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Biomasses et compositions relatives des communautés de macroinvertébrés associées à différents types d'habitats au lac Saint-Pierre (Québec, Canada)

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Biomasses et compositions relatives des communautés de macroinvertébrés associées à différents types d'habitats au lac Saint-Pierre (Québec, Canada)

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RÉSUMÉ

La partie sud du lac Saint-Pierre (fleuve Saint-Laurent, Québec), reçoit d'importantes concentrations de nutriments qui contribuent au développement, en amont, d'un imposant lit de végétation agissant comme un marais-filtrant naturel. La réduction de la concentration de nitrate qui en découle modifie la communauté de métaphyton en aval, passant de chlorophytes à la cyanobactérie *Lyngbya wollei*, avec des conséquences inconnues sur les invertébrés phytophiles. Les objectifs de cette thèse étaient de comparer les communautés de macroinvertébrés dans les macrophytes submergées, de l'amont vers l'aval, et de déterminer l'influence de deux types de métaphyton (Chlorophycées et Cyanobactéries) sur la biomasse et la composition taxonomique des macroinvertébrés. La biomasse totale des invertébrés a diminué de ~95 à <15 mg g^{-1} de macrophytes de l'amont vers l'aval, en corrélation avec la diminution de la biomasse des macrophytes. Les taxons favorisés par les conditions eutrophes de l'amont (Chironomides, Oligochètes) ont été remplacés par des taxons plus mobiles en aval (Amphipodes), aptes à utiliser l'hétérogénéité de l'habitat. Les communautés de macroinvertébrés différaient aussi entre les types de végétation. Les Gastéropodes dominaient la biomasse des invertébrés dans les macrophytes et les chlorophytes, alors que les cyanobactéries supportaient une biomasse plus élevée d'Amphipodes. Les chlorophytes supportaient une biomasse importante de macroinvertébrés, mais leur contribution à la biomasse totale des macroinvertébrés de la station était négligeable comparativement aux macrophytes. En aval, cependant, la cyanobactérie filamenteuse (*Lyngbya wollei*) supportait près de 25% de la biomasse de macroinvertébrés. La diminution en aval de la biomasse et de

l'accessibilité des macroinvertébrés dans les cyanobactéries pourraient réduire l'accès à cette ressource pour les poissons littoraux et les oiseaux aquatiques.

ABSTRACT

Along the south shore of the fluvial Lake Saint-Pierre (St. Lawrence River, Québec), important inputs of nutrients contribute to the development of a large weed bed upstream, which acts like a natural water purification system. The resulting reduction in nitrate modifies the metaphyton community downstream, where chlorophytes are replaced by the cyanobacterium *Lyngbya wollei*, a shift exerting unknown consequences on phytophilous invertebrates. The objectives of this study were to compare the macroinvertebrate communities inhabiting the submerged macrophytes along an upstream-downstream gradient, and to determine the influence of the two type of metaphyton (Chlorophytes and Cyanobacteria) on the biomass and taxonomic composition of macroinvertebrates. The total biomass of invertebrates was reduced from ~95 upstream to <15 mg g^{-1} of macrophytes downstream; this reduction of invertebrate biomass was also correlated to lower vegetation biomass. Taxa associated to eutrophic conditions in the upstream area (Chironomids, Oligochaetes) were replaced by more mobile taxa downstream (Amphipods), better adapted to use the heterogeneity of this habitat. Macroinvertebrate communities also differed between vegetation types. Gastropods dominated the biomass of invertebrates in macrophytes and chlorophyfes, while cyanobacteria supported a higher biomass of Amphipods. Chlorophytes supported an important biomass of macroinvertebrate, but their contribution to the total biomass of the invertebrate community at a station was negligible, compared to macrophytes. However, the filamentous cyanobacterium (*Lyngbya wollei*) found at the downstream sites supported almost 25% of the total biomass of macroinvertebrates. Consequently, the reduction of the macroinvertebrate

biomass downstream, combined to reduced accessibility of the invertebrates in cyanobacteria could result in lower resource availability for littoral fish and aquatic birds.

MOTS CLÉS

Cyanobactéries, lac Saint-Pierre, *Lyngbya wollei*, macroinvertébrés, macrophytes, métaphyton, nitrate.

KEY WORDS

Cyanobacteria, *Lyngbya wollei*, Lake Saint-Pierre, macroinvertebrates, macrophytes, metaphyton, nitrate.

TABLE DES MATIÈRES

LISTE DES TABLEAUX

CHAPITRE 1

CHAPITRE 2

LISTE DES FIGURES

CHAPITRE 1

CHAPITRE 2

LISTE DES ABRÉVIATIONS

Al= Algues filamenteuses (ou métaphyton)

ANC= Ancylidae

AMP= Amphipoda

BIT= Bithynidae

CHI= Chironomidae

CLA= Cladocera

COL= Couleur

COND= Conductivité

COP= Copepoda

DIN= Azote inorganique dissous (Dissolved inorganic nitrogen)

DIST= Distance de l'embouchure des effluents

DM ou dm= Masse sèche (Dry mass)

DO= Aval (Downstream)

DOC= Carbone organique dissous

GAS= Gastropoda

HYD= Hydra

HCA= Hydrachnida

MACRO= Macrophytes

SM= Matières en suspension (Suspended matter)

OLI= Oligochaeta

OTH= Autres (somme de tous les taxons de macroinvertébrés ayant une biomasse <0.5 mg g^{-1} dm de macrophytes)

OST= Ostracoda

PHY= Physidae

PLA= Turbellaria

PBD= Planorbidae

TDP= Phosphore total dissous (total dissolved phosphorus)

TN= Azote total (total nitrogen)

TRI= Trichoptera

UP= Amont (Upstream)

VAL= Valvatidae

VIV= Viviparidae

ZOO= Zooplancton (Cladocera, Copepoda et Hydra)

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INTRODUCTION GÉNÉRALE

Les macroinvertébrés phytophiles sont fréquemment utilisés comme indicateurs biologiques pour le suivi de l'état des écosystèmes aquatiques (Stephenson et al., 1994; Pinel-Alloul et al., 1996; Kashian et Burton, 2000; Nichols et Norris, 2006; Tall et al., 2008), comme par exemple dans les cas d'eutrophisation accélérée des milieux humides (Batzer et al., 1999; Liston et Trexler, 2005). L'intérêt que les macroinvertébrés suscitent réside tout d'abord dans leur importance en tant que maillon central du réseau trophique. Ils font le lien entre les producteurs primaires et les autres consommateurs tels que les poissons, les amphibiens et les oiseaux aquatiques (Krull, 1970; Mittlebach, 1981). La diversité des macroinvertébrés résulte de la grande variété de cycles vitaux (long ou court), de modes d'alimentation (détritivores, brouteurs, filtreurs, prédateurs, etc.) et de locomotion (nageurs, fouisseurs, sessiles, etc.), témoignant des différences majeures de capacité d'adaptation de chaque taxon aux variations de l'environnement (Rosenberg et Resh, 1993; Österling et Pihl, 2001; White et Irvine, 2003; De Sousa et al., 2008). Les communautés d'invertébrés peuvent être caractérisées selon la biomasse, l'abondance, la richesse spécifique, les relations entre les espèces et les variations temporelles et spatiales de la communauté (Rosenberg et Resh, 1993). La résistance à la pollution, aux fortes concentrations en nutriments et à l'anoxie dans la colonne d'eau diffère aussi entre les groupes (Shieh et al., 1999; McCormick et al., 2004; Ortiz et Puig, 2007; De Sousa et al., 2008), permettant ainsi de déterminer quels facteurs de stress présents dans le milieu affectent la communauté. Une récente étude réalisée au lac Saint-Pierre a démontré le potentiel de l'utilisation des

communautés d'invertébrés associés aux macrophytes émergentes et aux sédiments pour distinguer les sites fluviaux des sites impactés par l'apport de nutriments des tributaires (Tall et al., 2008).

Au lac Saint-Pierre, le développement massif de végétation à l'embouchure des tributaires situés en amont a pour effet de ralentir le courant dans les herbiers, favorisant la sédimentation des particules et la rétention des nutriments (Hudon et Carignan, 2008). En présence de conditions favorables, de grandes masses d'algues filamenteuses vertes se développent également dans cette région (Vis et al., 2008). Ce système agit comme un marais-filtrant naturel qui purifie les eaux provenant des rejets agricoles. Plusieurs expériences en mésocosmes ont démontré que la nitrification-dénitrification de l'azote par les bactéries constitue le principal mécanisme de rétention de nutriments dans les milieux humides artificiels (Tanner et al., 2002; Stottmeister et al., 2003; Maltais-Landry et al., 2009). La concentration de nitrate de la masse d'eau du sud du lac Saint-Pierre varie de >300 $\mu g\ N\ L^{-1}$ à l'embouchure des tributaires à <20 $\mu g\ N\ L^{-1}$ en aval des milieux humides (Vis et al., 2008), reproduisant ainsi les résultats d'expériences de mésocosmes à l'échelle de l'écosystème. La diminution de nitrate est aussi associée à un changement dans la communauté d'algues filamenteuses, passant d'une communauté diversifiée de chlorophytes en amont à une monoculture de la cyanobactérie benthique *Lyngbya wollei* en aval (Vis et al., 2008).

La prolifération d'algues filamenteuses (ou métaphyton) est un problème récurrent des écosystèmes aquatiques (Stevenson et al., 1996). Une importante masse d'algues peut entraîner notamment des épisodes d'anoxie dans la colonne d'eau, une

augmentation du pH suite à l'assimilation du HCO_3 ou le remplacement des autres producteurs primaires tel que les macrophytes. Le métaphyton peut aussi avoir des conséquences économiques négatives en réduisant l'attrait des plans d'eau pour la baignade et la navigation de plaisance. Cependant, ces producteurs primaires représentent une source importante de nourriture et d'abri pour les invertébrés (Dodds et Gudder, 1992; Stevenson et al., 1996; Salovius et Bondsdorff, 2004).

Présentation du site d'étude

Le lac Saint-Pierre (fleuve Saint-Laurent, Québec, Canada) est le dernier lac fluvial d'importance avant l'estuaire du Saint-Laurent. Il a une superficie d'environ 300 km^2. Sa profondeur moyenne (~3m) ainsi que la vitesse moyenne du courant (<0,5 m s^{-1}) sont faibles dans l'ensemble du lac, à l'exception d'un chenal de navigation central, excavé progressivement depuis le milieu du $XIX^{ième}$ siècle (>11,3 m, >0,5 m s^{-1}). Les conditions physiques et chimiques sont très variables spatialement, particulièrement entre les masses d'eau du nord, riches (TP 30-175 µg L^{-1}) et brunes, du centre, claires et peu turbides (SM 2-12 mg L^{-1}), et du sud, beaucoup de matières en suspension (SM 10-50 mg L^{-1}) et concentrations élevées en nutriments (TP ≥30 µg L^{-1}) (Hudon et Carignan, 2008; Vis et al., 2007). La production primaire annuelle est d'environ 105 g C m^{-2} a^{-1} (Vis et al., 2007). Les milieux humides couvrent jusqu'à 85% de la superficie du lac, bien qu'ils puissent diminuer de près de 50% lors des années de faible niveau d'eau (Vis et al., 2007). Ces

milieux humides supportent une importante biodiversité, servant entre autre de zone de reproduction ou de repos pour plus de 300 espèces de poissons et d'oiseaux.

Le côté sud du lac, en particulier, est caractérisé par des problèmes d'eutrophisation due à un apport excessif de nutriments par plusieurs tributaires situés en amont et qui drainent des bassins versants agricoles. Les concentrations élevées de nutriments favorisent la croissance d'un imposant lit de macrophytes submergées et émergentes aux abords de l'embouchure des tributaires. Les fortes biomasses de végétation favorisent la rétention des nutriments dans le milieu, la diminution de l'impact des vents sur les berges et le ralentissement du courant (Stevenson et al., 1996; Clarke, 2002).

Changements dans la communauté suite à la diminution de nitrate

Un apport important de phosphate et de nitrate, comme cela est observé en amont, entraîne l'eutrophisation du système, favorisant le développement d'importantes biomasses de producteurs primaires (revue de littérature par Carpenter et al., 1998). Ces biomasses élevées de producteurs primaires supporteront ainsi des densités et des biomasses plus élevées de macroinvertébrés (Cyr et Downing, 1988a; Shieh et al., 1999; Giorgi et al., 2005; Rennie et Jackson, 2005). Cependant, la diminution du nitrate dans la colonne d'eau, tel qu'observée en aval, serait susceptible de modifier les communautés végétales, non seulement par la diminution de la biomasse mais aussi en occasionnant un changement dans les espèces

dominantes et en modifiant la teneur en nutriments des producteurs primaires dont les invertébrés se nourrissent (Moss, 1976; Kraufvelin et al., 2006).

Plusieurs études ont montré l'impact de concentrations élevées de phosphate sur les invertébrés aquatiques (pour des exemples, voir Cyr et Downing, 1988a; Shieh et al., 1999; Shieh et al., 2003; McCormick et al., 2004). Cependant, peu d'études, à notre connaissance, ont évalué les changements induits par une diminution du nitrate sur les communautés de macroinvertébrés. Il est donc difficile de prévoir quels seront les effets de ce changement dans les conditions du milieu sur les différents taxa du lac Saint-Pierre. Néanmoins, en se basant sur les résultats des études concernant l'effet du phosphate sur les macroinvertébres, on peut supposer que les taxons caractéristiques des milieux eutrophes, tel que les oligochètes et les chironomides, seront dominants aux sites en amont (Shieh et al., 1999; McCormick et al., 2004; Tall et al., 2008). De plus, on peut s'attendre à ce que des milieux humides recevant des rejets agricoles présentent une plus faible richesse spécifique que ce qui était originellement retrouvé (Chipps et al., 2006). On peut donc présumer que les taxons plus sensibles aux perturbations, particulièrement les grandes larves d'insectes (Shieh et al., 1999; McCormick et al., 2004; Ortiz et Puig, 2005; De Sousa et al., 2008), seront favorisés par les faibles concentrations en nitrate observées en aval. La communauté de macroinvertébrés épiphytiques du côté sud du lac Saint-Pierre pourrait donc présenter des différences significatives entre l'amont et l'aval.

Comparaison de la communauté dans différents types de végétation

Cependant, le passage d'une communauté de chlorophytes en amont à une communauté de cyanobactéries en aval pourrait aussi modifier la communauté de macroinvertébrés. Les algues filamenteuses et les macrophytes peuvent être des sources de nourriture pour les macroinvertébrés épiphytiques (Lodge et al., 1998; Jones et al., 1999; Salovius et Bonsdorff, 2004), bien qu'ils servent principalement de support aux particules en suspension et aux épiphytes dont ceux-ci se nourrissent (Cattaneo et al., 1993, Jeffries, 1993; Brönmark et Vermaat, 1998). Le niveau de complexité de l'habitat influencera donc d'autant plus l'espace disponible aux macroinvertébrés pour se nourrir (Jeffries, 1993; García-Criado et al., 2005; McAbendroth et al., 2005). Une forte densité et une architecture complexe de la végétation offrent aussi un abri plus efficace contre les prédateurs vertébrés tel que les poissons (Crowder et Cooper, 1982; Dodds et Gudder, 1992). Ainsi, les algues filamenteuses procurent une meilleure protection aux ostracodes que les feuilles non-disséquées de la Vallisnérie (Mbahinzireki et al., 1991). Cependant, certaines études n'ont pu démontrer de relation entre le niveau de complexité du couvert végétal et la communauté de macroinvertébrés (Cyr et Downing, 1988b).

En plus des différences architecturales, les algues filamenteuses et les macrophytes présentent des caractéristiques écologiques très variées. Ainsi, dans les milieux lotiques, les algues filamenteuses sont souvent éphémères et susceptibles à la dérive, ce qui rend ce type d'habitat plus instable et imprévisible, diminuant la richesse et l'abondance de la communauté d'invertébrés (Norkko et al., 2000; Salovius et Kraufvelin, 2004). La capacité des invertébrés à coloniser les algues

filamenteuses dépend en grande partie de leurs caractéristiques fonctionnelles (Norkko et al., 2000). Ainsi, les espèces plus mobiles telles que les chironomides et les ostracodes sont plus aptes à utiliser les algues filamenteuses et à résister à la dérive, alors que les herbivores et les animaux moins mobiles comme les gastéropodes préfèrent les plantes vasculaires (Norkko et al., 2000; Salovius et Kraufvelin, 2004). De plus, les invertébrés capables de se déplacer aisément pourront occuper durant le jour la végétation offrant la meilleure protection plutôt que la meilleure valeur nutritive alors que la faune plus sédentaire devrait trouver le meilleur compromis entre la protection contre la prédation et l'accès aux ressources de qualité (Kraufvelin et al., 2006, Mbahinzireki et al., 1991).

Par conséquent, les communautés de macroinvertébrés retrouvées dans les macrophytes vasculaires et dans les algues filamenteuses présentent souvent des différences notables. En général, les algues filamenteuses ont une capacité de support importante puisqu'elles offrent un bon abri face aux prédateurs et une variété de ressources nutritives (détritus, épiphytes) (Kraufvelin et al., 2006). Cependant, certaines études ont montré que la richesse taxonomique et la diversité étaient plus importantes dans les macrophytes, malgré une abondance et une biomasse de macroinvertébrés plus élevées aux sites où les algues filamenteuses étaient dominantes (McCreary Waters et San Giovanni, 2002). D'autres ont plutôt établi que la biomasse était plus faible dans les algues filamenteuses alors que la densité était plus grande dans les milieux dominés par les macrophytes (Olson et al., 1995). Ces résultats en apparence contradictoires pourraient provenir du fait que la réponse des invertébrés à la végétation n'est pas linéaire : une augmentation de 30 à 50% de la

couverture spatiale par les algues filamenteuses est bénéfique pour la communauté épibenthique, puisqu'elle augmente l'hétérogénéité et la variété de ressources disponibles, tandis qu'une augmentation de 90% est négative pour plusieurs groupes (Pihl et al., 1995).

Au lac Saint-Pierre, il a été démontré que la biomasse des macroinvertébrés était plus élevée dans les algues filamenteuses vertes que dans les macrophytes submergées et émergentes, alors que la diversité taxonomique était plutôt reliée aux conditions physiques et chimiques de l'eau (Tessier et al., 2007). Les macrophytes submergées occupent plus de 85% (260 km^2) de la superficie du lac entre juin et octobre (Vis et al., 2007). Les chlorophytes filamenteuses constituent donc un habitat localisé et éphémère, bien que supportant les biomasses d'invertébrés les plus élevées (Tessier et al., 2007). Par contre, la découverte en 2005 de cyanobactéries benthiques couvrant une surface importante du côté sud du lac pourrait modifier de façon inconnue la communauté de macroinvertébrés dans cette région. Des masses de *Lyngbya wollei* ont été observées dès le début de mai (observations personnelles) et leur position près des sédiments lors de l'échantillonnage devrait rendre ces masses plus stables que les masses flottantes de chlorophytes.

La présence de composés analogues à la saxitoxine dans les cellules de la *Lyngbya* (communication personnelle, C. Hudon et A. Cattaneo) pourrait diminuer le taux de croissance et de reproduction des herbivores, comme cela fut démontré avec la microcystine (Gérard et Poullain, 2005; Gérard et al., 2008). La présence de toxine peut par contre stimuler le broutage chez certaines espèces (Nagle et al., 1998; Camacho et Thacker, 2006; Capper et al., 2006). Par ailleurs, la carence en nitrate

dans la région pourrait se répercuter dans la qualité nutritive des cyanobactéries ou celle des épiphytes qu'elles supportent, en étant plus faible que celle des algues filamenteuses vertes. Bien que n'ayant jamais été caractérisée, la communauté d'épiphytes sur les algues filamenteuses au lac Saint-Pierre présente probablement des différences significatives au niveau des espèces entre l'amont et l'aval, en particulier dans les régions où les concentrations de nitrate sont faibles (Moss, 1976; Giorgi et al., 2005). Les invertébrés sont souvent sensibles à une variation dans le type et la qualité des ressources nutritives (Brendelberger, 1995; Kraufvelin et al., 2006; Schneider et Sager, 2007).

Puisque l'eutrophisation des milieux humides et la prolifération de cyanobactéries benthiques seront des problèmes majeurs au lac Saint-Pierre pour les années à venir, il est important de connaître la faune phytophile qui y est associée. Bien que les cyanobactéries ne soient pas considérées comme des algues au sens strict, leur architecture semblable à celle des chlorophytes reflète leur appartenance au même groupe fonctionnel, ce qui nous a permis de comparer les différents types de végétations dans le cadre de cette thèse.

Objectifs et hypothèses

Les deux principaux objectifs de cette thèse sont, tout d'abord, de comparer les communautés de macroinvertébrés dans les milieux humides riches de l'amont avec celles de l'aval, dans la région de faibles concentrations en nitrate. Pour ce faire, nous étudierons les communautés de macroinvertébrés phytophiles échantillonnées

dans un seul type de végétation, soit les macrophytes vasculaires. Les communautés seront comparées en termes de biomasse totale, de distribution en taille et de composition taxonomique. Deux stations d'échantillonnages seront situées dans la section du milieu humide située à 2-4 km de l'embouchure des rivières Yamaska et Saint-François, et trois stations situées à 9 km et plus en aval de l'embouchure des tributaires. Pour cet objectif, deux méthodes d'échantillonnage ont été utilisées, une boîte de plastique rectangulaire et un troubleau. L'utilisation de deux méthodes d'échantillonnage permettra de comparer la communauté de macroinvertébrés présente dans la colonne d'eau (troubleau) et celle retrouvée directement dans la végétation (boîte). Le troubleau devrait intercepter des organismes épibenthiques plus mobiles que sédentaires (Henke et Batzer, 2005). Ainsi, on s'attend à ce que les gros omnivores ou prédateurs bons nageurs se retrouvent plutôt dans la colonne d'eau, tandis que les petits détritivores ou herbivores devraient être plutôt retrouvés dans la végétation. Il sera donc possible de comparer les biomasses et les différents taxons capturés par les deux engins, dans le but de déterminer lequel est le plus approprié pour répondre à nos questions et ainsi diminuer la charge de travail de terrain et de laboratoire pour les futurs échantillonnages.

