UNIVERSITÉ DU QUÉBEC À MONTRÉAL

TRANSFERT DE MÉTHYLMERCURE ET STRUCTURE DES RÉSEAUX TROPHIQUES CHEZ LES MACROINVERTÉBRÉS LITTORAUX

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« *Cambia di celu, cambierai di stella* ».

Proverbe corse.

« *If all mankind were to disappear, the world would regenerate back to the rich state of equilibrium that existed ten thousand years ago. If insects were to vanish, the environment would collapse into chaos* ».

Edward O. Wilson

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Dans le cadre de l'étude de cas du fleuve St Laurent du réseau COMERN, l'objectif général de la thèse était de déterminer le rôle des macroinvertébrés littoraux dans le transfert de méthylmercure (MeHg) dans l'écosystème du lac St Pierre.

Le premier chapitre était consacré à la contribution quantitative des invertébrés non consommables (« impasses trophiques ») au transfert de MeHg vers les poissons. Pour cela, les concentrations en mercure total (THg) et en MeHg chez quatre groupes fonctionnels de macroinvertébrés littoraux (brouteurs, détritivores, prédateurs consommables, prédateurs non consommables) ont été mesurées. Les résultats ont montré que les prédateurs non consommables présentaient les plus fortes concentrations en THg, en MeHg ainsi que la plus forte proportion de MeHg/THg de tous les groupes fonctionnels. La charge (concentration × biomasse) de MeHg des prédateurs non consommables représentait de 10 à 36% du réservoir de MeHg des invertébrés phytophiles. Cette proportion élevée de MeHg séquestrée dans des impasses trophiques pourrait contribuer à expliquer les faibles concentrations en Hg mesurées chez les poissons du lac St Pierre. Nos résultats montrent que les organismes non consommables doivent être pris en compte dans les modèles prédictifs de contamination des écosystèmes par le Hg afin d'éviter de surestimer les quantités de MeHg biodisponibles pour les poissons.

Dans le deuxième chapitre, l'objectif était de déterminer les liens entre la source de matière organique (MO) et la contamination au MeHg chez les macroinvertébrés littoraux consommateurs primaires. Une approche isotopique a été appliquée pour répondre à cet objectif. Les sources autochtones (épiphytes et macrophytes) étaient majoritaires dans la MO assimilée par les consommateurs primaires, avec une proportion plus faible de MO allochtone (matières particulaires en suspension notamment). Le MeHg/THg chez les macroinvertébrés était corrélé positivement avec les proportions d'épiphytes, alors ces dernières étaient corrélées négativement avec la fraction de Hg inorganique. Cette découverte peut faire supposer que la voie d'entrée principale du MeHg dans les réseaux trophiques littoraux se situe dans les épiphytes. Les consommateurs primaires pourraient alors moduler le transfert de MeHg vers les niveaux trophiques supérieurs suivant qu'ils s'alimentent de sources de MO à forte ou à faible concentration en MeHg.

Le troisième chapitre traitait de l'influence du groupe fonctionnel (brouteur, collecteur, fragmenteur, omnivore, prédateur, prédateur-hématophage, piqueur-suceur) et des variables spatiotemporelles (année, mois, station d'échantillonnage) sur la signature de $\delta^{15}N$ des macroinvertébrés littoraux du lac St Pierre. La station était le facteur le plus important pour expliquer les variations de $\delta^{15}N$, suivie du mois d'échantillonnage et du groupe fonctionnel. Les organismes de la rive sud, très

influencée par les apports d'azote inorganique agricole avaient des valeurs de $\delta^{15}N$ plus élevées que ceux de la rive nord qui reçoit des apports du Bouclier Canadien. La signature de $\delta^{15}N$ des organismes a augmenté d'environ 3‰ durant la période d'échantillonnage, de mai à septembre, soit l'équivalent d'un niveau trophique. L'enrichissement du $\delta^{15}N$ des herbivores aux prédateurs était en moyenne de 1.6‰, ce qui est inférieur aux 3.4‰ généralement considérés chez les organismes de la zone pélagique. Puisque le fractionnement isotopique n'est pas homogène dans tout le réseau trophique, nous conseillons d'employer des valeurs de fractionnement spécifiques aux niveaux trophiques considérés, afin de mieux reconstruire les réseaux trophiques littoraux.

Dans le dernier chapitre, les rôles de l'habitat et de l'architecture des macrophytes sur la biomasse et l'abondance des invertébrés phytophiles étaient étudiés. Nous avons aussi calculé une estimation à l'échelle du lac de la biomasse de macroinvertébrés associée aux différents types d'habitats macrophytiques afin d'estimer les effets quantitatifs de changements de végétation sur les communautés de macroinvertébrés. La biomasse, l'abondance et la richesse des communautés d'invertébrés étaient plus élevées dans les habitats de macrophytes submergées que dans ceux de macrophytes flottantes et émergentes. Les macrophytes avec une architecture complexe n'hébergeaient pas significativement plus de biomasse de macroinvertébrés que celles avec une architecture plus simple. Dans le cas d'une baisse de niveau d'eau du lac St Pierre nous avons prédit que la biomasse totale d'invertébrés phytophiles diminuerait de 16% à l'échelle du lac.

Dans les réseaux trophiques littoraux, il apparaît que les flux d'énergie et de MeHg ne sont pas parfaitement superposés. Premièrement, les bas niveaux trophiques constitués par les macroinvertébrés consommateurs primaires sont capables d'effectuer une modulation des flux de MeHg suivant la nature de leurs sources de MO. Deuxièmement, parmi les consommateurs secondaires une proportion non négligeable du réservoir de MeHg ne sera que peu ou pas disponible pour le transfert vers les poissons. La faible différence de $\delta^{15}N$ entre les consommateurs primaires et secondaires nous permet d'émettre des doutes quant à l'utilité de cet outil en tant que traceur du niveau trophique d'un organisme de la zone littorale comparé au $\delta^{13}C$.

Mots clés: macroinvertébrés, zone littorale, méthylmercure, réseaux trophiques, impasses trophiques, isotopes stables, milieux humides, lac St Pierre.

INTRODUCTION GÉNÉRALE

Contexte général de l'étude

Depuis le milieu du XX^{ème} siècle et la catastrophe de Minamata (Japon), le mercure (Hg) est devenu un constant objet d'attention de la part des chercheurs et des autorités sanitaires de nombreux pays. La principale forme organique du Hg, le méthylmercure (MeHg) possède deux caractéristiques importantes : 1) la capacité de se bioaccumuler (ses concentrations mesurées dans les organismes sont supérieures à celles mesurées dans le milieu ambiant); 2) la bioamplification, en particulier en milieu aquatique, c'est-à-dire que ses concentrations augmentent avec le niveau trophique d'un organisme (Cabana et Rasmussen, 1994; Cabana *et al.*, 1994; Lucotte *et al.*, 1999). Ces deux propriétés sont couplées à de puissants effets neurotoxiques (Lebel *et al.*, 1996; Boening, 2000). Qui plus est, le Hg est très volatil, notamment sous sa forme élémentaire Hg^0 et peut donc être aérotransporté et se déposer dans les systèmes éloignés de toute source de pollution (Jackson, 1997; Landers *et al.*, 1998). Via des processus de méthylation en milieu aquatique, le Hg inorganique (Hg^{2+} principalement) est transformé en MeHg et peut ensuite contaminer tout le réseau trophique puisque c'est essentiellement par l'alimentation que le MeHg se bioaccumule (Hall *et al.*, 1997). Ce MeHg constitue alors un danger sournois pour la santé humaine et animale car la simple consommation de poissons de haut niveau trophique peut conduire à des intoxications chroniques, et ce en dehors même des zones ponctuelles de contamination (Lebel *et al.*, 1996; Lucotte *et al.*, 2005).

Le Hg pouvant être présent dans tous les compartiments des écosystèmes (transport atmosphérique), les recherches multi- et interdisciplinaires doivent être privilégiées afin de mieux comprendre son cycle biogéochimique. Au Canada, le COMERN

(Réseau de recherches concertées sur le mercure – Collaborative Mercury Research Network, 2001-2006) s'est donné pour objectif « d'intégrer les efforts de recherches [...] pour en arriver à une meilleure compréhension, à l'échelle des écosystèmes, des processus qui contrôlent les échanges et l'accumulation du mercure dans la région nord du continent américain*. »

Un des aspects novateurs du COMERN est l'approche par « étude de cas » (*case study*) s'adressant à un écosystème ou un type d'écosystèmes. Cette approche est originale puisqu'elle est à la fois holistique dans sa nature (tous les aspects scientifiques pertinents par rapport à la problématique mercurielle sont traités) et transversale dans son application, au niveau des équipes de recherche mais aussi par ses liens avec les acteurs communautaires et politiques. La présente thèse fait partie de l'étude de cas consacrée au fleuve St Laurent (Québec). Une part importante de l'alimentation de plusieurs communautés vivant le long du fleuve St Laurent est constituée de poissons. Ceci est particulièrement vrai dans la région du lac St Pierre, le plus grand lac fluvial du St Laurent (Vis *et al.*, 2003). En plus de la détermination de l'exposition humaine au Hg, l'étude de cas portait sur une étude intégrée de la transformation biogéochimique et des flux de Hg au sein des terres humides du lac St Pierre (Amyot *et al.*, 2004). Les processus biogéochimiques et écologiques dans les milieux humides ou la zone littorale (les deux systèmes étant étroitement imbriqués au lac St Pierre) sont encore peu connus, mais certaines études ont montré qu'ils pourraient constituer des sites favorables à la méthylation, et s'avérer donc des sources nettes de MeHg (St. Louis *et al.*, 1994). Plus en détails, les équipes interdisciplinaires de l'étude de cas ont étudié les flux de Hg dissous et particulaire dans le lac (Caron, 2007), les échanges de Hg gazeux à l'interface air-eau (Poissant *et al.*, 2004), la contamination des poissons (Simoneau *et al.*, 2005), la spéciation du Hg dans les sédiments (Zhang *et al.*, 2004) et la méthylation dans les complexes

* http://www.unites.uqam.ca/comern/whofr/cadre.html

macrophytes-épiphytes (Planas *et al.*, 2004). La présente étude est principalement consacrée au transfert de MeHg dans les réseaux trophiques de macroinvertébrés liés aux macrophytes littorales. Elle est donc en lien direct avec les études « en amont » portant sur la méthylation et celles « en aval » sur les concentrations en MeHg des poissons, et en lien indirect avec toutes les autres. Avant d'exposer ci-après nos objectifs spécifiques, il nous faut tout d'abord bien définir les communautés d'organismes à l'étude et leur milieu.

Macroinvertébrés phytophiles et zone littorale

Le terme « macroinvertébré » rassemble étymologiquement les invertébrés aquatiques observables à l'oeil nu. De façon pratique, ces animaux sont ceux retenus dans des filets de maille de 200 à 500 µm ou plus grossière (Rosenberg et Resh, 1993). On trouve des macroinvertébrés dans tous les types de milieux aquatiques d'eau douce, bien qu'ils soient pauvrement représentés dans la zone pélagique des lacs (la famille des Chaoboridae étant l'exception notable). Par contre, dans les autres compartiments d'eau douce, des mares temporaires à la zone benthique des plans d'eau permanents, des ruisseaux intermittents aux plaines d'inondation des grands fleuves, les macroinvertébrés forment des communautés importantes (Rosine, 1955; Lalonde et Downing, 1992). Les insectes sont le groupe taxonomique souvent le mieux représenté, que ce soit en nombre d'individus ou de taxons avec pas moins de 12 ordres comprenant 30 000 espèces recensés en eau douce (Willams et Feltmate, 1992). Étant donné que les insectes sont avant tout d'origine terrestre, les évolutionnistes ont tendance à séparer les ordres d'insectes en deux groupes, à savoir les ordres d'envahisseurs primaires et ceux d'envahisseurs secondaires. Les envahisseurs primaires sont les insectes ayant colonisé le milieu aquatique à une période très ancienne (Dévonien de l'ère Primaire, Ross, 1965) et dont la majorité des

espèces sont désormais aquatiques. Chez les ordres d'envahisseurs secondaires, les premiers fossiles retrouvés en milieu aquatique sont plus récents et seulement un faible pourcentage des espèces est réellement aquatique. Parmi les envahisseurs primaires on trouve principalement les éphéméroptères, plécoptères, odonates, et trichoptères. Les envahisseurs secondaires sont en grande partie représentés par les hémiptères, les coléoptères, et les diptères. Au côté des insectes, on retrouve des mollusques (gastéropodes et bivalves surtout), des crustacés (amphipodes, isopodes, décapodes, cladocères, copépodes), des annélides (achètes, oligochètes), des nématodes, et des plathelminthes (Cyr et Downing, 1988). Les autres taxons d'invertébrés microscopiques (rotifères, protozoaires, etc.) ne font pas partie des macroinvertébrés et ne seront pas traités ici.

Dans les systèmes lentiques c'est souvent dans la zone littorale que l'on retrouve les communautés de macroinvertébrés les plus diversifiées. Strayer (1985) a d'ailleurs remarqué que la richesse spécifique du benthos ne fait que décroître au delà de 1 m de profondeur, avec une perte d'environ 10 espèces par m. C'est également au sein de la zone littorale que l'on retrouve la plus forte production secondaire lacustre (Brinkhurst, 1974). En règle générale, la densité et la richesse des communautés de macroinvertébrés sont toujours plus élevées sur des substrats de végétaux vivants que sur d'autres types de substrats d'un même écosystème (Watkins *et al.*, 1983; Rasmussen et Rowan, 1997). Un déclin des assemblages de macrophytes d'un lac est d'ailleurs souvent suivi d'une chute de la biomasse zoobenthique (Davies, 1982). Un grand nombre de facteurs ont été identifiés pour expliquer les liens intimes entre macroinvertébrés phytophiles (ou phytomacrobenthos) et macrophytes. Tout d'abord, les plantes aquatiques, de par leur structure tridimensionnelle procurent une plus grande surface de colonisation, puis de peuplement pour les invertébrés (Krecker, 1939; Cheruvelil *et al.*, 2002). Ensuite, elles offrent un support physique, protégeant de nombreuses espèces contre la turbulence dans les rivières ou les lacs en

amortissant l'énergie des vagues (Spence, 1982; Rasmussen et Rowan, 1997). Les macrophytes peuvent constituer une indispensable source d'oxygène lors des périodes hypoxiques, par leur production primaire et celle de leurs épiphytes mais aussi parce que certaines espèces de coléoptères et diptères tirent leur O_2 directement de vacuoles percées dans les macrophytes (Houlilan, 1970). Les plantes aquatiques servent également de défense primaire (évitement du prédateur) pour les espèces de macroinvertébrés cryptiques (Watkins *et al.*, 1983) et peuvent ainsi contribuer à réduire les risques de prédation sur ces organismes. Les macrophytes favorisent aussi la collecte de matière organique pour les macroinvertébrés herbivores, que ce soit en augmentant le taux net de sédimentation des particules (Benoy et Kalff, 1999), comme substrat pour le périphyton (Cattaneo, 1983; Gosselain *et al.*, 2005), ou bien comme source alimentaire *stricto sensu* (Sheldon, 1987; Elger et Lemoine, 2005). Finalement, les macrophytes jouent un rôle fondamental dans l'ontogénie et la phénologie de certains organismes. Par exemple, les macrophytes émergentes sont indispensables au dernier stade larvaire (instar) de plusieurs espèces d'odonates (libellules et demoiselles) qui les utilisent comme support d'escalade afin d'effectuer leur métamorphose dans le milieu aérien (Westfall et Tennessen, 1996). Les feuilles et les tiges de macrophytes servent également de sites de reproduction et de dépôt des oeufs d'un très grand nombre de macroinvertébrés (Pinder, 1986). Certaines espèces de Chironomidae ont même établi des relations quasi-symbiotiques avec des plantes aquatiques en passant la majeure partie de leur stade larvaire à l'intérieur des tiges de macrophytes (Coffman et Ferrington, 1996). La zone littorale est donc d'une grande valeur pour les processus écologiques et pour les communautés qu'elle héberge. Il nous reste à démontrer l'influence de ces particularités écologiques et biocénotiques sur le cycle biogéochimique du Hg.

