Université de Montréal

Patrons de distribution des crustacés planctoniques dans le fleuve Saint-Laurent

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Patrons de distribution des crustacés planctoniques dans le fleuve Saint-Laurent

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Résumé

La recherche porte sur les patrons de distribution longitudinale (amont-aval) et transversale (rive nord - rive sud) des communautés de crustacés planctoniques qui ont été analysés le long du fleuve Saint-Laurent entre le lac Saint-François et la zone de transition estuarienne, à deux hydropériodes en mai (crue) et en août (étiage). Les données zooplanctoniques et environnementales ont été récoltées à 52 stations réparties sur 16 transects transversaux en 2006. Au chapitre 1, nous présentons les principaux modèles écosystémiques en rivière, une synthèse des facteurs influençant le zooplancton en rivières et les objectifs et hypothèses de recherche. Au chapitre 2, nous décrivons la structure des communautés de zooplancton dans trois zones biogéographiques du fleuve et 6 habitats longitudinaux, ainsi que les relations entre la structure du zooplancton et la distribution spatiale des masses d'eau et les variables environnementales. Au chapitre 3, nous réalisons une partition de la variation des variables spatiales AEM (basées sur la distribution des masses d'eau) et des variables environnementales pour évaluer quelle part de la variation du zooplancton est expliquée par les processus hydrologiques (variables AEM) et les conditions locales (facteurs environnementaux). Le gradient salinité-conductivité relié à la discontinuité fleuve-estuaire a déterminé la distribution à grande échelle du zooplancton. Dans les zones fluviales, la distribution du zooplancton est davantage influencée par la distribution des masses d'eau que par les facteurs environnementaux locaux. La distribution des masses d'eau explique une plus grande partie de la variation dans la distribution du zooplancton en août qu'en mai.

Mots-clés : analyse canonique de redondance (ACR), cartes de vecteurs propres asymétriques (AEM), complexité spatiale de rivière, fleuve Saint-Laurent, masses d'eau, modélisation écologique, patrons de distribution spatiale du zooplancton, réseau hydrologique directionnel et qualité de l'eau, partition de la variation

Abstract

The research aims to determine the distribution patterns of crustacean plankton along the longitudinal (west-east) and transversal (north shore - south shore) axes of the St. Lawrence River between Lake Saint-François and the estuarine transition zone, during two hydroperiods in May (high discharge) and August (low discharge). The zooplankton samples and the environmental data were collected at 52 stations distributed along 16 transversal transects in 2006. In chapter 1, we present the theoretical concepts of river ecosystem models, and a synthesis on the generative processes driving zooplankton spatial patterns in rivers. We also present our research objectives and hypotheses. In chapter 2, we describe spatial patterns of the zooplankton community structure in three biogeographic zones of the St. Lawrence and 6 longitudinal habitats, together with the relationships between zooplankton spatial structure and water masses spatial distribution and environmental characteristics. In chapter 3, we perform a variation partitioning procedure on spatial variables AEM (based on water masses spatial distribution) and environmental variables in order to assess how much of the zooplankton variation is explained by hydrological processes (AEM variables) and local conditions (environmental factors). The salinity-conductivity gradient related to the fluvial-estuary discontinuity determines the large-scale spatial patterns of the crustacean zooplankton. In the fluvial zones, the zooplankton distribution patterns are more influenced by the water masses spatial structure than by local environmental factors. The spatial distribution of the water masses explained more of the spatial structure of zooplankton communities in August than in May.

Keywords : Asymmetric Eigenvector Maps (AEM), ecological modeling, directional hydrological network and water quality, redundancy analysis (RDA), river spatial complexity, St. Lawrence River, water masses, zooplankton spatial distribution patterns, variation partitioning

Table des matières

Liste des tableaux

Chapitre 1: Introduction générale

Chapitre 2 : Zooplankton spatial distribution patterns in the St. Lawrence River

Chapitre 3: Effects of hydrological and environmental processes on zooplankton spatial distribution patterns in the St. Lawrence River

Annexe A

Liste des figures

Chapitre 1: Introduction générale

Chapitre 2 : Zooplankton spatial distribution patterns in the St. Lawrence River

Chapitre 3: Effects of hydrological and environmental processes on zooplankton spatial distribution patterns in the St. Lawrence River

Liste des sigles et abréviations

Chapitre 1: Introduction générale

Chl*a* : Chlorophylle *a*

FP : Modèle *Flood Pulse* (Junk et al. 1989)

LSF : Lac Saint-François

LSL : Lac Saint-Louis

LSP : Lac Saint-Pierre

MOD : Matière organique dissoute

PT : Phosphore total

RCC : *River Continuum Concept* (Vannote et al. 1980)

RPM : *River Productivity Model* (Thorp et Delong 1994)

SDC : *Serial Discontinuity Concept* (Ward et Stanford 1983)

ZTE : Zone de transition estuarienne

ZTM : Zone de turbidité maximale

Chapitre 2 : Zooplankton spatial distribution patterns in the St. Lawrence River

aCDOM : Chromophoric dissolved organic matter absorbance

ACR : Analyse canonique de redondance

Chl*a* : Chlorophyll *a*

ETZ : Estuarine transition zone

FC : Fluvial corridor

FEZ : Fluvial estuary zone

FSZ : Fluvial section zone

GL : Great Lakes waters

k_dPAR : PAR extinction coefficient

LSF : Lake Saint-François

LSL : Lake Saint-Louis

LSP : Lake Saint-Pierre

MTZ : Maximum turbidity zone

OTT : Ottawa River waters
PAR : photosynthetically active radiation (400-700 nm)
RDA : Redundancy analysis
SLR : St. Lawrence River
SPM : Suspended particulate matter
TDS : Total dissolved solids
TN : Total nitrogen
TP : Total phosphorus
WM1 : Great Lakes water mass
WM2 : Mixed waters of the Great Lakes and the Ottawa River
WM3 : Ottawa River water mass
WM4 : Mixed waters of the Great Lakes and the Richelieu River
WM5 : Québec City water mass
WM6 : Estuarine transition zone water mass

Chapitre 3: Effects of hydrological and environmental processes on zooplankton spatial distribution patterns in the St. Lawrence River

aCDOM : Chromophoric dissolved organic matter absorbance
AEM : Asymmetric Eigenvector Maps
AEMs : AEM variables
ASS : l'Assomption River waters
Chl*a* : Chlorophyll *a*
CV : Coefficient of variation
DOC : Dissolved organic carbon
FC : Fluvial corridor
FE : Fluvial Estuary
FS : Fluvial Section
GL : Great Lakes waters
LSF : Lake Saint-François
LSL : Lake Saint-Louis
LSP : Lake Saint-Pierre

MASK : Maskinongé River waters
MIP : Mille Îles and des Prairies Rivers waters
OTT : Ottawa River waters
PAR : Photosynthetically active radiation (400-700 nm)
K_dPAR : PAR extinction coefficient
QC : Québec City waters
RDA : redundancy analysis
RICH : Richelieu River waters
SLR : St. Lawrence River
SPM : Suspended particulate matter
TDS: Total dissolved solids
TN : Total nitrogen
TP : Total phosphorus

Chapitre 4 : Conclusion générale

AEM : Vecteurs propres asymétriques
ZTE : Zone de transition estuarienne

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Chapitre 1 : Introduction générale

1.1 Fleuves et modèles théoriques

Plusieurs modèles théoriques ont été proposés pour comprendre les mécanismes influençant les communautés biologiques des fleuves, ces grandes rivières dynamiques et complexes.

Le modèle *River Continuum Concept* (RCC) de Vannote et al. (1980) propose que les fleuves sont des continuums longitudinaux dans lesquels la dynamique d'un écosystème en aval est intimement liée aux processus en amont, à la lithologie et la géomorphologie locales (Thorp et Delong 1994). Selon ce modèle, la majeure partie des particules fines de matière organique, dérivée des processus en amont, constitue la principale source de carbone organique pour les réseaux trophiques des grandes rivières. Les apports de particules grossières de matière organique venant de la végétation riveraine adjacente sont par contre considérés insignifiants à cause de la très grande largeur des fleuves. La production primaire *in situ* est sévèrement limitée par la profondeur et la turbidité inorganique, la respiration étant alors plus importante que la production primaire.

Le *Serial Discontinuity Concept* (SDC) de Ward et Stanford (1983) intègre l'effet des diverses retenues (réservoirs, lacs fluviaux, etc.) au modèle RCC. Ces retenues, avec des courants plus faibles et des temps de résidence plus longs, représentent des discontinuités au sein du continuum. Celles-ci modifient les paramètres physiques et biologiques en aval, dépendamment de leur position (ordre hydrologique).

Le modèle *Flood Pulse* (FP) de Junk et al. (1989) quant à lui met l'emphase sur l'importance des apports de matière allochtone provenant de la plaine inondable pour les réseaux trophiques des fleuves. Lors de crues saisonnières, et lorsque la plaine inondable d'une rivière est vaste, la biomasse animale au sein du chenal tirerait ses ressources en majeure partie des apports en matière organique de la plaine inondable et non du transport longitudinal en provenance de l'amont. En effet, la matière organique de la plaine inondable serait plus labile que les particules fines de matière organique du chenal et donc plus assimilable par les organismes à la base des réseaux trophiques. Enfin, l'accessibilité et la rétention de la matière organique au sein du chenal seraient fonction de la fréquence et de la durée des crues, ainsi que de la superficie de la plaine d'inondation.

Thorp et Delong (1994) ont développé le *River Productivity Model* (RPM) en réponse aux 3 modèles précédents. Ces derniers auraient surestimé l'importance des nutriments en provenance des ruisseaux de tête (RCC) ou de la plaine inondable (FP) dans le contrôle des réseaux trophiques des grandes rivières. Ces modèles auraient aussi sous-estimé le rôle de la production primaire locale au sein du chenal et des apports de matière organique en provenance de la végétation littorale. Le RPM soutient que la production autochtone et les apports directs de carbone organique de la végétation riveraine représentent ensemble la principale source de carbone contrôlant les réseaux trophiques dans les fleuves avec plaine inondable étroite. Dans les fleuves possédant une vaste plaine inondable, la production primaire autochtone (particulièrement du phytoplancton) contribuerait significativement à la productivité secondaire. Le carbone provenant de sources allochtones (ruisseaux de tête, plaine inondable et tributaires) constitue la plus grande partie de la matière organique transportée et benthique. Mais comme les particules de matière organique transportée sont pour la plupart réfractaires, leur valeur pour les réseaux trophiques fluviaux s'en trouve réduite (contrairement aux hypothèses des modèles RCC et FP). À l'opposé, le carbone autochtone et les apports allochtones directs de la végétation riveraine sont proportionnellement plus importants parce qu'ils sont labiles et donc plus facilement assimilables par les organismes hétérotrophes microbiens (Wetzel 2001).

En définitive, l'applicabilité des différents modèles varie en fonction de la taille du fleuve et de sa morphologie. Le modèle RCC serait plus approprié pour les ruisseaux de tête et les petites rivières; l'application du modèle FP se limiterait aux fleuves entourés d'une vaste plaine inondable (Sedell et al. 1989) tandis que le modèle RPM serait plus représentatif des fleuves avec une plaine inondable étroite (Thorp et Delong 1994). Le modèle RCC préconise des changements graduels de conditions physiques, chimiques et biologiques le long de la rivière. Le modèle SDC souligne l'existence de discontinuités (zones lentiques) qui peuvent faire varier les facteurs environnementaux ponctuellement et plus loin en aval de la rivière. La plupart des grandes rivières montrent des caractéristiques associées à ces deux modèles et les niveaux de discontinuité dans celles-ci sont influencés par les variations saisonnières de débit.

La rivière Spree en Allemagne (Köhler 1994) coule à travers une retenue et plusieurs lacs peu profonds. On peut donc concevoir la rivière Spree comme une séquence de tronçons à courant fort entrecoupés de zones à courant plus faible (retenue et lacs fluviaux). Au printemps, le phytoplancton lacustre, adapté à l'hydrodynamisme dynamique des lacs non stratifiés, pouvait croître ou maintenir son abondance dans le chenal tout au long de la rivière, conformément à l'hypothèse du continuum (RCC). Le scénario était différent en été, où la biomasse du phytoplancton, adapté à une stratification intermittente des lacs, était réduite de moitié en aval de la rivière. De plus, la biomasse de phytoplancton avait augmenté drastiquement dans la retenue Spremberg, constituant une discontinuité importante (selon le modèle SDC) dans le patron de biomasse. Cette rivière montre alors une combinaison des caractéristiques des deux modèles, avec un effet continuum fort pendant la crue printanière, et des discontinuités plus nettes résultant des retenues et des lacs en été, quand le débit est faible.

De même, une étude sur le phytoplancton dans le fleuve Saint-Laurent (Hudon et al. 1996) a aussi montré les caractéristiques des 2 modèles. Dans le chenal principal, un nombre plus grand d'espèces de phytoplancton était conservé dans les zones lotiques le long de la rivière au printemps, l'entraînement par les courants forts uniformisant le phytoplancton et augmentant ainsi la continuité conformément au modèle RCC. D'autre part, les lacs fluviaux avaient une composition de phytoplancton significativement différente de celle du tronçon en amont et influençaient celle de l'aval, conformément au modèle SDC.

D'autres fleuves et rivières sont des exemples de continuum ou de discontinuum. Dans la rivière Ohio (États-Unis), le lac de tête et les bassins ne changeaient pas significativement la diversité ni l'abondance du zooplancton à l'intérieur du chenal principal (Thorp et al. 1994). Le lac Saint-Pierre au sein du fleuve Saint-Laurent influence les communautés de rotifères et de crustacés en aval (Basu et al. 2000a). Dans la rivière Garonne (France), un des réservoirs présentant un pic de chlorophylle *a* (Chl*a*) faisait augmenter l'abondance de diatomées benthiques en aval (Améziane et al. 2003).

Supportant le modèle FP, Saunders et Lewis (1989) ont souligné l'importance des corps d'eau adjacents, comme les habitats de la plaine inondable, dans le contrôle du zooplancton des grandes rivières. Baranyi et al. (2002) ont observé que la biomasse moyenne du zooplancton dans la plaine d'inondation de la rivière Danube (Europe) était 3.5 fois plus élevée que les valeurs trouvées précédemment par Reckendorfer et al. (1999) dans le chenal à la même hauteur. Ceci suppose que la plaine inondable pourrait agir comme source d'éléments nutritifs et d'organismes pour le chenal. Dans la rivière Ohio, malgré une productivité potentiellement plus élevée dans la plaine inondable que dans le chenal, Thorp et al. (1994) n'ont pas observé de différence dans l'abondance de zooplancton entre les bassins avec plaine inondable réduite et le bassin possédant une vaste plaine d'inondation.

1.2 Facteurs influençant le zooplancton dans les grandes rivières

Les facteurs dominants influençant la distribution du zooplancton de rivière sont différents de ceux du zooplancton lacustre. Dans les lacs, ces facteurs varient selon l'échelle spatiale. Au niveau régional, la variation spatiale (inter-lacs) de la biomasse du zooplancton est corrélée positivement au phosphore total (PT) (Pinel-Alloul et Ghadouani 2007). Au niveau local, la biomasse du zooplancton varie en fonction de la température, la stratification du lac, la chimie des eaux, la conductivité, le pH et le calcium, la prédation par les poissons et les invertébrés (Pinel-Alloul et Ghadouani 2007). Dans les fleuves, l'hydrologie (temps de résidence, débit et courant) joue un rôle primordial dans le contrôle des communautés de zooplancton (Basu et Pick 1996; Kim et Joo 2000; Baranyi et al. 2002; Viroux 2002), suivi de facteurs biotiques tels que la présence de lits de macrophytes, la Chl*a* et la prédation par les poissons (Pinel-Alloul et Ghadouani 2007).

1.2.1 Temps de résidence

Le temps de résidence des eaux est un facteur déterminant pour le zooplancton de rivière (Lair 2006). Des temps de résidence plus longs sont généralement associés à des réseaux trophiques plus complexes, une biodiversité plus grande et une plus grande productivité (Frenette et al. 2006). Pace et al. (1992) ont montré qu'un temps de résidence plus long dans les rivières, les lacs et les estuaires est accompagné par une augmentation de la biomasse de zooplancton. À cause de leur temps de développement relativement long, les crustacés ne peuvent établir de grandes populations et biomasses que lorsque les conditions lentiques dominent sur de longues périodes (Köhler 1994; Baranyi et al. 2002; Lair 2006). Par exemple dans la rivière Danube (Europe), l'abondance des crustacés augmentait exponentiellement à des temps de résidence supérieurs à deux semaines (Baranyi et al. 2002). Dans ces conditions, les grands crustacés à développement lent deviennent plus importants et sont susceptibles de dominer la communauté (Viroux 1997, 2002; Ietswaart et al. 1999).

1.2.2 Température

La biomasse du zooplancton est généralement positivement corrélée à la température (Wetzel 2001). Celle-ci peut faire diminuer le temps de développement et augmenter le taux de croissance du zooplancton en laboratoire (Amblard et Pinel-Alloul 1995). La température a influencé l'abondance et la composition du macrozooplancton pendant l'été au lac Léman (Suisse et France) (Pinel-Alloul et al. 1999), et Thorp et al. (1994) ont observé une corrélation positive entre la densité du zooplancton et la température dans la rivière Ohio.

1.2.3 Matière organique et pénétration de la lumière

La majorité des crustacés planctoniques ont un régime herbivore/détritivore (Wetzel 2001). Leur abondance est donc influencée par les nutriments (phosphore et azote) qui font augmenter la biomasse des algues, et par la matière organique qui constitue une source de nourriture et affecte la pénétration de la lumière dans la colonne d'eau (Wetzel 2001). La matière organique dissoute (MOD) sert de nourriture aux bactéries, qui à leur tour, peuvent être mangées par le zooplancton (Wetzel 2001). La MOD peut généralement être classée en 2 catégories : 1) la MOD labile, de faible poids moléculaire (< 1 kDa) est facilement assimilable par les bactéries hétérothrophes (Stedmon 2004; Berggren et al. 2010; Massicotte et Frenette 2011). Elle provient essentiellement de l'exudation par des organismes photosynthétiques tels que les macrophytes et le phytoplancton (Findlay et Sinsabaugh 2003; Massicotte et Frenette 2011). 2) La MOD réfractaire provient généralement d'écosystèmes terrestres et est introduite dans le milieu aquatique par le ruissellement et l'écoulement de l'eau souterraine (Findlay et Sinsabaugh 2003). Elle est principalement composée d'acides humiques et fulviques de poids moléculaire élevé (> 1 kDa) et est considérée comme résistant mieux à la dégradation bactérienne (Amon et Benner 1996; Massicotte et Frenette 2011). La MOD est aussi altérée par des processus abiotiques tels que la photominéralisation (Stedmon et al. 2007; Spencer et al. 2009; Zhang et al. 2009), la sédimentation, et la floculation (von Wachenfeldt et Tranvik 2008; Massicotte et Frenette 2011).

La pénétration de la lumière dans la colonne d'eau affecte les organismes aquatiques de plusieurs façons. Elle affecte la production de MOD labile, la production primaire (croissance des algues et des macrophytes), la vue et le comportement des poissons et larves de poisson et plusieurs autres processus (Frenette et al. 2006). La composition spectrale de la lumière dans la colonne d'eau peut également influencer la composition lipidique et la stoechiométrie des algues, influençant du même coup la qualité de la nourriture et le transfert de nutriments aux niveaux trophiques supérieurs (Rai et al. 1997; Frenette et al. 1998; Sterner et Elser 2002; Frenette et al. 2006). La photodégradation de la MOD chromophorique par le rayonnement UV protège les organismes aquatiques contre ses effets délétères (Morris et Hargreaves 1997; Zhang et al. 2007). L'extinction du rayonnement UV dans la colonne d'eau est aussi augmentée par le carbone organique particulaire (Belzile et al. 2002; Vincent et al. 2001; Smith et al. 1999; Frenette et al. 2003).

1.2.4 Phytoplancton

Le phytoplancton est une source majeure de nourriture pour le zooplancton. La biomasse de Chl*a*, les nutriments et l'état trophique (PT) sont des facteurs majeurs influençant la biomasse de zooplancton dans les lacs (Köhler 1994; Pinel-Alloul et Ghadouani 2007; Wetzel 2001)**.** Dans leur étude sur 31 rivières en Ontario et au Québec, Basu et Pick (1996) ont trouvé une corrélation positive entre la Chl*a* et le PT et une faible corrélation positive entre la Chl*a* et la biomasse de zooplancton. La biomasse du zooplancton a aussi été positivement corrélée au phytoplancton dans la rivière Rideau (Canada), une rivière à courant faible (Basu et Pick 1997). Quelques études indiquent que la biomasse et l'abondance du zooplancton dans les rivières sont beaucoup plus basses que dans les lacs de concentrations en nutriments et en Chl*a* similaires (Köhler 1994; Basu et Pick 1997).

Dans les rivières, le phytoplancton est sujet à des conditions hydrologiques sub-optimales. En effet, la turbidité importante dans le chenal fait diminuer la pénétration de la lumière dans la colonne d'eau et donc la biomasse du phytoplancton (Wetzel 2001). Dans le fleuve Saint-Laurent (Hudon 1996), les faibles intensités lumineuses dues à la turbidité dans le chenal principal font probablement diminuer l'abondance du phytoplancton lors de son transport en aval. De plus, un temps de résidence trop court ne permet pas au phytoplancton de se développer suffisamment pour maintenir son abondance dans le chenal. Basu et Pick (1996) suggèrent que la biomasse algale est régie par les nutriments plutôt que par le temps de résidence lorsque celui-ci est d'environ 3 jours et plus. Ces auteurs ont trouvé que la relation entre la Chl*a* et la biomasse totale de zooplancton devenait significative après avoir contrôlé pour le temps de résidence.

Contrairement au chenal, les conditions dans les zones littorales peu profondes à courant faible favorise la rétention du plancton local (Lewis 1988; Moss et Ball 1989) où l'intensité lumineuse est plus élevée (Hudon 1996). Le phytoplancton dans les écosystèmes tempérés est fortement contrôlé par les variations saisonnières dans la luminosité et la température de l'eau (Hudon 2000).

1.2.5 Macrophytes

Les macrophytes jouent un rôle clé dans la structure et le fonctionnement des organismes associés à leur habitat (Martin et al. 2005). Ils diminuent la vitesse du courant, favorisant ainsi la sédimentation, et modulent l'hétérogénéité lumineuse et les concentrations de carbone organique dissous et de MOD chromophorique (Martin et al. 2005; Frenette et al. 2006; Lapierre et Frenette 2009; Massicotte et Frenette 2011). Les macrophytes au lac Saint-Pierre (fleuve Saint-Laurent) sont une source nette de MOD labile (Lapierre et Frenette 2009; Massicotte et Frenette 2011). Ils ont aussi une influence très importante sur le zooplancton de rivières, formant des milieux riches et productifs où celui-ci peut se développer (Wetzel 2001). Dans une étude sur les lacs Saint-François et Saint-Pierre dans le fleuve Saint-Laurent, Basu et al. (2000b) ont observé que la biomasse totale du macrozooplancton était 9 fois plus élevée à l'intérieur de lits de macrophytes (en moyenne 180 µg/L, poids sec) que dans les zones d'eau libre et les zones comprenant très peu de végétation (en moyenne 20 µg/L, poids sec). Les macrophytes peuplant les zones littorales peu profondes à l'abri du courant supportent des populations abondantes d'algues périphytiques, qui peuvent potentiellement contribuer à la biomasse de plancton quand elles sont remises en suspension (Hudon 1996; Whitton 1975; Wetzel 1983). C'est le cas du fleuve Saint-Laurent (Hudon 1996) où les zones riches en macrophytes dans les lacs fluviaux en été possédaient des biomasses d'algues périphytiques en suspension plus élevées que dans le chenal principal.

Parce que le zooplancton peut détecter les courants et modifier son comportement de nage en conséquence, les lits de macrophytes dans les zones littorales peu profondes peuvent fournir des abris contre la dérive pour les organismes à grande capacité natatoire (Viroux 1997), comme les cladocères de grande taille et les copépodes adultes. Basu et al. (2000a) et Viroux (1999) ont observé des diminutions dans l'abondance des crustacés planctoniques dans le chenal principal comparativement aux zones riches en macrophytes de l'exutoire des lacs Ontario et Saint-Pierre (fleuve Saint-Laurent) et des berges de la Moselle (France). Walks et Cyr (2004) ont comparé deux types d'exutoires de lacs fluviaux: des exutoires peu profonds riches en macrophytes et des exutoires profonds sans macrophyte. Les zones littorales des exutoires peu profonds riches en macrophytes étaient dominées par les cyclopoïdes, tandis que des zones littorales profondes sans macrophyte étaient dominées par *Bosmina longirostris*. Walks et Cyr (2004) ont alors supposé que les cyclopoïdes, dominant la communauté zooplanctonique dans les macrophytes, évitaient la dérive. La prédation par les poissons benthivores et planctivores diminue de façon remarquable dans les lacs peu profonds riches en macrophytes (Wetzel 2001). Le littoral sert alors de refuge pour les cladocères pélagiques. De la même façon, Viroux (1999) propose que les zones avec densités élevées de macrophytes dans la Moselle peuvent servir de refuge pour les grands cladocères contre la prédation par les poissons.

1.2.6 Prédation

Selon Jack et Thorp (2002), la prédation par les poissons serait un facteur important dans les rivières. La prédation par les poissons fait diminuer la biomasse et modifie la structure en taille et la composition des communautés de zooplancton. En effet, les poissons planctivores sélectionnent les individus de grande taille et de ce fait favorisent les individus de petite taille. Dans l'étude en enclos pélagique de Jack et Thorp (2002) dans la rivière Ohio (États-Unis), les taux de croissance du cyclopoïde *D. thomasi* ont fortement diminué après l'introduction de larves de poissons tandis que ceux des nauplies et des rotifères avaient augmenté. Les grandes densités et la grande taille de *D. thomasi* dans cette rivière auraient favorisé le choix de cette proie par les poissons. L'augmentation des nauplies et des rotifères avec la biomasse des poissons a pu provenir d'une diminution de leur prédation par *D. thomasi*, puisque les copépodes peuvent se nourrir de nauplies et de rotifères (Jack et Thorp 2002; Thorp et al. 1994).

1.3 Patrons de distribution du zooplancton dans la zone fleuve-estuaire

La distribution du zooplancton des grandes rivières est influencée par les variations longitudinales (amont-aval), transversales (rives-large) et saisonnières (crue-étiage) des conditions physiques, chimiques et biologiques.

1.3.1 Patrons de distribution longitudinale (amont-aval)

1.3.1.1 Le chenal au niveau fluvial

À l'intérieur du chenal des grandes rivières, l'advection intense et la turbidité ont des effets marqués sur la diversité et la production secondaire nette du zooplancton (Thorp et al. 1994). Dans cet environnement, le zooplancton dérive massivement vers l'aval et la production des algues diminue à cause de la turbulence (Casper et Thorp 2007). Selon Frutos et al. (2006), les milieux turbides favoriseraient les rotifères qui sont mieux adaptés à la turbulence et à de grandes concentrations de solides en suspension. La plupart des espèces planctoniques dominantes ont des cycles de vie relativement rapides ou sont principalement benthiques (Wetzel 2001); c'est pourquoi le chenal principal des grandes rivières du monde est généralement dominé par les rotifères et les petits cladocères (Lair 2006) comme c'est le cas pour les rivières Ohio (Thorp et al. 1994), Nakdong (Kim et Joo 2000), Paraguay (Frutos et al. 2006), Meuse (Viroux 1997) et les 31 rivières de l'Ontario étudiées par Basu et Pick (1996).

Toutefois, malgré toutes les contraintes que subissent les crustacés au sein du chenal, plusieurs auteurs y ont relevé une augmentation amont-aval de leur abondance et de leur diversité (Frutos et al. 2006). Basu et Pick (1997) et Kim et Joo (2000) ont décelé une augmentation de la densité du zooplancton vers l'aval dans les rivières Rideau (Canada) et Nakdong (Corée), respectivement. Selon plusieurs auteurs (Köhler 1994; Basu et Pick 1996; Walks et Cyr 2004), le zooplancton peut généralement se développer au sein du chenal des grandes rivières, quand celles-ci sont assez longues pour lui permettre de croître et de se reproduire lors de son transport vers l'aval. Cependant, d'autres auteurs ont obtenu des patrons longitudinaux différents, selon lesquels l'abondance du zooplancton n'augmente pas nécessairement de manière prévisible vers l'embouchure des rivières (Basu et Pick 1997; Viroux 1997). Cette variabilité dans le patron longitudinal des fleuves reflète la complexité des facteurs affectant le zooplancton à l'intérieur du chenal, ces facteurs incluant entre autres l'hydrologie et les influences anthropiques (Kim et Joo, 2000).

1.3.1.2 Les lacs fluviaux et autres retenues

Les lacs fluviaux et autres retenues, possédant généralement des profondeurs et vitesses de courant plus faibles et ayant donc un temps de résidence plus long, peuvent constituer des sources de zooplancton pour les grandes rivières (Basu et al. 2000a, 2000b; Wetzel 2001; Walks et Cyr 2004). Basu et al. (2000b) ont obtenu des résultats supportant cette hypothèse dans 2 lacs fluviaux (lac Saint-François et lac Saint-Pierre) du fleuve Saint-Laurent, où la biomasse du macrozooplancton à l'exutoire (~50 µg/L, poids sec) était beaucoup plus élevée que la biomasse à l'entrée des lacs (< 20 µg/L, poids sec). Cette augmentation dans la biomasse était due au transfert d'organismes à partir des lits de macrophytes marginaux vers le chenal central dans la partie aval des lacs où les eaux latérales entraient dans le chenal. Basu et al. (2000b) ont suggéré que les lacs fluviaux agissent comme des sources de plancton, lequel est transporté en aval pendant les années de développements importants de macrophytes littoraux. Dans une autre étude sur le fleuve Saint-Laurent (Basu et al. 2000a), tous les groupes de zooplancton avaient vu leur abondance diminuée à la sortie du lac Ontario et celle-ci était restée basse plus loin en aval. À l'exutoire du lac Saint-Pierre, la densité de rotifères avait de beaucoup augmenté, tandis que celle des crustacés était légèrement plus élevée. Dans leur étude sur 4 lacs en Ontario (Canada), Walks et Cyr (2004) ont établi que la morphologie des berges affectait le mouvement du zooplancton en aval des lacs fluviaux. En effet, les exutoires de 2 de ces lacs, drainant des zones littorales plus profondes, avait permis le transport d'une plus grande biomasse de zooplancton que les deux autres lacs peu profonds possédant des lits de macrophytes. Toutefois, ces effets disparaissaient à l'intérieur de 50 m en aval du lac. Comme ces études l'indiquent, les retenues et les lacs fluviaux peuvent constituer des sources ponctuelles de zooplancton, soit à l'intérieur même de la retenue et dans la courte zone immédiatement en aval.

1.3.1.3 La zone de transition estuarienne

Les patrons de distribution longitudinale du zooplancton dans la zone fleuve-estuaire (chenal principal au niveau fluvial jusqu'à la zone de transition estuarienne (ZTE)) sont grandement affectés par la discontinuité dans les facteurs hydrologiques et le gradient de salinité reliés à la ZTE.

La zone de turbidité maximale

La zone de turbidité maximale (ZTM), située en amont de plusieurs estuaires là où les eaux douces rencontrent la mer, comporte généralement des concentrations très élevées de plancton (Dodson et al. 1989; Frenette et al. 1995; Lapierre et Frenette 2008) pouvant supporter des pouponnières de poissons (Barnard et al. 2003; Winkler et al. 2003; Roman et al. 2005). Il s'y produit une rétention physique des organismes et des particules inorganiques due à un temps de résidence prolongé, résultant de l'hydrodynamisme typique de la ZTE (Dodson et al. 1989; Frenette et al. 1995; Winkler et al. 2003). Il en résulte une turbidité et des concentrations de matières organiques particulaires élevées (Martineau et al. 2004). La combinaison de pics de biomasse algale et de turbidité élevée a été observée dans plusieurs ZTE à des salinités variant de 0 à 4 psu (Lapierre et Frenette 2009).

Les processus hydrodynamiques comme la stratification, le mélange turbulent et l'advection peuvent être des facteurs majeurs déterminant les communautés planctoniques autotrophes et hétérotrophes dans les écosystèmes marins et d'eau douce (Frenette et al. 1995). Dans la ZTM, la circulation estuarienne et les processus de piégeage qui l'accompagnent contrôleraient les relations trophiques et les gradients dans la structure de la communauté planctonique (Winkler et al. 2003), et seraient responsables de l'accumulation du zooplancton et du phytoplancton dans la ZTE (Roman et al. 2001). Pour Pinel-Alloul et Ghadouani (2007), les patrons de circulation des eaux représentent le facteur générateur d'hétérogénéité spatiale du zooplancton le plus important dans les estuaires. Le couplage de l'hydrodynamisme avec les producteurs primaires, la migration verticale journalière et les interactions trophiques est aussi un facteur important (Pinel-Alloul et Ghadouani 2007).

Débit fluvial et phytoplancton d'eau douce

La variable clé contrôlant l'écosystème de la ZTM est probablement le débit qui agit directement en contrôlant la position du front eau douce/eau salée, l'étendue de la recirculation estuarienne, et les temps de résidence des eaux et des particules (Winkler et al. 2003). Les apports en eau douce vont aussi influencer la température et la pénétration de la lumière (Vincent et Dodson 1999). Dans la Baie Chesapeake, les plus grandes biomasses de phytoplancton et de zooplancton ont été trouvées au printemps, quand les apports en eaux douces étaient supérieurs au débit moyen (Roman et al. 2005). Le piégeage et le recyclage rapide des nutriments en provenance des eaux douces à l'intérieur de l'estuaire peuvent également contribuer à la grande productivité typique des estuaires (Dodson et al. 1989). Par exemple dans la ZTE du fleuve Saint-Laurent, une large gamme de substrats organiques est disponible pour la production bactérienne (Winkler et al. 2003). De plus, l'advection d'une biomasse importante de phytoplancton (Vincent et al. 1996) vers la ZTM du Saint-Laurent, combinée à un temps de résidence de 15 jours (Simons et al. 2006) du phytoplancton à l'intérieur de la ZTM, serait en grande partie à l'origine des pics de Chl*a* qui y sont observés (Lapierre et Frenette 2008). En effet, la Chl*a* de la ZTM était positivement reliée à la turbidité, alors qu'elle n'était pas reliée ou était reliée négativement aux facteurs de croissance du phytoplancton comme la lumière et les nutriments. Les ratios d'isotopes stables du soufre du phytoplancton dans la ZTM étaient différents de ceux du périphyton local et correspondaient à ceux du périphyton provenant des eaux douces en amont (Lapierre et Frenette 2008).

Le zooplancton

Le zooplancton est abondant dans la ZTE du Saint-Laurent (Winkler et al. 2003) et dans les estuaires de la Baie Chesapeake (Roman et al. 2005). Le zooplancton se nourrit principalement du phytoplancton riverain et autochtone également abondant dans la ZTM du Saint-Laurent (Winkler et al. 2003; Martineau et al. 2004; Lapierre et Frenette 2008). Dans la ZTE du Saint-Laurent, la baisse marquée des concentrations de Chl*a* à des salinités légèrement supérieures à celles où l'on trouve le pic de Chl*a*, semble couplée aux pics de biomasse de zooplancton et d'ichtyoplancton, ce qui vient appuyer l'hypothèse selon laquelle cette baisse est attribuable au broutage intensif par le zooplancton (Winkler et al. 2003; Martineau et al. 2004; Lapierre et Frenette 2008). De plus, le calanoïde *E. affinis*, dominant le zooplancton dans la ZTM du Saint-Laurent, dans les estuaires de la Baie Chesapeake (Roman et al. 2005) et de la rivière Columbia (Haertel et al. 1969), semble le brouteur le plus important des producteurs primaires dans ces écosystèmes et dans plusieurs autres estuaires (Winkler et al. 2003). Dans la ZTM du Saint-Laurent, à marées montante et descendante (périodes durant lesquelles la vitesse du courant est maximale), le frottement du fond marin induisant une remise en suspension des particules et des organismes fait augmenter la turbidité et l'abondance des harpacticoïdes dans la colonne d'eau (Barnard et al. 2003).

1.3.2 Patrons de distribution transversale (rives-large)

On observe généralement une augmentation de l'abondance des crustacés dans les régions littorales par rapport au chenal (Basu et al. 2000b; Baranyi et al. 2002). Celles-ci possèdent souvent des zones lentiques (méandres, lits de macrophytes, etc.) qui peuvent permettre l'établissement de populations stables de zooplancton (Köhler 1994). Il existe en effet une corrélation positive importante entre la disponibilité des zones lentiques et l'abondance du zooplancton dans les rivières (Baranyi et al. 2002). Les zones littorales de la rivière Ohio (Thorp et al. 1994) et du fleuve Saint-Laurent (Basu et al. 2000b), ainsi que la plaine inondée de la rivière Danube (Baranyi et al. 2002) avaient des abondances de crustacés supérieures à celles du chenal principal. De plus, Viroux (1997) attribuait la présence continue des microcrustacés dans la Moselle (France) à la disponibilité de zones lentiques le long des berges où les cladocères et les copépodes pouvaient se développer à l'abri du courant.

Ces zones d'eaux calmes peuvent localement recréer des conditions de vrais lacs et constituer de véritables sources de zooplancton pour la rivière. Dans leur étude sur une section du fleuve Saint-Laurent, Casper et Thorp (2007) avaient trouvé des femelles ovigères *Bosmina* sp. dans les zones d'eaux mortes littorales. Les avantages reliés aux zones littorales (abondance de nourriture, diminution du courant et de la turbidité, lieu de reproduction) étaient supérieurs aux inconvénients (prédation accrue par les poissons planctivores) pour cette espèce.

Des études sur la dynamique du zooplancton ont montré une contribution significative des tributaires à l'abondance et à la diversité (Thorp et al. 1994; Viroux 1999; Améziane et al. 2003) ou à la dilution (Kim et Joo 2000) du zooplancton riverain. Ceux-ci contribuent donc à la discontinuité dans la rivière au niveau des zones littorales. Cependant, leur influence était toujours ponctuelle ou minime pour les tributaires de moindre importance.

1.3.3 Patrons de distribution temporelle (crue et étiage)

Les variations saisonnières (crue et étiage) et ponctuelles (fortes et faibles précipitations) du débit déterminent le temps de résidence et la vitesse du courant propres aux divers habitats de la rivière.

