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Influence des liens sédimentaires sur la distribution du périphyton et des juvéniles de
saumon atlantique (*Salmo salar*) dans une rivière du Bouclier canadien

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Mémoire présenté à la Faculté des études supérieures en vue de l'obtention du grade de
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Université de Montréal
Faculté des études supérieures

Ce mémoire intitulé :
Influence des liens sédimentaires sur la distribution du périphyton et des juvéniles de
saumon atlantique (*Salmo salar*) dans une rivière du Bouclier canadien

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RÉSUMÉ

Le Concept de Discontinuité des Liens suggère que les zones ou points de recrutement de sédiments créent une série de liens sédimentaires pouvant structurer les composantes physiques et biologiques d'une rivière. Quoique certaines études supportent cette hypothèse, leur effet sur la distribution du périphyton et des poissons demeure inconnu. De plus, la stabilité temporelle du rôle potentiel joué par les liens sédimentaires n'a pas été vérifiée puisque les précédentes études utilisent des données récoltées durant une année.

L'objectif de cette étude était d'évaluer la relation entre la biomasse de périphyton, les densités de tacons de saumon atlantique et la structure d'une série de liens sédimentaires dans une rivière du Bouclier canadien durant trois périodes estivales (2003, 2004 et 2005). La biomasse de périphyton a été estimée avec une approche tactile et les densités de tacons ont été estimées en apnée.

Nos résultats suggèrent que la biomasse de périphyton n'est pas affectée par les liens sédimentaires. Par contre, ceux-ci semblent structurer la distribution spatiale des tacons et la variabilité inter annuelle de ce rôle est généralement expliquée par la nature et le type de lien sédimentaire ainsi que le débit annuel de la rivière.

Key words: Concept de Discontinuité des Liens, liens sédimentaires, Bouclier canadien, rivière, distribution spatiale, variabilité inter annuelle, périphyton, poissons, tacons, saumon atlantique

ABSTRACT

The Link Discontinuity Concept suggests that sediment recruitment zones or points create a series of sedimentary links that may determine the structure of physical and biological components. Although few studies support the role of sedimentary links on biological components of rivers, their effects on the distribution of periphyton and fish remains to be documented. In addition, the temporal stability of that role has not been tested because previous studies used data collected during a single year.

The purpose of our study was to assess the relationship between the biomass of periphyton, the density of Atlantic salmon parr, and the structure of a series of sedimentary links of a Canadian Shield river during 2003, 2004, and 2005. Periphyton biomass was estimated using a tactile approach. Parr density was estimated by underwater observations.

Our results suggest that the biomass of periphyton is not affected by sedimentary links. However, sedimentary links played a role in the distribution of Atlantic salmon parr. The inter annual variability of that role is generally consistent and derivation from it can be explained by the nature and type of sedimentary links, and the annual flow regime of the river.

Key words: Link Discontinuity Concept, sedimentary links, Canadian Shield, river, spatial distribution, inter annual variability, periphyton, fish, Atlantic salmon parr

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LISTE DES ABRÉVIATIONS

%	Pourcentage / Pourcentage
665v	Absorbance at 665 nm / Absorbance à 665 nm
750v	Absorbance at 750 nm / Absorbance à 750 nm
A	Length of the longest axis of a rock / Longueur du plus long axe d'une roche
ANOVA	Analysis of variance / Analyse de variance
B	Length of the median axis of a rock / Longueur de l'axe médian d'une roche
C	Length of the shortest axis of a rock / Longueur du plus court axe d'une roche
cm	Centimeter / Centimètre
Chl <i>a</i>	Microalgal chlorophyll <i>a</i> / Chlorophylle <i>a</i> microalgal
CL	Cell length used for spectrophotometer reading / Longueur de cellule utilisée pour la lecture spectrophotométrique
D50	Mean substrate size / Taille moyenne du substrat
DFRM	Distance From River Mouth / Distance à l'embouchure
E.P.A.	Environmental Protection Agency / Agence de protection environnementale
F-value	Computed Fisher statistical value / Valeur statistique calculée de Fisher
FPC	Flood Pulse Concept / Concept de pulsation des crues
FRM	From River Mouth / À l'embouchure
GIS	Geographic Information System / Système d'information géographique

LDC	Link Discontinuity Concept / Concept de discontinuité des liens
m	Meter / Mètre
mg	Milligram / Milligramme
p	Probability / Probabilité
PB	Periphyton biomass / Biomasse de périphyton
p_{perm}	Permutational probability / Probabilité permutatonnelle
r	Pearson linear correlation r / r de la corrélation linéaire de Pearson
R^2_{adj}	Adjusted R square / R carré ajusté
RBP	Rapid Bioassessment Protocol / Protocole de bioévaluation rapide
RCC	River Continuum Concept / Concept de continuité en rivière
RPSL	Relative Position in Sedimentary Link / Position relative dans un lien sédimentaire
s	Second / Seconde
S	Surface area of rock estimated / Aire de surface estimé d'une roche
SDC	Serial Discontinuity Concept / Concept de discontinuité sérielle
SMR	Sainte-Marguerite River / Rivière Sainte-Marguerite
U.S.	United States / États-Unis
UK	Underwater Kinetics™
μ S	Micro Siemens / micro Siemens
VE	Volume of ethanol used for extraction / Volume d'éthanol utilisé pour l'extraction
VF	Filtered volume of detached algae / Volume filtré de périphyton
VT	Total volume of detached algae / Volume total de périphyton

« In everyone's life, at some time, our inner fire goes out.
It is then burst into flame by an encounter with another human being.
We should all be thankful for those people who rekindle the inner spirit. »

Albert Schweitzer

1952 Nobel Peace Prize

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À mes parents,
pour leur amour, leur soutien et leurs encouragements,
sans qui je ne serais pas devenue celle que je suis aujourd'hui...

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INTRODUCTION GÉNÉRALE

Plusieurs modèles conceptuels ont été proposés pour expliquer la structure des composantes physiques, chimiques et biologiques des rivières. Suivant l'axe longitudinal (i.e. amont-aval) d'une rivière, le concept de continuité en rivière (River Continuum Concept - RCC; Vannote et al. 1980) met l'emphase sur le continuum d'ajustements physique (e.g. largeur, profondeur, vitesse d'écoulement, température, luminosité, etc.), chimique (e.g. matière organique, oxygène, etc.) et trophique (e.g. importance relative des communautés de producteurs et consommateurs). Selon le RCC, l'importance de la végétation riveraine dans cette partie de la rivière assure l'entrée allochtone (i.e. provenant de l'extérieur de la rivière : feuilles mortes, débris ligneux) de matière organique nécessaire afin de subvenir aux besoins énergétiques des organismes d'une part, mais l'ombrage créé par le couvert végétal limite la production autochtone (i.e. provenant de l'intérieur de la rivière : photosynthèse) d'autre part. Ensuite, à mesure que la rivière s'élargit et que l'ombrage diminue, la synthèse autochtone de matière organique par la photosynthèse des algues et des plantes aquatiques augmente graduellement (Naiman et al. 1987; Minshall et al. 1983; Thorp et al. 1998). Quant à elle, la matière organique particulaire fine, issue de la décomposition de la matière organique particulaire grossière (e.g. feuilles mortes, débris ligneux) par les bactéries et les invertébrés, est transportée par le courant vers l'aval de la rivière où l'ombrage causé par la végétation riveraine devient négligeable. Par contre, la production autochtone peut éventuellement être limitée par la profondeur et la turbidité de l'eau dans la partie aval.

Toujours selon le RCC, les changements longitudinaux dans les attributs physiques des rivières ainsi que dans l'origine et la forme de la matière organique sont accompagnés par un changement en dominance des différents groupes d'invertébrés (Vannote et al. 1980) : 1- les déchiqueteurs, qui utilisent la matière organique particulaire grossière de concert avec les communautés microbiennes; 2- les collecteurs, qui utilisent la matière organique particulaire fine filtrée dans la colonne d'eau ou amassée dans les sédiments; 3- les brouteurs, qui se nourrissent d'algues fixées au substrat (e.g. périphyton, épipelon, etc.); et 4- les prédateurs, qui se nourrissent parmi ces différents groupes. Ainsi, la partie amont de la rivière convient plus particulièrement aux déchiqueteurs, ensuite les brouteurs et, finalement, les collecteurs vers l'aval (Cushing et al. 1983; Minshall et al. 1985; Greathouse and Pringle 2006). Les prédictions du RCC concernant les poissons sont beaucoup moins détaillées que pour les algues et les invertébrés. Les communautés de poissons retrouvées en amont des rivières sont caractérisées par une faible productivité et une faible diversité. Elles sont majoritairement représentées par des espèces d'eaux froides, surtout insectivores. La productivité et la diversité, avec la prévalence d'espèces de poissons piscivores et d'eaux plus chaudes, augmentent vers l'aval (Walters et al. 2003; Goldstein and Meador 2004; Thomas and Hayes 2006).

La variabilité géomorphologique naturelle et les perturbations anthropiques dans les rivières sont reconnues depuis longtemps comme ayant le potentiel d'influencer les prédictions du RCC (Vannote et al.; Poole 2002). Par exemple, le concept de discontinuité sérielle (Serial Discontinuity Concept - SDC; Ward and Stanford 1983; Stanford 1988), habituellement appliqué aux rivières à débits contrôlés, est basé sur le

principe que les transitions abruptes entre les segments adjacents de rivière ayant une structure physique différente (i.e. d'un canyon à une plaine d'inondation, d'une rivière à un réservoir) peuvent influencer la progression longitudinale anticipée par le RCC. De façon similaire, le concept de pulsation des crues (Flood Pulse Concept - FPC; Junk et al. 1989; Tockner et al. 2000) met l'accent sur l'effet saisonnier des interactions latérales entre les rivières et leurs plaines d'inondation pour expliquer la structure et la dynamique des communautés. Quant à eux, les tributaires peuvent accélérer ou renverser la progression amont-aval des attributs biologiques prédite par le RCC puisque leur composition chimique (e.g. charge en nutriments, concentration et type de particules en suspension), physique (e.g. température, taille et forme du substrat, volume et débit d'eau) et biologique (e.g. patrons des communautés, niveaux trophiques) diffère de la rivière où ils se jettent (Bruns et al. 1984; Minshall et al. 1983; Minshall et al. 1985). Le concept de discontinuité des liens (Link Discontinuity Concept - LDC; Rice and Church 1998; Rice 1999; Rice et al. 2001) suggère que l'entrée de sédiments grossiers à partir des tributaires, ou tout autre source latérale de sédiments secs (e.g. glissement de terrain, dépôts glaciaires), crée une série de liens sédimentaires. Chaque lien est un segment de rivière, délimité en amont par une source de substrat grossier, le long duquel le transport fluvial sélectif donne naissance à un affinement classique vers l'aval (e.g. de blocs, à galets, au gravier, puis finalement parfois jusqu'au sable) et ce jusqu'à ce qu'une autre source de substrat grossier initie un nouveau lien. Le taux d'affinement à l'intérieur des liens est variable et dépend surtout des facteurs géomorphologiques qui caractérisent la dynamique de la portion de rivière en question. Ces changements locaux en composition du substrat (forme et taille) influencent la stabilité et la complexité du lit et, par conséquent, l'habileté des organismes de coloniser différents types d'habitats et de

trouver refuge, nourriture, partenaire, etc. (Rice et al. 2001; Rice et al. 2001). Ainsi, le LDC diffère surtout du RCC non seulement dans la manière de considérer l'effet des changements physiques sur les organismes dans le système, mais aussi par le fait que les processus considérés se situe à une échelle intermédiaire (10^0 - 10^2 Km contrairement à la rivière complète i.e. 10^2 - 10^4 Km).

