potential of a habitat to provide refuge from predation (Zamzow et al. 2010, Camacho and Thacker 2013), competition (Edgar 1983), and physical disturbance (Fenwick 1976) is influenced by its architecture, which defines the number, size, shape, and arrangement of habitable spaces and structures for a given organism (Hacker and Steneck 1990). Mats of *L. wollei* should be an efficient refuge since filamentous and branched algae have been shown to present a higher density of interstitial spaces and branches than those of foliose and leathery macrophytes in marine system (Hacker and Steneck, 1990). With respect to food, aquatic macroinvertebrates can feed either directly on the vegetation (macrophytes and metaphyton) or indirectly on epiphytes, fungi, bacteria, and protozoa associated with it (Cattaneo 1983, Kitting et al. 1984, Christie et al. 2009). Additionally, a temporal and spatial segregation between refuge and food acquisition has been observed for marine amphipods hiding during the day and foraging at night in different vegetation types (Edgar 1983, Aumack et al. 2011).

To better understand the ecological role of benthic cyanobacteria in the aquatic food web, we used laboratory multiple-choice experiments under light/dark conditions comparing amphipods' selection between *L. wollei*, natural and artificial mats of different architecture and food potential. The outcome would indicate whether the strong association of amphipods with cyanobacterial mats was related to shelter from predators (Duffy and Hay 1991, Camacho and Thacker 2013), to selection for high food quantity or palatability (Buschmann 1990, Schneider and Mann 1991), or to both. We interpreted the substratum preference pattern observed in the choice experiments by keeping into account carbon, nitrogen (N), and chlorophyll-a (Chl-a) content of the different substrata and the presence and quality of epiphytes. We expected amphipods to select mats offering the best cover in the light treatment and to select the most nutritious substratum (N%, C:N, Chl-a, epiphyte quantity and quality) in the dark treatment. Additionally, isotopic analyses (δ^{13}C and δ^{15}N) were used to test *in situ* consumption of different vegetation types.

5.3 Material and Methods

5.3.1 Field collection

Amphipods and aquatic vegetation were collected on 3 dates in August and September 2012 at several sites in the littoral zone of the St. Lawrence River, namely two fluvial lakes located near Montreal, Quebec, Canada (Lake Saint-Pierre: 46.17451 N, -72.802652 W and

Lake Saint-Louis: 45.42764 N, -73.846065 W). Water at these sites was turbid (Secchi depth 30-50 cm) with moderate conductivity (257-266 µS cm^{-1}) and nutrient concentrations (TP=29-82 µg P L^{-1}; TN=377-950 µg N L^{-1}), and relatively high DOC (4-6 mg C L^{-1}) (Lévesque, unpubl. data). Since no filamentous chlorophytes bearing epiphytes were found during sampling, additional samples of *Rhizoclonium*, previously found in SLR (Cattaneo et al., 2013),were collected in an urban pond (Beaubien Park; 45.51573 N, -73.608688 W) located close to Université de Montréal.

5.3.2 Laboratory handling

Upon arrival to the laboratory, amphipods and vegetation were kept separately in filtered (Whatman GF/C glass fiber filters) aerated water from sites where *L. wollei* was collected. Amphipods, identified as *Gammarus fasciatus* (confirmed on fixed animals after the experiments) and with a body length ≥7 mm to exclude small juveniles, were sorted from mats of *L. wollei* and held in laboratory aquaria under ambient temperature (20-24 °C) and light (~13 µE m^{-2} s^{-1}) and used within 1-2 d of collection.

Natural and artificial mats

In our choice experiments, we contrasted the benthic cyanobacterium *Lyngbya wollei* with the filamentous chlorophytes *Rhizoclonium* and *Spirogyra,* all of which typically occur in the St. Lawrence River. Furthermore, to differentiate between refuge and food, we used black acrylic wool as an artificial substratum with similar habitat architecture to *L. wollei.* Wool was either deployed for 28d in Lake Saint-Pierre close to *L. wollei* mats to allow epiphyte colonization or placed 24h before the experiment in aerated filtered water.

Quantity and quality of food offered to amphipods was assessed by measuring carbon, nitrogen, and Chl-a content of all types of mats tested in the experiments. Identifications and measurements of algal and wool filament width for 5-15 filaments of each type were made under an optical microscope (Leitz Orthoplan, Wetzlar, Germany) fitted with a calibrated ocular micrometer. Loosely attached epiphytes and debris were manually removed from weighted subsamples of natural and artificial mats by gentle shaking in water. Epiphytic algae, thus resuspended, were concentrated by centrifugation, then frozen and freeze dried. A subsample of epiphyte suspension was fixed in Lugol's and used for microscopical measurement (x400) of the percentage of cyanobacteria, diatoms, or a detritus-sediment-heterotrophic microorganism mix (N=50 fields). After epiphyte removal, subsamples of *L. wollei* and the filamentous chlorophytes were frozen, freeze dried, and ground to powder. Carbon and N content of epiphytes and algal filaments was determined with a Fisons Elemental Analyser 1108 CHNS-O. Chl-a content in epiphytes (mg DM g^{-1} substratum) and in algal filaments (% tissue content) was measured after 24h extraction in 95% ethanol and reading their absorbance spectrophotometrically before and after acidification (Nusch 1980).

Light measurements

We considered the percentage of light absorbed by the different mats as a proxy of their capacity to hide *G. fasciatus* from predators. For this measurement, we placed mats of similar size as those used in the experiments (1 g wet mass) in an aquarium under 10 cm of filtered water and measured the proportion of incident light intensity (Photosynthetically active radiation, PAR) under the mat by placing an optic sensor (JAZ; Ocean Optics, USA) under the aquarium glass. We repeated these measurements 6 times for each mat type. We measured a blank with no mats to correct for the percentage of light absorbed by water and aquarium glass.

Choice experiments: experimental setup

Three experiments were performed offering to *G. fasciatus* a choice between *L. wollei* and various natural (*Spirogyra* and *Rhizoclonium* in Experiments I and II, respectively) and artificial filamentous mats (Experiment III). In Experiments II and III, mats were offered with (natural) and without (clean) the loosely attached epiphytes to investigate the influence of food quantity in the choice of the amphipods. This was not possible in Experiment I because *Spirogyra* is naturally devoid of epiphytes. All experiments were carried out in the laboratory, during daytime, under ambient temperature (20-24°C) and light (~13µE m^{-2} sec^{-1}) roughly corresponding to 1% of outdoor daylight. These conditions closely resemble those occurring just above *L. wollei* mats in the Saint Lawrence River (Levesque et al. 2012).

For each experiment, we used 8 glass rectangular aquaria (20 x 40 cm) filled with 8 L (to about 10 cm depth) of filtered water from the collection site. In each aquarium, *G.*

fasciatus was offered a choice between 4 different mats (1g wet mass) positioned in the aquarium corners (N=8 per treatment for experiments II and III). Experiment I was an exception because only 2 mat types (repeated twice, N=16 per treatment) were offered to G. *fasciatus*. The position of each mat in the different corners of successive aquaria was randomly allocated. Four of the 8 aquaria were covered with an opaque box to determine whether light influenced the amphipod substratum choice. At the beginning of the experiment, 50 amphipods were released in the middle of each of the 8 aquaria, representing a density of 625 individuals m^{-2}, which is in the natural range observed in the St. Lawrence River (0-1594 ind. m^{-2}) (Palmer and Ricciardi 2004). All experiments were run for 5h to allow amphipods enough time to settle within the selected substratum. Generally, amphipods settled in a substratum after 15min and little movement occurred afterwards. At the end of the experiment, a plastic separator was inserted in each aquarium and amphipods on each substratum were counted.