Le deuxième objectif de cette étude était de caractériser les communautés de macroinvertébrés supportées par différents types de végétation, soit les algues filamenteuses vertes, les cyanobactéries benthiques et les macrophytes vasculaires. Les communautés seront aussi comparées en termes de biomasse totale, de composition taxonomique et de distribution en taille. Seulement la boîte de plastique

a été utilisée lors de cet échantillonnage puisque les macroinvertébrés spécifiques à chaque type de végétation devaient être ciblés.

Pour atteindre ces deux objectifs, deux campagnes d'échantillonnage ont eu lieu, les 22-24 août 2006 et les 19-21 septembre 2006. Cependant, de fortes pluies à la mi-août ont entraîné l'augmentation rapide du niveau de l'eau du lac et le détachement vers l'aval des masses d'algues filamenteuses flottantes, rendant ainsi impossible la comparaison entre les chlorophytes et les cyanobactéries pour cette période d'échantillonnage. Seulement les échantillons du mois de septembre seront donc analysés pour cette thèse. Les abondances brutes obtenues par les échantillons de troubleaux du mois d'août sont cependant présentés en annexe (Annexe V)

La comparaison des communautés d'invertébrés permettra d'évaluer la biomasse et l'accessibilité des macroinvertébrés pour les organismes situés aux échelons supérieurs du réseau trophique. Il sera aussi possible de déterminer comment les changements subséquents dans la communauté végétale les influenceront. Ultimement, les modifications de la communauté de macroinvertébrés sur une vaste région du lac Saint-Pierre pourraient avoir un impact sur le reste du réseau trophique, particulièrement sur les poissons littoraux qui utilisent les milieux humides comme zone de fraie, d'alevinage et d'alimentation pour les juvéniles et les adultes.

Pour la comparaison entre les différents habitats végétaux, nous supposons que les algues filamenteuses supporteront une plus grande biomasse totale d'invertébrés, composée d'individus de plus grande taille parce qu'elles offrent une

meilleure protection que les macrophytes contre la prédation. Pour les chlorophytes, on s'attend à ce qu'elles soient un habitat important pour les taxons opportunistes, bien qu'il s'agisse d'une structure très localisée et éphémère (Tessier, 2007). Dans le cas des cyanobactéries, on s'attend à ce que la communauté des invertébrés y soit différente de celle qui se trouve associée aux chlorophytes et que la biomasse y soit plus faible. Bien que présentant les mêmes avantages sur le plan architectural, l'attrait des cyanobactéries pour les macroinvertébrés pourrait être moins prononcé que pour les chlorophytes en raison de la présence de composés nocifs et de la plus faible qualité nutritive des cyanobactéries ou de celle des épiphytes qu'elles supportent. Plusieurs facteurs indirects ou non-mesurés durant l'échantillonnage pourraient aussi avoir un impact sur les différents groupes de macroinvertébrés, comme par exemple la diminution de la concentration de l'oxygène dissous durant la nuit engendrée par les fortes biomasses d'algues filamenteuses (McCormick et al., 2004). On s'attend donc à ce que les groupes dominants diffèrent entre les deux types d'algues filamenteuses et les macrophytes, puisque la capacité d'adaptation à un habitat diffère selon le mode de vie de chaque taxon.

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CHAPITRE 1

Biomass gradient of phytophilous macroinvertebrate communities at increasing distance from nutrient-rich tributaries flowing into a large fluvial lake

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ABSTRACT

In the south-upstream area of Lake Saint-Pierre, a fluvial lake of the St. Lawrence River (Canada), the waters originating from two nutrient-rich tributaries became depleted in dissolved nutrients after flowing through a natural wetland. Over a 14-km distance, marked decreases in dissolved inorganic nitrogen (from 320 to 5 μg N L^{-1}), total phosphorus (from 29 to 9 μg P L^{-1}) and macrophyte biomass (from > 200 to < 100 g m^{-2}) occurred, coinciding with the appearance of benthic cyanobacterial mats (from 0 to 12 g m^{-2}). Phytophilous macroinvertebrate communities were compared along a distance gradient from inflow of tributaries, with 2 stations in the rich wetland and 3 in the downstream oligotrophic region. Macroinvertebrates closely associated with the vegetation were sampled with a rectangular plastic box (5.7L) closed directly on the macrophytes while a D-frame net (30cm width) allowed additional sampling of loosely-attached invertebrates in the water column. The plastic box sampled systematically higher biomass than the D-frame net, although the latter method captured more rare species. Total macroinvertebrate biomass (mg g^{-1} of macrophytes dry mass) measured with the plastic box dropped five-fold between upstream and downstream stations. Gastropods represented 47-92% of the community total biomass at all five stations. Dominant taxa of other groups shifted from taxa characteristic of eutrophic status (Oligochaetes and Chironomids) at the upstream stations to Amphipods and Bithynidae at the downstream stations. The three downstream stations also sustained systematically less total biomass of every size class, with no individuals larger than 4 mg found at these stations. Assimilation/transformation of nitrogen originating from agricultural tributaries by

wetlands in the upstream area induced a sharp reduction of the biomass of macrophytes and invertebrates downstream, thus potentially affecting the carrying capacity of the aquatic ecosystem.

INTRODUCTION

Wetlands are considered with growing interest as a purification system for agricultural and urban waste waters (Tanner et al., 2002; Stottmeister et al., 2003; Stewart and Downing, 2008). Aquatic environments receiving major inputs of agricultural runoffs experience elevated nutrient levels and changes in their biota, resulting in the disappearance of sensitive taxa, increased biomass of resistant species, and blooms of metaphyton (Moss, 1976; Valiela et al., 1997). Experiments measuring the level of contaminants and nutrients retained by different assemblages of aquatic plants demonstrated that the principal process occurring in constructed wetlands is microbial nitrification-denitrification, with the level of efficiency depending on the conditions of the mesocosm (Stottmeister et al., 2003; Ouellet-Plamondon et al., 2006; Maltais-Landry et al., 2009).

In Lake Saint-Pierre, a fluvial lake of the St. Lawrence River (Canada), farmland tributaries flow directly in a natural wetland supporting large amounts of submerged and emergent macrophytes. As water slowly makes its way through the vegetation, dissolved inorganic nitrogen concentrations decrease markedly: nitrate concentrations fell from >300 μg in the wetlands to <20 μg N L^{-1} downstream (Vis et

al., 2008). This wetland acts as a natural water-purifier system, reproducing mesocosm experiences at the scale of the ecosystem.

Macroinvertebrates are commonly used to evaluate and monitor the condition of aquatics systems (White and Irvine, 2003; McCormick et al., 2004; Ortiz and Puig, 2007; De Sousa et al., 2008). Macroinvertebrates responses to variations of their environment, including pollutants input, are taxon-specific (Rosenberg and Resh, 1993; McCormick et al., 2004). The importance of invertebrates also stems from their position at the center of the trophic network, between primary producers and higher predators. Environmental variables, such as nutrient concentrations, water current, depth, and light intensity are major factors affecting aquatic invertebrate communities (Power, 1992; White and Irvine, 2003; Baumgärtner et al., 2008). In particular, nutrient concentrations can directly influence type, abundance, and quality of available food resources (Cyr and Downing, 1988; Brendelberger, 1995; Schneider and Sager, 2007).

Macrophytes are an important substrate for macroinvertebrates, usually supporting higher biomass than the sediments and providing a more stable environment than metaphyton (Norkko et al., 2000; Della Bella et al., 2005). Macrophytes offer a suitable habitat to the epiphytic community by retaining nutrient-rich suspended matter and epiphytes that invertebrates forage on, reducing water current and wind exposure, offering protection against fish predation and returning nutrients from sediments to the water column (Crowder and Cooper, 1982; Gregg and Rose, 1982; Cattaneo, 1983; Dibble et al., 1996; Lodge et al., 1998; Jones et al., 1999; Clarke, 2002; Kraufvelin et al., 2006). Thus, macrophytes density and

diversity can affect both biomass and dominant taxa of the macroinvertebrate community (Brown et al., 1988; Cyr and Downing, 1988; Jeffries, 1993; Cheruvelil et al., 2002; Strayer et al., 2003; García-Criado et al., 2005; Giorgi et al., 2005; Thomaz et al., 2008), as invertebrates may show a preference for certain macrophyte species (Dudley and D'Antonio, 1991; Olson et al., 1995).

The main objective of this study was to compare phytophilous macroinvertebrate communities of the fluvial Lake Saint-Pierre between the upstream area, which was characterized by high nutrient concentrations and high submerged macrophyte biomass, and the downstream area, where nitrate was chronically deficient and submerged macrophyte beds were dispersed (Vis et al., 2008). The natural processes occurring along the south shore of Lake Saint-Pierre allowed to examine the effects of nutrient removal by wetlands on the macroinvertebrate community at the ecosystem scale. We expect that the upstream area will sustain higher biomass of macroinvertebrates and will be dominated by taxa characteristics of richer environments, such as Oligochaetes and Chironomids, while the more oligotrophic downstream area should exhibit a lower invertebrate biomass, dominated by taxa adapted to patchy environments, such as Amphipods and Zooplankton.

METHODS

Study site

Lake Saint-Pierre (LSP) (≈300 km^2; 46°12'N, 72 ° 49'W) supports wetlands with high biodiversity and was classified as a Ramsar site in 1998 and as a UNESCO

World Biosphere Reserve in 2000. Shallow shorelines (mean depth ~3m), slow current (<0.5 m s^{-1}) and gentle slopes allow growth of dense emergent and submerged aquatic vegetation, which can cover up to 85% of the lake (260 km^2, mean biomass 54 g dry mass m^{-2}) at the peak of the season (Hudon, 1997; Vis et al., 2007). A man-made navigation channel (≥11.3m deep, 250m wide) runs at the center of the lake, thus isolating three distinct water masses (north, central and south). The north and south water masses receive high nutrient inputs from farmland tributaries, causing the eutrophication of the shorelines, while the central mass is characterized by clear water coming from the Great Lakes (Hudon and Carignan, 2008). Sampling was carried out along the south shore of LSP, at five stations located at increasing distance of the mouth of two tributaries (St. François and Yamaska Rivers) (Figure 1). Stations 1 and 2 were located in the upstream area, where macrophyte biomass and nutrient concentrations were high. Station 2 was the only one where large mats of filamentous chlorophytes were observed. Stations 3, 4 and 5 were located further downstream, and were characterized by a lower biomass of macrophytes, accompanied by the benthic cyanobacterium *Lyngbya wollei*. These stations coincided with the previously documented gradient of water quality and vegetation types (Vis et al., 2008).

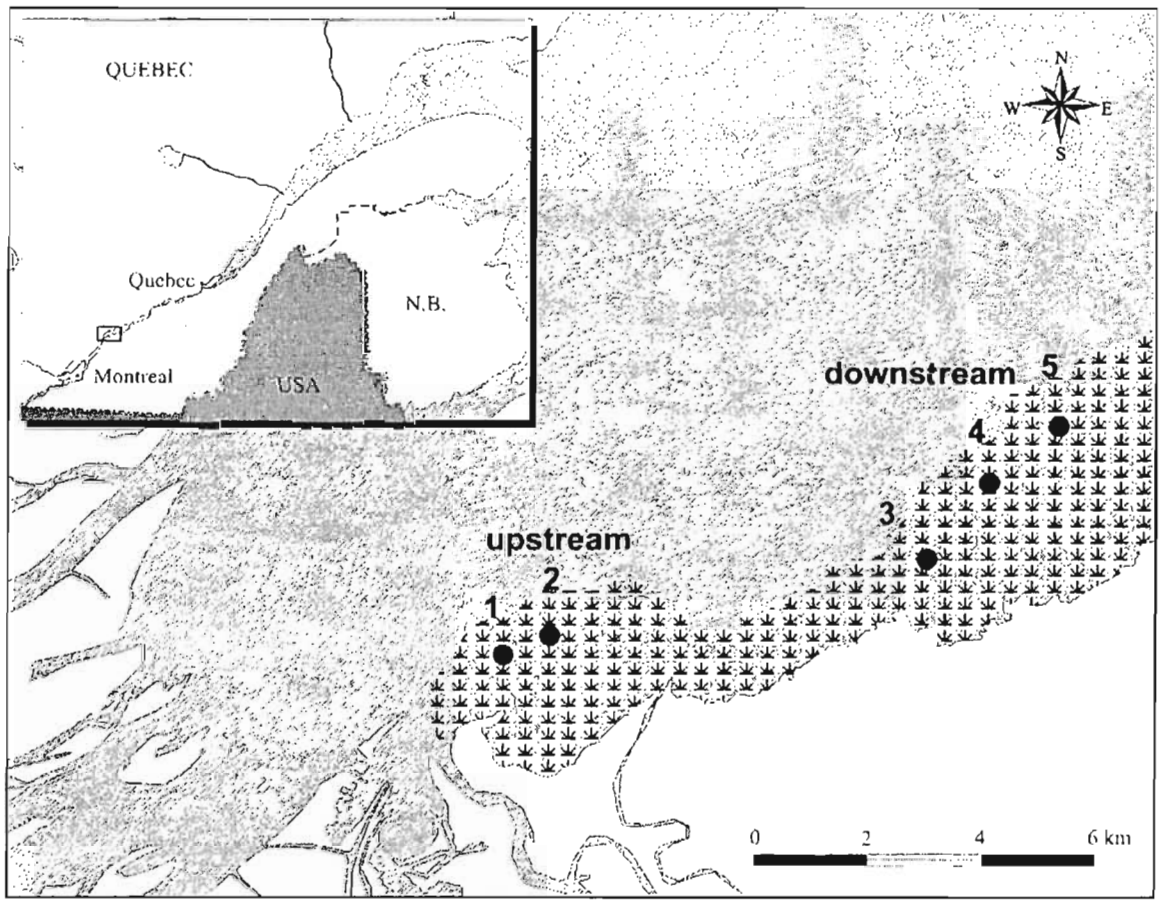
Sampling

Field sampling was carried on September 19 and 21, 2006. Water characteristics measured from the boat included conductivity (µS/cm), pH, water temperature (°C), and dissolved oxygen (ppm and %) recorded with a YSI 600 XLM multiprobe (YSI Inc., Yellow Springs, Ohio). Current velocity was measured at a depth of 30 cm (FlowTracker acoustic Doppler velocimeter; SonTek/YSI, San Diego,

Calif.). Water samples were collected at 30 cm below the surface and were subsequently analysed for total phosphorus (TP) (Environnement Canada, 2005), total nitrogen (TN) (LACHAT Continuous Flow Quick-Chem 8000), and suspended particulate matter (SPM) (American Public Health Association, 1998). Samples were filtered (Whatman GF/C) for analysis of total dissolved phosphorus (TDP), ammonium (NH_4), nitrite-nitrate (NO_2-NO_3), dissolved organic carbon (DOC) and colour (Pt-Co) (Environment Canada, 2005). Dissolved inorganic nitrogen (DIN) was calculated as the sum of ammonium and nitrite-nitrate concentrations.

Epiphytic macroinvertebrates were collected in shallow water (<1m), using two different sampling gears. First, a D-frame net (30 cm width, mesh of 500 µm) was passed through the vegetation over a distance of 4m during 1 minute, with vertical movements over the entire water column (from 5 cm below the surface to 5 cm above the bottom). Second, the phytophilous fauna closely associated to the macrophytes was sampled using a rectangular transparent plastic box (volume of 5.7 L; Downing and Cyr, 1985), which was closed gently by a diver around the vegetation at 2-3m away from the area previously sampled by the D-frame net. The content of the plastic box was passed through a sieve (500 µm) to retain floating macroinvertebrates and vegetation. The plastic box allowed quantitative sampling of epiphytic invertebrates, while the D-frame net selected invertebrates from the water column or more loosely attached to the vegetation. We assumed that macroinvertebrates sampled by the D-frame net would represent the community easily accessible to the vertebrate predators.

Figure 1. Study site (Lake Saint-Pierre, St. Lawrence River, Quebec). Stations 1 and 2 were located in the upstream area of Lake Saint-Pierre, near the mouth of the Yamaska and Saint-François rivers; stations 3, 4 and 5 were located downstream. The 1-m isobath from bathymetric charts (dotted lines) and the area of mixed submerged and emergent wetland vegetation () are indicated.


QUEBEC
Quebec
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6 km

Biomass of the submerged vegetation at a station was estimated from samples collected with a double-headed rake (35 cm width) passed on the bottom over a distance of 1m (Yin et al., 2000). Collected vegetation was sorted on the boat to separate macrophytes and metaphyton, wringed out of excessive water and weighted. Two replicates were used to estimate the macrophyte biomass at the location of each previously collected macroinvertebrate replicate. Estimates of mean macrophytes wet biomass were converted into dry mass (g m^{-2}, dm) using previously defined relationships (Hudon and Lalonde, 1998). When present, a sub-sample of metaphyton was preserved with Lugol for identification under the microscope.

Sampling sequence was organised to carry out first the least disturbing activities for the habitat: water sampling was made from the boat, invertebrates (D-frame net and plastic box) were collected by a single operator (on foot), and finally, vegetation biomass was raked following the same path as the D-frame net sampling. Macroinvertebrate and vegetation sampling was repeated at 5 spots located systematically around the boat, two on the left side, one in front, and two on the right side.

Macroinvertebrate sorting

Macroinvertebrate samples were preserved in ethanol (70%) until sorting under a dissecting microscope. Most invertebrates were identified to the order level. Gastropods, the dominant group, were identified to the family level. Three replicates out of the five collected at each station with the D-frame net and the plastic box were

analysed (n=15 for each sampling gear). Samples from station 2 contained important masses of filamentous algae, which were sub-sampled. Vegetation in a replicate was divided in 15 approximately equal sub-samples, which were sorted until >1000 organisms were collected. Sub-samples not sorted for macroinvertebrates were inspected rapidly to remove bigger individuals and weighted separately. The total abundance in the complete sample was estimated with a simple multiplication.

After sorting out the invertebrates, macrophytes and filamentous algae enclosed within the plastic box were rinsed of debris, dried (48 h at 60°C) and weighted (± 0.05 mg). Invertebrates were measured using an image analyzer system connected to a dissecting microscope (Image Pro-Plus; Media Cybernetics Inc., Bethesda Md). For each Gastropod family, at least 50 individuals were measured in all replicates. For the other invertebrate groups, all individuals within the replicate sample showing the highest abundance were measured, at each station. Body length measurements were transformed in dry biomass using length-biomass equations (see Annex I for references). To examine the size structure of the community at each station, invertebrate individual body mass (µg) were grouped in $\log_2$ increasing size classes.

To allow the comparison of invertebrate biomass between sampling gear and with other studies, values of invertebrate abundance in the D-frame net (nb/sample) were transformed in areal biomass values (mg m^{-2}). This was done by considering the area sampled by the D-frame net (4 m long x 30 cm width). For each taxon, areal abundances were transformed in biomass (mg m^{-2}) using the mean biomass estimated with the measurements from the plastic box samples at the same station.

Macroinvertebrate dry biomass from the plastic box (mg g^{-1} of vegetation) were transformed into areal biomass (mg m^{-2}) using the mean macrophyte biomass at each station (g m^{-2}, n=10 rakes). A model-I regression analysis was performed to compare results from the two sampling devices.

Statistical analyses

In order to compare the global variation of the community between stations, we performed a multivariate analysis of variance (MANOVA) on the matrix of biomass of the 23 taxa found at the 5 stations (three replicats per station, n=15),. This analysis was computed using the anova function with permutation test on a redundancy analysis (R-package, Ihaka and Gentleman, 1996). The association of macroinvertebrate taxa with stations, environmental variables and the two sampling gears were assessed using redundancy analyses (rdaTest function, R-package, Legendre and Durand, 2009). Matrices of binary codes were used in these analyses for stations and sampling methods. To minimize the impact of double-zeros (absence), biomass data (y_{ij}) were transformed prior to analysis using the equation $y_{ij}'=\sqrt{(y_{ij}/y_{i+})}$ (Hellinger transformation, Legendre and Gallagher, 2001).

RESULTS

The environmental characteristics at the five stations showed a strong spatial variation (Table 1). Upstream stations 1 and 2 had high nutrient concentrations (TP >15 μg P L^{-1}, TN~700 μg N L^{-1}, NO_2-NO_3 >300 μg N L^{-1}), high macrophyte biomass (220 and 670 g m^{-2} dry mass, respectively), and high turbidity (suspended solids >4.5 mg L^{-1}) (Table 1). As water slowly percolated through the aquatic vegetation, nitrate concentrations dropped below the detection level, which also corresponded to a decrease in water conductivity. This decline was associated at downstream stations 3, 4, and 5, with low macrophyte biomass (140, 39 and 108 g m^{-2}, respectively) and the presence of thick mats of the benthic cyanobacterium *Lyngbya wollei*. Macrophytes were dominated by *Vallisneria americana* at all stations. *Potamogeton richardsonnii* co-dominated at stations 3 and 4. Noticeable amounts of floating mats of filamentous chlorophytes (*Hydrodictyon* sp. and *Oedogonium* sp.) were widespread in the upstream section but were present in our samples at station 2 only (Table 1).