À partir de leurs résultats, Rice et al. (2001) montrent que le nombre de groupes taxonomiques de macroinvertébrés décroît de l'amont vers l'aval de certains liens sédimentaires, bien que le patron ne soit pas clair pour tous les liens étudiés. Ces résultats suggèrent que le LDC pourrait expliquer les discontinuités dans le patron de distribution spatiale des macroinvertébrés. Par contre, l'étude portait uniquement sur l'effet des liens sédimentaires sur la diversité des communautés de macroinvertébrés dans les rivières alpines de l'Ouest canadien. Aussi, l'étude ne couvre qu'une seule année d'échantillonnage. Dans ce contexte, il est difficile d'évaluer l'utilité du LDC dans d'autres régions géographiques, le rôle structurant des liens sédimentaires sur les autres composantes biotiques de la rivière, ainsi que la stabilité temporelle de ce rôle.

Dans les régions non-alpines où les rivières sont formées par des processus glaciaires (Bouclier canadien; Bouclier baltique), le recrutement de substrat grossier est souvent non associé aux points d'entrée des tributaires, mais plutôt à la présence de vallées tels des canyons de roche-mère, des terrasses fluvio-glaciaires ou de larges éventails alluviaux datant de l'âge périglaciaire (Church et Ryder 1972). Davey et Lapointe (2007) ont proposé une extension au LDC dans l'objectif d'étendre son application à ce type de rivières, où les liens sédimentaires sont initiés par des sources non ponctuelles de substrat grossier. Ils ont démontré que le cadre théorique du LDC

pouvait non seulement fonctionner pour ce type de paysage, mais également que l'utilisation de son extension leur a permis de mieux modéliser et comprendre les processus physiques sous-jacents à la dynamique en rivière dans l'objectif d'identifier adéquatement les sites de fraie du saumon atlantique dans une rivière du bouclier canadien.

Le premier objectif de notre étude était d'évaluer l'applicabilité du LDC pour expliquer la distribution spatiale du périphyton et des poissons dans une rivière située dans le bouclier canadien. Nous voulons tester l'hypothèse que les tendances de l'amont vers l'aval en taille du substrat peuvent être les premiers prédicteurs de la distribution des organismes dont l'habitat est hautement lié aux caractéristiques locales du substrat. Nous nous attendons à ce que les biomasses de périphyton soient plus élevées dans la partie amont des liens sédimentaires. Plusieurs études ont montré que la biomasse de périphyton est corrélée positivement avec la taille du substrat puisque le substrat grossier offre une meilleure stabilité physique (protection contre les crues épisodiques : Tett et al. 1978; Ruhrmann 1990; Cattaneo et al. 1997) ainsi que des avantages trophiques (meilleure exposition au courant et aux nutriments : Hynes 1970; Uehlinger 1991). Nous nous attendons aussi à ce que l'abondance des poissons soit plus élevée dans la partie amont des liens sédimentaires à cause d'une production primaire anticipée plus élevée ainsi qu'une meilleure protection contre le courant grâce à la présence de blocs (Heggenes and Borgstrom 1991; Bouchard et Boisclair 2008). Le deuxième objectif était d'évaluer la variabilité inter annuelle du rôle des liens sédimentaires sur la distribution des poissons.

Afin d'atteindre ces objectifs, la biomasse de périphyton ainsi que les densités de poissons ont été échantillonnées à l'intérieur de quatre liens sédimentaires (L1, L4, L6 et L8) de la rivière Sainte-Marguerite, Saguenay, Québec. La biomasse de périphyton a été échantillonnée en 2005 dans les quatre liens sédimentaires et les densités de poissons en 2003, 2004 et 2005 à l'intérieur de deux (L6 et L8), trois (L1, L4 et L8) et quatre liens sédimentaires (L1, L4, L6 et L8) respectivement. Les sites échantillonnés (longueur de 200 m) ont été distribués de manière à rendre compte adéquatement de l'affinement du substrat dans l'axe amont-aval de chaque lien sédimentaire. Les biomasses de périphyton ont été estimées à l'aide d'une version modifiée de la méthode tactile présentée dans le protocole de bio évaluation rapide de l'agence de protection de l'environnement des Etats-Unis (U.S. E.P.A. Rapid Bioassessment Protocol; Barbour et al 1999). Les densités de poissons ont été estimées par deux plongeurs en apnée qui échantillonnaient à contre-courant deux transects orientés approximativement parallèle à la rive.

Notre étude s'est concentrée particulièrement sur le saumon atlantique comme espèce de poisson, plus spécifiquement les juvéniles âgés de I et II ans (i.e. tacons). Ce stade de vie est intéressant pour plusieurs raisons. Tout d'abord, nous pouvons les observer tout au long de la rivière étudiée. De plus, leur comportement territorial est reconnu (Saunders et Gee 1964; Heggenes et Borgstrom 1991). Ceci devrait faciliter l'établissement de relations entre les densités de tacons et leur environnement. Ensuite, un déclin des stocks mondiaux de saumon Atlantique depuis les trois dernières décennies suscite beaucoup d'attention (Parrish et al. 1998; Boisclair 2004). Les causes exactes de ce déclin restent indéfinies, mais la diminution de la qualité des habitats d'eau

douce pourrait jouer un rôle important (Dodson et al 1998) considérant que les juvéniles y naissent et s'y développent durant leurs stades précoces (Poff et Huryn 1998). De plus, étant donné qu'il est plus aisé d'étudier et d'intervenir dans ce type d'habitat plutôt que dans l'océan, il semble important de bien les connaître et les comprendre afin d'adopter des mesures de gestion et des stratégies de conservation efficaces. Dans ce contexte, toute information relative au rôle structurant des liens sédimentaires et à la stabilité temporelle de ce rôle sur la distribution spatiale des tacons s'avère pertinente.

Assessment of the structural role of sedimentary links on the spatial distribution of periphyton and fish in a Canadian Shield river.

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Introduction

Several conceptual models have been proposed to represent the changes of physical, chemical, and biological attributes along the upstream-downstream axis of rivers. The River Continuum Concept (RCC; Vannote et al. 1980) presumes relatively continuous changes of the physical attributes of unperturbed rivers (*e.g.* width, depth, flow velocity, temperature, and light) and focuses on the interactions between the origin and the transformation of matter and the structure of communities. According to the RCC, biological production in headwaters is largely determined by the input of coarse particulate organic matter from terrestrial origin. As river width increases and shading decreases downstream, the synthesis of organic matter inside rivers (photosynthesis by algae and plants) increases (Naiman et al. 1987; Minshall et al. 1983; Thorp et al. 1998). In addition, the decomposition of coarse organic particulate matter by bacteria and invertebrates results in the formation of gradually finer particulate organic matter that is flushed downstream. The longitudinal changes in the physical attributes of rivers and in the origin and the form of the organic matter are accompanied by changes in the dominance of invertebrates from shredders upstream, to scrapers, and to collectors downstream (Cushing et al. 1983; Minshall et al. 1985; Greathouse and Pringle 2006). The predictions of the RCC regarding fish are much less detailed than for algae and invertebrates. Headwaters are expected to be inhabited by low productivity, low diversity fish communities dominated by cool water species. Productivity and diversity, together with the prevalence of warm water fish, are expected to increase downstream (Walters et al. 2003; Goldstein and Meador 2004; Thomas and Hayes 2006).

Natural geomorphic variability and anthropogenic disturbances along rivers have long been recognized to have the potential to affect the predictions made by the RCC (Vannote et al. 1980; Poole 2002). For instance, the Serial Discontinuity Concept (SDC; Ward and Stanford 1983; Stanford et al. 1988) is based on the principle that abrupt transitions (e.g. from flowing in a canyon to flowing in a flood plain; from flowing in a channel to flowing in a reservoir) may affect the upstream-downstream progression of the biological attributes anticipated by the RCC. While this concept is generally applied to model the effects of reservoirs along regulated rivers, a similar concept, the Flood Pulse Concept (FPC; Junk et al. 1989; Tockner et al. 2000), focuses on the effects of the seasonal interactions between a river and its floodplain on the structure and the dynamics of communities. Tributaries, which represent inputs of water that differ from the river in which they flow in terms of nutrient content, temperature, and particle loading may either accelerate or reverse the upstream-downstream progression of biological attributes of rivers predicted by the RCC (Bruns et al. 1984; Minshall et al. 1983, 1985). The Link Discontinuity Concept (LDC; Rice et al. 2001a) suggests that, in alpine rivers, the punctual inputs of coarse substrate at some tributaries, or other dry lateral point sources of coarser material such as valley-side landslides, create a series of sedimentary links (Rice and Church 1998; Rice 1999; Davey and Lapointe 2007). Each link is a river segment delimited upstream by a source of coarser substrate along which selective fluvial transport leads to a classic downstream fining trend (e.g. from boulders, to cobble reaches, then to gravel and often even to sand bed reaches) until another source of coarse substrate initiates a new link. Within-link downstream fining rates are variable and depend on segment scale geomorphic factors. It has been hypothesized (Rice et al. 2001) that this link structure determines the upstream-downstream structure

of various physical (river slope and currents, channel type) and biological variables. Such reach-scale changes in substrate composition (size and form) are expected to affect the stability and the complexity of riverbeds and hence the ability of organisms to colonize a habitat, to find a refuge, to exploit food resources, and to encounter mates. The LDC therefore differs from RCC by its focus on processes occurring at the intermediate scale of river segments ($10^0 - 10^2$ km instead of the complete river i.e. $10^2 - 10^4$ km) and its emphasis on effects of the physics of the systems on organisms. Rice et al. (2001*a*; 2001*b*) found that the number of taxonomic groups of macro-invertebrates and the abundance of specific macro-invertebrates changed from the upstream to the downstream limits of some sedimentary links but the patterns were not clear in all the links sampled. Their study suggests that the LDC may potentially explain some of the discontinuities in macro-invertebrate spatial distribution patterns along rivers. However, Rice et al. (2001*a*; 2001*b*) assessed the effect of link discontinuities on macro-invertebrates only in high relief, alpine watersheds of western Canada. Similarly, sampling was done during a single year. However, it is presently difficult to assess the structuring role played by sedimentary links on other components of the biota, in various regions and types of river landscapes, and the temporal stability of this role.

Coarse substrate recruitment in rivers flowing in non-alpine landscapes that have been shaped by glacial processes (e.g. Canadian Shield; Baltic Shield) may be related to tributaries but is often also associated valley sections modified during glacial eras, such as long bedrock canyons, extended glacio-fluvial terraces or large alluvial fans of periglacial age undercut by the river (Church and Ryder 1972). Davey and Lapointe (2007) proposed an extension of the LDC for non-alpine, lower relief landscapes where

sedimentary links are often initiated by such non-point sources of coarse substrate, rather than at tributary point sources of coarse sediments. They showed that this extended LDC could be used to model and better understand the physical processes of river dynamics in order to identify the distribution of Atlantic salmon spawning habitats in a Canadian Shield river.

The first objective of this study was to evaluate the utility of the extension of the LDC to explain the spatial distribution of periphyton and fish in a river located in a low-relief landscape. We test the simpler hypothesis that geomorphically imposed, downstream trends in stream substrate size can be first order predictors of distribution for organisms whose habitat are closely tied to reach-scale substrate characteristics. We hypothesized that periphyton biomass should be higher in coarser composition reaches located near the upstream limit of sedimentary links. Periphyton biomass has been shown to be positively correlated with substrate size because large particles offer physical stability (protection against flood disturbances: Tett et al. 1978; Ruhrmann 1990; Cattaneo et al. 1997) and trophic advantages (exposure to flow and nutrients: Hynes 1970; Uehlinger 1991). However, it is not clear how the along-link variations in bed shear stress at baseflow (higher upstream), or in local sand supply and consequent algae abrasion during small spates, could affect these expected, longitudinal patterns of periphyton biomass. We also hypothesized that fish abundance may be higher in reaches located near the upstream limit of sedimentary links because of the higher primary productivity and the better protection against the flow provided by boulders (Heggnes 1991; Bouchard and Boisclair 2008). The second objective was to assess the inter-annual variability of the role played by sedimentary links in determining fish distribution.