Importance de la zone littorale dans les transferts de MeHg

L'importance qualitative et quantitative de la zone littorale dans le cycle du Hg peut être potentiellement considérable, pour trois raisons : (1) puisqu'elle est située entre le milieu terrestre et le milieu aquatique *stricto sensu*, la zone littorale sert d'écotone à la plupart des processus écologiques (transferts de carbone, de nutriments, de contaminants; Kalff, 2002; Desrosiers *et al.*, 2005). Les macroinvertébrés qui y vivent peuvent alors représenter des maillons de transfert importants entre les processus en amont et les niveaux trophiques supérieurs (poissons notamment) ainsi que vers les zones pélagique et benthique des lacs, y compris pour le transfert de MeHg. (2) Dans de nombreux systèmes, c'est dans cette zone que la plus grande part des flux d'énergie et de MeHg vont s'opérer, que ce soit parce que ce sont des lacs peu profonds comme le lac St Pierre où la majorité de la production primaire a lieu dans la zone littorale (Vis, 2004), ou bien parce que le rendement énergétique de la zone benthique est supérieur à celui de la zone pélagique à cause de la taille supérieure des macroinvertébrés par rapport au zooplancton en tant que proies pour les poissons (Vander Zanden *et al.*, 2006). (3) La troisième raison est liée au phénomène de méthylation. La méthylation a principalement lieu en milieu aquatique et est gouvernée par de nombreuses variables (Ullrich *et al.*, 2001). Traditionnellement, la couche supérieure des sédiments a été le site potentiel de méthylation le plus étudié (Compeau et Bartha, 1984; Gilmour *et al.*, 1992; Zhang et Planas, 1994; Guimarães *et al.*, 2000) mais un corpus croissant d'études démontre qu'elle a aussi lieu dans les assemblages de périphyton (Planas *et al.*, 2004; Desrosiers *et al.*, 2006). Les algues étant une source de matière organique plus digeste que les détritus sédimentaires, la charge de MeHg transférée vers les niveaux trophiques supérieurs pourrait être plus élevée chez le périphyton que par les sédiments. Dans tous les cas les invertébrés constitueraient le lien entre les systèmes de méthylation et les niveaux trophiques supérieurs.

Bien qu'il existe des études sur la contamination du benthos profond ou émergent des réservoirs (Tremblay et Lucotte, 1997; Hall *et al.*, 1998; Tremblay *et al.*, 1998) les recherches sur les dynamiques de transfert du MeHg chez les macroinvertébrés dans la zone littorale sont très peu nombreuses (Cleckner *et al.*, 1998; Allen *et al.*, 2005). Chez ces organismes, plusieurs aspects importants qui s'avéreraient des seuils critiques pour la compréhension du cycle du MeHg n'ont pas encore bénéficié de recherches poussées: (1) le lien entre palatabilité des macroinvertébrés et leur concentration en MeHg, ce qui aurait une influence sur le transfert de MeHg vers les niveaux trophiques supérieurs; (2) la modulation qui peut être opérée par les invertébrés consommateurs primaires dans les flux de MeHg vers les niveaux trophiques supérieurs suivant leur source de matière organique; (3) la dimension verticale (niveaux trophiques) dans les réseaux trophiques de macroinvertébrés; (4) l'aspect quantitatif des liens entre les invertébrés phytophiles et leur substrat de macrophytes. Ces quatre aspects constituent chacun un chapitre de cette thèse, ils sont exposés succinctement ci-dessous.

Chapitre I : Les impasses trophiques – un aspect méconnu du cycle du Hg

Plus que dans la zone benthique profonde, les communautés littorales de macroinvertébrés sont composées d'un grand nombre de taxons d'envahisseurs secondaires tels que les coléoptères et les hémiptères, qui ont la particularité d'effectuer la totalité de leur cycle vital en milieu aquatique, les adultes étant souvent nectoniques ou pleustoniques (Wallace et Anderson, 1996). Au sein de la colonne d'eau, les adultes de ces ordres devraient alors être vulnérables à la prédation des poissons, pourtant, à l'exception des Corixidae, les hémiptères et les coléoptères sont dédaignés par leurs prédateurs potentiels. En fait, il a été observé au niveau des glandes métathoraciques et pygidiales chez quasiment tous les hémiptères et

coléoptères aquatiques diverses molécules dont l'odeur et/ou le goût répugnants servent à dissuader les poissons de les consommer (Eisner et Meinwald, 1966; Blum, 1981; Eisner et Aneshansley, 2000). Il en résulte que ces insectes ne subissent que très peu de pression de prédation (Lokensgard *et al.*, 1993; Wallace et Anderson, 1996). On parle alors d'« impasses » ou de « culs-de-sac » trophiques. Cette propriété peut être d'une grande importance dans le cas du cycle du MeHg puisque la quantité de MeHg retenue dans ces organismes au cours de leur ontogénie pourrait ne pas être transférée aux niveaux trophiques supérieurs. Qui plus est, la quasi-totalité des espèces d'impasses trophiques étant des prédateurs, leurs concentrations en MeHg n'en seraient alors que plus élevées (Cleckner *et al.*, 1998; Allen *et al.*, 2005). Connaître l'importance quantitative des impasses trophiques et la proportion de MeHg qui y est séquestrée est alors capitale pour correctement évaluer les transferts de MeHg dans les réseaux trophiques et éviter de surestimer les quantités de MeHg disponibles pour les poissons. Pour le premier chapitre nous avons émis l'hypothèse que les prédateurs non consommables (coléoptères et hémiptères essentiellement) présentaient de plus fortes concentrations que tous les autres groupes fonctionnels, y compris les prédateurs consommables. Nous avons également voulu déterminer l'importance quantitative (charge de MeHg) des prédateurs non consommables dans le transfert de MeHg au sein des réseaux trophiques littoraux.

Chapitre II : Sources de matière organique des consommateurs primaires et MeHg

De part leur position intermédiaire dans les réseaux trophiques, les macroinvertébrés s'avèrent cruciaux pour le transfert de MeHg entre les systèmes de méthylation et les poissons. En effet, il existe de bonnes corrélations entre les concentrations en MeHg des invertébrés et celles des poissons (Wong *et al.*, 1997; Lucotte *et al.*, 1999; Allen *et al.*, 2005). Une variation des concentrations en MeHg

des macroinvertébrés aurait alors tout lieu de se répercuter plus haut dans le réseau trophique. Suivant qu'ils privilégient des sources de matière organique potentiellement riches (ex : périphyton) ou presque dépourvues de MeHg (ex : végétaux d'origine terrestre) les invertébrés consommateurs primaires pourraient moduler les flux de MeHg vers les niveaux trophiques supérieurs. Cependant, la plupart des invertébrés consommateurs primaires ont un régime alimentaire opportuniste (Cummins et Klug, 1979; Jacobsen et Sand-Jensen, 1995; Zah *et al.*, 2001). Ils peuvent donc inclure plusieurs sources potentielles de matière organique dans leur alimentation. Avec l'utilisation croissante des rapports isotopiques des isotopes stables du carbone et de l'azote ($\delta^{13}C$, $\delta^{15}N$) et des nouveaux logiciels d'équations de mélange (Phillips et Cregg, 2003; Benstead *et al.*, 2006) il est dorénavant possible d'estimer les proportions des différentes sources de matière organique dans l'alimentation de ces organismes. Cependant, seul un très petit nombre d'études ont été menées jusqu'à présent à l'aide de ces nouveaux outils sur les macroinvertébrés et aucune en lien avec le MeHg. Le but de ce chapitre est donc de coupler ces mesures de proportion de matière organique dans le régime alimentaire des invertébrés avec leurs valeurs de contamination au MeHg, pour vérifier s'il existe une relation entre ces deux variables.

Chapitre III : Niveaux trophiques des macroinvertébrés – utilisation des isotopes stables de l'azote ($\delta^{15}N$)

Le $\delta^{15}N$ est progressivement devenu un outil populaire pour l'étude des réseaux trophiques (Peterson et Fry, 1987). En effet, le fractionnement isotopique de l'azote entre les consommateurs et leurs proies (par une excrétion préférentielle de l'isotope léger ^{14}N) se traduit par une augmentation progressive du $\delta^{15}N$ verticalement dans le réseau trophique. Le niveau trophique d'un organisme est donc positivement corrélé avec son $\delta^{15}N$, avec un facteur d'enrichissement assez constant, évalué à 3.4‰

(Minagawa et Wada, 1984; Vander Zanden et Rasmussen, 2001; Post, 2002). En corrigeant pour les variations susceptibles de se produire à la signature de base (souvent un producteur ou consommateur primaire) il est possible de reconstruire assez fidèlement le réseau trophique d'un système aquatique (Vander Zanden *et al.*, 1997; Peterson, 1999). Pourtant, nos connaissances des réseaux trophiques d'invertébrés littoraux demeurent parcellaires. Par exemple, il existe des modes d'alimentation très diversifiés chez ces organismes, des brouteurs d'algues aux macroprédateurs tels que les Belostomatidae (hémiptères), en passant par les collecteurs de matière organique, les fragmenteurs, les ectoparasites, etc. Cette diversité de modes d'alimentation complexifie les réseaux trophiques de macroinvertébrés, complexité qui devrait logiquement se refléter dans les valeurs de $\delta^{15}N$ de ces animaux. De plus, il a été démontré que la valeur théorique d'augmentation du $\delta^{15}N$ par niveau trophique (3.4‰) n'est valide que pour des sources de nourriture très protéiques comme les poissons (McCutchan *et al.*, 2003). La valeur de fractionnement chez les macroinvertébrés devrait alors différer de 3.4‰, et les implications pourraient être majeures dans l'étude des réseaux trophiques aquatiques d'eau douce, en particulier lors de l'emploi d'équations de mélange (*mixing models*) et des relations entre niveau trophique et concentrations en MeHg. L'objectif de ce chapitre était de quantifier l'influence des modes d'alimentation sur le $\delta^{15}N$ des macroinvertébrés tout en tenant compte des éventuelles influences concurrentes (facteurs spatiotemporels).

Chapitre IV : Biomasse des macroinvertébrés et lits de macrophytes

Les changements climatiques à l'échelle mondiale sont prévus d'affecter les niveaux d'eau de certains systèmes aquatiques (Coops *et al.*, 2002). Les lacs peu profonds qui sont souvent les lacs les plus productifs (Straškraba, 1980) et hébergent

une grande quantité de lits de macrophytes et les macroinvertébrés qui y sont associés, risquent alors de subir des modifications hydrologiques majeures. Le passage de lits de plantes submergées à haute surface de colonisation à des marais de plantes émergentes à faible surface utilisable pour les invertébrés devrait se répercuter sur la phytomacrofaune (Cyr et Downing, 1988). Encore une fois, le lien trophique entre les invertébrés et les poissons risque d'être modifié car une diminution du niveau des lacs peu profonds par exemple non seulement restreindrait le volume de l'habitat des poissons mais pourrait affecter la biomasse et la distribution des invertébrés qui leur servent de proies. De tels changements quantitatifs dans la biomasse piscicole et invertébrée pourraient à moyen terme avoir potentiellement des conséquences importantes sur les transferts et la partition du Hg (Surette *et al.*, 2006).

D'après les problématiques exposées dans les paragraphes précédents (importance des impasses trophiques, relation entre MeHg et alimentation des invertébrés, comportement du $\delta^{15}N$ des réseaux trophiques de macroinvertébrés, influence des habitats de macrophytes sur les communautés) nous avons pu définir les objectifs de cette thèse de doctorat :

1 – Chez les macroinvertébrés littoraux, évaluer l'importance des impasses trophiques au transfert de MeHg aux niveaux trophiques supérieurs.

2 – Déterminer les sources d'alimentation des invertébrés littoraux et étudier les liens entre source d'alimentation et contamination au MeHg

3 – Évaluer l'influence des groupes fonctionnels et des modes d'alimentation des invertébrés sur leur signature en $\delta^{15}N$.

4 – Étudier les relations quantitatives entre habitat de macrophytes et biomasse et richesse des communautés d'invertébrés phytophiles.

CHAPITRE I

ASSESSING THE IMPORTANCE OF MACROINVERTEBRATE TROPHIC DEAD-ENDS IN THE LOWER TRANSFER OF METHYLMERCURY IN LITTORAL FOOD WEBS

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Résumé : Les concentrations en mercure total et méthylmercure ([THg] et [MeHg]) ont été mesurées chez les macroinvertébrés littoraux du lac St Pierre, Québec, Canada. Le groupe fonctionnel (détritivore, brouteur, prédateur consommable, prédateur non consommable) expliquait la plus forte proportion de la variation de [MeHg] comparé au temps (année, mois) et à l'espace (station, rive). Les plus fortes [THg] et [MeHg] ont été trouvées chez les prédateurs non consommables appartenant à des familles de coléoptères et d'hétéroptères. Les détritivores et les brouteurs montrèrent les plus faibles concentrations alors que les prédateurs consommables étaient intermédiaires. Les prédateurs non consommables présentaient également les plus forts pourcentages de MeHg ([MeHg]/[THg]), avec certains taxons proches de 100%. De tels pourcentages ne sont habituellement observés en eau douce que chez les poissons piscivores. La charge de MeHg (concentration × biomasse) chez les prédateurs non consommables représentait 10% du réservoir de MeHg de la communauté des macroinvertébrés. Cette quantité importante de MeHg est séquestrée dans des impasses trophiques aquatiques et pourrait expliquer partiellement les faibles [MeHg] mesurées chez les poissons comparées aux [MeHg] des macroinvertébrés du lac St Pierre et des autres écosystèmes d'eau douce avec des zones littorales étendues. Nous recommandons de tenir compte des organismes non consommables dans les modèles de cycle du Hg afin de ne pas surestimer les quantités de MeHg disponibles pour les poissons.

Mots clés: macroinvertébrés, impasses trophiques, méthylmercure, bioamplification, lac St. Pierre.

Abstract: Total mercury and methylmercury concentrations ([THg], [MeHg]) were measured in littoral macroinvertebrates from Lake St. Pierre, Quebec, Canada. Functional groups (detritivore, grazer, edible predator, inedible predator) explained the greatest fraction of [MeHg] variation compared to time (year, month), and space (station and shore). Greatest [THg] and [MeHg] were found in inedible predators mostly from families of heteropterans and coleopterans. Detritivores and grazers exhibited the lowest Hg concentrations while edible predators were intermediate. Inedible predators also had the highest percentage of MeHg ([MeHg]/[THg]), with some taxa close to 100%. Such high percentages are seldom observed in freshwater organisms other than piscivorous fish. MeHg burden (concentrations × biomass) in inedible predators accounted for 10% of the MeHg pool for the whole invertebrate community. These relatively significant quantities of MeHg are sequestrated in aquatic "trophic dead-ends" and could partly explain the low [MeHg] measured in fish, compared to [MeHg] of macroinvertebrates from Lake St. Pierre and other freshwater ecosystems with large littoral zones. We recommend taking into account the inedible organisms in Hg cycling models in order to avoid a possible overestimation of the MeHg pool available to fish.

1.1) INTRODUCTION

Monomethylmercury (MeHg) is considered a global threat to human and ecosystem health because of its neurotoxicity and accumulation in food webs through biomagnification (Boening 2000). Since fish consumption is the main pathway for MeHg to enter the human body, several studies considered factors affecting MeHg concentrations ([MeHg]) in fish (MacCrimmon et al. 1983; Cabana et al. 1994; Simoneau et al. 2005). However, other components of the mercury (Hg) food web have often been overlooked. For example, benthic macroinvertebrate have received less attention than pelagic invertebrates as prey organisms for fish. The few reported data demonstrate that [MeHg] in macroinvertebrates can be very high (Tremblay et al. 1996; Hall et al. 1998; Désy et al. 2000). Since macroinvertebrates constitute an important food source for juvenile and adult fish they play a crucial role in energy transfer in lakes (Bertolo et al. 2005). This fact should be even more important in shallow lakes with large littoral zones covered with aquatic plants where invertebrates dwelling in macrophytes constitute a larger fraction of the prey of insectivorous and juvenile piscivorous fish, and where pelagic phytoplankton productivity does not account for a large part of total productivity (Vis et al. 2007). In systems where periphyton productivity is important, Hg methylation rates may be high thus leading to elevated [MeHg] in epiphytic biofilms (Cleckner et al. 1998). Hence, littoral invertebrates may constitute a crucial link between the Hg methylating environment of epiphytes and top predators.