5.3.3 Stable isotope analysis

Isotopic analyses ($\delta^{13}C$ and $\delta^{15}N$) were carried out on *G. fasciatus* (N=7 with 10 whole individuals per replicate) and its potential food sources: *Lyngbya wollei* (N=8) and its epiphytes (N=8), two filamentous chlorophytes composed of *Spirogyra* (N=1) and *Hydrodyction* (N=4), collected in Lake Saint-Pierre and Lake Saint-Louis. *Rhizoclonium* was not analysed for stable isotope because it was absent of our sites during sampling. Additionally, we measured the isotopic signature ($\delta^{13}C$ and $\delta^{15}N$) of the ribbon-forming macrophyte *Vallisneria americana* Michx (N=5), the most commonly observed submerged macrophyte in the St. Lawrence River, and its epiphytes (N=4), as potential *in situ* food sources. *Vallisneria americana* was not used in choice experiments since amphipods were found on this macrophyte in densities ~10 times less to those found in mat of *L. wollei* (Tourville Poirier et al. 2010). Prior to analyses, amphipods were starved for 24h to allow gut clearing and pooled (10 whole individuals per sample) before analysis. Filamentous algae and *V. americana* were carefully washed in tap water to remove all detritus and invertebrates using tweezers. All samples were freeze-dried and then ground to a fine powder using a mortar and a pestle for determination of carbon and nitrogen stable isotope signatures (G.G. Hatch Stable Isotope Laboratory, University of Ottawa, Canada). Elemental and isotopic analyses were carried out on weighed amounts of powdered samples inside tin capsules using Vario EL III (Elementar, Germany), Conflo II and DeltaPlus XP IRMS (ThermoFinnigan, Germany). The data were normalized using internal standards previously calibrated with international standards IAEA-CH-6, IAEA-NBS22, IAEA-N1, IAEA-N2, USGS-40, USGS-41; analytical precision (2 SD) was ±0.2‰ (Pella 1990).

5.3.4 Isotope mixing model

We used a multiple sources dual isotope mixing model (Phillips and Gregg, 2003; Parnell et al., 2010) to reconstruct the natural diet of *G. fasciatus*. Specifically, we used the mixing model SIAR that estimates dietary habits by fitting a Bayesian model (Parnell et al., 2010). SIAR accounts for variation in consumer (*G. fasciatus*), source and isotopic discrimination values (i.e., the change in isotope ratio from source to consumer tissue) and allows inclusion of concentration dependence. We performed a mixing model assuming the general trophic discrimination value of δ15N=2.3±0.18‰ and δ13C=0.5± 0.13‰ (McCutchan et al. 2003).

5.3.5 Statistical analysis

We compared mean proportions of light absorbed by the different substrata with Kruskal-Wallis nonparametric analysis of variance (np-ANOVA; package 'stats') followed by multiple comparisons of medians (package 'pgirmess') in the R statistical program (version 2.12.2, R Development Core Team 2011, Austria).

For multiple choice experiments, we compared mean proportions of amphipods (arcsine-transformed) among the treatments (substratum and light/dark with interaction) with mixed effect modeling using replicate aquaria as the random factor for the intercept (Zuur et al., 2009) (R- package 'nlme') For each experiment, a reduced model was constructed using stepwise backward deletion of non-significant (p>0.05) terms from the global model following the procedure described in Zuur et al. (2009). Since random effect was never significant, differences between substrata and light/dark conditions were tested as main effects with generalized least square (GLS). When a significant effect was detected, multiple comparisons were then made (function glht of R package 'multicomp').

Additionally, the relationship between the proportion of light absorbed by each substratum and the proportion of amphipods selecting each one was modelled using type II ranged major axis (RMA) regression (Legendre and Legendre, 2012) ('lmodel2' package), since both variables are subject to measurement errors (Legendre and Legendre, 2012).

5.4 Results

5.4.1 Characterization of the substrata

The different mats offered to the amphipod *Gammarus fasciatus* had contrasting morphological characteristics and provided widely different tissue elemental composition, epiphyte abundance and light absorbance (Table 5.1 and 5.2). *Lyngbya wollei* is a benthic cyanobacterium characterized by large filaments (54 µm diameter), which include a thick sheath (10 µm). *Rhizoclonium* with large (95 µm-thick) unbranched filaments is architecturally similar to *L. wollei*. Both *L. wollei* and *Rhizoclonium* supported large amounts of epiphytes with similar percentages of diatoms and cyanobacteria and rather high presence of a detritus-sediment-heterotrophic microorganisms mix (67 and 70%, respectively; Table 5.1). Spirogyra filaments (65 µm diameter) surrounded by mucilage formed diffuse mats, largely devoid of epiphytes. Filaments of acrylic wool were by far the widest with 1911 µm of diameter. Epiphyte cover on *in situ* colonized wool was mixed with a high percentage of detritus-sediment-heterotrophic microorganisms (84%; Table 5.1).

In comparison to other substrata and their epiphytes, *Lyngbya wollei* had the lowest C:N ratio (6.8) and the highest N content (5.4%, same as the single sample of *Spirogyra*). *Lyngbya wollei* exhibited intermediate chl-a content in its tissues (0.7%), lower than *Spirogyra* (1.3%) but higher than *Rhizoclonium* and *Vallisneria* (<0.5%). *Lyngbya wollei* supported higher biomass of epiphytes than other vegetation types, although the low Chl-a content and high C:N ratio of epiphytes together with their composition (%) indicated a large detritic component (Table 5.1).

The potential of different mats to offer visual refuge was estimated by comparing the proportion of light (PAR) they absorbed. All mat types absorbed at least 89% of the incident light, but *Spirogyra* absorbed significantly less light than natural mats of *L. wollei* (p=0.002) and *Rhizoclonium* (p=0.006) and the colonized acrylic wool (p≤0.001) (Table 5.2). Natural mats of *L. wollei* and *Rhizoclonium* absorbed similar proportions of light (median values ~97.5%, p>0.999). Removing loosely attached epiphytes and debris from the mats of *L. wollei* and *Rhizoclonium*, did not significantly influence their light absorption (p=0.247, and p=0.930, respectively). In contrast, a significant difference in light absorption (~8%, p<0.001) occurred between uncolonized acrylic mats and those colonized *in situ*, owing to the coarse texture of the acrylic fibers, which favored sediment accumulation within large gaps in their loose matrix.

Table 5.1 Mean±SE (N) of different characteristics of the substrata offered to Gammarus fasciatus in multiple-choice experiments (MC) and considered in stable isotope analyses (SI). NA: not applicable, ND: not determined.

	Lyngbya (MC, SI)	*Spirogyra* (MC, SI)	*Rhizoclonium* (MC)	Acrylic wool (MC)	*Vallisneria* (SI)
Filament width (μm)	54±2 (5)	65±1 (5)	95±3 (15)	1911±38 (5)	5334±646 (6)
Nitrogen (% tissue content)	5.4±0.2 (11)	5.4 (1)	2.7±0.4 (6)	NA	3.2±0.2 (7)
Carbon:Nitrogen (mass ratio)	6.8±0.2 (11)	8.2 (1)	15.8±2.3 (6)	NA	11.8±0.9 (7)
Chl-a (% tisssue content)	0.65±0.17 (10)	1.29 (1)	0.35±0.01 (6)	NA	0.47±0.06 (6)
Epiphyte composition (% cyanobacteria/diatoms/sediment-detritus)	14/18/68	NA	16/14/70	2/14/84	32/14/54
Epiphyte N (%)	1.5±0.2 (10)	NA	ND	0.2±0.01 (2)	2.6±1.1 (2)
Epiphyte C:N (mass ratio)	10.1±0.9 (10)	NA	ND	7.9±0.3 (2)	8.1±1.4 (2)
Epiphyte Chl-a (mg DM g^{-1} substratum)	0.35±0.07 (15)	NA	0.14±0.04 (3)	0.46±0.13 (3)	1.18±0.04 (6)
Epiphyte biomass (g DM g^{-1} substratum)	1.03±0.34 (11)	undetectable	0.15±0.04 (3)	2.21±0.11 (3)	0.57±0.17 (6)

Table 5.2 Proportion of incident light absorbed (median and range, N=6) by 1 g (wet mass) mat of filamentous substratum supporting either their natural epiphytes (natural) or after manual removal of epiphytes (clean). Substratum for which median differ significantly ($p < 0.05$) are identified by different letters (Kruskal-Wallis nonparametric analysis of variance (np-ANOVA) followed by multiple comparisons of medians).