Materials and methods

Study area and biota

The study was conducted in the Sainte-Marguerite River (SMR; 48°09'21"N 69°33'51"W). This river is located on the north shore of the Saint-Lawrence estuary in Québec, Canada (Figure 1). The SMR consists of two main branches, the Principal and the Northeast, which drain similar sized sub-basins, totaling 2115 km² of drainage area. Mean annual peak daily and mean summer daily discharges at the gauging station located in the Principal branch at 43 km from the river mouth (FRM) are respectively 70 m³·s⁻¹ and 3.6 m³·s⁻¹ (Davey and Lapointe 2007). The Principal branch of the SMR, which constitutes our sampling area, has a mean width of 22 m at peak discharge in the spring and a mean depth of less than 1 m during the summer period (Hedger et al. 2006). Davey and Lapointe (2007) delineated ten sedimentary links in the Principal branch of the SMR. However, further geomorphological analyses indicated that the Principal branch of the SMR comprises only nine sedimentary links further referred to as L1 to L9 (from upstream to downstream; M. Lapointe, Dept. of Geography, McGill University, personal communication), none of which were triggered by a tributary input. These links were produced by the input of coarse (boulder) substrate from glacio-fluvial terraces and valley-side talus deposits of Paraglacial age (Church and Ryder 1972; Davey and Lapointe 2007). The high variability (in terms of link length, substrate size at the upstream and downstream ends of each link, downstream fining rate, etc.) in the SMR provides a valuable opportunity to test the response of algae and Atlantic salmon parr distribution in the context of the LDC (Table 1). While the upper reaches of many links are relatively straight, boulder rapid channel types, pool-riffle sequences dominate the

reach scale structure of the cobble to gravel, middle and lower parts of sedimentary links. Upstream on the RSM, small trees and bushes on the riverbanks and a narrower channel slightly reduce sunlight at the riverbed. Sunlight at the riverbed downstream is not affected by riparian vegetation because riverbanks are mostly cobble bars. Overall, shading by riparian vegetation accounted for less than 10% of the river surface. The SMR was perturbed by the rectification of meanders (41 to 52 km FRM, link L6) during the construction of a provincial highway in early 1960s and embankments were made to stabilize the shores (Talbot and Lapointe, 2000). Except for this highway, the watershed is relatively free of anthropogenic perturbation (Bouchard and Boisclair 2008).

The main components of the periphyton community of the SMR are diatoms (Bacillariophyceae), which include mainly *Tabellaria spp.*, *Eunotia spp.*, *Novicula spp.*, *Synedra spp.*, *Gomphonema spp.*, as well as some filamentous algae (Chlorophyta; Rasmussen and Trudeau 2007). Eight fish species are found in the SMR: Atlantic salmon (*Salmo salar*), Brook trout (*Salvelinus fontinalis*), Blacknose dace (*Rhinichthys atratulus*), Longnose dace (*Rhinichthys cataractae*), Longnose sucker (*Catostomus catostomus*), American eel (*Anguilla rostrata*), Sea lamprey (*Petromyzon marinus*), and Fallfish (*Semotilus corporalis*). However, this study focused exclusively on parr of Atlantic salmon because they are ubiquitous in the SMR. Age I+ and II+ parr were treated indiscriminately because there is a size overlap between the two age classes (Guay et al. 2000).

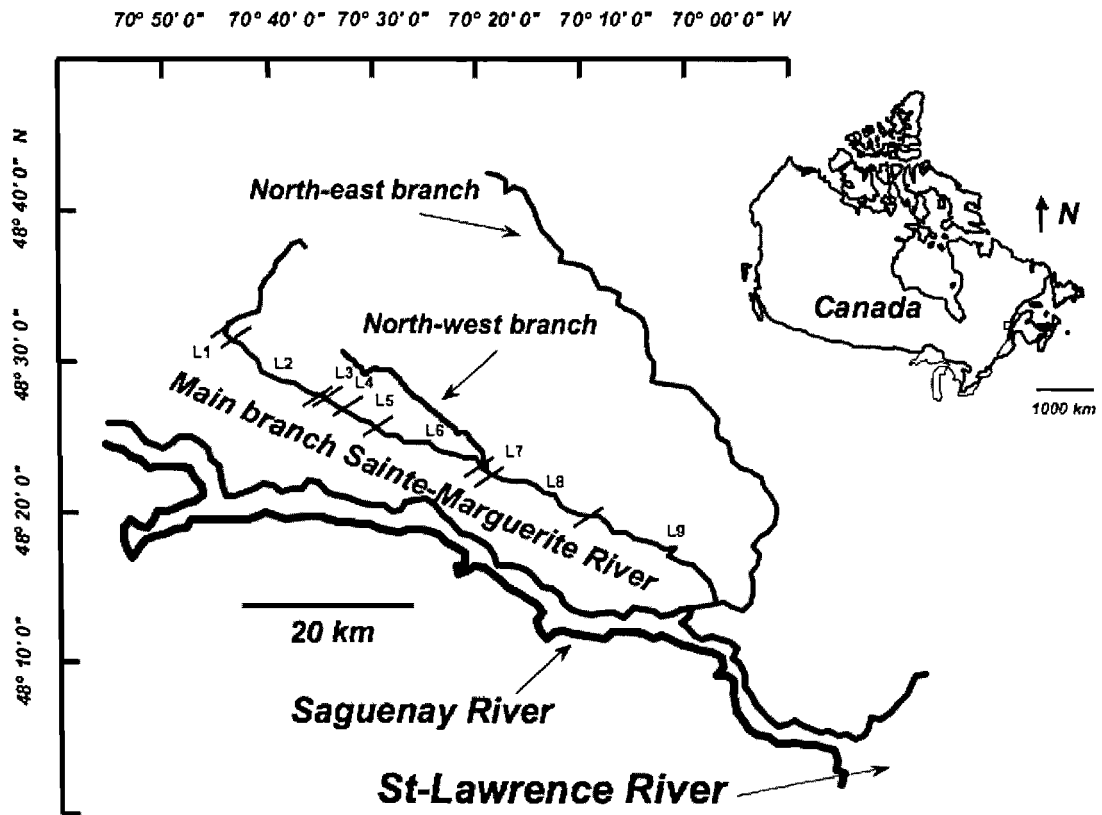


Figure 1. Map of the Sainte-Marguerite River watershed (Quebec, Canada). Bold lines perpendicular to the river represent limits of the nine sedimentary links of the main branch of the SMR.

Table I. Total lengths, D50 in upstream and downstream parts, bedrock and sand reaches presence, and source cause of the nine links in the SMR.

Link	Total length (Km)	D50 upstream (cm)	D50 downstream (cm)	Bedrock reach (Y/N)	Sand reach (Y/N)	Cause of link source
L1	2.6	29.0	14.7	Y	N	Canyon
L2	14.5	6.7	2.8	Y	Y	Glacio-fluvial
L3	1.1	24.7	9.2	Y	N	Glacio-fluvial
L4	3.5	18.1	13.6	Y	Y	Glacio-fluvial
L5	6.5	20.5	5.9	N	Y	Glacio-fluvial
L6	16.8	10.4	9.6	N	Y	Glacio-fluvial
L7	1.6	11.5	9.4	N	Y	Alluvial fan
L8	14.4	14.1	6.3	N	Y	Glacio-fluvial
L9	26.5	12.0	36.0	N	N	Glacio-fluvial

Spatial and temporal context

Four of the nine sedimentary links of the Principal branch of the SMR were selected for study because they represented a wide range of conditions: L1, L4, L6, and L8 (Figure 1). L1 (2.6 km) and L4 (3.5 km) are among the shortest, and L6 (16.8 km) and L8 (14.4 km) are among the longest links of the Principal branch of the SMR. While L1 and L4 are located in the upstream half, L6 and L8 are located in the downstream half of the Principal branch of the SMR. In addition, L6 differs from all other links studied because it is located in a part of the SMR that was subjected to the rectification of meanders and consequently still undergoes enhanced sand transport in its cobble reaches. Five to seven reaches of 200 m were sampled in each sedimentary links (Table 2). These reaches were selected to best represent the upstream-downstream variations of environmental conditions within individual links. Each 200 m reach was further divided in twenty sections of 10 m for periphyton and salmon sampling.

Sampling was conducted from June 27th to August 5th 2003, from July 27th to August 11th 2004, and from July 5th to 22nd 2005. Periphyton was sampled only in 2005 while parr were sampled in 2003, 2004, and 2005 (Table 2). Consequently, inter-annual variations of the distribution of periphyton could not be assessed, but inter-annual variations of the distribution of parr were assessed for L1 (2004, 2005), L4 (2004, 2005), L6 (2003, 2005), and L8 (2003, 2004, 2005).

Table II. Distribution of the 200 m reaches sampled for fish within the nine total combinations of sedimentary links and years. Periphyton was sampled in the links identified only in 2005.

Year	Link	L1	L4	L6	L8
2003		-	-	6	7
2004		5	7	-	7
2005		5	7	7	6

Physical variables

For each 10-m longitudinal section of any 200 m reach, three estimates were taken for water depth, flow velocity (at 40% of the water column from the bottom of the river), and substrate composition (percent contribution of eight size classes of substrate within an area of 1.5 m²). Substrate size was determined by the length of the median axis of particles. The eight substrate size classes used were clay, silt, sand (< 2 mm), gravel (2-32 mm), pebble (32-64 mm), cobble (64-250 mm), boulder (250-1000 mm), metric boulder (> 1000 m), and bedrock. Water depth, flow velocity, and substrate composition were noted in the thalweg (part of the cross section of the river where depth and flow rate are highest) as well as on the shore farthest from the thalweg (minimum depth of 25 cm), and at a point in the middle in these two locations. When no distinct thalweg was perceived, this location was replaced by the middle of the river. The average water depth, velocity, and percent cover by substrate size class in any given 200 m reach were obtained by averaging the values noted within this reach. Two variables were used to describe the position of all reaches along the upstream-downstream axis of the river. First, the distance of each reach from river mouth (DFRM) was measured using geographic information software (GIS; ArcView 8 ®). Second, the relative position of every reach within sedimentary links (RPSL) was calculated using GIS by dividing the distance to the upstream boundary of the sedimentary link by the total length of the sedimentary link considered (0 = upstream limit of a sedimentary link; 1 = downstream limit of a sedimentary link). This enabled us to compare response variables (periphyton biomass and parr density) in links of different lengths.

Periphyton biomass

Periphyton biomass was estimated in five reaches of L1, seven reaches of L4, seven reaches of L6, and six reaches of L8 in 2005 (Table 2). Ten estimates of periphyton biomass were obtained within each section of these reaches at the same three locations and at the same time as the description of physical conditions. Periphyton biomass was estimated using a modified version of the U.S. E.P.A. Rapid Bioassessment Protocol (RBP; Barbour et al. 1999). This method may be used to assess periphyton biomass more rapidly than traditional substrate sampling and laboratory analysis. The RBP consists in touching substrate selected haphazardly to assess the periphyton thickness, and hence, the approximate periphyton biomass on the substrate. Periphyton biomass was represented by four RBP classes of periphyton thickness (1= rough substrate with no visual evidence of microalgae; 2= slimy substrate, but no visually evident accumulation of microalgae; 3= evident accumulation of a microalgae forming a layer less than 1 cm thick; 4= evident accumulation of a microalgae forming a layer thicker than 1 cm). This permitted the estimation of a total of 600 RBP estimates of periphyton thickness per reach (10 RBP estimates x 3 locations x 20 sections of 10 m per reach).