In vegetated littoral environments of lakes and lentic waters of rivers, the invertebrate fauna is unique because it is not dominated by insect larvae as in lotic environments. Instead aquatic adults of insect species named "secondary invaders" (Hynes 1984) because of their recent terrestrial origin, constitute a non negligible share of the invertebrate community, along with non-insect taxa like gastropods and amphipods. The majority of the imago stages of insect species living in vegetated

water bodies, mostly heteropterans and coleopterans, have developed chemical defenses that render them unpalatable (Eisner and Aneshansley 2000). Thus, they are resistant to predation and are seldom eaten by fish (Polhemus 1996). Though fish are able to exclude some heteropterans and coleopterans from small lakes (Bendell and McNicol 1987), it is not well known whether it is caused by predation or competitive exclusion. It has been experimentally demonstrated that largemouth bass Micropterus salmoides, force fed with edible worms coated with Dineutus hornii (Coleoptera, Gyrinidae) abdominal gland secretion rejected the prey (Eisner and Aneshansley 2000). A decade-long field survey of the stomach contents of 18 fish species of the St. Lawrence River revealed that heteropterans and coleopterans constituted a negligible part of the fish diet (Latour et al. 1980). Large individuals of heteropterans and coleopterans are not only weakly affected by fish predation but can even become top predators in fishless lakes (Runck and Blinn 1994) and turn out to be pests in fish nurseries (Wilson 1958; Le Louarn and Cloarec 1997). Because of their trophic position and low predation pressure, inedible predatory insects are more susceptible to MeHg accumulation than edible ones. They may also have the potential to live longer than edible predators and hence accumulate even greater [MeHg]. The MeHg pool these invertebrates represent would thus be unavailable to aquatic predators, including fish.

The goal of this study was to assess the contribution of inedible predatory insects to the MeHg pool in the macroinvertebrate littoral communities in a large fluvial lake, Lake St. Pierre, which receives high Hg loadings from its tributaries (Quémerais et al. 1999; Caron and Lucotte, in press) and which hosts extensive macrophyte beds. We tested the following hypotheses: 1) variations in [MeHg] in macroinvertebrates are better explained by trophic factors than by spatial differences in Hg loadings; 2) the amount of Hg that is sequestrated in inedible predators is equal or greater to that represented by edible predators.

1.2) MATERIALS AND METHODS

1.2.1) Study site

Lake St. Pierre is a large fluvial lake of the St. Lawrence River (46°02-05'N 72°39'W) southern Quebec, Canada. Its macrophyte beds represent one fifth and three-quarters of all St. Lawrence River wetlands and marshes respectively (Langlois et al. 1992). These wetlands are highly productive (Tessier et al. 1984) with macrophytes and attached epiphytes contributing up to 70% of lake primary production (Vis et al. 2007). There are three markedly distinct water masses flowing in Lake St. Pierre: brown, dissolved organic carbon (DOC) rich waters from the Ottawa River inflow and other Canadian Shield tributaries arriving on the northern section of the lake (Vis et al. 2003). Clear waters from Lake Ontario flow in the central channel, and tributaries draining extensively farmed lands bring turbid waters from the Appalachian region on the southern section of Lake St. Pierre (Vis et al. 2003). The central channel is part of the St. Lawrence Seaway; it is artificially dredged and prevents the mixing of the north and south water masses. High Hg loadings are associated with terrigenous organic matter (TOM) in the south shore tributaries (Quémerais et al. 1999) in contrast to lower ones brought by the north shore tributaries that have more forested watersheds. Hg loads from the southern main tributaries (Richelieu, Saint-François, and Yamaska rivers) have been estimated between >120 mol Hg•year^{-1} (Caron and Lucotte, *in press*) and 733 mol Hg•year^{-1} (Quémerais et al. 1999). Tributaries from the north shore (Maskinongé, Rivière-du-Loup, and Yamachiche rivers) discharge comparatively little Hg: 4 mol Hg•year^{-1}. Dissolved THg concentrations are low in Lake St. Pierre, averaging 1.50 ng•L^{-1} in the south shore tributaries and 1.14 ng•L^{-1} elsewhere (Caron and Lucotte, *in press*). MeHg concentrations are generally below 1 ng•L^{-1} at all stations. Suspended

Particulate Matter bound Hg usually represents 40% of total Hg present in the water column.

1.2.2) Collecting and sorting invertebrates

Sampling was conducted monthly from July to September 2003 and from May to September 2004 at four sites in Lake St. Pierre. Two sites were situated in the brown waters of the north shore of the lake, (GIR, MAS) and two others on the turbid waters of the south shore (ADF, BSF). Invertebrates were collected in macrophytes beds, with a Plexiglas modified (15 × 35 × 25 cm) Downing box (Downing 1984). The sampler was immersed in the water between the surface and 1.5 m deep and then slowly closed, capturing both vagile and phytophilous invertebrates. Six replicates were collected at each station, in May and June in 2004 and nine replicates from July to September in 2003 and 2004. An aquatic hand net was used as a complement to catch very fast moving insects like Dytiscidae and Gyrinidae. All bulk samples were sieved through a 500 µm net, and macroinvertebrates were separated from macrophytes by vigorous hand shaking in a plastic container filled with lake water. Macroinvertebrates were pre-sorted in order to isolate predators from prey, and kept in Nalgene™ jars filled with lake-water for at least 4 hours, which is the travel time from sampling site to laboratory.

1.2.3) Macroinvertebrate identification and Hg analysis

Organisms were kept frozen at -80°C prior to analysis. Invertebrates were identified usually to family or genus. Shells of gastropods were removed manually

with stainless steel tweezers. For taxonomic identification, the following keys were used: Merrit and Cummins (1996) for insects, Clarke (1981) for gastropods and Pennak (1953) for other macroinvertebrates. We grouped the samples into four functional groups: grazers (including all invertebrates feeding on live plants), detritivores (invertebrates feeding on dead plants and animals), edible predators/parasites (called edible predators hereafter) and inedible predators (insects seldom eaten by fish because of their chemical defenses, Eisner and Meinwald 1966). The following taxa, Heteroptera _ Belostomatidae (Lokensgard et al. 1993), Gerridae and Mesoveliidae (Bronmark et al. 1984), Notonectidae (Pattenden and Staddon 1968), Pleidae (Maschwitz 1967), Coleoptera _Dytiscidae (Swevers et al. 1991) and Gyrinidae (Eisner and Aneshansley 2000) were included in the latter group. Though they belong to heteropterans, Corixidae (water boatmen) were not included in the inedible predators group because they are heavily preyed upon by fish and other predators (Polhemus 1996). Hydracarina (~~water~~ mites) might also be unpalatable to fish (Kerfoot 1982) but a more recent review only found anecdotal evidence of mite rejection by fish predators (Zhang 1998) so for the purpose of this study they were considered as edible.

All instruments used for Hg analysis were rinsed once with 10% HCl and twice with nanopure™ water. Invertebrates were freeze-dried for 48 h, and to avoid manipulation and possible contamination, ground with a glass rod directly in the vial. Sub-samples were then weighed on an electro balance (AT201 Mettler Toledo™, Canada). Each individual taxon was kept in a separate vial. Because the mean weight of our samples was often below 5 mg dry weight (DW), we used THg and MeHg analysis methods described by Pichet et al. (1999). These methods allow for the processing of small samples, as little as < 1 mg DW. Total Hg concentrations ([THg]) were obtained with cold vapor fluorescence atomic spectrometry (CVFAS; Bloom 1989) with a detection limit of 1 $ng \cdot g^{-1}$. The sole difference with Bloom method was

that Hg was not pre-concentrated in a gold column but is injected directly. Reproducibility was verified with the National Research Council of Canada standard TORT-2 (lobster hepatopancreas). The measured concentrations of TORT-2 were always within the certified value of 270 ± 60 $ng \cdot g^{-1}$ DW. For MeHg analyses, a saponification technique with a detection limit of 0.6 pg of MeHg, modified from Bloom (1989) by Pichet et al. (1999) was used. Briefly, the digestion of 0.5-5 mg DW invertebrate was performed in 0.5 mL of a KOH/MeOH (1 g•4 mL^{-1}) solution during 8 hours at 68°C. MeHg was then converted to methyl-ethyl Hg (MeEtHg) with sodium tetraethylborate in a buffered solution at pH 4.5. MeEtHg was then trapped in a column, separated by gas chromatography and quantified using CVAFS. The reproducibility of the method was verified by analyzing two National Research Council Standard Reference Materials DORM-1 (dogfish muscle) and TORT-2 that yielded a mean value ± SD of 742 ± 93 (n=37) and 157 ± 17 $ng \cdot g^{-1}$ DW (n=11), as compared to the certified values of 731 ± 60 $ng \cdot g^{-1}$ DW and 152 ± 13 $ng \cdot g^{-1}$ DW. Samples that lead to proportions of MeHg above 115% of THg were discarded.

1.2.4) Data treatment

Values of [MeHg] were log transformed prior to statistical analysis. We used factorial test effect models (JMP 5.1, SAS Institute, Cary, North-Carolina) to take into account the influence of temporal (2 years and 5 months), spatial (4 stations, 2 shores), and trophic level (4 functional groups) categorical variables on [MeHg] (SAS Institute Inc. 1991, Uryu et al. 2001). For each statistical level, comparisons between groups based on adjusted values (least-squared means, LSM) were performed with ANOVA and Tukey-Kramer Honestly Significant Differences (HSD).

For each taxon (t) and each sample we calculated MeHg burden, which represents a quantitative method to estimate the MeHg pool per functional group, in addition to measurements of [MeHg].

We calculated MeHg burden with the following equation:

(1) $\text{MeHg burden}_t = [\text{MeHg}]_t \times W_t$

Where MeHg burden_t is in ng; $[\text{MeHg}]_t$ in ng.g^{-1} DW; and W_t in ng DW for each taxon of invertebrates. Then, the MeHg burdens of each taxon t (t_1, t_2,...t_n) within a given functional group (a) at a given station (9 Downing boxes) and at each month were added:

(2) $\text{MeHg burden}_a = \text{MeHg burden}_{t1a} + \text{MeHg burden}_{t2a} + \ldots + \text{MeHg burden}_{tna}$

The MeHg burden share of a functional group (a) among four functional groups (a,b,c,d) is calculated with the following equation:

(3) $\%\text{share}_a = (\text{MeHg burden}_a / (\text{MeHg burden}_a + \text{MeHg burden}_b + \text{MeHg burden}_c + \text{MeHg burden}_d)) \times 100.$

In addition, we also calculated the MeHg burdens per individual (i) of each taxon in order to have an estimated amount of MeHg available per prey item of fish:

(4) $\text{MeHg burden}_i = \text{MeHg burden}_t / n_i$

Where n_i is the number of individuals within a sample of a taxon t.

1.3) RESULTS

1.3.1) THg and MeHg concentrations

In Lake St. Pierre, macroinvertebrate [THg] ranged from a mean <50 ng $Hg \cdot g^{-1}$ DW in trichopteran families to a mean >250 ng $Hg \cdot g^{-1}$ in heteropterans and predatory coleopterans (Table 1). Simuliidae larvae (Diptera) had the lowest concentrations (30 $ng \cdot g^{-1}$ DW) while *Ranatra* sp. (Heteroptera: Nepidae i.e., scorpion bugs) was the taxa with the greatest [THg] (406 $ng \cdot g^{-1}$ DW). Trends in [MeHg] were similar to those observed in [THg]. Mean [MeHg] ranged from 11 in *Odontomyia* sp. (Diptera: Stratiomyidae) to 378 $ng \cdot g^{-1}$ DW in *Ranatra*. On a functional group basis, the most elevated [THg] were found in inedible predators, grazers had the lowest [THg] and detritivores and edible predators [THg] were situated between these two groups (Fig. 1.1). As for [THg], [MeHg] were greatest in inedible predators, followed by predators, detritivores and finally, grazers, which again exhibited the lowest concentrations. Overall the mean proportions of MeHg to THg ([MeHg]/[THg]) values were high, above 50% MeHg, even in primary consumers. [MeHg]/[THg] respectively ranged from 61% ±1 to 69% ±4 in grazers and detritivores and from 80% ±3 to 90% ±4 in edible and inedible predators.

The test effect models 1 and 2 were both designed with three categorical variables (Table 1.2). All variables but year were highly significant. Model 1 explained slightly more of the variance of the macroinvertebrates [MeHg] than model 2 ($r^2 = 0.15$ compared to $r^2 = 0.11$). In models 3 and 4, functional group was added to models 1 and 2 as a categorical variable. Functional group was very highly significant ($p < 0.0001$) for both models and accounted for a much larger share of the variation ($r^2 = 0.47$) than the other variables. Additionally, the mean square of functional group

was one order of magnitude greater than the mean squares of the other significant variables combined (month, model 3 and 4, and shore, model 4, Table 1.2).

Comparisons of [MeHg] among functional groups showed that inedible predators had significantly greater [MeHg] than all the other functional groups, including edible predators and detritivores, while grazers had the lowest [MeHg] (Tukey HSD, $p < 0.05$). [MeHg] of invertebrates from the south shore of the lake were greater than those from the north shore (ANOVA, $p < 0.05$), consistent with the reported larger Hg loadings to the southern section. Temporal differences between years were insignificant but the differences among sampled months were highly significant. Indeed, invertebrates collected in June exhibited greater [MeHg] than those collected in the other months (Tukey HSD, $p < 0.05$). Three distinct patterns of [MeHg] monthly variations were observed among the main taxa collected in Lake St. Pierre (Fig. 1.2). The first pattern was a steady increase of [MeHg] during the season (Zygoptera). The second pattern was an acute drop of [MeHg] in July followed by a modest increase or decrease thereafter (Corixidae, *Neoplea*, Pulmonata). In the third pattern, there were nearly constant [MeHg] over the sampling season (*Gammarus*).

1.3.2) MeHg burden

Individual transfers of MeHg in food webs in stations where inedible predators are present are summarized in Fig. 1.3, with an example of a hypothetical littoral aquatic food web comprising three trophic levels. When expressed by the relative functional groups contribution by station and month of sampling, MeHg burden varied between 0 and 59 ng MeHg DW (Table 1.3). Grazers had the greatest mean MeHg burden (71% ±6), followed by predators (10% ±3), inedible predators (10% ±4) and detritivores (9% ±4). If only stations and months with a presence of inedible

predators were considered the relative mean MeHg burdens of the functional groups were 36% ±12 for grazers, 36% ±10 for inedible predators, 16%±6 for predators, and 12%±7 for detritivores.

1.4) DISCUSSION

1.4.1) Variations of [THg], [MeHg], and MeHg burdens

Functional group was the most important variable explaining differences in [MeHg] in macroinvertebrates, despite the fact that Hg loads are several orders of magnitude greater in the southern section of Lake St Pierre than in the northern one (Quémerais et al. 1999) and that dissolved THg concentrations were 25% greater in the south shore tributaries compared to the rest of the lake (Caron and Lucotte, *in press*). It has been observed that Hg loads from tributaries may not mirror [Hg] in water or sediments. Indeed the importance of the spring ice out and the shallowness of the lake might be unfavourable to Hg retention because sediments are easily resuspended during high water episodes and then flushed downstream. Jackson (1993) hypothesized that the inorganic Hg received by a system is not enough to explain MeHg bioaccumulation in the food webs. Indeed Hg methylation rates at the base of the food web (Desrosiers et al. 2006a) and/or number of trophic levels (Cabana et al. 1994) appear as the most important factors in determining the pool of MeHg, especially in the case of littoral macroinvertebrates which rely more on epiphytes than on sediments for their organic matter source.

After functional group, the second most significant variable that contributed to differences in [MeHg] was the month at which samples were collected. Within the

sampling period (May to September) of our study, covering most of the ice-free season, the invertebrates collected in the first week of June had the greatest [MeHg]. This is surprising since in northern temperate latitudes higher Hg methylation rates are usually measured in mid-summer (Ullrich et al. 2001, Desrosiers et al. 2006a). However, [MeHg] in organisms may not mirror the peak of methylation rate because spring floods could increase the release of MeHg in the water column from the surrounding wetlands (St. Louis et al. 1994; Desrosiers et al. 2006b). Thus, MeHg may be available for the food webs at the beginning of the ice-free season. In addition, the phenology of the insect larvae is another important feature that should be considered in monthly [MeHg] differences. Indeed, the replacement of the over-wintering organisms by the newly hatched generation may explain why [Hg] in insects like Corixidae or *Neoplea* decreased from May-June to July and then increased towards the end of the summer while the long-lived, large bodied predators like Damselfly (Zygoptera) showed a constant increase of [MeHg]. This increase could result from a longer ontogeny and the higher trophic positions of the preys eaten by the older instars of Zygoptera. On the contrary, taxa that have short-lived, overlapping generations like the primary consumers amphipods or gastropods showed modest changes in [MeHg]. But overall, in spite of differences in temporal and spatial conditions, the greatest dissimilarities of [MeHg] and MeHg burdens took place among functional groups.