	Light absorbed (%)	
Lyngbya (natural)	97.7^{ab}	(97.1-98.8)
Lyngbya (clean)	94.0^{bcd}	(92.0-95.1)
Spirogyra (natural)	89.2^{d}	(87.9-90.7)
Rhizoclonium (natural)	97.4^{abc}	(96.6-98.2)
Rhizoclonium (clean)	96.5^{abcd}	(94.9-97.1)
Acrylic wool (colonized)	99.8^{a}	(99.5-100.0)
Acrylic wool (clean)	92.1^{cd}	(89.9-92.8)

5.4.2 Substratum choice experiments

Gammarus fasciatus selected mats of *L. wollei* in significantly larger proportion than *Spirogyra* (Experiment 1, Table 5.3 and Fig. 5.1a). The amphipods showed no preference between mats of *L. wollei* and mats of *Rhizoclonium*, regardless of the amounts of epiphytes (Experiment II, Table 5.3 and Fig. 5.1b). Finally, *G. fasciatus* markedly preferred the acrylic mats colonized by epiphytes to cleaned *L. wollei*, with an intermediate selection for *L. wollei* mats with their natural epiphyte cover and clean acrylic mats (Experiment III, Table 5.3 and Fig. 5.1c). In all three experiments, the light/dark treatment, accomplished by covering 4 of the 8 aquaria with an opaque box, did not affect the substratum choice of *G. fasciatus* (Experiment I, GLS, p=0.98, df=2; Experiment II, GLS, p=0.99. df=2; Experiment III, GLS, p=0.97. df=2).

Across all experiments, amphipod preference towards the different filamentous substrata was significantly correlated with their light absorption capacity (R^2=0.53, N=7, p=0.034; Fig. 5.2).

5.4.3 Isotopic signatures of amphipods and their food sources

Isotopic signatures ($\delta^{15}N$ and $\delta^{13}C$) of the different types of vegetation were distinct (Fig. 5.3a). *Lyngbya wollei* and its epiphytes were considerably more $\delta^{13}C$ depleted than the other vegetation types. The two chlorophytes, *Hydrodictyon* and *Spirogyra*, exhibited large difference in their $\delta^{15}N$ and $\delta^{13}C$ signature. *Gammarus fasciatus* had a $\delta^{13}C$ signature which lay between those of *L. wollei* and the epiphytes of *V. americana* (Fig. 5.3a).

The mixing model indicated that *L. wollei* constitute the most important part of the diet of *G. fasciatus* with a mean±SD of 36.5±12.4%, followed its epiphytes with a mean value of 24.3±13.3% (Fig. 5.3b). The mat forming chlorophytes *Hydrodictyon* and epiphytes of *V. americana* seemed to constitute ~13% of the *G. fasciatus* diet, whereas *V. americana* and the filamentous chlorophytes *Spirogyra* appear less important food sources for *G. fasciatus* (<8%).

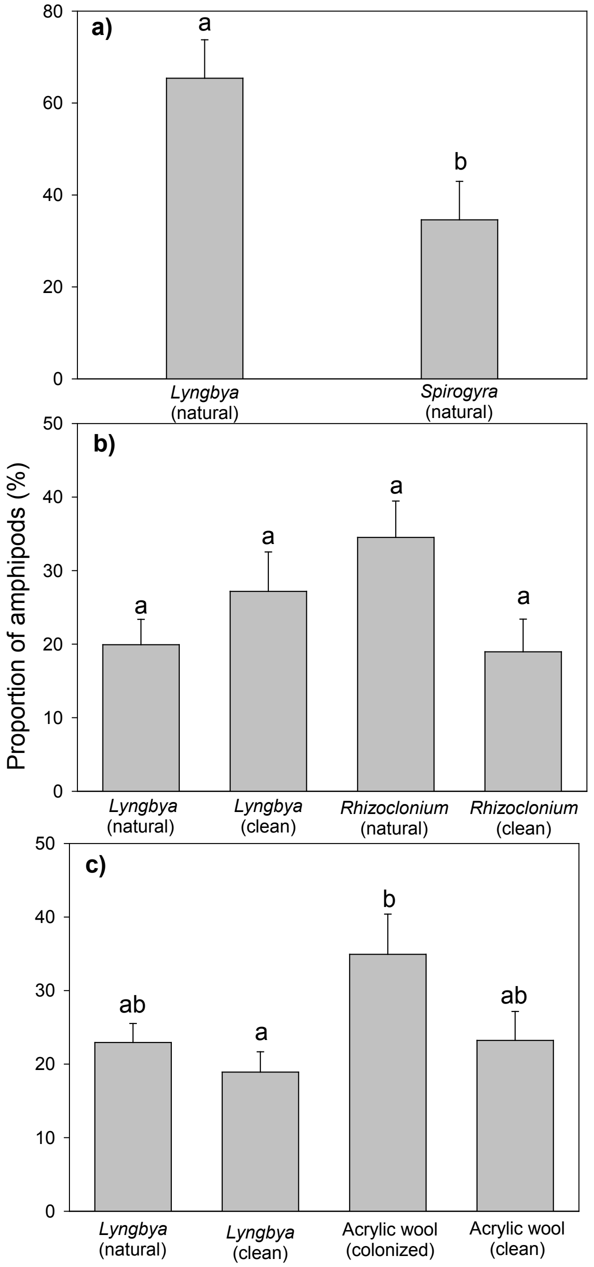

Figure 5.1 Proportion of *G. fasciatus* individuals found (mean±SE; grey bars with error bars) within different mat types after choice experiments. a) Experiment I, choice between *L. wollei* and *Spirogyra*; b) Experiment II, choice between *L. wollei* and *Rhizoclonium* supporting either their natural epiphytes (natural) or after manual epiphyte removal (clean); c) Experiment III, choice between *L. wollei* and acrylic wool with and without (clean) epiphytes. Substrata for which means differed significantly ($p < 0.05$) are identified by different letters (mixed effect modeling followed by multiple comparisons).

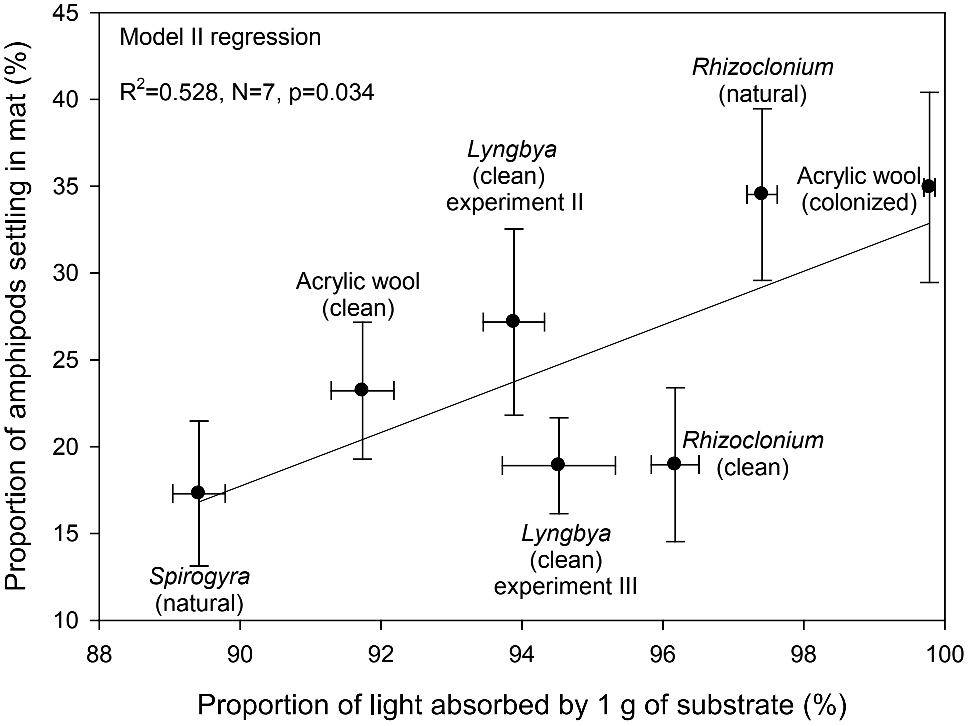

Figure 5.2 Relationship observed in choice experiments between the proportion of amphipods settling in a given substratum and the proportion of light absorbed by 1 g (wet mass) of that substratum. Natural mat of *Lyngbya* were excluded as it was the comparative element used in all experiment. Data were arcsine-transformed before the regression; the probability of a significant relationship was determined from 9999 permutations.