Lors des crues, le débit élevé provoque une forte augmentation de la vitesse du courant et le temps de résidence en est considérablement diminué. Dans ces conditions, les abondances de zooplancton diminuent (Thorp et al. 1994; Viroux 1997, 2002; Ietswaart et al. 1999; Kim et Joo 2000; Baranyi et al. 2002). Cette diminution est causée d'une part par un taux de mortalité et une dérive élevée du zooplancton (Tockner et al. 1999; Casper et Thorp 2007) et d'autre part par un temps de résidence trop court pour permettre son développement (Viroux 1997). Les rotifères et les petits cladocères (*Bosmina*), ayant des temps de génération courts et une reproduction parthénogénétique, dominent alors les grands cladocères filtreurs (*Daphnia*) et les copépodes (Viroux 1997; Baranyi et al. 2002). Un fort débit peut aussi faire diminuer la température (Ietswaart et al. 1999) et la concentration de Chl*a* (Thorp et al. 1994), et faire augmenter la turbidité (Viroux 1997; Fruget et al. 2001; Baranyi et al. 2002). Ces facteurs peuvent à leur tour influencer la distribution du zooplancton.

En période d'étiage, le faible débit provoque une diminution de la vitesse du courant et une augmentation du temps de résidence. Des zones lentiques favorables au développement des crustacés sont alors plus nombreuses, permettant ainsi l'établissement de populations aux abondances généralement élevées. Dans la rivière Nakdong (Kim et Joo 2000), l'abondance du zooplancton était significativement plus élevée au printemps et à l'automne (étiage) qu'en été et en hiver lors des précipitations intenses de la mousson.

De plus, l'alternance de crue et d'étiage modifie l'influence des différents compartiments de la rivière (lacs fluviaux et tronçons) entre eux, par une augmentation (débit élevé) ou une diminution (faible débit) de leur connectivité.

1.4 Objectifs et hypothèses de recherche

Cette étude s'inscrit dans le projet *Lampsilis*, regroupant des chercheurs de l'Université du Québec à Trois-Rivières, de l'Université du Québec à Rimouski et de l'Université de Montréal. Cette équipe a réalisé 3 missions scientifiques de 8 jours à bord du bateau de recherche *Lampsilis* en 2006. Il s'agit de la première mission d'envergure englobant 3 des 4 zones hydrographiques du fleuve Saint-Laurent, sur lesquelles on a recueilli sur 8 jours des données physiques, chimiques et biologiques. Ce projet a été financé par le Conseil de recherches en sciences naturelles et en génie du Canada et le Fonds de recherche du Québec - Nature et technologies.

Le projet *Lampsilis* avait pour but d'étudier l'hétérogénéité spatiale longitudinale, transversale et verticale de certains processus biologiques, physiques et chimiques dans les différents habitats caractéristiques du fleuve Saint-Laurent, soient les lacs fluviaux (lac Saint-François (LSF), lac Saint-Louis (LSL) et lac Saint-Pierre (LSP)), la ZTE et les tronçons fluviaux (corridor fluvial et estuaire fluvial)). L'objectif était d'établir la connectivité entre ces habitats, i. e. de caractériser le transfert de matière d'un milieu à l'autre.

Les objectifs spécifiques étaient variés; ils comptaient l'identification et la caractérisation spectrale des masses d'eau, la biodisponibilité des nutriments et de la matière organique dissoute, la variation spatio-temporelle des structures de communauté de bactéries, de protistes et de zooplancton et de leur qualité alimentaire, ainsi que la caractérisation de la faune benthique et de ses interactions avec la matière organique. Des données spectrales, biochimiques et trophiques ont été récoltées sur l'ensemble du fleuve Saint-Laurent, en couvrant les différentes zones hydrographiques jusqu'à la ZTE en amont de l'estuaire moyen.

Notre étude fait partie du volet zooplancton du projet *Lampsilis*. En effet, elle vise à évaluer les distributions longitudinale (Ouest-Est) et transversale (Rive nord - Rive sud) des crustacés planctoniques de Cornwall à l'Île aux Coudres, au mois de mai et d'août 2006. Notre analyse porte sur la composition taxonomique des échantillons de surface de zooplancton récoltés lors des expéditions du *Lampsilis* en mai et en août 2006. L'identification du zooplancton a été faite au niveau des grands groupes (cladocères, calanoïdes, cyclopoïdes, harpacticoïdes, amphipodes et mysidacés), allant jusqu'au genre ou à l'espèce pour les taxa dominants de crustacés. Les données environnementales du *Lampsilis* ainsi que sur la distribution modélisée des masses d'eau ont été utilisées dans le cadre de deux études séparées. L'objectif de la recherche est d'établir la relation entre la distribution des crustacés planctoniques dans le fleuve Saint-Laurent et la distribution des masses d'eau et leurs caractéristiques physico-chimiques et biologiques. Les hypothèses de départ sont: 1) que la distribution du zooplancton est liée à la distribution des masses d'eau et 2) que les facteurs physiques liés à l'hydrologie et à la transition estuarienne dominent les facteurs chimiques (nutriments) et biologiques (Chl*a*) liés à la distribution transversale des masses d'eau dans le contrôle de la répartition des crustacés planctoniques.

Dans la première partie (Chapitre 2), nous avons comparé la richesse spécifique, l'abondance et la structure des communautés de crustacés planctoniques entre les 3 zones hydrographiques du fleuve Saint-Laurent (le tronçon fluvial, l'estuaire fluvial et la ZTE de l'estuaire moyen) au printemps (crue) et en été (étiage). Parce que la géomorphologie et le gradient de salinité sont à la base des processus écologiques et des distributions d'espèces, nous nous attendons à trouver des variations importantes dans la diversité et la structure de la communauté de zooplancton entre les différentes régions hydrographiques du Saint-Laurent et entre les hydropériodes. Nous avons également déterminé les relations entre les communautés de zooplancton et la distribution spatiale ainsi que les caractéristiques des masses d'eau le long du système fleuve-estuaire et dans les zones fluviales (d'eau douce) seulement. Nous avançons l'hypothèse que les facteurs hydrologiques reliés à la ZTE et à la distribution des masses d'eau contrôlent principalement la distribution du zooplancton à grande échelle le long du système fleuve-estuaire tandis que les discontinuités transversales des masses d'eau et leurs caractéristiques environnementales expliqueraient la distribution spatiale du zooplancton dans la zone fluviale. Les facteurs hydrologiques contrôleraient davantage la répartition du zooplancton lors de la crue au printemps que lors de la période d'étiage en été.

Dans la deuxième partie (Chapitre 3), nous voulons quantifier l'importance relative des processus hydrologiques unidirectionnels et environnementaux sur la distribution spatiale du zooplancton dans les eaux douces du Saint-Laurent. Pour ce faire, nous avons utilisé une méthode statistique développée récemment, soit les cartes de vecteurs propres asymétriques (AEM; Blanchet et al. 2008a, 2008b, 2010, 2011)) qui permet de générer des variables spatiales directionnelles modélisant la distribution des masses d'eau en mai et en août. Nous avons fait l'hypothèse que la distribution spatiale du zooplancton est davantage reliée à la distribution longitudinale directionnelle des masses d'eau et à leur mélange latéral partiel qu'aux conditions environnementales locales. Les processus hydrologiques directionnels devraient avoir des effets plus marqués que les conditions environnementales locales sur la distribution du zooplancton au printemps quand le débit et les courants sont forts, et inversement en été lorsque le débit est faible et que les discontinuités transversales des masses d'eau sont plus prononcées.

Le projet nécessitait un encadrement multidisciplinaire par plusieurs membres du GRIL spécialistes en écologie du zooplancton (Bernadette Pinel-Alloul), en écologie fluviale (Jean-Jacques Frenette) et en analyse spatiale (Pierre Legendre). L'expertise en hydrologie provient de Jean Morin et Olivier Champoux (Service météorologique du Canada, Environnement Canada).

Bernadette Pinel-Alloul, Pierre Legendre et Jean-Jacques Frenette sont mes codirecteurs. Bernadette Pinel-Alloul a supervisé l'ensemble de mon travail tout au long de ma maîtrise. Pierre Legendre a fourni son expertise sur les analyses statistiques pertinentes pour la recherche. Jean-Jacques Frenette a fourni les données environnementales, conçu et réalisé le plan d'échantillonnage. Les échantillons de zooplancton nécessaires à la recherche ont été récoltés par Patrice Thibeault et traités par Ginette Méthot (agente de recherche) et des étudiants aux cycles supérieurs du GRIL (Groupe de Recherche Interuniversitaire en Limnologie et Environnement Aquatique). Jean Morin et Olivier Champoux ont produit les simulations menant aux schémas de distribution des masses d'eau utilisés dans les deux articles du mémoire. Lama Aldamman a fait l'identification des harpacticoïdes à l'espèce pour les mois de mai et d'août. Pour ma part, j'ai fait l'analyse en laboratoire du zooplancton (tri et identification) et tous les calculs statistiques ayant mené aux résultats, et j'assume seule la revue de littérature et la rédaction des articles figurant dans mon mémoire.

1.5 Site d'étude : le fleuve Saint-Laurent

Le système hydrographique Saint-Laurent - Grands Lacs (Figure 1, p18) draine plus de 25 % des réserves mondiales d'eau douce et son bassin de drainage s'étend sur 1 610 000 km^2. Ce système influence très fortement les processus environnementaux de l'Amérique du Nord (Direction générale des eaux intérieures 1990). Les eaux du fleuve Saint-Laurent (Figure 2, p19) subissent des modifications de leurs propriétés physico-chimiques tout au long de leur parcourt, soit par l'apport des tributaires, le mélange avec les eaux salées de l'Atlantique, par les saisons ou encore par les activités humaines (CSL 1996).

Le fleuve Saint-Laurent se classe au 16^e rang mondial pour son débit annuel moyen (12 600 m^3/s à Québec) (CSL 1996). Il est recouvert d'une couche de glace de la mi-décembre au début d'avril (CSL 1996). Le dégel engendre la crue printanière durant laquelle les débits du fleuve et de ses affluents sont plus élevés. Les débits moyens du fleuve Saint-Laurent et de ses principaux tributaires, au cours de la semaine d'échantillonnage du *Lampsilis* en mai et août 2006, sont présentés au tableau I (p20). Ces données ont été obtenues à partir des débits journaliers mesurés à des stations hydrométriques. Certains débits journaliers ont été mesurés directement aux centrales de Beauharnois (station hydrométrique 02MC010 (Environnement Canada (EC)); fleuve Saint-Laurent) et Carillon (station 02LB024 (EC); rivière des Outaouais), et à LaSalle (Montréal) (station 02OA016 (EC); fleuve Saint-Laurent). Des équations de relations de bassins ont été appliquées aux mesures de débits journaliers provenant des stations hydrométriques des rivières tributaires pour obtenir leurs valeurs à l'exutoire (Olivier Champoux, EC). Les débits du Saint-Laurent et des tributaires lors des campagnes d'échantillonnage en 2006 étaient considérablement plus élevés en mai qu'en août, excepté à la centrale de Beauharnois, où le débit était supérieur en août. La contribution plus importante des tributaires au fleuve Saint-Laurent pendant la crue au mois de mai est mise en évidence par la hausse marquée de son débit à la hauteur de Trois-Rivières.

1.5.1 Les régions hydrographiques

Le fleuve Saint-Laurent (Figure 2, p19) est composé de 4 régions hydrographiques se distinguant par leur hydrodynamisme (courants et marées), salinité, climat et géomorphologie (CSL 1996). Trois d'entre elles ont été échantillonnées lors des missions du *Lampsilis* : le tronçon fluvial, l'estuaire fluvial et l'estuaire moyen (CSL 1996). Le tronçon fluvial, situé dans une région

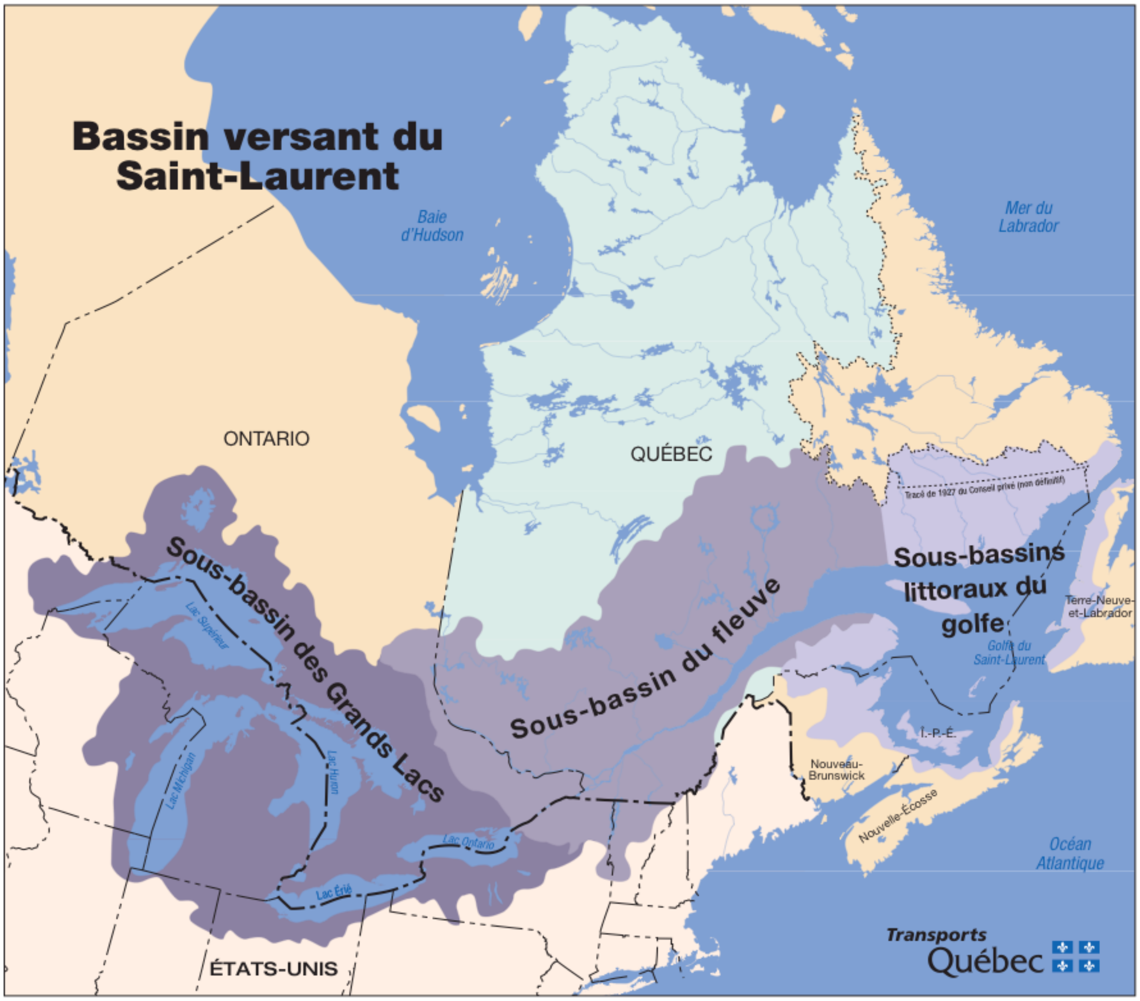

Figure 1 Bassin versant du fleuve Saint-Laurent.
Source: Service de la géomatique (2005), Environnement Canada, Centre Saint-Laurent

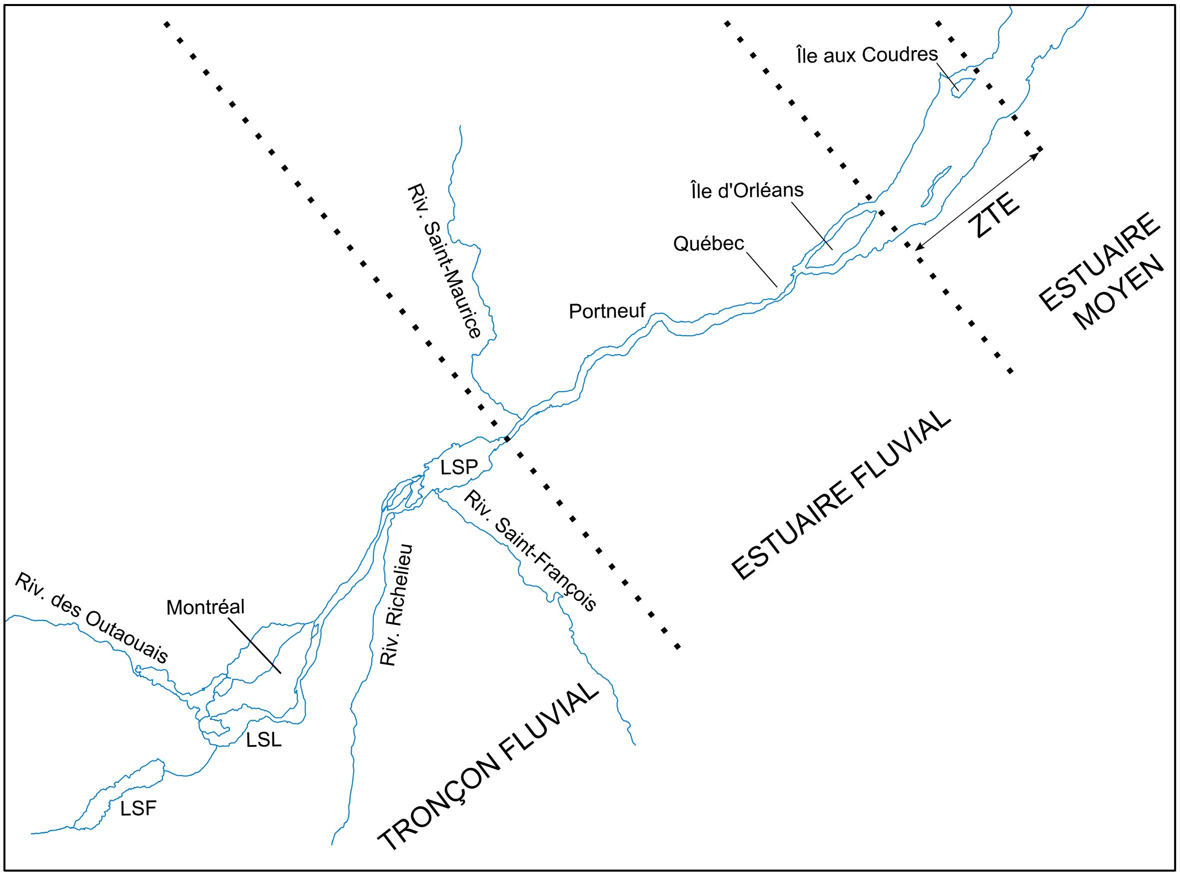

Figure 2 Zone étudiée du fleuve Saint-Laurent comprenant les trois zones hydrographiques (Tronçon fluvial, Estuaire fluvial, Estuaire moyen) et la zone de transition estuarienne (ZTE). Lac Saint-François (LSF), Lac Saint-Louis (LSL), Lac Saint-Pierre (LSP).

Tableau I Débits moyens (m^3/s) du fleuve Saint-Laurent et de ses principaux tributaires à l'exutoire au cours des 2 campagnes d'échantillonnage du *Lampsilis* du 23 au 30 mai et du 8 au 15 août 2006.

	Mai	Août
Fleuve Saint-Laurent		
Beauharnois	6203	6771
LaSalle	7909	7668
Sorel	9892	8920
Trois-Rivières	11447	9505
Rivières tributaires		
des Outaouais	2347	1399
l'Assomption	178	45
Richelieu	810	387
Yamaska	182	23
Saint-François	338	138
Maskinongé	67	11

Source: Olivier Champoux (Environnement Canada)

Tableau II Caractéristiques physiques et chimiques (moyenne (écart type, nombre de relevés) de la masse d'eau des Grands Lacs (Cornwall) et de celle de la rivière des Outaouais (Carillon) de mai 1995 à mai 1996.

	Grands Lacs (Cornwall)	Rivière des Outaouais (Carillon)
Conductivité (uS/cm)	295 (16, 30)	95 (21, 32)
Matières en suspension (mg/L)	0.78 (0.44, 30)	8,2 (11.4, 32)
Coefficient d'extinction lumineuse (K, m^{-1})	0.31 (0.04, 2)	1.32 (0.03, 2)
Phosphore total (mg P/L)	0.008 (0.003, 13)	0.031 (0.019, 14)

Source: Adapté de Hudon 2000

Tableau III Valeurs moyennes des variables physiques et des concentrations en ions majeurs dans les principales masses d'eau du Saint-Laurent entre 1985 et 1990. ( ): nombre de relevés.

	Grands Lacs	**Rivière des Outaouais**	**Mélange Grands Lacs - rive sud**	**Mélange Grands Lacs - des Outaouais - rive nord**	**Eaux de Québec**
Variables physiques					
Conductivité (uS/cm)	305 (220)	80 (127)	272 (41)	171 (126)	244 (189)
Couleur apparente (unité Pt-Co)	13 (146)	62 (91)	56 (26)	86 (85)	48 (137)
Turbidité (UTN)	1,4 (154)	4,2 (92)	6,4 (29)	8,6 (92)	6,0 (153)
MES (mg/L)	2,5 (154)	6.0 (92)	15.0 (29)	14,3 (91)	12,2 (153)
Ions majeurs					
Dureté (mg/L de CaCO3)	123,4 (153)	29,2 (92)	104,8 (29)	61,5 (92)	95,4 (153)
Calcium (mg/L)	36,3 (153)	8,3 (92)	31,0 (29)	17.7 (92)	27.9 (153)
Magnésium (mg/L)	7,9 (154)	2,1 (92)	7,1 (29)	4.2 (92)	6.3 (153)
Sodium (mg/L)	10,8 (154)	3,0 (92)	10,7 (29)	7.2 (92)	9.6 (153)
potassium (mg/L)	1,38 (154)	0,81 (92)	1.5 (29)	1.17 (92)	1.32 (153)
Chlorures (mg/L)	22.2 (154)	4,3 (92)	19.9 (29)	11.9 (92)	18.2 (153)
Sulfates (mg/L)	27,7 (154)	10,5 (92)	26.4 (29)	16.7 (92)	23.5 (153)

Source: Adapté de CSL 1996

fortement industrialisée, s’étend sur 240 km de Cornwall (Ontario) jusqu’à l’exutoire du lac Saint-Pierre (EMR 1975). Cette portion du fleuve comporte des rapides, des lacs (LSF, LSL, LSP), des îles et îlots ainsi que plusieurs aménagements hydrauliques (CSL 1996). Son eau est douce et son régime hydrodynamique est légèrement influencé par les ondes de marée au LSP (Godin 1979).

L’estuaire fluvial s’étend sur 160 km (EMR 1975) à partir de l’extrémité est du LSP jusqu'à la pointe est de l’Île d’Orléans (CSL 1996). En amont de Québec, l’estuaire fluvial est un corridor peu sinueux dont la largeur varie entre 3 et 5 km. La profondeur du chenal principal varie généralement de 13 à 40 m entre Trois-Rivières et Québec, un chenal de navigation étant maintenu par dragage à une profondeur d’au moins 11 m sur une largeur de 240 m (CSL 1996) - il est à noter que les valeurs de superficie et de profondeur moyennes du fleuve Saint-Laurent varient en fonction de la saison (Jean-Jacques Frenette, communication personnelle). En aval de Québec, le fleuve s’élargit rapidement et atteint 15 km à l’extrémité est de l’Île d’Orléans, cette dernière formant la seule île importante de l’estuaire fluvial. Le chenal longeant la rive sud de l’Île d’Orléans est dragué sur 300 m afin d’y maintenir une profondeur minimale de 12.5 m (Ministère du Conseil exécutif 1985) tandis que la profondeur du chenal au nord de l’île est inférieure à 10 m. De l’exutoire du LSP jusqu’à Portneuf, l’écoulement des eaux douces s’effectue vers l’aval sans renversement des courants, permettant aux masses d’eau en provenance des différents tributaires du Saint-Laurent de s’écouler sans mélange important et donc de conserver leurs caractéristiques physicochimiques respectives (CSL 1996). En aval de Portneuf, la marée devient de plus en plus forte jusqu’à Québec et il se produit un renversement des courants à marée montante, accentuant l’effet de mélange des masses d’eau. Les eaux demeurent toutefois douces jusqu’à l’extrémité est de l’Île d’Orléans (CSL 1996).

Le moyen estuaire (Figure 3, p22) couvre une distance de 150 km (EMR 1975) de la pointe est de l’Île d’Orléans jusqu’à l’embouchure du Saguenay, avec une largeur moyenne de 17 km. Cette section comporte une cinquantaine d’îles et d’îlots, les plus importants étant l’archipel de l’Île aux Grues, l’Île aux Coudres, les Îles de Kamouraska, l’Île aux Lièvres et l’Île Verte. (CSL 1993). Le moyen estuaire compte 3 chenaux d’écoulement d’une profondeur généralement supérieure à 10 m. Dans la ZTE (Figure 2, p19), entre l’Île d’Orléans et l’Île aux Coudres, 2 chenaux longent les rives nord et sud du Saint-Laurent, le troisième traversant le fleuve du nord au sud entre l’Île aux Coudres et l’archipel de l’Île aux Grues. C’est dans la ZTE que se produit le mélange des eaux douces du fleuve et des eaux salées de l’Atlantique. À cet endroit, les forts courants du fleuve

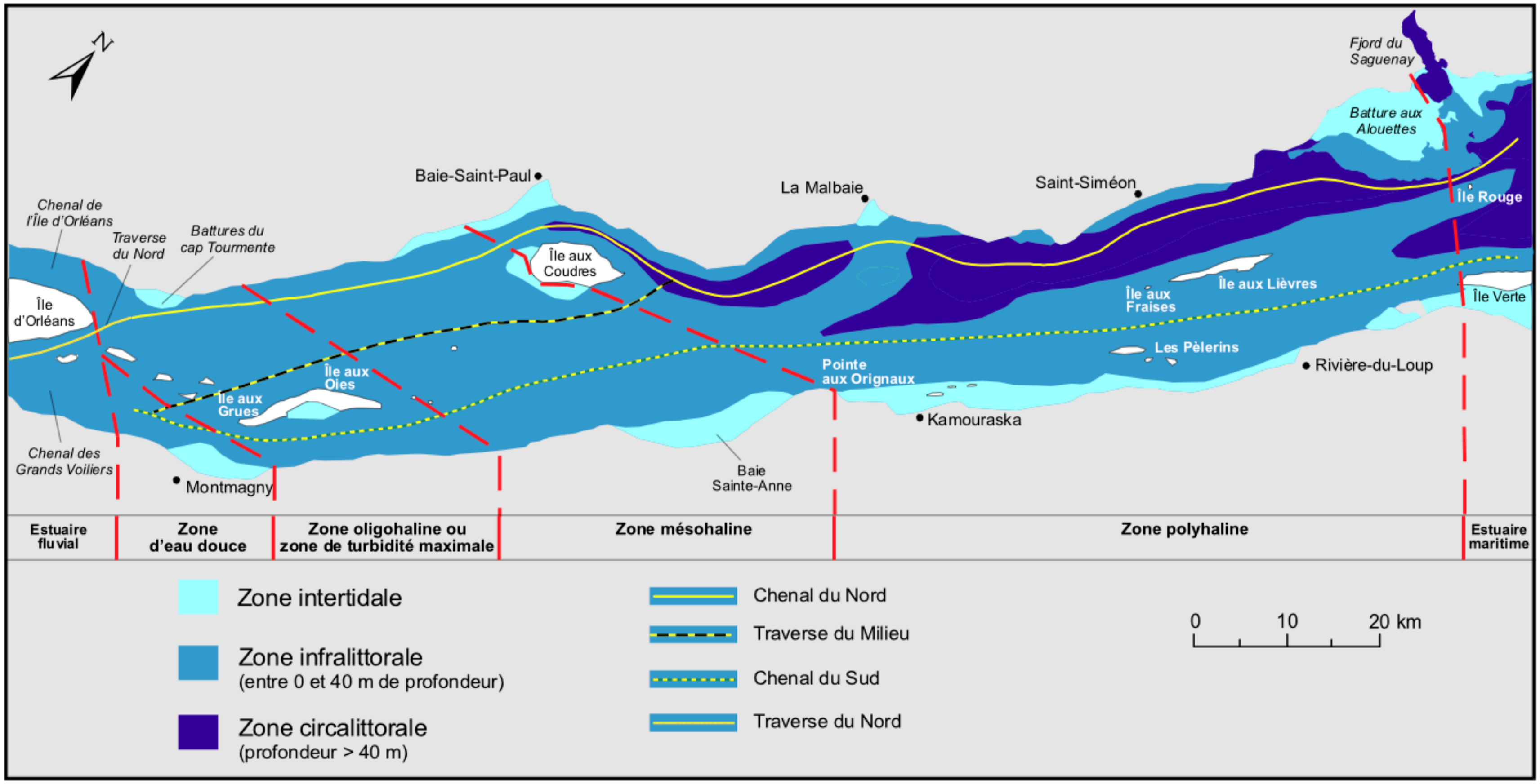

Figure 3 Zonation de l'estuaire moyen en fonction de la bathymétrie et du gradient amont-aval des conditions physico-chimiques.
Source : CSL 1996, adapté de CSL et Université Laval 1991

atteignent les eaux marines soumises à la marée; il se produit alors un très fort brassage des eaux et la remise en suspension des sédiments dû au frottement du fond marin, rendant les eaux saumâtres et très turbides (CSL 1996). Cette section de l'estuaire est partiellement mélangée avec une circulation en 2 couches : une intrusion des eaux salées vers l'amont le long du fond (surtout au niveau du chenal du nord), et un écoulement de surface vers la mer comprenant des eaux mélangées (Gagnon et Lacroix 1981). Les conditions physiques et chimiques particulières de la ZTE limitent le développement des espèces végétales et animales d'eau douce et d'eau salée et la diversité des espèce y diminue.

Les ondes de la marée semi-diurne, pénétrant dans l'estuaire depuis l'océan Atlantique, s'amplifient jusqu'à l'Île d'Orléans sur la rive sud et jusqu'à l'Île aux Coudres sur la rive nord (Godin 1979). Les marées atteignent leur hauteur maximale (6.9 m à la vive eau) à la pointe est de l'Île d'Orléans (Pêches et Océans 1992). En amont de l'île, elles s'atténuent graduellement jusqu'au LSP. À Québec, les marées moyennes sont de 4.1 m alors que les marées de vive eau atteignent 5.8 m. La marée produite à Québec a un débit impressionnant de 55 000 $m^{3/}s$ (CSL et Université Laval 1991), ce débit étant plus de 4 fois supérieur au débit moyen du fleuve au même endroit (12 100 m^3/s) (CSL 1993). À marée descendante, ces 2 débits combinés engendrent un débit instantané de 75 000 m^3/s et des courants de 3.0 m/s (Verrette 1990). Dans la ZTE, à Montmagny, le débit moyen total (débits du fleuve et de la marée) est estimé à 90 000 m^3/s (CSL et Université Laval 1991).

1.5.2 Les masses d'eau

À Montréal, le Saint-Laurent reçoit annuellement, en moyenne, 80 % de ses eaux des Grands Lacs et 16 % (jusqu'à 50% lors des crues printanières) de la rivière des Outaouais (CSL et Université Laval 1991). Leurs eaux et celles des tributaires y forment des masses d'eau aux caractéristiques physico-chimiques distinctes, qui coulent côte à côte, parfois sur de longues distances, avant de se mélanger.

Les eaux des Grands Lacs (Cornwall) et celles de la rivière des Outaouais (Carillon), avant leur confluence dans le fleuve Saint-Laurent, présentent des caractéristiques physico-chimiques très différentes (Hudon 2000; Tableau II, p20). D'une part, les eaux très claires ($K = 0.3\ m^{-1}$) des Grands Lacs sont caractérisées par des concentrations de matières en suspension extrêmement faibles (< 1 mg/L), une conductivité modérément élevée (295 µS/cm) et de faibles concentrations de PT (0.008 mg P/L) (Hudon 2000). Leur degré relativement élevé de minéralisation est dû au bassin inférieur des Grands Lacs, en grande partie d'origine sédimentaire, et leurs très faibles concentrations de matières en suspension proviennent de leur importante sédimentation dans le lac Ontario, qui est la source du fleuve (CSL 1996).

Au contraire, les eaux de la rivière des Outaouais qui draine le Bouclier canadien (CSL 1996; Hudon 2000; Hudon et Carignan 2008) ont une clarté (K = 1.3 m^{-1}) et une conductivité (95 µS/cm) moins élevées, avec des concentrations de matières en suspension (8 mg/L) et en nutriments (PT = 0.03 mg P/L) plus élevées (Hudon 2000).

Le Saint-Laurent compte 5 masses d'eau principales (Tableau III, p 20) et 9 autres masses d'eau de moindre importance associées aux principaux tributaires (CSL 1996). Les 5 masses d'eau principales sont 1) les eaux des Grands Lacs, 2) les eaux de la rivière des Outaouais, 3) les eaux de mélange des Grands Lacs et des tributaires de la Rive-Sud (mélange Grands Lacs – rive sud), 4) les eaux de mélange des rivières des Outaouais et l'Assomption et des Grands Lacs à l'est de la rivière l'Assomption (mélange Grands Lacs - des Outaouais - rive nord), 5) les eaux de la région de Québec. Les rivières Saint-Louis, Châteauguay, l'Assomption, Richelieu, Yamaska, Nicolet, Saint-Maurice, Bécancour et Jacques Cartier forment les 9 masses d'eau secondaires à leur confluence avec le fleuve Saint-Laurent.

La masse d'eau des Grands Lacs se distingue par ses eaux plus minéralisées, avec une conductivité d'environ 300 µS/cm et des concentrations élevées d'ions majeurs (Tableau III, p20). Les eaux brunes (chargées en acides humiques) de la rivière des Outaouais ont une conductivité (80 µS/cm) et des concentrations en ions majeurs plus faibles à cause du caractère moins altérable des roches métamorphiques du Bouclier canadien (CSL 1996). La couleur apparente, la turbidité et les matières en suspension sont plus faibles dans les eaux vertes des Grands Lacs et le mélange Grands Lacs - rive sud que dans les eaux de la rivière des Outaouais et du mélange Grands Lacs - des Outaouais - rive nord. Les eaux des affluents de la rive sud sont moyennement minéralisées et très chargées en matières en suspension (CSL 1996).

Les lacs fluviaux, situés dans le tronçon fluvial, sont des bassins d'eau douce assez larges pour être considérés comme des lacs mais dont l'écoulement est typique d'un fleuve. Le LSF, ayant une profondeur moyenne de 6 m (Environnement Canada 2010), reçoit les eaux des Grands Lacs qui s'écoulent en une seule masse d'eau (CSL 1996). Il reçoit moins de 2% de ses apports des tributaires. Le LSL, avec une profondeur moyenne de 3 m (Environnement Canada (2010), reçoit deux masses d'eau principales : les eaux vertes des Grands Lacs qui s'écoulent le long de la rive sud et dans le chenal de navigation du Saint-Laurent ainsi que les eaux brunes humiques de la rivière des Outaouais, partiellement mélangées à celles des Grands Lacs en rive nord (CSL 1996). Le LSP constitue l'une des composantes majeures de l'écosystème du Saint-Laurent. Situé en aval des autres lacs fluviaux du Saint-Laurent, il est bordé par la plus vaste plaine d'inondation en eaux douces du Québec, atteignant une superficie de plus de 600 km^2 en période de crue (Environnement Canada 2010). À l'exception du chenal de navigation dont la profondeur minimale est de 11.3 m, le LSP se caractérise par sa faible profondeur (moins de 3 m). Les 3 masses d'eau principales s'écoulant au LSP sont 1) les eaux des Grands Lacs (au centre), 2) les eaux de mélange des Grands Lacs et des tributaires de la Rive-Sud (au sud) et 3) les eaux de mélange des Grands Lacs, de la rivière des Outaouais et des tributaires de la Rive-Nord (au nord) (CSL 1996; Hudon et Carignan 2008).

Les caractéristiques des masses d'eau regroupent les concentrations en matière organique dissoute chromophorique, en solides en suspension et en pigments comme la chlorophylle. Ces facteurs contribuent ensemble à la distribution et à la composition des masses d'eau des lacs fluviaux au sein du tronçon fluvial (Frenette et al. 2003). L'origine d'une masse d'eau, les variations du niveau d'eau et du débit modifient les caractéristiques physico-chimiques de ces masses d'eau et la portion de la surface du lac qu'elles couvrent (Hudon et Carignan 2008). La chimie des masses d'eau peut influencer la distribution du zooplancton de façon directe en fonction des conditions du pH, des nutriments et des ressources algales et de façon indirecte en affectant la pénétration de la lumière. La pénétration de la lumière photosynthétique et des UV influence à son tour la distribution du zooplancton (Frenette et al. 2003, 2006). Le zooplancton produit dans le bassin versant peut aussi être transporté jusqu'au fleuve par les tributaires, lesquels peuvent modifier ponctuellement la composition et l'abondance du plancton (Hudon 1996).

Dans l'estuaire fluvial (Figure 2, p19), entre l'exutoire du lac Saint-Pierre et Porneuf, la marée ralentit l'écoulement des eaux sans toutefois engendrer le renversement des courants. Par conséquent, les masses d'eau des affluents se mélangent peu dans ce tronçon, et les 3 masses d'eau principales du LSP continuent leur écoulement en aval. Au-delà de Portneuf, l'effet de la marée est plus accentué et produit un renversement du courant à marée montante, engendrant une homogénéisation verticale et transversale des caractéristiques physico-chimiques des eaux. Les eaux de cette région (les eaux de Québec) forment la 5^e masse d'eau principale du Saint-Laurent.

1.5.3 Le plancton dans la zone fluviale

Quelques auteurs ont évalué l'évolution des communautés de phytoplancton et de zooplancton dans le fleuve Saint-Laurent en aval du lac Ontario. Mills et al. (1981), Mills et Forney

(1982) et Twiss et al. (2010) ont étudié le plancton dans le tronçon international du Saint-Laurent sur une distance de 160-180 km (entre le lac Ontario et Cornwall) à l'hiver 1978, aux périodes printemps-été 1976 à 1978 et à l'été 2008, respectivement. L'étude de Basu et al. (2000a) a couvert le fleuve Saint-Laurent du lac Ontario jusqu'à Trois-Rivières (Québec) sur une distance de 425 km. Ces auteurs ont observé une diminution des biomasses de phytoplancton et de zooplancton lors de leur transport vers l'aval. La diminution du plancton en aval du lac Ontario survenait en grande partie dès son entrée dans la zone fluviale (Mills et Forney 1982; Basu et al. 2000a; Twiss et al. 2010). De même, la composition taxonomique du phytoplancton (Mills et al. 1981; Twiss et al. 2010) et du zooplancton (Mills et Forney 1982) variait peu en aval du lac Ontario, appuyant encore l'hypothèse d'une contribution majeure du lac Ontario au plancton du fleuve Saint-Laurent (Mills et al. 1981; Mills et Forney 1982; Twiss et al. 2010). Twiss et al. (2010) attribuait en grande partie la diminution du phytoplancton en aval dans le tronçon international du fleuve Saint-Laurent au broutage par la communauté benthique (larves filtreuses d'insectes et moules de la famille Dreissenidae), tandis que la diminution du zooplancton serait due en partie aux changements abrupts dans l'environnement physique du fleuve, provoquant une augmentation de la vitesse du courant et de la turbulence (Mills et Forney 1982).