Microalgal chlorophyll *a* (Chl *a*) concentration is a good indicator of periphyton biomass (Wetzel and Likens 2000). We estimated the Chl *a* concentration corresponding to the four RBP classes of periphyton thickness by collecting ten rocks (substrate with a median axis between 32 and 64 mm) for each RBP class. Each rock was brushed in laboratory in a known volume of water to detach algae. Samples were filtered on Gelman type A/E glass-fiber filters (1 μm pore size) and kept frozen until analysis. Chl *a* concentrations were estimated after extracting Chl *a* from filters immersed in 95 %

ethanol for 24 h (Nusch 1980). Extracts were read with a spectrophotometer (Spectronic Genesys 5 type) at 665 nm and 750 nm (Lorenzen 1967; Marker 1972). Periphyton biomass (PB; mg Chl *a*·m⁻²), expressed as the mass of Chl *a* per unit of rock surface area were estimated by assuming that two thirds of a rock is available for periphyton growth (Bergman and Peters 1980):

$$PB = \frac{(((13.7 \cdot (665v - 750v)) - (5.76 \cdot (649 - 750v))) \cdot VE \cdot VT \cdot 10)}{(0.66 \cdot S \cdot CL \cdot VF)} \quad (\text{equation 1})$$

where 665v and 750v are respectively the absorbance at 665 and 750 nm, VE is the volume of ethanol used for extraction (12 mL), VT is the total volume of detached algae (mL), VF is the filtered volume of detached algae (mL), CL is the cell length used for spectrophotometer reading (cm), and S is the surface area of rock (cm²) estimated following Graham et al. (1988):

$$S = 1.15 \cdot (A \cdot B + A \cdot C + B \cdot C) \quad (\text{equation 2})$$

where A is the length of the longest axis (cm), B is the length of the median axis (cm), and C is the length of the shortest axis (cm) of each rock sampled. Rocks were measured using calipers (± 0.05 cm). Average periphyton biomass per reach was estimated in two steps. First, we replaced the RBP class assigned to the 600 rocks sampled in this reach by the anticipated mean periphyton biomass corresponding to their respective RBP class. Second, we averaged the subsequent 600 estimates of mean periphyton biomass.

Parr density

Parr density in each section was estimated by two observers who simultaneously snorkeled, in an upstream direction, two 10-m long transects oriented approximately parallel to shore. One transect was located less than 2 m from shore at a minimum depth of 30 cm, and another was located approximately in the middle of the river (i.e. 5 to 15 m from the shore depending on the river width). The two transects were therefore positioned relative to features of the river that could be easily identified by snorkellers (the shores) and that allowed the estimation of fish density over a wide range of environmental conditions within each section. Parr density in a reach was estimated a maximum of three days before or after physical conditions were noted within this reach. Water discharge varied by less than $0.8 \text{ m}^3 \cdot \text{s}^{-1}$ (21% of average flow) over this interval. We recognize that visual observations performed while snorkelling, like many other methods, provides only a relative index of fish density. Although the SMR is wadeable during average summer flows, snorkelling is the only method that can be applied everywhere and over the complete range of environmental conditions found in this river (Bouchard and Boisclair 2008). Hence, estimates of fish density obtained by snorkelling could not be calibrated with other methods because of the difficulty, for instance, to efficiently operate electrofishing gears in 1 m of water with flows of $0.7\text{-}0.8 \text{ m} \cdot \text{s}^{-1}$. Sampling performed to estimate parr densities was done at night (22h00-03h00). This further explains the utility of transects positioned relative to the shores instead of the thalweg (difficult to identify at night). No sampling was done when it rained or within one day of a rain event. Night sampling was performed because previous studies showed that estimates of parr densities, in the SMR and elsewhere, are significantly higher

during the night than during the day (Gries et al. 1997; Johnston et al. 2004; Imre and Boisclair 2005). In addition, it has been shown in the SMR that parr densities estimated at night are less variable and less affected by meteorological conditions than during the day, when high cloud cover affects fish sighting (Girard et al. 2003; Bédard et al. 2005; Imre and Boisclair 2005). Hence, snorkelling at night was employed because it could be used everywhere in the SMR, it eliminated the problem of having to deal with different biases inherent to different sampling methods, and it provided estimates that, while relative are reliable.

Parr were observed using underwater lighting systems (UK Sunlight C4). The light beam was directed towards water surface to minimize fish disturbance (Gries et al. 1997). For each 10-m section, the two snorkelers counted the number of parr observed. They also evaluated the average distance (to their right and to their left) at which parr could be seen and correctly identified. The maximum distance was 2 m on both sides of observers and it varied with water depth, substrate composition, and water turbidity. Parr density ($\text{fish} \cdot 100 \text{ m}^{-2}$) in each transect was obtained by dividing the number of parr observed by the surface area sampled in this transect (average distance \cdot 2 sides \cdot 10 m). The average parr density in any given 200 m reach was obtained by averaging parr densities in transects included within the reach.

Statistical analysis

Variations of water depth and flow velocity along sedimentary links were tested with a two-way ANOVA with no interaction. The first factor was the upstream or downstream third of sedimentary links, given by the RPSL, and the second factor was the studied year. Variations of the average percent contribution of sand and boulder were

tested with a one-way ANOVA. The only factor was the upstream or downstream third of sedimentary links because substrate composition at one site did not vary from one year to another. Variations of Chl *a* biomass among the four classes of periphyton thickness were tested with a one-way ANOVA. For each combination of sedimentary links and years, the linear correlation coefficient (Pearson *r*) was used to measure the dependence between periphyton biomass and DFRM, periphyton biomass and RPSL, parr density and DFRM, parr density and RPSL, and parr density and periphyton biomass. The correlation between periphyton biomass, average parr density, and RPSL was estimated using a one-tailed test because we expected periphyton biomass and parr density to be higher at the upstream than at the downstream limit of sedimentary links. However, because we have no *a priori* concerning the correlation between periphyton biomass and DFRM, parr densities and DFRM, and parr density and periphyton biomass, a two-tailed test was used (correlation between the variables in the reference population is different than zero; $\rho \neq 0$). Pearson linear correlations were estimated by permutation (number of permutation = 999 times) because of low sample size ($n=5$ to 7 , 200 m long sample units, per sedimentary link). The inter-annual variability of parr density was tested for each sedimentary link using a one-way ANOVA in which parr density in the reaches sampled for a given combination of link and year were used as replicates. All statistical analyses were done using permutation tests on untransformed values because original data did not meet the assumptions of ANOVA and no data transformation procedure could correct this situation (Legendre and Legendre 1998). Statistical analyses were realized with the open source R language (www.r-project.org).

Results

Average water depth in the upstream third of sedimentary links during sampling ranged from 0.36 (L6, Upstream; Table 3) to 0.57 m (L8, Upstream). Corresponding values for the downstream third of sedimentary links were 0.38 (L1, Downstream) and 0.63 m (L6, Downstream). Although water depth generally tended to increase from the upstream to the downstream third of sedimentary links, these differences were never statistically significant ($0.626 < p_{\text{perm}} < 1.000$). One exception was L6 ($p_{\text{perm}} = 0.004$) which is characterized by the presence of meanders in its downstream third, and hence, by a statistically significant increase of average water depth in this area. Among-year differences in water depth were not statistically significant ($0.198 < p_{\text{perm}} < 0.832$) except for L8 where water depth in 2003 was 15.8 to 15.3 % lower than in 2004 and 2005 respectively ($0.007 < p_{\text{perm}} < 0.037$). Average flow velocity ranged from 0.19 (L6, Downstream) to $0.52 \text{ m}\cdot\text{s}^{-1}$ (L6, Downstream). The average flow velocity decreased significantly from the upstream to the downstream third of all sedimentary links ($0.004 < p_{\text{perm}} < 0.013$). Among-year differences in flow velocities were not statistically significant ($0.173 < p_{\text{perm}} < 0.907$) except for L4 where flow velocities were 58.1% higher in 2004 than in 2005 ($p_{\text{perm}} = 0.014$). As anticipated, the average percent contribution of sand to riverbed composition was lower in the upstream than in the downstream third of sedimentary links (Table 3). This difference was statistically significant for three out of four links: L4 ($p_{\text{perm}} = 0.020$), L6 ($p_{\text{perm}} = 0.017$), and L8 ($p_{\text{perm}} = 0.009$). The average percent contribution of sand was ranging from 3.5 (L4) to 6.1 % (L6) in the upstream third and from 25.1 (L4) to 41.4 % (L6) in the downstream third of these links. The downstream increase of sand was less pronounced and not statistically significant in L1

($p_{perm} = 0.153$) with the average percent contribution of sand was ranging from 6.0 % in the upstream third of sedimentary links to 11.4 % in the downstream third. On average, boulders covered from 13.3 (L6) to 39.5 % (L4) of the riverbed in the upstream third of typical sedimentary links. Boulders were rare in the downstream third of all sedimentary links studied (average contribution to riverbed from 0.05 to 1.8%). The percent contribution of boulders to riverbed was always significantly higher ($0.001 < p_{perm} < 0.031$) in the upstream than in the downstream thirds of sedimentary links. The description of substrate composition within the sedimentary links studied support the expectations that particle fining does occur along the upstream-downstream axis of the links sampled and that particle fining is more pronounced in some links (L4 and L8) than others (L1 and L6).

Table III. Description of the physical conditions observed within the upstream, middle, and downstream river reaches (mean value \pm standard deviation) of each sedimentary link studied. The n represents the sampling size for each line. Data used for the two-way ANOVAs with no interaction are in italic. Statistically significant differences are identified with letters in exponent.

Link	Position	Average water depth (m)	Average flow velocity ($\text{m}\cdot\text{s}^{-1}$)	Sand (%)	Gravel (%)	Pebble et cobble (%)	Boulder et metric boulder (%)
L1	Upstream (n = 90)	<i>0.38 \pm 0.06</i>	<i>0.56 \pm 0.08</i>	<i>6.0 \pm 0.3</i>	<i>9.9 \pm 3.0</i>	<i>63.0 \pm 7.5</i>	<i>20.8 \pm 10.1^f</i>
	Middle (n = 90)	<i>0.32 \pm 0.01</i>	<i>0.47 \pm 0.01</i>	<i>6.5 \pm 0.4</i>	<i>15.8 \pm 3.7</i>	<i>73.3 \pm 1.3</i>	<i>3.9 \pm 1.6</i>
	Downstream (n = 90)	<i>0.38 \pm 0.10</i>	<i>0.42 \pm 0.07</i>	<i>11.4 \pm 7.8</i>	<i>20.5 \pm 4.6</i>	<i>64.4 \pm 11.1</i>	<i>1.8 \pm 1.8^f</i>
L4	Upstream (n = 90)	<i>0.42 \pm 0.05</i>	<i>0.46 \pm 0.11</i>	<i>3.5 \pm 1.5^c</i>	<i>7.1 \pm 1.4</i>	<i>49.7 \pm 9.1</i>	<i>39.5 \pm 10.2^g</i>
	Middle (n = 90)	<i>0.46 \pm 0.07</i>	<i>0.31 \pm 0.09</i>	<i>7.9 \pm 3.6</i>	<i>18.1 \pm 6.2</i>	<i>57.8 \pm 5.9</i>	<i>13.2 \pm 7.7</i>
	Downstream (n = 90)	<i>0.46 \pm 0.13</i>	<i>0.27 \pm 0.09</i>	<i>25.1 \pm 13.4^c</i>	<i>38.1 \pm 15.0</i>	<i>30.6 \pm 4.6</i>	<i>0.05 \pm 0.04^g</i>
L6	Upstream (n = 120)	<i>0.36 \pm 0.06^a</i>	<i>0.31 \pm 0.03^b</i>	<i>6.1 \pm 4.1^d</i>	<i>17.2 \pm 8.3</i>	<i>55.8 \pm 2.6</i>	<i>13.3 \pm 5.7^h</i>
	Middle (n = 120)	<i>0.35 \pm 0.07</i>	<i>0.35 \pm 0.10</i>	<i>6.5 \pm 2.0</i>	<i>35.3 \pm 13.4</i>	<i>51.5 \pm 10.6</i>	<i>2.8 \pm 1.6</i>
	Downstream (n = 60)	<i>0.63 \pm 0.01^a</i>	<i>0.19 \pm 0.03^b</i>	<i>41.4 \pm 14.3^d</i>	<i>39.6 \pm 21.7</i>	<i>13.5 \pm 12.4</i>	<i>1.0 \pm 1.7^h</i>
L8	Upstream (n = 150)	<i>0.57 \pm 0.09</i>	<i>0.52 \pm 0.10</i>	<i>5.5 \pm 2.8^e</i>	<i>14.3 \pm 7.6</i>	<i>47.9 \pm 18.0</i>	<i>32.0 \pm 23.6ⁱ</i>
	Middle (n = 150)	<i>0.54 \pm 0.06</i>	<i>0.42 \pm 0.08</i>	<i>11.2 \pm 9.0</i>	<i>25.6 \pm 9.1</i>	<i>60.5 \pm 15.2</i>	<i>1.4 \pm 2.3</i>
	Downstream (n = 150)	<i>0.57 \pm 0.08</i>	<i>0.35 \pm 0.06</i>	<i>37.3 \pm 24.3^e</i>	<i>54.7 \pm 21.8</i>	<i>4.5 \pm 2.9</i>	<i>0.5 \pm 0.7ⁱ</i>