Comparison between stations

Twenty-three taxa, including the 6 families of Gastropods, were identified in the plastic box samples (Table 2). Total macroinvertebrate biomass was the highest at the most upstream station (95.8 mg g^{-1} of macrophytes, dm), followed by the second station (76 mg g^{-1}) and then rapidly declined downstream (8.1, 14.8 and 12.9 mg g^{-1}, in stations 3, 4, and 5, respectively) (Table 2, Figure 2). This pattern was mostly

Table 1. Environmental characteristics and vegetation biomass at 5 stations in Lake Saint-Pierre, in September 2006.

Variables	**1**	**2**	**3**	**4**	**5**
Sampling date	2006/09/21	2006/09/21	2006/09/19	2006/09/19	2006/09/19
Distance from effluents mouth (km)	2.35	3.78	9.74	11.67	13.26
Depth (m)	0.65	0.65	0.84	0.67	0.92
Temperature (^{0}C)	15.10	14.75	18.58	18.42	18.32
Conductivity (μS cm^{-1})	219	226	192	191	185
Current speed (cm s^{-1})	4.0	0.5	2.3	3.7	4.5
pH	8.59	7.96	8.9	9.09	8.86
O_2 (% sat)	50.0	30.6	46.6	43.5	32.2
O_2 (ppm)	5.03	3.10	4.36	4.07	3.05
K_{water}	2.13	2.24	0.59	2.37	1.12
TDP (μg P L^{-1})	13	9	7	8	8
TP (μg P L^{-1})	29	17	9	14	9
NH_4 (μg N L^{-1})	0	3	13	8	5
NO_2-NO_3 (μg N L^{-1})	320	330	0	0	0
TN (μg N L^{-1})	691	709	339	362	354
DOC (mg C L^{-1})	6.80	6.64	6.74	6.79	7.04
Color (Pt-Co)	32.96	31.60	26.78	28.5	26.43
Suspended matter (mg L^{-1})	4.7	5.8	0.5	6.7	1.0
Macrophytes (g m^{-2}, dm)	220.3	670.1	140.3	39.1	107.8
Cyanobacteria (g m^{-2}, dm)	0.0	0.0	9.67	4.3	12.2
Chlorophytes (g m^{-2}, dm)	0.0	0.8	0.0	0.0	0.0

Table 2. Mean total biomass (mg g^{-1} of macrophytes, dm) of macroinvertebrate taxa sampled with a plastic box at 5 stations in Lake Saint-Pierre (n=3 for each station).

Taxon	**Code**	**Mean Total Biomass (mg g^{-1}, dm) mean± s.d.**				
		1	2	3	4	5
Turbellaria	PLA	0.1 ±0.05	1.9 ±0.8	0.3 ±0.1	_	0.024 ±0.04
Mollusca						
Gastropoda	GAS	88.5 ±16.5	54.4 ±18.3	3.8 ±1.7	11.2 ±15.5	8.4 ±8.3
Ancylidae	ANC	3.2 ±3.1	0.9 ±0.5	0.4 ±0.4	0.5 ±0.8	0.2 ±0.07
Bithynidae	BIT	37.1 ±4.1	24.1 ±11.7	2.6 ±1.7	8.3 ±6.5	8.3 ±6.5
Physidae	PHY	6.1 ±7.9	24.3 ±21.7	0.8 ±0.8	0.06 ±0.07	_
Planorbidae	PBD	31.8 ±10.0	0.6 ±0.5	_	_	_
Valvatidae	VAL	4.9 ±1.1	_	_	_	_
Viviparidae	VIV	5.4 ±1.0	4.5 ±4.1	_	2.4 ±3.6	0.3 ±0.5
Annelida						
Oligochaeta	OLI	0.9 ±0.03	10.1 ±7.9	0.2 ±0.03	0.05 ±0.04	0.4 ±0.2
Hydrachnida	HCA	0.005 ±0.003	0.01 ±0.0004	0.002 ±0.001	0.005 ±0.002	0.002 ±0.003
Insecta						
Diptera						

Chironomidae larvae	CHI	5.1 ±2.5	0.7 ±0.5	2.1 ±0.5	0.3 ±0.2	0.6 ±0.8
Chironomidae pupae	NYM	0.5 ±0.3	0.06 ±0.05	0.05 ±0.02	_	0.4 ±0.7
Ephemeroptera	EPH	0.008 ±0.01	_	_	_	0.03 ±0.05
Heteroptera	HET	_	0.1 ±0.03	_	_	_
Lepidoptera	LEP	0.09 ±0.08	0.2 ±0.1	0.3 ±0.3	0.08 ±0.1	_
Odonata	ODO	_	_	0.06 ±0.08	_	0.01 ±0.02
Trichoptera	TRI	0.06 ±0.03	1.0 ±0.7	0.1 ±0.1	0.05 ±0.05	0.1 ±0.2
Crustacea						
Amphipoda	AMP	0.1 ±0.07	3.0 ±0.7	0.3 ±0.1	2.8 ±2.3	1.3±1.7
Cladocera	CLA	0.2 ±0.1	1.0 ±0.5	0.01 ±0.005	0.007 ±0.007	0.04 ±0.01
Copepoda	COP	0.04 ±0.03	0.2 ±0.1	0.002 ±0.001	0.002 ±0.001	0.007 ±0.009
Ostracoda	OST	0.003 ±0.001	0.01 ±0.008	0.02 ±0.007	0.004 ±0.005	0.009 ±0.01
Hydra	HYD	0.2 ±0.1	2.4 ±0.4	0.9 ±0.1	0.2 ±0.3	1.3 ±0.7
Nematoda	NEM	_	_	0.05 ±0.03	_	0.3 ±0.4
Total Biomass		95.8 ±14.1	76.0 ±25.3	8.1 ±1.4	14.8 ±11.5	12.9 ±8.5

influenced by Gastropod biomass, which declined with distance from the tributaries (Table 2). Multivariate analysis of variance showed that macroinvertebrate biomass differed significantly between stations ($F=7.659$, $p<0.001$), but subsequent analyses demonstrated that only station 2 was significantly different from the other stations ($F=18.01$, $p=0.002$). Station 1 had the highest total biomass as a result of the very high gastropod biomass found at this station. In contrast, station 2 exhibited a higher biomass of all taxa except gastropods and chironomids, which dominated at station 1 (Table 2). The total invertebrate biomass was lowest at the three downstream stations (Table 2). This decline in the total biomass of the invertebrate community coincided with the decline in DIN and macrophyte biomass observed along the transect (Figure 2).

The response of macroinvertebrate groups to environmental conditions was taxa-specific (Figure 3). Three Gastropod families (Planorbidae, Physidae and Valvatidae) were positively correlated to the upstream stations. Amphipods were associated to conditions of low macrophyte biomass and total nitrogen, observed downstream at stations 4 and 5 (Figure 3). The other macroinvertebrate taxa that had their variance explained at more than 50% by the RDA analysis are associated with either one of the middle stations 2 and 3, which also exhibited intermediate levels of the environmental characteristics and macrophyte biomass (Figure 3).

Gastropods dominated the macroinvertebrate communities, their average biomass representing between 47% (station 3) and 92% (station 1) of the total community (Table 2). Although Bithynidae biomass declined with distance from tributaries, their relative importance in the Gastropod community increased

Figure 2. Dissolved inorganic nitrogen (DIN; $\mu g\ N\ L^{-1}$), macrophyte biomass (mean ± s.d., $g\ m^{-2}$, dm) and total macroinvertebrate biomass (mean ± s.d., $mg\ g^{-1}$ macrophytes, dm) observed at 5 stations in Lake Saint-Pierre located at different distance from the mouth of tributaries (km).

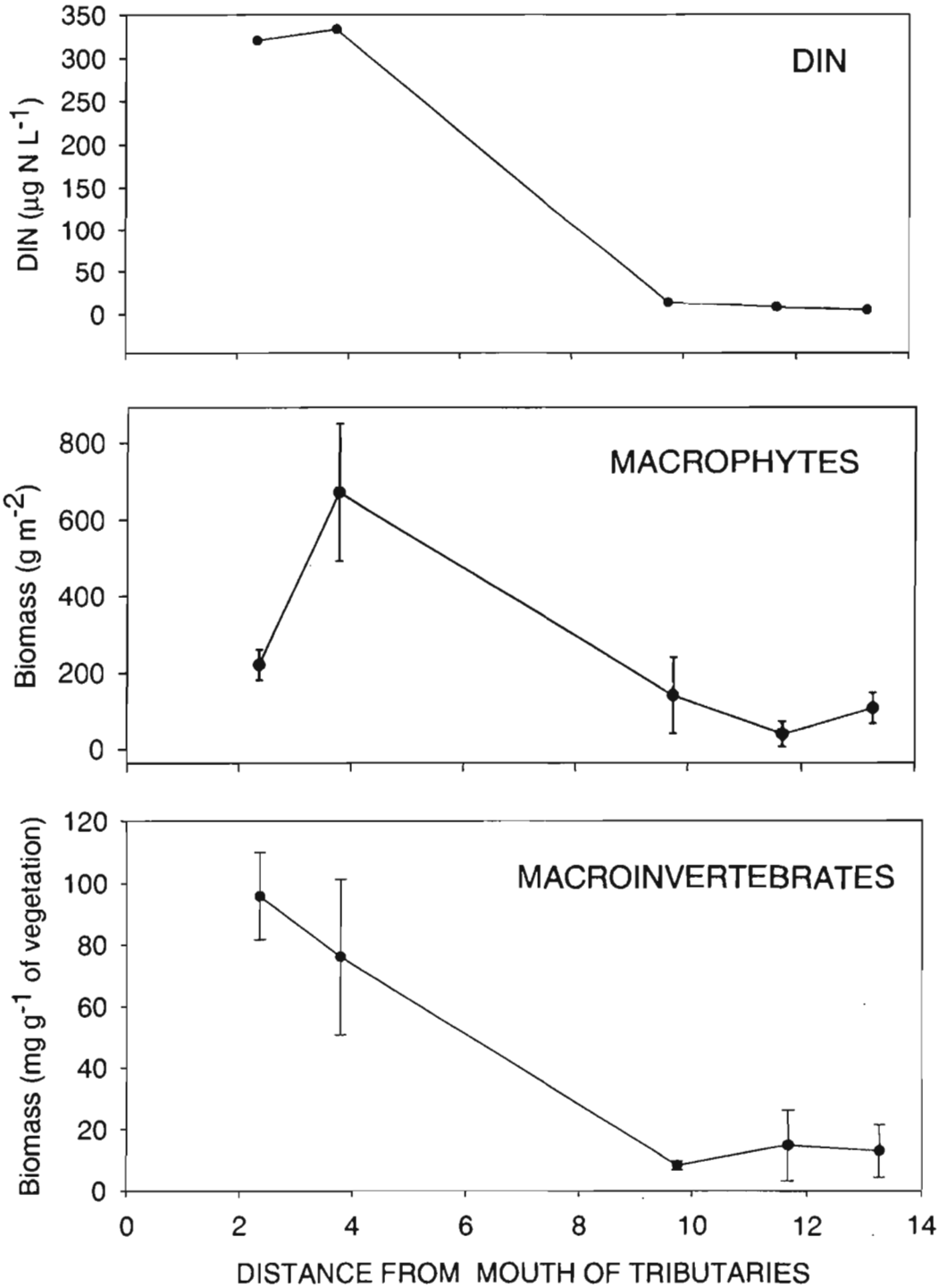
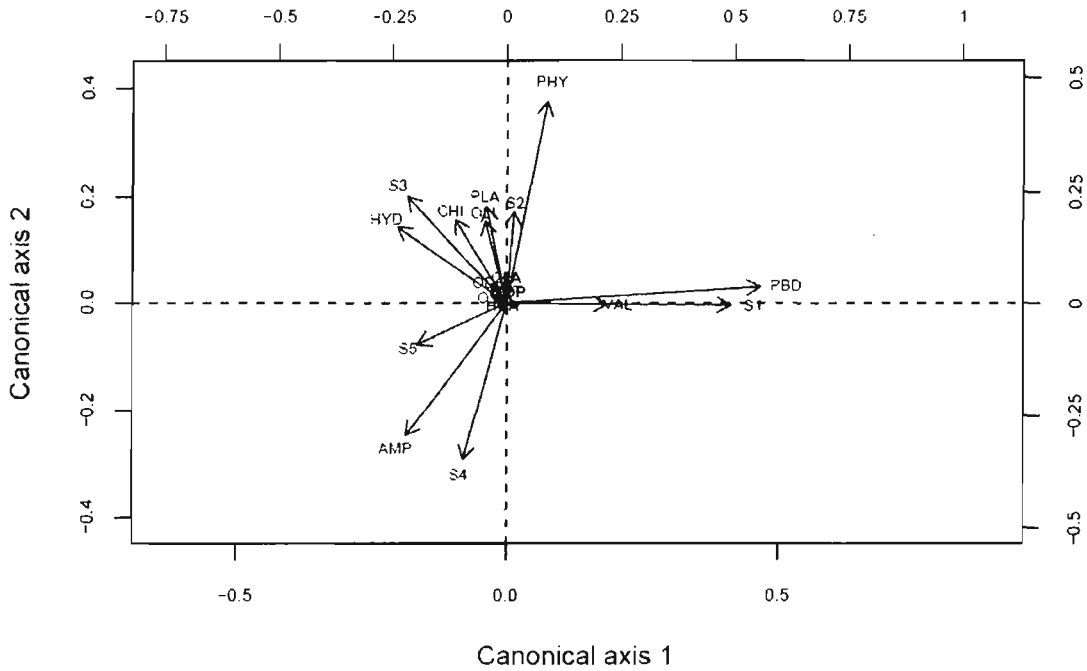
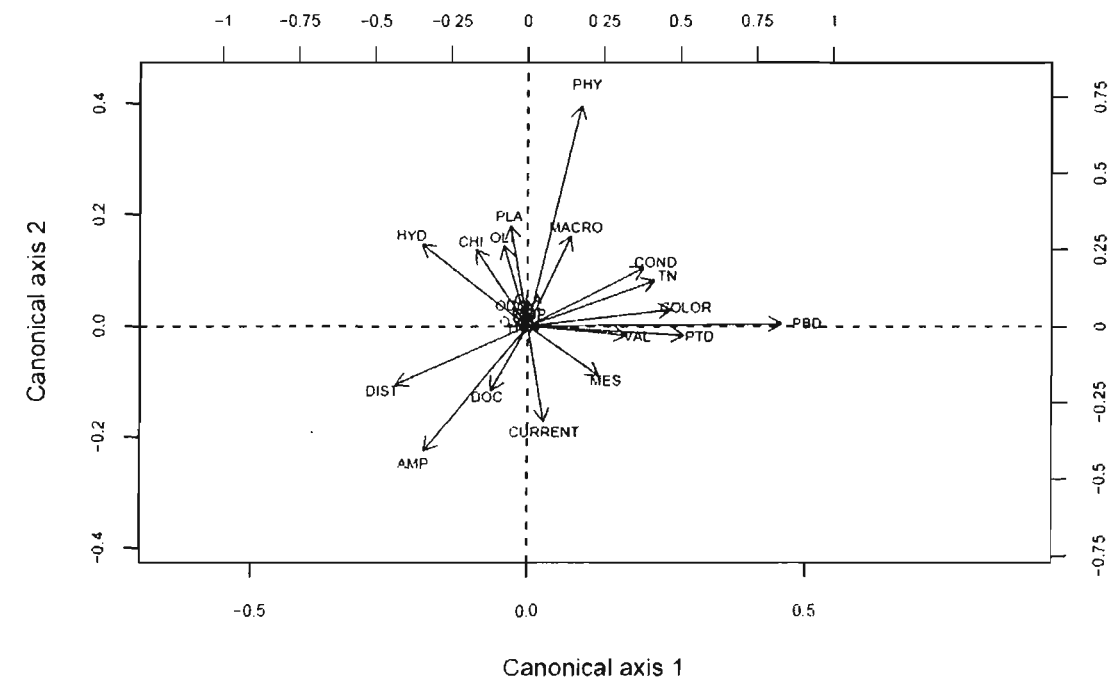

DIN
DIN (µg N L-1)
350
300
250
200
150
100
50
0
MACROPHYTES
Biomass (g m-2)
800
600
400
200
0
MACROINVERTEBRATES
Biomass (mg g-1 of vegetation)
120
100
80
60
40
20
0
0
2
4
6
8
10
12
14
DISTANCE FROM MOUTH OF TRIBUTARIES

Figure 3. Redundancy Analysis (RDA) biplots of macroinvertebrate taxa sampled in macrophytes with a plastic box (mean total biomass in mg g^{-1} of macrophytes, dm) associated to stations (Panel A, adjusted R^2=0.514) and environmental variables (Panel B, adjusted R^2=0.494). Taxa codes are indicated in Table 2.

A.


-0.75
-0.5
-0.25
0
0.25
0 5
0.75
1
PHY
S3
PLA
CHI
S2
HYD
PBD
VAL
S1
S5
AMP
S4
0.4
0.2
0.0
-0.2
-0.4
0.5
0.25
0
-0.25
-0.5
-0.5
0.0
0.5
Canonical axis 2
Canonical axis 1

B.


-1
-0.75
-0.5
-0 25
0
0 25
0.5
0.75
1
PHY
PLA
MACRO
HYD
CHI
COND
TN
SOLOR
PBD
VAL
PTO
MES
DIST
DOC
CURRENT
AMP
0.4
0.2
0.0
-0.2
-0.4
0.75
0.5
0.25
0
-0.25
-0.5
-0.75
-0.5
0.0
0.5
Canonical axis 2
Canonical axis 1

(Figure 4A).They represented 41 and 44% of the Gastropods at the first two stations and rose to 69, 74 and 94% at the three downstream stations. Station 1 held all 6 Gastropod families. Valvatidae was the first to disappear at station 2, while Planorbidae was absent from station 3 and beyond. Only three families remained at station 5 which was dominated by Bythinidae (94%), with small biomass of Ancylidae and Viviparidae (3% each) (Figure 4A).

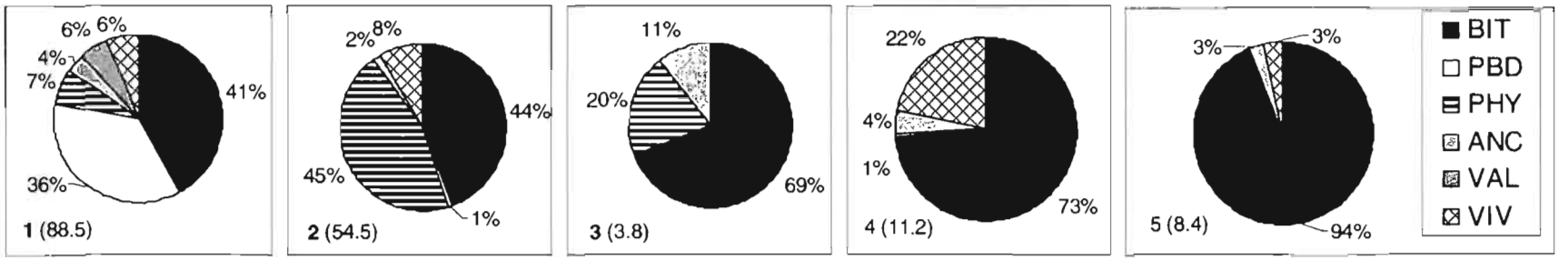
A shift in the dominant taxa along the transect could also be observed for the rest of the macroinvertebrate community (Figure 4B). Chironomids dominated at station 1 and 3, but represented less than 15% of the total biomass at the other three stations. Oligochaetes were important at station 2 only. Amphipods dominated at the three downstream stations with a maximum at station 4, where they represented 81% of the biomass other than the Gastropods (Figure 4B). The size distribution of the whole community showed that stations 1 and 2 had systematically higher total invertebrate biomass for each class size than the three downstream stations, which also lacked organisms weighting more than 4 mg (Figure 5).

Comparison between sampling devices

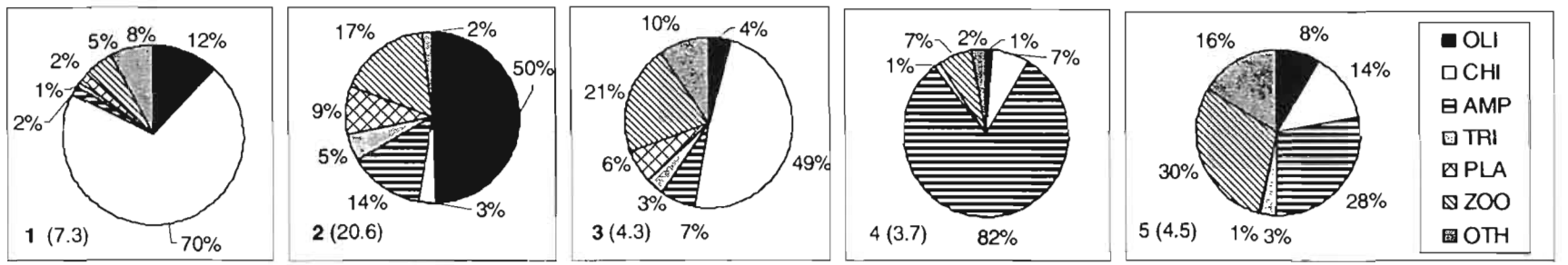
The D-frame net collected all seventeen taxa that were sampled with the plastic box, with the addition of Pelecypoda (Appendix 1). Gastropods also dominated communities sampled with the D-frame net, representing between 56% (at station 2) and 97% of total biomass (at station 1). However, neither device succeeded in capturing all types of invertebrates at a single station. Five taxa were sampled with

Figure 4. Proportion per g of macrophytes (dm) of the total biomass of Gastropod families (A) and the other macroinvertebrate taxa (B), at five stations in Lake Saint-Pierre (n=15), collected with the plastic box. ZOO= sum of Cladocerans, Copepods and Hydra, OTH=sum of other macroinvertebrate taxa that had a biomass <0.5 mg g^{-1} of macrophytes. Numbers in brackets indicate total invertebrate biomass (mg g^{-1} of macrophytes), at each station.