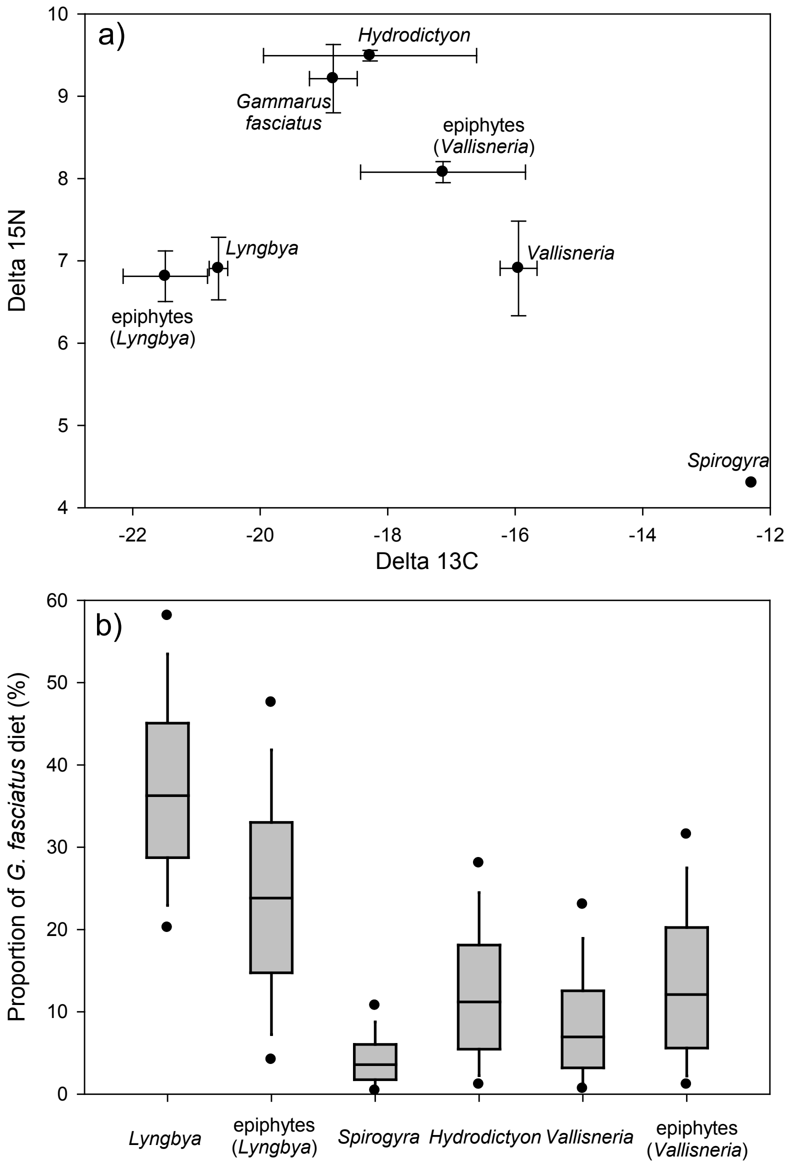

Figure 5.3 a) Average (±SE) isotopic signature of δ13C (X-axis) and δ15N (Y-axis) for *Gammarus fasciatus* (N=12) and potential food sources: *Lyngbya wollei* (N=9), epiphytes of *L. wollei* (N=9), *Vallisneria americana* (N=5), epiphytes of *V. americana* (N=4), filamentous chlorophytes (N=7). b) Box plot of the proportion of each potential food source consumed by the amphipod *Gammarus fasciatus* estimated from the mixing model. For each plot, the boundary of the box indicates the 25th and 75th percentiles, the line within the box marks the median, whiskers above and below the box indicate the 5th and 95th percentiles and dots indicate outliers.

5.5 Discussion

5.5.1 Refuge: light avoidance and habitat architecture

Our first question was whether mats of *Lyngbya wollei* are chosen by amphipods primarily as a refuge from predation. In our experiment, we used the proportion of light absorbed in PAR by the mats as a proxy for habitat architecture, which is notoriously difficult to quantify (Warfe et al. 2008). Wavelengths in PAR (400-700 nm) encompass the visual spectrum of crustaceans in freshwater usually ranging between 515 and 635 nm (Marshall et al 2003). In our experiments, *Gammarus fasciatus* consistently selected the substratum offering the best cover (highest light absorption), regardless of the tissue elemental composition or epiphyte abundance of the available substrata. Despite its high N and Chl-a tissue content, *Spirogyra* (Experiment I) was avoided in favor of *L. wollei*. In addition to the poor shading capacity of *Spirogyra*, the loose mats of its mucilage-covered filaments may have offered a low refuge potential presenting few interstitial spaces for cryptic *Gammarus* (Hacker and Steneck 1990). *Rhizoclonium* provides similar shading as *L.wollei*, but was not discriminated by *Gammarus*, despite its lower N and Chl-a tissue content and lower epiphyte biomass than the cyanobacterium (Experiment II). *In situ* however, amphipods that hide in benthic mats of cyanobacteria receive less than 1% of incident light (Levesque et al. 2015, accepted in Freshwater Science) and would likely be better hidden from fish predators than within mats of chlorophytes that generally floats at the surface. Biomass of *G. fasciatus* was indeed 3-fold higher in mats of *L. wollei* than in metaphytic chlorophytes in the St. Lawrence River (Tourville Poirier et al., 2010). Acrylic wool (Experiment III) was the favored substratum by *G. fasciatus* likely because its large fibrous filaments (1911 µm) trapped a mix of epiphytes, detritus, and sediments that blocked nearly all the light. Nevertheless, these acrylic mats were obviously not a food source and their epiphytes comprised a lot of inorganic sediments as indicated by their extremely low N content.

Our findings agree with the well-known amphipod light avoidance (negative phototaxy; Phipps, 1915; Clemens, 1950), which is likely associated with predation escape (Zamzow et al., 2010; Camacho & Thacker, 2013). In laboratory experiments, *Hyalella azteca* chose mats of *L. wollei* over those of *Rhizoclonium* in the presence of Bluegill Sunfish because the cyanobacterium offered best survivorship (Camacho and Thacker, 2013). A habitat architecture that provides hiding from predators is crucial (Zamzow et al., 2010) and often valued more than food (Norderhaug, 2004) by marine amphipods. Indeed, amphipods were more abundant on marine macroalgae providing refuge from predation than on vegetation they preferentially fed on, both in laboratory and *in situ* (Duffy and Hay, 1991; Lasley-Rasher et al., 2011).

Dense algal mats such as those of *L. wollei*, may provide a shelter not only from predators but also from microturbulence, since amphipods tend to avoid current by hiding and foraging within dense algal mats clinging to filaments with their gnathopods (Clemens 1950). At low to medium density of *G. fasciatus*, the habitat architecture of cyanobacterial mats may reduce intraspecific competition (Edgar 1983). At high density, predation on other invertebrates and/or intraguild predation by *G. fasciatus* might prevent overgrazing of the mat via top-down control (Dick and Platvoet 1996, Kelly et al. 2002).

5.5.2 Food source: quality and quantity

We also asked whether *G. fasciatus* would use *L. wollei* and its epiphytes as a food source and not just as a shelter. Although *Lyngbya wollei* is generally considered a poor nutritional source (Camacho & Thacker, 2006), our results from elemental composition (N%, C:N ratio) and isotopic analysis challenge this hypothesis.

In terms of nutritional value, *Lyngbya wollei* was the best food source tested with the highest N content and lowest C:N ratio. Food with elevated N content and low C:N ratio is usually valued by consumers (Sterner & Hessen, 1994) because it is associated with high protein content, which increases invertebrate fitness and growth rates (Cruz-Rivera & Hay, 2000). *Lyngbya wollei* is considered a poor food choice because of its toxin content (Carmichael et al., 1997; Lajeunesse et al., 2012). Amphipods captured in mats of *L. wollei* indeed showed some sign of physiological stress, as evidenced by the higher activities of acetylcholinesterase and glutathione-S-transferase when compared to amphipods from sites devoid of the cyanobacterium (Gelinas et al., 2013). Despite consistent presence of the saxitoxin analogue LWTX-1 in all samples collected from St. Lawrence River (range 0.3-153 μg LWTX-1 g^{-1} DM, Hudon, unpublished data), our laboratory results as well as field observations (Tourville Poirier et al., 2010) showed that amphipods were not deterred by *L. wollei*. Similarly, three out of four gastropods, when offered a choice between *L. wollei* and filamentous chlorophytes, were either indifferent or attracted to the cyanobacterium (Visconti et al., 2014). Additionally, the toxin-producing *Lyngbya majuscula* was consumed by some marine mezograzers, including two amphipods in multiple choice assays (Cruz-Rivera & Paul, 2006).