The RBP classes of periphyton thickness assigned to individual rocks sampled in the study area ranged from 1 (37.9% of the rocks) to 4 (2.1% of the rocks) with 47.2% of the rocks assigned an RBP class of 2. The mean periphyton biomass (\pm standard deviation) that corresponded to the different RBP classes ranged from 0.45 ± 0.16 (RBP class 1) to 11.08 ± 6.03 mg Chl *a* \cdot m⁻² (RBP class 4; Figure 2). The permutational ANOVA showed that all pairs of RBP classes were significantly different ($p_{\text{perm}} < 0.001$) except for RBP classes 2 and 3 ($p_{\text{perm}} = 0.365$). Periphyton biomasses from RBP classes 2 and 3 were therefore combined and averaged (1.35 ± 0.93 mg Chl *a* \cdot m⁻²). The average periphyton biomass per reach ranged from 0.45 to 2.44 mg Chl *a* \cdot m⁻² (mean among reaches \pm standard deviation = 1.16 ± 0.43 mg Chl *a* \cdot m⁻²; Figure 3). Average periphyton biomass did not vary significantly among reaches ($p_{\text{perm}} = 0.107$). There was no statistically significant correlation between average periphyton biomass and DFRM ($r = -0.06$; $p_{\text{perm}} = 0.796$). Our results suggested the existence of higher periphyton biomass in the sedimentary link located close to the middle of the SMR (L6; Figure 3). However, multiple regression analysis using periphyton biomass of all reaches as dependent variable and DFRM and DFRM² as independent variables produced no statistically significant model ($R^2_{\text{adj}} = 0.03$; $p = 0.27$). There was no statistically significant correlation between average periphyton biomass and RPSL in any of the sedimentary links ($-0.72 < r < 0.17$; $0.07 < p_{\text{perm}} < 0.65$; Table 4). No statistically significant quadratic model could be fitted to these data ($0.09 < p < 0.67$; $0.37 < R^2_{\text{adj}} < 0.54$) except for L8 ($p = 0.0499$; $R^2_{\text{adj}} = 0.77$). This suggested that periphyton biomass in the two reaches located in the middle of L8 may be 44.7 to 57.3 % higher the average value estimated for this sedimentary link.

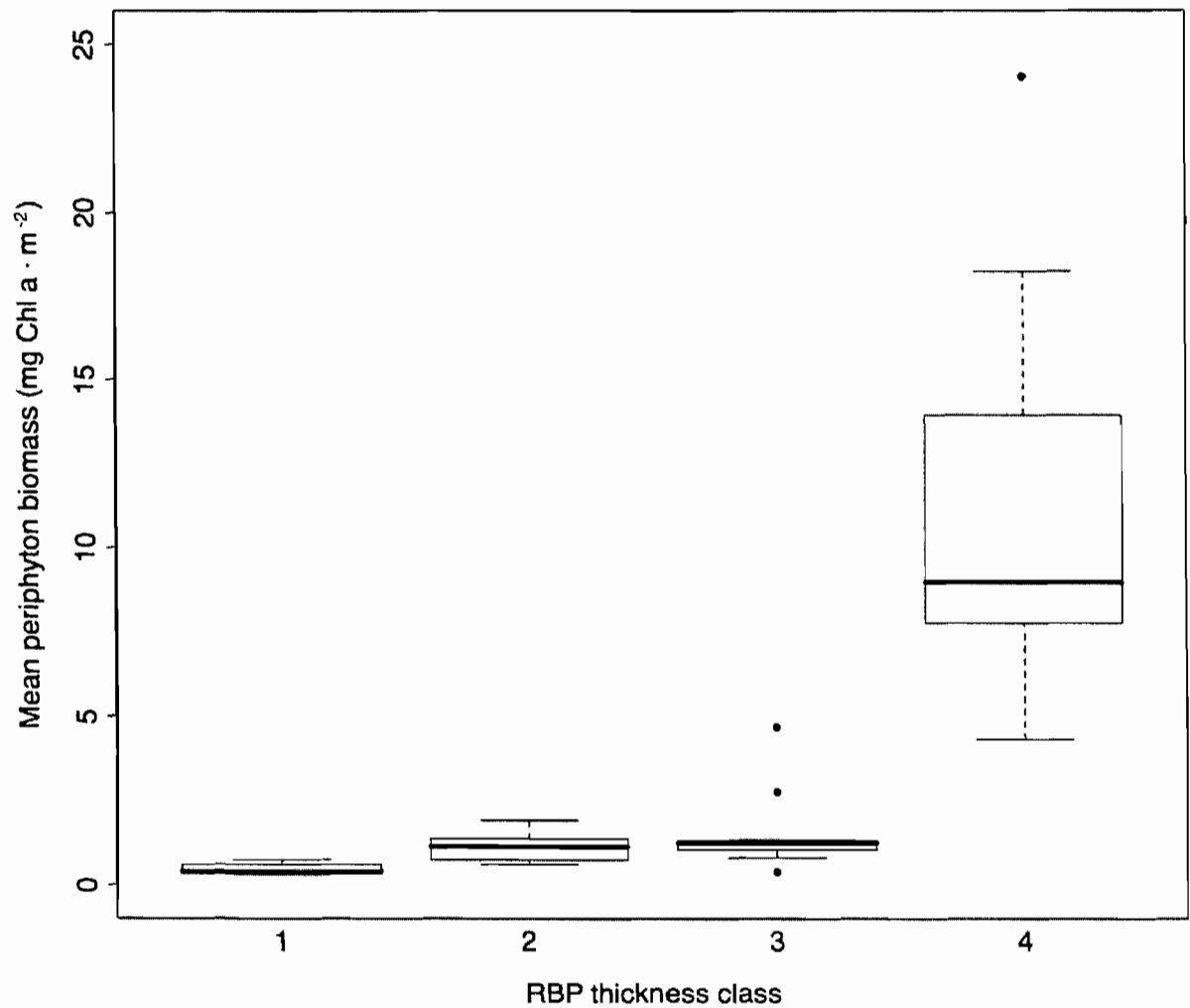


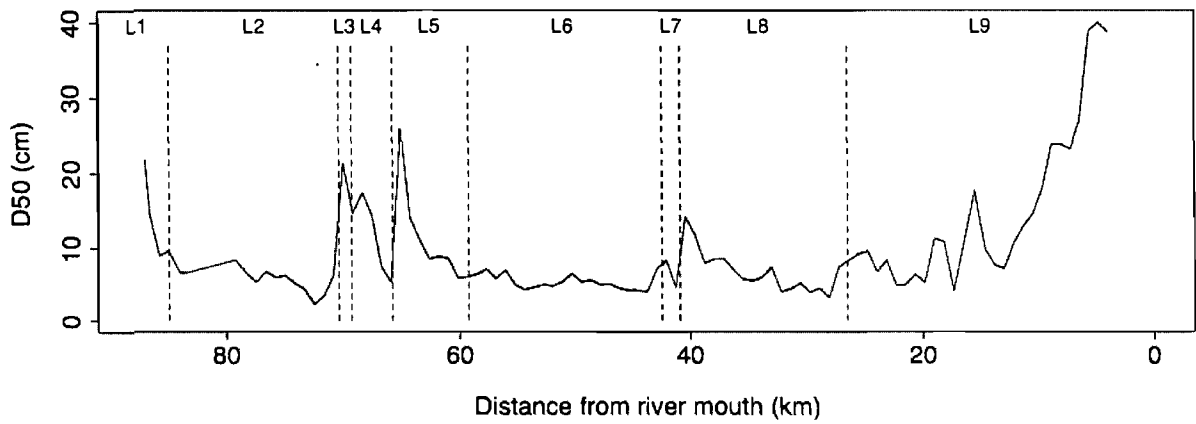
Figure 2. Box plot showing the mean periphyton biomass (mg Chl *a* · m⁻²) for the four RBP classes of thickness. The box plot shows the 10th, 25th, 75th, and 90th percentiles. The line in the middle of the boxes represents the median and the solid black circles represent the outliers.

Parr densities estimated at the scale of reaches ranged from 0.69 to 15.88 parr·100m⁻² (average ±standard deviation for all reaches and sedimentary links=5.71±4.34 parr·100m⁻²) in 2003, from 1.46 to 18.25 parr·100m⁻² (7.38±5.10 parr·100m⁻²) in 2004, and from 1.75 to 12.69 parr·100m⁻² (5.98±2.93 parr·100m⁻²) in 2005 (Figure 3). Average parr densities did not vary significantly among years (all reaches and sedimentary links sampled within a year used as replicates; F-value =0.003; p_{perm}=0.96). However, average parr density varied significantly between years for L1 (F-value=11.03; p_{perm}=0.027). Average parr density for this sedimentary link decreased 2.5-fold between 2004 (11.40±3.55 parr·100m⁻²) and 2005 (4.60±2.88 parr·100m⁻²). The other sedimentary links studied (L4, L6 and L8) displayed no such among-year variability (0.255<F-value<0.385; 0.397<p_{perm}<0.693). Average parr density in reaches tended to increase from 2.00 (at 29.55 km FRM) to 14.25 parr·100m⁻² (at 86.48 km FRM) with DFRM in 2004 ($r = 0.476$; p_{perm} = 0.048). However, no such trend was observed in 2003 and 2005 (-0.260< r <0.146; 0.210<p_{perm}<0.675).