A


6%
6%
4%
7%
41%
36%
1 (88.5)
2%
8%
44%
45%
1%
2 (54.5)
11%
20%
69%
3 (3.8)
22%
4%
1%
73%
4 (11.2)
3%
3%
94%
5 (8.4)
BIT
PBD
PHY
ANC
VAL
VIV

B


5%
8%
12%
2%
1%
2%
70%
1 (7.3)
17%
2%
50%
9%
5%
14%
3%
2 (20.6)
10%
4%
21%
6%
49%
3%
3 (4.3)
7%
7%
4 (3.7)
82%
7%
2%
1%
1%
16%
8%
14%
30%
28%
5 (4.5)
1%
3%
OLI
CHI
AMP
TRI
PLA
ZOO
OTH

the plastic box but not with the D-frame net in at least one station, whereas nine taxa identified in the D-frame net were not found in the plastic box samples. Taxa found solely in one of the two sampling devices occasionally included large insects such as Odonata and Ephemeroptera (D-frame net) but usually represented a low biomass (<0.5 mg g^{-1}) (Table 2 and Appendix 1).

Total macroinvertebrate biomass collected by the plastic box was 35-fold (at stations 3 and 5) to 300-fold (at station 2) higher than that estimated by the D-frame net (Appendix 1). This trend was observed for most groups sampled by each gear (Figure 6). Comparison of the mean biomass of each taxon estimated by the two methods at each station yielded a significant exponential relationship ($p<0.001$, adjusted $R^2=0.49$) (Figure 6). Multiple analysis of variance showed an interaction between the two sampling gear and the stations, meaning that the invertebrate biomass sampled with the two devices varied differently between stations ($F=7.6198$, $p<0.001$). Both stations ($F=1.93$ $p=0.046$) and sampling methods ($F=4.22$, $p<0.001$) were significant factors explaining macroinvertebrate biomass variance. The RDA analysis (adjusted $R^2=0.57$) corroborates that most invertebrate taxa are strongly associated to sampling with the plastic box and station 2, with the exception of Gastropod families Planorbidae and Valvatidae, which are correlated to station 1 (Figure 7).

Figure 5. Size distribution of the entire macroinvertebrate community, at each station, measured from samples collected with the plastic box.

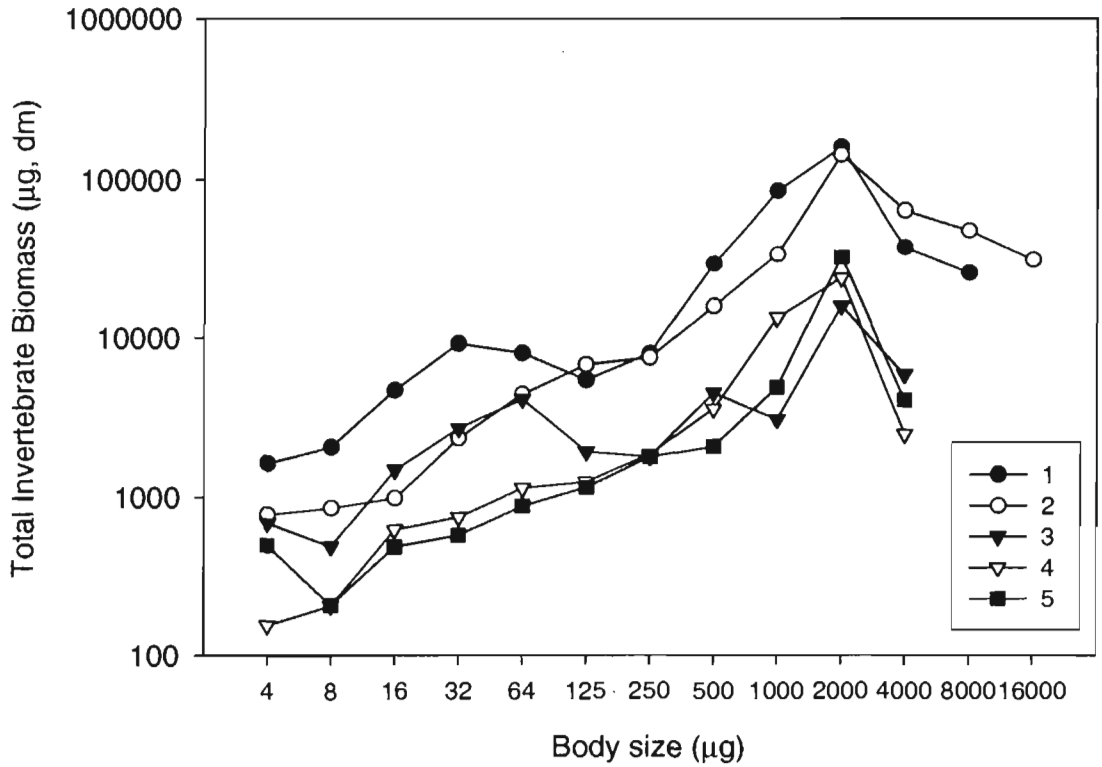

1000000
100000
10000
1000
100
Total Invertebrate Biomass (µg, dm)
4
8
16
32
64
125
250
500
1000
2000
4000
8000
16000
Body size (µg)
1
2
3
4
5

Figure 6. Comparison of macroinvertebrate biomass (mg m^{-2}) estimated with a D-frame net and a plastic box. Points are the mean total biomass of a taxon, at each station (n=125). Upstream (stations 1-2) and downstream (3, 4, 5) stations are indicated by open and closed symbols respectively.

Figure 7. Redundancy analysis (RDA) of macroinvertebrate taxa biomass (mg m^{-2}) sampled with a D-frame net (NET) and a plastic box (BOX), at 5 stations in Lake Saint-Pierre.

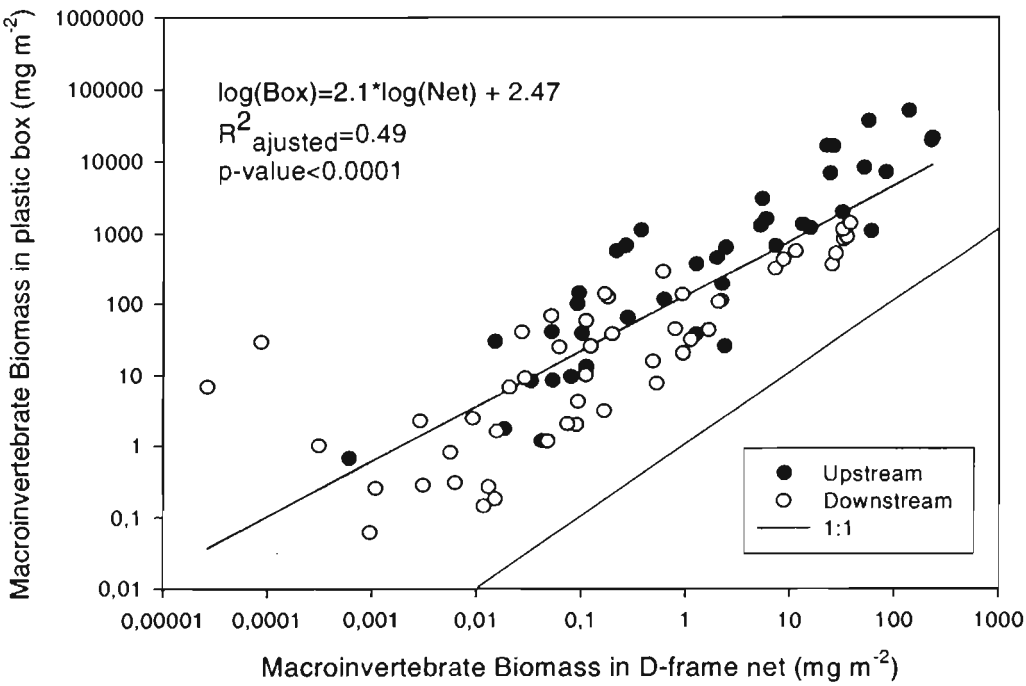


Figure 6.

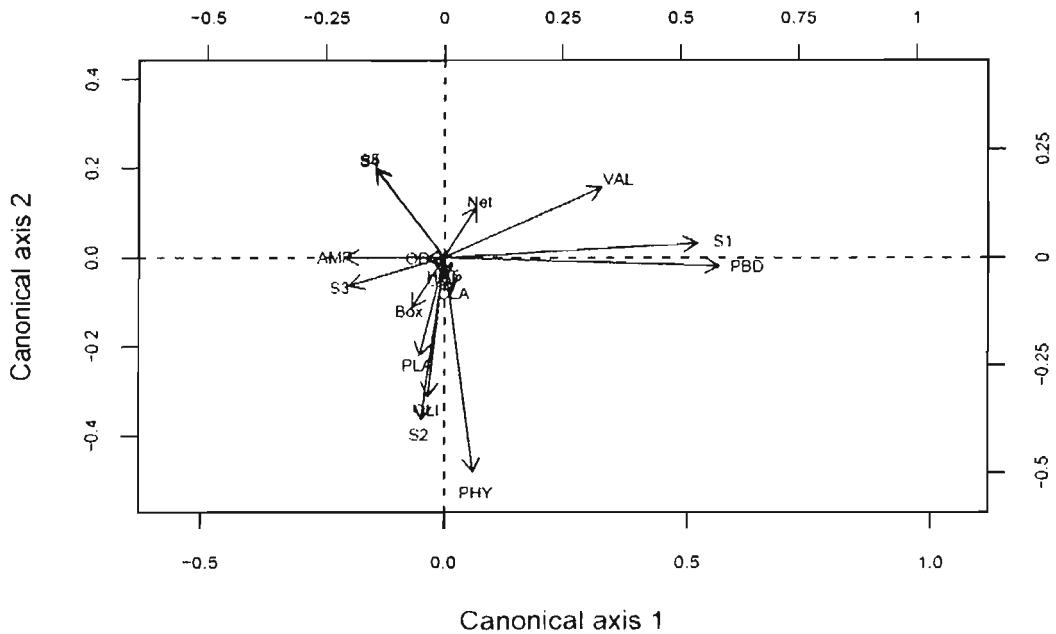


Figure 7.

DISCUSSION

Comparison between stations

Three indirect factors can be brought forward to explain spatial changes in the macroinvertebrate community associated to a major reduction in nitrates. First, macroinvertebrate densities and biomass are often related to macrophyte densities (Cyr and Downing, 1988; Shieh et al., 1999; Giorgi et al., 2005). High nutrient levels can lead to increased primary producers which represent food resources to macroinvertebrates (Cyr and Downing, 1988; Schneider and Sager, 2007). Dense macrophyte beds could also lower predation pressure by littoral fish (Rennie and Jackson, 2005). The lack of large organisms noted at the last three downstream stations, where macrophytes were sparse, may support the predation hypothesis. Second, food quality may have an incidence on growth and reproduction rate of many invertebrate taxa (Brendelberger, 1995; Kraufvelin et al., 2006). Stable isotope analyses performed simultaneously to this study showed that *Vallisneria* nitrogen content was reduced at the downstream stations (2.4 versus 3.6 % N g^{-1} dm; unpublished data). Finally, nutrient concentrations in water can affect the species composition of the vegetation, particularly metaphyton and epiphytes (Moss, 1976). The shift from chlorophytes to the cyanobacterium *Lyngbya wollei* might affect the macroinvertebrate community (Chapter 2). Although epiphytes were not identified and quantified, the lack of nitrate may have affected their quality and quantity (Hagerthey and Kerfoot, 2005; Vuorio et al., 2005). Many invertebrate taxa are

sensitive to shifts in epiphyte availability, as they represent a primary food source for the macroinvertebrates (Cattaneo et al., 1993; Schneider and Sager, 2007). Considering that space availability, protection against predation and variety and availability of food are major factors influencing habitat choice by macroinvertebrates (Mbahinzireki et al., 1991; Cheruvelil et al., 2002; Kraufvelin et al., 2006), it is not surprising that a decrease in invertebrate biomass was associated with the reduced macrophyte biomass at the downstream stations.

Dominating taxa also shifted along the transect as distance from tributaries increased downstream. Chironomids and Oligochaetes, usually associated with eutrophic conditions (Shieh et al., 1999; Shieh et al., 2003; De Sousa et al., 2008; Tall et al., 2008), had their highest biomass upstream. Surprisingly, Oligochaetes, which are typically found in the sediments (Tall et al., 2008), had a relatively important biomass at station 2. This occurrence might be explained by the presence of filamentous chlorophytes, in which they can crawl. Sensitive taxa such as large insect larvae (Ephemeroptera, Odonata) were scarce in our samples, suggesting that conditions might not be optimal in the lake (Shieh et al., 1999; Ortiz and Puig, 2007; De Sousa et al., 2008), although September is not the most favourable season for sampling insect larvae. The high variability of macrophyte and metaphyton biomass induced patchiness to which not all invertebrates are well adapted to (Chase et al., 2001). Mobile taxa, such as Amphipods, benefited from habitat heterogeneity by exploiting more efficiently resources for nutrition and protection. Amphipods are also generally associated with highly dissected macrophytes (Brown et al., 1988) and efficiently utilize metaphyton mats (Salovius and Bondsorff, 2004). Less mobile taxa

might have difficulties in patchy environments. This could explain why the biomass of all Gastropod families decreased with distance from the inflow. Only Bithynidae seemed to resist at conditions prevailing at the last station.

Comparison of sampling devices

The use of a second sampling method brought complementary results to this study, as the D-frame net yielded lower biomass estimates and a different species composition from those obtained using the plastic box. The D-frame net sampled a larger distance and thus succeeded better at collecting larger and more mobile organism such as insect larvae and Gastropods. Given that the laboratory analysis of net samples was generally less time consuming, more replicates could be collected and analyzed, thus increasing the chances of finding rare taxa. However, the D-frame net was less effective in sampling invertebrate taxa closely-attached to the macrophytes, such as Lepidopterans and Ancylidae. Consequently, the D-frame net might be of interest to evaluate the invertebrate community in the water-column, which is easily available to littoral fish. It is also the device usually used for bioassessment protocols (Friberg et al., 2006; Tall et al., 2008), and was shown to have the smallest variation between samples (Turner and Trexler, 1997). However, the exponential relationship obtained after the comparison of the biomass of each taxa sampled with the two methods suggests that the higher the biomass, the higher is the underestimation with samples from the D-frame net. The two sampling methods can thus fulfill different needs: the plastic box allows a quantitative follow-up of the

epiphytic macroinvertebrate community whereas the D-frame net can be more cost-efficient for a qualitative assessment of species richness.

Nevertheless, both sampling devices lead to the conclusion that macro-invertebrate biomass was reduced at increasing distance from the mouth of nutrient-rich tributaries. High concentrations of nutrients increased the carrying capacity of the upstream area, which resulted in higher biomass of macroinvertebrates, thus increasing prey abundance for fish. Although water purification by its slow passage through a wetland brought back dissolved nutrient levels to a more oligotrophic state, this induced a major impact on the macroinvertebrate community and consequently reduced the available resources for vertebrate predators in a large section of the lake. This observation raises the dilemma of the overall effects of nutrient removal on aquatic ecosystems, since the return of a system to its pristine, oligotrophic state also results in a decrease of its carrying capacity for vertebrate fauna.

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APPENDIX 1

Mean total biomass (mg g^{-1} of macrophytes, dm) of macroinvertebrate taxa sampled with a D-frame net at 5 stations in Lake Saint-Pierre (n=3 for each station). Multivariate analysis of variance of the biomass of the 23 taxa between stations was not significant (F=2.25, p=0.096).

Taxon	Code	Mean Total Biomass (mg m^{-2}, dm) mean± s.d.				
		1	2	3	4	5
Turbellaria	PLA	0.008 ±0.01	6.3 ± 1.3	0.24 ± 0.22	_	_
Mollusca						
Gastropoda	GAS	221.4 ±41.5	47.6 ±27.5	18.0 ±5.6	5.4 ±3.3	42.1 ±17.6
Ancylidae	ANC	0.28 ±0.19	0.23 ±0.10	0.14 ±0.24	_	_
Bithynidae	BIT	42.2 ±4.9	21.0 ±14.9	16.2 ±6.4	4.4 ±2.3	39.2 ±17.5
Physidae	PHY	13.1 ±1.9	17.9 ±7.2	1.7 ±1.4	_	0.06 ± 0.07
Planorbidae	PBD	94.2 ±31.4	1.4 ±2.0	_	_	_
Valvatidae	VAL	62.2 ±14.9	1.1 ±1.1	_	0.9 ±1.1	1.3 ±1.8
Viviparidae	VIV	9.4 ±0.1	5.9 ±5.9	_	_	1.5 ±1.7
Pelecypoda	PEL	_	0.01 ±0.02	_	0.003 ± 0.005	_
Annelida						
Oligochaeta	OLI	2.4 ±0.2	27.8 ±12.7	0.16 ±0.10	0.07 ±0.05	0.04 ±0.03
Hydrachnida	HCA	0.05 ±0.008	0.077 ±0.01	0.006 ±0.001	0.014 ±0.006	0.0009 ±0.0001
Insecta						
Diptera						

Chironomidae larvae	CHI	0.46 ±0.37	2.4 ±0.9	0.89 ±0.03	0.10 ±0.03	0.05 ±0.02
C. pupae	NYM	0.12 ±0.03	0.087 ±0.15	0.02 ±0.03	_	0.33 ±0.58
Ephemeroptera	EPH	0.03 ±0.05	0.22 ±0.38	0.28 ±0.09	0.03 ±0.05	0.22 ±0.05
Heteroptera	HET	_	0.20 ±0.17	_	_	_
Lepidoptera	LEP	_	0.16 ±0.28	_	_	_
Odonata	ODO	0.016 ±0.028	0.03 ±0.06	0.47 ±0.07	_	0.064 ±0.056
Trichoptera	TRI	0.13 ±0.15	7.5 ±2.2	0.85 ±0.10	0.086 ±0.043	0.46 ±0.48
Crustacea						
Amphipoda	AMP	1.6 ±0.6	28.8 ±27.1	1.4 ±0.5	1.1 ±0.7	1.1 ±0.67
Cladocera	CLA	1.65 ±0.85	2.2 ±0.9	0.016 ±0.007	0.006 ±0.004	0.1 ±0.03
Copepoda	COP	0.05 ±0.03	0.62 ±0.26	0.004 ±0.004		0.009 ±0.003
Ostracoda	OST	0.001 ±0.0009	0.03 ±0.01	0.003 ±0.003	0.004 ±0.001	_
Hydra	HYD	0.04 ±0.04	5.0 ±3.7	0.17 ±0.07	0.028 ±0.014	0.11 ±0.11
Nematoda	NEM	_	0.0008±0.0004	0.00004±0.00008	0.006 ±0.005	0.0001 ±0.0002
Total Biomass		228.0 ±42.6	12985.1 ±66.5	22.5 ±6.3	6.8 ±4.0	44.6 ±17.3

CHAPITRE 2

DO BENTHIC CYANOBACTERIA AND FILAMENTOUS CHLOROPHYTES AFFECT MACROINVERTEBRATE COMMUNITIES IN A LARGE FLUVIAL LAKE?

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ABSTRACT

The fluvial Lake Saint-Pierre (St. Lawrence River, Canada) supports both wetlands with high nutrient level and areas depleted in nitrate, creating a shift in the metaphytic community from chlorophytes to the cyanobacterium *Lyngbya wollei*. We examined the effect of metaphyton presence and compositon on the epiphytic macroinvertebrates. We measured the biomass, taxonomic composition, and size distribution of macroinvertebrate communities associated with metaphyton and adjacent macrophytes at two stations, collecting four replicates for each combination of vegetation and station. The upstream station was near the input of agricultural tributaries and was characterized by the presence of metaphytic chlorophytes. At the downstream station, where nitrate concentrations were low, *Lyngbya wollei* was abundant near the bottom. *Vallisneria americana* was the dominant macrophyte at both sites. The macroinvertebrate total biomass was higher at the upstream station (68.1 and 69.3 mg g^{-1} of vegetation dm for metaphytic chlorophytes and macrophytes, respectively). In the downstream section, *Lyngbya* supported 38.3 mg g^{-1} and macrophytes had the lowest biomass of the four habitats sampled (12.4 mg g^{-1}). Gastropods were dominant in these habitats (between 43 and 73%), except in the cyanobacteria where Amphipods dominated (59%). Oligochaetes, Trichopterans and littoral zooplankton were strongly associated with the upstream station and in particular with the metaphytic chlorophytes. At the scale of the station, the relative contribution of macroinvertebrates supported by chlorophytes to the total biomass of the phytophilous invertebrate community was insignificant (0.1%), compared to adjacent macrophytes, while invertebrates associated to the cyanobacteria represented

25% of the total biomass at the downstream station. The rich upstream site supported a 71-fold higher biomass of epiphytic macroinvertebrates per m^2 than the downstream area. Such reduction of macroinvertebrates biomass and availability in the downstream portion of Lake Saint-Pierre may decrease the carrying capacity of this ecosystem for high-level consumers, such as fishes and aquatic birds.

INTRODUCTION

Proliferation of filamentous algae chlorophytes and cyanobacteria (metaphyton) is a recurrent problem in streams (Dodds et al., 2002), rivers (Leland and Porter, 2000, Sabater et al., 2003), lakes (Havens et al., 2003, Hagerthey and Kerfoot, 2005), marine estuaries (Kuffner and Paul, 2001, Elmetri and Bell, 2004), and wetlands (Wu and Mitsch, 1998; Vis et al., 2008). Excessive algal growth is a well-documented consequence of eutrophication of aquatic ecosystems by nutrient-rich agricultural and/or urban waste waters (Leland and Porter, 2000; Dodds et al., 2002; Sabater et al., 2003).