Le phytoplancton lacustre entrant dans une grande rivière est soumis à des changements majeurs dans l'hydrodynamisme : la turbulence due à l'advection homogénéise la colonne d'eau, exposant les algues à des intensités lumineuses élevées près de la surface et à des intensités très faibles dans les tronçons les plus profonds (Reynolds 1994; Hudon 1996). Des études ont souligné la continuité spatiale dans la composition taxonomique (Provencher 1976) et dans les concentrations en Chl*a* (Painchaud et al. 1993; Bertrand et Vincent 1994) dans la masse d'eau centrale du Saint-Laurent, où le courant est élevé (Hudon 1996). Dans l'étude de Hudon et al. (1996), 3 transects étaient étudiés dans le corridor fluvial entre Cornwall et Port Saint-François (quelques km en aval du LSP) dans le fleuve Saint-Laurent. Le pourcentage des espèces exclusives à un seul transect était faible (24%) en période de fort débit et élevé (33%) en période de faible débit, suggérant que l'entraînement physique vers l'aval avait un effet uniformisant très fort sur le phytoplancton, maintenant la continuité longitudinale dans le chenal principal.

En hiver, le phytoplancton était peu abondant dans le fleuve Saint-Laurent (Mills et al. 1981). La faible biomasse du zooplancton variait entre < 0.01 et $0.6\ g/m^2$ et se situait autour d'un dixième de la biomasse algale. La communauté zooplanctonique avait une faible diversité et était fortement dominée par le cyclopoïde *Diacyclops thomasi* tandis que le calanoïde *Leptodiaptomus* *minutus* et le cladocère *Bosmina sp*. étaient communs (Mills et al. 1981). En été, la biomasse totale de zooplancton était encore faible (< 10 mg/L, poids sec) (Basu et al. 2000a). Parmi les crustacés planctoniques, le cyclopoïde *D. thomasi* et les cladocères *Bosmina sp*., *Ceriodaphnia quadrangulata* et *Daphnia galeata mendotae* étaient communs (Mills et Forney 1982). Le patron de biomasse de zooplancton montrait de petites populations d'adultes tôt au printemps, et celle-ci atteignait un pic à la fin de juillet-début août (Mills et Forney 1982).

1.5.4 Le plancton dans la ZTE

La ZTE dans l'estuaire du Saint-Laurent contient des concentrations importantes de microplancton et de macroplancton supportant une pouponnière de poisson productive (Laprise et Dodson 1994; Vincent et Dodson 1999; Barnard et al. 2003; Winkler et al. 2003). Cette région est caractérisée par des gradients forts de plusieurs variables environnementales comme la salinité, la concentration en nutriments, la température et la pénétration de la lumière (Gagnon et Lacroix 1981; Winkler et al. 2003). Les concentrations de zooplancton et de particules en suspension, de même que la turbidité y sont élevées (Laprise et Dodson 1994; Frenette et al. 1995; Winkler et al. 2003; Barnard et al. 2003). La recirculation estuarienne et la marée causent la rétention physique des phytoplanctons allochtone et autochtone et du zooplancton d'eau saumâtre dominé par le calanoïde *E. affinis* et le mysidacé *Neomysis americana* (Winkler et al. 2003). Dans le fleuve Saint-Laurent, le plancton hétérotrophe représente une petite composante du microplancton total en eau douce, mais domine la biomasse totale à des salinités plus élevées (Winkler et al. 2003). Les consommateurs primaires dans la ZTE du Saint-Laurent sélectionnent le phytoplancton, qui, même s'il ne représente qu'une petite fraction du carbone sestonique, supporte ultimement la productivité élevée de la ZTE (Martineau et al. 2004). Lapierre et Frenette (2008) indiquent que le pic de biomasse de phytoplancton trouvé dans la ZTM du Saint-Laurent ne peut pas s'expliquer seulement par la croissance locale. Le fait que ce phytoplancton présente un ratio d'isotopes stables du soufre représentatif des eaux douces indique que la plupart de la biomasse du phytoplancton de la ZTM provient des eaux douces en amont. Le calanoïde *E. affinis* joue un rôle important dans la dynamique trophique de l'estuaire moyen du Saint-Laurent où il se nourrit de phytoplancton (Winkler et al. 2003). Les conditions de croissance de *E. affinis* dans la zone d'eau douce en amont de la ZTM était reliée à l'abondance relative d'un type de seston probablement associé aux diatomées d'eau douce en provenance de l'amont (Pommier et al. 2010). Le taux ARN : ADN élevé de *E. affinis* à travers la ZTE par rapport à ceux observés dans des conditions optimales pour d’autres copépodes, ainsi que la présence à cet endroit de nombreuses femelles ovigères portant des spermatophores, suggère que la population estivale de *E. affinis* dans la ZTE du Saint-Laurent profite de bonnes conditions de croissance. Les prédateurs d’*E. affinis* les plus importants dans la ZTM sont les mysidacés et les larves de poulamon (*Microgadus tomcod*) et d’éperlan (*Osmerus mordax*) (Winkler et al. 2003).

Chapitre 2:
Zooplankton spatial distribution patterns in the St. Lawrence River

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2.1 Abstract

Herein we studied the spatial distribution and community structure of planktonic crustaceans and their generative processes along the fluvial-estuary section of the St. Lawrence River (Québec). Zooplankton and environmental data were surveyed at 52 sites distributed in 16 transects along three biogeographical zones: the fluvial section zone (FSZ), the fluvial estuary zone (FEZ), and the estuarine transition zone (ETZ). Two surveys were conducted in May and August 2006 between Cornwall (Ontario) and Île aux Coudres (Québec). To describe the spatial distribution of zooplankton groups (cladocerans, calanoid, cyclopoid and harpacticoid copepods, amphipods and mysids), we compared crustacean diversity and community structure among the three biogeographic zones during two different hydroperiods in May (high discharge) and August (low discharge). The global community structure of the zooplankton, as well as the community structure within each zooplankton group was also detailed in 6 longitudinal habitats along the survey area. To contrast transversal habitats, we compared diversity and abundance of zooplankton among sites depending on their location within transects (south, center and north) in 5 longitudinal habitats within the fluvial zones. We found that the crustacean assemblages differed significantly among biogeographic zones (especially between the fluvial zones and the brackish zone), the longitudinal habitats and the hydroperiods. We observed zooplankton enrichment in fluvial lakes and littoral zones, and successive decrease and increase in the main channel species richness, respectively within and at the outlet of Lake Saint-Pierre (LSP). We established the relationship between zooplankton distribution patterns and the spatial distribution of water masses and their physical and chemical characteristics at each hydroperiod. The salinity-conductivity gradient related to the fluvial-estuary discontinuity determined the large-scale zooplankton distribution while the spatial patterns of the water masses and their environmental conditions influenced zooplankton distribution within the fluvial zones.

Keywords: redundancy analysis (RDA); river spatial complexity; St. Lawrence River; water masses; zooplankton spatial distribution patterns

2.2 Résumé

Nous avons évalué la distribution spatiale et la structure de la communauté des crustacés planctoniques et leurs processus générateurs le long de la section fleuve-estuaire du fleuve Saint-Laurent (Québec). Les données environnementales et les échantillons de zooplancton ont été récoltés à 52 sites distribués dans 16 transects le long de 3 zones biogéographiques: le tronçon fluvial, l'estuaire fluvial et la zone de transition estuarienne. Deux campagnes d'échantillonnage ont été réalisées en mai et août 2006 entre Cornwall (Ontario) et l'Île aux Coudres (Québec). Pour décrire la distribution spatiale des grands groupes de zooplancton (cladocères, copépodes calanoïdes, cyclopoïdes et harpacticoïdes, amphipodes et mysidacés), nous avons comparé la diversité et la structure de la communauté des crustacés entre les 3 zones biogéographiques lors de 2 hydropériodes en mai (crue) et août (étiage). La structure globale de la communauté zooplanctonique ainsi que la structure de la communauté de chaque groupe de crustacés a aussi été détaillée dans 6 habitats longitudinaux successifs le long de la zone étudiée. Pour contraster les habitats transversaux, nous avons comparé la diversité et l'abondance du zooplancton entre les sites en fonction de leur position à l'intérieur des transects (sud, centre et nord) dans 5 habitats longitudinaux à l'intérieur de la zone fluviale. Nous avons trouvé que les assemblages de crustacés planctoniques variaient significativement entre les zones biogéographiques (particulièrement entre les zones fluviales (tronçon et estuaire fluviaux) et la zone saumâtre (zone de transition estuarienne)), les habitats longitudinaux et les hydropériodes. Nous avons observé une augmentation de l'abondance du zooplancton dans les lacs fluviaux et les zones littorales, ainsi qu'une augmentation de la richesse spécifique à l'intérieur du Lac Saint-Pierre suivie d'une diminution au passage dans l'exutoire. Nous avons établi les relations entre les patrons spatiaux de zooplancton et la distribution spatiale des masses d'eau et leurs caractéristiques à chaque hydropériode. Le gradient salinité-conductivité relié à la discontinuité fleuve-estuaire a déterminé la distribution à grande échelle du zooplancton alors que les patrons spatiaux des masses d'eau et leurs caractéristiques environnementales ont influencé le zooplancton dans les zones fluviales.

Mots clés: analyse canonique de redondance (ACR); complexité spatiale de rivière; fleuve Saint-Laurent; masses d'eau; patrons de distribution spatiale du zooplancton

2.3 Introduction

As the geomorphology and hydrology of rivers are of primary importance for fluvial biodiversity and ecological functions (Elosegi et al. 2010), much effort has been invested to understand how they drive *in situ* productivity. Rivers were first described as longitudinal continua (Vannote et al. 1980) in which abiotic and biotic factors change gradually. For Ward and Stanford (1983), river corridors were punctuated with different kinds of discontinuities such as fluvial lakes and reservoirs which could strongly affect the river ecology downstream. Junk et al. (1989) emphasized the floodplain contribution to river productivity, whereas Thorp and Delong (1994) considered local primary production within the channel and the organic matter input from littoral vegetation as important factors. Recently, rivers were considered as arrays of large "hydrogeomorphic patches" (Thorp et al. 2006) which determine different functional zones and biological communities. Despite all these efforts, we still lack theory and knowledge about river spatial complexity and how planktonic organisms respond to it.

As zooplankton is a key component of aquatic food webs in all ecosystems including rivers, a better understanding of their distribution is necessary to evaluate future changes in biodiversity and community structure resulting from global warming and other anthropogenic influences. Zooplankton in rivers is primarily governed by abiotic factors related to hydrology (discharge, current velocity and water residence time) (Basu and Pick 1996; Kim and Joo 2000; Baranyi et al. 2002; Viroux 2002; Lair 2006) followed by biotic factors such as macrophytes, chlorophyll *a*, and fish predation (Basu et al. 2000b; Pinel-Alloul and Ghadouani 2007). Rotifers and secondly small cladocerans (*Bosmina sp.*) dominate communities in most rivers around the world, thanks to their shorter development time and their reproduction by parthenogenesis which enable them to survive and proliferate in the current (Pourriot et al. 1997; Viroux 1997; Baranyi et al. 2002; Lair 2006). Although copepods are less adapted to river conditions, they still represent a considerable portion of the zooplankton due to their euryhalinity (Lee 1999) and their ability to escape unfavourable conditions by activating winter diapause and aestivation in the dried sediments of temporary waters (Lair 2006). As planktonic crustaceans need long water residence time to grow and reproduce (Viroux 1997; Ietswaart et al. 1999; Viroux 2002; Lair 2006), their abundance largely depends on the availability of slow flowing or stagnant habitats such as fluvial lakes, reservoirs or littoral dead zones. Similarly, hydroperiods greatly affect zooplankton: floods are disruptive for them (Baranyi et al. 2002), causing high drift and mortality (Tockner et al. 1999) whereas periods of low water favour them by providing lentic habitats.

The St. Lawrence River (SLR) is one of the largest river systems in the world, its surface area, including the Great Lakes, reaching 1.6 million km^2. With its mean annual discharge of 12 600 m^3/s at Québec City, the SLR is the river with the second largest discharge in North America, after the Mississippi. It encompasses three fluvial lakes and several islands and tributaries which render it physically heterogeneous. Several physicochemically distinct water masses flow alongside the SLR, conserving their respective properties for long distances before mixing altogether near Portneuf, due to the action of the tide. Previous studies of zooplankton in the St. Lawrence system focused on smaller portions with few sites and transects (Mills et al. 1981; Mills et Forney 1982; Basu et al. 2000a, 2000b; Twiss et al. 2010). Our study is one of the first to cover the SLR from Cornwall to the upper estuary downstream of Québec City, providing environmental and zooplankton data along both the longitudinal and transversal axes. Sampling was conducted during two hydroperiods, in May and August 2006, to compare the high-discharge period in the spring to the low-discharge period in the summer.

We compared zooplankton species richness, abundance and community structure among three biogeographical zones (the fluvial section, the fluvial estuary and the estuarine transition zones), 6 longitudinal habitats (3 fluvial lakes, 2 freshwater corridors and the estuarine transition zone) and 3 transversal habitats (north and south shores, main channel) during each hydroperiod. Because geomorphology and the salinity gradient form the basic structure modulating ecological processes and species distributions, we expected to detect important variations in zooplankton diversity and community structure among biogeographical zones of the SLR, and between the spring and summer hydroperiods. Differences in hydrological factors (current velocity, water residence time), biological factors (presence of extensive macrophyte beds) and river bed morphology among the longitudinal and transversal habitats would also be reflected by contrasting zooplankton abundances and community structure, depending on the hydroperiod.

We also determined how the zooplankton community structure is influenced by the spatial distribution and chemical features of the water masses along the fluvial estuary section, and in the fluvial zones only, during the spring and summer hydroperiods. In the SLR, we expected that hydrological factors related to the estuarine transition zone together with the distribution of water masses would primarily control the zooplankton large-scale distribution along the river-estuary section, whereas transversal discontinuities between the distinct water masses, as well as their environmental characteristics would explain the zooplankton spatial distribution in the fluvial zone. We also expected that the hydrological factors would have a stronger effect during the high-discharge hydroperiod in the spring than during the low-discharge hydroperiod in the summer, as spatial connectivity among habitats is influenced by discharge (Tockner et al. 2000; Frenette et al. 2006) and was found to be higher in the main channel of the SLR as for phytoplankton composition during spring high discharge (Hudon et al. 1996).

2.4 Methods

2.4.1 Study sites and biogeographic zones

The zooplankton sampling units and the environmental data were collected during two cruises of the research vessel *Lampsilis*, conducted during the spring (23-30 May) and summer (8-15 August) of 2006. A total of 52 stations, distributed along 16 transversal transects, were visited in three biogeographical zones of the SLR from Cornwall to Île aux Coudres along a 375 km transect (Figure 1, p35). Transects were positioned perpendicularly to the main east-to-west axis of the SLR. Locations of stations within each transect were determined in order to study the lateral heterogeneity of the SLR water masses. Meteorological conditions were uniform during each sampling cruises and water masses stability was validated by satellite images. The sampling periods reflected seasonal variations in discharge, as shown in Table I (p35). Tributaries discharge was much more important in May than in August, and that was reflected on the cumulative discharge of the SLR, mostly at Trois-Rivières, downstream of LSP and the confluence of the major St. Lawrence tributaries.

The fluvial section zone (FSZ; sites 1-35) is 240 km long from Cornwall in Ontario to the Lake Saint-Pierre outlet in Québec, and ranges from < 2 km to 10 km wide (CSL 1996). This freshwater zone encompasses three fluvial lakes (Lake Saint-François (LSF), Lake Saint-Louis (LSL) and Lake Saint-Pierre (LSP)), and one fluvial corridor (FC). There is no or very little tidal effect to this point. Fluvial lakes are wide, slow flowing (< 0.3 m/s with the exception of the central channel), and shallow, with depth averaging 6 m for LSF and 3 m in LSL and LSP, whereas the fast flowing (1 m/s) navigation channel is 11.3 to 15 m deep. The fluvial lakes are extensively colonized by submerged macrophyte beds (Hudon 1996; CSL 1996; Basu et al. 2000a, 2000b). The slow

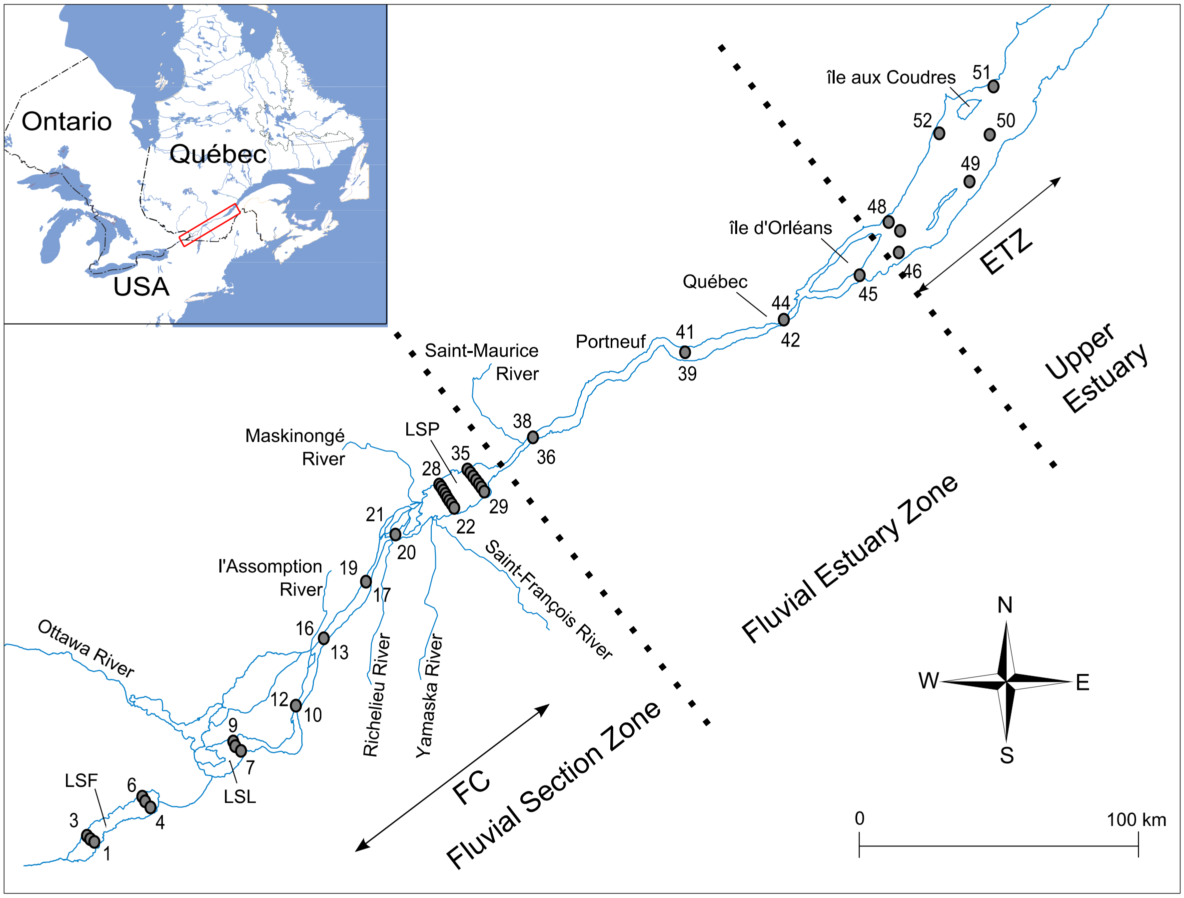

Figure 1 Distribution of the sampling sites in the 16 transects across the three biogeographical zones (Fluvial Section Zone, Fluvial Estuary Zone, Estuarine Transition Zone (ETZ)) of the St. Lawrence River (SLR). Lake Saint-François (LSF), Lake Saint-Louis (LSL), Lake Saint-Pierre (LSP), Fluvial corridor (FC).

Table I Mean discharge (m^3/s) in the St. Lawrence River (SLR) and at the outlet of its major tributaries during the sampling cruises in May 23-30 and August 8-15 2006.

	May	August
St. Lawrence River		
Montreal	7909	7668
Sorel (upstream of LSP)	9892	8920
Trois-Rivières (downstream of LSP)	11447	9505
Tributaries		
Ottawa River	2347	1399
l'Assomption River	178	45
Richelieu River	810	387
Yamaska River	182	23
Saint-François River	338	138
Maskinongé River	67	11

Source : Olivier Champoux (Environment Canada) flowing littoral areas in LSP would be isolated from the rapidly circulating central channel (Hudon 1996) during years of relatively low macrophytes development (Basu et al. 2000b), this transversal discontinuity limiting exchanges among the main northern, southern and central water masses. The main channel is fed by the clear waters of Lake Ontario, whereas the south and north shores receive waters from the tributaries.

The fluvial estuary zone (FEZ; sites 36-45) stretches more than 160 km from the LSP outlet to the eastern tip of Île d'Orléans (CSL 1996). River width ranges from 870 m near Québec City to 15 km at the eastern end of Île d'Orléans. Average water depth in the main channel varies from 13 to 40 m. The FEZ is composed of fresh waters and shows significant semidiurnal tides (averaging 4.1 m) at Québec City.

The upper estuary covers 150 km from the eastern tip of Île d'Orléans to the mouth of the Saguenay River. Average width is 17 km and depth varies from 100 to 300 m (CSL 1996). In this study, we included this section up to Île aux Coudres only, this portion being called the estuarine transition zone (ETZ; sites 46-52). In this region, high-intensity currents encounter tides which cause fresh and salt water mixing, strong upwelling currents and important sediment resuspension. Highly turbid waters on the north shore, especially in the area between Île d'Orléans and Île aux Coudres, originate from this sediment resuspension (CSL 1996).

Unfortunately, some sites in the FC (sites 10, 15 and 16) and the LSP (sites 22, 28, 29, 35) were not sampled due to technical problems during the sampling cruise in August. The lacking sites in LSP, which were located in the northern and southern shallow littoral zones, were probably richer in zooplankton, as these highly vegetated zones had considerably greater macrozooplancton biomass than in the open water during mid-summer (Basu et al. 2000b). Their loss may have significantly biased the results.

2.4.2 Environmental variables

At each site, water temperature (°C), conductivity (µS/cm), turbidity (NTU), pH and dissolved oxygen (mg/L) were measured *in situ* using a Conductivity Temperature Depth profiler (YSI 6600 EDS-M sensor array, Yellow Spring Instruments). A spectroradiometer-fluorometer (HFT: Satlantic hyperpro-Wetlab C Star) was used to determine underwater profiles of light irradiance and calculate by Simpson integration the light available for photosynthesis (PAR: 400-700 nm). Water samples were collected using an 8 liters GO-Flow water sampler (Model 1080;

General Oceanics) 1 m below the surface at each site. To measure chlorophyll *a* (Chl*a*), dissolved organic carbon (DOC; mg/L), total nitrogen (TN; mg/L), total phosphorus (TP; µg/L), total dissolved solids (TDS; mg/L), and chromophoric dissolved organic matter absorbance (aCDOM; m^{-1}), subsamples were drawn from the GO-Flow bottles into acid-washed polyethylene bottles. Chl*a* concentrations were measured with a Turner Designs 10–005R fluorometer, after sonication and 24 h extraction in 90% acetone at 4°C in the dark (Parsons et al. 1984). For nitrogen and phosphorus analyses, samples for soluble reactive phosphorus and nitrites + nitrates (NO_2 + NO_3) were prefiltrated on 45 mm diameter, 0.7-µm pore-size GFF filters (Millipore). All nitrogen and phosphorus analyses were performed according to APHA (1998). DOC measurements were undertaken as follows: at each sampling site, 200 ml of water was filtered through a 45 mm diameter, 0.2-µm nominal pore-size polycarbonate membrane (Isopore; Millipore). Membranes were pre-rinsed with 100 ml of MilliQ water to remove potential impurities. The filtrate was stored in acid-washed borosilicate bottles and kept in the dark at 4°C until analysis. DOC concentrations were determined with a total organic carbon analyzer (TOC-1010; OI Analytical, College Station, Texas, USA) by sodium persulfate digestion. aCDOM was measured with a Shimadzu UV-2401PC UV-Vis spectrophotometer (Shimadzu, Columbia, Maryland, USA) using a 1-cm quartz cell between 190 and 900 nm. See Frenette et al. (2006) and Massicotte and Frenette (2011) for calculations of the absorption coefficients.

2.4.3 Zooplankton sampling and analysis

Zooplankton was collected at each site using a conical net (1 m mouth opening, 153 µm mesh size) hauled horizontally at the same depth as for water collection. Zooplankton are generally longer than 153 µm (Wildlife Supply Company 1997-1998). Net filtered volume was measured with a flowmeter (General Oceanic). Upon collection, zooplankton organisms were split into fractions with a Folsom splitter. One/eight of each sampling unit was reserved for taxonomy and transferred to 250 ml plastic bottles. Zooplankton was narcotized with carbonated water and preserved in a buffered 4% sugar-formaldehyde solution and stored for later analysis (Prepas 1978). In the laboratory, a subsample was taken with a large opening pipette, transferred to a Ward rotative cell and analysed under a stereomicroscope (Ward 1955). Adult copepods were identified to species. The copepodite stages (C1-C5) were categorised to appropriate suborder (Calanoida, Cyclopoida, Harpacticoida), while nauplii were not enumerated. For cladocerans, amphipods and mysids, identification was carried up to species level when it was possible and adults were at least identified to genus level. Identification of cladocerans was made based on Edmonston (1959), Amoros (1984) and Hebert (1995). Identification of copepods was made following Hudson et al. (2003), Lesko et al. (2003a, 2003b), Lacroix (1981), Huys et al. (1996), Edmondson (1959), and Smith and Fernando (1978). We identified amphipods using Bousfield (1958) and Holsinger (1972), and mysids using Brunel (1960) and Brunel et al. (1998). Laboratory procedures are described in details in Pinel-Alloul et al. (1990). Counts of crustacean species were expressed as numbers of individuals per cubic metre accounting for subsampling fractionation during field collection and microscopic analysis.

2.4.4 Data analyses

To characterize the environment conditions and zooplankton community structure throughout the study area, data sets of environmental and crustacean variables were constructed by averaging the values of variables for each biogeographical zone and hydroperiod (Tables II (p40); III (p44) and IV (p47)). Global community structure of zooplankton along 6 longitudinal habitats - FSZ's LSF, LSL, FC and LSP, FEZ and ETZ - was represented by pie chart diagrams (Figure 3, p49) showing the relative abundances of the four main taxonomic groups (cladocerans, calanoids, cyclopoids and harpacticoids) at each site, for both hydroperiods. Diversity and abundances were exhibited along the longitudinal habitats of the fluvial zones (FSZ and FEZ) for each site or group of sites representing one of the 3 transversal habitats (north and south littoral zones, and main channel) in May and August (Figure 4, p51). In LSP where the two transects counted 7 sites, the sites 22, 23 and 29 were considered as southern sites, 24, 25, 30-32 as central sites, and 26-28, 33-35 as northern sites. We calculated the mean values of each group of sites for both transects. Histograms were used to illustrate the zooplankton species assemblages along the 6 longitudinal habitats. They represent the relative abundances of the dominant species recorded in the taxonomic groups: cladocerans (Figure 5, p53), calanoids (Figure 6, p54), cyclopoids (Figure 7, p56), harpacticoids (Figure 8, p57) and amphipods (Figure 9, p59), during the spring and summer hydroperiods. Redundancy analysis (RDA) was used to determine the relationships between zooplankton spatial distribution and environmental features, which included water masses dummy variables and physical and chemical variables). RDA is a multivariate extension of a multiple regression, or a direct gradient analysis approach that associates variation in taxonomic composition to environmental variables (ter Braak 1994; ter Braak and Smilauer 2002; Leps and Smilauer 2003). Tests of significance of the species-environment relationships were done by Monte Carlo permutation tests involving 9999 unrestricted permutations (Legendre and Legendre 1998). The variance inflation factor (VIF) of selected variables was kept under 10. We applied the log transformation (all sites) and no transformation (sites 1-45) on zooplankton data for May and the profiles of relative frequencies transformation for August as these treatments maximized the R^2 of the species-environment relationship for each hydroperiod. RDA was performed using two data sets. The first set featured the zooplankton distribution in relation to water masses and environmental variables in the whole river-estuary system (FSZ, FEZ and ETZ); the second set included only the fluvial zones (FSZ and FEZ).

We carried out forward selection of the environmental variables following the method proposed by Blanchet et al. (2008b) using the ***forward.sel()*** function of the R-language package packfor (Dray et al. 2007; R Development Core Team 2010). Firstly, a global RDA was done with all environmental variables and water mass dummy variables, using the ***rdaTest()*** function (R-laguage package rdaTest). If this model was significant at the 5 % level, its R^2_a was used as stopping criterion for the forward selection procedure, in addition to the 5% significance level. We performed the final RDA using only the selected variables to illustrate the relationships between the distribution of zooplankton species and the most important environmental and water mass variables.

2.5 Results

2.5.1 Water characteristics in the biogeographic zones

The FSZ and FEZ zones presented similar water chemical characteristics for both spring and summer hydroperiods (Table II, p40). Waters were slightly alkaline with pH varying from 7.5 to 8.1 in May and 7.7 to 8.8 in August. Water temperature ranged from 11.6 to 14.2 ºC in May and from 20.3 to 24.6 ºC in August. In May, waters were well saturated in oxygen (9.6 - 10.8 mg/L). Chl*a* concentrations (0.9 - 7 µg/L) indicated oligo-mesotrophic conditions. Water turbidity (0 - 98 NTU) and concentrations of DOC (2.1 - 10.5 mg/L) were highly variable in the FSZ, especially in August. Conductivity (23.5 - 298 µS/cm) and TDS (12 - 119 mg/L) were also highly variable in the fluvial zones in May and August. TN and TP concentrations varied greatly among sites and

Table II Water characteristics in the three biogeographical zones of the SLR at spring (May) and summer (August) hydroperiods. SD = standard deviation. * Dissolved oxygen data is not available in August due to damage in the YSI sensor.

May 2006	Fluvial Section Zone (N=33)		Fluvial Estuary Zone (N=10)		Estuarine Transition Zone (N=7)	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
pH	7.9 ± 0.2	7.5 - 8.1	7.8 ± 0.1	7.6 - 7.9	7.8 ± 0.1	7.7 - 7.8
Dissolved oxygen (mg/L)	10.2 ± 0.3	9.6 - 10.8	10.0 ± 0.2	9.6 - 10.2	10.1 ± 0.2	9.9 - 10.3
Turbidity (NTU)	7.3 ± 5.4	0 - 18.7	10.3 ± 2.2	6.6 - 14.2	47.5 ± 35.6	10.3 - 101.2
Chlorophyll *a* (Chl*a*, µg/L)	3.0 ± 0.7	1.4 - 4.3	3.4 ± 0.7	2.8 - 4.9	5.5 ± 5.3	0.9 - 22.3
Dissolved organic carbon (DOC, mg/L)	4.6 ± 1.6	2.4 - 9.6	5.7 ± 1.7	4.1 - 9.6	7.2 ± 9.8	3.0 – 39.6
Total nitrogen (TN, mg/L)	3.4 ± 0.6	2.2 - 4.5	2.5 ± 1	1.1 - 4.2	2.8 ± 1.2	1.0 – 5.2
Total phosphorus (TP, µg/L)	36.4 ± 19.2	8.4 - 83.7	51.7 ± 16.8	20.4 - 72.6	157± 141	28.4 – 475
PAR extinction coefficient (k_dPAR, m^{-1})	1.8 ± 0.8	0.5 - 3.3	2.3 ± 0.3	1.9 - 2.7	4.6 ± 2.5	1.5 - 10.2
Temperature (°C)	12.8 ± 0.7	11.6 - 14.2	13.3 ± 0.3	12.8 - 13.8	12.3 ± 1.9	7.7 - 13.8
Conductivity (µS/cm)	189 ± 43.1	99.0 - 232	160± 49.4	23.5 - 192	3695 ± 6339	176.6 – 18710
Total dissolved solids (TDS, mg/L)	94.0 ± 21.9	49.0 - 119	78.6 ± 24.0	12.0 - 91.0	653 ± 761	85.0 – 1705
Chromophoric dissolved organic matter absorbance (aCDOM, m^{-1})	8.1 ± 5.5	1.6 - 24.2	12.1 ± 3.5	8.9 - 21.0	7.8 ± 2.6	4.7 - 11.3
Latitude (decimals)	45.86 ± 0.40	45.11 - 46.27	46.62 ± 0.19	46.36 - 46.90	47.19 ± 0.18	46.97 - 47.46
Longitude (decimals)	-73.29 ± 0.55	-74.48 - -72.71	-71.74 ± 0.59	-72.50 - -70.89	-70.51 ± 0.22	-70.76 - -70.25

August 2006	Fluvial section zone (N=29)		Fluvial estuary zone (N=10)		Estuarine transition zone (N=7)	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
pH	8.3 ± 0.3	7.7 - 8 .8	8.2 ± 0.2	7.7 - 8.4	7.9 ± 0.2	7.7 - 8.3
Dissolved oxygen (mg/L)*	-	-	-	-	-	-
Turbidity (NTU)	7.8 ± 18.2	0.0 - 98.2	7.7 ± 2.8	2.5 - 12.5	44.0 ± 42.1	1.8 – 120.1
Chlorophyll *a* (Chl*a*, µg/L)	2.7 ± 1.6	0.9 - 7.0	2.9 ± 1.2	1.8 - 6.0	9.7 ± 13.4	0.6 - 54.8
Dissolved organic carbon (DOC, mg/L)	3.7 ± 1.8	2.1 - 10.5	4.3 ± 1.2	3.3 - 7.4	3.7 ± 0.8	2.0 - 5.4
Total nitrogen (TN, mg/L)	2.7 ± 1.1	0.5 - 5.2	2.6 ± 0.7	1.5 - 3.7	2.3 ± 0.9	0.9 - 3.6
Total phosphorus (TP, µg/L)	15.3 ± 8.9	4.5 - 44.7	19.8 ± 5.0	12.2 - 28.5	62.6 ± 49.4	17.5 - 150.6
PAR extinction coefficient (k_dPAR, m^{-1})	1.6 ± 1.0	0.4 - 4.9	1.9 ± 0.3	1.7 - 2.6	4.5 ± 3.8	0.9 - 14.5
Temperature (°C)	23.4 ± 0.8	20.3 - 24.6	22.5 ± 0.6	21.1 - 23.2	20.5 ± 3.5	12.2 - 23.2
Conductivity (µS/cm)	241 ± 53	91 - 298	206 ± 61	37 - 248	5242 ± 8173	218 - 23 700
Total dissolved solids (TDS, mg/L)	100.2 ± 21.4	36.0 - 119.0	87.3 ± 25.9	16.0 - 106.0	771.8 ± 754.9	93.0 - 1705
Chromophoric dissolved organic matter absorbance (aCDOM, m^{-1})	5.5 ± 6.2	0.8 - 31.4	7.8 ± 5.8	4.1 - 24.1	5.0 ± 1.7	2.4 - 6.7
Latitude (decimals)	45.86 ± 0.40	45.11 - 46.27	46.62 ± 0.19	46.36 - 46.90	47.19 ± 0.18	46.97 - 47.46
Longitude (decimals)	-73.29 ± 0.55	-74.48 - -72.71	-71.74 ± 0.59	-72.50 - -70.89	-70.51 ± 0.22	-70.76 - -70.25

hydroperiods (TN: 0.5 - 5.2 mg/L; TP: 4.5 - 83.7 µg/L). PAR extinction coefficient (k_dPAR; 0.4 - 4.9 m^{-1}) and aCDOM (0.8 - 31.4 m^{-1}) were also highly variable, particularly in August.

Water characteristics in the ETZ were very different from those of the fluvial zones (Table II, p 40). We observed very high increases in salinity, conductivity (176.6 - 23 700 µS/cm) and TDS (85 - 1705 mg/L) caused by the mixing of fresh and salt waters and the resulting particle resuspension. On average, waters were 4 times more turbid than in the fluvial zones although the range of variation was important (1.8 - 120 NTU in August). Higher concentrations in Chl*a* (up to 55 µg/L in August) and TP (up to 475 µg/L in May) pointed out the higher productivity of the ETZ compared to the fluvial zones. Water temperature in the ETZ was lower during both hydroperiods (7.7 - 13.8 ºC in May and 12.2 - 23.2 ºC in August) than upstream in the river.

2.5.2 Water masses distribution

The SLR is composed of several water masses with different physical and chemical characteristics, flowing side by side and mixing slightly or not at all over long distances. We recognized 6 main water masses (Figure 2, p42). Their distribution in the SLR during each sampling cruise were based on simulations of the 2D convection-diffusion DISPERSIM model (Champoux and Morin 2007; collaboration with Jean Morin, Environment Canada) and water masses maps from CSL (1996). The DISPERSIM model integrated simulations of the hydrodynamic HYDROSIM model (based on discharge and water levels measurements) and conductivity measurements. The results of the simulations were the relative contribution of the tributaries and the two main inputs (Great Lakes and Ottawa River) to the waters of each sampling site (not shown).