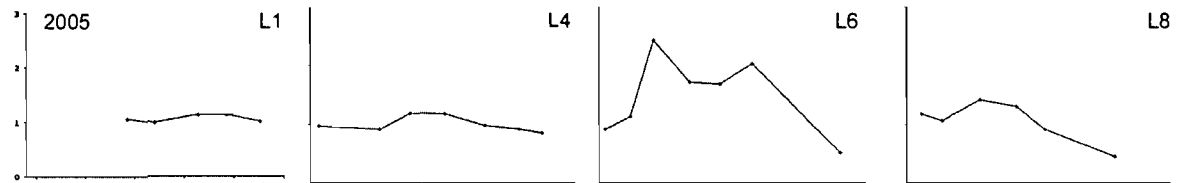
Beyond inter-annual environmental variability in reach-scale densities, the main hypothesis tested here is that relative (rather than absolute) parr abundances are related to along-link position. Average parr density among reaches within sedimentary links was generally correlated with RPSL. The correlation between average parr density and RPSL when all reaches, sedimentary links, and years are used as replicates was -0.52 (p_{perm}=0.001) supporting the expectation that, in general, average parr density decreases from the upstream to the downstream limits of sedimentary links. Individual analysis of the nine combinations of years and sedimentary links indicated the existence of a statistically significant correlation between average parr density and RPSL for six of

these combinations ($-0.90 < r < -0.33$; $0.005 < p_{\text{perm}} < 0.275$; Table 4) while 8 of the 9 are significant at the 10% level. In all these cases, average parr density decreased 1.2- to (L1; 2004) to 15.3- fold (L8; 2003) from the upstream to the downstream limits of sedimentary links. L8 was the temporally most consistent sedimentary link with statistically significant correlations between average parr density and RPSL for 2003 ($r = -0.75$; $p_{\text{perm}} = 0.025$), 2004 ($r = -0.65$; $p_{\text{perm}} = 0.048$), and 2005 ($r = -0.75$; $p_{\text{perm}} = 0.038$). In contrast, the correlation between average parr density and RPSL was statistically significant one of the two years for L1, L4, and L6 (Table 4).

There was no statistically significant correlation between average parr density and average periphyton biomass when this correlation was tested using the data for all reaches and sedimentary links as replicates ($r = 0.25$; $p_{\text{perm}} = 0.217$). Tests done for individual sedimentary links indicated that the correlation between parr density and average periphyton biomass was statistically significant only for L4 ($r = 0.73$; $p_{\text{perm}} = 0.047$).



Periphyton biomass (mg Chl *a* · m⁻²)



Parr density (fish · 100m⁻²)

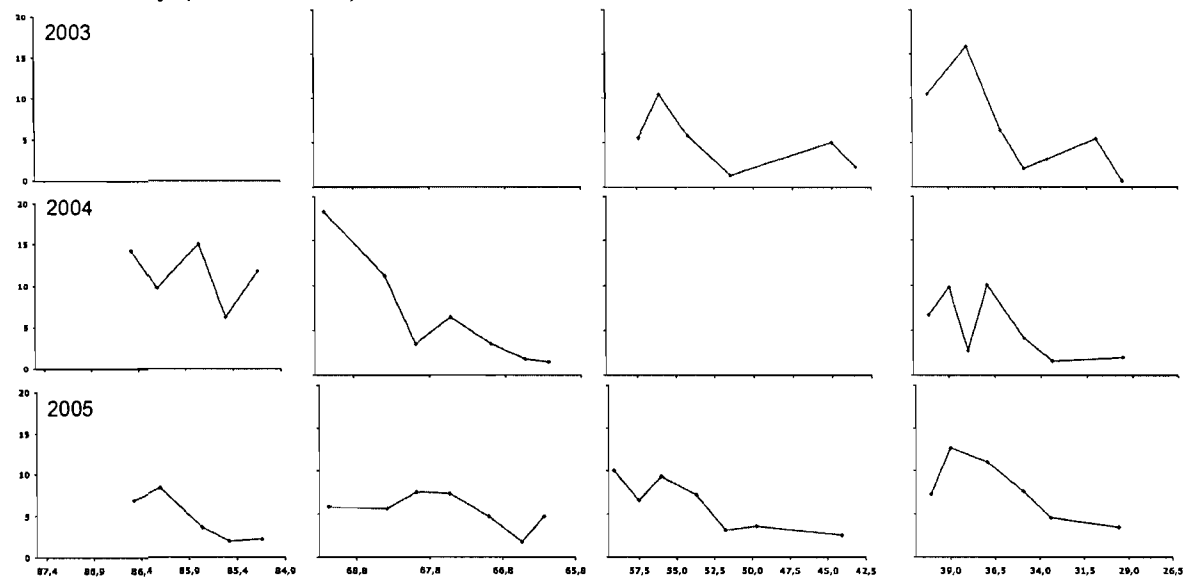


Figure 3. The variations of substrate size along the upstream-downstream axis of the complete river was represented by a 100-data point simple moving average to smooth the mean substrate size data (D50; length of the median axis of the particle located at the 50th percentile of the substrate size spectrum observed at a site) from Carbonneau et al. (2005).

Table IV. Linear correlation results (Pearson r and permutational probability) between periphyton biomass, parr density, and relative position in sedimentary link (RPSL) for all link and year combinations.

Link		L1	L4	L6	L8
Periphyton biomass	2005	$r = 0.1704$; $p_{\text{perm}} = 0.646$	$r = -0.3270$; $p_{\text{perm}} = 0.230$	$r = -0.2159$; $p_{\text{perm}} = 0.326$	$r = -0.7234$; $p_{\text{perm}} = 0.072$
Parr density	2003	-	-	$r = -0.5558$; $p_{\text{perm}} = 0.097$	$r = -0.7451$; $p_{\text{perm}} = 0.025$
	2004	$r = -0.3343$; $p_{\text{perm}} = 0.275$	$r = -0.9022$; $p_{\text{perm}} = 0.005$	-	$r = -0.6471$; $p_{\text{perm}} = 0.048$
	2005	$r = -0.8911$; $p_{\text{perm}} = 0.038$	$r = -0.5499$; $p_{\text{perm}} = 0.083$	$r = -0.8578$; $p_{\text{perm}} = 0.007$	$r = -0.7497$; $p_{\text{perm}} = 0.038$

Discussion

The present study does not support the hypothesis that the distribution of periphyton along the SMR does not simply covary with along link position. No statistically significant only one relationship between periphyton biomass and RPSL (L8) and it was marginally significant ($p = 0.072$). In addition, the only environmental variable that statistically correlates significantly with periphyton biomass is the percentage of pebble and cobble ($r = 0.40$, $p_{\text{perm}} = 0.03$). Four propositions may be listed to explain the lack of support for the existence of a statistically significant correlation between periphyton biomass and environmental variables. First, spatial variations may be difficult to detect or to properly quantify for variables like periphyton biomass that are known to be subjected to an important heterogeneity at the scale of single rocks or among rocks of individual sampling sites (Tett et al. 1978; Uehlinger 1991). In the present study, average periphyton biomass was estimated by assigning RBP class to 600 rocks distributed at random within each reach of 200 m specifically to insure a good representation of periphyton spatial heterogeneity. Second, the Rapid Bioassessment Protocol (RBP) may not be sufficiently sensitive to describe spatial variations of periphyton biomass. This proposition is not supported by our study. There was a statistically significant difference between the Chl *a* concentrations that were associated with the different RBP classes used during sampling. In addition, these Chl *a* concentrations varied widely among RBP classes (0.45, 1.35, and 11.08 mg Chl *a*·m⁻² respectively for RBP classes 1, 2-3 combined, and 4). Consequently, RBP has the potential to detect variations of periphyton biomass when these variations are larger than 3-fold. Third, floods or sudden rises in discharge above baseflow minor spates have long

been recognized to have a negative effect on periphyton biomass because substrate mobility or abrasion by suspended or saltating sand tend to scour periphyton (Biggs and Close 1989; Ruhrmann 1990; Cattaneo et al. 1997). Suspended and saltating loads may not be uniform within a link. The spatial structure of periphyton biomass variations within a given link could therefore be masked if floods or spates occur during or soon before the sampling of this link. In our study, periphyton was sampled in all the links from July 5th to 22nd 2005 (Julian day 186 to 203). During this sampling period, flow of the SMR trended downward and no major floods were noted: however a number of minor spates occurred (Figure 4). Data used to estimate periphyton biomass in any given individual link were collected within 3-4 days. While no bankfull floods capable of mobilizing coarse pavement substrate occurred during the sampling period, the smaller spates that occurred did put in saltation sands stored in pools, may have differentially depleted periphyton in sand rich sectors and thus be responsible for the lack of correlation between periphyton biomass and RPSL within individual links. Fourth, periphyton biomass and its perceived spatial structure may not be affected only by floods that occur within a sampling period but also by floods that occur before a sampling period (Uehlinger 1991; Biggs 1995). SMR was subjected to a flood event from June 17th to June 20th 2005 (Julian days 168 to 171). The peak flow during the flood ($105.7 \text{ m}^3 \cdot \text{s}^{-1}$) was equivalent to 3-fold the annual mean daily flow of the SMR ($32.3 \text{ m}^3 \cdot \text{s}^{-1}$ based on data collected since 1998). Such flood may be sufficient to significantly affect periphyton biomass (Biggs and Close 1989; Biggs and Smith 2002). This flood occurred 2 weeks before sampling the first sedimentary link (L1) and 4 weeks before sampling the last sedimentary link (L6) studied. Periods of 4 to 10 weeks of

relative flow stability may be required to permit the accumulation of periphyton biomass following a flood (Fisher and Grimm 1988; Uehlinger 1991; Lohman et al. 1992). In this context, the flood that occurred 2-4 weeks before periphyton was sampled may have affected our ability to elucidate the correlation between periphyton biomass and RPSL. Floods may also explain the difference between the biomass of Chl *a* we estimated in the SMR (0.45 to 2.44 mg·m⁻²) and that reported by Rasmussen and Trudeau (2007; 4.63 to 8.90 mg·m⁻²) for a sampling that took place in the SMR in July 2003. The SMR was affected by a smaller spring and earlier summer floods in 2003 (sampling year of Rasmussen and Trudeau 2007) than in 2005 (periphyton sampling year of the present study; Figure 4).