As suggested by dual isotope ($\delta^{15}N$ and $\delta^{13}C$) mixing model, the most important food source for *G. fasciatus* in our study was *L. wollei* representing 37% of the diet composition followed by its epiphytes (24%) and to a lesser extent by *V. americana* epiphytes and *Hydrodictyon* both with 13% of the diet. The high proportion of *L. wollei* in the diet was somewhat surprising, but amphipods that are opportunistic feeders (Clemens, 1950; Delong et al., 1993) have previously been shown to consume in similar proportion the marine cyanobacterium *L. majuscula* and macroalgae (Cruz-Rivera & Paul, 2006). In freshwater, although small amphipods such as *Hyallela* (≈ 7 mm) may not be able to graze on *L. wollei* (Camacho and Thacker, 2006), *Gammarus fasciatus* (≈ 13 mm) has strong mouthparts (MacNeil et al., 1999) that can likely chew through *L. wollei* thick polysaccharide sheath. Loosely attached epiphytes were not surprisingly an important component of amphipod diet since the latter can consume particles resuspended by their respiratory movements (Hudon, 1983). Epiphytes, which consist of a mixture of bacteria, fungi, protozoa, algae, and particulate organic matter (Cross et al., 2005), are considered a good food source for opportunistic feeders as the amphipods (Clemens, 1950; Delong et al., 1993). The macrophyte *V. americana* was not a prominent food for *G. fasciatus* in the St. Lawrence River as previously found for amphipods in the Hudson River (Cole & Solomon, 2012).

5.5.3 An ideal substratum for omnivorous *Gammarus*

Shelter was clearly favored over food by *G. fasciatus* in our substratum choice experiments. We expected that amphipods would select the most nutritious substratum under dark conditions but our results showed that the choice of *G. fasciatus* was not influenced by light/dark treatment. This is consistent with other results on freshwater (Shannon et al. 1994) and marine (Martinsmith 1994, Poore et al. 2000) gammarid amphipods whose substratum choice was not influenced by light/dark treatment either in laboratory or *in situ*. Other studies, however, suggested that amphipods seek shelter in the vegetation offering the best refuge during the day but forage in vegetation yielding best food at night (Buschmann 1990, Taylor 1998, Aumack et al. 2011).

Our results indicate that the omnivorous *G. fasciatus* finds both refuge and food in the dense *L. wollei* mats and does not need to leave the mat protection to forage elsewhere. Besides, saxitoxin-protected mats of *L. wollei* may deter predators (Camacho and Thacker, 2013) as reported in other chemically-protected marine vegetation (Duffy and Hay, 1994). This coincidence of opportunities may explain the high abundance of amphipods observed in *L. wollei* mats. However, the inaccessibility of these invertebrates for fish predators (Camacho and Thacker, 2013) might contribute to a decoupling between the benthic and pelagic food chain of the St. Lawrence River. Indeed, replacement of submerged aquatic vegetation by mats of *L. wollei* in the St. Lawrence River (Vis et al., 2008) has been associated with a drop in habitat complexity, a shift from mollusc to amphipod dominance, decrease in fish biomass, and poor yellow perch recruitment (Tourville Poirier et al., 2010; Hudon et al., 2012). These responses exemplify the complex sequence of impacts of proliferation of *L. wollei* on aquatic ecosystems.

5.6 Acknowledgements

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6. Conclusion générale

La problématique mondiale entourant l'augmentation des épisodes de floraisons de cyanobactéries, engendré par l'eutrophisation anthropique représente une réelle menace pour les écosystèmes aquatiques et la santé publique. Ces floraisons peuvent, entre autres, engendrer une réduction de la transparence de l'eau, une augmentation du pH, une diminution du CO_2 disponible, la production de toxines et de composés organiques volatils (goût et odeur), la création de zones hypoxiques et la dégradation de l'esthétisme de l'environnement. Ces effets peuvent avoir des conséquences écologiques notables, allant de changements de diversité des communautés aquatiques, jusqu'à des modifications sévères du réseau trophique, et ce sans compter les pertes économiques et les risques de contamination de l'eau potable. Il faut cependant apporter une nuance en mentionnant que les cyanobactéries sont une composante naturelle et normale du phytoplancton et du métaphyton des écosystèmes aquatiques lorsque leur dominance n'est pas favorisée par l'activité humaine. Elles dominent naturellement dans les environnement extrêmes tels que les sources thermales, les ruisseaux intermittents, les lacs hypersalins et les déserts chauds et froids. De plus, elles ont un fort potentiel dans le domaine de la biotechnologie où elles sont utilisées dans la production de molécules thérapeutiques, de biocarburants, de biofertilisants, de cellulose et pour les polyhydroxyalkanoates offrant une alternative biodégradable au plastique issu du pétrole.

Les cyanobactéries sont apparues, il y a environ 3.5 milliards d'années et sont de toutes évidences là pour rester, pour le meilleur et pour le pire. C'est dans cette optique que nous avons jugé nécessaire d'acquérir plus de connaissances au sujet de la cyanobactérie filamenteuse benthique *Lyngbya wollei* dont les épisodes de floraison, potentiellement toxiques et ayant un impact négatif sur les environnements aquatiques, sont de plus en plus reportés en Amérique du Nord (Hudon et al. 2014). Cette thèse a été conduite afin d'évaluer les facteurs environnementaux contrôlant la distribution, la biomasse et la saisonnalité de la cyanobactérie *L. wollei,* dans le fleuve Saint-Laurent et d'approfondir nos connaissances relativement à son rôle trophique. D'abord, nous avons étudié sa répartition ainsi que les conditions chimiques et physiques dans lesquelles cette cyanobactérie se retrouve le long d'un tronçon fluvial de 250 km du fleuve Saint-Laurent, entre Cornwall et Trois-Rivières. Nous avons utilisé ces données afin d'élaborer un modèle permettant de prédire son occurrence dans le Saint-Laurent. Par la suite, nous avons étudié les facteurs hydrologiques contrôlant ses variations de biomasse saisonnière et à fine échelle spatiale le long d'un gradient d'exposition au courant et aux vagues. Nous avons subséquemment évalué l'importance relative de *L. wollei* par rapport aux autres producteurs primaires benthiques du fleuve Saint-Laurent à l'aide d'une approche multi-échelle nous permettant de revisiter certains paradigmes du fonctionnement des grands fleuves. Finalement, nous avons exploré la place qu'occupe *L. wollei* dans la chaîne trophique du fleuve Saint-Laurent en approfondissant les mécanismes expliquant sa forte association avec l'amphipode *Gammarus fasciatus.*

Dans cette section, nous discuterons les principaux résultats de cette recherche en mettant l'accent sur leur originalité et sur leur importance dans la compréhension globale de l'écologie de la cyanobactérie *L. wollei*.

6.1 Prédiction du risque de prolifération de la cyanobactérie benthique *Lyngbya wollei* dans le fleuve Saint-Laurent

L'étude de la distribution à grande échelle (250 km) de *L. wollei* dans le tronçon fluvial du fleuve Saint-Laurent visait à déterminer l'ampleur de la problématique associée à cette cyanobactérie. *Lyngbya wollei* a été observé à 37 des 113 sites échantillonnés, atteignant une biomasse maximale de 46 g DM m^{-2}. Les biomasses récoltées dans le fleuve Saint-Laurent étaient similaires à celles observées dans le lac Érié (Bridgeman and Penamon 2010), mais jusqu'à 30 fois inférieures à celles retrouvées dans le sud-est des États-Unis (Beer et al. 1986, Speziale et al. 1991, Cowell and Silver Botts 1994). *Lyngbya wollei* n'a jamais été retrouvé dans la masse d'eau provenant du lac Ontario ni directement à l'embouchure des 31 tributaires échantillonnés.

Notre prédiction était que les zones littorales calmes du fleuve Saint-Laurent, situées en aval de tributaires riches en nutriments et en matières organiques allaient supporter des tapis de *L.wollei.* En effet, les tapis de filaments étaient généralement présents en aval de la confluence de petits tributaires qui irriguent des terres agricoles. Dans ces zones, l'écoulement lent d'eaux enrichies à travers la dense végétation submergée se traduisait par une diminution de la concentration d’azote inorganique dissous, alors que les concentrations de carbone organique dissous et de phosphore total dissous demeuraient élevées, produisant un rapport DIN:TDP faible.