In May (Figure 2a, p42), the clear waters originating from the Great Lakes (GL; WM1) fed LSF and constituted the main channel until Portneuf. Those waters are characterized by exceptionally low suspended particulate matter (SPM; 1 mg/L), DOC (2.5 mg/L) and TP (10 mg/L) concentrations with moderately high conductivity (294 µS/cm) (Hudon and Carignan 2008). In contrast, the Ottawa River (OTT; WM3) exhibits higher SPM (7.2 mg/L), DOC (6.1 mg/L), TP (34 mg/L) and lower conductivity (81 µS/cm) (Hudon and Carignan 2008). This more coloured and humic (CSL 1996) water mass flows into the Mille Îles and Des Prairies Rivers in Montréal and along the north shore of the FC to LSP, while it mixed with the GL (GL + OTT; WM2) along the north shore from LSL to Porneuf. The mixing of the Richelieu River waters (moderatly mineralized

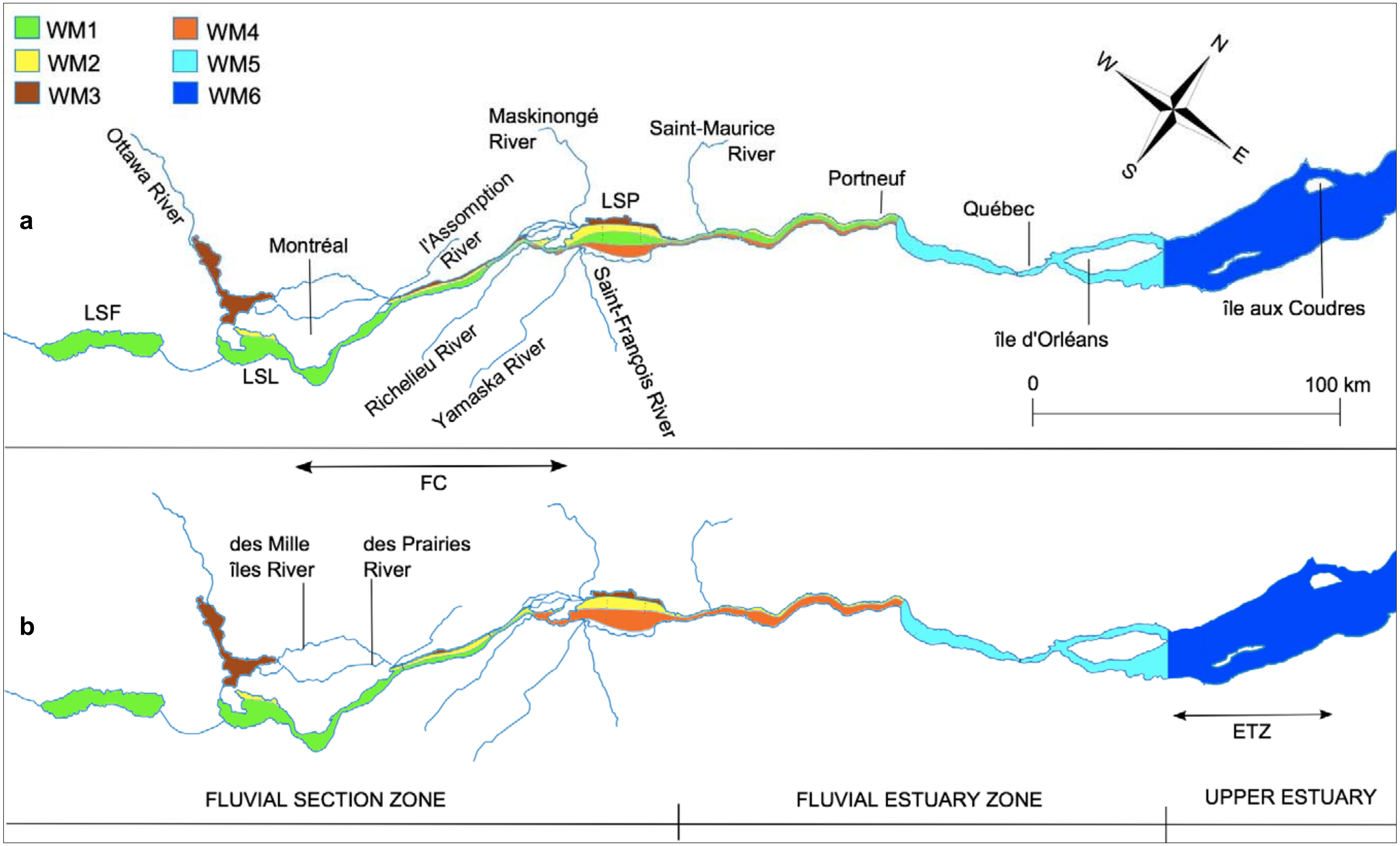

Figure 2 Water masses distribution in the SLR in May (a) and August (b). WM1: Great Lakes waters, WM2: Mixed waters of the Great Lakes and the Ottawa River/Mille Îles and des Prairies Rivers, WM3: Ottawa River waters, WM4: Mixed waters of the Great Lakes and the Richelieu River, WM5: Québec City waters, WM6: Waters of the Estuarine Transition Zone (ETZ). LSF: Lake Saint-François, LSL: Lake Saint-Louis, LSP: Lake Saint-Pierre, FC: Fluvial corridor.

(conductivity = 191 µS/cm) and highly turbid (SPM = 17.2 mg/L)) with the GL (GL + RICH; WM4) in the south shore of LSP and downstream until Portneuf formed the fourth main water mass. The waters downstream of Portneuf, which are completely homogenized due to the effect of the tide, forms the Québec City water mass (WM5). The ETZ water mass (WM6) is a mix of fresh and salt waters that extends from Île d'Orléans to Île aux Coudres.

In August (Figure 2b, p42), the central WM1 was markedly restricted in LSP where no sites were located in 100% GL waters: central sites of both transects passed directly from WM4 to WM2. This result seems contradictory with those of several studies on LSP, which found the GL water mass to constitute the main channel during summer (Frenette et al. 2003; Frenette et al. 2006; Vis et al. 2007; Hudon et Carignan 2008; Lapierre et al. 2008; Massicotte and Frenette 2011). This may partly be due to the use of different method for the establishment of water masses distribution. The present study used hydrodynamic and convection-diffusion models along with conductivity measurements, while the other studies used satellite imagery. This technique used color-producing agents such as chromophoric dissolved organic matter and suspended particulate inorganic matter (Frenette et al. 2006; Lapierre et al. 2008; Massicotte and Frenette 2011) as markers for the differentiation of water masses.

In the present study, even though one site was located in a water mass majorly constituted of the GL waters (up to 95%), it was classified as a mixed water mass. That is probably the reason why the GL water mass (WM1) disappeared from the water masses distribution in LSP during summer, contrary to previous findings. Only the water masses attributed to sampling sites were represented in Figure 2; we did not show all LSP water masses present during sampling.

2.5.3 Zooplankton diversity and abundance

In total, 72 crustacean taxa were identified in the 52 sampling units, including 23 cladocerans, 8 calanoids, 17 cyclopoids, 19 harpacticoids, 3 amphipods and 2 mysids (Table III, p44). Over the two hydroperiods (May and August) (Table IV, p47), the highest species richness (61 species) was observed in the FSZ (22 cladocerans, 6 calanoids, 16 cyclopoids, 14 harpacticoids and 3 amphipods), and the lowest species richness (22 species) in the ETZ (4 cladocerans, 3 calanoids, 2 cyclopoids, 8 harpacticoids, 3 amphipods and 2 mysids); the FEZ showed intermediate species richness (17 cladocerans, 3 calanoids, 13 cyclopoids, 8 harpacticoids, 2 amphipods and one

Table III Mean abundance (ind/m^3) ± standard deviation (SD) of crustacean groups and species in the biogeographical zones of the SLR. FSZ: Fluvial Section Zone, FEZ: Fluvial Estuary Zone, ETZ: Estuarine Transition Zone.

				May			**August**		
Group	**Family**	**Genus**	**Species**	**FSZ (N=33) mean ± SD**	**FEZ (N=10) mean ± SD**	**ETZ (N=7) mean ± SD**	**FSZ (N=29) mean ± SD**	**FEZ (N=10) mean ± SD**	**ETZ (N=7) mean ± SD**
Cladocerans	Bosminidae	*Bosmina*	*coregoni*	4.9 ± 11.5	4.0 ± 7.7	0.3 ± 0.9	3.9 ± 7.1	0.6 ± 1.8	
	Bosminidae	*Bosmina*	*sp.*	52.6 ± 75.2	59.1 ± 48.8	18.8 ± 34.9	75.7 ± 219	24.9 ± 28.3	26.9 ± 63.2
	Chydoridae	*Acroperus*	*sp.*	0.1 ± 0.8			4.8 ± 17.4		
	Chydoridae	*Alona*	*guttata*		0.04 ± 0.1				
	Chydoridae	*Alona*	*sp.*	1.4 ± 2.3	0.4 ± 0.9		5.9 ± 13.2	5.5 ± 10.4	
	Chydoridae	*Alonella*	*sp.*	0.1 ± 0.4			4.1 ± 13.3	0.2 ± 0.4	
	Chydoridae	*Camptocercus*	*sp.*	0.03 ± 0.2			5.7 ± 16.8	6.1 ± 14.2	
	Chydoridae	*Chydorus*	*brevilabris*	0.2 ± 1.0					
	Chydoridae	*Chydorus*	*sp.*	16.2 ± 20.0	5.4 ± 7.1	0.3 ± 0.9	12.7 ± 62.0	1.8 ± 2.2	
	Chydoridae	*Eurycercus*	*sp.*		0.04 ± 0.1	0.3 ± 0.9	0.8 ± 1.6	0.2 ± 0.6	
	Chydoridae	*Leydigia*	*quadrangularis*	0.3 ± 1.2	0.2 ± 0.6				
	Chydoridae	*Leydigia*	*sp.*				1.0 ± 3.9	0.1 ± 0.2	
	Chydoridae	*Pleuroxus*	*denticulatus*	0.05 ± 0.3	0.6 ± 2.0				
	Chydoridae	*Pleuroxus*	*sp.*		0.4 ± 1.2		2.0 ± 9.6	0.04 ± 0.1	
	Chydoridae	-	-	1.4 ± 2.6			3.6 ± 11.0	0.6 ± 1.8	
	Daphniidae	*Ceriodaphnia*	*sp.*	0.03 ± 0.1			11.2 ± 17.8	3.7 ± 7.9	
	Daphniidae	*Daphnia*	*ambigua*	0.3 ± 0.9	0.4 ± 1.2			0.2 ± 0.6	
	Daphniidae	*Daphnia*	*catawba*	0.3 ± 1.1	0.4 ± 1.2		0.03 ± 0.1		
	Daphniidae	*Daphnia*	*longiremis*	0.4 ± 1.2	0.2 ± 0.7				
	Daphniidae	*Daphnia*	*parvula*	0.1 ± 0.3					
	Daphniidae	*Daphnia*	*pulex*	0.03 ± 0.1					
	Daphniidae	*Daphnia*	*pulicaria*	0.4 ± 1.1	0.04 ± 0.1			0.3 ± 0.7	
	Daphniidae	*Daphnia*	*retrocurva*	0.5 ± 2.2			0.1 ± 0.5		
	Daphniidae	*Daphnia*	*sp.*	1.8 ± 3.8	0.8 ± 1.8	4.1 ± 11.0	6.4 ± 17.2	0.2 ± 0.5	
	Daphniidae	*Scapholeberis*	*kingi*	0.2 ± 1.1					
	Daphniidae	*Scapholeberis*	*sp.*				0.1 ± 0.4		
	Daphniidae	-	-				0.1 ± 0.4		
	Holopediidae	*Holopedium*	*sp.*		0.2 ± 0.6				
	Ilyocryptidae	*Ilyocryptus*	*spinifer*				0.1 ± 0.4	1.2 ± 2.2	
	Polyphemidae	*Polyphemus*	*sp.*				0.4 ± 2.1		
	Sididae	*Diaphanosoma*	*brachyurum*	0.5 ± 2.7					
	Sididae	*Diaphanosoma*	*sp.*	0.2 ± 1.3			8.6 ± 33.2	0.7 ± 1.5	
	Sididae	*Sida*	*sp.*				2.4 ± 4.9	3.0 ± 2.9	
Total	**7**	**17**	**at least* 23**	**81.9 ± 94.6**	**72.2 ± 52.4**	**23.9 ± 33.9**	**149 ± 321**	**49.1 ± 50.4**	**31.6 ± 68.7**

Calanoids		Copepodites		7.8 ± 9.0	16.9 ± 13.2	449 ± 682	84.2 ± 209	172 ± 151	1249 ± 1872
	Acartiidae	*Acartia*	*longiremis*			344 ± 900			23.4 ± 29.9
	Diaptomidae	*Leptodiaptomus*	*minutus*	0.2 ± 0.9					
	Diaptomidae	*Leptodiaptomus*	*sicilis*	0.2 ± 0.9	0.4 ± 0.8		0.1 ± 0.4		
	Diaptomidae	*Skistodiaptomus*	*oregonensis*	0.1 ± 0.6			0.7 ± 1.3	0.5 ± 1.5	
	Diaptomidae	*Skistodiaptomus*	*reighardi*	0.05 ± 0.3			0.4 ± 1.0		
	Temoridae	*Epischura*	*lacustris*	0.4 ± 1.2					
	Temoridae	*Eurytemora*	*affinis*	0.003 ± 0.02		153 ± 181	4.0 ± 7.3	16.2 ± 15.8	709 ± 1601
	Temoridae	*Eurytemora*	*herdmani*			0.7 ± 1.8			1.5 ± 4.1
Total	**3**	**5**	**8**	**8.7 ± 9.3**	**17.3 ± 12.9**	**947 ± 1507**	**89.4 ± 210**	**188 ± 159**	**1990 ± 3408**
Cyclopoids		Copepodites		230 ± 239	315 ± 211	141 ± 137	33.7 ± 39.5	10.9 ± 5.3	0.8 ± 1.7
	Cyclopidae	*Acanthocyclops*	*carolinianus*	0.2 ± 1.2					
	Cyclopidae	*Acanthocyclops*	*robustus*	0.2 ± 0.6	0.4 ± 1.0		1.2 ± 4.2	1.2 ± 2.5	
	Cyclopidae	*Acanthocyclops*	*venustoides*	0.5 ± 1.8	0.04 ± 0.1		0.02 ± 0.1		
	Cyclopidae	*Diacyclops*	*nanus*	0.04 ± 0.2					
	Cyclopidae	*Diacyclops*	*thomasi*	12.1 ± 13.5	14.4 ± 13.2	10.1 ± 11.2	0.1 ± 0.3		
	Cyclopidae	*Eucyclops*	*elegans*	0.3 ± 1.6			0.2 ± 1.0	0.3 ± 0.6	
	Cyclopidae	*Eucyclops*	*pectinifer*	1.3 ± 2.6	0.04 ± 0.1		29.6 ± 144	2.3 ± 4.9	
	Cyclopidae	*Eucyclops*	*prionophorus*	0.5 ± 1.2	0.2 ± 0.5		1.2 ± 2.4	0.04 ± 0.1	
	Cyclopidae	*Halicyclops*	*fosteri*					29.8 ± 94.2	507 ± 780
	Cyclopidae	*Macrocyclops*	*albidus*				0.05 ± 0.2	0.2 ± 0.6	
	Cyclopidae	*Mesocyclops*	*americanus*	0.04 ± 0.2			0.4 ± 1.7	0.4 ± 0.8	
	Cyclopidae	*Mesocyclops*	*edax*	0.2 ± 0.9	0.04 ± 0.1		3.4 ± 16.9		
	Cyclopidae	*Microcyclops*	*rubellus*	0.5 ± 1.6	0.6 ± 1.2		1.7 ± 6.1	0.3 ± 0.7	
	Cyclopidae	*Orthocyclops*	*modestus*	0.04 ± 0.2					
	Cyclopidae	*Paracyclops*	*chiltoni*	0.1 ± 0.4			1.1 ± 4.4	0.2 ± 0.6	
	Cyclopidae	*Paracyclops*	*poppei*	0.04 ± 0.2					
	Cyclopidae	*Tropocyclops*	*prasinus*	2.3 ± 6.0	2.9 ± 3.7		2.5 ± 5.6	0.4 ± 0.7	
Total	**1**	**10**	**17**	**248 ± 253**	**333 ± 222**	**151 ± 136**	**73.9 ± 156**	**46.0 ± 89.6**	**514 ± 781**

Harpacticoids		Copepodites		1.0 ± 2.7	0.1 ± 0.2	107 ± 169	0.7 ± 1.3		
	Ameiridae	*Nitokra*	*hibernica*	1.5 ± 3.6	1.7 ± 2.8		3.4 ± 4.1	1.3 ± 1.9	0.1 ± 0.3
	Ameiridae	*Nitokra*	sp.	0.2 ± 1.0			0.1 ± 0.4		
	Canthocamptidae	*Attheyella*	*americana*	0.1 ± 0.7			0.005 ± 0.03		
	Canthocamptidae	*Bryocamptus*	*hiemalis*	0.05 ± 0.3					
	Canthocamptidae	*Bryocamptus*	*hutchinsoni*				0.03 ± 0.1		
	Canthocamptidae	*Bryocamptus*	*minutus*	0.3 ± 1.7					
	Canthocamptidae	*Bryocamptus*	*nivalis*		0.7 ± 1.9				
	Canthocamptidae	*Bryocamptus*	*zschokkei*	0.2 ± 0.7					
	Canthocamptidae	*Canthocamptus*	*robertcokeri*	0.3 ± 1.7					
	Canthocamptidae	*Canthocamptus*	*sp.*				0.03 ± 0.2		
	Canthocamptidae	*Canthocamptus*	*staphylinoides*	1.5 ± 4.1					
	Canthocamptidae	*Canthocamptus*	*vagus*	0.2 ± 0.7					
	Canthocamptidae	*Elaphoidella*	*bidens*	0.1 ± 0.4	0.3 ± 1.0	0.4 ± 1.1	0.2 ± 0.5	0.1 ± 0.2	
	Canthocamptidae	*Heteropsyllus*	*nunni*	0.1 ± 0.8			0.2 ± 0.8	0.1 ± 0.2	
	Canthocamptidae	*Mesochra*	*alaskana*	0.7 ± 2.4	0.3 ± 0.9		0.5 ± 2.3	2.5 ± 6.7	
	Diosaccidae	*Schizopera*	*borutzkyi*	0.1 ± 0.4	2.7 ± 3.2	5.6 ± 13.7	1.1 ± 1.6	1.3 ± 2.9	
	Ectinosomatidae	*Halectinosoma*	*curticorne*		0.2 ± 0.7	343 ± 479			391 ± 847
	Ectinosomatidae	*Microstella*	*norvegica*			2.6 ± 6.9			
	Laophontidae	*Onychocamptus*	*mohammed*	0.6 ± 1.6	0.4 ± 1.4	0.4 ± 1.1	9.9 ± 39.9	2.4 ± 3.4	
	Tachidiidae	*Microarthridion*	*falax*			0.2 ± 0.5			
	Tachidiidae	*Microarthridion*	*littorale*			2.1 ± 3.9			14.1 ± 30.2
Total	**6**	**12**	**at least 19**	**6.9 ± 8.0**	**6.6 ± 4.8**	**462 ± 641**	**16.1 ± 39.2**	**7.6 ± 11.0**	**410 ± 889**
Amphipods		Juveniles		0.7 ± 0.7	0.6 ± 0.6	0.5 ± 0.9	0.2 ± 0.6	0.2 ± 0.2	5.3 ± 11.7
	Gammaridae	*Echinogammarus*	*ischnus*	0.04 ± 0.1	0.4 ± 0.5	0.5 ± 1.4	0.02 ± 0.1	0.1 ± 0.1	0.1 ± 0.2
	Gammaridae	*Gammarus*	*sp.*	0.01 ± 0.04	0.008 ± 0.03		0.7 ± 3.3	0.1 ± 0.2	2.4 ± 5.0
	Hyalellidae	*Hyalella*	*azteca*	0.02 ± 0.1		0.1 ± 0.4			
Total	**2**	**3**	**at least 3**	**0.8 ± 1.5**	**1.6 ± 1.2**	**1.6 ± 2.6**	**0.9 ± 3.4**	**0.4 ± 0.4**	**7.6 ± 17.2**
Mysids	Mysidae	*Mysis*	*stenolepis*			0.2 ± 0.4			0.06 ± 0.1
	Mysidae	*Mysis*	*sp.*					0.009 ± 0.03	
	Mysidae	*Neomysis*	*americana*			0.1 ± 0.1			
	Mysidae	*Neomysis*	sp.						5.3 ± 9.3
Total	**1**	**2**	**at least 2**			**0.2 ± 0.6**		**0.009 ± 0.03**	5.4 ± 9.5
Total	**20**	**49**	**at least 72**	**347**	**431**	**1584**	**331**	**292**	**2960**

*at least: Taxa which were not identified to species level were not counted in the total number of species when at least one other known species of the same genus was present.

Table IV Abundance (mean ± SD; ind/m^3) and species richness (nb. species) of 6 major crustacean groups in each biogeographical zone of the SLR in May and August, and means over the two hydroperiods.

	Abundance			**Species richness**		
	May			**May**		
	FSZ N=33	**FEZ N=10**	**ETZ N=7**	**FSZ N=33**	**FEZ N=10**	**ETZ N=7**
Cladocerans	82.0 ± 94.6	72.2 ± 52.4	19.1 ± 35.3	at least* 18	at least 11	at least 4
Calanoids	8.2 ± 9.2	17.1 ± 12.9	943 ± 1508	6	1	3
Cyclopoids	251 ± 253	334 ± 223	147 ± 141	15	8	1
Harpacticoids	8.4 ± 11.3	6.9 ± 4.3	462 ± 641	at least 13	7	7
Amphipods	0.8 ± 1.5	1.6 ± 1.2	1.6 ± 2.6	3	2	2
Mysids	-	-	0.2 ± 0.6	-	-	2
Total	**351 ± 350**	**432 ± 278**	**1573 ± 1308**	**55**	**29**	**19**
	August			**August**		
	FSZ N=29	**FEZ N=10**	**ETZ N=7**	**FSZ N=29**	**FEZ N=10**	**ETZ N=7**
Cladocerans	161 ± 342	60.5 ± 62.9	31.6 ± 68.7	at least 17	at least 14	1
Calanoids	88.9 ± 215	188 ± 159	1990 ± 3408	4	2	3
Cyclopoids	74.8 ± 156	46.7 ± 90.9	514 ± 781	12	10	1
Harpacticoids	19.1 ± 47.7	8.9 ± 12.4	410 ± 889	at least 9	6	3
Amphipods	1.0 ± 3.5	0.3 ± 0.3	7.6 ± 17.2	2	2	2
Mysids	-	0.009 ± 0.03	5.4 ± 9.5	-	1	2
Total	**344 ± 594**	**304 ± 250**	**2960 ± 5003**	**44**	**35**	**12**
	May and August			**May and August**		
	FSZ N=62	**FEZ N=20**	**ETZ N=14**	**FSZ N=62**	**FEZ N=20**	**ETZ N=14**
Cladocerans	119 ± 245	66.4 ± 56.7	25.3 ± 52.9	at least 22	at least 17	at least 4
Calanoids	45.9 ± 151	103 ± 140	1467 ± 2590	6	3	3
Cyclopoids	169 ± 229	190 ± 222	331 ± 572	16	13	2
Harpacticoids	13.4 ± 33.8	7.9 ± 9.1	436 ± 745	at least 14	8	8
Amphipods	0.9 ± 2.6	1.0 ± 1.1	4.6 ± 12.2	3	2	3
Mysids	-	0.004 ± 0.02	2.8 ± 7.0	-	1	at least 2
Total	**348 ± 476**	**368 ± 266**	**2266 ± 3586**	**61**	**44**	**22**

*at least: Taxa which were not identified to species level in Table II were not counted in the total number of species when at least one other known species of the same genus was present within one biogeographical zone for each hydroperiod and over the two hydroperiods.

mysid for a total of 44 species). Total species richness was higher in May than in August in the FSZ and the ETZ, whereas it was slightly lower in May than in August in the FEZ.

Opposite to species richness, abundance of crustaceans over the two hydroperiods was relatively low in the FSZ and the FEZ (348-368 ind/m^3) but very high in the ETZ (2266 ind/m^3) (Table IV, p47). Abundance of zooplankton remained the same from May to August in the FSZ (351 ± 350 and 344 ± 594 ind/m^3), declined slightly from May to August in the FEZ (432 ± 278 and 304 ± 250 ind/m^3), and increased significantly in the ETZ (1573 ± 1308 and 2960 ± 5003 ind/m^3) especially in August. This is mainly due to the large increase of calanoids and cyclopoids in this area during the summer hydroperiod. In the FSZ, cladocerans ($p = 0.06$, Mann–Whitney–Wilcoxon paired test) and calanoids ($p < 0.001$) were more abundant in August than in May, while the opposite was true for the cyclopoids ($p < 0.001$). In the FEZ, calanoids abundance was still lower ($p < 0.01$) and that of the cyclopoids higher ($p < 0.01$) in August than in May. Community structure differed greatly between the fluvial and estuarine zones, and between hydroperiods (Table IV, p47). In the fluvial zones (FSZ and FEZ), the cyclopoid copepods were dominant in May (251 ± 253 and 334 ± 223 ind/m^3: 72-77%) whereas in August the cladocerans dominated in the FSZ (161 ± 342 ind/m^3: 47%), and so did the calanoids in the FEZ (188 ± 159 ind/m^3: 62%). In the ETZ, euryhaline calanoids dominated the community in May and August (943 ± 1508; 1990 ± 3408 ind/m^3: 60-67%). In August, the abundance of euryhaline species of cyclopoids also greatly increased in the ETZ compared to May, whereas the abundance of harpacticoid species remained similar during both hydroperiods. Amphipods and mysids were also more frequent in this zone, whereas cladocerans abundance decreased from the fluvial zones to the ETZ.

The relative zooplankton community composition at each site along the fluvial-estuary section is shown in Figure 3 (p49). In May, little variation was observed in the zooplankton composition within the fluvial zones (FSZ and FEZ), where cyclopoids (black) were dominant, along with the subdominant cladocerans (yellow). No clear difference was observed among the fluvial lakes, the FC and the FEZ. A break in the longitudinal pattern occurred at the salinity-conductivity discontinuity between the FEZ and the ETZ, where the euryhaline harpacticoids (blue) dominated the maximum turbidity zone (ZTM). They were replaced by the calanoids (red) downstream. In August, cladocerans and calanoids dominated the fluvial zones while cyclopoids were still common. Cladocerans were slightly more abundant than calanoids in the fluvial lakes. Within the FEZ, the first transect had a composition similar to that of the LSP, which was replaced

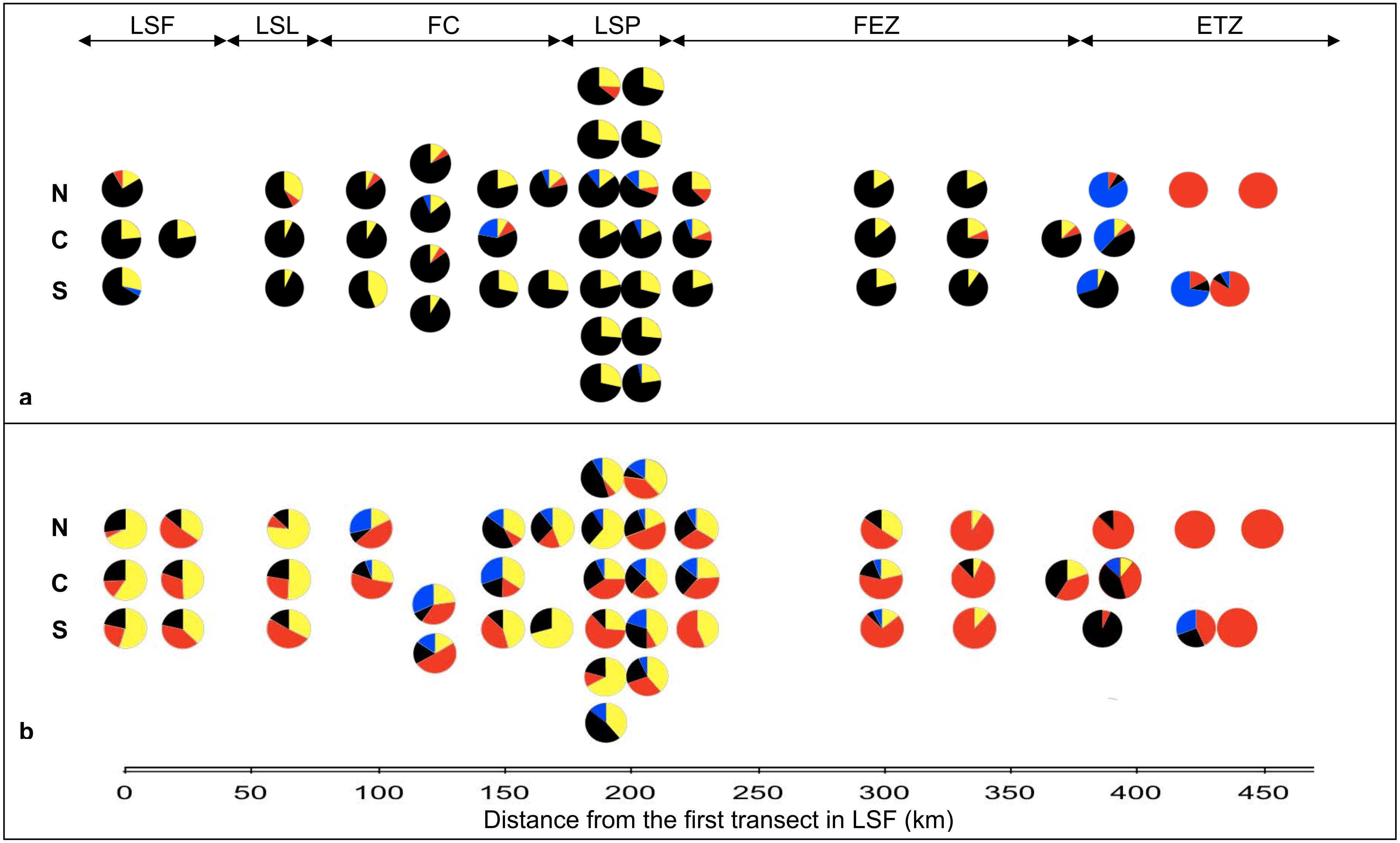

Figure 3 Relative composition (pie charts) of the zooplankton community (major groups: cladocerans (yellow), calanoids (red), cyclopoids (black), harpacticoids (blue)) at each site depending on the distance (km) from the first transect in Lake Saint-François, in May (a) and August (b). Groups representing less than 5% of one site total abundance were not represented. LSF = Lake Saint-François, LSL = Lake Saint-Louis, FC = Fluvial corridor, LSP = Lake Saint-Pierre, FEZ = Fluvial Estuary Zone, ETZ = Estuarine Transition Zone. The letters N, C and S in front of the sites represent respectively the northern, central and southern portion of the transects.

downstream by a community dominated by the calanoids. The ZTM seemed to appear earlier in the SLR, as the euryhaline cyclopoid *H. fosteri* arose at site 45 (Île d'Orléans). This species dominated the ZTM along with the subdominant calanoids and harpacticoids. In the second part of the ETZ, calanoids represented nearly the total abundance of zooplankton. For both hydroperiods, no clear pattern in the zooplankton composition was observed among southern, central and northern sites of the transects.

Abundances and species richness of sites depending on their location (north, center, south) within transects are shown in Figure 4 (p51). In May, zooplankton abundance for any position tended to decrease from LSL to FC, while it increased within the LSP. Within the main channel, the passage from the LSP to the FEZ was immediately followed by a decrease in zooplankton abundance, which considerably increased afterwards from the first to the second transect in the FEZ. In August, abundances along the SLR was generally low (≤ 200 ind/m^3) regardless of the position within transects. Abundances along the south shore were higher in LSL, LSP and the FEZ. In the main channel, abundances increased within the LSP, while abundances in the northern sites remained generally low except in LSL where we found the highest zooplankton abundance of the whole study.

Globally, for both hydroperiods, abundances tended to increase in LSL and LSP while it decreased and remained low in the FC. Along the south shore, abundances were lowest in the FC and highest in the LSP. Within the main channel, abundances were highest in the first portion of LSF and in the FEZ downstream of Portneuf in May while they were highest in LSP during summer. Along the north shore, zooplankton concentrations were highest in LSL for both hydroperiods. Most of the times, the southern site exhibited higher abundance than the central site within a single transect. No clear general pattern was observed as for species richness distribution throughout the study area, for both hydroperiods. Within the main channel, species richness was relatively high in the first transect of LSP. Then, it decreased towards the second LSP transect and increased again downstream from the LSP outlet until the confluence of the Saint-Maurice River and the SLR into the FEZ. In August, there seemed to be an increase of the species richness within the main channel in the FC. However, we should consider the results in LSP cautiously, as few sites located at both ends of the two transects were not sampled.

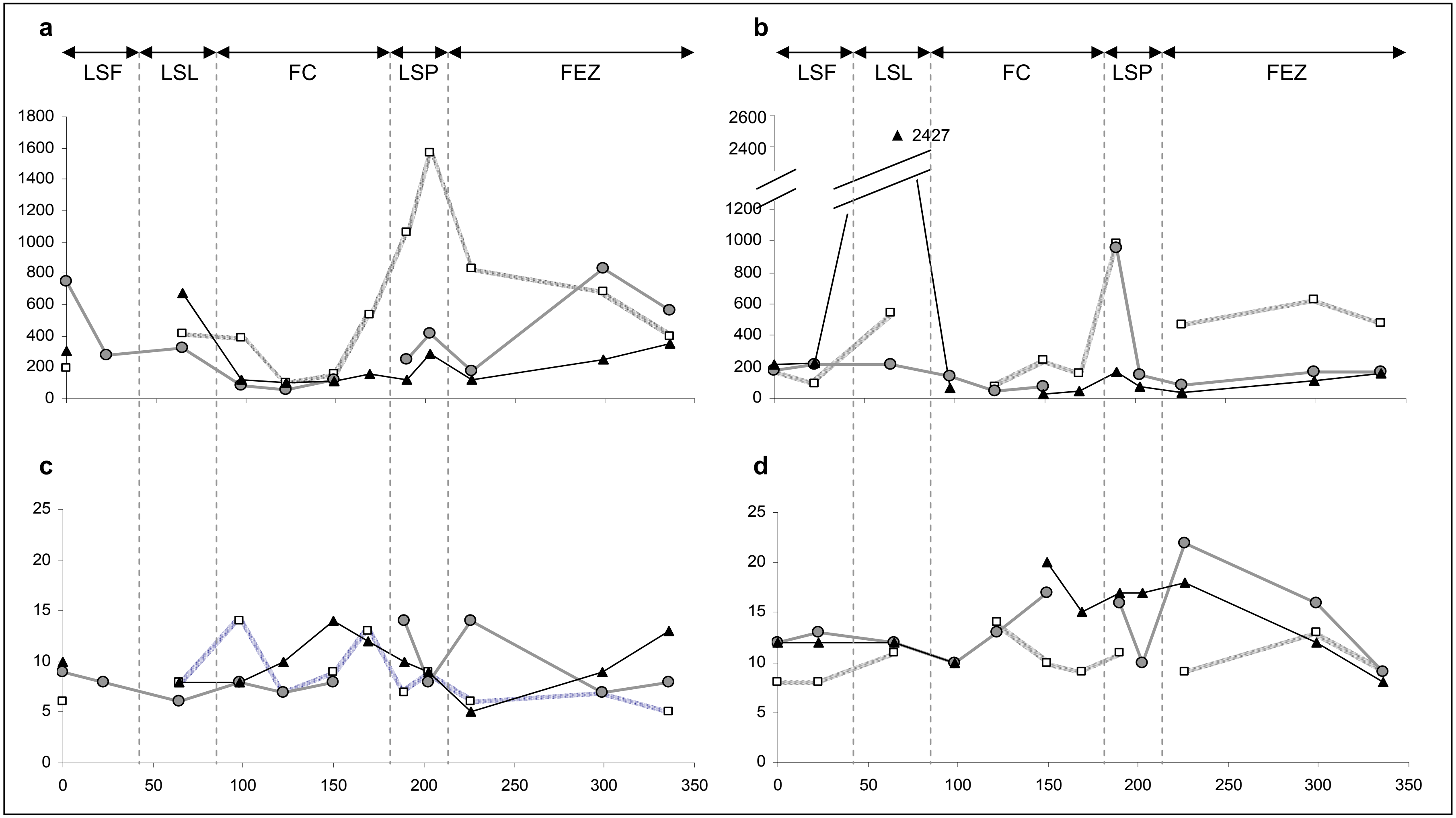

Figure 4 Mean abundance (ind/m^3; a) May; b) August) and species richness (nb. species; c) May; d) August) of zooplankton for each portion of transect (white squares: southern portion; grey circles: central portion; black triangles: northern portion) in the longitudinal habitats of the SLR fluvial zone (LSF = Lake Saint-François, LSL = Lake Saint-Louis, FC = Fluvial corridor, LSP = Lake Saint-Pierre, FEZ = Fluvial Estuary Zone) depending on the distance (km) from the first transect in Lake Saint-François.

2.5.4 Occurrence and spatial distribution of cladocerans

During both hydroperiods (Figures 5a and 5b, p53), the mean densities of cladocerans in each region differed little except in LSL where it was five times higher in August (404 ind/m^3) than in May (76 ind/m^3). The FC downstream of Montréal and the ETZ contained fewer cladocerans whereas the LSP had a maximum density in August (123 ind/m^3). *Bosmina sp.* dominated in almost all regions during both hydroperiods. In May (Figure 5a), *Chydorus sp.* ranked second in all the fluvial regions, followed by *Daphnia sp.* in LSF and FC. *Bosmina sp.* represented more than 95% of the cladoceran abundance in the ETZ region. In August (Figure 5b), *Bosmina sp.* was less dominant and several species were better represented. LSF contained *Ceriodaphnia sp.* and *Daphnia sp.*, with chydorid species and a few *Diaphanosoma sp*., *Polyphemus sp.* and *Sida sp*. LSL was mainly composed of *Bosmina sp.* along with other species. The composition of the FC and FEZ was similar, with roughly the same proportion of *Bosmina sp*., *Alona sp.*, *Camptocercus sp*., *Ceriodaphnia sp.* and other species. Between them, LSP had a similar composition with much more *Chydorus sp.*, whereas only *Bosmina sp.* was found in the ETZ region.

2.5.5 Occurrence and spatial distribution of calanoids

Most of the calanoid copepods were found as copepodite stages during each hydroperiod; adult calanoids occurred in very low abundances in the fluvial zones (Table III, p44). In May, *Epischura lacustris* was the most abundant in the LSF (Figure 6a, p54), along with *S. oregonensis* and a few specimens of other species. *Leptodiaptomus minutus* and *L. sicilis* occurred in LSL, whereas *L. minutus* and *S. oregonensis* dominated the FC. Species richness was higher in LSP, which contained *E. lacustris* and *L. sicilis* with a few specimens of *L. minutus* and *S. oregonensis*. *Leptodiaptomus sicilis* occurred in low numbers in the FEZ, while the euryhaline calanoids *Acartia longiremis* and *Eurytemora affinis* were very abundant in the ETZ with a few specimens of *Eurytemora herdmani* (Table III). In August (Figure 6b, p54), the calanoid community structure was more homogeneous in the three biogeographical zones than in May. *Eurytemora affinis* was dominant in all zones and reached very high densities in the ETZ (Table III). *Skistodiaptomus oregonensis* was relatively abundant in the fluvial zones and was replaced by *A. longiremis*, *E. affinis* and a few of *E. herdmani* in the ETZ (Table III).