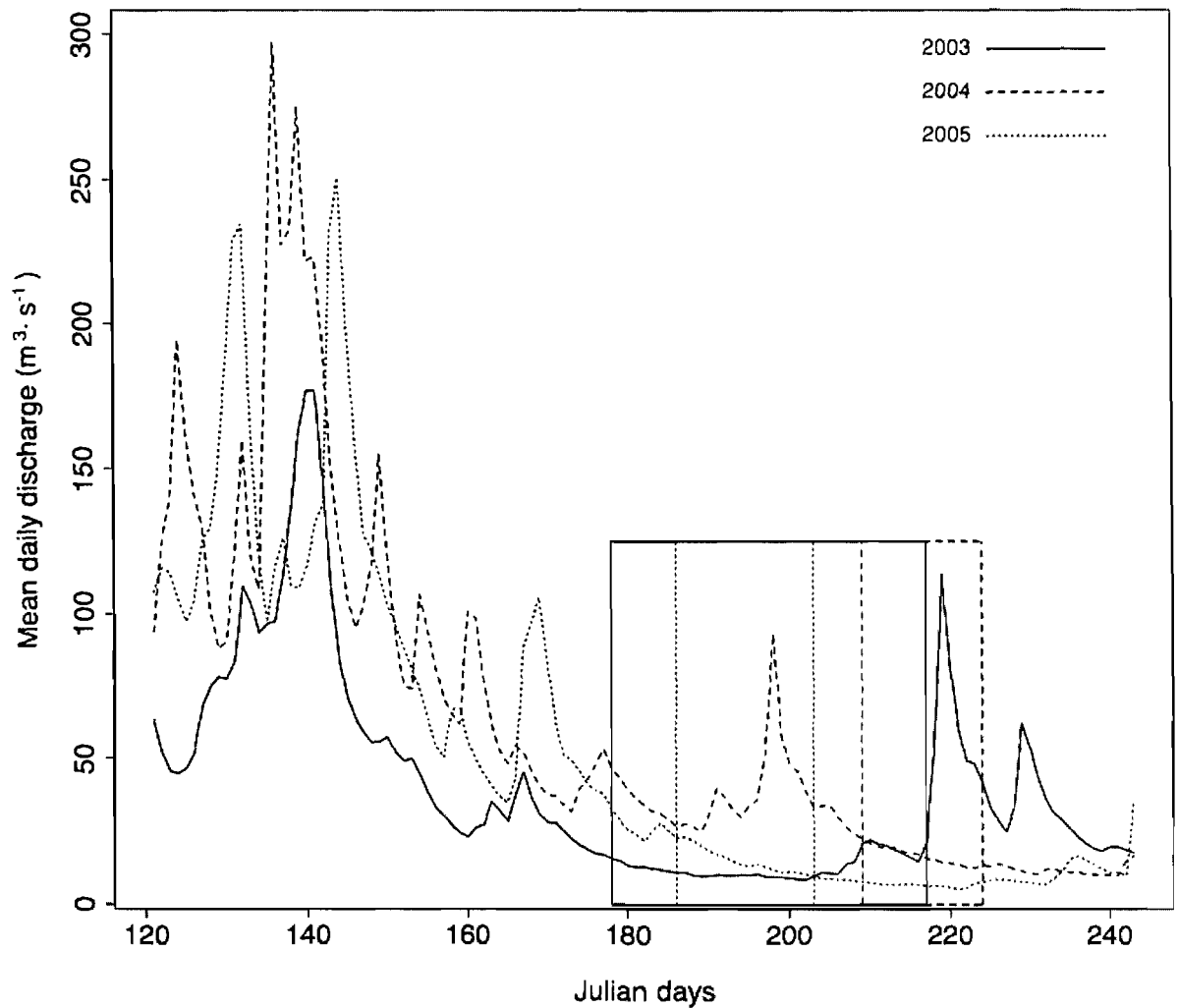


Figure 4. Annual hydrographs of the mean daily discharge (in cubic meter per second) in the SMR for the 2003 (solid line), 2004 (dotted line), and 2005 (dotted-dashed line) summer periods, Julian days 121 to 243. Boxes show the sampling periods for respective summer. Source data from the hydrological monitoring of the gauging station #062803, located at 1.7 km upstream from river mouth on the northeast branch of the Saint-Marguerite River (SMR). Centre d'expertise hydrique du Québec. Ministère du Développement durable, de l'Environnement et des Parcs.

Strong statistically significant correlations were found between average parr density and RPSL for six of the nine combinations of sedimentary links and years (8 of the 9 at $p=0.10$) for which these correlations could be tested. Hence, our analyses generally support the hypothesis that average parr density tends to decrease from the upstream to the downstream limit of sedimentary links. By extension, the present study also supports the suggestion that sedimentary links may play a role in structuring the spatial distribution of the parr. This interpretation is similar to that proposed by Rice et al. (2001) for macro-invertebrates. However, a detailed comparison between the results of the present study and those of Rice et al. (2001a) is hindered by the difference in the statistical methods used to assess the effect of sedimentary links on the biota. These authors compared dissimilarity indices calculated for pairs of samples collected around lateral sediment source (*i.e.* limits of sedimentary links) to indices calculated for pairs of samples within sedimentary links. They found that dissimilarity indices were larger between sites that straddled limits of sedimentary links than between sites within links. Visual examination of their Figures 6 and 7 nevertheless suggests that, as in the present study, sedimentary links could contribute to explain the distribution patterns of the biota on most occasions.

The perceived role of sedimentary links in structuring parr distribution varied between years. While the correlations between average parr density and RPSL were always negative (indicating a decrease of parr density from the upstream to the downstream limit of sedimentary links in all links and all years) these correlations changed from statistically significant in one year to not statistically significant at $p=0.05$ in another year for three of the four sedimentary links studied (Table 4). However, even if this may indicate that the correlation is absent between the variables, it may

also be caused by the lack of detection power of the analysis or the simply the noise in our data. The inter annual variability of the correlation between average parr density and RPSL may be related to two attributes that can affect fish distribution patterns and that can vary among years. First, fish distribution patterns have been suggested to vary with average fish density (Rangeley and Kramer 1998; Shepherd and Litvak 2004). Results obtained for L1 are consistent with the suggestion that changes in average parr density in this link (2.5-fold difference; $p < 0.027$) between 2004 (11.40 ± 3.55 parr $\cdot 100\text{m}^{-2}$) and 2005 (4.60 ± 2.88 parr $\cdot 100\text{m}^{-2}$) may affect the correlation between parr density and RPSL (not statistically significant in 2004 but significant in 2005 at lower densities). However, the statistical significance of the correlation between average parr density and RPSL also changed between years for L4 and L6 but average parr density did not vary significantly between years in these sedimentary links. Second, given the propensity of parr of Atlantic salmon to select a habitat based on flow velocity and water depth (Morantz et al. 1987; Heggenes e al. 1991; Guay et al. 2000), it could be suggested that flow variations between years may affect the correlation between average parr density and RPSL. This issue is difficult to address because flow often determined the time at which sampling for fish occurred during the present study. For instance, the average flow in the SMR in July 2004 was 1.4- to 1.5-fold higher than that in 2003 and 2005. This forced us to delay the description of fish distribution in 2004 to July 27th. One consequence of this delay is that the sampling periods used to quantify fish distribution in 2004 and 2005 do not overlap (Figure 4). It is unclear if time of sampling could affect the perceived relationship between average parr density and RPSL. Nevertheless, few findings indicate that flow (or even time of sampling

within the summer) may not be responsible for the presence or the lack of statistically significant correlations between average parr density and RPSL. Despite relatively similar flows during the sampling periods (and an overlap in the timing of the sampling), the correlation between average parr density and RPSL in L6 changed from not statistically significant in 2003 to statistically significant in 2005 (Table 4). In contrast, while both the flow and the timing of the sampling varied widely among 2003, 2004, and 2005, the correlation between average parr density and RPSL was always statistically significant in L8. One element that may compromise any attempt (or its rationale) to confirm the existence, and to identify the causes, of inter-annual variations of the structuring effect of sedimentary links on the distribution of parr of Atlantic salmon is the range of the p-values associated with the correlations that are defined as statistically significant ($0.007 < p_{\text{perm}} < 0.048$) or not ($0.083 < p_{\text{perm}} < 0.097$) for eight of the nine combinations of sedimentary links and years for which this correlation could be tested. This situation is best illustrated by the finding of an unambiguously significant negative correlation ($r = -0.52$; $p_{\text{perm}} = 0.001$) between average parr density and RPSL when data from all reaches, sedimentary links, and years are combined. When compared to the percentage of boulders, which is the traditional environmental variable strongly correlated to parr densities (Heggenes 1991; Bouchard and Boisclair 2008), the correlation seems to be slightly lower ($r = 0.49$; $p_{\text{perm}} = 0.001$) than with RPSL. In addition, our results also suggest that percentage of boulders and RPSL are statistically and strongly correlated with each other ($r = -0.71$; $p_{\text{perm}} = 0.001$). Hence, while parr distribution may be affected by numerous environmental variables (Bouchard and Boisclair 2008), the present analyses suggest that the LDC formulated by Rice et al. (2001a) may be extended to low relief landscape (Davey and Lapointe

2007), and that this extension of the LCD contributes to explain the variation of fish distribution patterns along the upstream-downstream axis of rivers. In our study, the LDC explains about as much variation in parr densities than traditional environmental variables such as the percentage of boulders because both variables are highly correlated. However, the LDC may provide a conceptual framework that could explain more variation in other species distribution provided that they are correlated to other environmental features, such as habitat disposition, that cannot be described by a single environmental variable like in our study.

Acknowledgments

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CONCLUSION GÉNÉRALE

Le premier objectif de notre étude était d'évaluer l'applicabilité du LDC pour expliquer la distribution spatiale du périphyton et des poissons dans une rivière située dans le bouclier canadien. Premièrement, notre étude ne supporte pas l'hypothèse que la distribution du périphyton est structurée par les liens sédimentaires dans la rivière Sainte-Marguerite. En effet, la relation entre la biomasse de périphyton et la position relative dans un lien sédimentaire ne s'est avérée statistiquement significative que dans un seul des quatre liens sédimentaires étudié (L8), et ce de façon marginale ($p = 0.72$). De plus, la seule variable environnementale corrélée statistiquement avec le périphyton est le pourcentage combiné de caillou et galet ($r = 0.40$, $p_{perm} = 0.03$). Plusieurs hypothèses sont explorées pour expliquer l'absence de corrélation entre les deux variables : la haute variation spatiale du périphyton à l'échelle du microhabitat (Tett et al. 1978; Uehlinger 1991), la critique de la méthode d'échantillonnage (Barbour et al. 1999), la mobilité du substrat ainsi que l'abrasion durant un événement de crue (Biggs and Close 1989; Ruhrmann 1990; Cattaneo et al. 1997) et, finalement, le temps écoulé depuis la dernière crue (Uehlinger 1991; Biggs 1995). Dans le cas de notre étude, seule la dernière hypothèse ne peut être réfuté. En effet, le rétablissement de la biomasse et de la structure spatiale du périphyton après une crue dépend de l'intensité de cette dernière ainsi que du temps écoulé depuis le dernier événement (Uehlinger 1991; Biggs 1995). Or, notre échantillonnage s'est déroulé dans une période de moins de 4 semaines après une crue équivalente à plus de 3 fois la moyenne journalière annuelle dans la rivière Sainte-Marguerite. Plusieurs auteurs ont démontré qu'une telle crue

pourrait être suffisamment sévère pour perturber l'abondance et la structure spatiale du périphyton et que le rétablissement de celui-ci après un tel événement pourrait requérir de 4 à 10 semaines (Fisher and Grimm 1988; Biggs and Close 1989; Uehlinger 1991; Lohman et al. 1992; Biggs and Smith 2002). Dans ce contexte, il est difficile d'évaluer si l'absence de corrélation entre la biomasse de périphyton et la position relative dans le lien sédimentaire est réelle ou expliquée par le fait que la période de rétablissement depuis le dernier événement de crue n'a pas été suffisante lors de notre étude.

Deuxièmement, notre étude supporte l'hypothèse que la distribution des tacons est structurée par les liens sédimentaires dans la rivière Saint-Marguerite. En effet, la relation entre la densité de tacons et la position relative dans un lien sédimentaire s'est avérée statistiquement significative dans six des neuf combinaisons années et liens sédimentaires étudiés (8 des 9 à $p = 0.10$). Nos analyses montrent que les densités de tacons tendent à décroître de l'amont vers l'aval des liens sédimentaires. Cette interprétation est similaire à celle proposée par Rice et al. (2001) à propos des macroinvertébrés, même si la comparaison de nos résultats avec ceux de Rice et al. (2001) s'avère difficile notamment à cause de différences au niveau des méthodes statistiques utilisées. Nous suggérons que d'autres études du même type soient menées afin d'amasser plus d'information de manière à supporter nos hypothèses avec plus de certitude.