In Lake St. Pierre, [MeHg]/[THg] were always high even at the grazer trophic level (over 50%), and reached almost 100% in predators of both types (edible and inedible). Among primary consumers, the more generalist feeders such as amphipods had the highest ratios, probably because of a substantial feeding upon animal tissues (Pennak 1953; Tate and Hershey 2003). On the contrary, herbivorous taxa like snails that scrape algae had a relatively lower [MeHg]/[THg] ($\approx$ 50% on average). Elevated [MeHg] and [MeHg]/[THg] in macroinvertebrates living in the macrophyte beds

could be linked to the high Hg methylation rates observed in Lake St. Pierre epiphytes (Hamelin et al. 2004). It has been hypothesized that newly methylated Hg is most rapidly transferred in the food webs (Desrosiers et al. 2006a).

The bottom-up increase of Hg between primary and secondary consumers is consistent with the expected biomagnification of Hg as a function of trophic level (Cabana et al. 1994) but this has been rarely demonstrated in littoral food webs (Cleckner et al. 1998; Allen et al. 2005). These findings contradict some previous studies like those of Parkman and Meili (1993) and Tremblay et al. (1996) that showed greater [THg] in detritivores than in predators and explained these discrepancies by the characteristics of the detritic material. Samples of the latter studies included a mixture of littoral and bottom dwelling macroinvertebrates of boreal lakes. This habitat contrasts radically with the lush macrophyte beds of Lake St. Pierre where the community is dominated by scrapers and not detritivores. Given that detritus have a poor nutritive value, detritivores must ingest large quantities of sediment material that is rich in inorganic Hg. In contrast, the majority of macroinvertebrates of Lake St Pierre feed on epiphytic algae (unpublished data, F. Cremona, Université du Québec à Montréal) that have a higher nutritive value than detritus and sustain Hg methylation.

1.4.2) MeHg bioaccumulation in inedible predators

Among functional groups, inedible predators had the greatest [MeHg] and [MeHg]/[THg] of all macroinvertebrates. In some taxa, [MeHg]/[THg] were close to 100%; such high ratios have only been reported so far in piscivorous fish (Bloom 1992). In Lake St. Pierre [MeHg] of inedible predators are indeed comparable to the [Hg] of 400 mm walleye (*Sander vitreus* Mitchil; Simoneau et al. 2005). Previous

research conducted in two strikingly different systems, namely, the Canadian Boreal lakes (Allen et al. 2005) and the wetlands in the Everglades (Cleckner et al. 1998) have also found that Notonectidae (an inedible predator) was the invertebrate taxon most contaminated with MeHg. Although no account had been advanced to explain the greater [MeHg] in inedible predators, we advance that are the life span of the inedible predators and their trophic status are likely factors explaining the greatest [MeHg] in inedible predators. We can presume that organisms that receive little predation pressure are more likely to reach their maximum life expectancy and thus accumulate more Hg. Indeed, this has been observed in insects not eaten by fish because of their large size (Wong et al. 1997). Furthermore, in our study it is not only the size that causes predation avoidance but rather chemical defenses of the potential prey. The high [MeHg] in some inedible macroinvertebrates could also be explained by their fluid feeding mode. For example the heteropterans and some coleopterans are piercers-suckers that ingest only the soft tissues of their prey compared to other predators that are chewers. Heteropterans (excluding corixids) inject enzymes into the body of their prey to dissolve internal organs and suck the resulting body fluids. In our study, minute (2 mm) *Neoplea* sp. feeding mainly upon the soft parts of microinvertebrates also exhibited very high [MeHg] compared to larger bodied Zygoptera, which usually prey on whole organisms. MeHg concentrations are generally lower in the exoskeleton of organisms compared to other body parts (Boudou et al. 1991). In our samples, the [MeHg] in exuvia of macroinvertebrates (Anisoptera, Gomphidae) was ten-fold smaller than those of whole post-molt adult body (unpublished data, F. Cremona, Université du Québec à Montréal). The importance of feeding mode for [MeHg] was also observed in our study between the larvae and the adults of Gyrinidae (whirligig beetles). Whirligig beetle larvae feed exclusively on body fluids of their prey and had thrice greater [MeHg] than those of the adults who are also predatory but chewers instead of fluid feeders. The fact that adult Gyrinidae are able to prey on terrestrial invertebrates falling on the water surface, and thus integrate terrestrial organic matter less contaminated in MeHg could

also explain their relatively low [MeHg] compared to larvae. A final explanation of high [MeHg] of fluid-feeding inedible predators is that this feeding mode allows invertebrates to handle and kill larger prey than engulfing predators and thus receive MeHg from more contaminated, larger-bodied preys. Indeed, Dytiscidae larvae or Belostomatidae are usually able to ingest prey items the same size or larger than themselves (Peckarsky 1982; Tate and Hershey 2003).

1.4.3) Relative MeHg burdens of functional groups and implications for MeHg transfer to fish

Woodward and Hildrew (2002) addressed the lack of a quantitative approach in food web research, and their observation can also be applied to studies on contaminant biomagnification. Thus, MeHg burdens take into account the importance (in terms of biomass) of a given trophic level in the Hg transfer to the upper trophic levels; this information cannot be obtained using solely MeHg concentrations. In Lake St. Pierre, grazers constituted four fifths of the biomass (unpublished data, F. Cremona, Université du Québec à Montréal) but they only accounted from one-third to three-quarters of the MeHg pool, contrasting with inedible predators that had ten times less biomass but constituted one tenth of the MeHg pool. These trophic dead-ends thus limit during their lifetime the pool of MeHg that could be transferred to fish by secondary consumers in the aquatic food web. It is not known if these insect carcasses are edible by fish, but it can be hypothesized that as soon as defensive compounds decompose, nothing would prevent these organisms from entering the food web via detritivores.

The presence of inedible predators in a food web could explain some paradoxes about Hg contamination in fish. This may be the case in Lake St. Pierre where [Hg] in walleye are consistently lower than those found in many boreal Quebec lakes

(Simoneau et al. 2005) while those of invertebrates are equal or greater (Tremblay et al. 1996). In the Simoneau et al. (2005) study the low [Hg] in fish with respect to their prey was explained by higher fish growth rates in Lake St. Pierre compared to the other lakes. However, the majority of the MeHg found in fish flesh comes from their diet (Hall et al. 1997) and thus food web structure and food chain length (Cabana et al. 1994) might also be important. We propose an alternative hypothesis to explain lower that expected [Hg] in fish when inedible predators are present. The fish that feed more on littoral zone should rely on lower trophic levels prey compared to those that feed in a milieu without inedible predators. The presence of trophic dead-ends may thus explain lower Hg concentrations in fish from eutrophic lakes in general (Rudd and Turner 1983; Hanten et al. 1998), and in Lake St. Pierre in particular, because many eutrophic systems are shallow and usually have vegetated beds on their littoral zones, which inedible predators favor (Polhemus 1996; Bouchard 2004).

To our knowledge, this study is the first to take into account inedibility of the organisms in MeHg transfert in aquatic ecosystems. We have demonstrated that when inedible consumers are present, they have the greatest MeHg concentrations in the littoral zone. We also have shown that 10% of the macroinvertebrate MeHg pool is sequestrated in inedible organisms and thus hardly available to fish consumers. We thus recommend a better characterization of the littoral invertebrate communities in order to establish better predictive models of mercury transfert in aquatic food webs, especially in the littoral zone and in wetlands. Indeed, if researchers do not take into account inedibility in studies of Hg transfert in ecosystems, this could lead to an overestimation of MeHg available to fish and impair the accuracy of these models.

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Table 1.1
Compilation of the mean [MeHg] and [THg] (ng Hg•g^{-1} DW ± SE) in invertebrates from Lake St. Pierre sampled in 2003 and 2004

Taxon	Functional group[a]	[THg]	N	[MeHg]	n
Annelida					
Glossiphonidae	P	91 ± 11.91	23	41 ± 17.56	6
Mollusca	G				
Prosobranchia		85 ± 7.5	58	40 ± 6.27	47
Pulmonata		81 ± 5.44	110	37 ± 4.96	75
Arachnidia					
Araneae	P	282	1	—	—
Hydracarina	P	134 ± 13.46	18	55 ± 30.46	2
Crustacea					
Gammarus fasciatus	G	60 ± 5.77	98	45 ± 5.25	67
Hyalella azteca	G	49 ± 18.06	10	38 ± 13.6	10
Asellus sp.	D	119 ± 11.42	25	67 ± 12.97	11
Insecta					
Ephemeroptera					
Baetidae	D	76 ± 13.12	19	79 ± 19.23	5
Heptageniidae	G	134	1	—	—
Odonata	P				
Coenagrion sp.		120 ± 7.9	52	110 ± 9.38	21
Libellula sp.		85 ± 28.60	2	—	—
Aeschnidae		85.5±23.99	4	107.5 ± 52.5	2
Heteroptera					
Belostoma sp.	IP	143 ± 23.35	6	121 ± 24.83	3
Callicorixa sp.	P	113 ± 8.62	14	99 ± 9.86	19
Gerris sp.	IP	176	2	—	—
Ranatra sp.	IP	406	1	378	1
Notonecta sp.	IP	236 ± 20.19	6	242 ± 16.25	7
Neoplea sp.	IP	162 ± 11.91	23	150 ± 11.93	13
Mesoveliidae	IP	159 ± 32.44	3	163 ± 30.46	2
Trichoptera					

Taxon	Functional group[a]	[THg]	N	[MeHg]	n
Hydroptilidae	G	63 ± 21.23	2	—	—
Leptoceridae	D	68 ± 20.18	8	37 ± 19.36	6
Limnephilidae	D	37 ± 32.44	3	—	—
Phryganeidae	D	33	1	—	—
Lepidoptera					
Pyralidae	G	46 ± 25.55	5	—	—
Coleoptera					
Dytiscidae (A)[b]	IP	220 ± 32.98	3	177 ± 24.83	3
Dytiscidae (L)	IP	195 ± 28.56	4	—	—
Gyrinidae (A)	IP	155 ± 21.59	3	39	1
Gyrinidae (L)	IP	212 ± 32.98	4	148	1
Curculionidae	G	82	1	—	—
Haliplidae (A)	G	76	1	—	—
Hydrophilidae (L)	P	79	1	—	—
Diptera					
Odontomyia sp.	D	79 ± 32.98	3	11	1
Chironominae	D	81 ± 8.81	42	61 ± 11.10	15
Orthocladiinae	G	73 ± 9.52	36	40 ± 9.17	22
Tanypodinae	P	36	1	—	—
Sciomyzidae	P	113	1	—	—
Simuliidae	D	30 ± 32.98	3	33	1

Note: —, no data available.
[a]D = detritivore, G = grazer, IP = inedible predator, P = predator.
[b]A = adult, L = larvae.

Table 1.2
Test effect model of log ([MeHg] in ng•g^{-1} DW) in invertebrates with selected categorical explanatory variables

	Sum of	df	Mean square	F ratio	*p*	r^2
Model 1						0.15
Year[a]	0.08	1	0.08	0.15	0.69	
Month[b]	15.21	4	3.80	7.35	0.0001	
Station[c]	15.12	3	5.04	9.74	<0.0001	
Model 2						0.11
Year	0.63	1	0.63	1.16	0.28	
Month	15.70	4	3.92	7.26	<0.0001	
Shore[d]	6.04	1	6.04	11.18	0.0009	
Model 3						0.47
Year	0.60	1	0.60	1.88	0.17	
Month	14.85	4	3.71	11.46	<0.0001	
Station	2.06	3	0.68	2.12	0.09	
Func.	68.72	3	22.90	70.71	<0.0001	
Model 4						0.47
Year	0.70	1	0.70	2.18	0.14	
Month	15.21	4	3.80	11.77	<0.0001	
Shore	1.72	1	1.72	5.32	0.02	
Func.	77.45	3	25.82	79.91	<0.0001	

[a]2003, 2004
[b]May, June, July, August, September.
[c]ADF, BSF, GIR, MAS.
[d]north, south.
[e]detritivore, grazer, predator, inedible predator.

Table 1.3

Methylmercury burden of each functional group and its relative contribution to the total MeHg burden represented by nine Downing boxes (ng MeHg) for each sampling effort

	Det.[a]	Gra.[b]	E.P.[c]	I.P.[d]	Total burden[e]	% Det.[f]	% Gra.	% E.P.	% I.P.
2003-07 BSF	0	0	4.55	6.95	11.50	0	0	39.56	60.44
GIR	0	20.59	0.79	0	21.38	0	96.31	3.69	0
2003-08 ADF	0	59.53	0	0	59.53	0	100	0	0
BSF	0	1.26	6.74	12.03	20.03	0	6.29	33.65	60.05
GIR	0	22.44	0	0	22.44	0	100	0	0
2003-09 ADF	0	6.40	0	0	6.40	0	100	0	0
BSF	0.12	13.77	2.61	0	16.50	0.73	83.44	15.83	0
GIR	0	28.67	0	0	28.67	0	100	0	0
MAS	0	20.35	5.37	0	25.72	0	79.12	20.88	0
2004-05 ADF	0	0.17	0	0	0.17	0	100	0	0
BSF	0.35	0.58	0	0	0.94	37.87	62.13	0	0
MAS	2.91	1.86	0	2.91	7.67	37.88	24.20	0	37.92
2004-06 ADF	0	2.95	0	0	2.95	0	100	0	0
BSF	0	3.52	0.91	0.51	4.93	0	71.27	18.38	10.35
GIR	0.35	5.44	3.00	0	8.79	4.01	61.89	34.10	0
MAS	13.23	3.94	0	0	17.17	77.03	22.97	0	0
2004-07 ADF	0.60	2.06	2.55	0	5.20	11.44	39.59	48.97	0
BSF	0.05	3.24	0.22	6.13	9.65	0.56	33.55	2.30	63.59
GIR	0.14	6.26	1.22	0	7.62	1.87	82.18	15.95	0
MAS	0	0.65	0	0.06	0.71	0	91.36	0	8.64
2004-08 ADF	0.37	9.94	0	0	10.31	3.63	96.37	0	0
BSF	1.93	29.34	2.54	0	33.81	5.71	86.79	7.50	0
GIR	0.45	31.76	0	0	32.21	1.41	98.59	0	0
MAS	0.12	2.25	0	0	2.37	4.96	95.04	0	0
2004-09 BSF	30.59	20.39	12.44	6.83	70.24	43.55	29.03	17.71	9.72
GIR	0	2.88	0	0	2.88	0	100.0	0	0

Table 1.3
continued

[a]Detritivores.
[b]Grazers.
[c]Edible predators.
[d]Inedible predators.
[e]Total burden = Det. + Gra. + E.P. + I.P.
[f]% Det. = (Det. / (Det. + Gra. + E.P. + I.P.)) × 100. See equation **(3)**.

1.6) FIGURE CAPTIONS

Fig. 1.1: Mean MeHg (black columns) and THg (white columns) concentrations ($ng.g^{-1}$ DW ±SE) of the four macroinvertebrate functional groups sampled in Lake St. Pierre.

Fig. 1.2: Monthly means (± SE) of macroinvertebrate MeHg concentrations for the two years of sampling. Only the dominant taxa found at least in four out of five samples are shown. Functional groups are ♦: detritivores, ●: grazers, ■: predators, and ▼: inedible predators.

Fig. 1.3: Schematic representation of individual MeHg burdens (10^{-3} ng Hg) and [MeHg] ($ng \cdot g^{-1}$ DW; italics and in brackets) in littoral macroinvertebrate potential prey to fish. Lower row represents macroinvertebrate primary consumers; middle row represents macroinvertebrate secondary consumers. Crossed lines represent inedible organisms that are avoided by fish. Drawings represent from left to right: i) lower row, Bithyniidae (Prosobranchia), Physidae (Pulmonata), Chironominae (Diptera), and Gammaridae (Amphipoda); ii) middle row: Notonectidae (Heteroptera), Coenagrionidae (Odonata), and Dytiscidae (Coleoptera). Macroinvertebrates drawings are modified from Bouchard (2004).