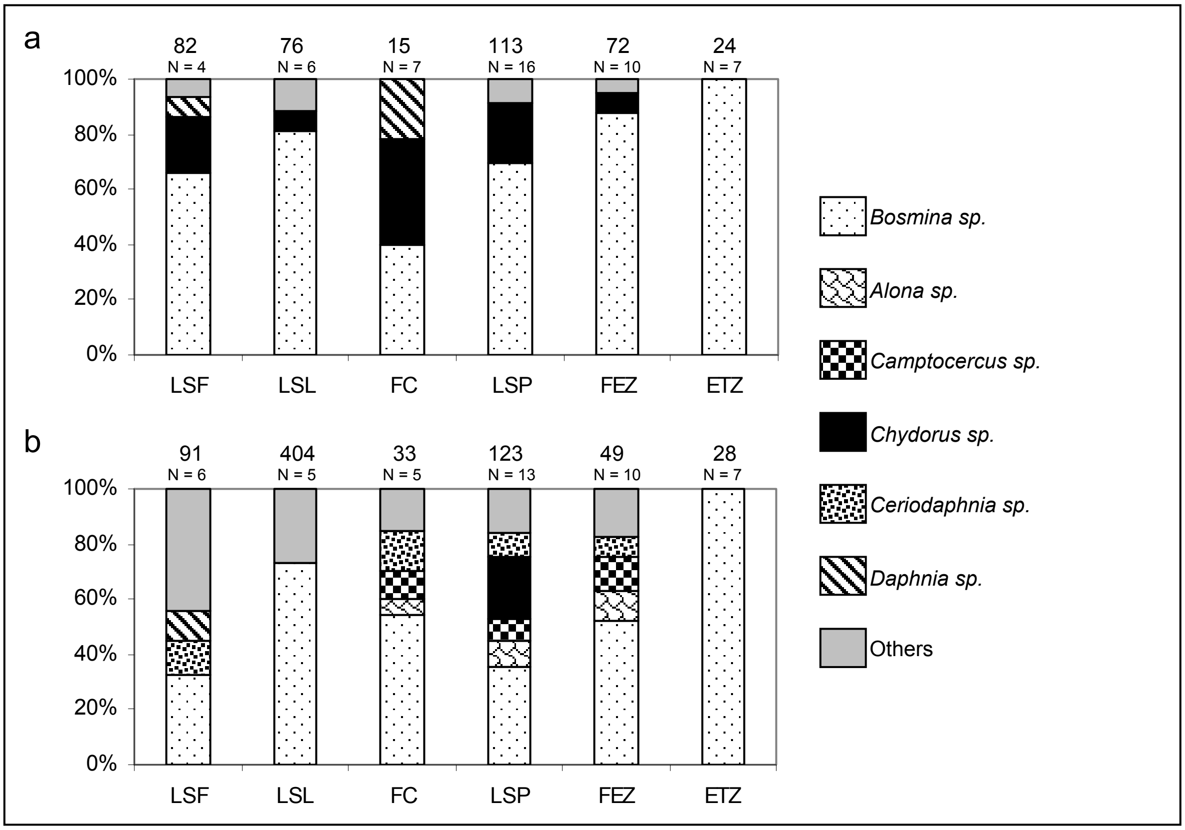

Figure 5 Relative abundance of the 6 most frequent genera of cladocerans in 6 sections of the SLR in May (a) and August (b). Lake Saint-François (LSF; sites 1-6), Lake Saint-Louis (LSL; sites 7-12), Fluvial corridor (FC; sites 13-19), Lake Saint-Pierre (LSP; sites 20-38), Fluvial Estuary Zone (FEZ; sites 39-45), Estuarine Transition Zone (ETZ; sites 46-52). Species representing less than 5% of total density were not shown. 'Others' contains identified less frequent species. The number above each bar is the mean abundance (ind/m^3) of the cladocerans for each longitudinal habitat.

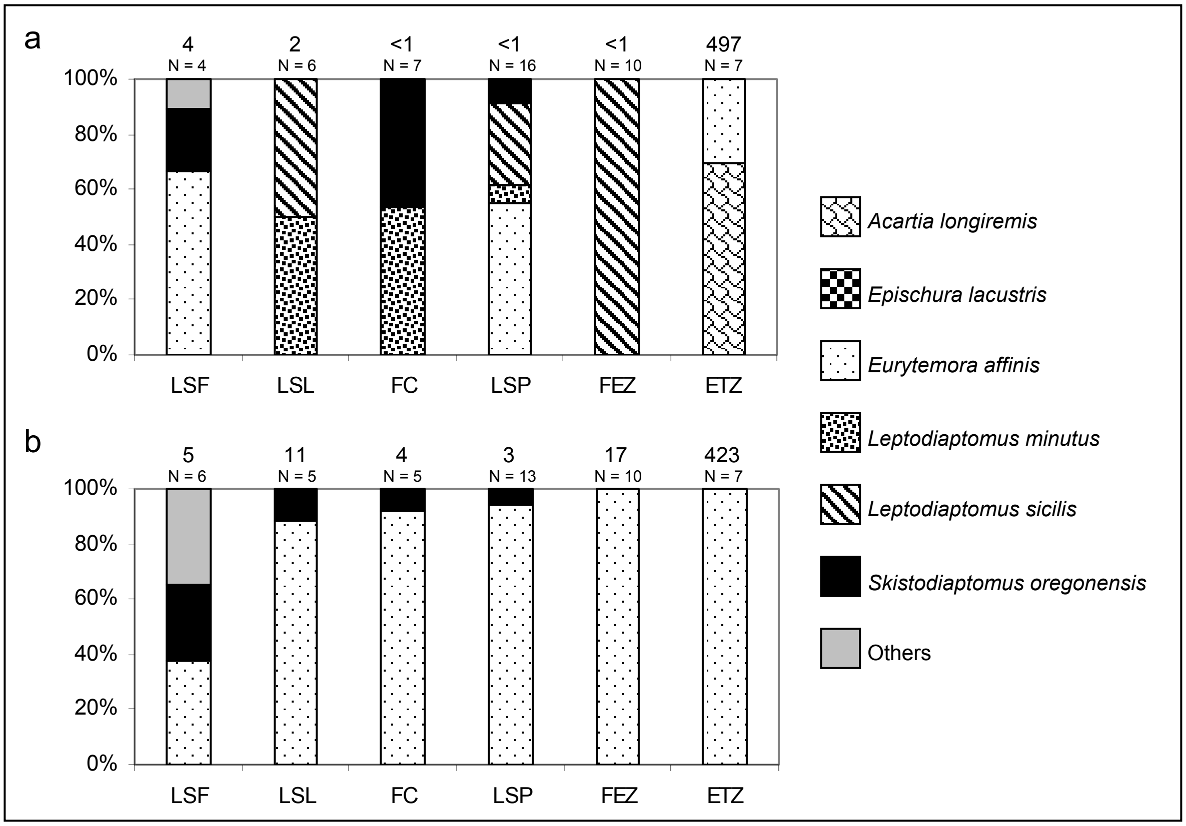

Figure 6 Relative abundance of the 6 most frequent genera of calanoid copepods in 6 sections of the SLR in May (a) and August (b). Lake Saint-François (LSF; sites 1-6), Lake Saint-Louis (LSL; sites 7-12), Fluvial corridor (FC; sites 13-19), Lake Saint-Pierre (LSP; sites 20-38), Fluvial Estuary Zone (FEZ; sites 39-45), Estuarine Transition Zone (ETZ; sites 46-52). Species representing less than 5% of total density were not shown. 'Others' contains identified less frequent species. The number above each bar is the mean abundance (ind/m^3) of the calanoids for each longitudinal habitat.

2.5.6 Occurrence and spatial distribution of cyclopoids

The cyclopoid copepod community structure was very different between hydroperiods and biogeographical zones. In May (Figure 7a, p56; Table III, p44), most of the populations were found as copepodite stages. Adults of *Diacyclops thomasi* were the most frequently found in all regions and were the only cyclopoids that reached the ETZ. The freshwater cyclopoid species *Tropocyclops prasinus*, *Eucyclops pectinifer* and *Eucyclops prionophorus*, were subdominant in the fluvial zones. Some cyclopoids (*Acanthocyclops venustoides*, *Acanthocyclops carolinianus*, *Mesocyclops edax*, *Eucyclops elegans* and *Microcyclops rubellus*) occurred in very low numbers (Table III) while other cyclopoids were very rare (*Diacyclops nanus*, *Mesocyclops americanus*, *Orthocyclops modestus*, *Paracyclops chiltoni*, *Paracyclops poppei*). In August (Figure 7b, p56; Table III), adult cyclopoids were more common than in May. *Eucyclops pectinifer*, *M. edax*, and *T. prasinus* were more frequent in the FSZ, associated with fewer *E. prionophorus, Acanthocyclops robustus*, *M. rubellus* and *P. chiltoni*. The dominant species *D. thomasi* in May was rarely found in August, and peaked in LSF. The estuarine cyclopoid *Halicyclops fosteri*, not found in the FSZ, was dominant in the FEZ, and highly increased in the ETZ.

2.5.7 Occurrence and spatial distribution of harpacticoids

As for other groups, the harpacticoid community structure differed greatly among biogeographic zones and between hydroperiods. In May (Figure 8a, p57; Table III, p44), the harpacticoid populations were diverse in the fluvial zones. *Canthocamptus staphylinoides* dominated the community in LSF with *Canthocamptus robercokeri*. LSL included low numbers of *Attheyella americana*, *Bryocamptus zschokkei* and *Canthocamptus vagus* specimens. In the FC, *Nitokra hibernica* was the most frequently found with fewer *Mesochra alaskana* and other species. Total abundance was more evenly distributed among the dominant species (*C. staphylinoides, M. alaskana, N. hibernica* and *Onychocamptus mohammed*) in LSP. *Schizopera borutzkyi* was the most frequently found in the FEZ, along with *N. hibernica* and very few specimens of *O. mohammed* and other species. The euryhaline species *Halectinosoma curticorne*, found in the eastern part of the FEZ, reached high abundance in the ETZ; *S. borutzkyi*, *Microarthridion littorale*, *Microstella norvegica* also occurred frequently in this zone, whereas other species (*Elaphoidella bidens*, *Microarthridion falax*, *O. mohammed*) were relatively rare. In August (Figure 8b, p57; Table III)

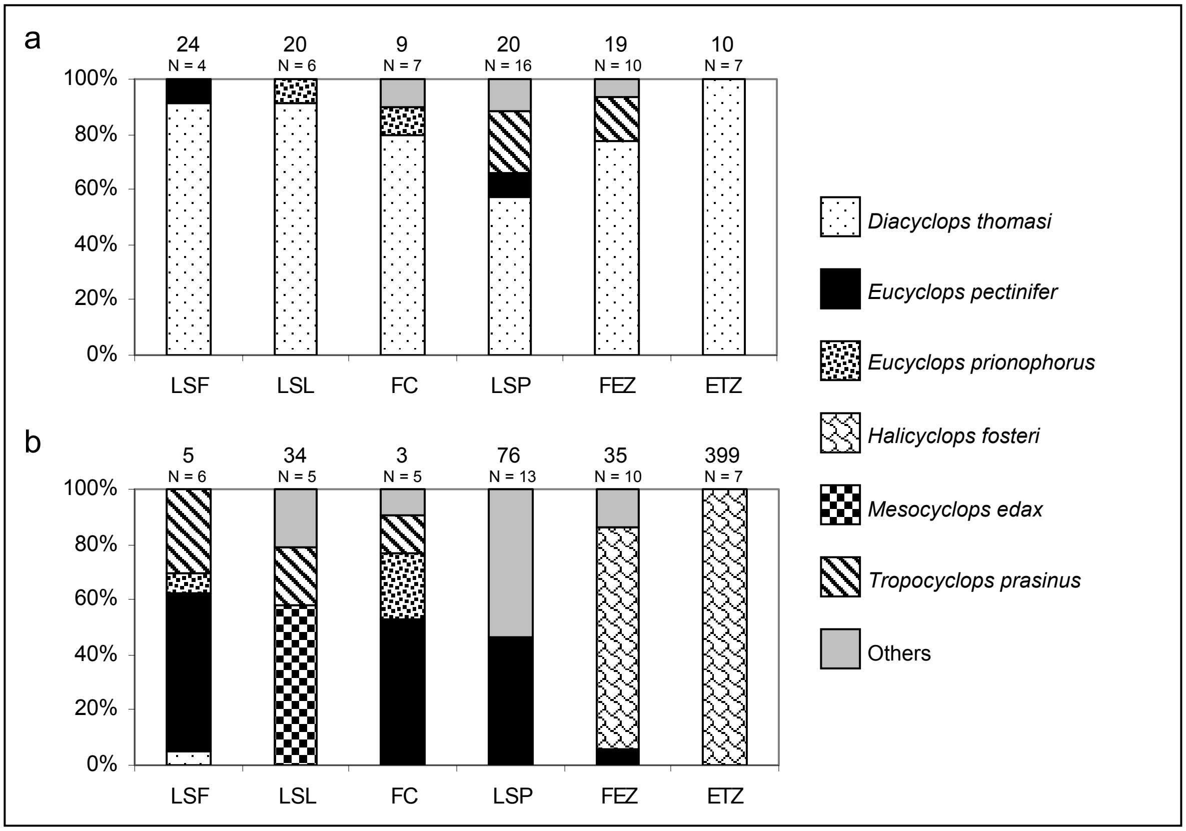

Figure 7 Relative abundance of the 6 most frequent genera of cyclopoid copepods in 6 sections of the SLR in May (a) and August (b). Lake Saint-François (LSF; sites 1-6), Lake Saint-Louis (LSL; sites 7-12), Fluvial corridor (FC; sites 13-19), Lake Saint-Pierre (LSP; sites 20-38), Fluvial Estuary Zone (FEZ; sites 39-45), Estuarine Transition Zone (ETZ; sites 46-52). Species representing less than 5% of total density were not shown. 'Others' contains identified less frequent species. The number above each bar is the mean abundance (ind/m^3) of the cyclopoids for each longitudinal habitat.

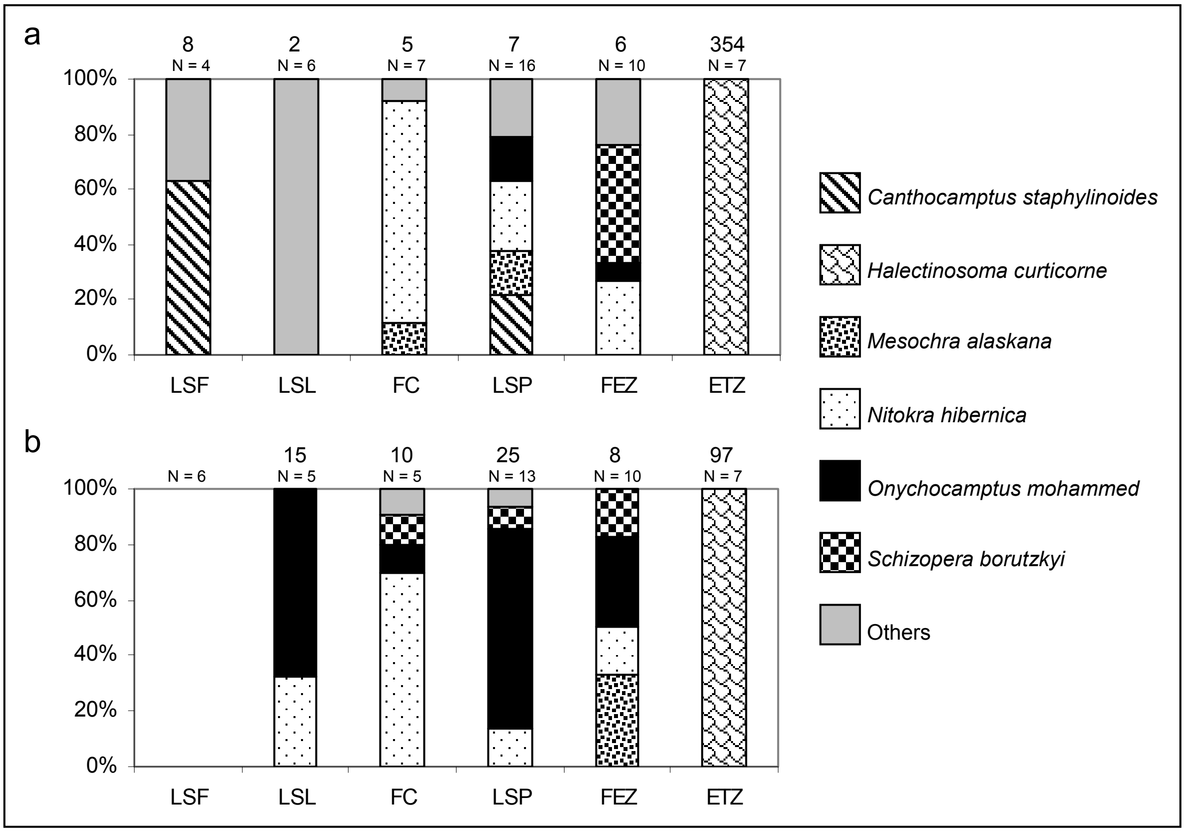

Figure 8 Relative abundance of the 6 most frequent genera of harpacticoid copepods in 6 sections of the SLR in May (a) and August (b). Lake Saint-François (LSF; sites 1-6), Lake Saint-Louis (LSL; sites 7-12), Fluvial corridor (FC; sites 13-19), Lake Saint-Pierre (LSP; sites 20-38), Fluvial Estuary Zone (FEZ; sites 39-45), Estuarine Transition Zone (ETZ; sites 46-52). Species representing less than 5% of total density were not shown. 'Others' contains identified less frequent species. The number above each bar is the mean abundance (ind/m^3) of the harpacticoids for each longitudinal habitat.

N. hibernica, *O. mohammed* and *S. borutzkyi* were the most frequent species in the FSZ. The FEZ also included these species with the co-dominant *M. alaskana*, while the ETZ region included high densities of *H. curticorne* associated to smaller populations of *M. littorale* and a few specimens of *N. hibernica*.

2.5.8 Occurrence and spatial distribution of amphipods and mysids

Amphipods were very few compared to the copepods and cladocerans, and culminated in the ETZ region in August (Table III, p44). Juveniles largely dominated the amphipod surface populations during both hydroperiods (Figure 9, p59). Very few specimens were large enough to permit identification to the species level. The only species identified in our study were *Gammarus sp.* (probably *fasciatus*), *Echinogammarus ischnus* and *Hyalella azteca*. To our knowledge, no other amphipod species have been identified in the St. Lawrence freshwaters, whereas *Gammarus tigrinus* inhabits the ETZ region (Winkler et al. 2003). Juveniles were mainly Gammaridae, but many could not be identified at this level. In May, *E. ischnus* was found all along the fluvial-estuary section, being more important from LSP to ETZ. Few specimens were identified as *Gammarus sp.* (probably *G. fasciatus*) in LSL, LSP and FEZ. A small number of *H. azteca* was found in LSP and ETZ. In August, *Gammarus sp.* dominated *Echinogammarus sp.* along the continuum, but was not found in the FC. Very few specimens of *Echinogammarus sp.* were found in LSL, FEZ and ETZ, whereas *H. azteca* was absent.

In May, a few mysids (1.6 ind/m^3) were found at site 49 in the ETZ (Figure 1, p35). In August, their area was extended: they were found in very low numbers at sites 42 (FEZ) and 46 (ETZ), and were more frequent in more saline waters at sites 48 (23 ind/m^3) and 49 (15 ind/m^3). *Mysis stenolepis* was present during both hydroperiods, while *Neomysis americana* was found in May and *Neomysis sp.* in August (Table III, p44).

2.5.9 Environmental influence on crustacean spatial distribution

We assessed the relationships between environmental features (water masses, chemical characteristics) and crustacean community structure along the river-estuary section (Figure 10, p60) and in the fluvial zones only (Figure 11, p61). The results of the forward selection are presented in Table V (p62). The spatial distribution of species along the whole river-estuary section during the

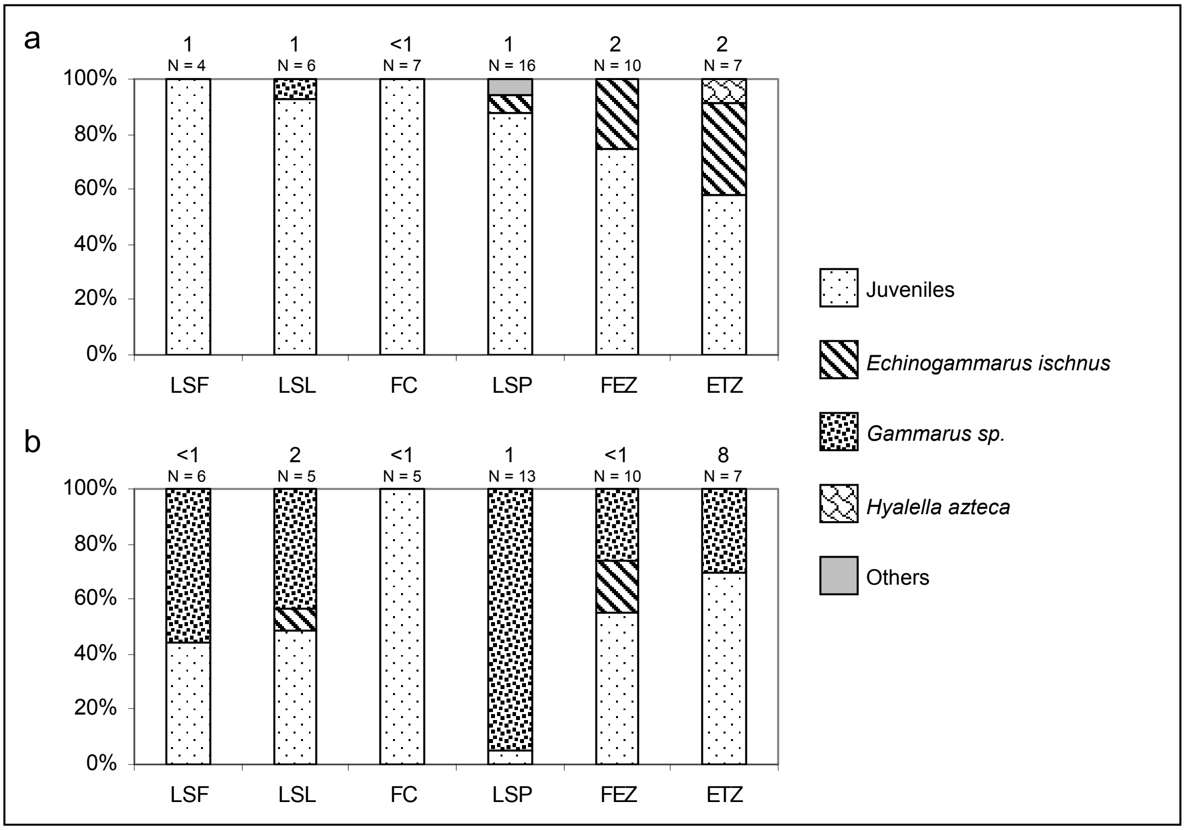

Figure 9 Relative abundance of the 6 most frequent genera of amphipods in 6 sections of the SLR in May (a) and August (b). Lake Saint-François (LSF; sites 1-6), Lake Saint-Louis (LSL; sites 7-12), Fluvial corridor (FC; sites 13-19), Lake Saint-Pierre (LSP; sites 20-38), Fluvial Estuary Zone (FEZ; sites 39-45), Estuarine Transition Zone (ETZ; sites 46-52). Species representing less than 5% of total density were not shown. 'Others' contains identified less frequent species. The number above each bar is the mean abundance (ind/m^3) of the amphipods for each longitudinal habitat.

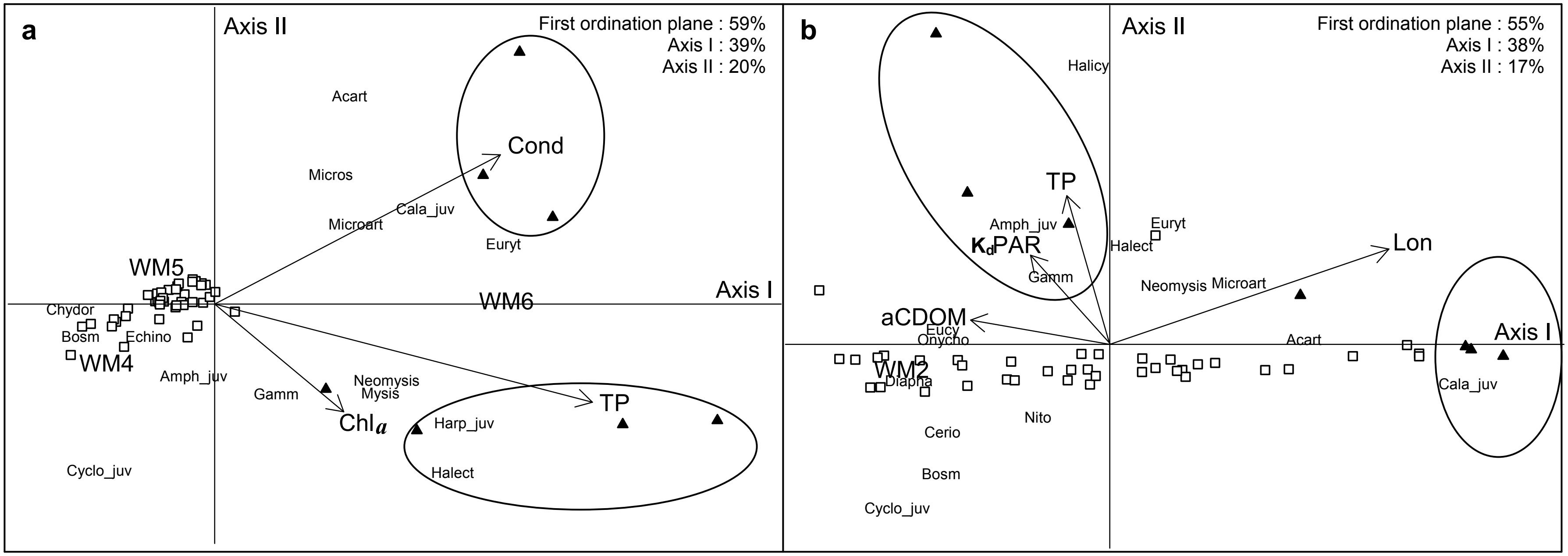

Figure 10 Biplots of the environmental variables (water masses and water characteristics), and zooplankton genera in the first ordination plane of the RDA based on the whole river-estuary section in May (a) and August (b). Fluvial zones (FSZ and FEZ): sites 1-45 (empty squares). Estuarine transition zone (ETZ): sites 46-52 (black triangles). **Cladocerans**: Bosm: *Bosmina sp.*; Chydor: *Chydorus sp.*; Diapha: *Diaphanosoma sp.*; Cerio:*Ceriodaphnia sp*. **Calanoids**: Cala_juv: Calanoid copepodite stages; Acart: *Acartia longiremis*; Euryt: *Eurytemora affinis*. **Cyclopoids**: Cyclo_juv: Cyclopoid copepodite stages; Halicy: *Halicyclops fosteri*; Eucy: *Eucyclops sp*. **Harpacticoids**: Harp_juv: Harpacticoid copepodite stages; Halect: *Halectinosoma curticorne*; Microart: *Microarthridion sp.*; Micros: *Microstella norvegica*; Nito: *Nitokra hibernica*; Onycho: *Onychocamptus mohammed*. **Amphipods**: Amphi_juv: Amphipod juveniles; Echino: *Echinogammarus ischnus*. Gamm: *Gammarus sp.* **Mysids**: *Mysis sp.*; *Neomysis sp*. **aCDOM**: Chromophoric dissolved organic matter absorbance, **Chl*a***: Chlorophyll *a*; **Cond**: Conductivity; **Lon**: Longitude; **K$_d$PAR**: PAR extinction coefficient; **TP**: Total phosphorus, **WM2**: Mixed waters of the Great Lakes and the Ottawa River; **WM4**: Mixed waters of the Great Lakes and the Richelieu River. **WM5**: Québec City waters; **WM6**: Waters of the ETZ. The contributions to the explanation of total zooplankton variance of axis I, axis II and the first ordination plane of the RDA are presented in the upper right corner of each panel.

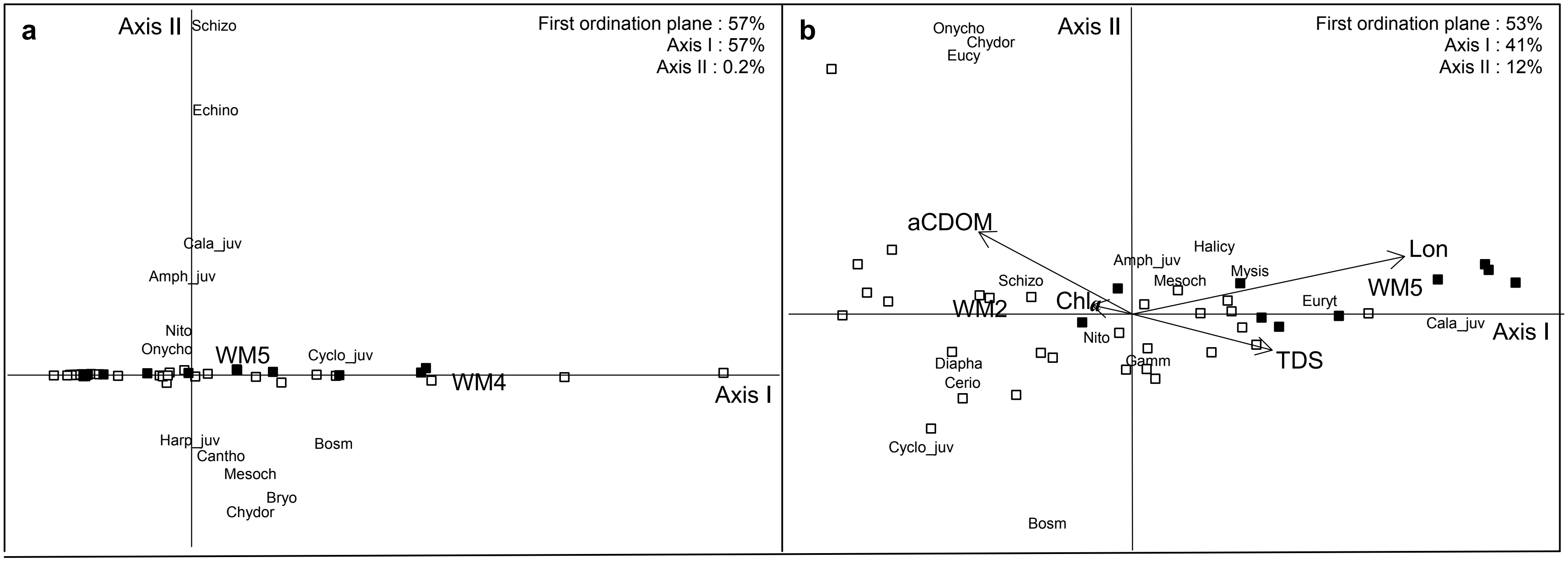

Figure 11 Biplots of the environmental variables (water masses and water characteristics), and zooplankton genera in the first ordination plane of the RDA based on the fluvial zones in May (a) and August (b). Fluvial section zone (FSZ): sites 1-35 (empty squares). Fluvial estuary zone (FEZ): sites 36-45: black squares. **Cladocerans**: Bosm: *Bosmina sp.*; Chydor: *Chydorus sp.*; Diapha: *Diaphanosoma sp.*; Cerio: *Ceriodaphnia sp*. **Calanoids**: Cala_juv: Calanoid copepodite stages; Euryt: *Eurytemora affinis*. **Cyclopoids**: Cyclo_juv: Cyclopoid copepodite stages; Eucy: *Eucyclops sp.*; Halicy: *Halicyclops fosteri*. **Harpacticoids**: Harp_juv: Harpacticoid copepodite stages; Bryo: *Bryocamptus sp.*; Cantho: *Canthocamptus sp.*; Mesoch: *Mesochra alaskana*; Nito: *Nitokra hibernica*; Onycho: *Onychocamptus mohammed*; Schizo: *Schizopera borutzkyi*. **Amphipods**: Amphi_juv: Amphipod juveniles; Echino: *Echinogammarus ischnus*; Gamm: *Gammarus sp.* **Mysids**: Mysis: *Mysis stenolepis.* **aCDOM**: Chromophoric dissolved organic matter absorbance; **Chl*a***: Chlorophyll *a*; **Lon**: Longitude; **TDS**: Total dissolved solids; **WM2**: Mixed waters of the Great Lakes and the Ottawa River, **WM4**: Mixed waters of the Great Lakes and the Richelieu River; **WM5**: Waters of the ETZ. The contributions to the explanation of total zooplankton variance of axis I, axis II and the first ordination plane of the RDA are presented in the upper right corner of each panel.

Table V Selected variables and cumulated R^2_a during forward selection of environmental variables for the river-estuary section (all sites) and the fluvial zones (sites 1 to 45) during the spring (May) and summer (August) hydroperiods. Chl*a* = Chlorophyll *a*, Cond = Conductivity, aCDOM = Chromophoric dissolved organic matter absorbance, Lon = Longitude, K_dPAR = PAR extinction coefficient, TDS = Total dissolved solids, TP = Total phosphorus, WM2 = Mixed waters of the Great Lakes and the Ottawa River/Milles Îles and des Prairies Rivers, WM4 = Mixed waters of the Great Lakes and the Richelieu River, WM5 = Québec City waters.

	River-estuary section		Fluvial zones	
May	WM6	0.34	WM4	0.49
	Cond	0.52	WM5	0.55
	WM4	0.56		
	TP	0.59		
	Chl*a*	0.6		
	WM5	0.62		
August	Lon	0.20	WM5	0.24
	TP	0.41	aCDOM	0.35
	K_dPAR	0.49	TDS	0.39
	aCDOM	0.55	WM2	0.44
	WM2	0.58	Lon	0.46
			Chl*a*	0.51

spring hydroperiod (May) (Figure 10a, p60) was strongly influenced by the salinity-conductivity gradient and the water mass of the ETZ (WM6), characterized by high values of TP and conductivity. The first ordination plane of the RDA, the axes I and II explained respectively 59%, 39% and 20% of the total variance; it showed a clear discrimination between the fresh waters (sites 1-45: empty squares, negative part of axis I) in the fluvial zones and the brackish waters (sites 46-52: black triangles, positive part of axis I) in the ETZ. The upper estuary can be separated in two parts: the nutrient-enriched maximum turbidity zone (MTZ) with the highest TP and Chl*a* values (sites 47 to 49; encircled black triangles, negative part of axis II) and farther east, a region with maximum conductivity (sites 50 to 52; encircled black triangles, positive part of axis II). The MTZ community was composed of epibenthic species - probably transported upwards to the surface waters by ascendant currents - such as the harpacticoid (copepodite stages and adults) *H. curticorne*, mysids species (*M. stenolepis* and *N. americana*), and amphipods (*Gammarus sp.*). The calanoid *E. affinis* was also abundant in the MTZ, as well as in more saline waters (encircled black triangles, positive part of axis II) with calanoid (copepodite stages and adults) *A. longiremis*, along with a few specimens of the harpacticoids *M. littorale* and *M. norvegica* which were only found in this area. Cyclopoid copepodite stages, the cladocerans *Bosmina sp.* and *Chydorus sp.* as well as the amphipods *E. ischnus* were associated to the fluvial zones and the WM4 and WM5 water masses. In summer (Figure 10b, p60), the separation between fresh (negative part of axis II) and brackish (positive part of axis II) waters was weakened but still present. The first ordination plane of the RDA explained 55% of total variance, with the contributions of axis I (38%) and axis II (17%) (Figure 10b). Again, there was the distinction between nutrient-enriched and less clear waters (higher TP and K_dPAR; sites 46, 47 and 49; encircled black triangles, negative part of axis I) and the adjacent more saline region with higher longitudes (sites 50 to 52; encircled black triangles, positive part of axis I). The copepods *H. fosteri*, *E. affinis* and *H. curticorne* dominated the MTZ region, along with the amphipods *Gammarus sp.* and juveniles. In the transition between these two environments, site 48 in the north channel of the ETZ possessed most of the *Neomysis sp.* and *M. littorale* specimens. *Acartia longiremis* was abundant in this area and in the easternmost region (positive part of axis I), which contained a lot of calanoid copepodite stages. In the negative part of axis II, the freshwater sites on the left are represented by the cyclopoid (copepodite stages and adults) *Eucyclops sp.*, the harpacticoid *O. mohammed* and *N. hibernica* and the cladocerans *Diaphanosoma sp.*, *Ceriodaphnia sp.* and *Bosmina sp.*, associated with higher aCDOM and WM2 flowing in the mid channel and along the north shore of the river. Few sites located in the eastern part of the FEZ (sites 39 to 44) were dominated by calanoid copepodite stages.

When considering only the fluvial zones, the first ordination plane of the RDA in May (Figure 11a, p61) explained 57% of total variation distributed almost exclusively on axis I (57%). The fluvial zones, dominated by cyclopoid copepodite stages, were not distinguishable. The FSZ (empty squares) contained slightly larger proportion of *Bosmina sp.* and cyclopoids, associated to the WM4 flowing along the south shore of the LSP, while the eastern part of the FEZ (black squares) represented by WM5 (sites 39 to 45) contained a larger proportion of calanoids, harpacticoids and amphipods, although this trend is not visible in Figure 3 (p49). In August (Figure 11b, p61), the fluvial zones were better differentiated. The first ordination plane of the RDA explained 53% of total zooplankton variance (axis I: 41%, axis II: 12%). On the positive part of axis I, the FEZ sites were associated to WM5 with high longitude and TDS values. This area was dominated by calanoid copepodite stages and adults *E. affinis* with numerous *H. fosteri* and a few *Mysis sp.*, these last two found at one site only. On the negative part of axis I, the FSZ was dominated by cyclopoid copepodite stages, the cladocerans *Bosmina sp.*, *Diaphanosoma sp.* and *Ceriodaphnia sp.*, along with the harpacticoid *S. borutzkyi*. This region was characterized by WM2 flowing north and in mid channel from the FC to the outlet of LSP, associated with aCDOM and Chl*a* concentrations. Site 22, located on the upper left side, reached maximum aCDOM value and counted numerous *O. mohammed*, *Chydorus sp.* and *Eucyclops sp*.