Metaphyton exerts both positive and negative effects on the aquatic environment, as it is an important primary producer (Stevenson et al., 1996), which retains (Wu and Mitsch, 1998) and releases nutrients in the system (Keiper and Foote, 1999; Kraufvelin et al., 2006). In addition, metaphytic algae support a diversified macroinvertebrate fauna (Liston and Trexler, 2005; Tessier et al., 2007), as they

support periphyton used by invertebrate grazers (Cattaneo, 1983; Valiela et al., 1997) and serve as a refuge from fish predation (Mbahinzireki et al., 1991, Pihl et al., 1995; Kraufvelin et al., 2006). Conversely, filamentous algal blooms may exert a negative impact on macroinvertebrate communities by amplifying daily dissolved oxygen variations and by inducing episodic events of hypoxia or anoxia (Valiela et al., 1997). In addition, some species, mostly cyanobacteria, may also produce toxins (Onodera et al., 1997; Gérard et al., 2008) or have morphological structures (thick sheath) (Camacho and Thacker, 2006), which may provide protection against grazers. Blooms of filamentous algae are usually dominated by chlorophytes (Valiela et al., 1997), although massive developments of benthic cyanobacteria have been recently documented in many systems with low N:P ratios (Sabater et al., 2003; Albert et al., 2005; Vis et al., 2008).

Macroinvertebrates are a crucial trophic link between primary producers and vertebrate consumers. Because of their high abundance and their diversified response to environmental changes, they are a useful tool for evaluating the impacts of anthropogenic perturbations, particularly eutrophication (Rosenberg and Resh, 1993; McCormick et al., 2004). In fact, macroinvertebrates are often used as bioindicators of aquatic ecosystem quality (White and Irvine, 2003; McCormick et al., 2004; Ortiz and Puig, 2007; De Sousa et al., 2008). However, only few studies have compared communities in different vegetation habitats within the same aquatic system, showing different levels of spatial variations between taxa (McCreary Waters and San Giovanni, 2002, White and Irvine, 2003; Liston and Trexler, 2005, Tessier et al., 2007).

Metaphyton and vascular macrophytes differ very much in their architecture and surrounding environment (epiphytes, dissolve oxygen concentrations), which can influence the associated macroinvertebrate community (Jeffries, 1993; Rosenberg and Resh, 1993; Norkko et al., 2000; Salovious and Kraufvelin, 2004). Although one gram of metaphyton supports considerably higher biomass of macroinvertebrates than submerged and emergent macrophytes, their impact is often considered negligible at the whole-lake scale, because blooms of filamentous algae are short-lived and spatially dispersed (Tessier et al., 2007). Changes in the dominant vegetation type (between macrophytes and metaphyton) could lead to a shift in the dominant invertebrate species (Liston and Trexler, 2005), possibly resulting from changes in growth and reproduction rate of specific macroinvertebrate groups. Consequently, the effects of filamentous algae on the macroinvertebrate fauna could vary depending on the bloom's magnitude and invertebrate species involved (Pihl et al., 1995).

Our study was designed to assess the impact of the presence and the type of metaphyton (chlorophytes and cyanobacteria) on the phytophilous macroinvertebrate community. We compared the macroinvertebrates found at two stations located in a 30-km-long widening of the St. Lawrence River (Lake Saint-Pierre), where vascular macrophytes (*Vallisneria americana*) grew in combination with either filamentous chlorophytes (upstream site) or with filamentous cyanobacteria (downstream site). An earlier study (Vis et al., 2008) showed that, as nutrient-rich water slowly flowed along the south shore of the river through submerged plant beds, metaphyton communities initially dominated by filamentous chlorophytes were progressively

replaced by benthic cyanobacterial mats (*Lyngbya wollei*). As macroinvertebrates are a crucial link of the trophic network, we wanted to assess the effects of such shift in metaphyton composition on this community. Consequences could be important, as Lake Saint-Pierre represents a major area for fish spawning and bird nesting. First, we characterized macroinvertebrates assemblages found on each vegetation type, macrophytes and metaphyton, in terms of their biomass, taxonomic composition and size distribution. Second, we assessed the relative importance of metaphyton as a support for invertebrates at the scale of the station, taking into account the areal biomass of each vegetation type.

METHODS

Study area

Lake Saint-Pierre (LSP; 46°12'N, 72 ° 49'W) is a large fluvial lake (~300 km^2) of the Saint-Lawrence River, located about 65 km downstream of Montreal (Figure 1). The river broadens to 10–12 km in LSP proper; this section of the river is relatively shallow (mean depth ~3 m) and slow-flowing (<0.5 m s^{-1}), with the exception of a 250 m wide, man-made (1854–2001) central navigation channel (>11 m deep). This fluvial lake is characterized by large, sheltered bays and shallow sloping shoreline that supports large emergent marshes and extensive beds of submerged aquatic vegetation to a depth of about 3 m (Hudon, 1997). During the

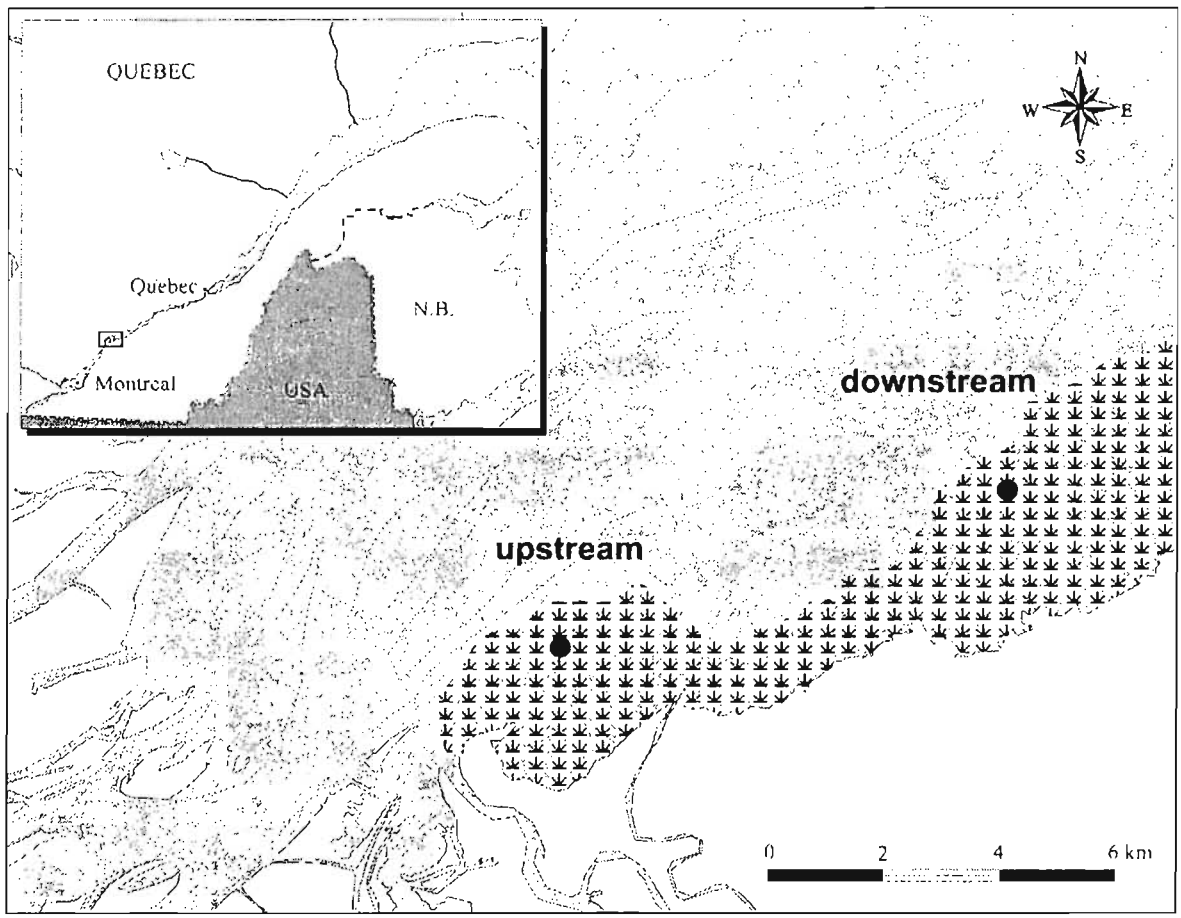
summer, submerged aquatic plants cover 260 km^2 (85%) of the lake surface area (mean biomass 54 g dry mass m^{-2}) and represent an annual production of 8700 tonnes (t) of carbon (Vis et al., 2007). Lake Saint-Pierre was classified as a UNESCO World Biosphere Reserve (in 2000) and as a Ramsar site (in 1998), as it represents the last major freshwater area for wetlands and wildlife before the estuary. The lake is undergoing eutrophication due to excessive input of nutrients by tributaries draining agricultural lands (Hudon and Carignan, 2008).

Sampling

Late summer is usually the season with the highest vegetation biomass (Vis et al., 2006). A preliminary sampling carried on 22-24 August, 2006, showed that intensive rainfalls in mid-August 2006 had elevated the water level and eliminated the floating mats of chlorophytes, preventing comparison with cyanobacterial mats and macrophytes for these dates (unpublished data). Therefore, only samples collected on 19-21 September, 2006 were kept for this study. At each station, water temperature (°C), conductivity (µS/cm), pH and dissolved oxygen (ppm and %) were measured at 30 cm below the surface with a YSI 600 XLM multiprobe (YSI Inc., Yellow Springs, Ohio). Current velocity was measured at a depth of 30 cm (FlowTracker acoustic Doppler velocimeter; SonTek/YSI, San Diego, Calif.). Water samples were collected below the surface and brought back to the laboratory for analyses of suspended particulate matter (SPM) (American Public Health

Association, 1998), total phosphorus (TP) (Environnement Canada, 2005) and total nitrogen (TN) (LACHAT Continuous Flow Quick-Chem 8000). Samples were

Figure 1. Study site (Lake Saint-Pierre, St. Lawrence River, Quebec), with the two sampling stations, Upstream and Downstream. The area of mixed submerged and emergent vegetation () and 1-m isobath from bathymetric charts (dotted lines) are indicated.


QUEBEC
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filtered (Whatman GF/C) for analysis of total dissolved phosphorus (TDP), ammonium (NH_4), nitrite-nitrate (NO_2-NO_3), dissolved organic carbon (DOC) and colour (Pt-Co) (Environnement Canada, 2005).

Submerged vegetation was collected over a 1-m bottom strip, using a 35-cm-wide, double-headed rake (Yin et al., 2000). Mean plant biomass and dominant vascular species composition was estimated from 8-10 rake samples collected systematically around the boat, at each site after sampling the macroinvertebrates. The vegetation was sorted between filamentous algae and macrophytes, washed and weighted on the boat after wringing out excess water. Wet mass of each vegetation type was converted to dry mass using previously published equations (Hudon and Lalonde, 1998). Filamentous algae were subsampled and preserved in Lugol for microscopic identification at the laboratory. For an easier interpretation, chlorophytes and cyanobacteria are grouped as metaphyton (or filamentous algae) in this study, considering their similar architecture.

Macroinvertebrates sampling

Macroinvertebrates associated with metaphyton (Al) and macrophytes (Macro) were sampled at the upstream (Up-Al and Up-Macro) and downstream stations (Do-Al and Do-Macro). At each station, macrophytes and metaphyton growing side by side were collected separately using a rectangular transparent plastic box (volume of 5.7 L) closed gently around the vegetation by a diver (Downing and Cyr, 1985). This device allowed quantitative sampling of all invertebrates, including

those loosely associated with the vegetation. Four replicates of the two vegetation types were collected at each station. The water in the box was washed through a 500 µm sieve to retain floating invertebrates and invertebrates were sorted under a binocular microscope. All organisms were preserved in ethanol (70%) until analysis. Most invertebrates were identified to the order level. Gastropods, the dominant group, were identified to the family level. Cladocerans and Heteropterans were also identified to the family level to obtain a better estimate of their biomass by length-mass relationships, but analyses were made at the order level, as for the other groups.

After sorting the invertebrates and rinsing off the debris, macrophytes and filamentous algae retained by the plastic box were dried (48 h at 60°C) and weighted (± 0.05 mg) to estimate macroinvertebrate density per gram of vegetation dry mass (dm). Invertebrate length was measured using an image analyzer system connected to a dissecting microscope (Image Pro-Plus; Media Cybernetics Inc., Bethesda Md). Samples containing more than 50 individuals of each gastropod family were sub-sampled for size measurements. Size of other invertebrate groups was obtained by measuring all individuals of the replicate with most organisms, at each station. Body lengths measurements were transformed in dry mass (dm) using previously documented length-biomass equations (see Annex I for references). To examine the size structure of the communities, invertebrates were grouped in $\log_2$ increasing size classes.

Biomass of invertebrate taxa were expressed as mg g^{-1} of vegetation (dm). These values were subsequently multiplied with the mean area-specific biomass of

metaphyton or macrophytes at each station, estimated on the field with the double-headed rake (g vegetation dm m^{-2}), to obtain the mean areal total biomass of macroinvertebrates at the upstream and downstream stations (mg dm m^{-2}). These values were used to estimate the relative contribution of algae, compared to macrophytes, to the biomass of the phytophilous macroinvertebrate community at each station.

Statistical analyses

The global variations of the invertebrate assemblages found in the four habitats was assessed from a multivariate analysis of variance (MANOVA), performed on the matrix of biomass of the 21 taxa and the 6 families of Gastropods, collected in the samples from algae and macrophytes of the upstream and downstream stations (four replicates per combination of vegetation type and station, n=16). This analysis was computed using the ANOVA function with permutation test on a redundancy analysis (R-package, Ihaka and Gentleman, 1996).The association between major macroinvertebrate taxa and vegetation types was assessed using a redundancy analyses (rdaTest function, R-package, Legendre and Durand, 2009). A matrix of binary codes for vegetation types and stations was used in this analysis. To minimize the impact of double-zeros (absence), biomass data (y_{ij}) were transformed prior to analysis using the equation $y_{ij}'=\sqrt{(y_{ij}/y_{i+})}$ (Hellinger transformation, Legendre and Gallagher, 2001).

RESULTS

Characteristics of sampling stations

Sampling stations were located 8 km apart, along the south shore of Lake Saint-Pierre (Figure 1), in shallow (< 1 m), slow-flowing (< 5 cm s^{-1}) beds of submerged aquatic vegetation (Table 1). Both stations were dominated by *Vallisneria americana,* interspersed with *Potamogeton richardsonii* and *Heteranthera dubia* (upstream only). Biomass of submerged macrophytes was 17-fold higher at the upstream than at the downstream station (670 and 39 g dm m^{-2}, respectively). At the upstream station, three filamentous chlorophytes: *Hydrodiction* (72%), *Oedogonium* (27%) and *Spirogyra* (1%) formed sparse mats close to the water surface (0.8 g dm m^{-2}). In contrast, the cyanobacterium *Lyngbya wollei* (99%), with only traces of chlorophytes (*Oedogonium* and *Rhizoclonium*, 1%), formed dense mats (4 g dm m^{-2}) on the bottom of the downstream station.

Water chemistry indicated that both stations were under the influence of the Saint-François River, characterized by colored (colour ≈30 Pt-Co units), DOC-rich (≈6.5 mg C L^{-1}) waters of moderate conductivity (≈ 200 µS cm^{-1}). Both stations were characterized by similar, moderate concentrations of TP (≈ 15 µg P L^{-1}), TDP (≈ 9 µg P L^{-1}), dissolved organic nitrogen (≈ 350 µg N L^{-1}) and NH_4 (≈ 5 µg N L^{-1}); however, NO_2-NO_3 concentrations dropped from 300 to <20 µg N L^{-1} as water slowly percolated through the macrophytes bed, as documented earlier (Vis et al., 2008; Hudon and Carignan, 2008).

Table 1. Physical, chemical and biological characteristics of the upstream and downstream sampling stations in Lake Saint-Pierre.

Variables	**Upstream**	**Downstream**
Sampling date	2006/09/21	2006/09/19
Depth (m)	0.65	0.67
Temperature (°C)	14.75	18.42
Conductivity ($\mu S\ cm^{-1}$)	226	191
Current speed ($cm\ s^{-1}$)	0.5	3.7
pH	7.96	9.09
O_2 (% sat)	30.6	43.5
O_2 ($mg\ L^{-1}$)	3.10	4.07
K (m^{-1})	2.24	2.37
Colour (Pt-Co)	31.6	28.5
Suspended matter ($mg\ L^{-1}$)	5.8	6.7
Water chemistry		
DOC ($mg\ C\ L^{-1}$)	6.64	6.80
TDP ($\mu g\ P\ L^{-1}$)	9	8
TP ($\mu g\ P\ L^{-1}$)	17	14
NH_4 ($\mu g\ N\ L^{-1}$)	3	8
NO_3 ($\mu g\ N\ L^{-1}$)	330	0
TN ($\mu g\ N\ L^{-1}$)	709	362
Vegetation characteristics		
Macrophytes ($g\ dm\ m^{-2}$)	670	39
Cyanobacterium *Lyngbya wollei* ($g\ dm\ m^{-2}$)	0.0	4.0
Chlorophytes ($g\ dm\ m^{-2}$)	0.8	0.0

Macroinvertebrate community

A total of 22 macroinvertebrate taxa were identified, three of which were exclusively found upstream (Heteroptera Corixidae, Hirudinae and Odonata) and five exclusively downstream (Coleoptera Elmidae, Ephemeroptera, Nematoda, Pelecypoda and Tipulidae) (Table 2). Six families of gastropods were also identified. Ten taxa had a total biomass of more than 0.5 mg g^{-1} of vegetation (dm) in at least one habitat (Amphipods, Chironomids larvae, Cladocerans, Copepods, Gastropods, Hydra, Oligochaetes, Ostracods, Planarians and Trichopterans).

Overall, the upstream station supported a higher total biomass of macroinvertebrates in both types of vegetation (algae: 68.1; macrophytes: 69.3 mg g^{-1} of vegetation, dm) than in the cyanobacterial mats (38.3 mg g^{-1}) and the macrophytes (12.4 mg g^{-1}) found at the downstream station (Figure 2). Vegetation type (filamentous algae and macrophytes, $F=5.4$, $p=0.002$) and station (upstream and downstream, $F=11.1$, $p\leq0.001$) both induced a significant difference in invertebrates biomass (non-parametric multivariate analysis of variance). Gastropods dominated macroinvertebrate biomass in Lake Saint-Pierre, representing between 43 and 73% of the total biomass found in the chlorophytes and the macrophytes (Figure 2). However, Amphipods were the dominant group (59%) associated with the benthic cyanobacterium *Lyngbya wollei* (Figure 2).

Table 2. Mean total biomass (mg g^{-1} vegetation dm) for the major taxa of macroinvertebrate found in the four sampling habitats (n=4 for each habitat).

Taxon	Code	Mean Total Biomass (mg g^{-1} vegetation, dm) ± s.d.			
		Upstream		Downstream	
		Algae	Macrophytes	Algae	Macrophytes
Turbellaria	PLA	2.0 ±0.6	1.9 ±0.7	1.8 ±1.3	0.2 ±0.1
Mollusca					
Gastropoda	GAS	26.7 ±16.5	49.2 ±18.2	4.9 ±2.6	9.1 ±8.5
Ancylidae	ANC	0.5 ±0.3	0.8 ±0.5	0.01 ±0.02	0.4 ±0.7
Bithynidae	BIT	9.6 ±8.3	22.0 ±10.4	4.0 ±3.1	6.9 ±6.0
Physidae	PHY	12.5 ±7.0	21.2 ±18.8	0.2 ±0.3	0.05 ±0.07
Planorbidae	PBD	0.9 ±0.5	1.3 ±1.5	0.02 ±0.04	_
Valvatidae	VAL	0.05 ±0.06	0.6 ±1.1	0.3 ±0.6	_
Viviparidae	VIV	4.0 ±7.3	3.4 ±4.1	0.3 ±0.4	1.8 ±3.2
Pelecypoda	PEL	_	_	0.008 ±0.007	_
Annelida					
Hirudinea	HIR	0.03 ±0.06	_	_	_
Oligochaeta	OLI	12.7 ±5.8	9.3 ±6.7	0.4 ±0.2	0.03 ±0.04

Hydrachnida	HCA	0.03 ±0.01	0.01 ±0.005	0.01 ±0.01	0.004 ±0.002
Insecta					
Coleoptera	COL	_	_	0.2 ±0.4	_
Diptera					
Chironomidae					
Larvae	CHI	2.2 ±0.9	0.6 ±0.4	3.8 ±2.0	0.3 ±0.2
Pupae	NYM	0.2 ±0.3	0.06 ±0.04	0.08 ±0.1	_
Tipulidae	TIP	_	_	0.004 ±0.008	_
Ephemeroptera	EPH	_	_	0.002 ±0.003	_
Hemiptera					
Corixidae	HEC	0.07 ±0.003	0.08 ±0.15	_	_
Hibridae	HEH	0.13 ±0.02	0.08 ±0.04	0.06 ±0.1	0.008 ±0.02
Lepidoptera	LEP	0.08 ±0.1	0.2 ±0.1	0.002 ±0.004	0.1 ±0.1
Odonata	ODO	0.0006 ±0.001	_	_	_
Trichoptera	TRI	6.4 ±2.4	1.0 ±0.6	0.1 ±0.1	0.07 ±0.05
Crustacea					

Amphipoda	AMP	8.2 ±2.7	2.8 ±0.7	25.4 ±7.8	2.5 ±2.0
Cladocera	CLA	3.5 ±1.6	1.0 ±0.6	0.08 ±0.03	0.006 ±0.006
Copepoda	COP	1.5 ±1.2	0.2 ±0.1	0.4 ±0.2	0.001 ±0.001
Ostracoda	OST	0.02 ±0.01	0.04 ±0.01	0.7 ±0.4	0.003 ±0.004
Hydra	HYD	3.8 ±1.9	2.8 ±0.9	0.4 ±0.3	0.2 ±0.3
Nematoda	NEM	–	–	0.03 ±0.03	–
Total Biomass (mg g^{-1} vegetation dm)		68.1 ±10.6	69.3 ±24.7	38.3 ±7.7	12.4 ±10.5

Composition of the entire invertebrate community was contrasted between vegetation types and stations using a Redundancy Analysis (RDA, Figure 3). The first axis distinguished between assemblages found at the two stations, whereas the second axis divided macrophytes from metaphyton. The analysis explained 57% of the total variance of the community (adjusted R^2). Stations were differentiated on the basis of the biomass of Oligochaetes and Physidae, which prevailed upstream, and Amphipods, which dominated downstream. Macrophytes at both stations were primarily associated to Viviparidae and Bithynidae, while most other groups, including Chironomids and Zooplankton taxa, were strongly associated to metaphyton.