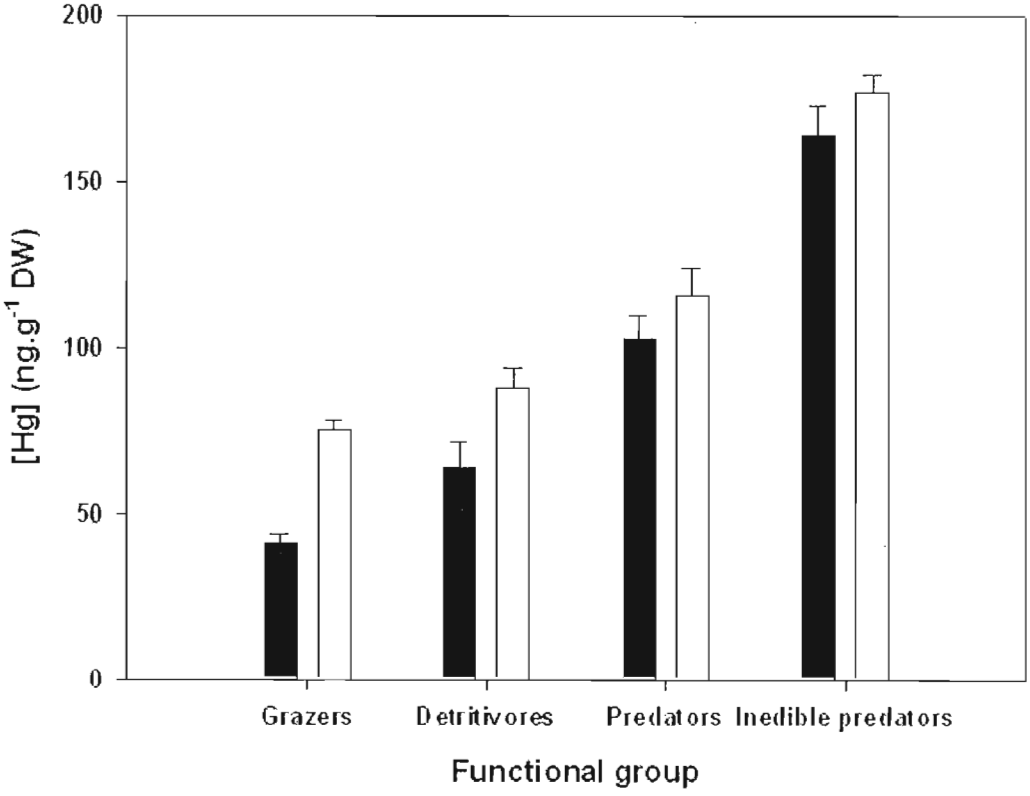
200
150
100
50
0
[Hg] (ng.g-1 DW)
Grazers
Detritivores
Predators
Inedible predators
Functional group

Fig. 1.1

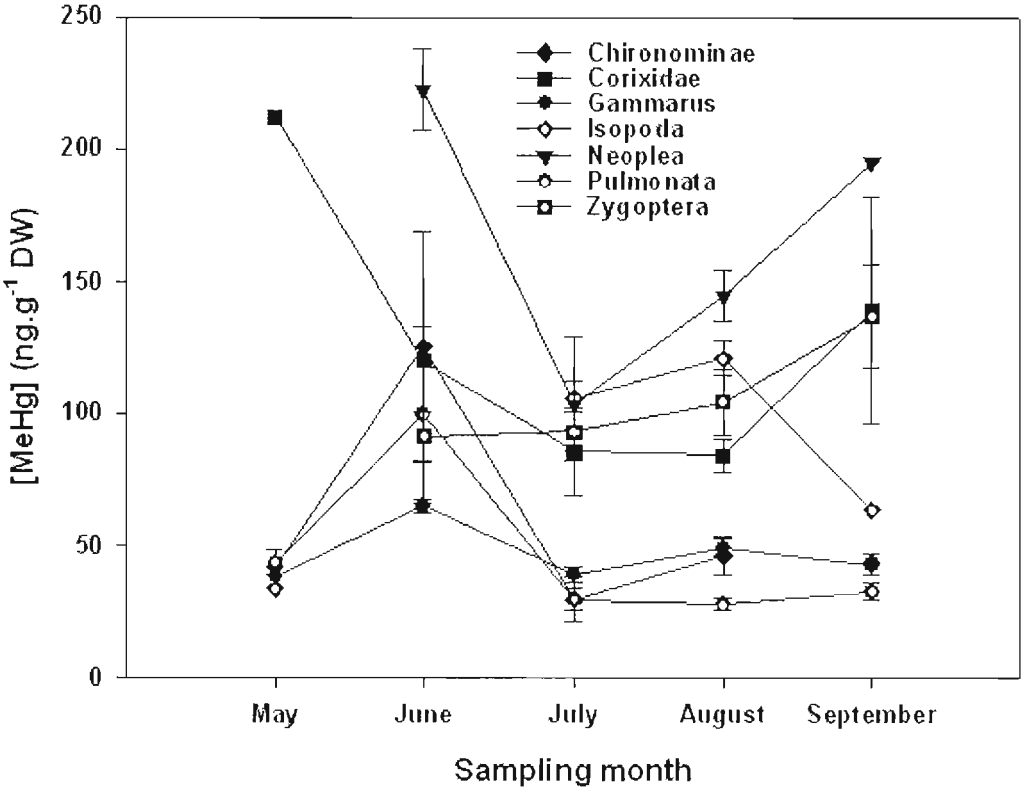
250
200
150
100
50
0
[MeHg] (ng.g-1 DW)
Chironominae
Corixidae
Gammarus
Isopoda
Neoplea
Pulmonata
Zygoptera
May
June
July
August
September
Sampling month

Fig. 1.2

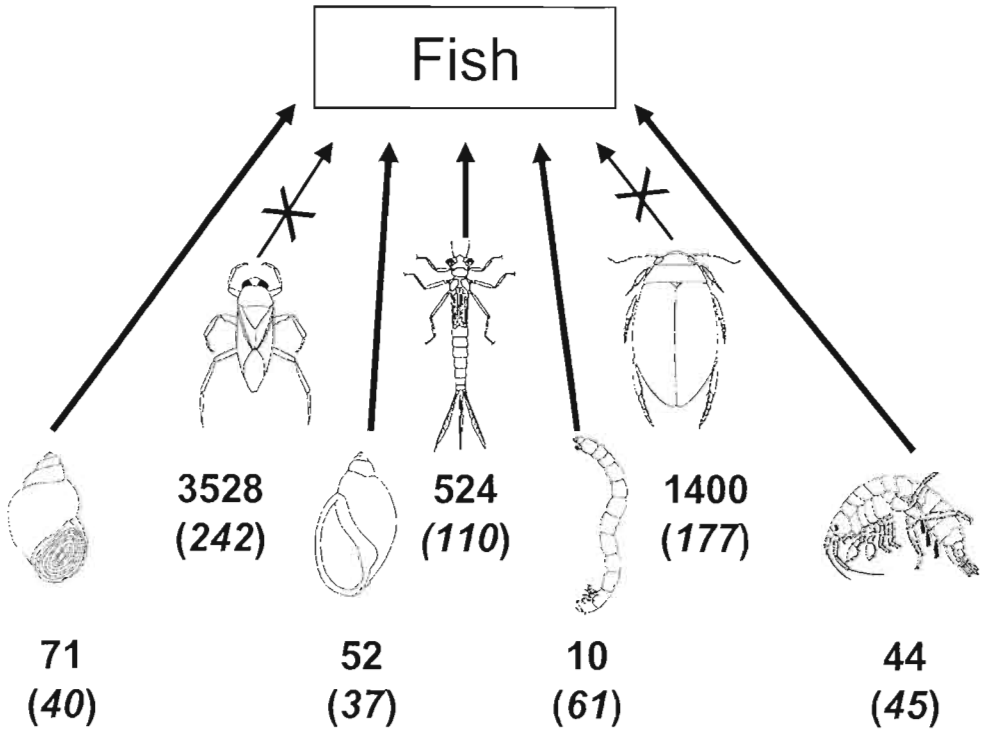

Fig 1.3

1.7) REFERENCES

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CHAPITRE II

SOURCES OF ORGANIC MATTER AND METHYLMERCURY IN LITTORAL MACROINVERTEBRATES: A STABLE ISOTOPE APPROACH

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Résumé:
1. L'objectif de cette étude était de déterminer les sources de matière organique (MO) et de méthylmercure (MeHg) des macroinvertébrés d'eau douce consommateurs primaires.
2. Les rapports isotopiques des isotopes stables du carbone et de l'azote ($\delta^{13}C$, $\delta^{15}N$) des sources (épiphytes, macrophytes, matières particulaires en suspension _MPS) et des consommateurs invertébrés furent mesurés dans un lac fluvial recouvert d'assemblages macrophytiques (émergentes et submergées).
3. Pour déterminer la contribution relative de chaque source de MO à l'alimentation des macroinvertébrés nous avons utilisé le modèle IsoSource qui examine toutes les combinaisons possibles de solutions pour chaque source.
4. Les résultats montrent que les sources autochtones littorales (épiphytes et, dans une moindre mesure, macrophytes) sont prépondérantes dans l'alimentation des macroinvertébrés, surtout au début de l'été (juillet). Plus tard (août), les MPS allochtones constituent une source de MO non négligeable pour les consommateurs primaires.
5. La proportion d'épiphytes dans l'alimentation des macroinvertébrés était corrélée positivement avec leur pourcentage de MeHg. Il n'y avait pas de relation entre la proportion de MPS assimilée et la contamination au Hg des consommateurs invertébrés. Ces résultats suggèrent que les épiphytes constituent la voie d'entrée privilégiée pour le MeHg dans les réseaux trophiques littoraux.

Mots clés: macroinvertébrés d'eau douce, modèle IsoSource, périphyton, isotopes stables, réseaux trophiques, méthylmercure, zone littorale.

Abstract:
1. The main objective of this study was to assess sources of methylmercury (MeHg) for freshwater littoral macroinvertebrates primary consumers.
2. Isotopic ratios of carbon and nitrogen stable isotopes ($\delta^{13}C$, $\delta^{15}N$) of sources (epiphytes, macrophytes, suspended particulate matter _SPM) and of macroinvertebrates consumers were measured in a fluvial lake with an extensive macrophytes beds (emergent and submerged).
3. To determine the relative contribution of each OM source to macroinvertebrate diets we used the IsoSource model that examines all possible combinations of solutions for each source
4. Results show that autochthonous littoral sources (epiphytes and to a lesser extent, macrophytes) are preponderant in the diet of macroinvertebrates, especially in early summer (July). Later (August), allochthonous SPM constitutes a non-negligible OM-source to the primary consumers.
5. The proportion of epiphytes in macroinvertebrate diet was positively correlated with the percentage of MeHg in their tissues. There was no relationship between SPM assimilation and Hg contamination in macroinvertebrate consumers. These results

suggest that epiphytes constitute the privileged path of entry for MeHg in littoral food webs.

2.1) INTRODUCTION

River-wetland systems are characterized by complex food webs, which span both terrestrial and aquatic environments (Haines & Montague, 1979). The composition of organic matter (OM) in river-wetland systems is determined by the mixing of terrestrial, lacustrine, and riverine sources (Albuquerque & Mozeto, 1997; Hedges et al., 1986). One of the most difficult problems in these systems is identifying the major sources of OM available to aquatic consumers. Indeed, the great temporal and spatial variability in autochthonous production and allochthonous OM in wetlands represents a major obstacle (Hedges et al., 1986). Furthermore, as organisms seldom rely on a unique food source during their ontogeny and a plethora of sources are potentially available to a consumer at the same time (Peterson, 1999). For macroinvertebrate primary consumers in wetlands, there are generally three groups of food sources: epiphytic algae, macrophytes (mostly submerged and emergent), and suspended particulate matter (SPM; Cummins, 1973; Lamberti & Moore, 1984; Frost et al., 2002).

Determining the OM source of lower trophic levels in wetlands is essential because wetlands are considered net exporters of environmental pollutants like mercury (Hg) to other systems (St. Louis et al., 1994). In wetlands, inorganic Hg is thought to be methylated by micro-organisms into methylmercury (MeHg) which is biomagnified up to food web consumers (Cabana and Rasmussen, 1994; Sampaio da Silva et al., 2005).This methylated form of Hg, is a ubiquitous neurotoxic metal and a concern for freshwater ecosystem health worldwide (Lucotte et al., 1999; Boening, 2000). Important macroinvertebrate OM sources like macrophyte-epiphytes systems have been described as major methylating sites (Cleckner et al., 1999; Guimarães et al., 2000; Hamelin, Planas & Amyot, 2004). Thus, in order to trace MeHg contamination in those systems it would be useful to determine OM source as well.

In the last few decades, the use of stable isotopes in food web studies has provided a time-integrated method for assessing OM sources available to consumers (Peterson & Fry, 1987; Junger & Planas, 1993, 1994; Peterson, 1999; Hershey et al., 2006). Until recently, most studies used two stable isotopes and a two end-members model to assess the contribution of OM sources (Post 2002). Phillips (2001) demonstrated that, for n isotopic signatures, if the number of sources is greater than n+1, a unique solution establishing proportions of each OM source cannot be obtained. This means that, in studies using two stable isotope signatures, the maximum number of sources a given organism may feed on is three, forcing researchers to give preference to some sources and exclude others. This leads to an underestimation of the widespread omnivory of invertebrates (Zah et al., 2001), and would partially be responsible for the pooling of sources in large categories that correspond to "signals" i.e., autochthonous vs. allochthonous, pelagic vs. littoral (e.g., France, 1995) instead of elucidating the particular proportion of each source. To deal with the multiple potential food sources, Phillips & Cregg (2003) have proposed a method that examines all possible combinations of solutions with a small increment (<1‰) for each source. They also developed a computer program named "IsoSource" which gives the most probable (in percentages) solutions. This approach is relatively new and has not yet been employed extensively in aquatic food webs, but recent studies indicated a good potential for food web partitioning (Benstead et al., 2006; Herwig et al., 2007).

With this tool, we aim to assess the contribution of the different OM sources to the diets of wetland macroinvertebrates and the relationship of diet partitioning with MeHg accumulation. We considered the following OM sources in the studied macrophyte beds: epiphytes (periphyton attached to submerged and emergent macrophytes), macrophytes (submerged and emergent), and SPM.

2.2) METHODS

2.2.1) Study site

Our study was conducted in a fluvial lake of the St. Lawrence River, Lake St. Pierre, located in Southern Quebec, Canada (46°08'N 072°39'W). Macrophyte beds thrive in the shallow (<6m) topography of the lake and cover 80% of the surface area of Lake St. Pierre (300 km^2; Vis, Hudon & Carignan, 2003). The lake presents three distinct water masses of different origins: the brown waters of the north shore, rich in dissolved organic carbon (DOC), are under the influence of the Ottawa River and other Canadian Shield tributaries and differ remarkably from the south shore waters. Tributaries from the south shore drain agricultural fields and carry turbid, nutrient rich waters. Between these two water masses clear waters from the Great Lakes flow through the artificially dredged (>11m) navigation channel, preventing the other two water masses from mixing (Vis et al., 2003).

Sampling was carried out between 0 and 1.5 m depth, at the summer macrophytes biomass peak in July and in August 2004 at two stations on Lake St-Pierre, Girodeau Island (GIR) near the north shore and Baie St. François (BSF) on the south shore. Both sites were covered in submerged and emergent aquatic macrophytes. GIR macrophyte cover was constituted mostly of *Scirpus fluviatilis* (Torr.) and *Potamogeton perfoliatus* (L.) in July and *S. fluviatilis* and *Elodea canadensis* Rich. in August while BSF was covered with *Typha angustifolia* L. and *Myriophyllum spicatum* L. in July and *T. angustifolia* and *Ceratophyllum demersum* L. in August.

2.2.2) Sampling of macroinvertebrate consumers

A modified Downing box (Downing & Rigler, 1984), with an increased capacity of 13 L and a handheld aquatic net were used to sample macroinvertebrates. Invertebrates were separated from their host plants by vigorous shaking. Content was sieved on a 500 μm net and kept in Nalgene™ jars filled with lake-water. In the laboratory, organisms were identified and grouped together according to taxon composition, determined in general to the family level (Pennak, 1953; Clarke, 1981; Merrit & Cummins, 1996). When the number of individuals collected for a given taxon was insufficient for the stable isotopes analysis organisms from a higher taxonomical level were grouped together. According to some recent studies (Kaehler & Pakhomov, 2001; Jardine et al., 2005) gut clearing only marginally influences consumer stable isotope ratios, thus organisms were not gut cleared.

2.2.3) Sampling of OM sources

Macrophytes and epiphytes — Because of differences in macrophyte $\delta^{13}C$ signatures (Peterson & Fry, 1987; Keough et al., 1998), all dominant submerged and emergent macrophytes were sampled at each site. In the strata from the surface to a depth of 60cm, 9 field replicates of both macrophyte types and of their associated epiphytes were sampled using 0.68 L Pac-man boxes (Downing & Rigler, 1984, modified by C. Vis, Environment Canada, Burlington, Ontario). Once in the laboratory, epiphytes were separated from macrophytes by mechanical shaking (9 min in a Red Devil® paint shaker, method previously tested for removing epiphytes without destroying algal cells). Two aliquots/field replicate of the epiphyte suspension were filtered on pre-combusted and pre-weighted GF/C filters and then kept frozen until analysis.