Selon nos modèles, le DOC (effet positif), le TP (effet négatif) et le DIN:TDP (effet négatif) sont les variables les plus importantes pour expliquer la répartition de *L. wollei*. L'association entre une concentration élevée de DOC (>6 mg C L^{-1}) et la présence de *L. wollei* suggère un effet stimulant des apports de carbone organique provenant du bassin versant, tout comme chez l'espèce marine *L. majuscula* (Albert et al. 2005). Une partie de cette dépendance pourrait être reliée aux besoins en fer de cette espèce, puisque cet élément est fortement lié à la matière organique en eau douce (Hassler et al. 2009), et que le Fe est essentiel au processus de fixation de l'azote atmosphérique. Une autre explication de la correspondance entre *L. wollei* et les apports des tributaires agricoles serait que les apports en carbone organique favorisent l’hétérotrophie comme voie énergétique alternative (Burkholder et al. 2008). L’utilisation du carbone organique par *L. wollei* pourrait de surcroit être favorisée par les conditions à l'intérieur du tapis, incluant l’absence de luminosité et l'anoxie. Les différences de conditions entre l'intérieur des tapis et la colonne d'eau, le recyclage interne des nutriments et l'apport des sédiments (Stevenson et al. 2007) pourraient expliquer la relation négative entre la présence de *L. wollei* et les nutriments (N et P). Ce résultat à tout le moins contre-intuitif souligne l'importante différence entre les cyanobactéries planctoniques et benthiques et appelle à la prudence lors des généralisations sur les conditions favorables aux proliférations de cyanobactéries.

La biomasse de *Lyngbya wollei* était négativement reliée à l'abondance des macrophytes, un phénomène fréquemment observé dans d'autres milieux (Macbeth 2004, Stevenson et al. 2007, Vis et al. 2008, Bridgeman and Penamon 2010). En effet, *L. wollei* semble une espèce opportuniste possédant une grande tolérance aux faibles concentrations de nutriments et de luminosité, lui permettant de coloniser des milieux peu propices aux autres végétaux et ainsi d'éviter la compétition. Sa dominance dans plusieurs environnements semble liée aux perturbations anthropiques et son apparition est un symptôme de la dégradation des écosystèmes plutôt qu’une cause en soi.

Cette étude est la première à développer des modèles prédictifs de la présence et de la biomasse de *L. wollei* en fonction des variables chimiques et physiques du milieu. Ces modèles simples (2-4 variables), validés à l'aide de données indépendantes, ont prédit avec exactitude le risque de prolifération de *L. wollei* dans 72 % à 92 % des cas. Ces succès de prédictions sont comparables à ceux obtenus par Hamilton et al. (2009), qui ont prédit avec succès (aire sur la courbe ROC de 0.91) l'occurrence temporelle des floraisons de *L. majuscula* dans la baie de Deception en Australie avec un modèle bayésien similaire au nôtre avec comme meilleur prédicteur la moyenne mensuelle des températures minimales. De tels modèles simples sont des outils faciles à utiliser par les gestionnaires de l'environnement.

6.2 L'exposition aux vagues et le courant contrôlent l'accumulation de biomasse de la cyanobactérie benthique *Lyngbya wollei* dans un grand lac fluvial.

Comme *L. wollei* peut croître dans une large gamme de nutriments et de luminosité (Hudon et al. 2014), nous avons testé l'hypothèse que l'accumulation de biomasse, tant du point de vue spatial que temporel, était contrôlée par l'exposition aux vagues et au courant dans le fleuve Saint-Laurent. Pour ce faire, nous avons mesuré la biomasse et la condition (C, N, P contenu dans les tissus) de *L. wollei* à 21 occasions entre avril 2009 et octobre 2011, incluant une fois sous la glace en mars 2010, à 10 sites localisés le long d'un gradient d'exposition au vent, vagues et courant dans une baie du fleuve Saint-Laurent où la présence de cette cyanobactérie avait constamment été observée lors d'échantillonnages précédents. Les tapis de *L. wollei,* étant simplement déposés sur les sédiments, ils sont particulièrement influencés par le mouvement de l'eau à l'interface des sédiments.

Du point de vue spatial, nous avons constamment mesuré d'importantes biomasses (>30 g DM m^{-2}) aux sites localisés entre 100 et 250 m de la berge. Le courant et le REI, un indice d'exposition aux vagues basé sur le fetch ainsi que la direction et la vélocité des vents, expliquaient 60.5% de la variation de biomasse de *L. wollei* aux sites avec une profondeur >1m. Le site le moins profond était vulnérable à l'action des vagues et supportait peu de *L. wollei*. Deux études au lac Érié ont obtenu des résultats similaires, alors que *L. wollei* était absent près des berges où la profondeur était <1 m (Bridgeman and Penamon 2010, Panek 2012). Nous avons mis en relief l'effet combiné du courant induit par le débit du fleuve et généré par l'action des vagues sur les patrons d'accumulation de biomasse durant la saison de croissante.

Au niveau temporel, nous avons observé des différences interannuelles de biomasse entre nos trois années d'étude aux 2 sites où la biomasse était maximale. Effectivement, en 2010, année avec un faible débit, la biomasse était élevée (maximum de 101 g DM m^{-2}) alors que pour 2009 et 2011, années avec un débit plus élevé, les biomasses étaient plus faibles (maximum de75 et 58 g DM m^{-2}, respectivement). La biomasse de *L. wollei* augmente lentement de mai à octobre et reste élevée avec 50% de filaments sénescents durant l'hiver. Au printemps, le vent et la crue délogent les matelas et réduisent les biomasses à leur niveau minimal. Malgré d'importantes variations annuelles de biomasse dans le fleuve Saint-Laurent, la composition stœchiométrique (C, N, P) était relativement constante. *Lyngbya wollei* semblait légèrement limité par le P selon les seuils pour les algues benthiques (Hillebrand and Sommer 1999). Les variations annuelles de biomasses étaient le mieux expliquées par le niveau d'eau au cours des 15 derniers jours (45%), qui agissait comme un *proxy* du débit alors que le vent n'était pas un facteur significatif aux sites étudiés. Une étude récente a effectivement montré que la diminution de débit dans les sources de Floride serait en bonne partie responsable de l'augmentation de couverture de *L. wollei* (King 2014).

Notre étude est l'une des rares à quantifier l'exposition aux vagues et au courant de façon quantitative et la première à les mettre en relation avec la biomasse des tapis de cyanobactéries. Nos résultats ont une importance particulière dans un contexte de changement climatique alors que les prévisions indiquent une baisse de niveau du fleuve Saint-Laurent (D'Arcy et al. 2005) ainsi qu'une augmentation en fréquence et en intensité des tempêtes de vents et de pluies (Croley 2003). D'une part, cette diminution de débit risque d'augmenter la superficie colonisable par *L. wollei* et d'autres parts, les forts vents risquent de déloger les tapis et de les rejeter sur la berge, ce qui engendrerait des pertes économiques ainsi que des problèmes de santé publique et d'ordre esthétique.

6.3 Les facteurs environnementaux structurant la communauté de producteurs primaires benthiques à différentes échelles dans le fleuve Saint-Laurent

L'objectif de recherche était de déterminer l'influence de l'échelle spatiale sur le contrôle de la biomasse des producteurs primaires benthiques (*Lyngbya wollei,* macrophytes et épiphytes) par les variables environnementales et les répercussions que cela entraîne sur notre interprétation des modèles théoriques fluviaux. Pour ce faire, nous avons mesuré la biomasse de ces trois types de producteurs primaires (PP) ainsi que les variables environnementales dans trois lacs fluviaux du tronçon fluvial (250 km) du St-Laurent. Nous avons partitionné les variations de biomasse entre les variables environnementales et trois échelles spatiales, soit fluviale, inter-lac et intra-lac, afin de déterminer l'échelle d'action des variables environnementales sur le contrôle des biomasses.

Les biomasses des communautés de PP benthiques du fleuve Saint-Laurent étaient contrôlées, au niveau environnemental, par la conductivité et phosphore total. La conductivité reflétait les changements de l'amont vers l'aval de la géologie et de l'utilisation du territoire du bassin versant du Saint-Laurent. D'autres études rapportent également l'importante influence de la conductivité sur les biomasses et la composition de la végétation aquatique à grande échelle (Biggs 1995, Capers et al. 2010, O'Hare et al. 2012, Alahuhta and Heino 2013). L'importance du phosphore total met en évidence les différentes stratégies d'acquisition des nutriments utilisées par nos trois groupes de PP benthiques. Les épiphytes dépendent des concentrations de nutriments de la colonne d'eau (Vadeboncoeur and Steinman 2002), alors que les macrophytes utilisent l'absorption racinaire pour acquérir leurs nutriments des sédiments (Carignan and Kalff 1980, Barko and Smart 1986) et les tapis de cyanobactéries utilisent une combinaison de ces deux sources de nutriments et font en plus du recyclage à l'intérieur du tapis (Stevenson et al. 1996).