2.6 Discussion

Our study presents for the first time a description of the macrozooplankton community structure in the whole St. Lawrence fluvial-estuary section and its relationship to water mass distributions and their physical and chemical characteristics. In addition, two species - *Echinogammarus ischnus* and *Halicyclops fosteri* - were found in the St. Lawrence ETZ region for the first time in the present study. It should be reminded, however, that missing data in August from both shores in LSP may have significantly biased the results.

2.6.1 Zooplankton diversity and abundance

As we expected, freshwater and brackish crustacean communities of the SLR were very different in their species richness, abundance, and community structure. The number of species in the ETZ was lower than in the fluvial zones (FSZ and FEZ), because only euryhaline species can tolerate a wide range of salinity. Moreover, those euryhaline species were found in high abundance in the ETZ, compared to FSZ and FEZ. The powerful mixing of freshwater and marine salt waters in the ETZ causes the entrapment of very high concentrations of phytoplankton, protists and euryhaline zooplankton, which proliferate in this nutrient-rich environment and support a larval fish nursery (Frenette et al. 1995; Dauvin and Dodson 1990; Barnard et al. 2003). The low abundance of crustacean zooplankton found in the fluvial zones is typical of large rivers (Lair 2006). High discharge and current velocity are greatly unfavourable to crustaceans with longer development times like copepods.

In the FSZ and FEZ, the dominance of the cyclopoids in May is probably due to their life cycle. In fact, the cyclopoids generally reactivate from winter diapause as copepodite stage IV (Hudson et al. 2003; Pinel-Alloul and Alekseev 2004) which allows the adult cyclopoids in the St. Lawrence to seize the important food resources available in the spring and dominate the zooplankton. The dominance of the cyclopoids in the SLR has already been reported during winter (Mills et al. 1981), and during the spring-summer period (Mills and Forney 1982). In August, the cladocerans dominated the FSZ while the calanoids were the most abundant downstream in the FEZ. The more extensive littoral zones especially in the three shallow lakes of the FSZ would have favoured the cladocerans which are known to prefer the littoral to the main channel in the SLR (Casper and Thorp 2007). The calanoids, surviving generally as resting eggs during winter (Hudson et al. 2003; Gyllström and Hansson 2004) became adults during August. Casper and Thorp (2007) found that calanoids in a portion of the SLR avoided fish predation in littoral zones by inhabiting the offshore habitats near the main channel. This is in agreement with our results, which indicate a higher abundance of calanoids in the FEZ corridor than in the FSZ which contains wide littoral zones.

When considering zooplankton abundance and diversity among longitudinal and transversal habitats, we observed that: 1) abundances were generally higher in the fluvial lakes (LSL and LSP) and in the southern littoral zones, especially within the last two lakes; 2) species richness in the main channel decreased within the LSP and subsequently increased downstream between LSP outlet and the next transect in the FEZ. Many authors have suggested that fluvial lakes can act as zooplankton sources in rivers as their lower depth and current velocities favour the establishment of slow flowing-stagnant zones with high water residence times, therefore allowing development of abundant zooplankton population (Basu et al. 2000a, 2000b; Wetzel 2001; Walks and Cyr 2004). In the same way, increases in zooplankton abundance from main channels towards littoral zones have been observed many times (Thorp et al. 1994; Basu et al. 2000b; Baranyi et al. 2002). Littoral zones frequently contain slackwaters areas enabling the development of stable zooplankton populations (Köhler 1994). Moreover, fluvial lakes and littoral zones are frequently characterized by extensive macrophytes developments. The macrophytes are known to greatly improve growth conditions of zooplankton (Wetzel 2001; Basu et al. 2000b), by reducing water residence time (Martin et al. 2005) and protecting zooplankton from drifting (Viroux 1997; Walks and Cyr 2004) and predation by benthivorous and planktivorous fishes (Viroux 1999; Wetzel 2001).

The longitudinal pattern of species richness into the main channel observed in LSP may be interpreted as follows: the river widening at the entrance in the LSP and the corresponding diminution of waters velocities reduced the longitudinal continuity within the central channel, compared to corridor sections. More organisms could have escaped the main channel by drifting passively towards and remain into littoral zones and macrophytes beds where current velocities are lower (Lair 2006). The same phenomenon is expressed in the opposite way when waters flow through LSP outlet: the confluence of the three main water masses occasioned the replenishment in zooplankton from the different alongshore communities into the main channel, thereby enhancing its species richness during both hydroperiods.

2.6.2 Cladocerans

Bosmina sp. was the most abundant cladoceran along the whole study area during both hydroperiods, whereas *Chydorus sp.* was subdominant in the fluvial zones in May and in LSP in August. Those small taxa are known to dominate the zooplankton in most rivers all over the world (Lair 2006). Their small size and their ability to escape predation by sinking without causing turbulence (Balcer et al. 1984) are great advantages compared to bigger and more predated zooplankton species. The genus *Daphnia* was the third most important cladoceran and was subdominant in LSF during both hydroperiods and in the FC in May. This cladoceran seemed to have drifted from the Great Lakes on longer distances in the SLR during the spring high discharge than in August where it was only significantly abundant in LSF. Hudon (2000) observed the same pattern with phytoplankton.

2.6.3 Copepods

In the fluvial zones, the copepods were the most abundant as copepodite juvenile stages as observed in other rivers (Pourriot et al. 1997; Kobayashi et al. 1998). Among the dominant cyclopoids of the fluvial zones, all species are widely distributed throughout North America except for *E. prionophorus* (Hudson and Lesko 2003) and were observed in all the Great Lakes. In spring, *D. thomasi* was probably drifting from the Great Lakes where it was the most abundant copepod (Hudson et al. 2003). There, it was found encysted as fourth instar copepodite stage IV in late summer and emerged at spring (Napela 1985). One of the smallest cyclopoid species *T. prasinus* is present throughout the year and is very common in the Great Lakes. It is concentrated in surface waters in the summer and fall (Balcer et al. 1984). *Eucyclops pectinifer* is one of the most common benthic littoral cyclopoids in North America and is the most collected *Eucyclops* in the Great Lakes nearshore habitats (Hudson and Lesko 2003). *Eucyclops prionophorus,* another benthic species sparsely distributed in the Great Lakes, appears to replace *E. pectinifer* in deeper waters. The large *M. edax* was observed as copepodite stage V in Lake Superior in June and July. Their progeny matured in late August and they spend winter in diapause in the bottom sediment until the following spring (Selgeby 1975). This species presents a similar life history in the SLR where adults were the most abundant during the summer hydroperiod.

Although *E. lacustris* was rarely collected in Lake Ontario (Balcer et al. 1984) and contrary to what was generally the rule in Wisconsin lakes (Torke 2001), this species was found to dominate the calanoid communities including its associated species *S. oregonensis* and *L. minutus* in the LSF and LSP during spring. The carnivorous *E. lacustris* and the herbivorous species *L. minutus*, *L. sicilis* and *S. oregonensis* were far less abundant in the fluvial zones of the SLR than in the Great Lakes. Density of *E. lacustris* varied from 33 ind/m^3 in Lake Superior to 4900 ind/m^3 in Lake Erie. *Leptodiaptomus minutus* was most abundant in Lake Huron and Lake Michigan (245-2700 ind/m^3), whereas *L. sicilis* was more numerous in Lake Superior; density of *S. oregonensis* ranged from less than 1 ind/m^3 in Lake Superior to more than 2000 ind/m^3 during summer in Lake Erie (Balcer et al. 1984; Makarewicz et al. 1995).

Among the harpacticoids, *N. hibernica***,** widely distributed in Europe (Hudson and Lesko 2003) is common along the weedy margins of large rivers and lakes. It was first observed in North America in Lake Ontario (Czaika 1978). After being introduced in Lake Ontario, it colonised the other Great Lakes except Lake Superior. In the SLR, *N. hibernica* was dominant only in the FC where it seemed favoured over the other harpacticoid species. *Canthocamptus staphylinoides* is one of the most frequently found species in the Great Lakes (Robertson and Gannon 1981). It was also found to be relatively abundant on May in the SLR, but disappeared in August. This disappearance is probably due to its diapause which happens in late summer or early fall in the Great Lakes where at least 50% of all adult canthocamptids (including *C. staphylinoides*) were found encysted on the lake bottoms (Nalepa 1985). The euryhaline *S. borutzkyi* (Monchenko 1967) was introduced into the Great Lakes probably by ballast water exchange. It was first discovered in Lake Michigan in 1998, where it reached maximum abundance at the deeper sites (Horvath et al. 2001). In the SLR, this species was more important in the FEZ especially in May, where water conductivity and depth increased. *Onychocamptus mohammed* is distributed worldwide in fresh and saline inland waters. This species had not been reported in the Great Lakes until the 1990s. This harpacticoid was first recorded in Lake Ontario in 1992-93, and then in Lake Erie and Lake St. Clair in 2000. This suggests that this harpacticoid species may have been introduced in Lake Ontario; from there, it spread in the SLR where it was most commonly collected with *N. hibernica*, and *E. pectinifer* as observed in the Great Lakes.

In the ETZ, only a few euryhaline copepod species reached very high abundances. In May, the calanoid *A. longiremis* and the harpacticoid *H. curticorne* were the two dominant copepods along with fewer *E. affinis* and a low number of *D. thomasi*. In August, the calanoid *E. affinis* became dominant with the cyclopoid *H. fosteri* and the harpacticoid *H. curticorne*. *Eurytemora affinis* and *A. longiremis* are typically found in river estuaries and coastal bays in eastern North America (Heinsle 1966; Steinberg and Condon 2009). These estuarine calanoids can sustain strong and frequent salinity variations caused by mixing of fresh and saline waters and alternating tides. Lawrence et al. (2004) and Michalec et al. (2010) indicated a preference of *E. affinis* for low to medium salinities. The freshwater cyclopoids *D. thomasi* was probably drifting in the ETZ from upstream where it was abundant. *Halicyclops fosteri* inhabits temperate estuaries such as the Delaware Bay (Aurand and Daiber 1979) and the York River estuary (Steinberg and Condon 2009). To our knowledge, it was found for the first time in the St. Lawrence ETZ during this study. *Halectinosoma curticorne* was only found in the ETZ along with very few of the other estuarine harpacticoids, *M. littorale* and *M. norvegica*. These species were already recorded in the *Catalogue of the marine invertebrates of the Estuary and Golf of the St. Lawrence* (Brunel et al. 1998).

2.6.4 Amphipods

Echinogammarus ischnus is an invasive euryhaline Ponto-Caspian species first found in North America in 1995 in the Detroit River (Witt et al. 1997). By 2002, it had extended to all of the Great Lakes and downstream in the SLR to Québec City (Palmer and Ricciardi 2005). This species is replacing the native amphipod *G. fasciatus* in the Great Lakes. In the St. Lawrence, the two species coexist, but *G. fasciatus* remains dominant (Palmer and Ricciardi 2004). In our study, *E. ischnus* was found up to site 47 in the ETZ, downstream of Québec City. This is the first observation of that species as far downstream in the river. As for dominance patterns, *E. ischnus* was more common throughout the study area in May whereas *Gammarus sp.* was rare. This could be due to the high spring discharge that favoured zooplankton inputs from the Great Lakes where *E. ischnus* is abundant. Moreover, Palmer and Ricciardi (2004) found that *E. ischnus* was more abundant in areas of strong currents, while *G. fasciatus* did better on algal substrate in slower flowing areas in the St. Lawrence. That could explain why *G. fasciatus* was dominant in August, the summer hydroperiod providing larger macrophyte areas and more slowly flowing habitats.

2.6.5 Mysids

In May, few mysids were found in the ETZ. In August, they were found in very low numbers in the FEZ and were more frequent in ETZ where waters reach maximum turbidity. *Mysis stenolepis* was present during both hydroperiods, while *N. americana* was only formally identified in May but probably dominated the group of *Neomysis sp.* found in August. Theses species occur in many estuaries of northeastern North America (Winkler et al. 2007) and reach high densities in the ETZ region of the St. Lawrence (Dodson et al. 1989; Frenette et al. 1995; Winkler et al. 2007).

2.6.6 Influence of distribution and characteristics of water masses on crustacean communities

We showed that the longitudinal discontinuity in water masses and the conductivity-turbidity gradient were the source of most of the species variation found along the river-estuary section of the SLR. Laprise and Dodson (1994) indicated that water retention caused by the estuarine recirculation, and the strong salinity gradient in the ETZ of the SLR as seen in this study, were the main drivers controlling the fresh and brackish zooplankton communities. A strong distinction could be made between communities of the fresh and brackish waters and also between those of the upstream and downstream regions of the ETZ. In August, the same communities were isolated although in a less clear pattern. During both hydroperiods, the salinity-turbidity longitudinal gradient was the primary driver of zooplankton spatial variation. Contrary to our hypothesis, the hydrological effects were not stronger during the spring high discharge than during the summer low discharge.

Within the fluvial zones only, the zooplankton distribution was strongly related to the water masses and their characteristics. In May, the only two variables retained by the model were the water mass dummy variables WM4 and WM5, whereas WM2 and WM5 were selected in August.

In May, *Bosmina sp.* and cyclopoid copepodite stages were slightly associated to WM4, while calanoids, harpacticoids and amphipods were associated to WM5 in the eastern part of the FEZ. *Bosmina sp.* and the cyclopoid copepodite stages may have been favoured in WM4 along the south shore of LSP where extensive macrophyte beds are found. Being not well suited for swimming, they may have avoided drifting by inhabiting the macrophytes. The calanoids were found to prefer offshore habitats in the SLR (Casper and Thorp 2007); this may be the reason why they seem more abundant in the FEZ corridor containing less littoral shallow habitats. The combined action of discharge and tides in the totally homogenized WM5 may be responsible for the higher abundance of harpacticoids and amphipods in surface waters along the eastern part of the FEZ, as these taxa are epibenthic.

In August, two water mass dummy variables were still selected in the model: WM2 was associated to aCDOM and Chl*a*, whereas WM5 was related to higher values of longitude and TDS. The communities of the FSZ and FEZ could be easily differentiated: on the one hand, FSZ has a typical freshwater community dominated by cyclopoids and cladocerans; on the other hand, the FEZ contained higher proportions of the calanoid *E. affinis*, and represented the farthest freshwater habitat upstream for the cyclopoid *H. fosteri* and the mysid *Mysis sp.* Those taxa are known to inhabit estuaries (Aurand and Daiber 1979; Winkler et al. 2007), and could, due to their euryhalinity, penetrate the freshwaters in the eastern part of the FEZ. The WM5 possesses many properties that could have enabled these species to survive and dominate in a freshwater environment: compared to the whole FSZ, the eastern part of the FEZ exhibited higher TDS concentrations, associated with corresponding higher turbidity and slightly lower temperatures and PAR penetration. These environmental conditions are more similar to those of the typical environment of the estuarine species compared to the FSZ. Changes in TDS ionic composition can exclude some species while promoting population growth of others (Weber-Scannell and Duffey 2007). The proximity of the WM5 to the ETZ could have enhanced its concentrations in minerals, thereby reducing the range of tolerant species; this may be partly responsible for the observed changes in the zooplankton community structure. In the FSZ, the cyclopoid copepodite stages and many cladoceran species were associated to the coloured and humic WM2, which contains high aCDOM and Chl*a* concentrations. The chromophoric dissolved organic matter (CDOM), largely composed of humic substances, is responsible for most of the UV attenuation in the water column (Helbing et al. 2003). UV radiation has many effects on aquatic environments processes and organisms, among which the inhibition of photosynthetic algae and the generation of DNA damage in zooplankton and fishes within shallow water habitats (Helbing et al. 2003). Zooplankton as well as phytoplankton were thus protected against deleterious effects of UV within the CDOM-rich WM2. The dominant freshwater zooplankton species could also benefit from higher algal biomass (Chl*a* concentrations) in the macrophytes-rich and highly productive littoral habitats (Basu et al. 2000b) where WM2 flows. Macrophytes offer well-suited habitats for zooplankton development in temperate rivers (Lair 2006). In the SLR, zooplankton abundance was 9 times higher in the macrophytes beds of the fluvial lake littoral zones compared to the river channel (Basu et al. 2000b).

2.7 Acknowledgements

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Chapitre 3 :

Effects of hydrological and environmental processes on zooplankton spatial distribution patterns in the St. Lawrence River

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Jean-Jacques Frenette et Jean Morin

En préparation pour la revue ***Ecology***

3.1 Abstract

Herein we study the community structure of planktonic crustaceans and their generating processes along two biogeographical zones of the St. Lawrence River (Québec). Our purpose was to evaluate how the spatial structure of the characteristically distinct and contiguous water masses influenced the distribution of crustacean groups (cladocerans, calanoids, cyclopoids and harpacticoids) during spring (high discharge) and summer (low discharge) hydroperiods. Zooplankton and environmental data were sampled at 44 sites distributed in 12 transects along the Fluvial Section (FS) and the Fluvial Estuary (FE) of the St. Lawrence River in May and August 2006. Using the Asymmetric Eigenvector Maps (AEM) framework, we created four different theoretical flow models (connection diagrams) based on water mass distributions established for each hydroperiod. The resulting sets of AEM variables (AEMs) and environmental data were submitted to redundancy analysis (RDA) combined with a forward selection procedure to obtain parsimonious models. We determined the best AEM model (which led to the highest R^2_a) for May and August and compared the results between the two hydroperiods. Variation partitioning was used to assess how much of the zooplankton variation is explained by hydrological processes (AEMs) and local conditions (environmental factors). The selected AEMs from the best AEM model explained 40 % of total variation of crustacean distribution in May and 59 % in August, indicating a greater control by the water masses spatial structure on zooplankton during the low discharge in August than in May. In May, total phosphorus (TP), turbidity and conductivity explained 33 % of zooplankton variation, while no environmental variables were retained during the forward selection procedure in August. In May, the variation partitioning of the zooplankton data between selected AEMs and environmental variables explained 53 % of total zooplankton variation, with 20% explained by directional spatial structure of water masses (AEMs), 13% by local conditions (environmental variables), and 20% by the spatially structured portion of the environmental variables (common fraction).

Keywords : Ecological modeling, directional hydrological network and water quality, zooplankton spatial distribution patterns, St. Lawrence River, Asymmetric Eigenvector Maps (AEM), variation partitioning.

3.2 Résumé

Dans cette étude nous évaluons la structure de la communauté de crustacés planctoniques et leurs processus générateurs le long de deux zones biogéographiques du fleuve Saint-Laurent (Québec). Notre objectif était d'évaluer comment la structure spatiale des masses d'eaux contiguës aux caractéristiques distinctes influence la distribution de certains groupes de crustacés (cladocères, calanoïdes, cyclopoïdes et harpacticoïdes) au printemps (débit élevé) et en été (débit faible). Les échantillons de zooplancton ainsi que les variables environnementales ont été récoltés à 44 stations réparties sur 12 transects le long du tronçon fluvial et de l'estuaire fluvial du fleuve Saint-Laurent. En utilisant la méthode des cartes de vecteurs propres asymétriques (AEM), nous avons créé 4 modèles d'écoulement (diagrammes de connectivité) différents basés sur des distributions de masses d'eau établies à chaque hydropériode. Les séries de variables AEM ainsi obtenues et les variables environnementales ont été soumises à une analyse canonique de redondance (ACR) suivie d'une sélection progressive pour obtenir des modèles parcimonieux. Nous avons déterminé le meilleur modèle AEM (celui ayant mené au R^2_a le plus élevé) pour les mois de mai et d'août et avons comparé les résultats entre les deux hydropériodes. Une partition de la variation a été utilisée pour évaluer quelle part de la variation du zooplancton est expliquée par les processus hydrologiques (variables AEM) et les conditions locales (facteurs environnementaux). Les variables AEM sélectionnées à partir du meilleur modèle expliquaient 40% de la variation totale de la distribution des crustacés au mois de mai et 59% au mois d'août, indiquant un contrôle plus fort de la structure spatiale des masses d'eau sur le zooplancton pendant la période d'étiage au mois d'août qu'au mois de mai. Au mois de mai, le phosphore total, la turbidité et la conductivité expliquaient 33% de la variation du zooplancton, alors qu'aucune variable environnementale n'a été retenue par la sélection progressive au mois d'août. En mai, le partitionnement de la variation des données de zooplancton entre les AEM et les variables environnementales sélectionnées expliquaient 53% de la variation totale du zooplancton, avec 20% expliqués par la structure spatiale directionnelle des masses d'eau (variables AEM), 13% par les conditions locales (variables environnementales) et 20% par la portion structurée spatialement des variables environnementales (fraction commune).

Mots clés : cartes de vecteurs propres asymétriques, fleuve Saint-Laurent, Modélisation écologique, patrons de distribution du zooplancton, réseau hydrologique directionnel et qualité de l'eau, partition de la variation.

3.3 Introduction

Rivers conceptual models have first emphasized their continuum properties (Vannote et al. 1980) in which downstream ecosystem dynamics were closely linked to upstream processes. Ward and Stanford (1983) thereafter distinguished fluvial corridors of reservoirs or fluvial lakes, which represented discontinuities affecting processes downward the river. Primary production within the floodplain (Junk et al. 1989) and river channel, together with inputs from littoral vegetation (Thorp and Delong 1994), were subsequently stressed as important factors controlling riverine food webs. Recently, Thorp et al. (2006) considered rivers as an array of large hydrogeomorphic patches determining different functional zones and biological communities.

The St. Lawrence system, including the Great Lakes, is one of the largest freshwater systems in the world. Its surface area of 1.6 million km^2 is the third largest in North America and it drains more than 25% of the Earth's freshwater reserves (CSL 1996). One of its fluvial lakes – Lake Saint-Pierre – is fringed by the most expansive freshwater floodplain in Québec, its surface reaching 600 km^2 during floods.

Along its longitudinal axis, the St. Lawrence River (SLR) can be seen as a series of connected habitats consisting of corridors and fluvial lakes, eventually entering a tidal zone near Québec City. We consider these habitats as discontinuities or patches that possess their own physical and biological properties. The deep and fast flowing main channel may strengthen the connections between these habitats and perhaps form a distinct compartment by the time it reaches the Québec City region, where water masses are mixed and homogenized.

The SLR is made up of several distinct water masses, flowing side by side, each of which possesses its own chemical characteristics (CSL 1996; Frenette et al. 2006). On the one hand, there is initially little mixing between them, they can be seen as discontinuities on the transversal axis. On the other hand, taken longitudinally, each distinct water mass also forms a continuum of physicochemical conditions along the river. The St. Lawrence system can therefore be considered as a mosaic of interconnected habitats demonstrating varying degrees of continuity depending on the hydroperiod (high or low discharge). The Lake Saint-Pierre possesses a huge floodplain which may intervene in the control of biological production as proposed by Junk et al. (1989) in a tropical environment.

Zooplankton in rivers around the world is generally dominated by rotifers and small cladocerans, thanks to their shorter development time and parthenogenetic reproduction which enable them to survive and proliferate in the current (Baranyi et al. 2002; Viroux 1997; Lair 2006). Less adapted to turbulent river conditions, copepods still compose an important part of riverine zooplankton, owing to their euryhalinity (Lee 1999) and their ability to withstand unfavourable conditions by activating winter diapause and aestivation in the dried sediments of temporary waters (Lair 2006). The main zooplankton distribution patterns in rivers include increasing abundance from upstream to downstream in the main channel (Frutos et al. 2006; Basu and Pick 1997; Kim and Joo 2000) and from the fast flowing main channel to the slow flowing littoral zones (Köhler 1994; Thorp and Delong 1994; Viroux 1997; Baranyi et al. 2002; Casper and Thorp 2007), reservoirs or fluvial lakes (Walks and Cyr 2004; Basu et al. 2000a, 2000b; Wetzel 2001). The hydroperiods also modulate zooplankton distribution, the high discharge during spring sharply decreasing zooplankton abundance while the low discharge during mid-summer tends to increase populations (Baranyi et al. 2002).

In this study, the SLR was sampled along the freshwater section between Cornwall and Québec City. This is one of the first time that such a large part of the SLR is covered (see Massicotte and Frenette 2011), providing zooplankton and environmental data both in its longitudinal and transversal axes. Indeed, previous studies of zooplankton on the SLR freshwater segment covered smaller portions with few sites and transect (Mills et al. 1981; Mills and Forney 1982; Basu et al. 2000a, 2000b; Twiss et al. 2010). Sampling was conducted at two hydroperiods in May and August 2006 in order to compare the high-discharge spring and the low-discharge summer hydroperiods.

Our objective was to quantify the relative importance of spatial and environmental processes on the zooplankton spatial distribution patterns in the freshwater portion of St. Lawrence system. We used the new Asymmetric Eigenvector Maps (AEM; Blanchet et al. 2008a; 2011) method of analysis to create spatial variables modeling water mass distributions in May and August. Four different flow models (connection diagrams) were created for each hydroperiod. The resulting sets of AEM variables (AEMs) and the corresponding environmental variables were submitted to redundancy analysis (RDA) combined with a forward selection procedure to obtain parsimonious models. Variation partitioning was applied using the selected variables to assess the effects of hydrological processes (AEMs) and local conditions (environmental factors) on the species data. We determined the best AEM model (the one which led to the highest R^2_a) for May and August and compared the results between the two hydroperiods. We hypothesized that zooplankton spatial distributions were more strongly related to the longitudinal unidirectional distribution of water masses and their partial transversal mixing than to local environmental factors. We also hypothesized that the unidirectional hydrological process should have greater effects than local environmental conditions on zooplankton distribution during the spring hydroperiod with high discharge and currents, and inversely during the summer hydroperiod with low discharge and stronger transversal discontinuities.

3.4 Material and methods

3.4.1 Study sites and biogeographical zones

Zooplankton and environmental data were collected during two cruises of the research vessel *Lampsilis*, conducted during spring (23 to 30 May) and summer (8 to 15 August) 2006. A total of 44 sites, distributed along 12 transversal transects, were visited in two biogeographical zones of the SLR from Cornwall to Québec City (Figure 1, p79). Locations of stations within each transect were determined in order to study the lateral heterogeneity of the SLR water masses. Meteorological conditions were uniform during each sampling cruises and water masses stability was validated by satellite images. Unfortunately, some sites in the fluvial corridor (sites 15, 16) and Lake Saint-Pierre (sites 28, 29, 35) were not sampled due to technical problems during the sampling cruise in August. Their loss may have significantly biased the results.

The fluvial section (FS; sites 1-35) is 240 km long from Cornwall in Ontario to the Lake Saint-Pierre outlet in Québec, its width varying from < 2 km to 10 km wide (CSL 1996). This freshwater zone encompasses three fluvial lakes (Lake Saint-François (LSF), Lake Saint-Louis (LSL) and Lake Saint-Pierre (LSP)), and one fluvial corridor (FC) from Montréal. There is no or very little tidal effect up to this point. The SLR fluvial lakes are wide, slow flowing (< 0.3 m/s with the exception of the central channel) and shallow, with depth averaging 6 m for LSF and 3 m in LSL and LSP, whereas the fast flowing (1 m/s) navigation channel is 11.3 to 15 m deep. The fluvial lakes are extensively colonized by submerged macrophyte beds (Hudon 1996; CSL 1996; Basu et al. 2000b).

The fluvial estuary (FE; sites 36-44), composed of freshwaters, stretches more than 160 km from the LSP outlet to the eastern tip of Île d'Orléans. Width ranges from 870 m near Québec City

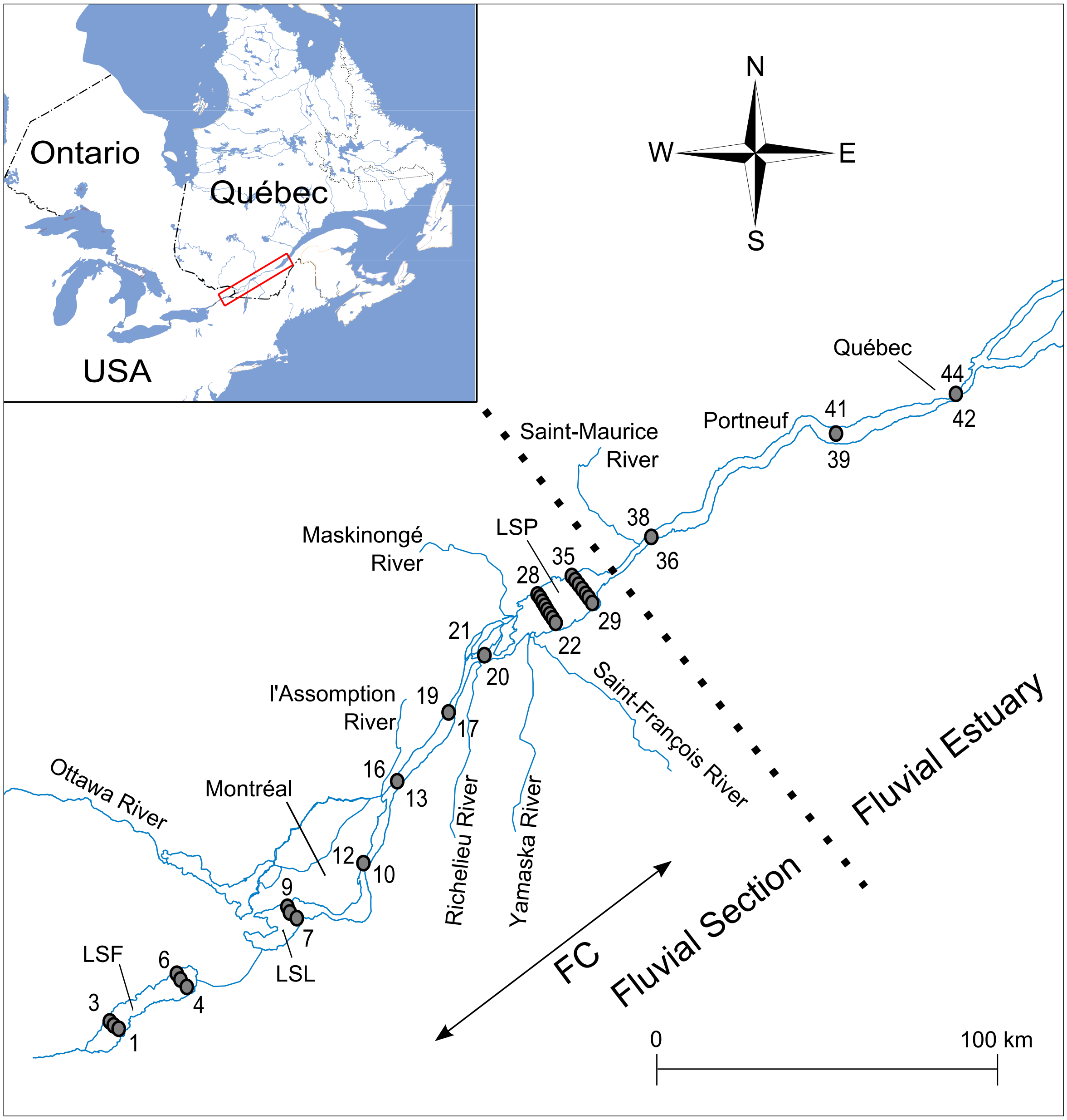

Figure 1 Distribution of the sampling sites in the 12 transects across two biogeographical zones (Fluvial Section (FS) and Fluvial Estuary (FE)) of the St. Lawrence River (SLR). Lake Saint-François (LSF), Lake Saint-Louis (LSL), Lake Saint-Pierre (LSP), Fluvial corridor (FC).

to 15 km at the eastern end of Île d'Orléans. Average water depth in the main channel ranges 13 to 40 m (CSL 1996). The effect of the tides becomes increasingly important downriver, and downstream Portneuf, the waters are completely homogenized.

3.4.2 Water masses distribution

The SLR is composed of several water masses with different physical and chemical characteristics, flowing side by side and mixing slightly or not at all for long distances. The sampling sites in the present study were distributed in 6 main water masses (Figure 2, p81).

The clear waters of the Great Lakes (GL; green) are characterized by exceptionally low suspended particulate matter (SPM; 1 mg/L), dissolved organic carbon (DOC; 2.5 mg/L) and total phosphorus concentrations (TP; 10 mg/L) with moderately high conductivity (294 µS/cm) (Hudon and Carignan 2008). In contrast, the more coloured and humic Ottawa River waters (OTT; brown) exhibits higher SPM (7.2 mg/L), DOC (6.1 mg/L), TP (34 mg/L) and lower conductivity (81 µS/cm) (CSL 1996; Hudon and Carignan 2008). The Richelieu River waters (RICH) are moderatly mineralized (conductivity = 191 µS/cm) and contains high SPM concentrations (17.2 mg/L).

Water masses distributions in the SLR during each sampling cruise were based on water masses mixture data (Annexe A: Table Ia, pii) and water masses map from CSL (1996). Water masses mixture data (Annexe A: Table Ia) for sites 10-35 were generated by simulations of the 2D convection-diffusion DISPERSIM model (Champoux and Morin 2007). This model performed the spatial distribution of the water masses by mapping conductivity gradient, this physical property being conservative in time and space. Moreover, each of the SLR water masses possesses its own signature (Champoux and Morin 2007). Firstly, the HYDROSIM model simulated the hydrodynamic conditions of each sampling cruise based on discharge and water levels measurements. The results of the simulations were then validated by other water levels measurements. The DISPERSIM model then integrated the simulated hydrodynamics along with depth and conductivity measurements to calculate a diffusivity coefficient, which led to the mapping of conductivity, and thus, of the water masses. The resulting simulations were then validated by other conductivity measurements. Results from convection simulation model were previously used in several habitats models and ecosystem response modelling (Champoux and Morin 2007). The same general water masses map from CSL (1996) was used to establish the spatial distribution of water masses for both hydroperiods for sites 1-9 and 36-44. We have

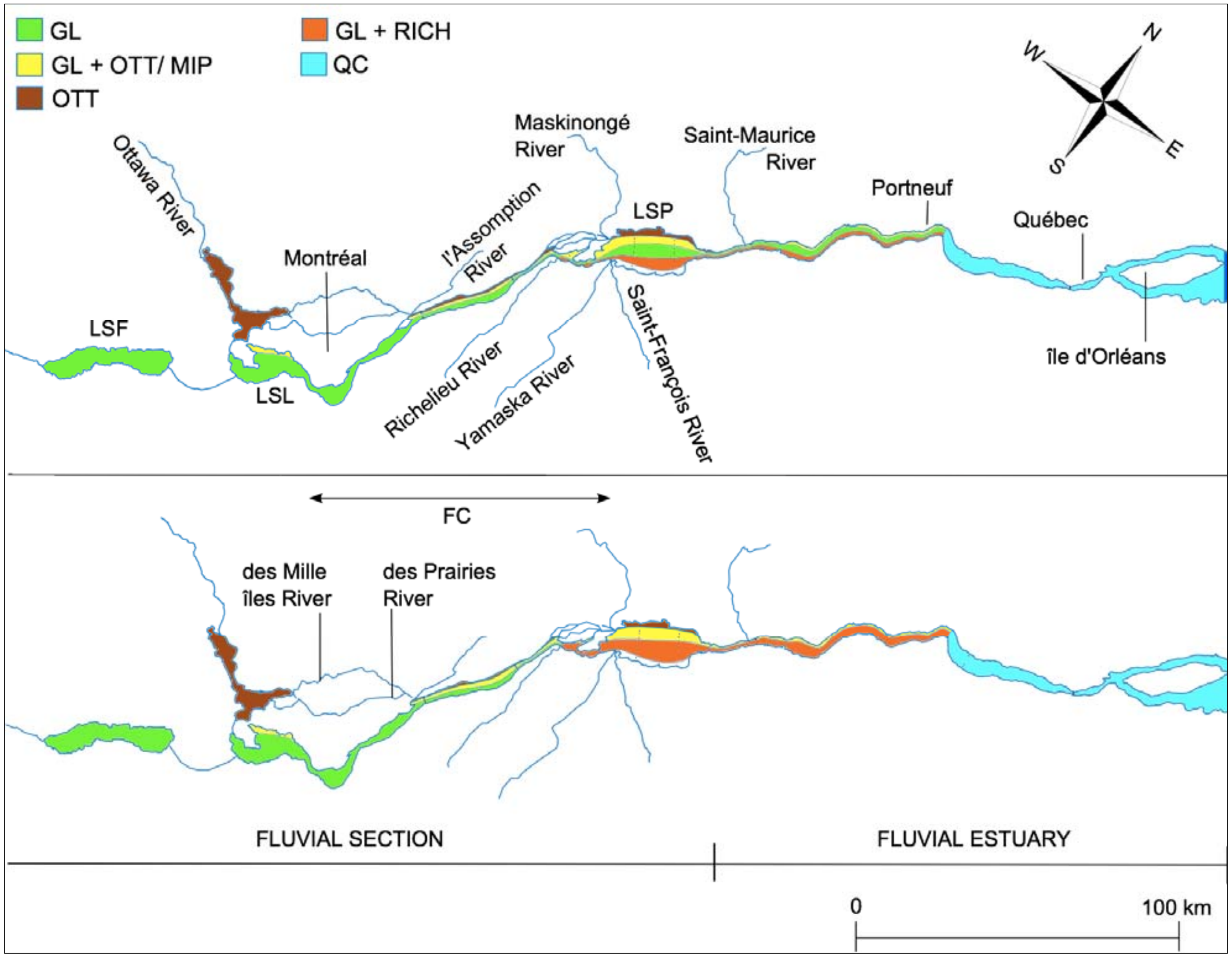

Figure 2 Water masses of the SLR (a) in May and (b) in August. Green = Great Lakes waters (GL), Yellow = Mixed waters of GL and Ottawa River (OTT) or Mille Îles and des Prairies Rivers (MIP), Brown = Mixed waters of OTT and l'Assomption River (ASS), Orange = Mixed waters of GL and Richelieu River (RICH), Blue = Québec City waters (QC). LSF = Lake Saint-François, LSL = Lake Saint-Louis, LSP = Lake Saint-Pierre, FC = Fluvial corridor.

attributed the LSP central water mass composition to the central water mass downstream until the Québec City water mass, for each hydroperiod.

In May, in the FS, the GL fed LSF and constituted the main channel. The OTT flowed into the Mille Îles and Des Prairies Rivers in Montréal and along the north shore of the FC to LSP, while it mixed with the GL (GL + OTT) along the north shore from LSL to LSP. The mixing of the RICH and the GL (GL + RICH) in the south shore of LSP formed the fourth main water mass. In the FE section, water masses coming from LSP flowed in a laminar way till upstream of Québec City, where the waters become homogenized by the tide. This water mass is called the Québec City waters (QC) (Figure 2, p81). In August, the water masses distribution differed markedly from that of May, because of the apparent disappearance of the GL water mass around the entrance into LSP. In fact, sites of the two LSP transects passed directly from a GL + RICH water mixture to a GL + OTT water mixture, going north. However, the RICH and OTT water masses were never mixed together (Annexe A: Table Ia, pii); this implies that a fine pure GL plume was conserved along the SLR until the Québec City waters.