SPM — SPM in Lake St. Pierre represents in summer a mixture of allochthonous terrestrial detritus with a significant fraction of autochtonous matter (Caron et al., in press). Integrated water samples were collected for SPM using an electric pump equipped with a 210 µm filter followed by a 64 µm filter. The pre-filtered water was then treated by ultrafiltration using a Pellicon filter system by Millipore® with a 0.45 µm Durapore® membrane. This process concentrates 50 to 100 L of water into a volume of 1 L. The ultrafiltered water was then transferred to four 250 ml Nalgene® bottles and stored in a freezer until analysis. More details about SPM collection can be obtained in Rheault (2000).

2.2.4) Isotopes and Hg analyses

Samples were frozen at –80°C, a preservation method little susceptible to alteration of sample isotope ratios (Ponsard & Amlou, 1999). The macroinvertebrate samples contained between 3 and 100 individuals. Gastropods shells and opercula which are susceptible to modify $\delta^{13}C$ signature were manually removed prior to analysis. Samples were then freeze-dried for 24 hours and grounded manually with a 10% HCl rinsed glass rod. For the epiphytes, filters were dried in an oven at 40°C until constant weights were achieved. Carbon to Nitrogen atomic ratio (C/N) which is an indicator of nutritive value (lower is more nutritive) was measured in OM sources by a Carlo-Erba™ at the Geochemistry geodynamics Research Center (GEOTOP-UQÀM-McGill).

Isotopic analyses were performed with an Isotopic Resolution Micromass™ mass spectrometer. Isotopic ratios were expressed in parts per thousand (‰) between the sample and a reference material following the standard equations (Verardo, Froelich & McIntyre, 1990):

(1) $\delta^{13}C = [(^{13}C/^{12}C_{sample}/^{13}C/^{12}C_{standard}) - 1] \times 1000$

(2) $\delta^{15}N = [(^{15}N/^{14}N_{sample}/^{15}N/^{14}N_{standard}) - 1] \times 1000$

For C, this reference is Vienna Pee Dee Belemnite (VPDB) and for N, it is atmospheric nitrogen (N_2). Repeated analyses of an internal standard (n=3 for each group of 20-50 samples) resulted in typical precision of ± 0.1‰ for $\delta^{13}C$ and ± 0.2‰ for $\delta^{15}N$.

Total Hg (THg) and methylmercury (MeHg) were analyzed using Bloom's (1989) method modified by Pichet et al. (1999). Inorganic Hg was calculated by the difference between THg and MeHg concentrations in $ng.g^{-1}$ dry weight (DW).

2.2.5) Data treatment

At each station (BSF, GIR) and for each sampling month (July, August), six OM sources were considered to be available to invertebrate consumers: submerged macrophytes, emergent macrophytes, epiphytes growing on submerged macrophytes, epiphytes growing on emergent macrophytes, and SPM. The predicted isotopic value for each combination was computed using IsoSource software (Phillips & Cregg, 2003). All possible contributions of each source combination (0-100%) were examined using specified small (1%) increments with a tolerance value starting at 0.05‰. If mixture isotopes were outside the polygon delineated by the food end members, the tolerance value was incrementally increased by 0.05‰ up to 0.2‰. We reported the range as the 1st to the 99th percentile of source contribution distributions as recommended by Phillips & Cregg (2003). Relatively high minimum contributions indicate significant sources.

We assumed a 0.4‰ fractionation for $\delta^{13}C$ carbon isotopes per trophic level for all organisms (Post, 2002). For $\delta^{15}N$, we applied McCutchan et al. (2003)'s fractionation of 2.2‰ for herbivorous organisms (feeding on emergent and submerged macrophytes and their respective epiphytes). The mean 2.3‰ fractionation reported by McCutchan et al. (2003) for mixed diet organisms was applied to SPM, as seston may contain vegetal material and micro-organisms. At each station and for a given month, the signatures of the primary producers sources were all significantly different (Tukey HSD, $p<0.05$) with a few exceptions. At BSF, the signatures of the epiphytes growing on *M. spicatum* and *T. angustifolia* in July were merged according to the a priori aggregation method (Phillips, Newsome & Cregg, 2005) because they were not significantly different (Tukey HSD, $p>0.05$). We did the same for the epiphytes on *C. demersum* and *T. angustifolia* in August. Non-significant differences (Tukey HSD, $p>0.05$) were also observed for the signatures of the macrophyte *E. canadensis* and of its epiphytes at GIR station in August. In that case, given that herbivores generally prefer epiphytes to underlying macrophytes, we only used the signature of the epiphytes. As recommended by Philipps & Cregg (2003), for graphical representation, mean as well as minimum and maximum proportions for each source were used. Sources were grouped into three major categories: epiphytes, macrophytes, and SPM. Isotopic signatures and Hg concentrations of organisms between sampling months and stations were compared with ANOVA, or Tukey Honestly Significant Differences (HSD) tests when more than two groups were being compared (SAS Institute Inc., 1991). Relationships between organic matter source proportions and other variables were calculated using Pearson pair-wise correlations.

2.3) RESULTS

2.3.1) C/N ratios and isotopic signatures of OM sources and primary consumers

OM sources — C/N atomic ratios varied among OM source categories. Epiphytes presented the lowest ratios, SPM and submerged macrophytes intermediate ones, and emergent macrophytes the highest. Epiphyte C/N ratios varied from 8.5 for epiphytes collected on *S. fluviatilis* at GIR in August to 14.8 for epiphytes on *T. angustifolia* at the BSF station in August (Table 2.1). For macrophytes, the C/N ratio varied between 30 and 129 for emergent plants, and between 11.5 and 27.7 for submerged macrophytes. The C/N ratios of the SPM were comprised between 12.4 and 24. Temporal variations in C/N ratios were observed for all sources. For the two emergent macrophyte species and for epiphytes on emergent and submerged macrophytes, C/N ratios increased up to 4 times between July to August (Table 2.1). On the other hand, C/N ratios for SPM and submerged macrophytes decreased between July and August; however the macrophyte species collected in July were not the same ones found in August.

At each station and for each month, carbon signatures provided a good discrimination (at least >2‰; Fig. 2.1) among aquatic OM primary producer sources. Discrimination for $\delta^{15}N$ was narrower than for $\delta^{13}C$ (>1‰). Epiphytes in emergent plants had a distinct signature in relation to their host (>4‰ for $\delta^{13}C$ and >2‰ for $\delta^{15}N$). Differences between $\delta^{13}C$ of epiphytes sampled on emergent and on submerged plants were conspicuous. The $\delta^{13}C$ of epiphytes from emergent host plants were at least >6‰ depleted in relation to the epiphytes from submerged plants (Fig. 2.1c and 2.1d).

The signatures of OM in Lake St. Pierre encompassed a wide range of isotopic values. $\delta^{13}C$ extended roughly over a 20‰ scale, with the most depleted C signature occurring for the submerged macrophyte *C. demersum* at BSF in August (–31.3±0.4‰) and the most enriched for SPM at GIR in July (–11.3‰, Table 2.1, Fig. 2.1b,c). The $\delta^{15}N$ varied between 7‰ and 15‰, the lowest average was 4.5±0.3‰ for emergent *S. fluviatilis* at GIR in August, while the highest average signature was measured in epiphytes growing on *C. demersum* at BSF in August (12.9±0.6‰). The spatial distribution of $\delta^{13}C$ signatures indicated that OM sources were more depleted in BSF than in GIR, particularly in August, while the reverse was observed for $\delta^{15}N$ values. Temporal variations were found in SPM signatures at the two stations, $\delta^{13}C$ and $\delta^{15}N$ shifted by –5‰ and 2.3‰ respectively in BSF and by –4 and 2‰ in GIR from July to August.

Primary consumers — After correction for fractionation, a majority of taxa fell within the polygons delineated by the OM source end members, suggesting that the main OM sources have successfully been sampled at each station and each month (Fig. 2.1). Signatures of both isotopes differed less between macroinvertebrate taxa than between the OM sources. The $\delta^{13}C$ signatures extended from –27.1‰ in Prosobranchia to –13.6‰ in Pulmonata and the $\delta^{15}N$ from 6.9‰ in Baetidae to 12‰ in Pulmonata (Table 2.2), which corresponds to two trophic levels when employing a 2.2-2.3‰ fractionation per trophic level. Similarly to OM sources, the majority of invertebrate taxa present at both stations tended to be more depleted in $\delta^{13}C$ and more enriched in $\delta^{15}N$ at BSF compared to GIR (ANOVA, *Gammarus fasciatus* in July $p<0.05$ for $\delta^{13}C$, $p<0.001$ for $\delta^{15}N$; *G. fasciatus* in August $p<0.0001$ for $\delta^{13}C$ and $\delta^{15}N$; Prosobranchia in August $p<0.001$ for $\delta^{13}C$, $p<0.0001$ for $\delta^{15}N$; Pulmonata in August $p=0.15$ for $\delta^{13}C$, $p<0.001$ for $\delta^{15}N$). Monthly variations in N signatures were observed, with $\delta^{15}N$ increasing from July to August while $\delta^{13}C$ varied little (ANOVA, *G. fasciatus* at BSF $p=0.29$ for $\delta^{13}C$, $p<0.05$ for $\delta^{15}N$; *G. fasciatus* in GIR $p=0.57$ for $\delta^{13}C$, $p<0.01$ for $\delta^{15}N$).

2.3.2) Contributions of the different OM sources

There was a strong variability in the contributions of each OM source to consumer diet (Table 2.3). The majority of OM in invertebrate diets came from autochthonous matter (epiphytes and macrophytes), with a minor influence of allochthonous matter (SPM). At BSF, epiphytes (July) and epiphytes-macrophytes (August) constituted the bulk of the diet of primary consumers with a minimum contribution never lower than 52%. At GIR, the invertebrates shifted from a mixed diet in July to a more epiphytes-macrophytes oriented diet in August.

Taxonomic differences were generally unconspicuous. Within the Gastropoda class, Pulmonata exhibited a more detritivore diet compared to Prosobranchia individuals. Insects (Baetidae, Leptoceridae, Chironominae, and Orthocladiinae) were generally a little more phytophageous than other classes.

2.3.3) Hg concentrations of invertebrates

THg concentrations ranged between 35 $ng.g^{-1}$ DW in Prosobranchia, to 191 $ng.g^{-1}$ DW in Baetidae (Table 2.2). MeHg concentrations were comprised between 25 $ng.g^{-1}$ DW in Prosobranchia and 131 $ng.g^{-1}$ DW in Amphipods. The percentage of MeHg relative to THg in primary consumers ranged from 32% in Baetidae in August to 86% in some *G. fasciatus*. THg and MeHg concentrations were more elevated in August than in July (test effect model followed by ANOVA, $p<0.05$), while they did not differ between stations (ANOVA, $p>0.05$). The mean adjusted concentrations of THg increased from 64±8 $ng.g^{-1}$ DW in July to 89±7 $ng.g^{-1}$ DW in August while MeHg concentrations only rose from 45±4 to 56±4 $ng.g^{-1}$ DW during the same period of time. Thus, MeHg/THg diminished in macroinvertebrates from July to August.

2.3.4) Relationships between OM sources and Hg concentrations

There were significant relationships between OM sources calculated from IsoSource outputs and Hg concentrations in macroinvertebrate primary consumers (Table 2.4). The proportion of macrophytes in the diet was correlated with THg concentrations (Pearson correlation coefficient = 0.72, $p<0.001$) and MeHg concentrations, but with a lower correlation coefficient ($r = 0.61$, $p<0.05$). The percentage of epiphyte contribution to the consumer diet was correlated positively with %MeHg ($r = 0.58$, $p<0.05$) and negatively with THg ($r = -0.61$, $p<0.05$). No relationship was found between Hg concentrations in primary consumers and SPM assmilated ($p>0.05$).

2.4) DISCUSSION

2.4.1) Contribution of the OM sources to macroinvertebrate diet

In contrast to the study by Herwig et al. (2007) conducted in the floodplain of the Mississippi River, the majority of consumers signatures in the St. Lawrence River fell within the mixing polygon defined by the potential OM sources. Among the OM sources considered, epiphytes and macrophytes made the greatest contributions to the diets of Lake St. Pierre macroinvertebrate primary consumers. SPM also constituted a non negligible food source, although mostly in August when SPM was enriched in N (lower C/N ratio).

The IsoSource model output data indicated that there is a considerable variation in the contribution of each source for a given taxon, often from 0 to 50% or more. This large range in contributions is due to the array of possible solutions calculated by the IsoSource model (Phillips & Cregg, 2003). At some stations, for instance at BSF in

July, the range is narrower, as indicated by the clustering of primary consumers in one corner of the mixing polygon. On the other hand, at GIR in August, the signatures of the consumers are roughly equidistant from several organic matter sources. In this latter case, additional information is needed to discriminate among food provenances. Knowledge of the consumer organic matter preferences as well as of the palatability of the sources could permit a narrowing of the range of possible solutions given by the IsoSource model. Most taxa of littoral macroinvertebrate primary consumers in our study are mainly opportunistic feeders (Clarke, 1981; Jacobsen & Sand-Jensen, 1995; Merrit & Cummins, 1996; Tate & Hershey, 2003). These organisms have fairly unspecialized mouth parts, such as the chewing mandibles of amphipods, chironomids, mayflies, caddisflies, or the radulae of gastropods that can collect detritus, algae in the periphytic biofilm and macrophyte tissue (Clarke, 1981; Carlsson & Brönmark, 2006). Thus, they could potentially feed on any of the food sources if their nutritional quality was similar.

The C/N ratios are indicators of the nutritional quality of the food sources (Tuchman et al., 2003). Their large variation range thus illustrates the considerable differences in edibility of the various OM sources available and could influence selective feeding by primary consumers. For example, the C/N ratio of decaying *T. angustifolia* at BSF in August was 130, nearly ten times the ratio for epiphytes growing on this macrophyte species. Herbivores are thus very unlikely to use this OM source once they have scraped the epiphyte film covering it. Macroinvertebrate herbivores usually assimilate the food source with greater nutrient content when different sources are available (Rincón & Martínez, 2006). On the other hand, when the C/N ratios of macrophytes and epithytes are very close to each other, macroinvertebrates might potentially assimilate both OM sources indiscriminately. This was probably the case, for example, for *C. demersum*, epiphytes, and SPM that had similar C/N ratios (11.5, 9.4, and 12.4 respectively) in August at BSF. Thus, N-rich particulate matter could also constitute a substantial trophic support for macroinvertebrates. As suggested by three indicators of invertebrate feeding preferenda, i.e., (1) $\delta^{13}C$ and $\delta^{15}N$ of the OM

sources and of the consumers, (2) output data from IsoSource, and (3) nutritional quality of the sources as indicated by C/N ratios, macroinvertebrates at BSF appeared to switch from an epiphyte diet in July to a mix of epiphytes, submerged macrophytes and SPM in August.

At GIR, however, OM preferences could not be as clearly established. C/N ratio rankings of the sources (epiphytes < SPM < submerged macrophytes < emergent macrophytes) were to some extent similar to what had been observed at BSF. In spite of C/N ratios indicating that host plants were slightly less nutritive than the overlying epiphytes (C/N =10.9 for the epiphytes and 16.2 for the plant) invertebrates may have included *E. canadensis* in their diet. At GIR in August, the macroinvertebrate herbivores may also have ingested *S. fluviatilis* (C/N ratio = 71) as a trophic support despite its high C/N ratio. If this plant is not considered in the diet, no other OM source could explain the $\delta^{13}C$ signatures below –19‰ found in consumers at this station in August.

The contribution of macrophytes to aquatic herbivorous invertebrate diets seems surprising since they are generally considered little nutritive compared to algae (Kitting, Fry & Morgan, 1984; Brönmark, 1989; Suren & Lake, 1989). But several studies report invertebrates grazing upon live (Sheldon, 1987; Jacobsen & Sand-Jensen, 1995; Elger & Willby, 2003; Elger & Lemoine, 2005; Carlsson & Brönmark, 2006) and decaying (James et al., 2000) aquatic vascular plants. Carlsson & Brönmark (2006) observed individuals of the herbivorous snail *Pomacea canaliculata* grazing on the soft parts of macrophytes from the inside out after having penetrated in the plant via a decaying spot in the fibrous cuticle. At our sampling sites we observed the same behaviour in amphipods and some chironomid taxa. These organisms derive protection from predators and decreased competition with other herbivores for food in exchange for a less nutritive, but plentiful OM source (Merrit & Cummins, 1996). This trade-off may be more common in late summer (August) when competition for food is high since grazer populations are very well established and the amount of periphytic algae is reduced by overgrazing (Cattaneo, 1983).