Une large portion de la variation de biomasse des PP benthiques était expliquée par les variables environnementales structurées spatialement à toutes les échelles; un résultat commun dans les études multi-échelles sur les communautés biologiques (Pinel-Alloul et al. 1995, Capers 2000, Alahuhta and Heino 2013). L'importance de l'échelle intra-lac seule pourrait être attribuable aux processus biologiques autogéniques (par exemple, la compétition et le broutage) ou aux facteurs environnementaux agissant à une échelle spatiale plus fine que celle étudiée (<10 km). Ce résultat indique également que des actions locales, à l'échelle du bassin versant de petits tributaires agricoles, peuvent être très efficaces dans la gestion de l'intégrité des communautés de PP benthiques. La faible importance de l'échelle fluviale, longue de 250 km, montre que la communauté de PP benthiques à une capacité de dispersion inférieure à cette échelle. Compte tenu de l'importance cruciale des macrophytes submergées comme habitat de la microfaune et des poissons qui s'en nourrissent, la qualité de l'eau de l'ensemble des tributaires du Saint-Laurent est susceptible d'exercer un impact cumulatif majeur sur les écosystèmes fluviaux. Notre étude illustre que la somme des effets locaux peut exercer indirectement un effet global significatif.

Cette étude est la première à utiliser une approche multi-échelle spatialement explicite intégrant les variables environnementales afin de revisiter certains concepts quant au fonctionnement des grands fleuves. En effet, nous avons utilisé les PP benthiques comme modèle de référence pour tester si leur abondance et composition dans le fleuve Saint-Laurent sont régies par 1) les gradients chimiques et physiques amont-aval décrits par le *River Continum Concept* (Vannote et al. 1980) et ses modifications (Elwood et al. 1983, Ward and Stanford 1983, Junk et al. 1989, Ward and Stanford 1995) ou 2) par l'agencement d'agrégats d'habitat aux propriétés eco-géomorphologiques différentes décrit dans le *Riverine Ecosystem Synthesis* (RES) (Thorp et al. 2006) qui stipule que les grands fleuves sont une mosaïque constitué d'agrégats d'habitat discrètement arrangés. Nous avons observé certains gradients amont-aval dans les zones littorales du SLR où l'eau devenait progressivement plus turbide, enrichie en carbone organique dissous et en nutriments. La biomasse totale des PP benthiques diminuait tel que prédit par le RCC, mais uniquement pour les macrophytes. Aussi, bien qu'une forte biomasse de macrophytes ait été mesurée en aval du barrage Moses-Saunders, la superficie de milieu humide n'augmentait pas de l'amont vers l'aval comme prédit par le *Serial Discontinuity Concept* (Ward and Stanford 1995). Donc, les patrons spatiaux le long du SLR sont seulement partiellement attribuables aux gradients longitudinaux et sont mieux décrits par l'assemblage hétérogène d'agrégats d'habitat induits par l'activité humaine à fine échelle avec les tributaires et à large échelle avec les barrages.

6.4 Les tapis de cyanobactéries benthiques servent de refuge et de nourriture à l'amphipode *Gammarus fasciatus*

Les tapis de *L. wollei* sont généralement considérés comme un mauvais habitat (Hudon et al. 2012) et une piètre ressource alimentaire (Camacho et Thacker 2006). Pourtant, de grandes biomasses de l'amphipode *Gammarus fasciatus* ont été retrouvées dans les tapis de *L. wollei* du fleuve Saint-Laurent (Tourville Poirier et al. 2010). Nous avons donc examiné le rôle écologique de *L. wollei* en tant que refuge et source de nourriture en présentant différents choix de substrats filamenteux (*Lyngbya wollei*, les chlorophytes *Rhizoclonium* et *Spirogyra* ainsi que des filaments synthétiques d'acrylique) en condition lumière/obscurité et *in situ* avec des analyses d'isotopes stables ($\delta^{13}C$ et $\delta^{15}N$). Nous nous attendions à ce que les amphipodes choisissent le substrat offrant le plus de couverture dans le traitement lumière et le plus nutritif (de N%, C:N, Chl-a, quantité et qualité des épiphytes) en conditions d'obscurité.

Sans égard au traitement lumière/obscurité, *Gammarus fasciatus* a toujours choisi le substrat offrant la meilleure protection de la lumière (Acrylique > *Lyngbya* = *Rhizoclonium* > *Spirogyra*). La présence de saxitoxines, la composition élémentaire des tissus ainsi que l'abondance et la composition des épiphytes n'ont pas influencé la sélection de *G. fasciatus.* Nos résultats concordent avec la phototaxie négative de *G. fasciatus* associée à l'évitement des prédateurs (Phipps 1915, Clemens 1950). En effet, l'amphipode *Hyalella azteca* préférait les tapis de *L. wollei*, offrant un meilleur taux de survie, à ceux de la chlorophyte filamenteuse *Rhizoclonium* en présence du crapet arlequin lors d'expériences de laboratoire (Camacho & Thacker, 2013).

In situ, *L. wollei* et ses épiphytes constituaient respectivement 36 et 24% de la diète de *G. fasciatus,* alors que les chlorophytes, les macrophytes et leurs épiphytes représentaient une plus petite fraction de sa diète. Ce résultat semble surprenant, mais il est corroboré par le riche contenu en azote des filaments de *L. wollei* et leur faible ratio C:N, deux propriétés prisées par les consommateurs primaires (Sterner and Hessen 1994).

Cette étude est la première à montrer que les tapis de cyanobactéries en eau douce peuvent être à la fois un bon habitat et une source de nourriture, incluant les filaments eux-mêmes, leurs épiphytes et la microfaune associée, pour les invertébrés omnivores tels que les amphipodes. Ces résultats apportent une nuance importante à la vision unilatérale voulant que les tapis de cyanobactéries soient un habitat de piètre qualité en montrant que certains organismes omnivores et tolérants utilisent cet habitat avec efficacité.

6.5 Perspectives

Cette thèse représente un apport important aux connaissances portant sur l'écologie de la cyanobactérie filamenteuse benthique *L. wollei*. Nous avons défini sa niche écologique et sa phénologie dans le fleuve Saint-Laurent en considérant les facteurs physiques et chimiques à fine et à grande échelle. Nous avons élaboré des modèles prédictifs facilement utilisables par les gestionnaires afin de prédire la distribution de *L. wollei.* Nous avons également établi son importance relative face aux autres producteurs primaires benthiques en plus d'avoir déterminé une portion du rôle écologique que cette cyanobactérie en tant qu'habitat et sources de nourriture pour les macroinvertébrés omnivores. Au final, les proliférations de *L. wollei* semblent une conséquence de la dégradation de la qualité de l'eau par l'apport matière organique et de nutriments provenant de certains tributaires enrichis. Cette dégradation devrait s'accentuer durant les prochaines années selon les prévisions du réchauffement climatique, ce qui favorisera les floraisons de *L. wollei* dans le fleuve Saint-Laurent si certaines mesures visant à limiter les apports en nutriments et en matière organique ne sont pas mises en œuvre. Il apparait donc urgent d'intégrer les besoins des organismes vivants et des habitats à ceux des humains quant à la gestion du niveau et de la qualité de l'eau du fleuve Saint-Laurent.

Cette thèse ouvre également la porte à de futures études. D'abord, la compréhension des différentes voies métaboliques et énergétiques (Burkholder et al. 2008) en œuvre chez *L. wollei* permettrait de mieux cerner la vaste palette de conditions environnementales permettant à *L. wollei* de survivre et/ou croître en Amérique du Nord. Ensuite, la taxonomie précaire de *L. wollei* à grande échelle nécessite une étude de la génétique à l'échelle du continent nord-Américain afin de déterminer les conditions environnementales favorisant les trois différents sous-groupes déjà caractérisés (Joyner et al. 2008). Aussi, des recherches décrivant les différents composés bioactifs produits par les trois sous-groupes de *L. wollei,* dont les toxines et leurs effets sur différents organismes vivants, sont nécessaires afin de bien cerner les risques potentiels pour la santé publique et les écosystèmes (Hudnell 2008). La relation entre les tapis de *L. wollei* et les macrophytes submergées reste également à approfondir. Finalement, la relation toxines-facteurs environnementaux mérite un approfondissement afin de comprendre dans quelles conditions les floraisons de *L. wollei* deviennent potentiellement dangereuses.