Le deuxième objectif de notre étude était d'évaluer la variabilité inter annuelle du rôle des liens sédimentaires sur la distribution des poissons. Malgré le fait que la corrélation entre la densité de tacons et la position relative dans un lien sédimentaire est toujours négative (indiquant une diminution de la densité de tacons de l'amont vers

l'aval des liens sédimentaires pour tous les liens et toutes les années), les corrélations d'une année à l'autre pour un même lien changent de statistiquement significative à statistiquement non significative dans trois dans quatre liens sédimentaires étudiés. Par contre, l'étendue des probabilités associées aux corrélations entre la densité de tacons et la position relative dans un lien sédimentaire pour huit des neuf combinaisons année et liens sédimentaires se situe entre $0.007 < p_{perm} < 0.048$ pour des corrélations qui sont définies comme statistiquement significative et $0.083 < p_{perm} < 0.097$ pour des corrélations qui sont définies comme statistiquement non significative. Ces légères variations pourraient s'expliquer par deux phénomènes qui varient d'année en année soient la variation inter annuelle en densité moyenne globale des poissons dans une rivière (Rangeley and Kramer 1998; Shepherd and Litvak 2004) et la variation inter annuelle dans le régime hydrographique de la rivière (Morantz et al. 1987; Heggenes et al. 1991; Guay et al. 2000). Finalement, une relation négative ($r = -0.52$) et statistiquement significative ($p_{perm} = 0.001$) est trouvée lorsque nous combinons les données de tous les sites, tous les liens sédimentaires et toutes les années. Lorsque nous utilisons une corrélation simple entre les densités de tacons et le pourcentage de blocs (variable classique utilisée pour décrire la distribution des tacons dans d'autres études; Heggenes 1991; Bouchard and Boisclair 2008), nous obtenons une corrélation similaire ($r = 0.49$; $p_{perm} = 0.001$). Dans les faits, la corrélation entre le pourcentage de blocs et la position relative dans un lien sédimentaire est hautement significative ($r = -0.71$; $p_{perm} = 0.001$). Ainsi, malgré le fait que la distribution des tacons dépende de nombreuses variables environnementales (Bouchard and Boisclair 2008), les résultats de notre étude suggèrent que le LDC, formulé par Rice et al. (2001) et remanié par Davey et Lapointe (2007), a le potentiel d'expliquer une partie importante de la variation du

patron de distribution des poissons dans l'axe amont-aval des rivières. Dans notre étude, le LDC explique autant de variation dans les densités de tacons qu'une variable environnementale traditionnelle (i.e. pourcentage de blocs) puisque ces deux variables sont hautement corrélées.

En conclusion, nos résultats montrent qu'une variable locale (i.e. le pourcentage de blocs) pourrait suffire à prédire adéquatement la qualité des habitats de tacons le long de la rivière étudiée. Bien que la position relative dans un lien sédimentaire donné par le LDC explique la distribution des tacons, l'information qu'elle apporte s'avère redondante à celle fournie par les variables locales. Notons, cependant, que cette étude a été menée sur une seule rivière du Québec. L'importance d'une variable locale pourrait avoir une influence différente sur la distribution des tacons dans d'autres rivières dont les caractéristiques contextuelles diffèrent de celle étudiée. De plus, le LDC présente un cadre conceptuel intéressant qui pourrait contribuer à expliquer plus de variation dans la distribution d'autres espèces qui répondent à d'autres caractéristiques fluviales, telles que la disposition relative d'habitats dans une rivière, qui ne peut être décrite par une seule variable environnementale comme dans notre étude. Par conséquent, il serait intéressant de mener des études similaires à celle-ci sur des rivières et des espèces présentant des organisations spatiales différentes de la rivière Sainte-Marguerite et des tacons.

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Annexe

Tableau Annexe. Données brutes récoltées pendant l'échantillonnage et utilisées pour les analyses statistiques.

Année	Lien	Site #	DFRM (en Km)	Densité de tacons (en poisson·100 m ⁻³)	Biomasse de périphyton (en mg Chl <i>a</i> ·m ⁻³)	RPSL	Argile (en %)	Limon (en %)	Sable (en %)	Gravier (en %)	Caillou (en %)	Galet (en %)	Bloc (en %)	Bloc métrique (en %)	Profondeur (en m)	Vitesse (m ² ·s)
2003	L6	247	57,375	5,50	-	0,13	0,00	1,92	8,42	27,83	23,67	33,67	4,42	0,08	0,36	0,26
2003	L6	242	56,010	10,44	-	0,21	0,00	1,00	3,26	24,56	27,51	30,74	12,94	0,00	0,29	0,34
2003	L6	234	54,195	5,75	-	0,31	0,00	0,00	3,25	51,56	35,41	9,78	0,00	0,00	0,25	0,51
2003	L6	222	51,460	1,31	-	0,47	0,00	0,00	7,08	47,17	31,58	10,83	3,17	0,17	0,41	0,32
2003	L6	193	45,011	5,00	-	0,85	0,00	4,17	27,16	64,60	3,99	0,08	0,00	0,00	0,62	0,21
2003	L6	188	43,487	2,25	-	0,94	0,92	4,50	41,08	25,92	20,81	6,77	0,00	0,00	0,64	0,20
2003	L8	176	40,080	10,50	-	0,06	0,00	0,00	0,67	8,29	6,69	26,01	52,50	5,84	0,52	0,58
2003	L8	166	37,968	15,88	-	0,20	0,00	0,00	2,66	33,90	34,47	24,22	4,75	0,00	0,43	0,58
2003	L8	160	36,131	6,31	-	0,33	0,00	1,18	7,28	16,70	23,49	47,84	3,35	0,18	0,49	0,29
2003	L8	156	34,915	2,06	-	0,41	0,00	0,08	3,41	29,28	29,27	37,95	0,00	0,00	0,46	0,47
2003	L8	146	33,642	3,13	-	0,50	0,08	0,00	26,43	39,65	21,15	12,68	0,00	0,00	0,59	0,36
2003	L8	135	30,990	5,44	-	0,69	1,73	2,15	3,92	86,03	4,93	0,91	0,33	0,00	0,50	0,44
2003	L8	130	29,557	0,69	-	0,79	2,32	1,33	56,83	37,18	1,50	0,83	0,00	0,00	0,52	0,31
2004	L1	358	86,480	14,25	-	0,40	0,00	0,50	5,63	9,40	19,60	34,93	26,87	3,07	0,43	0,52
2004	L1	357	86,201	9,75	-	0,51	0,00	0,07	6,07	12,73	29,67	41,43	8,30	1,23	0,34	0,50
2004	L1	355	85,763	15,00	-	0,68	0,00	0,20	6,23	18,37	34,83	37,60	2,73	0,03	0,32	0,46
2004	L1	354	85,481	6,25	-	0,79	0,00	2,00	5,77	23,53	37,33	30,10	1,23	0,03	0,32	0,43
2004	L1	353	85,142	11,75	-	0,91	0,00	4,83	24,33	22,33	30,13	18,20	0,17	0,00	0,51	0,29
2004	L4	292	69,184	18,25	-	0,03	0,00	0,10	3,20	5,87	17,20	32,83	34,17	6,63	0,47	0,55
2004	L4	289	68,387	11,08	-	0,26	0,00	0,07	5,70	6,33	17,53	40,50	28,67	1,20	0,44	0,56
2004	L4	288	67,983	3,50	-	0,37	0,00	0,00	5,47	10,53	26,67	34,67	22,50	0,17	0,48	0,41
2004	L4	286	67,525	6,50	-	0,51	0,00	0,03	10,57	19,23	31,33	28,80	7,70	2,33	0,46	0,34
2004	L4	285	66,993	3,50	-	0,66	0,67	12,83	11,13	18,87	30,57	20,20	5,40	0,33	0,60	0,41
2004	L4	283	66,537	1,79	-	0,79	0,03	7,87	10,47	56,43	19,27	5,87	0,07	0,00	0,62	0,30
2004	L4	282	66,229	1,46	-	0,88	0,00	0,17	32,83	30,50	25,07	11,40	0,03	0,00	0,45	0,37
2004	L8	176	40,080	6,75	-	0,06	0,00	0,00	4,37	8,47	7,33	19,00	39,33	21,50	0,60	0,64

2004	L8	172	38,978	9,83	-	0,13	0,00	0,00	7,00	9,00	9,50	35,50	36,83	2,17	0,70	0,45
2004	L8	166	37,962	2,75	-	0,20	0,00	0,00	7,50	14,63	31,83	38,00	7,87	0,17	0,47	0,55
2004	L8	163	36,921	10,08	-	0,27	0,00	0,00	7,77	11,60	24,33	37,67	9,63	9,00	0,64	0,55
2004	L8	156	34,912	4,17	-	0,41	0,00	0,37	16,33	27,63	32,83	22,83	0,00	0,00	0,53	0,40
2004	L8	145	33,379	1,58	-	0,52	0,00	0,00	2,43	13,10	45,17	33,63	2,50	3,17	0,55	0,56
2004	L8	130	29,551	2,00	-	0,79	3,17	0,00	34,67	52,63	6,53	1,47	1,53	0,00	0,69	0,34
2005	L1	358	86,480	6,90	1,07	0,40	0,00	0,02	6,37	5,83	15,23	43,97	21,93	6,65	0,43	0,68
2005	L1	357	86,201	8,38	1,00	0,51	0,00	0,00	6,10	11,58	21,97	45,18	14,17	0,92	0,31	0,53
2005	L1	355	85,763	3,58	1,14	0,68	0,00	0,03	6,80	13,17	23,48	50,77	5,00	0,00	0,33	0,47
2005	L1	354	85,481	1,96	1,14	0,79	0,00	0,92	7,13	19,53	28,92	42,58	0,92	0,00	0,28	0,45
2005	L1	353	85,142	2,21	1,02	0,91	0,00	2,90	17,83	26,15	25,65	26,97	0,50	0,00	0,51	0,41
2005	L4	292	69,184	5,83	0,98	0,03	0,00	0,02	2,32	7,27	11,68	25,38	46,50	6,83	0,41	0,38
2005	L4	289	68,387	5,63	0,92	0,26	0,00	0,05	2,95	9,05	18,88	34,90	31,83	2,33	0,37	0,35
2005	L4	288	67,983	7,54	1,19	0,37	0,00	0,00	3,63	12,93	25,22	35,33	22,47	0,42	0,40	0,30
2005	L4	286	67,525	7,33	1,17	0,51	0,00	1,20	4,82	18,32	29,70	34,38	8,08	3,50	0,40	0,21
2005	L4	285	66,993	4,71	0,98	0,66	2,92	0,27	11,63	28,50	27,42	22,78	4,33	2,15	0,43	0,23
2005	L4	283	66,537	1,75	0,92	0,79	0,00	8,70	17,63	43,37	24,63	5,67	0,00	0,00	0,48	0,17
2005	L4	282	66,229	4,71	0,85	0,88	0,00	7,90	39,48	22,07	18,15	12,32	0,08	0,00	0,29	0,23
2005	L6	253	59,157	10,00	0,92	0,02	0,00	1,93	11,10	11,52	13,33	41,53	20,58	0,00	0,39	0,32
2005	L6	248	57,507	6,56	1,13	0,12	0,00	9,77	6,73	12,55	19,33	37,67	13,95	0,00	0,44	0,33
2005	L6	242	56,011	9,33	2,44	0,21	0,00	23,40	0,90	9,67	15,55	36,10	14,38	0,00	0,34	0,31
2005	L6	232	53,677	7,19	1,71	0,34	0,00	4,80	6,20	23,75	32,22	29,78	2,42	0,83	0,33	0,37
2005	L6	224	51,748	3,13	1,68	0,46	0,00	3,17	7,12	22,47	29,00	35,12	3,13	0,00	0,35	0,32
2005	L6	216	49,693	3,58	2,04	0,58	0,00	11,47	8,70	31,63	28,00	15,95	2,42	1,83	0,41	0,24
2005	L6	190	44,076	2,56	0,52	0,90	0,00	4,02	55,85	28,17	3,17	5,82	2,98	0,00	0,62	0,16
2005	L8	176	40,080	7,27	1,17	0,06	0,00	0,12	3,00	10,72	7,93	17,13	43,58	17,52	0,59	0,59
2005	L8	172	38,978	12,69	1,06	0,13	0,00	1,12	9,48	12,88	8,03	23,40	41,33	3,75	0,64	0,46
2005	L8	163	36,921	11,02	1,42	0,27	0,00	0,03	5,43	16,40	19,78	37,17	15,03	6,15	0,62	0,53
2005	L8	156	34,912	7,63	1,30	0,41	0,00	3,27	10,80	24,92	31,60	29,27	0,15	0,00	0,49	0,36
2005	L8	145	33,379	4,56	0,91	0,52	1,23	2,58	7,93	18,87	34,42	32,37	0,85	1,75	0,63	0,36
2005	L8	130	29,551	3,46	0,45	0,79	0,97	0,08	53,75	43,00	0,87	1,08	0,25	0,00	0,58	0,31