Terrestrial OM inputs, illustrated partly in our study by SPM signature (Caron et al., in press), represented a smaller trophic support for macroinvertebrate primary consumers in Lake St. Pierre. This is in agreement with a recent study by Clapcott & Bunn (2003), which reported low contribution of C_4 plants to aquatic food webs, despite their widespread distribution and production, as may be the case for corn within the Lake St. Pierre watershed. This finding implies that the invertebrate food web in Lake St. Pierre mostly depends on autochthonous OM. Nevertheless, differences in $\delta^{15}N$ ratios between the south (BSF) and north (GIR) shore stations indicated that terrestrial inputs did influence the wetland. Organisms from the south shore tended to have a higher $\delta^{15}N$ signature, not because of their consumption of terrestrial detritus but because of the probable uptake of terrestrial, ^{15}N enriched, inorganic N by primary producers. This isotopic signal then appears to be propagated through the entire lake food web (Chapter III; Anderson & Cabana, 2005).

2.4.2) Links between Hg concentrations and OM sources

The IsoSource model has been employed in some food web studies (Hall-Aspland, Hall & Rogers, 2005; Benstead et al., 2006; Gerardo Herrera et al., 2006; Herwig et al., 2007), but no previously published work has employed this mixing model to approach the issue of contaminant transfer in food webs. In our study, we found a correlation between the mean contributions of some OM sources and the concentrations of THg and MeHg in consumers. Epiphytic biofilms seem to be an important source of MeHg for macroinvertebrate herbivores as indicated by the positive relationship between the MeHg/THg ratio and the percentage of epiphytes consumed by macroinvertebrates. This relationship, suggests that the MeHg in invertebrates comes mostly from epiphytes. In Lake St. Pierre, Hg results tend to demonstrate that macrophytes contain very low concentrations of both inorganic and

methylated mercury forms compared to epiphytes (S. Hamelin, Université du Québec à Montréal unpublished data). Inorganic Hg concentrations in macroinvertebrate herbivores represent a low percentage of the THg (Cremona et al., 2004). Hg transfer in littoral primary consumers seems to be only marginally linked to macrophyte consumption and more dependent on the fluctuations of methylation rates in epiphytes. In fact, high methylation rates have been observed in epiphytes (Cleckner et al., 1999; Mauro et al., 2004). The newly generated MeHg could then be quickly transferred to higher trophic levels as has been experimentally demonstrated by Branfireun et al. (2005). Our findings support the growing corpus of evidence on the importance of an epiphyte-mediated transfer of MeHg in freshwater systems.

Some studies have found that the natural abundance of $\delta^{15}N$ proved to be a reliable tool for predicting the transfer of Hg concentrations in pelagic and benthic food webs (Cabana & Rasmussen, 1994, 1996; Allen et al., 2005). These models did not seem to apply to predict Hg concentrations in macroinvertebrates from wetlands. In our study, $\delta^{15}N$ variability reflected OM source choice of herbivores in the IsoSource mixing polygon more than it did prey-predator relationships. In other words, the $\delta^{15}N$ signal of primary consumers represents the variability of the food web "baseline" for stable isotope studies of food webs as has already been reported (Vander Zanden, Cabana & Rasmussen, 1997; Post, 2002). Therefore, when only primary consumers are considered, $\delta^{15}N$ signatures are more indicators of the source of OM than of the trophic level. When the $\delta^{13}C$ was combined with $\delta^{15}N$ as a two-dimensional OM source indicator in the IsoSource mixing model, significant relationships were observed between Hg contamination (THg, MeHg, MeHg/THg) and the output variables from the IsoSource model.

2.5) CONCLUSION

Our results stress the significance of epiphytes as the point of entry for MeHg contamination in the aquatic food web, and macroinvertebrates as vectors of MeHg transfer to organisms at higher trophic levels such as piscivorous fish, and eventually to human consumers. We have demonstrated that invertebrate primary consumers in Lake St. Pierre marshes rely mostly on autochthonous OM sources, especially epiphytes, and to a lesser extent, aquatic macrophytes. Macroinvertebrates were nevertheless able to assimilate suspended particulate matter or even decaying macrophytes when epiphytes were less abundant. These findings are in agreement with a growing number of studies recognizing the importance of littoral organic matter in sustaining freshwater food webs (Vadeboncoeur, Vander Zanden & Lodge, 2002; Bertolo et al., 2005; Hershey et al., 2006; Vander Zanden et al., 2006). In a broader perspective, this study is linked to previous research emphasizing the importance of wetlands as privileged sites for MeHg production and trophic transfer in ecosystems. Our findings could eventually contribute to the debate on wetland restoration and maintenance, particularly in a place like Lake St. Pierre which provided more than half of the 1000 tons of fish commercially harvested in Québec fresh waters in 2004[†].

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[†] http://www.mapaq.gouv.qc.ca/Fr/Peche/Profil/pecheaquaculture/pechecommerciale

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Table 2.1

Mean ±SE of $\delta^{13}C$ and $\delta^{15}N$ signatures as well as C/N atomic ratios of organic matter sources at Baie St. François (BSF) and Girodeau Island (GIR) in summer

Organic matter sources	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	n	C/N	n
Macrophytes					
T. angustifolia (BSF, July)	-27.7±0.4	5.8±0.4	3	29.9	1
T. angustifolia (BSF, August)	-27.4±0.4	6.5±1	2	129.4	1
M. spicatum (BSF, July)	-20.7±0.5	7.4±0.4	2	27.7	1
C. demersum (BSF, August)	-31.3±0.4	12.5±1	2	11.5	1
S. fluviatilis (GIR, July)	-22±0.3	6.9±0.1	3	46.3	1
S. fluviatilis (GIR, August)	-28±0.1	4.5±0.3	2	71.6	1
P. perfoliatus (GIR, July)	-15.3±0.6	6.7±0.1	3	23.6	1
E. Canadensis (GIR, August)	-14.7±0.1	7.7±0.3	2	16.2	1
Epiphytes growing on:					
T. angustifolia (BSF, July)	-24.8±0.2	9.8±0.1	18	9.8±0.1	18
T. angustifolia (BSF, August)	-28±0.2	12.2±0.6	6	14.8±0.5	5
M. spicatum (BSF, July)	-24.1±0.3	9.8±0.3	6	7.4±0.2	6
C. demersum (BSF, August)	-27.5±0.2	12.9±0.6	6	9.4±0.4	6
S. fluviatilis (GIR, July)	-27.6±1.1	5.4±0.3	36	8.5±0.3	18
S. fluviatilis (GIR, August)	-19.6±0.5	10.7±0.2	6	9.2±0.2	6
P. perfoliatus (GIR, July)	-16.5±1.1	8.1±0.3	12	9.6±0.4	6
E. Canadensis (GIR, August)	-12.7±0.5	10.2±0.2	6	10.9±0.2	6
SPM (BSF, July)*	-17.7	4.6	1	23.9±0.4	3
SPM (BSF, August)*	-23.9	7.1	1	12.4±0.4	3
SPM (GIR, July)*	-11.3	4.8	1	17.7±2.8	3
SPM (GIR, August)*	-15.2	6.9	1	12.4±0.3	3

Note: * samples collected in 2003.

Table 2.2

Average ±SE of $\delta^{13}C$ and $\delta^{15}N$ signatures (in ‰), total and methylmercury concentrations ([THg], [MeHg] in $ng.g^{-1}$ DW) of macroinvertebrate primary consumers at BSF and GIR in July and August

Macroinvertebrate taxon	$\delta^{13}C$	$\delta^{15}N$	[THg]	[MeHg]	n
Baetidae (BSF, July)	-25.6	10.5	46	28	1
Baetidae (GIR, July)	-18.2	7.9	45	31	1
Baetidae (GIR, August)	-23.3	6.9	191	61	1
Chironominae (BSF, July)	-24.5	10.4	60	45	1
Chironominae (GIR, August)	19.5±0.4	8.4±0.6	77.5±11.5	55±18	2
Orthocladiinae (BSF, July)	-22.5±0.3	10.5±0.2	39.3±1.6	28.3±1.2	3
G. fasciatus (BSF, July)	-24.7±0.7	10.6±0.1	58±3	49±1	2
G. fasciatus (BSF, August)	-26±0.2	11.4±0.1	62.5±9.2	47.5±3.3	4
G. fasciatus (GIR, July)	-20±0.3	7±0.1	60±3.7	51.7±4.7	4
G. fasciatus (GIR, August)	-19.6±0.6	7.6±0.1	75.4±8.9	64.6±8.1	7
H. azteca (BSF, July)	-23.8±0.1	10.6±0.1	46±4.7	38±4	3
Amphipoda (GIR, August)	-22.6	7.6	181	131	1
Prosobranchia (BSF, July)	-27	9.7	88	50	1
Prosobranchia (BSF, August)	-27.1±0.4	11.2±0.2	111.9±6.7	53.7±4.6	8
Prosobranchia (GIR, August)	-17.5±0.6	9.1±0.1	34.7±16.2	25±8	2
Pulmonata (BSF, August)	-25.1±1	12±0.3	74.3±14.9	32.7±5.9	2
Pulmonata (GIR, July)	-13.6±0.1	7.4±0.1	51.5±4.5	22±7	2
Pulmonata (GIR, August)	-18.9±2.1	7.9±0.1	91±2	64±4	2
Leptoceridae (GIR, August)	-19.5	8.6	39	32	1

Table 2.3
Range of organic matter source contributions for macroinvertebrate consumers (in %) using the IsoSource mixing model (mean value in brackets)

	OM source		
	Epiphytes	Macrophytes	SPM
BSF July			
Baetidae	ns	ns	Ns
Chironominae	61-62 (61.5)	30-32 (31)	7-8 (7.5)
G. fasciatus	60-67 (63.5)	27-41 (34)	0-6 (2.5)
H. azteca	53-69 (61.6)	17-47 (31.7)	0-14 (6.7)
Orthocladiinae	41-70 (56.1)	3-59 (30.8)	0-27 (13.1)
Prosobranchia	ns	ns	Ns
GIR July			
Baetidae	0-75 (24)	21-60 (38.6)	26-44 (37.5)
G. fasciatus	ns	ns	Ns
Pulmonata	0-31 (9.7)	6-23 (13.9)	72-80 (76.5)
BSF August			
G. fasciatus	6-42 (24.5)	0-58 (27.6)	32-63 (47.9)
Prosobranchia	0-42 (21.7)	24-95 (58.7)	1-39 (19.6)
Pulmonata	46	0	54
GIR August			
Amphipoda	0-44 (21.6)	52-64 (58.5)	12-28 (20)
Baetidae	0-6 (2.4)	64-66 (65.1)	31-34 (32.5)
Chironominae	0-89 (43.5)	20-44 (32.2)	8-40 (24.4)
G. fasciatus	0-43 (20.8)	28-40 (34.3)	37-53 (44.9)
Prosobranchia	2-100 (60)	0-32 (15.5)	0-45 (24.5)
Pulmonata	0-60 (29)	20-36 (28.2)	32-53 (42.8)
Leptoceridae	0-99 (49.1)	18-45 (32.2)	1-37 (18.7)

ns : no solution

Table 2.4
Pearson pair-wise correlations of percentage of food source contributions (in %) and different forms of Hg concentrations (in $ng.g^{-1}$ DW) of macroinvertebrate primary consumers in Lake St. Pierre.
Significant correlations are presented in bold characters

Row	THg	MeHg	MeHg/THg	Epiphytes	Macrophytes	SPM
THg	1					
	0.78					
MeHg	**(0.0001)**	1				
	-0.47	0.09				
MeHg/THg	**(0.0424)**	(0.72)	1			
	-0.61	-0.35	0.58			
Epiphytes	**(0.0124)**	(0.18)	**(0.0178)**	1		
	0.72	0.61	-0.13	-0.43		
Macrophytes	**(0.0017)**	**(0.0114)**	(0.63)	(0.09)	1	
	0.02	-0.16	-0.48	-0.65	-0.40	
SPM	(0.95)	(0.55)	(0.058)	**(0.006)**	(0.1215)	1

2.7) FIGURE CAPTIONS

Fig. 2.1a: Mean ± SE of stable isotope ratios ($\delta^{15}N$ vs. $\delta^{13}C$) of OM sources (squares) and macroinvertebrate primary consumers (circles) from Lake St. Pierre BSF station in July 2004. Source ratios are corrected by +0.4‰ for $\delta^{13}C$, and +2.2‰ (epiphytes, macrophytes) or +2.3‰ (SPM) for $\delta^{15}N$ because of fractionation. Dotted lines represent mixing polygon limits.

Fig. 2.1b: Mean ± SE of stable isotope ratios ($\delta^{15}N$ vs. $\delta^{13}C$) of OM sources (squares) and macroinvertebrate primary consumers (circles) from Lake St. Pierre BSF station in August 2004. Source ratios are corrected by +0.4‰ for $\delta^{13}C$, and +2.2‰ (epiphytes, macrophytes) or +2.3‰ (SPM) for $\delta^{15}N$ because of fractionation. Dotted lines represent mixing polygon limits.

Fig. 2.1c: Mean ± SE of stable isotope ratios ($\delta^{15}N$ vs. $\delta^{13}C$) of OM sources (squares) and macroinvertebrate primary consumers (circles) from Lake St. Pierre GIR station in July 2004. Source ratios are corrected by +0.4‰ for $\delta^{13}C$, and +2.2‰ (epiphytes, macrophytes) or +2.3‰ (SPM) for $\delta^{15}N$ because of fractionation. Dotted lines represent mixing polygon limits.

Fig. 2.1d: Mean ± SE of stable isotope ratios ($\delta^{15}N$ vs. $\delta^{13}C$) of OM sources (squares) and macroinvertebrate primary consumers (circles) from Lake St. Pierre GIR station in August 2004. Source ratios are corrected by +0.4‰ for $\delta^{13}C$, and +2.2‰ (epiphytes, macrophytes) or +2.3‰ (SPM) for $\delta^{15}N$ because of fractionation. Dotted lines represent mixing polygon limits.

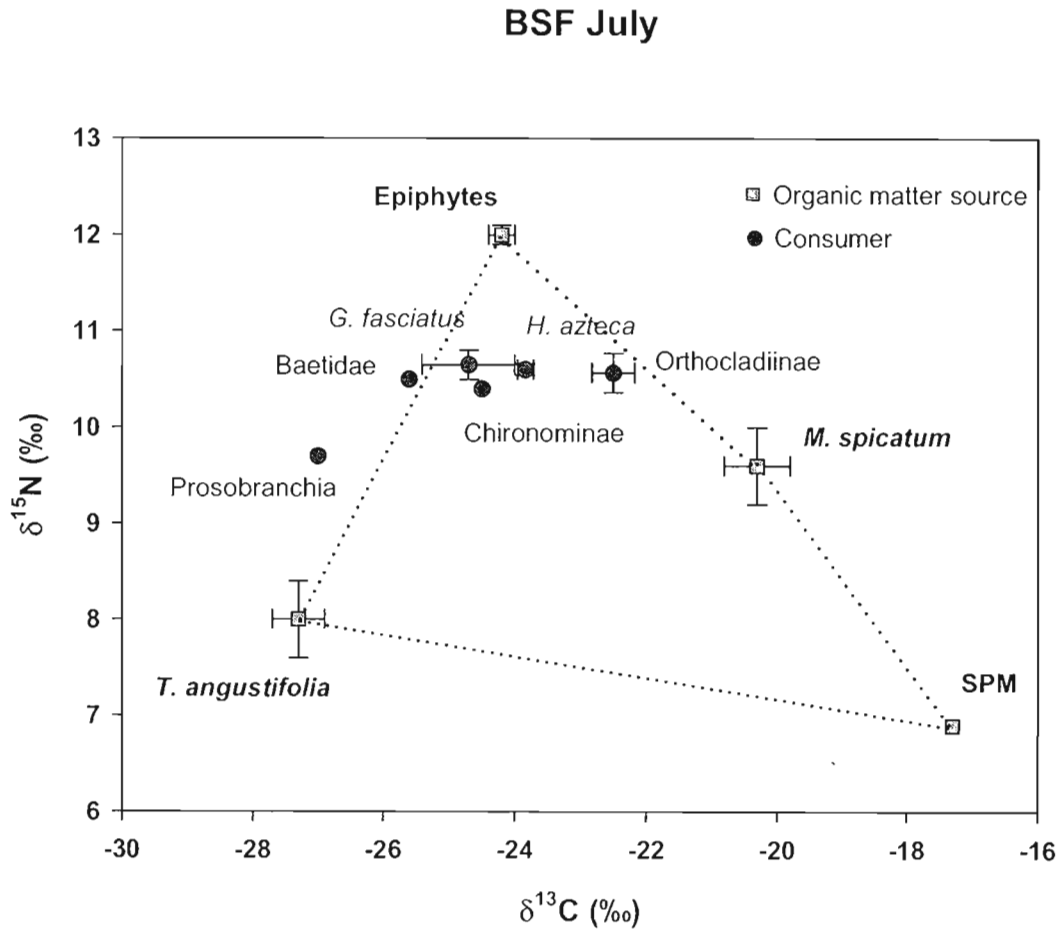
BSF July
Epiphytes
Organic matter source
Consumer
G. fasciatus
H. azteca
Baetidae
Orthocladiinae
Chironominae
M. spicatum
Prosobranchia
T. angustifolia
SPM
δ15N (‰)
δ13C (‰)
13
12
11
10
9
8
7
6
-30
-28
-26
-24
-22
-20
-18
-16