Investigating more closely the association between taxa and filamentous algae demonstrated that invertebrate groups responded differently to the shift from chlorophytes to cyanobacteria (Figure 2). Whereas Amphipods, Chironomids and Ostracods reached a higher biomass in the cyanobacteria than in the green algae, Gastropods, Oligochaetes and Trichopterans showed the opposite trend.

Examination of biomass trends of individual taxa between station and vegetation type (ANOVA) showed that Gastropods, particularly Physidae ($F=11.1$, $p=0.003$), Bithynidae ($F=7.72$, $p=0.015$) and Planorbidae ($F=5.33$, $p=0.008$), were significantly more abundant upstream, as were Oligochaetes ($F=23.8$, $p=0.003$). Within sites, a significantly higher biomass of Chironomids ($F=19.5$, $p=0.001$), Copepods ($F=7.36$, $p=0.001$), Ostracods ($F=11.6$, $p=0.001$), Cladocerans ($F=9.64$, $p=0.011$) and Amphipods ($F=15.7$, $p=0.002$) was recorded on metaphyton than on macrophytes.

Figure 2. Average total biomass (mg g^{-1} vegetation, dm) of macroinvertebrates in the metaphyton (Al) and macrophytes (Macro) of the upstream (Up-) and downstream (Do-) stations (n=16). OTH= sum of 12 macroinvertebrate taxa exhibiting a total biomass < 0.5 mg g^{-1} (dm) of vegetation. ZOO=Cladocera, Copepoda and Hydra.

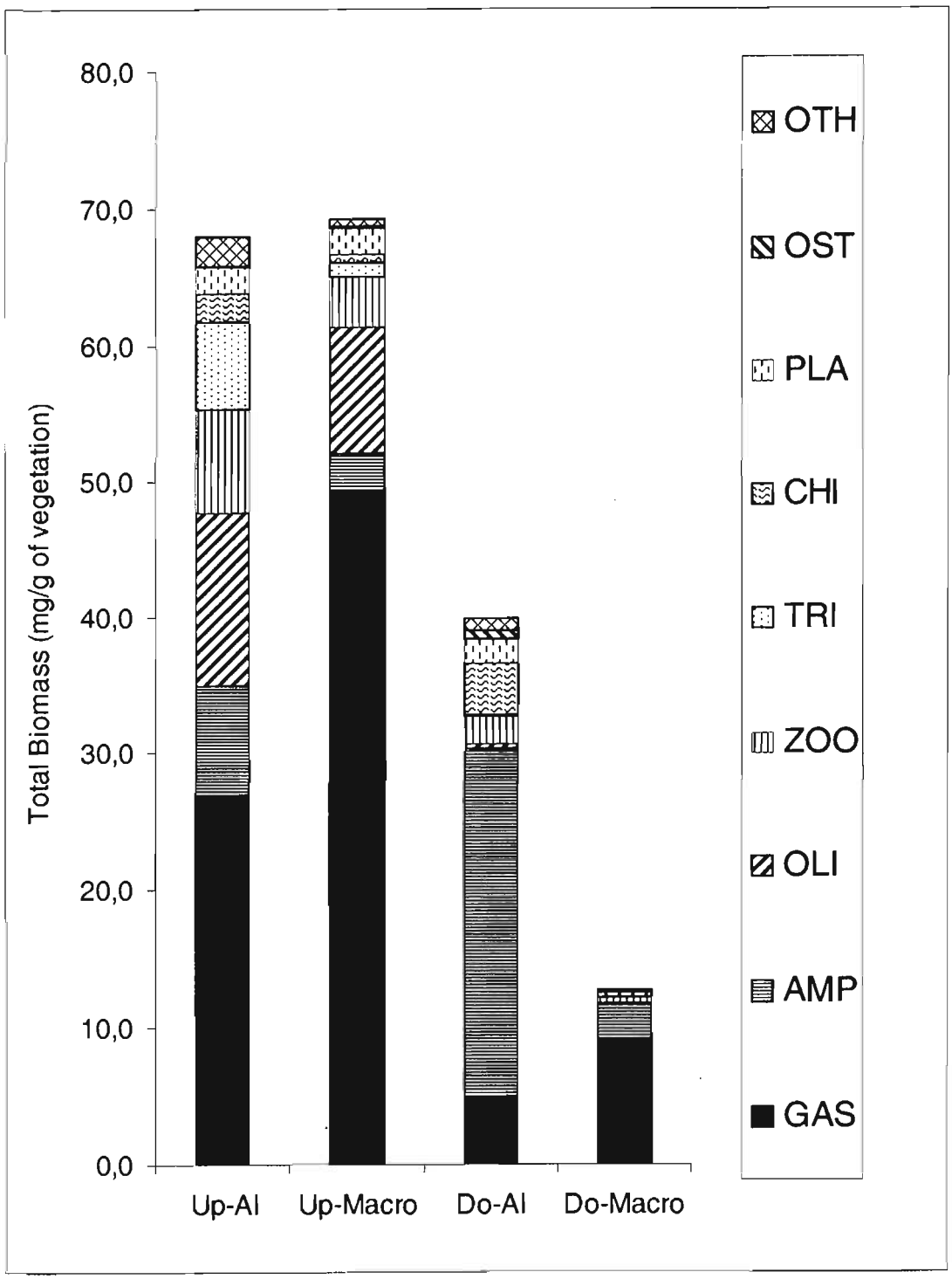
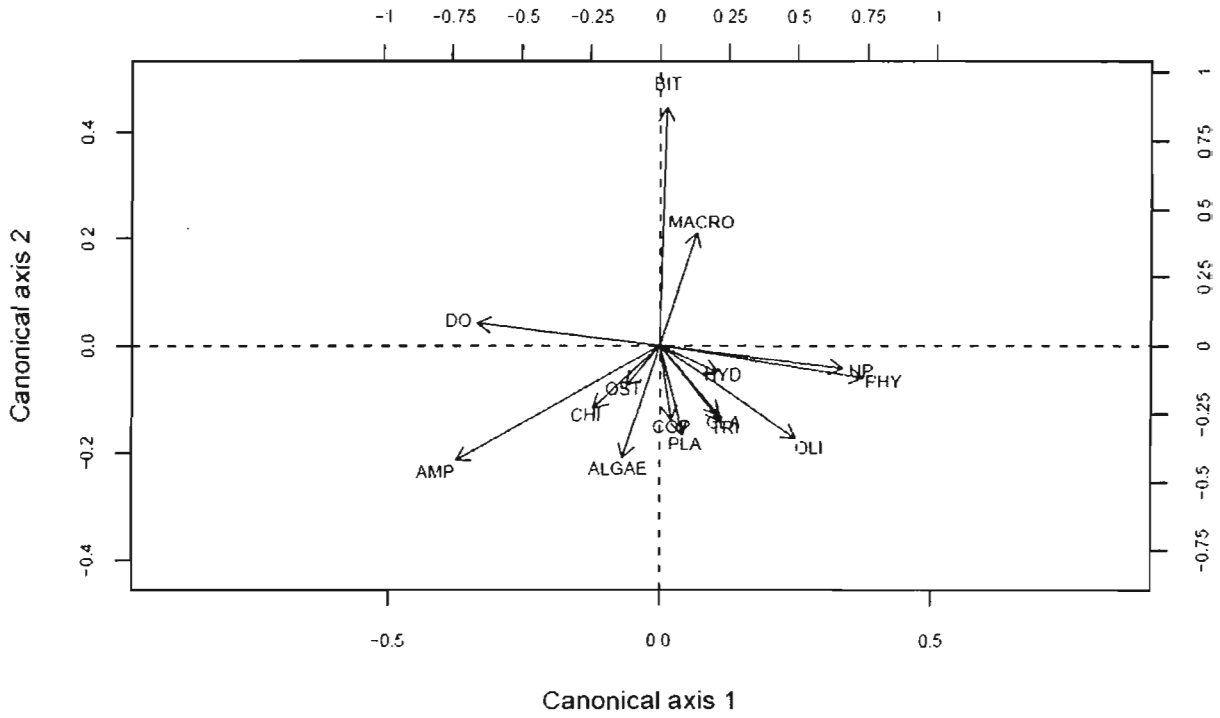

80,0
70,0
60,0
50,0
40,0
30,0
20,0
10,0
0,0
Total Biomass (mg/g of vegetation)
Up-Al
Up-Macro
Do-Al
Do-Macro
OTH
OST
PLA
CHI
TRI
ZOO
OLI
AMP
GAS

Figure 3. Redundancy analysis (RDA) of macroinvertebrate taxa biomass (mg g^{-1} vegetation, dm) sampled with a plastic box at two stations located upstream (UP) and downstream (DO) of Lake Saint-Pierre, in metaphyton (Algae) and macrophytes (Macro). Taxa whose variation contributed to explain more than 50% of the redundancy analysis are the only ones shown.


-1
-0.75
-0.5
-0.25
0
0.25
0.5
0.75
1
BIT
MACRO
DO
HYD
NP
PHY
OST
CHI
PLA
AMP
ALGAE
OLI
0.4
0.2
0.0
-0.2
-0.4
-0.5
0.0
0.5
Canonical axis 2
Canonical axis 1

Comparison of the size distribution of macroinvertebrates in each combination of vegetation type and station showed that the macrophytes from the downstream station supported systematically less biomass of each size class than the macroinvertebrate community found in the cyanobacteria of the same station and in both types of vegetation upstream (Figure 4). Invertebrates larger than 4 mg were also scarce downstream.

At the scale of the station, when the total biomass of invertebrates was calculated accounting for the areal biomass of each vegetation type (g dm m^{-2}), the mean biomass of each taxa was higher upstream than downstream. These differences were large, ranging from 3.6 fold for the Ostracods to 1750 fold for the Oligochaetes (Figure 5). Overall, the upstream station supported a total macroinvertebrate biomass of 46.5 g m^{-2} while a severely reduced biomass (0.65 g m^{-2}) was found downstream (Figure 5). When metaphyton contribution to the total macroinvertebrate areal biomass was distinguished from that of macrophytes, metaphytic chlorophytes supported only 0.1% of the upstream invertebrate community, whereas 25% of the macroinvertebrate biomass was associated with the benthic cyanobacterium *Lyngbya wollei* at the downstream station.

Figure 4. Size distribution of the invertebrate communities observed in macrophytes (Macro) and metaphyton (Al) at the upstream (Up-) and downstream (Do-) stations sampled in Lake St-Pierre.

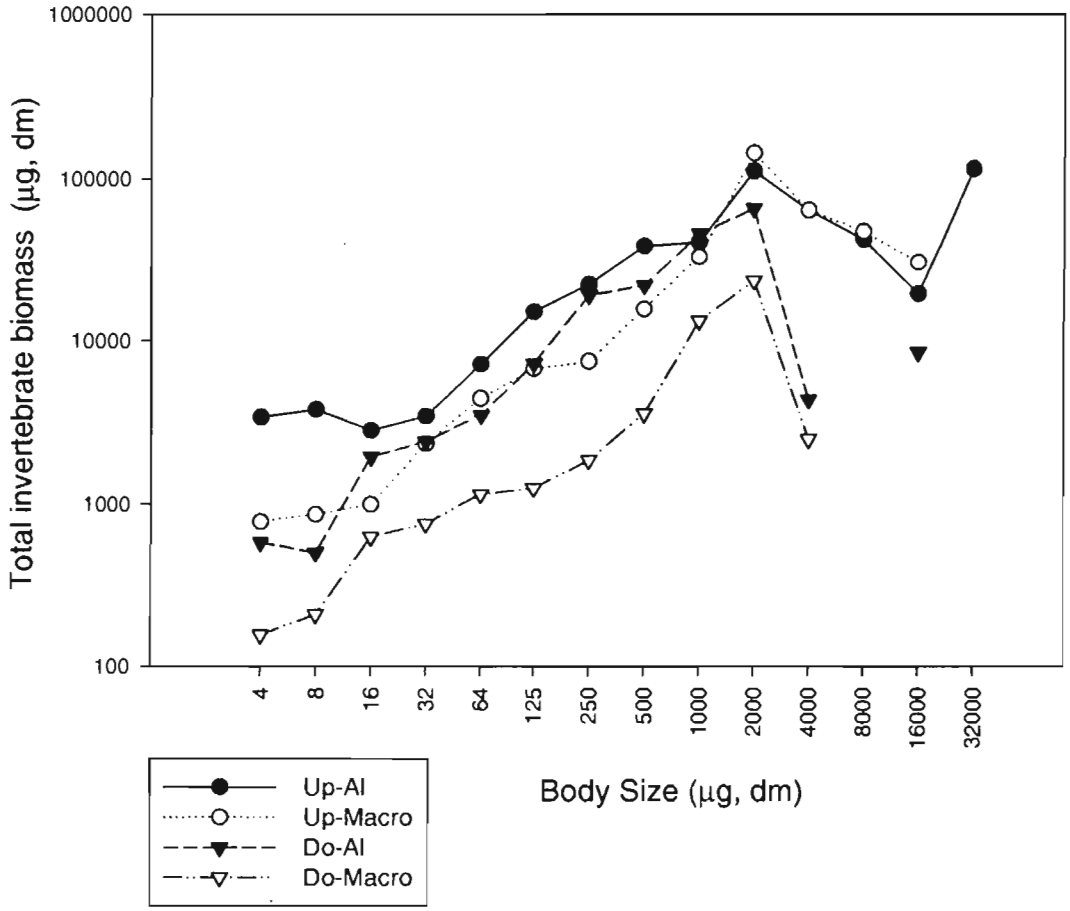
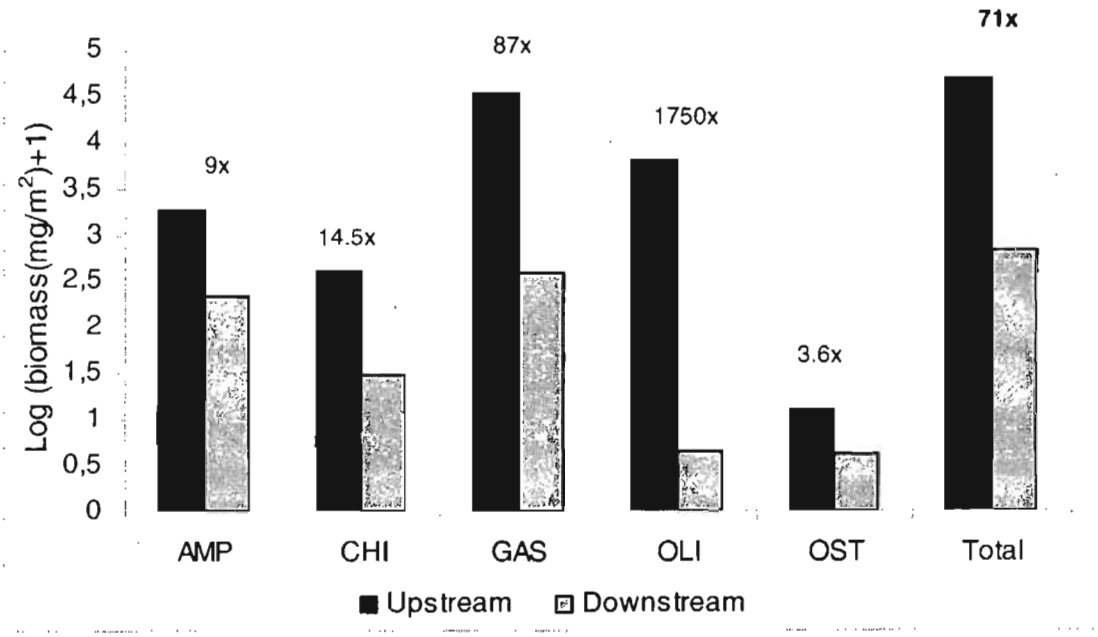

1000000
100000
10000
1000
100
Total invertebrate biomass (µg, dm)
4
8
16
32
64
125
250
500
1000
2000
4000
8000
16000
32000
Body Size (µg, dm)
Up-Al
Up-Macro
Do-Al
Do-Macro

Figure 5. Total biomass, at the scale of the station (mg m^{-2}), for major macroinvertebrate taxa. Results are log-transformed. For each taxon, the magnitude (X) of the difference in biomass between upstream and downstream is indicated.


Log (biomass(mg/m²)+1)
5
4,5
4
3,5
3
2,5
2
1,5
1
0,5
0
9x
14.5x
87x
1750x
3.6x
71x
AMP
CHI
GAS
OLI
OST
Total
Upstream
Downstream

DISCUSSION

Effect of environmental conditions at upstream and downstream stations

Macroinvertebrate assemblages differed between the upstream station, which supported high macrophyte biomass and was under the direct influence of enriched tributary inflow, and the downstream station, characterised by low macrophyte biomass and chronic deficiency of dissolved inorganic nitrogen.

Our results revealed that the macrophytes found upstream supported higher macroinvertebrate biomass per gram of vegetation than downstream (by a factor of 6X). This result agrees with earlier studies showing that macroinvertebrate densities are positively related to an increase of biomass and primary production of aquatic vegetation (Cyr and Downing, 1988; Strayer et al., 2003; Giorgi et al., 2005; Rennie and Jackson, 2005). Dense vegetation beds may also offer protection against fish predation (Rennie and Jackson, 2005). Invertebrate size spectrum observed in this study supported this hypothesis, as the sparse macrophytes of the downstream station hosted systematically smaller total biomass for each size class than the other three habitats. Thus, high resource availability and protection from predators at the upstream station could explain the large differences in invertebrate biomass observed between stations, the metaphyton as well as in the macrophytes.

The effect of nutrient enrichment at the upstream station was also revealed by the relative abundance of certain macroinvertebrate groups, as Oligochaetes, which typically dominate in eutrophic environments (Ortiz and Puig, 2007; De Sousa et al.,

2008). Massive developments of macrophytes and filamentous algae under nutrient-rich conditions may further induce periods of hypoxia in the water column (Valiela et al., 1997), under which conditions pulmonate gastropods (Physidae and Planorbidae) inhabiting floating chlorophytes mats could be favoured by their ability to use atmospheric oxygen at the surface.

Effect of vegetation types: metaphyton and macrophytes

Macroinvertebrate communities differed between the four different habitats sampled, in terms of total biomass, taxonomic composition and, to a lesser degree, size distribution. Within each station, macrophytes and metaphyton sustained different invertebrate communities. These dissimilarities may in part be explained by structural differences. Macrophytes were dominated by *Vallisneria americana*, which formed rosettes of linear, ribbon-like leaves above the bottom. At both stations, the fauna associated to macrophytes was dominated by gastropods, which might have been advantaged by the availability of such substratum to crawl and feed on (Salovius and Kraufvelin, 2004).

In contrast, metaphytic filamentous forms belonging to chlorophytes and *Lyngbya wollei* offered a similarly dissected, more complex structure than the structurally simple *Vallisneria americana*. The occurrence and abundance of different macroinvertebrate groups on metaphyton results from the combination of their behaviour, mobility, feeding habits, tolerance to stress and vulnerability to predators (Österling and Pihl, 2001). Mobile taxa, such as Cladocerans, Copepods,

Chironomids and Ostracods can benefit from the presence of metaphytic filamentous algae (Norkko et al., 2000). Since these mats are typically temporary, invertebrate taxa able to rapidly colonise new habitats and resist eventual drifting are favoured by this alternative habitat (Norkko et al., 2000; Salovius and Kraufvelin, 2004). Efficient swimmers like Amphipods may also hide from predators in the mats during the day and move away from it for feeding at night (Kraufvelin et al., 2006).

Nevertheless, the marked difference observed between communities inhabiting mats of chlorophytes and those of benthic cyanobacteria cannot be entirely explained by architecture. This difference between assemblages of invertebrates could result either by a disparity in the quality and quantity of food (mainly epiphytes) available or from different ecological characteristics of the two types of mats. Chlorophytes are usually more suitable food resources than cyanobacteria, which can deter grazing through production of toxins (Carmichael, 1981; Gérard et al., 2008). Differences in macroinvertebrate assemblages between cyanobacteria and chlorophytes could stem from the fact that the cyanobacterium *Lyngbya wollei* grows close to the sediments, whereas chlorophytes are found in the water column and at the surface, thus providing their associated fauna access to either benthic or pelagic and surface resources, respectively. Taxa usually associated to the sediments, Amphipods, Ostracods and to a lesser extent Chironomid larvae, had higher biomass in the cyanobacteria than in the chlorophytes despite the fact that the upstream station had generally more invertebrate biomass. Although Amphipods were previously associated to *Lyngbya* (Camacho and Thacker, 2006), to our knowledge it was never reported for Ostracods and Chironomids.