3.4.3 Environmental variables

At each site, water temperature (°C), conductivity (µS/cm), turbidity (NTU), pH and dissolved oxygen (mg/L) were measured *in situ* using a Conductivity Temperature Depth profiler (YSI 6600 EDS-M sensor array, Yellow Spring Instruments). A spectroradiometer-fluorometer (HFT: Satlantic hyperpro-Wetlab C Star) was used to determine underwater profiles of light irradiance and calculate by Simpson integration the light available for photosynthesis (PAR: 400-700 nm). Water samples were collected using an 8 liters GO-Flow water sampler (Model 1080; General Oceanics) 1 m below the surface at each site. To measure chlorophyll *a* (Chl*a*), DOC (mg/L), total nitrogen (TN; mg/L), TP (µg/L), total dissolved solids (TDS; mg/L), and chromophoric dissolved organic matter absorbance (aCDOM, m^{-1}), subsamples were drawn from the GO-Flow bottles into acid-washed polyethylene bottles. Chl*a* concentrations were measured with a Turner Designs 10–005R fluorometer, after sonication and 24 h extraction in 90% acetone at 4°C in the dark (Parsons et al. 1984). For nitrogen and phosphorus analyses, samples for soluble reactive phosphorus and nitrites + nitrates (NO2 + NO3) were prefiltrated on 45 mm diameter, 0.7-µm pore-size GFF filters (Millipore). All nitrogen and phosphorus analyses were performed according to APHA (1998). DOC measurements were undertaken as follows: at each sampling site, 200 ml of water was filtered through a 45 mm diameter, 0.2-µm nominal pore-size polycarbonate membrane (Isopore; Millipore). Membranes were pre-rinsed with 100 ml of MilliQ water to remove potential impurities. The filtrate was stored in acid-washed borosilicate bottles and kept in the dark at 4°C until analysis. DOC concentrations were determined with a total organic carbon analyzer (TOC-1010; OI Analytical, College Station, Texas, USA) by sodium persulfate digestion. aCDOM was measured with a Shimadzu UV-2401PC UV-Vis spectrophotometer (Shimadzu, Columbia, Maryland, USA) using a 1-cm quartz cell between 190 and 900 nm. See Frenette et al. (2006) and Massicotte and Frenette (2011) for calculations of the absorption coefficients.

3.4.4 Zooplankton sampling and analysis

Zooplankton was collected at each site using a conical net (1 m mouth opening, 153 µm mesh size) hauled horizontally at 1 m depth. Zooplankton are generally longer than 153 µm (Wildlife Supply Company 1997-1998). Net filtered volume was measured with a flowmeter (General Oceanic). Upon collection, zooplankton organisms were split into fractions with a Folsom splitter. One/eight of each sampling unit was reserved for taxonomy and transferred to 250 ml plastic bottles. Zooplankton was narcotized with carbonated water and preserved in a buffered 4% sugar-formaldehyde solution and stored for later analysis (Prepas 1978). In the laboratory, a subsample was taken with a large opening pipette, transferred to a Ward rotative cell and analysed under a stereomicroscope (Ward 1955), until at least 100 crustaceans per station were counted. Adult copepods were identified to species. The copepodite stages (C1-C5) were categorised to appropriate suborder (Calanoida, Cyclopoida, Harpacticoida), while nauplii were not enumerated. For cladocerans, amphipods and mysids, identification was carried up to species level when it was possible and adults were at least identified to genus level. Identification of cladocerans was made based on Edmonston (1959), Amoros (1984) and Hebert (1995). Identification of copepods was made following Hudson et al. (2003), Lesko et al. (2003a, 2003b), Lacroix (1981), Huys et al. (1996), Edmondson (1959), and Smith and Fernando (1978). We identified amphipods using Bousfield (1958) and Holsinger (1972), and mysids using Brunel (1960) and Brunel et al. (1998). Laboratory procedures are described in details in Pinel-Alloul et al. (1990). Counts of crustacean species were expressed as numbers of individuals per cubic metre accounting for subsampling fractionation during field collection and microscopic analysis.

3.4.5 Statistical analyses

The Asymmetric Eigenvector Maps (AEM) method is an eigenfunction-based spatial filtering technique that was developed for situations where a directional process may influence a response variable along a gradient (Blanchet et al. 2008a, 2011). Our hypothesis in the present study is that the directional hydrological process is the main factor influencing the distribution of planktonic crustacean groups in the SLR. The AEM method uses directional connection diagrams linking sampling sites and, optionally, weights attached to the edges (links) to generate spatial variables modeling species distribution.

3.4.5.1 Connection diagrams

We built directional connection diagrams (flow models, Figure 3, p85) based on the water mass distributions detailed above. Results from the simulations of the convection-diffusion model consisted in percentages of original water masses composing the water column at each site (Table Ia, pii). 6 main water masses have been established (Figure 3; Great Lakes (GL), mixed waters of the Great Lakes and the Ottawa River (GL + OTT) or the Mille Îles and des Prairies Rivers (GL + MIP), mixed waters of the Ottawa and l'Assomption Rivers (OTT + ASS), mixed waters of the Ottawa and Maskinongé Rivers (OTT + MASK), mixed waters of the Great Lakes and the Richelieu River (GL + RICH) and Québec City waters (QC)) and were attributed to the sites. For each hydroperiod, the sampling sites were represented into a connection diagram (Figure 3) with color codes reflecting their water mass categories. Edges relating two sites (or a tributary to a site) were established based on the modeled contribution of the upstream site to the water of the target site. The flow direction, which goes from top to bottom in Figure 3, was emphasized by adding a site 0 ('Origin', not shown) upstream of the study sites. The origin was connected to the most upstream study sites, sites 1, 2 and 3, as recommended by Blanchet et al. (2008a, 2011). Unfortunately, several sampling sites were not sampled (4 and 6 in May; 10, 15, 16, 28, 29 and 35 in August) due to technical problems. Sites 9 and 22 were not considered in both May and August because their water mixes were incompatible with those of the other sampling sites of the network.

For each hydroperiod, we created four flow models (connection diagrams), which differ by the importance given to the mixing of water masses and the influence of the tributaries. These models are: 'Mixing with tributaries', 'Mixing without tributaries', 'No mixing with tributaries' and 'No mixing without tributaries'. The connection diagrams represented in Figure 3 are the starting

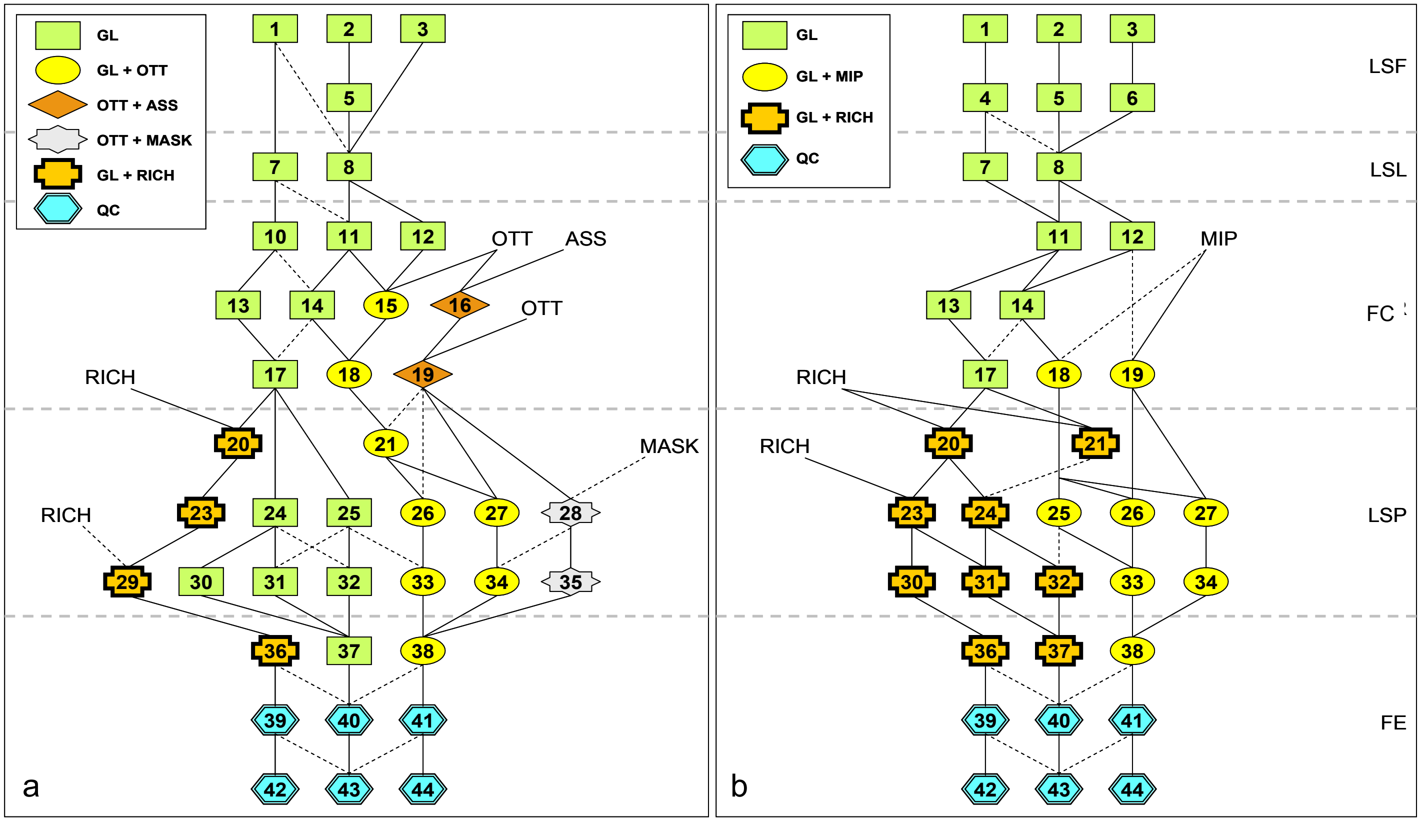

Figure 3 Connection diagrams used in May (a) and August (b) to generate the AEM eigenfunctions. The river flows from top to bottom of the maps. Each symbol identified by a number is a site. The form and color of a symbol relates a site to a water mass category: Green rectangle = Great Lakes waters (**GL**), Yellow ellipse = Mixed waters of GL and Ottawa River (**OTT**) or Mille Îles and des Prairies Rivers (**MIP**), Brown rhomb = Mixed waters of OTT and l'Assomption River (**ASS**), Grey stars = Mixed waters of OTT and Maskinongé River (**MASK**), Orange cross = Mixed waters of GL and Richelieu River (**RICH**), Blue hexagon = Québec City waters (**QC**). LSF = Lake Saint-François, LSL = Lake Saint-Louis, FC = Fluvial Corridor, LSP = Lake Saint-Pierre, FE = Fluvial Estuary. Dotted lines represent weak edges (low weight). The fictitious site 0, the weights on the edges and their identification numbers are not shown to simplify the figure.

models, ‘Mixing with tributaries’; they contain the maximum number of edges. To obtain the other models, we removed some edges according to the model. For models with no tributaries, we simply removed edges connecting tributaries to the network. For ‘no mixing’ models, we took off edges considered weak (dotted lines, see next paragraph).

3.4.5.2 Weights on the edges

In the AEM method, weights can be added to the edges to modulate the strength of the connections. We created AEMs either using weights or not. To compute the weights on the edges, we used the initial water masses percentage data (Table Ia, pii). Each site received a mixture of water masses indicated in percentages. We evaluated the contribution of an upstream site to the connected sites downstream on the basis of those water masses percentages. Simple calculations were used to determine the percentage of one water mass at one site reaching a connected site downstream. For example, in May, site 18 (Table Ia) was composed of 69 % of GL water and of 31% of OTT water. Two upstream sites (site 14: 100% of GL; site 15: 50% of GL and 50% of OTT) were connected to site 18 (Figure 3a, p85). We assessed the proportion of the OTT water mass (site 15) reaching site 18 as follows: 31/50 * 100 = 62%. Thus, site 15 waters contributed to 62% to site 18, and the balance (38%) was considered to be coming from site 14. In this way, for the ‘‘Mixing and tributaries’’ model, the sum of the incoming edge weights into a site is always 100%. When water masses percentage data was not available (sites 1-9 and 36-44; these sites were not covered by the convection-diffusion model), we distributed evenly the total weight (100%) among the incoming edges. For example, sites 39, 40 and 41 are all connected to site 43 (Figure 3); thus, the three edges entering site 43 each had a weight of 33.3%. The edges with weights under 20%, as well as some other doubtful edges, were considered to be weak (dotted line); they were removed from the ‘No mixing’ models.

3.4.5.3 Creating AEM eigenfunctions

Blanchet et al. (2008a, 2011) present a detailed account of the AEMs construction method. Here is a summary of the main steps: for each hydroperiod, (1) site-by-edge matrices (Table IIa, piii; Table IIIa (piv)) were constructed. In these tables, codes 1 are given to all edges (columns) that link a target site (row) to the origin (site 0), or stand along any downstream path between the target site and the origin. All edges that do not connect a target site to the origin receive code 0. (2) Weights were given to the edges by multiplying the values in each column of the site-by-edge matrix by the corresponding value in a weight vector (Table IVa, piv, Table Va piv). We also created sets of AEMs without applying weights on the edges; all edges received equal weights in these models. (3) To obtain the AEMs, we performed a singular value decomposition (SVD) of the site-by-edge matrices after centering them by columns. This operation can be performed by the ***aem()*** function of the R-language package AEM (Blanchet 2010). (4) We calculated a Moran's *I* coefficient of spatial correlation for each eigenfunction produced by the AEM procedure using the ***moran.I.multi()*** function of the R-language package AEM (Blanchet 2010). Only eigenvectors with a Moran's *I* above the expected value were considered to model positive spatial correlation and were kept for subsequent analyses.

3.4.5.4 Determination of the best AEM model

To determine the best AEM model for each hydroperiod, we performed a global RDA for each set of AEMs created from each flow model, using as response matrix of zooplankton data submitted to different transformations (Hellinger, species profiles, chord and chi-square) (Legendre and Gallagher 2001). The flow model and transformation combinations that produced the best explanations (highest R^2_a) for each survey were identified; several models were retained during this step. The AEMs in the retained models were submitted to a forward selection procedure to choose a single best model for each hydroperiod, based on the resulting R^2_a. We used two stopping criteria during the forward selection procedure, as proposed by Blanchet et al. (2008b): the R^2_a threshold produced by a first global RDA which contained all variables, and the α threshold = 0.05. Bubble plots representing the significant RDA axes of zooplankton distribution modeled by the best flow model in May and August were drawn to display the zooplankton spatial patterns.

3.4.5.5 RDA and variation partitioning

After performing forward selection on AEMs and environmental data using the two stopping criteria proposed by Blanchet et al. (2008b) (see above), we performed a RDA of the zooplankton groups with the environmental variables only (***rdaTest()*** function from package rdaTest in the R language (R Development Core Team 2011)) and computed a variation partitioning (Borcard et al. 1992) of the zooplankton groups between AEMs (hydrological process) and environmental variables (local conditions). This was done using the ***varpart()*** function from package VEGAN (Oksanen et al. 2011) in the R language.

3.5 Results

3.5.1 Environmental and zooplankton data in May and August

The sampling periods reflected seasonal variations in discharge, as shown in Table I (p89). Tributaries discharge was much more important in May than in August, and that was reflected on the cumulative discharge of the SLR, mostly at Trois-Rivières, downstream of LSP and the confluence of the major SLR tributaries.

In SLR freshwater zone, aCDOM, PAR extinction coefficient (k_dPAR) and TP showed the most important variations among sites (high coefficient of variation (CV)) in both hydroperiods, while Chl*a* was highly variable in August (Table II, p89). Most of the other variables were relatively similar in May and August. Conductivity and temperature increased in August while aCDOM and TP decreased. The waters were well oxygenated in May.

For the zooplankton community (Table III, p89), the mean abundance per site was higher in May than in August ($p < 0.01$, Mann-Whitney-Wilcoxon paired test), contrary to our expectations. Cladocerans were subdominant and equally abundant in both hydroperiods, but were proportionally more important in August. Calanoids were very few in May and turned to be dominant in August, while it was the opposite for the cyclopoids. Harpacticoids remained in low numbers during both hydroperiods. Nevertheless, it should be reminded that some sites in the FC (sites 10, 15 and 16) and the LSP (sites 28, 29, 35) were not sampled in August. The lacking sites in LSP, which were located in the northern and southern shallow littoral zones, were probably richer in zooplankton, as these highly vegetated zones (Hudon 1996; CSL 1996; Basu et al. 2000b) have considerably greater macrozooplancton biomass than in the open water during mid-summer (Basu et al. 2000b). Their loss may have significantly biased the results.

3.5.2 AEM models

The R^2_a statistics resulting from the global RDAs conducted using all AEM models (8 in May, 8 in August) are presented in Table IV (p90). In May, the chi-square transformation seemed the best suited for the zooplankton data. The choice of the most appropriate connection diagram did not seem an important criterion in maximizing the R^2_a statistic, while the weights on the edges did seem important: better results were always obtained with equal weights on all edges. In August, the species profile transformation (Legendre and Gallagher 2001) seemed to be the best transformation

Table I Mean discharge (m^3/s) in the St. Lawrence River (SLR) and at the outlet of its major tributaries during the sampling cruises in May 23-30 and August 8-15 2006.

	May	August
St. Lawrence River		
Montreal	7909	7668
Sorel (upstream of LSP)	9892	8920
Trois-Rivières (downstream of LSP)	11447	9505
Tributaries		
Ottawa River	2347	1399
l'Assomption River	178	45
Richelieu River	810	387
Yamaska River	182	23
Saint-François River	338	138
Maskinongé River	67	11

Source : Olivier Champoux (Environment Canada)

Table II Water characteristics of the SLR between Cornwall and Québec City during the spring (May) and summer (August) hydroperiods. Results showing important variations among sites (high coefficient of variation (CV)) are in bold. SD = standard deviation. *Dissolved oxygen data is not available in August due to damage in the YSI sensor.

	May (N=40)			August (N=36)		
Variables	Mean ± SD	Range	CV	Mean ± SD	Range	CV
Chromophoric dissolved organic matter absorption coefficient (aCDOM, m^{-1})	**8.4 ± 4.8**	**1.6 - 21**	**57**	**5.1 ± 4.3**	**0.8 - 24.1**	**84**
Chlorophyll *a* (Chl*a*, µg/L)	3.1 ± 0.7	1.4 - 4.9	23	**2.6 ± 1.4**	**0.9 - 7**	**54**
Conductivity (µS/cm)	187 ± 42	24 - 232	22	239 ± 50	37 - 298	20
Dissolved oxygen (mg/L)	10.2 ± 0.3	9.6 - 10.8	3	-	-	-
Dissolved organic carbon (DOC, mg/L)	4.7 ± 1.7	2.4 - 9.6	36	3.5 ± 1.1	2.1 - 7.4	31
PAR extinction coefficient (k_dPAR, m^{-1})	**1.9 ± 0.8**	**0.5 - 3.3**	**42**	**1.6 ± 0.8**	**0.4 - 4.9**	**50**
pH	7.9 ± 0.2	7.5 - 8.1		8 ± 0.4	6.4 - 8.5	
Total nitrogen (TN, mg/L)	3.2 ± 0.8	1.1 - 4.5	25	2.6 ± 1	0.5 - 5.2	38
Total phosphorus (TP, µg/L)	**40 ± 20**	**8 - 84**	**51**	**15.4 ± 6.9**	**4.5 - 40.9**	**45**
Total dissolved solids (TDS, mg/L)	90 ± 22	12 - 119	24	100 ± 20	16 - 119	20
Temperature (°C)	12.9 ± 0.6	11.6 - 13.9	-	23.2 ± 0.7	21.1 - 24.6	-
Turbidity (NTU)	7.9 ± 5	0 - 18.7	-	7.5 ± 16.3	0 - 98.2	-

Table III Mean abundance (ind/m^3) ± SD (standard deviation) and range of major crustacean groups. The dominant groups for each hydroperiod are in bold.

	May (N=40)		August (N=36)	
Large group	Mean ± SD	Range	Mean ± SD	Range
Cladocerans	**81 ± 87**	6 - 355	**74 ± 87**	9 - 483
Calanoids	9.4 ± 9.2	0 - 44.9	**112 ± 208**	0 - 1152
Cyclopoids	**263 ± 247**	32 - 1158	34 ± 40	4 - 223
Harpacticoids	8.5 ± 10.3	0 - 52.6	8 ± 10	0 - 43
Total	362		228	

Table IV R^2_a from the global RDA from AEM models with associated species data transformation. Highest R^2_a per hydroperiod and transformation are in bold. Connection diagram and transformation combinations with highest R^2_a values (outlined) were chosen for the forward selection procedure.

			Transformation			
	AEM Model	Weights on the links	Hellinger	Profiles of relative frequencies	Chord	Chi-square
May	Mixing + tributaries	yes	0.224	0	0	0.246
		no	**0.328**	0.108	0.041	**0.390**
	Mixing no tributaries	yes	0.228	0	0	0.149
		no	0.264	**0.113**	0.050	0.378
	No mixing + tributaries	yes	0.177	0	0	0.191
		no	0.277	0.072	0.020	0.359
	No mixing no tributaries	yes	0.138	0.043	0.002	0.125
		no	0.227	0.105	0.036	0.280
August	Mixing + tributaries	yes	0.552	0.580	0.522	0.447
		no	0.528	0.529	0.477	0.420
	Mixing no tributaries	yes	0.551	0.586	0.490	0.418
		no	0.535	0.533	0.472	0.455
	No mixing + tributaries	yes	**0.562**	0.584	**0.523**	**0.458**
		no	0.513	0.510	0.460	0.409
	No mixing no tributaries	yes	0.555	**0.596**	0.506	0.413
		no	0.402	0.395	0.380	0.299

for the zooplankton data. Contrary to May, non-evenly distributed weights on the edges were better to obtain high R^2_a values; none of the best results (outlined) arose from AEMs calculated without weights. As in May, the choice of connection diagram did not seem an important criterion.

The best combinations of connection diagrams and species data transformations (Table IV, p90, outlined) were submitted to forward selection of the AEMs in order to choose one best model-transformation for each hydroperiod. The R^2_a results of this exercise are in Table V (p92). In May, the best model was ‘Mixing without tributaries’ with equal weights on the edges (‘no weights on the edges’) and chi-square transformation of the zooplankton data, with a R^2_a of 0.395. In August, the model ‘No mixing without tributaries’ with weighted edges and the species profile transformation gave the best R^2_a (0.589). These results give us insights about the way zooplankton is driven by spatial connectivity between and within water masses.

General zooplankton community composition for both hydroperiods (Figure 4 p93) is shown in bubble plot maps of the first canonical axis of the zooplankton as a function of the selected AEMs from the best models. A single canonical axis was significant ($p < 0.01$) in each case. Black and white squares in bubble plots represent different zooplankton community composition. In May, zooplankton community in white squares is generally characterized by higher abundances of harpacticoids and calanoids, with a slight trend toward lower abundances of cyclopoids; the opposite was true in black squares. The AEM model thus indicates a general increase of calanoid and harpacticoid abundances, mainly in the LSF and the mixing zone area between the central (GL) and the northern (OTT) water masses from the FC to the outlet of LSP, whereas cyclopoids abundance tend to increase in LSL, the main channel (GL) through LSP and the FE. Cladocerans showed no clear trend between white and black squares.

In August, zooplankton spatial patterns were better defined. The zooplankton community was generally richer in cladocerans with fewer calanoids in the LSF, the northern and southern portions of LSP and upstream (white squares), while we found the opposite in the black squares. Cyclopoids were generally more numerous in the white squares, but this pattern was less clear. We found no clear trend for harpacticoids in August.

3.5.3 RDA and variation partitioning

In May, conductivity, turbidity and TP were the environmental variables retained by the forward selection ($R^2_a = 0.330$), using the chi-square transformation for zooplankton data. The first

Table V R^2_a of the canonical models using the selected AEM models and transformations selected in Table IV. The highest R^2_a for each month is outlined.

			Transformation		
	AEM Model	Weights on the links	Hellinger	Profiles of relative frequencies	Chi-square
May	Mixing + tributaries	no	0.155		0.305
	Mixing no tributaries	no			$\boxed{0.395}$
	No mixing + tributaries	no			0.352
August	Mixing + tributaries	yes		0.530	
	Mixing no tributaries	yes		0.483	
	No mixing + tributaries	yes	0.491	0.536	
	No mixing no tributaries	yes	0.555	$\boxed{0.589}$	

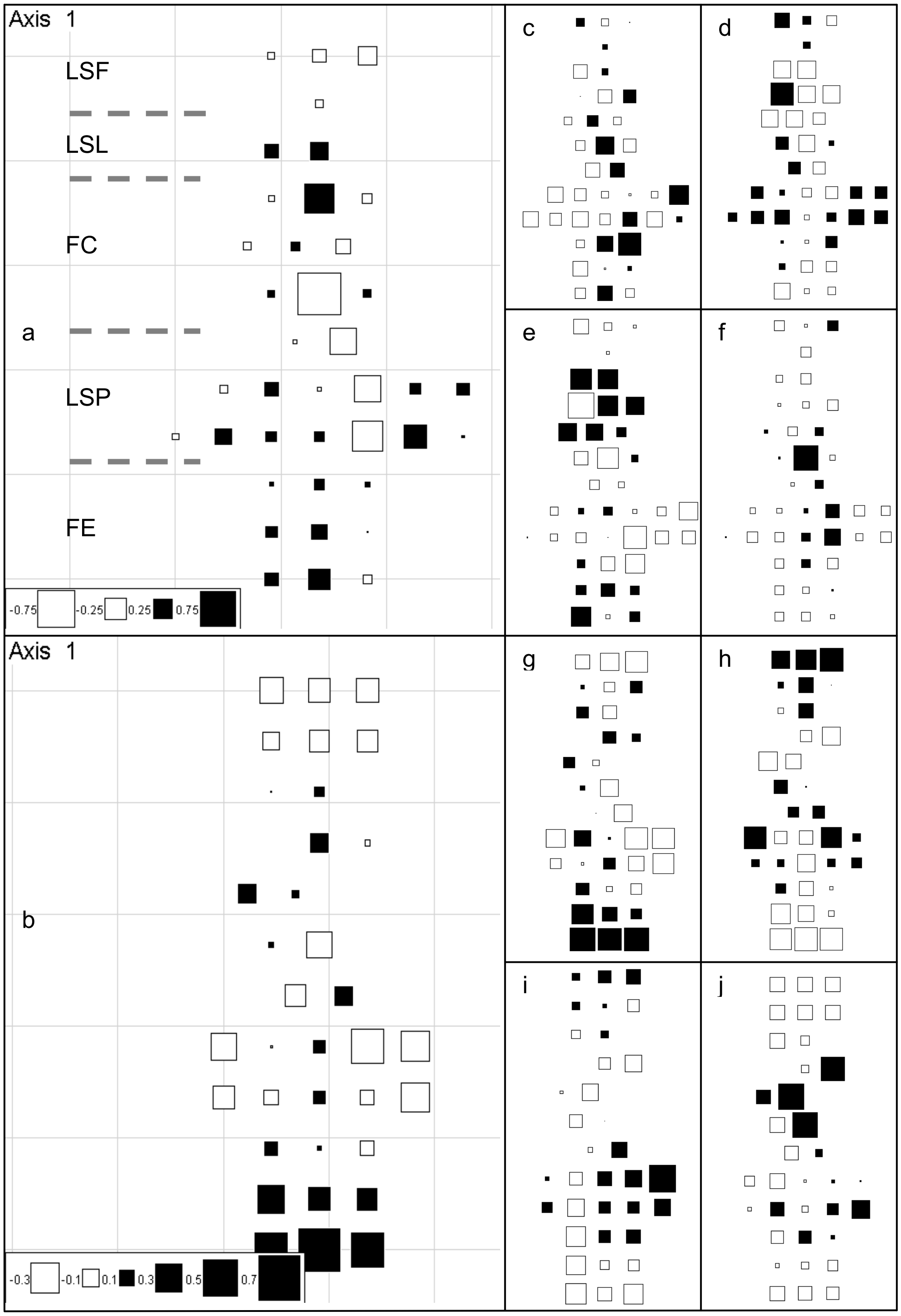

Figure 4 Bubble plot maps presenting the fitted value of zooplankton on canonical axis 1 of the best RDA model of selected AEMs (a) in May and (b) in August. In May, c (calanoids), d (cladocerans), e (cyclopoids), and f (harpacticoids) are bubble plots maps of the zooplankton groups chi-square-transformed abundances. In August, g (calanoids), h (cladocerans), i (cyclopoids) and j (harpacticoids) are bubble plots maps of the zooplankton groups abundances transformed by the species profiles transformation. Bubble size is related to the value associated to it. The color reflects the sign of the value (black = positive, white = negative). Signs are arbitrary in AEM eigenfunctions.

ordination plane of the RDA (Figure 5, p95) explained 36% of the zooplankton variation; axes I and II explained 25% and 11%, respectively. Harpacticoids were associated to higher turbidity and conductivity, while it was the opposite for the cyclopoids. Cladocerans were more important in richer habitats (higher TP concentrations), contrary to the calanoids.

The variation partitioning (Figure 6, p95) of the zooplankton data between the selected AEMs and the selected environmental variables explained 53% of total zooplankton variation, with 20% strictly explained by the directional spatial structure of water masses (AEMs), 13% by the local conditions (environmental variables), and 20% by the spatially structured portion of the environmental variables (common fraction). In August, no environmental variable was selected ($p > 0.1$ for the first variable of the model). Variation partitioning was thus useless; the zooplankton data only had a significant directional spatial structure representing $R^2_a = 0.589$.

3.6 Discussion and conclusion

3.6.1 Flow models and zooplankton transformations

Zooplankton distribution in the freshwaters of the SLR was not successfully explained by the flow model type, for both hydroperiods. That is to say, removing or not the effects of the tributaries or the weak lateral exchange between water masses did not dramatically change the results. The type of weights on the edges differed between hydroperiods. In May, equal weights always gave the best results. Thus, considering the exchanges between adjacent water masses and within a water mass as equally important seems to better reflect the hydrological conditions taking place in the SLR in period of high discharge than quantifying theses exchanges by the chemical composition of the original water masses. That suggests a greater exchange and mixing between the different water masses due to the high discharge during spring. In August, weighted edges increased the amount of explained variation. That is in accordance with the principle by which transfers are more difficult between stable and slow flowing water bodies.

Transformations of zooplankton data also greatly influenced the results in both hydroperiods. In May, the chi-square transformation gave the best results (Table IV, p90). Since this transformation gives extra weight to rare species (Legendre and Legendre 1998; Legendre and Gallagher 2001), these species may have contributed to the better explanation of zooplankton distributions. Indeed, when representing zooplankton groups in a rank-frequency diagram in May

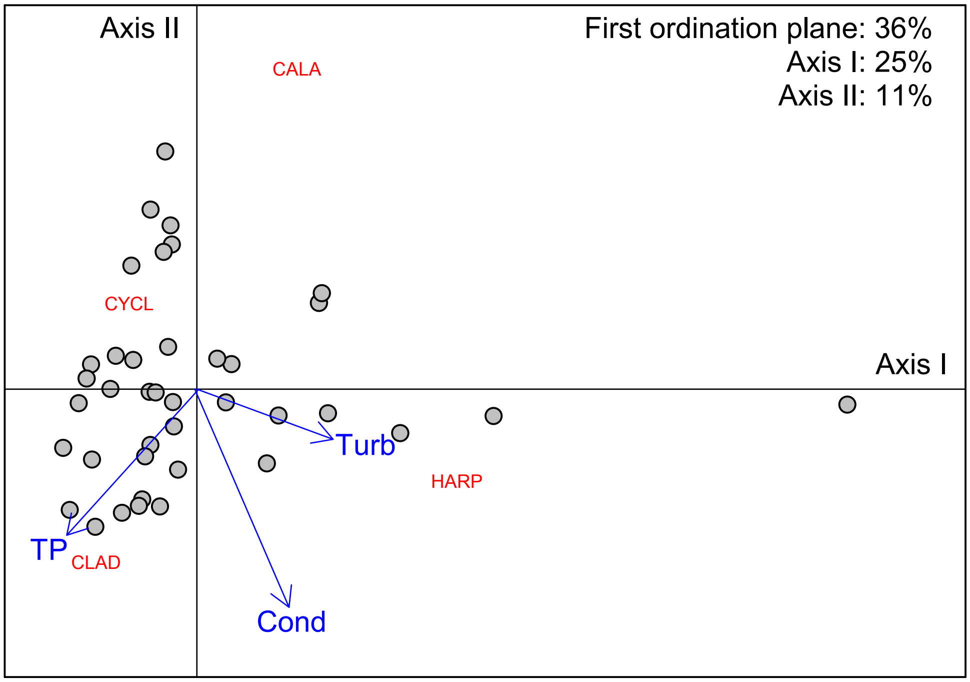

Figure 5 Biplot of the environmental variables and zooplankton groups in the first ordination plane of the RDA. Grey circles represent sampling sites. CLAD (cladocerans); CALA (calanoids); CYCL (cyclopoids); HARP (harpacticoids); Cond (Conductivity); TP (Total phosphorus); Turb (Turbidity). The contributions to the explanation of total variance of axis I, axis II and the first ordination plane of the RDA are presented in the upper right corner.

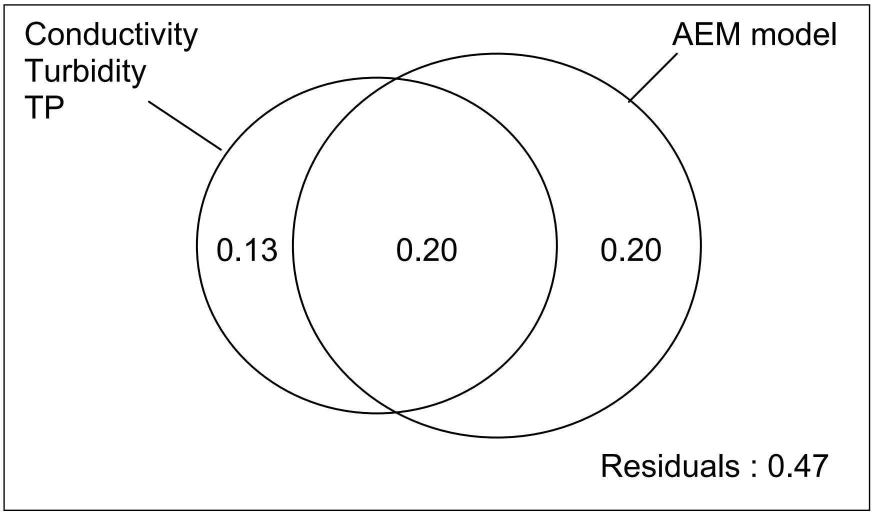

Figure 6 Variation partitioning results for May between the selected AEMs and Environmental variables illustrated by a Venn diagram. TP = Total phosphorus.

(graph not shown), we found that cyclopoids largely dominated the zooplankton, whereas calanoids and harpacticoids were rare. In August, the species profiles transformation, an unweighted variant of the chi-square transformation, led to the highest R^2_a. This transformation does not give high weights to rare species (Legendre and Gallagher 2001), so the less abundant groups did not influence the results in the same way as in May. Indeed, differences between the mean abundance of zooplankton groups per site were much smaller in August than in May.

3.6.2 Best flow models

In May, the zooplankton spatial pattern was best supported by the mixing model (Table V, p92), likely because of the powerful effect of the flood which would have increased lateral exchanges. The hydrological process accounted for 40% of total community variation. In August, water masses were well established and lateral exchanges between distinct water masses became unlikely. That is probably why the 'No mixing' model (R^2_a = 59%) best explained the zooplankton data. The stability of the water mass distribution could have reinforced the pattern described in Figure 3b (p85) which in turn could explain a larger portion of the variation than in May when waters were more turbulent.

3.6.3 Zooplankton composition spatial patterns

In May (Figure 4a, p93), calanoids and harpacticoids were more abundant in LSF and the main channel of LSP and upstream. As for calanoids, this could be due to their natural tendency to live in offshore habitats rather than littoral zones, where they were subjected to higher predation pressure in a portion of the SLR (Thorp and Casper 2007). The fact that they were associated to less rich habitats (lower TP concentrations) in the RDA support this hypothesis. The higher abundances of harpacticoids may be explained by the high current velocities flowing in shallow areas during the spring high discharge, which could have caused their resuspension in the water column. This hypothesis is consistent with the association of the harpacticoids to higher turbidity in the RDA. The cladocerans, which did not show any clear trend in Figure 4, were related to higher TP concentrations. Cladocerans are known to be more abundant in littoral slackwaters than in the main channel in the SLR (Casper and Thorp 2007). Productive slackwaters zones are non-evenly distributed along littoral zones; this may be the reason why cladocerans distribution was not clearly established. Cyclopoids, the most abundant zooplankton group in May, were more important in LSL and downstream, and in the Québec City waters. They were mainly constituted of copepodite stages which may have drifted in the main channel up to Québec City. They were also associated to low turbidity zones, as it would probably be the case if they were drifted into the main channel where depth was maximal and sediment far from the surface.

In August (Figure 4b, p93), the calanoids and cladocerans patterns were better defined. The cladocerans were more numerous in LSF, the LSP northern and southern portions and upstream region. Their development in the LSF and LSP is probably related to the development in summer of extensive macrophyte beds in littoral zones (Hudon 1996; CSL 1996; Basu et al. 2000b) where cladocerans (especially *Bosmina sp.*) are favoured compared to the main channel (Thorp and Casper 2007). In contrast, the dominant zooplankton group calanoids were more numerous in the main channel between LSL and the Québec City waters, where they were clearly the most abundant species. Their importance in this last tidal region may be due to the dominant euryhaline *E. affinis* and the homogenization of the water column which could have caused longer residence time.

3.6.4 Variation partitioning

Selected AEMs and environmental variables together explained half (53%) of the variation in May (Figure 6, p95), whereas AEMs alone explained 59% of the variation in August. Local conditions seemed therefore to have greater effects on zooplankton abundances in May (13%) than in August (0%) during which zooplankton distribution seems to be completely spatially structured. Those results are in agreement with our hypothesis predicting that zooplankton distribution patterns are more influenced by the water masses spatial structure than by local environmental factors.