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Annexe 1. Double-headed rake photograph and biomass calibration method

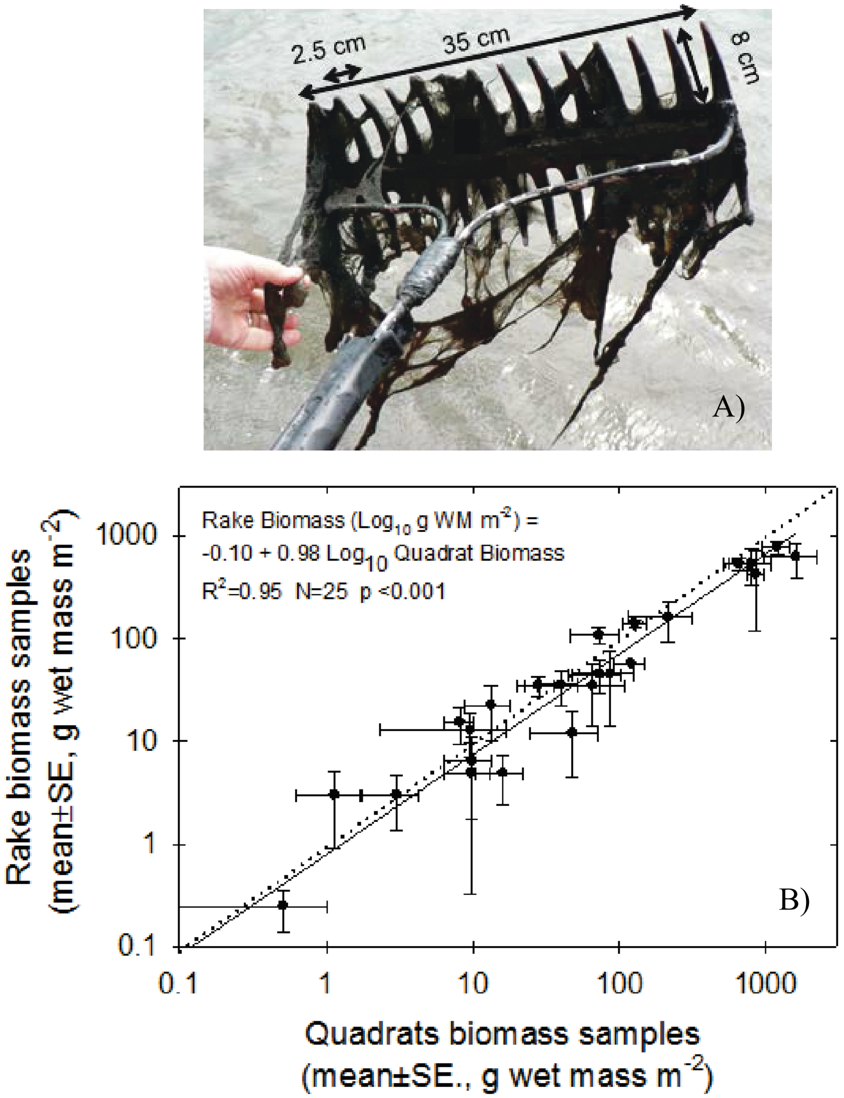

Fig. 1. A) Photograph of the double-headed rake used for sampling of *L. wollei* in the St. Lawrence River. The rake head was attached to a telescopic pole allowing sampling at sites with water depth up to 4 m. B) Relationship and regression equation between mean (±SE) *L. wollei* wet biomass (g m^{-2}) estimated from pairs of quadrats and rake samples (mean of 2-11 replicate pairs per site) collected at 25 sites in SLR with depth ranging from 0.75-3.0 m in 2006-2009.

Annexe 2. Calculation of wave height (H), period (T), and length (L)

Wave height (H) was calculated as:

$$H = 0.283 \tanh\left(0.53\left(\frac{g\,d}{U_a^2}\right)^{0.75}\right)\tanh\left(\frac{0.00565\left(\frac{g\,F}{U_a^2}\right)^{0.5}}{\tanh\left(0.53\left(\frac{g\,d}{U_a^2}\right)^{0.75}\right)}\right)\frac{U_a^2}{g}$$

where U_a is wind velocity, g is the acceleration due to gravity (m s^{-2}) and F is the effective fetch (m).

Wave period (T) was calculated as:

$$T = 7.54 \tanh\left(0.833\left(\frac{g\,d}{U_a^2}\right)^{0.375}\right)\tanh\left(\frac{0.0379\left(\frac{g\,F}{U_a^2}\right)^{0.333}}{\tanh\left(0.833\left(\frac{g\,d}{U_a^2}\right)^{0.375}\right)}\right)\frac{U_a^2}{g}$$

and L was estimated as:

$$L \approx 1.56\,T^2\sqrt{\frac{2\pi\,d}{1.56\,T^2}}$$

Annexe 3. RDA of all environmental factors explaining the biomasses of benthic primary producers of the St. Lawrence River

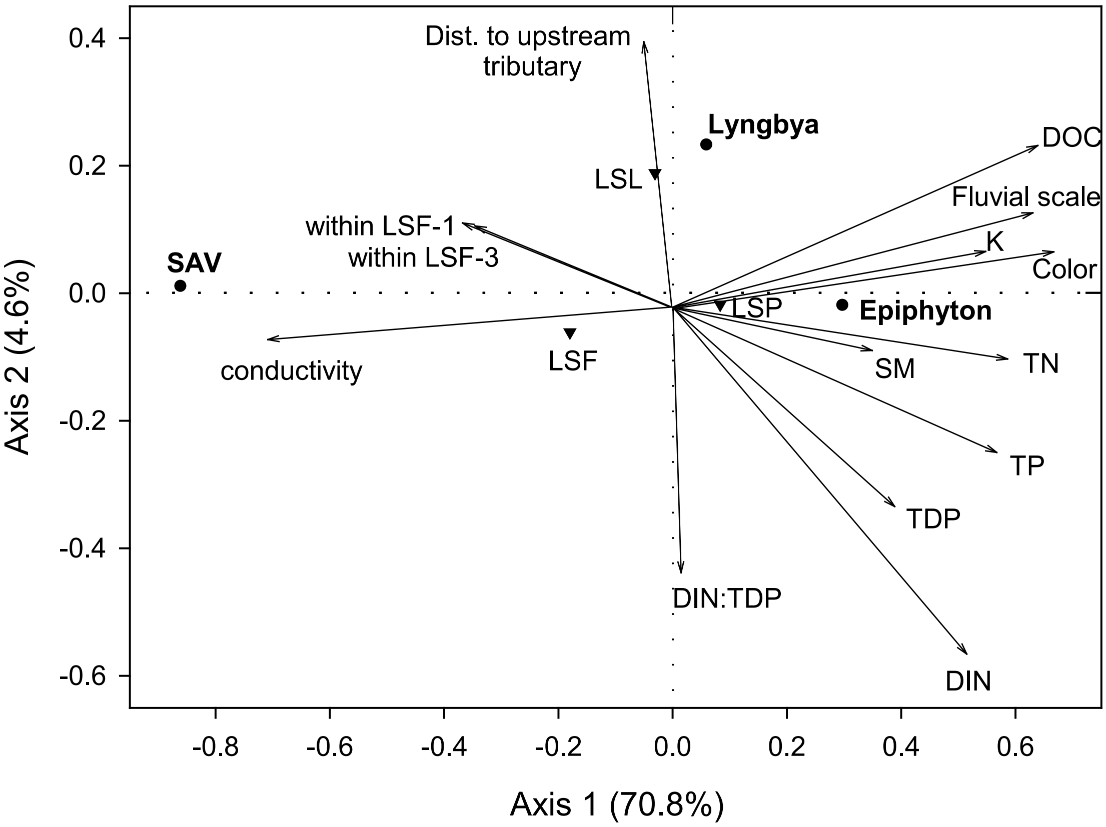

Fig. 4.4. Redundancy analysis (RDA) triplot with scaling type 2. Hellinger transformed biomasses of benthic PP are represented by filled circles. Quantitative environmental and spatial variables selected by forward selection are represented by arrows and centroids of the states of the qualitative variables by filled triangles. The analysis explained 59% of the PP biomass variance.