Generalization of results to the scale of the station (areal basis)

When results are expressed in biomass of macroinvertebrates at the scale of the station (mg m^{-2}), the downstream station appeared substantially poorer than the upstream station. These results are explained by a combination of higher total biomass of macroinvertebrates in vegetation and by higher macrophyte areal biomass upstream. As it was previously demonstrated, filamentous chlorophytes algae in Lake Saint-Pierre are an alternative but temporary habitat with high diversity and productivity, but submerged macrophytes support the majority of the macroinvertebrate biomass (Tessier et al., 2008). At the downstream station, however, submerged macrophytes are scarce and do not form dense patches as in the areas previously investigated (Tessier et al., 2008). Consequently, invertebrates inhabiting these macrophytes are more exposed to predation by fish (Crowder and Cooper, 1982). The cyanobacterium *Lyngbya wollei* sustained about a quarter of the station's macroinvertebrate biomass, while green algae only supported 0.1% of the biomass at the upstream site.

Therefore, despite the production of toxin (Carmichael et al., 1997; Onodera et al., 1997; unpublished data), *Lyngbya* seems to act as a refuge from fish predation for invertebrates and as a suitable alternative habitat from macrophytes in this area, contrary to expectations. Further more, benthic cyanobacteria support a different macroinvertebrate community than the other vegetation habitats of the lake, dominated mainly by mobile taxa such as Amphipods. As macroinvertebrates are the primary food resource for littoral fish, their substantially lower biomass downstream (>71-fold) and their reduced availability in the thick mats of *Lyngbya* could have

important consequences on the trophic chain. If conditions inducing the replacement of dense macrophyte beds by mats of *Lyngbya wollei* persist or spread, fish resources could be seriously jeopardized.

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CONCLUSIONS GÉNÉRALES ET PERSPECTIVES

Le lac Saint-Pierre est un milieu naturel de grand intérêt. Il est le dernier lac fluvial d'importance avant l'estuaire du Saint-Laurent et il soutient une superficie non négligeable de milieux humides ainsi qu'une grande biodiversité. Il est soumis à plusieurs pressions environnementales, telles que le contrôle du niveau d'eau en provenance des Grands Lacs, l'érosion de ses berges causée par une navigation commerciale sans cesse grandissante et de possibles projets d'élargissement de la voie maritime. En particulier, l'apport par des tributaires de rejets agricoles fortement chargés en nutriments en amont et la diminution marquée de nitrate observée en aval constitueront des problèmes majeurs pour le secteur sud du lac dans les années à venir. Les communautés de macroinvertébrés du lac Saint-Pierre ont déjà été étudiées à quelques reprises. Cependant, notre étude se distingue parce qu'elle a permis d'évaluer les conséquences de l'oligotrophisation d'un milieu aquatique sur les communautés de macroinvertébrés phytophiles, suite à l'assainissement des rejets agricoles par des marais humides naturels. Nous avons aussi pu déterminer, à une plus petite échelle, l'apport des algues filamenteuses vertes et des cyanobactéries à la communauté de la station.

Les communautés de macroinvertébrés ont varié de façon importante le long de la rive sud du lac. Les marais humides situés en amont, recevant de fortes concentrations en nutriments, supportaient d'importantes biomasses de producteurs primaires, qui eux-mêmes supportaient de très fortes biomasses de macroinvertébrés. À mesure que la distance depuis l'embouchure des tributaires augmentait, la diminution marquée du nitrate était corrélée à des lits de macrophytes réduits et de

plus en plus épars. Il s'en est suivi que la biomasse des invertébrés par gramme de macrophytes fut réduite par un facteur de 5 à 10. La moyenne de la biomasse individuelle des organismes était aussi plus faible, alors qu'aucun invertébré de plus de 4 µg n'a été mesuré aux trois stations de l'aval. Les Gastéropodes, qui étaient représentés par 6 familles à la station la plus en amont, ont perdu de leur diversité vers l'aval. La dernière station ne contenait plus que trois familles, dont la biomasse était représentée à 94% par les Bithynidae. Les différents taxons ont aussi montré des réponses variées le long du transect. Alors que la plus forte biomasse de Gastéropodes a été observée à la seule station où il n'y avait pas de masses d'algues filamenteuses, les Amphipodes ont augmenté en importance à mesure que l'on s'éloignait vers aval et les Oligochètes ont dominé à la seule station où des masses flottantes de chlorophytes entouraient les macrophytes.

Compte tenu que nous avons considéré tous les groupes de macroinvertébrés présents dans la communauté, l'identification des groupes n'a pas été poussée au-delà de la famille (Gastéropodes, Chironomidae) ou de l'ordre pour la plupart des autres taxons. La méthodologie de l'étude a requis le tri de près de 43 000 individus et la mesure d'environ 8 000 spécimens. Dans ces conditions, le nombre ainsi que le niveau d'analyse des échantillons ont forcément dû être axés sur certains aspects bien particuliers, quitte à omettre l'exploration de certaines avenues potentiellement intéressantes. Ainsi, bien que de nombreux travaux traitent des communautés de macroinvertébrés en classant les taxons selon leur mode de vie, cette analyse n'a pas été possible dans notre étude. Par exemple, pour beaucoup de taxons, les variations entre les différents modes de vie sont observables à des niveaux taxonomiques plus

approfondis que celui de la présente étude. Il en va de même pour plusieurs caractéristiques, telles que la résistance aux polluants ou à l'anoxie, qui peuvent varier entre les espèces. De plus, un trop grand nombre de critères de classification aurait dû être utilisé, puisque le mode de locomotion influence autant les taxons que le mode d'alimentation dans leur choix de substrat. Ainsi, des taxons bons nageurs peuvent avoir des modes d'alimentation très différents, étant filtreurs ou prédateurs. Nous croyons donc que réunir plusieurs ordres selon un seul critère pourrait cacher des réponses plus fines, notamment au niveau des groupes ayant de très faibles biomasses. Il s'agit cependant d'une avenue intéressante pour de futurs projets.

Les chlorophytes filamenteuses retrouvées en amont supportaient une biomasse totale de macroinvertébrés semblable aux macrophytes de cette région. Les différences se situaient surtout au niveau de la biomasse relative de certains taxons, alors que les Chironomides et les Trichoptères étaient plus importants dans les algues filamenteuses, et les Gastéropodes dans les macrophytes. Néanmoins, l'apport du métaphyton à la biomasse totale de la communauté à l'échelle de la station en amont a été négligeable par rapport aux macrophytes. En aval, cependant, la présence de cyanobactéries filamenteuses benthiques a modifié la dynamique de la communauté de macroinvertébrés. Contrairement à ce que l'on avait supposé, la cyanobactérie *Lyngbya wollei* n'est pas un désert biologique. Alors que les Gastéropodes dominaient dans tous les autres types de végétation et à toutes les stations le long du versant sud, les Amphipodes ont dominé dans la *Lyngbya wollei*. De plus, certains groupes comme les Chironomides, les Ostracodes et les Planaires, qui avaient une biomasse réduite dans les macrophytes en aval, ont semblé avoir trouvé refuge dans

l'épais tapis de métaphyton. Les biomasses plus élevées de macroinvertébrés ont été retrouvées dans la *Lyngbya*, plutôt que dans les macrophytes présentes aux mêmes sites. Compte tenu de la biomasse importante de cette cyanobactérie aux stations en aval, *Lyngbya* représentait un habitat plus significatif pour ce secteur que les algues filamenteuses vertes présentent aux stations en amont. Les cyanobactéries supportaient près de 25% de la population de macroinvertébrés de l'aval. Cependant, nos résultats suggèrent que les invertébrés colonisant les masses très denses de *Lyngbya* sont moins accessibles aux poissons littoraux que ceux présents dans les macrophytes. L'utilisation d'une deuxième méthode d'échantillonnage, un troubleau passé dans la colonne d'eau à travers la végétation, a permis d'appuyer ce point. La biomasse de la communauté récoltée par le troubleau était extrêmement réduite en aval, suggérant une quantité réduite d'invertébrés dans la colonne d'eau, et donc un accès limité des prédateurs vertébrés aux ressources nutritives que constituent les macroinvertébrés phytophiles.

Le côté sud du lac Saint-Pierre est donc soumis à des perturbations écologiques opposées mais également problématiques, soit l'eutrophisation de ses milieux humides en amont et l'oligotrophisation d'une importante région en aval. Cela pourrait entre autre avoir des conséquences pour la biodiversité du lac. En amont, les rejets agricoles par les tributaires favorisent le développement d'importantes masses d'algues filamenteuses flottantes ainsi que la dominance de taxons résistants aux perturbations tels que les Oligochètes et les Chironomides. En aval, la carence en nitrate est, quand à elle, corrélée à une réduction importante de la biomasse des producteurs primaires et donc à un appauvrissement de la communauté

d'invertébrés dans les macrophytes et dans la colonne d'eau. De plus, on ne connait pas les effets à long terme du développement de masses de cyanobactéries benthiques sur une grande superficie du lac. Les prédateurs vertébrés tels que les poissons littoraux, les amphibiens et les oiseaux aquatiques, qui utilisent le lac Saint-Pierre comme site de fraie ou de nidification, ont donc un accès réduit aux ressources sur une importante section de la rive-sud du lac. Une situation semblable a été observée ces dernières années au Lac Ontario, où la réduction des apports en phosphore et l'introduction de la moule zébrée ont coïncidé avec une diminution de la productivité et une augmentation de la clarté des eaux, avec des répercussion sur les réseaux trophiques, en particulier pour la productivité des communautés de poissons (Mills et al., 2003). Au lac Saint-Pierre, le problème ne réside pas dans le manque de nutriments en aval, mais plutôt dans la présence d'un débalancement des éléments nutritifs au sein d'un même milieu, ayant pour conséquence ultime le développement massif de cyanobactéries. La solution envisageable ne serait donc pas l'ajout de nitrate dans le système en aval, mais plutôt la diminution de la charge en nutriments, (particulièrement le phosphore) provenant des tributaires en amont, ce qui permettrait de réduire l'eutrophisation, entraînant la réduction du taux de dénitrification et donc rendant le système en aval moins favorable pour les cyanobactéries. Notre étude a ainsi permis de démontrer que les changements de biomasse et de composition spécifique des plantes aquatiques exercent un impact réel sur la faune qui y vit.

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ANNEXE I

Équations utilisées pour la transformation des longueurs (L, mm) des invertébrés en biomasses sèches (*DM*, mg)

Taxon	Equation (DM=)	Reference
Turbellaria	$0.0095*L^{(2.154)}$	Benke et al., 1999
Gastropoda		
Ancylidae	$0.2*10^{(2.6981*\log(L)-1.574)}$	Personal communication, Anne-Marie T. Poirier
Bithynidae	$0.2*10^{(2.7386*\log(L)-0.6639)}$	Personal communication, Anne-Marie T. Poirier
Physidae	$0.2*10^{(2.8315*\log(L)-1.183)}$	Personal communication, Anne-Marie T. Poirier
Planorbidae	$0.2*10^{(2.8044*\log(L)-1.0354)}$	Personal communication, Anne-Marie T. Poirier
Valvatidae	$0.2*10^{(3.1929*\log(L)-0.9339)}$	Personal communication, Anne-Marie T. Poirier
Viviparidae	$0.2*10^{(2.587*\log(L)-0.6342)}$	Personal communication, Anne-Marie T. Poirier
Pelecypoda	$0.0163*L^{(2.477)}$	Benke et al., 1999
Hirudinea	$10^{(0.1972*L-1.0646)}$	Mason 1977
Oligochaeta	$10^{(1.54698*\log(L)-2.2354)}$	Personal communication, Ginette Méthot
Hydrachnida	$3.682*L^{(2.761)}$	Rogers et al., 1977
Coleoptera Elmidae	$0.00737*L^{(2.879)}$	Benke et al., 1999
Diptera		
Chironomidae larvae	$10^{(2.1698*\mathrm{Log}(L)-2.5397)}$	Personal communication, Ginette Méthot
Chironomidae pupae	$10^{(2.82527*\log(L)-2.432)}$	Personal communication, Ginette Méthot
Tipulidae larvae	$10^{(2.681*\log(L)-2.5376)}$	Benke et al., 1999
Ephemeroptera	$10^{(2.69949*\log(L)-2.2839)}$	Personal communication, Ginette Méthot
Hemiptera		
Corixidae	$10^{(3.15673*\log(L)-2.2177)}$	Personal communication, Ginette Méthot
Hebridae	$10^{(2.788*\log(L)-2.1938)}$	Benke et al., 1999
Lepidoptera	$10^{(1.95341*\log(L)-1.6986)}$	Personal communication, Ginette Méthot

Odonata	$10^{(2.52555*\log(L) -2.3101)}$	Personal communication, Ginette Méthot
Tricoptera	$10^{(2.56254\log(L) -2.2317)}$	Personal communication, Ginette Méthot
Amphipoda	$10^{(2.521*\log(L) -2.2822)}$	Personal communication, Ginette Méthot
Cladocera		
Chydoridae	$e^{(2.1*\ln(L) +2.29)} *0.001$	Peters and Downing, 1984
Daphniiae	$e^{(3.81*\ln(L)+1.39)} *0.001$	Dumont et al., 1975
Sididae	$e^{(2.189*\ln(L)+2.0539)} *0.001$	Rosen, 1981
Copepoda	$0.00647724*L^{(2.1)}$	Dumont et al., 1975
Ostracoda	$0.041007*L^{(2.76063)}$	Tudorancea et al., 1979
Hydra	$0.03125*L^{(3)}$	Personal communication, Antonella Cattaneo
Nematoda	$0.001*L^{(3)}$	Personal communication, Antonella Cattaneo

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ANNEXE II

Densités estimées d'invertébrés (nb g^{-1} de végétation) retrouvées dans les réplicats échantillonnés avec la boîte de plastique. Pour les échantillons récoltés dans les macrophytes des stations 2 (amont) et 4 (aval), seulement les réplicats 2, 3 et 4 (station 2) et 1, 3 et 4 (aval) ont été utilisés pour les analyses du chapitre 1.

Station	Substrat	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL	CHI	NYM
1	MACRO	1	2,8	4,6	45,5	9,9	36,0	6,3	1,8	0	0	61,7	2,8	0	195	3,5
		2	4,1	31,4	35,5	4,1	74,5	8,5	2,5	0	0	62,4	5,2	0	350	11,8
		3	6,3	9,6	29,5	1,5	30,7	7,8	1,5	0	0	65,9	2,1	0	548	21,7
2	MACRO	1	21,4	1,1	11,8	12,4	2,8	1,7	0	0	0	806	18,6	0	12,9	0,6
		2	11,0	4,5	10,2	9,0	1,8	0	1,0	0	0	182	6,9	0	12,3	0
		3	28,8	1,8	32,0	8,5	0	0	0,7	0	0	1998	18,6	0	21,0	0,7
		4	20,6	7,4	18,5	15,3	1,1	0	0	0	0	1366	19,5	0	46,0	0,5
3	MACRO	1	3,8	3,2	3,2	1,6	0	0	0	0	0	38,6	1,1	0	123	2,1
		2	7,3	0,3	1,0	1,3	0	0	0	0	0	33,7	1,9	0	179	3,2
		3	3,8	2,6	1,5	2,1	0	0	0	0	0	50,0	1,8	0	199	4,1
4	MACRO	1	7,1	42,5	14,2	3,5	0	0	3,5	0	0	10,6	3,5	0	14,2	0
		2	3,8	1,3	2,6	0	0	0	0	0	0	2,6	1,3	0	31,9	0
		3	0,3	0	11,3	0	0	0	0	0	0	4,4	5,0	0	34,3	0

Station	Substrat	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL	CHI	NYM
4	MACRO	4	2,7	0	0,8	0,8	0	0	0,4	0	0	2,3	1,9	0	11,6	0
5	MACRO	1	0	2,1	0,7	0	0	0	0	0	0	132	4,1	0	200	1,4
		2	0	6,9	4,4	0	0	0	0	0	0	84,1	1,9	0	16,2	0,6
		3	2,6	0,6	12,2	0	0	0	0,6	0	0	43,8	19,3	0	23,2	0
2	AL	1	15,2	2,4	3,5	6,2	1,0	0,3	0,3	0	0	1749	45,3	0	75,0	0,7
		2	24,3	3,5	5,6	4,1	1,2	0	0	0	0	1526	27,7	0	59,8	3,9
		3	13,2	2,9	19,4	8,8	0	0,4	1,1	0	0	1077	27,1	0	33,3	0,7
		4	16,3	6,4	8,0	16,1	0,2	0	0,5	0	0,5	493	16,3	0	30,7	0,5
4	AL	1	13,3	0	8,4	0,4	0	0	0	0,9	0	60,5	3,2	0	58,4	1,9
		2	25,7	0,2	5,1	0,9	0,1	0,1	0,1	1,6	0	49,2	92,5	0,8	151,1	0,1
		3	3,1	0	2,5	0,6	0,2	0,2	0,2	0,2	0	35,2	46,9	0	126,6	0
		4	11,2	0	5,8	0	0	2,9	0	0	0	13,75	2,5	0	44,9	0,7

Station	Substrat	Réplicat	TIP	EPH	HEC	HEH	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
1	MACRO	1	0	0	0	0	0,4	0	2,5	1,1	27,9	4,2	2,1	12,7	0
		2	0	0,3	0	0	0	0	5,0	0,6	50,6	15,4	1,4	3,0	0
		3	0	0	0	0	0,3	0	7,5	0,3	16,9	5,4	1,5	4,8	0
2	MACRO	1	0	0	0,6	1,1	0,6	0	5,6	5,6	257	49,5	11,8	75,3	1,1
		2	0,2	0	0	3,5	0,6	0	2,7	6,1	140	37,1	1,2	35,8	0
		3	0	0	0	3,9	0,4	0	4,8	7,5	235	19,1	7,1	48,1	0
		4	0	0	0	2,1	1,6	0	11,1	9,5	403	93,0	5,8	46,0	0
3	MACRO	1	0	0	0	0	3,2	0,5	0,5	1,1	5,4	0,5	4,3	18,8	321
		2	0	0	0	0	0	0,6	2,9	1,6	4,8	1,9	10,8	17,2	115
		3	0	0	0	0	1,2	0,3	3,5	2,6	3,2	0,9	10,0	13,2	497
4	MACRO	1	0	0	0	0	0	0	0	42,5	7,1	3,5	0	135	0
		2	0	0	0	1,3	1,3	0	2,6	11,5	1,3	0	0	43,4	0

Station	Substrat	Réplicat	TIP	EPH	HEC	HEH	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
4	MACRO	3	0	0	0	0	1,7	0	1,7	12,4	0,6	1,1	0,8	9,1	0
		4	0	0	0	0	0	0	1,9	10,8	2,3	1,9	3,1	5,4	0
5	MACRO	1	0	0	0	0	0	0	2,1	2,1	8,9	0	3,4	9,6	4242
		2	0	0	0	0	0	0	0	0	6,9	3,1	0,6	29,9	46,7
		3	0	0,6	0	0	0	1,3	2,6	12,2	10,3	12,9	11,0	18,0	296
2	AL	1	0	0	0,3	4,5	0	0	40,7	51,2	966	1132	20,2	116	0
		2	0	0	0,2	6,8	0,5	0,2	20,7	31,3	577	304	10,2	95,7	0
		3	0,4	0	0	6,2	0,4	0	18,6	26,3	377	171	15,0	61,1	0
		4	0	0	0	6,1	0	0	25,0	28,6	411	487	14,6	31,2	0
4	AL	1	0	3,7	0	9,3	0	0	33,4	100	34,0	201	200	48,9	22,8
		2	0	0,4	0	0	0,1	0	9,6	69,3	34,2	487	453	14,6	80,6
		3	0	0	0	0	0	0	17,6	61,0	41,0	384	399	23,4	9,4
		4	0	0	0	0	0	0	5,8	119	15,2	119	85,1	4,3	0

ANNEXE III

Biomasses des taxons de macroinvertébrés (mg g^{-1} de végétation) pour chaque réplicat échantillonné avec la boîte de plastique. Pour les échantillons récoltés dans les macrophytes des stations 2 (amont) et 4 (aval), seulement les réplicats 2, 3 et 4 (station 2) et 1, 3 et 4 (aval) ont été utilisés pour les analyses du chapitre 1.