However, contrary to what was expected, the spatial structure of the water masses explained more of the spatial zooplankton community variation in August than in May, whereas local environmental factors (not spatially structured) explained more variation in May than in August. As higher discharge in May (Table I, p89) made the river more dynamic, a strong, stable hydrological spatial structure may not have been established and the zooplankton distribution pattern was less predictable. There was less dependence in May between zooplankton and the chemical characteristics of the water masses. In August, when we thought that the high stability of the slow flowing water masses would allow the environmental local conditions to influence zooplankton, we observed exactly the opposite. In fact, the water masses stability in August made the distribution of zooplankton more predictable and better related to the water mass distribution.

The higher amount of explained zooplankton variation in August may be partly due to the lacking sites in both north and south extremities of the two transects (sites 28, 29 and 35) in LSP. These more shallow (≤ 2 m depth) and highly vegetated (CSL 1996; Basu et al. 2000b) zones were probably richer in zooplankton because of their increased water residence time (Basu and Pick 1996), compared to the other sites more exposed to current. Thus, being located at both extremities of the shore-pelagic-shore gradient, they would have generated higher heterogeneity in August zooplankton data. Moreover, the lacking sites were possibly more affected by the LSP tributaries due to their greater proximity, further enhancing their differences with the other sites. Their lost likely flattened the zooplankton distribution and made it more predictable by the water masses distribution.

In August, the environmental variables that varied the most among sampling sites were aCDOM, Chl*a*, k_dPAR and TP (Table 2, p89). In spite of their high variation throughout the environment, they failed to explain zooplankton spatial distribution. The lack of relationship between these variables and zooplankton abundance may be due to the riverine environment itself: phytoplankton biomass (Chl*a*), nutrients and trophic status (TP) are major factors affecting zooplankton biomass in lakes (Köhler 1994; Wetzel 2001; Pinel-Alloul and Ghadouani 2007) but their influence in rivers is much less important. Basu and Pick (1996) only found weak positive correlations between Chl*a* and zooplankton biomass in 31 temperate rivers in Ontario and Québec (Canada). The relationship between Chl*a* and zooplankton became significant only after controlling for residence time. The same authors (1997) also found a more important relationship between those variables ($R^2 = 0.20$); however, it was in a river with low current velocities. Zooplankton biomass and abundance have been found to be much lower in rivers than in lakes of similar nutrients and Chl*a* concentrations (Köhler 1994; Basu et Pick 1997). As phytoplankton biomass has little effect on riverine zooplankton, the same applies to TP concentrations and K_dPAR, which act mainly on zooplankton through their influence on phytoplankton.

Furthermore, since zooplankton distribution in the SLR is majorly driven by advection (as suggests the high amount of spatially explained variation (40% in May and 59% in August)), the local conditions where sampling occurred could not have affected the zooplankton importantly, as the organisms were mainly coming from upstream.

3.6.5 Water masses distribution in the SLR

In August, the GL water mass disappeared from the water masses distribution near the entrance of LSP (Figure 2, p81). This last result seems contradictory with those of several studies on LSP, which found the GL water mass to constitute the main channel during summer (Frenette et al. 2003; Frenette et al. 2006; Vis et al. 2007; Hudon et Carignan 2008; Lapierre et al. 2008; Massicotte and Frenette 2011). This may partly be due to the use of different methods for the establishment of water masses distribution. Those last studies used satellite analysis to identify the LSP water masses, which can be divided up to 8 distinct water masses. This technique used color-producing agents such as chromophoric dissolved organic matter and suspended particulate inorganic matter (Frenette et al. 2006; Lapierre et al. 2008; Massicotte and Frenette 2011) as markers for the differentiation of water masses; those agents have been quantified from space by optical satellite sensors. The method used here for the mapping of LSP water masses was based on simulations of a 2D convection-diffusion model (Champoux and Morin 2007) which integrated simulations from a hydrodynamic model and conductivity measurements. Conductivity was used here to distinguish the water masses. This method enabled us to quantify the relative contribution of the tributaries and both main inputs (GL and OTT) to the waters of each sampling site. This way, we did not observe any site whose waters were made up to 100% GL waters.

In the particular case of the present study, the water mass distribution was established to fulfill the requirements for the construction of AEM connectivity diagrams. Even though one site was located in a water mass majorly constituted of the GL waters (up to 95%), it was classified as a mixed water mass. That is probably the reason why the GL water mass disappeared from the water mass distribution in LSP during summer, contrary to previous findings. Only the water masses attributed to each site were represented in Figure 2; we did not show all LSP water masses present during sampling.

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Chapitre 4 : Conclusion générale

Cette recherche présente le premier portrait sur la distribution des crustacés planctoniques dans l'ensemble du fleuve Saint-Laurent. Cette problématique a été abordée du point de vue de la connectivité entre les différentes masses d'eau et les composantes biophysiques du fleuve.

Dans l'axe longitudinal, les trois zones biogéographiques du fleuve (le tronçon fluvial, l'estuaire fluvial, la zone de transition estuarienne (ZTE) représentent un gradient dans l'hydrodynamisme, les variables physiques et la géomorphologie. Le plus fort gradient physique et chimique se trouve au niveau de la discontinuité salinité-conductivité entre les zones fluviales et la zone de transition estuarienne. À l'intérieur des zones fluviales, les lacs fluviaux, possédant de vastes zones lentiques peu profondes et densément peuplées de macrophytes (Hudon 1996; CSL 1996; Basu et al. 2000a, 2000b), se distinguent des corridors profonds à écoulement rapide (CSL 1996). Dans l'axe transversal, les masses d'eau aux caractéristiques distinctes, s'écoulant côte à côte et se mélangeant peu, forment des discontinuités physiques et chimiques. Les zones littorales peu profondes et végétalisées ont des courants plus faibles et un temps de résidence prolongé, comparées au chenal principal profond au débit élevé. Tous ces compartiments forment une mosaïque d'habitats qui génère la structure spatiale du zooplancton dans le fleuve Saint-Laurent. La connectivité entre les habitats dépend de l'hydropériode; la période de crues au printemps et la période d'étiage en été. Les conditions hydrologiques sont un facteur majeur déterminant la distribution des masses d'eau dans le fleuve Saint-Laurent (Champoux et Morin 2007). Les différences de débit observées entre mai et août ont fait changer la distribution des masses d'eau entre ces deux hydropériodes.

Au chapitre 2, nous avons déterminé que la discontinuité longitudinale entre les eaux douces et les eaux marines au niveau de la ZTE est le facteur qui régit la distribution du zooplancton à grande échelle. Dans la ZTE, quelques espèces euryhalines formaient une communauté très dense et peu diversifée, contrairement aux zones fluviales où les abondances étaient faibles et la richesse spécifique beaucoup plus élevée. Nous avons pu faire la distinction entre deux zones à l'intérieur de la ZTE; la partie amont formait la zone de turbidité maximale, avec des concentrations élevées d'animaux épibenthiques tels que les harpacticoïdes, les amphipodes et les mysidacés, et la partie aval plus riche en animaux pélagiques comme les calanoïdes. Deux espèces – *Halicyclops fosteri* et *Echinogammarus ischnus* – ont été répertoriées pour la première fois dans la ZTE du fleuve Saint-Laurent au cours de cette étude. À l'intérieur des zones fluviales, la distribution du zooplancton était fortement liée aux masses d'eau et à leurs caractéristiques. Nous avons observé une augmentation de l'abondance du zooplancton dans les lacs fluviaux (lac Saint-Louis et lac Saint-Pierre) et les zones littorales le long de la rive sud du fleuve. Les macrophytes, même s'ils ne faisaient pas partie des variables explicatives, ont pu influencer la distribution du zooplancton notamment dans les lacs fluviaux à l'intérieur du tronçon fluvial, où ils sont associés aux masses d'eau du nord et du sud.

Au chapitre 3, nous avons trouvé que la distribution du zooplancton dans la section fluviale est davantage influencée par la structure spatiale des masses d'eau que par les facteurs environnementaux locaux à l'intérieur des zones fluviales. Contrairement à notre hypothèse, la structure spatiale des masses d'eau a expliqué davantage la distribution du zooplancton en août qu'en mai, alors que les facteurs environnementaux (non structurés au niveau spatial) ont expliqué une plus grande part de la variation du zooplancton en mai qu'en août. En effet, la distribution des crustacés en été semblait exclusivement régie par la structure spatiale des masses d'eau.

Nos résultats suggèrent qu'en mai, les débits plus élevés ont fait du fleuve Saint-Laurent un milieu plus dynamique qu'en août, empêchant l'établissement d'une forte structure spatiale laminaire. En août, la plus grande stabilité des masses d'eau due aux débits plus faibles du fleuve Saint-Laurent et de ses tributaires a permis de renforcer la structuration spatiale du zooplancton, probablement parce que les échanges entre les masses d'eau étaient plus prévisibles et conformes aux modèles d'écoulement directionnel. De plus, la perte des stations aux deux extrémités des transects du LSP a probablement fait augmenter l'homogénéité dans la distribution spatiale du zooplancton, rendant celle-ci encore plus prévisible et adaptée au modèle d'écoulement des masses d'eau. Les variables qui variaient le plus entre les sites au mois d'août étaient pour la plupart des variables reliées plus directement au phytoplancton qu'au zooplancton (phosphore total, chlorophylle *a*, coefficient d'extinction de la lumière photosynthétique active). Or il est démontré que la biomasse du phytoplancton affecte beaucoup moins le zooplancton dans les rivières que dans les lacs (Köhler 1994; Basu et Pick 1996, 1997). Enfin, comme la distribution du zooplancton dans le fleuve Saint-Laurent est régie en grande partie par l'advection, les conditions environnementales locales n'ont pas pu l'influencer de façon importante, puisque la plupart du zooplancton échantillonné provenait d'habitats en amont.

En conclusion, nous avons démontré que la distribution spatiale du zooplancton dans le fleuve est liée à celle des masses d'eau. La discontinuité longitudinale des masses d'eau dans la zone de transition estuarienne détermine la structure spatiale du zooplancton à grande échelle, tandis que les discontinuités transversales des masses d'eau ainsi que leurs caractéristiques influencent la distribution du zooplancton dans les zones fluviales. L'hydropériode influence également les patrons de distribution du zooplancton et ses processus générateurs. Le zooplancton est davantage influencé par la distribution des masses d'eau que par les variables environnementales dont on a retiré la composante spatiale. Les modèles d'écoulement et la méthode des vecteurs propres asymétriques (AEM) ont fourni une bonne explication de la variation des communautés zooplanctoniques. En effet, dans cette étude, ils ont expliqué la majeure partie de la variation du zooplancton comparativement aux variables environnementales non structurées au niveau spatial. L'utilisation de cette méthode en complément avec d'autres variables (physiques, chimiques ou biologiques) est un atout majeur dans l'étude d'écosystèmes influencés par des processus directionnels. Ceci permet d'établir les effets relatifs de la structure spatiale d'un environnement et des variables environnementales locales.

Il aurait été intéressant dans cette étude de disposer de données sur la vitesse du courant, puisque le courant détermine en grande partie la connectivité des sites au sein d'une même masse d'eau. Nous aurions alors pu combiner la distribution des masses d'eau à la distribution des vitesses de courant dans le fleuve Saint-Laurent, ce qui aurait probablement mené à une meilleure explication de la distribution du zooplancton. De même, des données biotiques telles que la densité des macrophytes et l'abondance moyenne de larves de poissons ou de poissons adultes planctivores aurait pu fournir une explication supplémentaire dans les modèles.

Plus les modèles théoriques performent à expliquer les données d'espèces, plus notre compréhension des écosystèmes en est améliorée. Nous sommes alors mieux à même de prévoir les changements dans les communautés d'organismes en nous basant sur les variations dans la structure spatiale de leur environnement. Cette étude nous a permis d'évaluer les effets de l'hydrologie et de la dynamique des masses d'eau sur les communautés zooplanctoniques. Dans le contexte actuel des changements climatiques, des effets sur le régime hydrologique du Saint-Laurent sont à envisager. En étudiant les effets des masses d'eau sur le zooplancton, nous pouvons mieux comprendre cet écosystème et éventuellement mieux encadrer les politiques de conservation du fleuve Saint-Laurent. La description de la structure des communautés zooplanctoniques permettra dans le futur de témoigner de la diversité et de l'abondance du zooplancton avant plusieurs années de réchauffement climatique. On pourra alors en évaluer les impacts dans le futur.

Le zooplancton est une composante essentielle des milieux aquatiques, assurant le transfert de l’énergie et du carbone des producteurs primaires aux niveaux trophiques supérieurs tels que les poissons planctivores et piscivores, qui dépendent du zooplancton à au moins un stade de leur croissance. Notre étude est une des premières qui englobent le fleuve Saint-Laurent sur tout le continuum fleuve-estuaire, fournissant des données environnementales et zooplanctoniques sur les axes longitudinal et transversal. La présente étude et celle de Massicotte et Frenette (2011) sont les premières à avoir utilisé la méthode des vecteurs propres asymétriques dans une portion aussi importante du fleuve Saint-Laurent.

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Annexe A

Cette annexe comprend 9 tableaux. Les tableaux Ia à Va expliquent le cheminement de la création des fonctions AEM au chapitre 3. Les tableaux VIa et VIIa montrent les abondances des différents groupes de zooplancton, tandis que les tableaux VIIIa et IXa fournissent les données environnementales, à chaque station d'échantillonnage en mai et août 2006.

Table Ia Water masses mixture present at sampling sites (10-35) on the days of sampling (May 25-26, August 10-11 2006). The water mass column shows the proportion of each water mass present at the sites: Great Lakes (GL), south shore channel (SSC), Ottawa River (OTT), the Mille Îles and des Prairies Rivers (MIP), Richelieu River (RICH), Maskinongé River (MASK) and Québec City waters (QC). FC = Fluvial corridor, LSP = Lake Saint-Pierre.

				May	August
Section	Site	Latitude	Longitude	Water Mass (%)	Water Mass (%)
FC	10	45.5326	-73.5282	45 GL / 55 SSC	-
	11	45.5326	-73.5316	100 GL	84 GL / 16 SSC
	12	45.5328	-73.5371	100 GL	100 GL
	13	45.73298	-73.41667	100 GL	2 MIP / 99 GL
	14	45.7354	-73.4225	100 GL	1 MIP / 99 GL
	15	45.73628	-73.43353	50 GL / 50 OTT	-
	16	45.7402	-73.4365	48 ASS / 52 OTT	-
	17	45.9334	-73.213	100 GL	3 MIP / 98 GL
	18	45.9354	-73.2222	69 GL / 31 OTT	7 MIP / 93 GL
	19	45.9375	-73.2317	3 ASS / 97 OTT	75 MIP / 26 GL
LSP	20	46.0594	-73.077	60 GL / 40 RICH	75 GL / 25 RICH
	21	46.072	-73.0824	58 GL / 42 OTT	67 GL / 33 RICH
	23	46.1625	-72.8634	52 GL / 48 RICH	43 RICH / 57 GL
	24	46.1783	-72.8776	100 GL	26 RICH / 74 GL
	25	46.192	-72.8909	100 GL	6 MIP / 94 GL
	26	46.2012	-72.9015	51 GL / 49 OTT	39 MIP / 62 GL
	27	46.2058	-72.9076	36 GL / 64 OTT	52 MIP / 49 GL
	28	46.2139	-72.9149	96 OTT / 4 MASK	-
	29	46.2228	-72.7154	44 GL / 56 RICH	-
	30	46.2342	-72.733	100 GL	42 RICH / 58 GL
	31	46.2389	-72.7396	100 GL	30 RICH / 70 GL
	32	46.2441	-72.7472	100 GL	23 RICH / 77 GL
	33	46.2524	-72.7552	59 GL / 41 OTT	27 MIP / 74 GL
	34	46.2581	-72.7625	32 GL / 68 OTT	52 MIP / 48 GL
	35	46.265	-72.7697	85 OTT / 15 MASK	-

Table IIa Site-by-edge matrix for May

Edges

Sites	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	…	68
1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	…	0
2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	…	0
3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	…	0
5	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	…	0
7	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	…	0
8	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	…	0
10	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	…	0
11	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	…	0
12	1	1	1	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	…	0
13	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	…	0
14	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0	…	0
15	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	1	1	1	0	0	…	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	…	0
17	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	…	0
18	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	…	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	…	0
20	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	…	0
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	…	⋮
44	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	…	1

Table IIIa Site-by-edge matrix for August

Sites	Edges 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	…	58
1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	…	0
2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	…	0
3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	…	0
4	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	…	0
5	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	…	0
6	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	…	0
7	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	…	0
8	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	…	0
11	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	…	0
12	1	1	1	1	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	…	0
13	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	…	0
14	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0	…	0
17	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	…	0
18	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	1	…	0
19	1	1	1	1	1	1	0	1	1	1	0	0	1	0	0	0	1	0	0	0	…	0
20	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	…	0
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	…	⋮
44	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	…	1

Table IVa Weight vector for May

Edges

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	…	68
100	100	100	100	33.3	100	33.3	33.3	100	50	50	100	100	50	50	25	25	50	52	48	…	100

Table Va Weight vector for August

Edges

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	…	58
100	100	100	100	100	100	100	33.3	33.3	33.3	50	50	100	100	50	50	26	50	50	93	…	100

Tableau VIa Abondances (ind/m^3) de 6 groupes de zooplancton dans les eaux de surface aux stations échantillonnées en mai 2006.

Stations	Amphipodes	Calanoïdes	Cladocères	Cyclopoïdes	Harpacticoïdes	Mysidacés
1	0.4	10.6	56.4	130.5	0.0	0.0
2	0.0	22.0	165.2	534.3	22.0	0.0
3	1.9	12.0	46.0	224.1	22.0	0.0
5	0.0	12.6	59.8	206.1	1.6	0.0
7	0.7	3.0	29.7	374.9	7.4	0.0
8	0.1	15.5	21.7	285.2	0.0	0.0
9	0.4	49.1	233.2	386.6	0.0	0.0
10	0.5	15.3	160.2	202.1	11.4	0.0
11	0.6	0.8	6.6	72.2	1.6	0.0
12	1.0	8.2	8.2	99.1	0.0	0.0
13	0.6	2.8	7.5	83.7	3.8	0.0
14	1.2	4.6	5.9	61.0	0.7	0.0
15	0.2	1.2	5.6	32.1	2.4	0.0
16	0.1	5.7	11.5	81.2	2.9	0.0
17	0.3	3.8	42.4	108.9	5.7	0.0
18	0.0	11.2	10.0	69.2	25.7	0.0
19	0.2	1.3	22.9	85.4	2.7	0.0
20	0.2	2.5	138.9	382.0	14.9	0.0
21	0.0	12.2	21.4	114.5	9.2	0.0
22	0.2	6.6	251.3	628.3	0.0	0.0
23	0.0	0.0	319.0	889.4	29.0	0.0
24	0.1	6.5	81.2	298.9	9.7	0.0
25	0.3	2.9	14.6	72.1	3.9	0.0
26	0.5	4.5	15.7	86.4	11.2	0.0
27	0.3	3.9	30.9	86.1	0.0	0.0
28	1.3	13.1	31.5	77.2	1.1	0.0
29	1.2	1.1	355.2	1157.5	52.6	0.0
30	2.4	11.2	184.3	508.2	0.0	0.0
31	0.7	0.0	90.0	222.3	2.6	0.0
32	0.1	4.7	42.4	174.3	14.1	0.0
33	2.1	7.2	21.7	53.7	11.4	0.0
34	0.0	0.0	126.6	290.5	7.4	0.0
35	8.5	14.6	87.6	219.0	0.0	0.0
36	1.1	23.9	161.5	633.9	6.0	0.0
37	2.7	14.2	31.3	113.9	10.0	0.0
38	0.3	15.8	30.3	75.0	0.0	0.0
39	0.9	3.0	142.2	531.8	6.2	0.0
40	2.7	32.0	112.0	671.7	16.0	0.0
41	0.0	11.0	37.4	195.8	8.8	0.0
42	2.0	8.0	35.9	346.8	4.0	0.0
43	2.4	44.9	99.9	409.5	5.0	0.0
44	3.4	9.1	57.4	268.7	9.1	0.0
45	0.8	9.1	14.7	94.1	4.5	0.0
46	2.4	16.3	23.3	245.1	114.4	0.0
47	7.2	56.3	96.5	385.9	337.6	0.0
48	1.0	110.1	13.8	96.3	1156.1	0.0
49	0.4	369.1	0.0	218.6	1578.5	1.6
50	0.0	256.0	0.0	23.7	23.7	0.0
51	0.0	4096.0	0.0	0.0	0.0	0.0
52	0.0	1698.8	0.0	61.8	20.6	0.0

Tableau VIIa Abondances (ind/m^3) de 6 groupes de zooplancton dans les eaux de surface aux stations échantillonnées en août 2006.

Stations	Amphipodes	Calanoïdes	Cladocères	Cyclopoïdes	Harpacticoïdes	Mysidacés
1	0.2	42.0	94.9	37.3	0.0	0.0
2	0.0	27.3	104.6	45.5	0.0	0.0
3	0.2	11.4	146.2	60.1	0.0	0.0
4	0.0	37.8	34.3	19.7	0.0	0.0
5	0.0	66.7	104.6	41.5	0.0	0.0
6	0.0	115.8	77.9	29.5	0.0	0.0
7	0.3	279.6	180.4	85.7	0.0	0.0
8	0.6	56.6	105.1	46.5	10.1	0.0
9	6.2	247.0	1778.6	296.4	98.8	0.0
11	0.2	72.0	37.7	18.8	7.8	0.0
12	0.9	30.5	11.8	5.6	19.4	0.0
13	0.2	36.9	11.8	13.3	11.1	0.0
14	0.2	15.5	9.7	3.5	13.7	0.0
17	0.0	100.9	110.7	29.5	0.0	0.0
18	0.1	12.0	27.2	14.4	24.0	0.0
19	0.0	2.5	9.2	11.7	3.9	0.0
20	0.0	100.7	108.3	45.3	2.5	0.0
21	0.0	8.2	21.7	14.0	4.8	0.0
22	1.7	0.0	669.8	810.8	246.8	0.0
23	0.0	29.2	151.1	46.3	9.7	0.0
24	17.8	1152.0	483.1	223.0	0.0	0.0
25	0.1	15.8	9.8	10.9	2.8	0.0
26	0.0	1.4	40.3	20.5	5.5	0.0
27	0.0	15.3	104.9	125.3	20.5	0.0
30	0.0	48.5	61.6	37.3	11.2	0.0
31	0.0	84.9	84.9	16.6	33.1	0.0
32	0.0	41.1	14.8	19.7	4.9	0.0
33	0.0	20.7	35.2	22.6	11.7	0.0
34	0.0	5.1	26.8	19.1	12.8	0.0
36	0.0	249.9	194.3	18.5	9.3	0.0
37	0.6	29.5	19.2	19.9	11.0	0.0
38	0.1	11.6	13.0	10.2	3.2	0.0
39	0.2	464.6	85.4	32.0	42.7	0.0
40	0.2	98.3	36.1	26.2	9.8	0.0
41	0.0	55.0	37.0	15.9	4.2	0.0
42	0.1	410.1	52.9	13.2	0.0	0.1
43	0.5	137.3	10.4	19.1	1.7	0.0
44	1.0	138.1	12.4	7.1	3.5	0.0
45	0.3	285.4	144.6	304.4	3.8	0.0
46	0.9	48.9	0.0	896.0	0.0	0.0
47	46.3	592.8	186.3	711.3	220.2	0.0
48	0.3	8684.8	0.0	1005.1	257.7	59.4
49	0.0	325.7	0.0	193.9	232.6	14.9
50	0.0	969.8	0.0	19.4	0.0	0.0
51	0.0	1942.3	0.0	0.0	0.0	0.0
52	0.0	214.2	0.0	0.0	1.9	0.0

Tableau VIIIa Données environnementales dans les eaux de surface aux stations échantillonnées en mai 2006. Lat = Latitude, Lon = Longitude, aMODC = Absorbance de la matière organique dissoute chromophorique, Chl*a* = Chlorophylle *a*, COD = Carbone organique dissous, Cond = Conductivité, NT = Azote total, OD = Oxygène dissous, PT = Phosphore total, K_dRPA = Coefficient d'extinction du rayonnement photosynthétique actif, Sal = Salinité, STD = Solides totaux dissous, Tem = Température et Turb = Turbidité. Les données d'oxygène dissous (OD), de pH et de turbidité (Turb) aux stations 49 à 52 sont manquantes dû au bris de l'appareil CTD.

Stations	Lat décimales	Lon décimales	aMODC m^{-1}	Chl*a* µg/L	COD mg/L	Cond uS/cm	NT mg/L	OD mg/L	pH	PT µg/L	K_dRPA m^{-1}	Sal psu	STD mg/L	Tem °C	Turb NTU
1	45.1115	-74.446	1.909	1.426	2.585	220	3.007	10.369	8.030	10.800	0.547	0	116	11.766	0.000
2	45.1186	-74.4612	1.992	1.946	2.638	219	3.627	10.426	8.042	10.886	0.469	0	116	11.635	0.000
3	45.128	-74.4784	1.635	1.637	2.504	223	2.991	10.183	7.948	10.943	0.584	0	116	11.558	0.956
5	45.2273	-74.2145	1.902	1.693	2.428	215	3.540	10.558	8.026	8.449	0.584	0	116	12.061	0.146
7	45.3974	-73.7892	4.636	1.908	3.242	226	2.877	10.745	8.122	16.131	0.988	0	111	11.852	2.356
8	45.4099	-73.8103	3.715	1.792	4.805	163.15	3.791	10.827	8.092	26.512	1.075	0	80	12.724	1.433
9	45.4241	-73.8203	16.552	1.653	6.368	100.3	4.540	9.954	7.818	36.894	2.330	0	49	14.173	8.117
10	45.5326	-73.5282	7.833	3.239	4.149	232	4.001	9.775	7.812	83.686	2.802	0	119	12.333	14.826
11	45.5326	-73.5316	4.855	3.730	3.413	211	3.198	10.351	8.056	19.425	0.958	0	113	11.984	2.518
12	45.5328	-73.5371	3.811	3.451	3.413	211	3.198	10.494	7.991	17.545	1.015	0	113	11.887	2.768
13	45.733	-73.4167	4.217	3.598	3.309	205	2.829	10.540	8.006	14.020	1.031	0	108	12.154	3.247
14	45.7354	-73.4225	5.645	2.665	3.660	197.8	4.436	10.365	8.044	15.008	1.343	0	104	12.400	3.883
15	45.7354	-73.4225	5.645	2.633	6.030	129	3.595	10.319	7.871	36.026	2.047	0	64	13.405	18.721
16	45.7402	-73.4365	16.397	3.683	6.030	129	3.458	9.763	7.512	54.873	2.508	0	64	13.796	13.055
17	45.9334	-73.213	4.424	3.560	3.798	225	3.844	10.675	8.093	25.854	1.239	0	105	12.561	3.625
18	45.9354	-73.2222	6.061	3.314	3.798	225	3.173	10.322	8.003	26.633	1.449	0	105	12.967	17.200
19	45.9375	-73.2317	16.395	3.023	7.701	125.8	3.202	10.220	7.807	44.074	2.722	0	61	13.628	11.847
20	46.0594	-73.077	5.490	4.265	4.602	178.8	3.788	10.497	7.917	56.572	1.925	0	89	12.678	7.933
21	46.072	-73.0824	9.327	3.092	4.602	178.8	2.627	10.151	7.901	40.929	1.735	0	89	13.057	8.089
22	46.1472	-72.846	24.177	3.506	8.042	99	3.555	10.095	7.665	34.033	2.477	0	50	11.946	3.617
23	46.1625	-72.8634	5.398	3.198	3.874	210	3.198	10.339	7.987	50.200	1.651	0	104	12.685	6.774
24	46.1783	-72.8776	4.638	3.542	3.352	217	2.535	10.474	8.090	36.002	2.272	0	109	12.684	5.243
25	46.192	-72.8909	6.382	3.336	4.562	209	4.126	10.366	8.067	27.399	1.457	0	101	12.922	4.275
26	46.2012	-72.9015	9.726	3.212	5.045	185.75	3.152	9.943	7.775	47.765	2.388	0	87.5	13.229	9.377
27	46.2058	-72.9076	12.289	3.491	5.528	162.5	3.179	9.800	7.680	48.171	2.614	0	74	13.668	12.984
28	46.2139	-72.9149	15.246	2.969	6.025	117.4	3.592	9.552	7.597	57.005	3.235	0	56	13.143	15.325
29	46.2228	-72.7154	9.640	3.499	4.744	194.3	4.549	9.922	7.648	64.726	2.348	0	94	13.021	11.921
30	46.2342	-72.733	4.797	3.263	3.408	218	3.852	10.396	7.927	39.302	1.992	0	108	13.109	5.028

31	46.2389	-72.7396	4.746	3.078	4.379	226	2.215	10.380	7.969	41.420	1.377	0	107	12.695	4.768
32	46.2441	-72.7472	5.873	3.464	4.416	222	2.536	10.624	8.052	32.653	1.510	0	102	12.920	5.332
33	46.2524	-72.7552	10.976	2.824	4.068	222	3.484	9.821	7.746	34.867	2.254	0	106	13.288	8.167
34	46.2581	-72.7625	14.914	3.443	4.068	222	3.125	9.781	7.593	58.858	2.826	0	106	13.531	11.013
35	46.265	-72.7697	16.372	3.054	9.584	134.8	4.115	9.563	7.623	72.628	3.308	0	60	13.868	14.900
36	46.3581	-72.4882	13.751	4.936	7.436	165	2.312	10.060	7.920	72.575	2.017	0	83	13.336	8.400
37	46.3612	-72.4976	8.867	3.433	4.542	184	2.257	10.119	7.808	35.225	1.897	0	91	13.430	8.086
38	46.3625	-72.5002	21.017	2.897	9.551	23.5	1.070	10.113	7.629	20.369	2.357	0	12	13.111	6.621
39	46.6346	-71.7283	12.789	4.217	5.661	192.4	1.792	9.921	7.803	71.539	2.408	0	91	13.840	12.250
40	46.6393	-71.7283	9.760	3.563	6.399	182.1	4.211	10.216	7.837	50.162	2.067	0	88	13.202	9.948
41	46.6579	-71.7283	12.224	2.819	4.559	151.1	3.126	10.134	7.800	52.804	2.502	0	72	13.740	10.316
42	46.7476	-71.2677	10.253	3.335	5.901	175.8	3.293	10.035	7.891	55.792	2.448	0	88	13.285	11.321
43	46.7507	-71.271	10.511	3.178	4.114	177.7	3.309	9.644	7.636	37.753	2.448	0	87	13.285	10.671
44	46.753	-71.2737	10.525	2.987	4.688	171.1	1.418	9.716	7.635	67.098	2.420	0	86	13.197	11.346
45	46.9046	-70.8917	11.531	2.818	4.591	181.7	2.599	9.865	7.685	53.793	2.714	0	88	12.829	14.225
46	46.9673	-70.7226	11.324	3.309	4.586	192	1.733	10.000	7.785	57.251	3.241	0	88	12.857	21.350
47	47.0295	-70.6919	10.486	22.303	4.511	191	1.739	10.310	7.807	224.337	6.016	0	89	13.302	58.184
48	47.0584	-70.7598	9.016	9.003	4.281	176.7	2.197	9.891	7.801	303.979	10.177	0	87	13.235	101.244
49	47.1815	-70.3705	7.365	5.358	4.028	3310	1.904	-	-	370.413	5.440	2.1	1705	12.713	-
50	47.3166	-70.2728	5.027	1.761	3.973	16460	0.996	-	-	116.930	4.378	9.1	1705	8.422	-
51	47.4614	-70.2484	4.740	0.935	3.025	18710	3.219	-	-	43.252	1.521	15.4	1705	7.656	-
52	47.321	-70.5137	6.686	1.374	3.598	8630	3.297	-	-	110.285	3.681	6.5	1705	11.281	-

Tableau IXa Données environnementales dans les eaux de surface aux stations échantillonnées en août 2006. Lat = Latitude, Lon = Longitude, aMODC = Absorbance de la matière organique dissoute chromophorique, Chl*a* = Chlorophylle *a*, COD = Carbone organique dissous, Cond = Conductivité, NT = Azote total, PT = Phosphore total, K_dRPA = Coefficient d'extinction du rayonnement photosynthétique actif, Sal = Salinité, STD = Solides totaux dissous, Tem = Température et Turb = Turbidité. Les données d'oxygène dissous sont manquantes au mois d'août dû au bris de l'appareil CTD.

Stations	Lat décimales	Lon décimales	aMODC m^{-1}	Chl µg/L	COD mg/L	Cond µS/cm	NT mg/L	pH	PT µg/L	K_dRPA m^{-1}	Sal psu	STD mg/L	Tem °C	Turb NTU
1	45.1115	-74.446	0.882	1.591	2.289	284	3.843	7.34	4.548	0.562	0	118	24.167	0
2	45.1186	-74.4612	0.843	1.674	2.135	287	2.870	8.18	5.204	0.385	0	118	24.299	0
3	45.128	-74.4784	1.082	3.952	2.279	284	3.394	7.87	5.411	0.671	0	118	23.668	0
4	45.20192	-74.17055	3.284	1.208	3.102	271	1.504	8.43	7.999	0.504	0	111	24.000	0
5	45.2273	-74.2145	1.792	2.075	2.282	287	0.620	7.42	9.990	0.429	0	116	24.591	0
6	45.24218	-74.2356	2.777	2.520	2.595	298	2.797	8.45	9.830	0.672	0	119	24.249	0
7	45.3974	-73.7892	1.829	0.871	2.963	286	3.370	8.4	19.214	0.959	0	116	24.414	0
8	45.4099	-73.8103	2.236	0.871	2.686	283	1.483	8.37	8.878	1.126	0	114	23.375	0.738
9	45.4241	-73.8203	15.826	2.898	7.447	91	3.406	7.17	17.989	2.250	0	36	23.519	8.467
11	45.5326	-73.5316	1.974	2.457	2.408	278	2.600	8.43	11.202	0.721	0	117	23.796	1.592
12	45.5328	-73.5371	2.455	2.095	2.408	273	2.911	8.37	11.762	0.801	0	114	24.096	1.640
13	45.73298	-73.41667	1.987	2.180	2.581	275	1.838	8.31	8.207	1.221	0	115	23.460	0
14	45.7354	-73.4225	2.800	2.045	3.120	266	3.465	8.09	14.206	1.097	0	111	23.442	3.876
17	45.9334	-73.213	2.952	1.703	2.446	275	0.487	8.36	10.869	1.221	0	114	23.460	0
18	45.9354	-73.2222	3.975	1.109	3.029	253	2.915	8.06	18.402	1.473	0	108	23.088	5.065
19	45.9375	-73.2317	9.606	1.883	4.584	178	3.890	7.63	13.758	1.980	0	76	23.404	5.711
20	46.0594	-73.077	3.153	4.091	4.628	238	1.842	8.11	16.876	1.528	0	100	23.273	0
21	46.072	-73.0824	7.547	1.451	3.957	211	3.020	7.49	22.721	1.533	0	88	23.445	0
22	46.1472	-72.846	31.429	4.231	10.482	125	3.160	7.58	44.669	3.210	0	55	20.291	12.671
23	46.1625	-72.8634	5.578	7.009	3.685	233	3.357	8.28	17.982	4.894	0	98	22.815	98.241
24	46.1783	-72.8776	2.632	2.984	2.594	264	5.190	8.28	14.501	1.970	0	110	23.116	10.269
25	46.192	-72.8909	3.381	1.509	2.828	261	1.817	8.06	17.417	1.669	0	109	23.597	6.233
26	46.2012	-72.9015	8.758	2.273	4.464	190	2.189	7.91	40.906	1.707	0	80	22.976	6.176
27	46.2058	-72.9076	11.918	4.936	5.583	154	3.239	7.76	12.514	2.741	0	64	23.400	20.663
30	46.2342	-72.733	6.863	6.689	4.494	228	3.846	8.08	13.504	2.833	0	98	22.119	14.529
31	46.2389	-72.7396	3.238	4.837	2.820	250	2.440	8.05	13.593	1.625	0	106	22.501	6.310
32	46.2441	-72.7472	3.001	1.651	3.971	264	2.984	8.08	15.925	1.427	0	109	23.661	7.352
33	46.2524	-72.7552	5.808	2.059	3.983	220	3.098	7.81	16.501	2.016	0	93	23.246	9.793

34	46.2581	-72.7625	9.783	3.390	4.791	177	0.970	7.88	19.441	1.973	0	74	23.106	5.760
36	46.3581	-72.4882	4.051	2.158	3.310	248	2.960	8	16.300	1.874	0	106	22.063	5.650
37	46.3612	-72.4976	4.887	2.064	3.396	236	1.523	7.76	12.208	1.727	0	100	22.488	8.122
38	46.3625	-72.5002	24.080	1.845	7.412	37	3.215	6.4	15.531	2.134	0	16	21.120	2.542
39	46.6346	-71.7283	5.700	2.752	3.547	236	3.699	7.81	19.321	1.683	0	100	22.574	5.308
40	46.6393	-71.7283	5.226	2.128	3.571	232	1.852	7.64	23.923	1.700	0	98	22.722	9.725
41	46.6579	-71.7283	7.176	2.978	4.094	205	2.891	7.48	18.634	1.783	0	87	22.603	7.407
42	46.7476	-71.2677	6.174	2.763	3.800	226	3.065	7.86	28.458	1.720	0	95	22.995	8.067
43	46.7507	-71.271	6.382	2.554	5.305	224	2.161	7.98	16.190	2.160	0	94	22.857	12.452
44	46.753	-71.2737	7.796	3.956	4.229	200	1.968	7.83	22.398	1.794	0	84	22.795	8.478
45	46.9046	-70.8917	6.428	5.985	4.543	220	2.981	7.75	24.821	2.596	0	93	23.163	9.721
46	46.9673	-70.7226	6.748	9.894	3.780	222	3.477	7.57	105.921	2.685	0	93	23.178	29.863
47	47.0295	-70.6919	6.614	54.822	3.741	224	1.176	8.03	64.888	7.326	0	94	23.195	89.873
48	47.0584	-70.7598	5.635	3.053	3.794	2720	3.640	7.54	43.909	4.163	1.4	1164	21.830	34.138
49	47.1815	-70.3705	4.993	4.902	3.279	5790	1.710	7.89	29.351	4.295	3.5	1164	20.296	40.800
50	47.3166	-70.2728	2.386	1.238	2.963	23700	1.544	7.71	17.529	1.815	18.9	1164	12.158	9.767
51	47.4614	-70.2484	2.994	0.623	1.955	22900	3.304	7.66	18.615	0.913	18	1164	13.269	1.800
52	47.321	-70.5137	4.109	1.015	5.438	13560	3.472	7.76	31.262	1.620	9.2	1164	17.560	6.470