Station	Substrat	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL	CHI
1	MACRO	1	0,09	1,15	41,79	15,18	30,94	3,65	4,55	0	0	0,85	0,004	0	2,75
		2	0,13	6,77	35,28	2,64	42,20	5,40	6,51	0	0	0,10	0,008	0	4,93
		3	0,19	1,57	34,21	0,57	22,19	5,63	5,27	0	0	0,004	0,003	0	7,73
2	MACRO	1	2,04	0,55	15,73	11,66	3,36	2,26	0	0	0	6,93	0,01	0	0,34
		2	1,05	0,96	12,98	17,71	0,71	0	5,56	0	0	1,56	0,005	0	0,32
		3	2,74	0,30	36,24	6,74	0	0	8,08	0	0	17,16	0,01	0	0,55
		4	1,96	1,35	23,18	48,57	0,99	0	0	0	0	11,74	0,01	0	1,21
3	MACRO	1	0,20	0,79	4,59	0,38	0	0	0	0	0	0,17	0,001	0	1,55
		2	0,40	0,008	1,53	1,70	0	0	0	0	0	0,15	0,002	0	2,26
		3	0,21	0,44	1,77	0,20	0	0	0	0	0	0,22	0,003	0	2,51
4	MACRO	1	0,35	135,5	11,55	0,14	0	0	6,59	0	0	0,09	0,004	0	0,19
		2	0,19	0,04	2,85	0	0	0	0	0	0	0,02	0,002	0	0,42
		3	0,01	0	12,51	0	0	0	0	0	0	0,04	0,007	0	0,45

Station	Substrat	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL	CHl
4	MACRO	4	0,13	0	0,76	0,05	0	0	0,72	0	0	0,02	0,003	0	0,15
5	MACRO	1	0	0,30	0,78	0	0	0	0	0	0	0,56	0,001	0	1,57
		2	0	0,17	6,53	0	0	0	0	0	0	0,36	0,0005	0	0,13
		3	0,07	0,22	16,3	0	0	0	0,87	0	0	0,19	0,005	0	0,18
2	AL	1	1,79	0,72	2,31	9,02	0,91	0,12	0,35	0	0	18,36	0,05	0	3,31
		2	2,85	0,13	7,07	6,95	1,03	0	0	0	0	16,01	0,03	0	2,64
		3	1,54	0,47	21,56	11,48	0	0,07	15,02	0	0	11,30	0,03	0	1,47
		4	1,91	0,66	7,51	22,72	0,21	0	0,80	0	0,12	5,18	0,02	0	1,36
4	AL	1	1,77	0	8,41	0,008	0	0	0	0,01	0	0,66	0,001	0	2,31
		2	3,44	0,04	2,80	0,35	0,002	0,04	0,91	0,02	0	0,53	0,026	0,88	5,99
		3	0,41	0	1,34	0,56	0,074	0,04	0,18	0,002	0	0,38	0,01	0	5,02
		4	1,50	0	3,51	0	0	1,18	0	0	0	0,15	0,001	0	1,78

Station	Substrat	Réplicat	NYM	TIP	EPH	HEC	HEH	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
1	MACRO	1	0,13	0	0	0	0	0,10	0	0,03	0,20	0,10	0,02	0,004	0,31	0
		2	0,44	0	0,02	0	0	0	0	0,06	0,10	0,32	0,07	0,003	0,07	0
		3	0,80	0	0	0	0	0,16	0	0,09	0,06	0,10	0,03	0,003	0,17	0
2	MACRO	1	0,08	0	0	0,31	0,03	0,14	0	0,93	2,16	0,96	0,17	0,03	4,17	0
		2	0	0	0	0	0,10	0,16	0	0,44	2,35	0,52	0,13	0,003	1,98	0
		3	0,10	0	0	0	0,12	0,09	0	0,79	2,86	0,88	0,07	0,02	2,66	0
		4	0,07	0	0	0	0,06	0,40	0	1,84	3,65	1,51	0,32	0,02	2,54	0
3	MACRO	1	0,03	0	0	0	0	0,56	0,15	0,03	0,19	0,02	0,001	0,008	1,02	0,05
		2	0,05	0	0	0	0	0	0,01	0,18	0,27	0,01	0,004	0,02	0,93	0,02
		3	0,06	0	0	0	0	0,20	0,009	0,22	0,46	0,007	0,002	0,02	0,72	0,08
4	MACRO	1	0	0	0	0	0	0	0	0	5,52	0,015	0,003	0	0,63	0
		2	0	0	0	0	0,03	0,19	0	0,11	1,49	0,002	0	0	0,13	0
		3	0	0	0	0	0	0,01	0	0,07	1,62	0,001	0,001	0,002	0,08	0

Station	Substrat	Réplicat	NYM	TIP	EPH	HEC	HEH	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
4	MACRO	4	0	0	0	0	0	0	0	0,09	1,40	0,005	0,005	0,009	0	0
5	MACRO	1	1,18	0	0	0	0	0	0	0,38	0,55	0,02	0	0,006	0,65	0,74
		2	0,05	0	0	0	0	0	0	0	0	0,04	0,004	0,001	2,02	0,008
		3	0	0	0,09	0	0	0	0,03	0,06	3,26	0,05	0,02	0,02	1,22	0,05
2	AL	1	0,11	0	0	0,19	0,10	0	0	9,94	12,21	5,75	3,23	0,05	5,77	0
		2	0,61	0	0	0,09	0,15	0,23	0,002	5,06	7,46	3,43	0,87	0,03	4,75	0
		3	0,11	0	0	0	0,14	0,08	0	4,55	6,28	2,24	0,49	0,04	3,03	0
		4	0,07	0	0	0	0,13	0	0	6,11	6,81	2,45	1,39	0,04	1,54	0
4	AL	1	0,27	0	0,05	0	0,008	0	0	0,19	29,21	0,09	0,24	0,50	0,87	0,06
		2	0,01	0	0,005	0	0	0,008	0	0,05	20,14	0,09	0,59	1,14	0,26	0,07
		3	0	0	0	0	0	0	0	0,10	17,75	0,11	0,46	1,00	0,42	0,01
		4	0,05	0	0	0	0	0	0	0,03	34,53	0,04	0,14	0,21	0,08	0

Annexe IV. Biomasses de la végétation retrouvées dans les échantillons récoltés avec la boîte de plastique (g échantillon^{-1})

Échantillons 'Macrophytes'

Stations	1			2				3			4				5		
Réplicats	1	2	3	1	2	3	4	1	2	3	1	2	3	4	1	2	3
Macrophytes	2,84	3,64	3,32	2,70	4,89	2,82	4,09	1,86	3,14	3,40	0,30	0,78	3,62	2,60	1,46	1,60	1,33
Chlorophytes	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
Lyngbya wollei	_	_	_	_	_	_	_	_	_	_	0,003	_	_	_	_	_	0,22

Échantillons 'Algues filamenteuses'

Stations	2				4			
Réplicats	1	2	3	4	1	2	3	4
Macrophytes	1,24	5,06	2,49	2,46	0,30	0,48	_	_
Chlorophytes	1,65	1,30	0,24	1,78	_	_	_	_
Lyngbya wollei	_	_	_	_	1,96	8,86	5,19	2,76

Annexe V. Coordonnées géographiques des stations et abondances des macroinvertébrés dans les échantillons récoltés avec le troubleau (nb par réplicat) en août 2006.

Station	X	Y	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL
A	668805	5113015	1	1	2	16	2	0	0	0	0	0	4	3	0
			2	0	0	14	2	0	0	0	0	0	4	4	0
			3	0	0	9	0	0	0	0	0	0	0	0	0
			4	1	2	39	3	0	0	0	0	0	11	2	0
			5	0	0	16	0	0	0	1	0	0	5	0	0
B	663007	5110486	1	16	0	0	0	0	0	0	0	0	52	3	0
			2	15	17	8	6	3	0	3	0	0	112	27	0
			3	26	9	2	1	3	0	0	0	0	213	17	0
			4	11	2	4	3	1	1	1	0	0	78	7	0
			5	8	14	4	5	0	2	3	0	0	80	77	0

Station	X	Y	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL
C	663720	5110957	1	3	5	21	6	1	0	10	1	0	12	29	0
			2	0	0	31	4	2	0	6	0	0	4	15	1
			3	2	0	23	4	2	0	10	0	0	5	32	0
			4	2	0	39	3	1	0	3	0	0	1	15	0
			5	1	1	38	5	0	0	32	0	0	4	22	0
D	666210	5111599	1	0	0	6	0	0	4	0	1	0	3	14	0
			2	0	3	25	0	0	6	0	0	9	12	18	0
			3	0	0	50	0	2	12	0	0	0	13	22	0
			4	0	0	5	0	0	2	0	0	0	7	6	0
			5	1	0	42	0	3	4	0	1	0	33	19	0
E	669905	5114417	1	0	0	0	0	0	5	0	0	0	6	3	0
			2	0	0	0	0	0	12	0	1	0	2	5	0

Station	X	Y	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL
E	669905	5114417	3	1	0	2	0	0	5	0	0	0	1	6	0
			4	4	0	9	0	0	19	0	0	1	19	9	0
			5	0	0	5	1	0	10	0	0	0	1	2	0
F	671134	5115333	1	0	0	6	0	0	2	0	0	0	2	7	0
			3	0	0	0	0	0	1	0	0	0	3	3	0
			4	0	0	3	0	0	1	0	2	0	1	1	0
			5	0	0	0	0	0	0	0	0	0	1	2	0

Station	Réplicat	CHI	NYM	EPH	HET	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
A	1	3	0	12	0	0	2	0	4	25	0	0	0	0
	2	4	0	8	0	0	1	0	0	16	2	0	0	0
	3	3	0	9	0	0	0	2	0	6	0	0	0	0
	4	7	0	11	0	0	1	7	2	21	0	0	3	1
	5	1	0	14	0	0	0	2	1	11	1	1	1	
B	1	271	2	0	0	0	0	32	13	6	4	13	3	2
	2	134	4	11	0	0	1	61	104	25	24	20	1	5
	3	441	0	7	0	0	0	161	65	66	19	54	9	2
	4	70	0	2	1	0	0	45	18	28	2	6	7	4
	5	41	4	10	34	0	0	74	16	15	5	2	10	1
C	1	8	0	32	1	0	1	4	17	33	7	0	3	2
	2	1	0	18	3	0	0	4	6	24	6	0	1	0

Station	Réplicat	CHI	NYM	EPH	HET	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
C	3	11	0	35	2	0	0	4	14	19	5	0	4	0
	4	5	1	11	0	0	1	0	8	9	9	2	2	0
	5	30	0	7	0	0	0	0	5	8	0	0	0	0
D	1	3	1	5	0	0	0	2	1	29	0	2	3	2
	2	17	0	35	0	0	0	3	2	84	1	0	4	1
	3	21	0	19	0	0	1	2	1	62	1	1	23	0
	4	4	0	14	0	0	0	0	0	36	0	0	3	0
	5	31	1	16	0	0	0	10	8	69	0	0	13	4
E	1	3	2	0	0	0	0	1	0	6	0	2	0	0
	2	4	1	1	0	0	0	1	1	10	0	1	0	3
	3	5	1	1	0	0	0	2	3	7	0	0	1	2
	4	17	1	9	1	0	0	13	9	43	2	9	0	1

Station	Réplicat	CHI	NYM	EPH	HET	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
E	5	1	0	0	0	0	0	0	0	11	0	0	0	0
F	1	4	3	3	0	0	0	0	4	18	0	0	0	1
	3	2	0	2	0	0	0	0	2	0	0	1	0	0
	4	3	1	0	0	0	0	1	0	2	0	0	0	2
	5	1	0	0	0	0	0	0	1	0	0	0	0	0

Annexe VI. Coordonnées géographiques des stations et abondances des macroinvertébrés dans les échantillons récoltés avec le troubleau (nb par réplicat) en septembre 2006. La station 2B n'a pas été utilisée pour les analyses du chapitre 1.

Station	X	Y	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL
1	661355	5111332	1	1	3	89	16	123	71	14	0	0	245	27	0
			2	0	3	55	12	170	113	4	0	0	191	35	0
			3	1	0	71	13	109	148	7	0	0	118	22	0
			4	1	1	53	16	101	89	4	0	0	205	32	0
			5	0	1	44	14	205	144	4	0	0	223	43	0
2	662158	5111682	1	91	2	45	58	5	2	2	0	0	3312	146	0
			2	72	2	26	14	9	1	1	4	0	2174	114	0
			3	68	1	4	7	0	2	0	0	0	3752	103	0
			4	98	1	31	17	1	0	2	0	0	5708	147	0
			5	55	0	21	14	0	1	0	0	0	2186	122	0

Station	X	Y	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL
2B	662568	5111618	1	41	0	63	7	2	13	0	0	0	1953	228	0
2B	662568	5111618	2	57	1	32	0	1	1	0	0	0	1973	168	0
			3	27	0	17	3	1	0	0	22	0	2828	280	0
			4	38	1	212	28	2	21	2	0	0	1457	347	0
			5	32	0	70	7	0	2	0	32	0	6358	388	0
3	668807	5113067	1	6	0	20	3	0	0	0	0	0	31	4	0
			2	2	0	9	8	0	0	0	0	0	29	4	0
			3	2	1	49	10	0	0	0	1	0	11	7	0
			4	3	0	13	2	0	0	0	0	0	23	6	0
			5	11	3	20	2	0	0	0	0	0	74	6	0
4	669905	5114417	1	1	0	16	0	0	5	0	1	0	20	15	0
			2	0	0	1	0	0	0	0	0	0	17	18	0

Station	X	Y	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL
4	669905	5114417	3	1	0	11	1	1	2	0	2	0	11	16	0
			4	0	0	7	0	0	4	0	0	0	9	11	0
			5	0	0	6	0	0	1	0	1	0	4	8	0
5	671126	5115371	1	0	0	29	2	0	2	0	0	0	2	8	0
			2	0	0	50	1	0	0	3	0	0	7	4	0
			3	0	4	13	3	0	0	1	0	0	2	3	0
			4	0	0	35	3	0	1	1	0	0	22	4	0
			5	0	0	19	0	0	6	0	0	0	5	4	0

Station	Réplicat	CHI	NYM	EPH	HET	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
1	1	30	1	0	1	0	3	17	36	118	19	0	7	0
	2	45	5	0	0	0	1	30	13	130	16	0	4	0
	3	25	2	0	0	0	0	11	10	140	8	0	0	0
	4	24	3	1	0	0	0	5	6	394	6	1	0	0
	5	68	4	0	0	0	0	9	13	429	20	1	2	0
2	1	26	2	0	23	0	10	52	147	1335	301	31	274	2
	2	37	0	0	15	0	2	48	44	577	195	8	176	4
	3	79	0	0	1	0	0	43	39	475	135	18	19	5
	4	82	2	7	9	2	0	73	188	1046	313	14	131	9
	5	48	0	0	10	0	0	50	84	485	129	5	45	0
2B	1	168	0	0	0	0	0	61	116	1173	471	56	105	0
	2	116	0	0	0	0	0	89	42	780	537	57	346	0

Station	Réplicat	CHI	NYM	EPH	HET	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
2B	3	151	4	17	0	0	0	203	392	3735	3536	97	216	3
	4	62	0	0	0	5	0	44	75	1005	584	58	91	4
	5	259	19	0	0	0	0	127	197	2256	1366	159	133	13
3	1	25	2	4	0	0	15	26	11	7	1	1	9	0
	2	11	0	2	0	0	8	14	6	4	1	0	5	0
	3	9	1	3	0	0	11	16	17	7	1	2	0	0
	4	209	1	4	0	0	10	17	13	9	1	2	2	1
	5	33	4	3	0	0	11	18	11	10	6	4	4	0
4	1	6	1	0	0	0	0	1	38	22	2	10	4	5
	2	12	0	0	0	0	0	3	3	2	1	2	3	11
	3	18	0	0	0	0	0	2	33	5	5	10	1	4
	4	7	0	0	0	0	0	3	16	3	0	1	3	5

Station	Réplicat	CHI	NYM	EPH	HET	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
4	5	8	0	1	0	0	0	1	12	6	0	2	1	2
5	1	4	5	1	0	0	0	12	2	16	0	0	1	0
	2	10	0	2	0	0	2	1	8	18	5	0	0	2
	3	9	1	1	0	0	1	2	4	12	0	1	8	1
	4	12	0	2	0	0	2	4	5	32	10	0	4	0
	5	5	2	3	0	0	0	13	2	31	9	0	2	0

Annexe VII. Biomasse des macroinvertébrés (mg m^{-2}) de chacun des réplicats récoltés avec le troubleau en septembre 2006. La station 2B n'a pas été utilisée pour les analyses du chapitre 1.

Station	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL
1	1	0,025	0,50	74,2	14,9	73,0	38,3	33,2	0	0	2,8	0,036	0
	2	0	0,50	45,8	11,2	100,9	60,9	9,5	0	0	2,2	0,046	0
	3	0,025	0	59,2	12,1	64,7	79,8	16,6	0	0	1,4	0,03	0
	4	0,025	0,17	44,2	14,9	59,9	48,0	9,5	0	0	2,4	0,042	0
	5	0	0,17	36,7	13,1	121,6	77,6	9,5	0	0	2,6	0,057	0
2	1	7,3	0,38	46,1	39,8	2,3	2,4	9,7	0	0	23,7	0,09	0
	2	5,7	0,35	26,9	19,8	3,7	1,1	5,9	0,038	0	15,6	0,073	0
	3	5,4	0,18	4,1	9,9	0	2,2	0	0	0	26,9	0,065	0
	4	7,8	0,18	32,1	24,0	0,42	0	11,9	0	0	40,9	0,094	0
	5	0,50	0	21,7	19,8	0	1,1	0	0	0	16,7	0,078	0

Station	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL
2B	1	3,2	0	65,2	9,9	0,83	14,5	0	0	0	14,0	0,15	0
	2	4,6	0,18	33,1	0	0,42	1,1	0	0	0	14,1	0,11	0
	3	2,1	0	17,6	4,2	0,42	0	0	0,20	0	20,2	0,18	0
	4	3,0	0,18	219	39,5	0,83	23,5	11,9	0	0	10,4	0,22	0
	5	2,5	0	72,5	9,9	0	2,2	0	0,30	0	45,5	0,25	0
3	1	0,27	0	23,1	1,2	0	0	0	0	0	0,11	0,005	0
	2	0,090	0	10,4	3,3	0	0	0	0	0	0,11	0,005	0
	3	0,018	0,14	56,6	4,1	0	0	0	0	0	0,041	0,008	0
	4	0,14	0	15,0	0,83	0	0	0	0	0	0,085	0,007	0
	5	0,50	0,42	23,1	0,83	0	0	0	0	0	0,27	0,007	0
4	1	0,023	0	14,2	0	0	2,7	0	0,009	0	0,15	0,017	0
	2	0	0	0,89	0	0	0	0	0	0	0,13	0,020	0

Station	Réplicat	PLA	ANC	BIT	PHY	PBD	VAL	VIV	PEL	HIR	OLI	HCA	COL
4	3	0,023	0	9,8	0,046	0,57	1,1	0	0,018	0	0,082	0,018	0
	4	0	0	6,2	0	0	2,2	0	0	0	0,067	0,012	0
	5	0	0	5,3	0	0	0,55	0	0,009	0	0,030	0,009	0
5	1	0	0	32,8	0,093	0	1,1	0	0	0	0,007	0,002	0
	2	0	0	56,6	0,046	0	0	3,4	0	0	0,025	0,0009	0
	3	0	0,31	14,7	0,14	0	0	1,1	0	0	0,007	0,0007	0
	4	0	0	39,6	0,14	0	0,55	1,1	0	0	0,078	0,0009	0
	5	0	0	21,5	0	0	3,3	0	0	0	0,018	0,0009	0

Station	Réplicat	CHI	NYM	EPH	HET	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
1	1	0,35	0,031	0	0,024	0	0,14	0,17	5,5	0,61	0,074	0	0,14	0
	2	0,53	0,15	0	0	0	0,048	0,30	2,0	0,68	0,062	0	0,081	0
	3	0,13	0,062	0	0	0	0	0	1,5	0,73	0,031	0	0	0
	4	0,059	0,092	0,093	0	0	0	0	0,93	2,1	0,023	0,0015	0	0
	5	0,80	0,12	0	0	0	0	0,090	2,0	2,2	0,078	0,00015	0,040	0
2	1	0,97	0,25	0	0,57	0	0,46	7,1	47,1	4,2	0,88	0,068	12,6	0,0003
	2	1,4	0	0	0,35	0	0,10	6,6	13,9	1,8	0,57	0,018	8,1	0,0007
	3	2,9	0	0	0,024	0	0	5,9	12,3	1,5	0,39	0,040	0,88	0,0007
	4	3,0	0,26	0,65	0,23	0,48	0	10,1	60,1	3,3	0,91	0,030	6,1	0,0013
	5	1,8	0	0	0,23	0	0	6,9	26,8	1,5	0,38	0,011	2,1	0
2B	1	6,2	0	0	0	0	0	8,4	37,0	3,7	1,4	0,12	4,8	0
	2	4,3	0	0	0	0	0	12,2	13,3	2,4	1,6	0,13	15,9	0

Station	Réplicat	CHI	NYM	EPH	HET	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
2B	3	5,6	0,50	1,6	0	0	0	28,0	125	11,6	10,3	0,21	10,0	0,0006
	4	2,3	0	0	0	0,98	0	6,0	24,1	3,1	1,7	0,13	4,2	0,0005
	5	9,5	2,2	0	0	0	0	17,5	63,0	7,0	4,0	0,35	6,2	0,0018
3	1	0,26	0.026	0,37	0	0	0,72	1,4	1,6	0,014	0,002	0,002	0,41	0
	2	0,12	0	0,19	0	0	0,39	0,73	0,86	0,008	0,0015	0	0,23	0
	3	0,095	0,013	0,28	0	0	0,53	0,83	2,4	0,015	0,0015	0,003	0	0
	4	2,2	0,013	0,37	0	0	0,48	0,89	1,9	0,019	0,0015	0,003	0,090	0,0001
	5	0,35	0,052	0,28	0	0	0,53	0,94	1,6	0,021	0,0092	0,006	0,18	0
4	1	0,065	0,50	0	0	0	0	0,037	4,1	0,038	0,0012	0,024	0,049	0,0054
	2	0,13	0	0	0	0	0	0,11	0,33	0,003	0,0006	0,006	0,036	0,012
	3	0,20	0	0	0	0	0	0,074	3,6	0,009	0,0030	0,024	0,012	0,0043
	4	0,076	0	0	0	0	0	0,11	1,73	0,005	0	0,002	0,036	0,0054

Station	Réplicat	CHI	NYM	EPH	HET	LEP	ODO	TRI	AMP	CLA	COP	OST	HYD	NEM
4	5	0,087	0	0,093	0	0	0	0,037	1,30	0,010	0	0,005	0,012	0,0022
5	1	0,026	2,5	0,093	0	0	0	0,92	0,44	0,069	0	0	0,056	0
	2	0,065	0	0,19	0	0	0,096	0,076	1,78	0,078	0,0058	0	0	0,0003
	3	0,059	0,50	0,093	0	0	0,048	0,15	0,89	0,052	0	0,002	0,45	0,0001
	4	0,078	0	0,19	0	0	0,096	0,31	1,1	0,14	0,012	0	0,23	0
	5	0,033	1,0	0,28	0	0	0	1,0	0,44	0,13	0,010	0	0,11	0