Fig. 2.1a

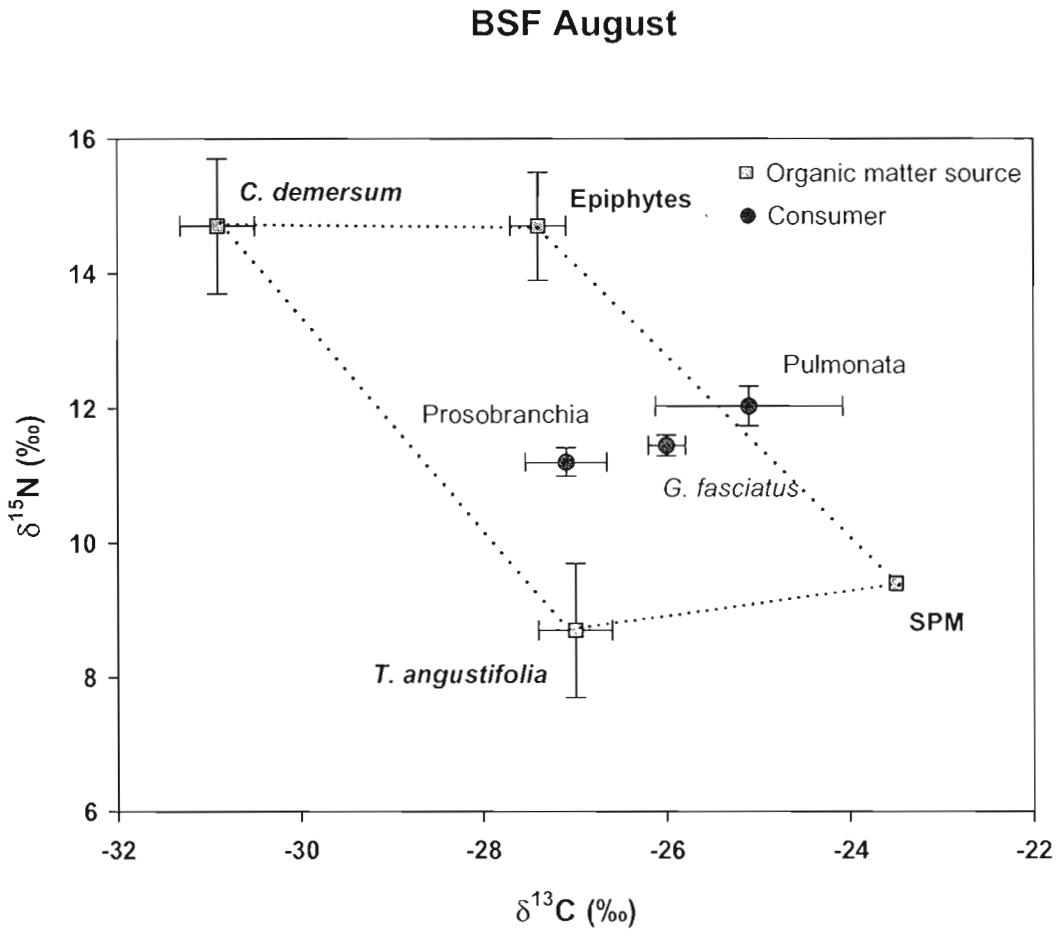
BSF August
Organic matter source
Consumer
C. demersum
Epiphytes
Pulmonata
Prosobranchia
G. fasciatus
SPM
T. angustifolia
16
14
12
10
8
6
-32
-30
-28
-26
-24
-22
δ15N (‰)
δ13C (‰)

Fig. 2.1b

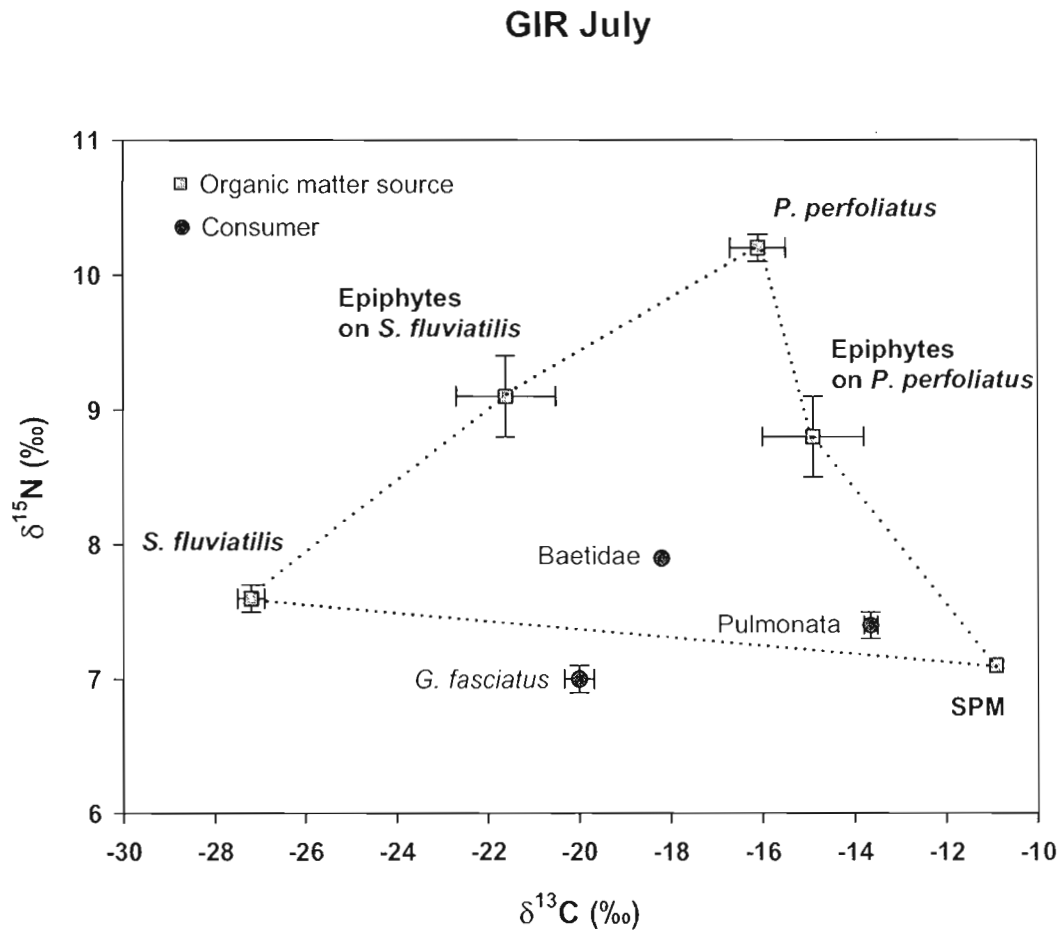
GIR July
Organic matter source
Consumer
P. perfoliatus
Epiphytes
on S. fluviatilis
Epiphytes
on P. perfoliatus
S. fluviatilis
Baetidae
Pulmonata
G. fasciatus
SPM
δ15N (‰)
δ13C (‰)
11
10
9
8
7
6
-30
-28
-26
-24
-22
-20
-18
-16
-14
-12
-10

Fig. 2.1c

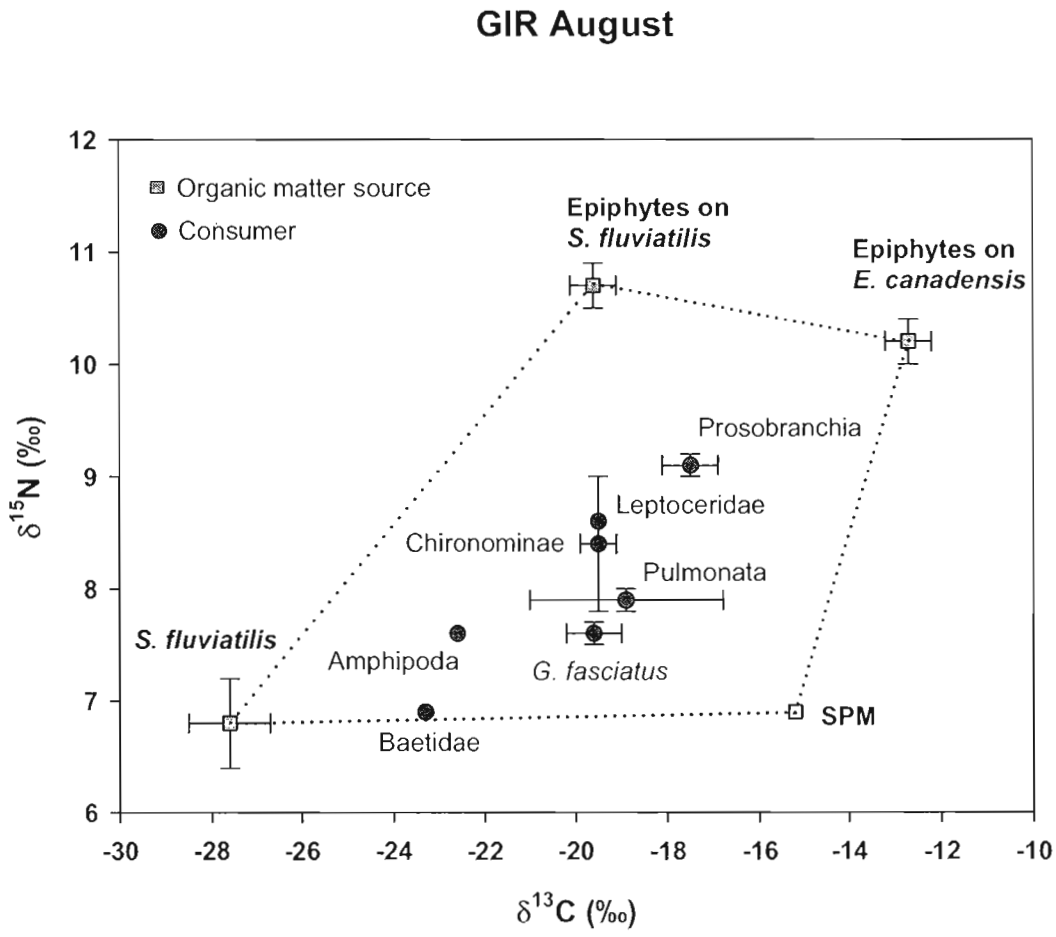
GIR August
Organic matter source
Consumer
Epiphytes on
S. fluviatilis
Epiphytes on
E. canadensis
Prosobranchia
Leptoceridae
Chironominae
Pulmonata
S. fluviatilis
Amphipoda
G. fasciatus
SPM
Baetidae
δ15N (‰)
δ13C (‰)
12
11
10
9
8
7
6
-30
-28
-26
-24
-22
-20
-18
-16
-14
-12
-10

Fig. 2.1d

2.8) REFERENCES

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CHAPITRE III

INFLUENCE OF FUNCTIONAL FEEDING GROUPS AND SPATIOTEMPORAL VARIABLES ON THE $\delta^{15}N$ SIGNATURE OF LITTORAL MACROINVERTEBRATES

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Résumé: L'enrichissement en $\delta^{15}N$ dans les réseaux trophiques de la zone littorale est encore mal connu malgré l'importance des macroinvertébrés dans les flux d'énergie lacustre. Nous avons voulu déterminer l'influence du groupe fonctionnel (brouteur, collecteur, fragmenteur, omnivore, prédateur, prédateur-hématophage, piqueur-suceur) et des variables spatio-temporelles (année, mois, station d'échantillonnage) sur la signature de $\delta^{15}N$ des macroinvertébrés littoraux. Nous avons échantillonné deux années de suite durant la période libre de glace les macroinvertébrés littoraux phytophiles du lac St Pierre, un grand lac fluvial du fleuve St Laurent, Québec, Canada. Les analyses du $\delta^{15}N$ montrent que la station est le facteur le plus important pour expliquer la variation du $\delta^{15}N$, suivie du mois d'échantillonnage, et du groupe fonctionnel. Les organismes échantillonnés sur la rive sud, soumises à de forts apports de matière organique et de fertilisants issus de l'agriculture, présentaient des valeurs de $\delta^{15}N$ plus élevées que ceux prélevés sur la rive nord dont le bassin versant draine la forêt boréale poussant sur le Bouclier Canadien. L'enrichissement des brouteurs aux prédateurs était de 1.6‰, ce qui est inférieur aux 3.4‰ généralement admis. Les fragmenteurs présentent les valeurs de $\delta^{15}N$ les plus basses alors que les prédateurs-hématophages ont les plus élevées. La signature de $\delta^{15}N$ des invertébrés a augmenté mensuellement durant l'été, pour une augmentation totale de 3‰ de mai à septembre. Il est donc recommandé de prendre en compte la station, le mois, et le groupe fonctionnel des organismes lors d'analyses des signatures de $\delta^{15}N$ des macroinvertébrés afin de caractériser correctement les réseaux trophiques littoraux.

Key words: macroinvertébrés, réseaux trophiques, zone littorale, isotopes stables.

Abstract: The $\delta^{15}N$ enrichment in littoral food webs is not well-known despite the importance of macroinvertebrates in lacustrine energy fluxes. We wanted to assess the influence of functional group (grazer, collector, shredder, predator, predator-hematophagous, predator-sucker) and spatiotemporal variables (year, month, station of sampling) on littoral macroinvertebrate $\delta^{15}N$ signatures. For two years, during the ice-free period phytophilous littoral macroinvertebrates were sampled in Lake St. Pierre, a large fluvial lake of the St. Lawrence River, Quebec, Canada. $\delta^{15}N$ analyses have shown that station was the most important factor for explaining $\delta^{15}N$ variation, followed by sampling month and functional group. The organisms sampled on the south shore, which is influenced by heavy inputs of agricultural organic matter and fertilizers exhibited higher $\delta^{15}N$ valuers than those sampled on the north shore which watershed is mostly constituted by Canadian Shield boreal forest. Grazer-to-predator enrichment valued 1.6‰, which is inferior to the 3.4‰ generally admitted in food-web research. Shredders exhibited the lowest $\delta^{15}N$ values and predators-hematophagous the highest ones. $\delta^{15}N$ signature of invertebrates increased monthly during summer, with an amplitude of 3‰ between May and September. We recommend better taking into account station, month and functional group in future research about littoral food webs and $\delta^{15}N$ signature analyses.

3.1) INTRODUCTION

Stable isotopes are increasingly being used in food webs studies (Allen et al., 2005; Walter et al., 2006). They are considered steady, time-integrated tools for taking into account effective assimilation of dietary items in organisms (Post, 2002). This is especially true when they are compared to traditional methods like stomach or gut contents that only provide a snapshot of the feeding habits of an organism (Hart & Lovvorn, 2002; Schindler, 2002). Stable N isotope signature ($\delta^{15}N$) in particular is used to position the trophic level of an organism or a group of organisms in a given of food web (Minagawa & Wada, 1984; Vander Zanden & Rasmussen, 2001). Higher trophic levels exhibit higher $\delta^{15}N$ values with respect to lower consumers or producers, with a typical increase of 3.4‰ per trophic level (Vander Zanden & Rasmussen, 2001; Post, 2002). This approach has been successfully tested in pelagic food web studies including a large variety of organisms, ranging from primary producers to top-end consumers (Yoshioka et al., 1994). $\delta^{15}N$ signature is even extensively used as tracer of biomagnifying persistent pollutants like PCB or methylmercury in aquatic pelagic food webs, with the highest trophic levels also being the most contaminated (Cabana & Rasmussen, 1994).

However, not much is known about $\delta^{15}N$ trophic enrichment into the aquatic littoral food webs. This lack of knowledge may be caused by an historical bias in favour of researches conducted in pelagic systems compared to littoral and benthic ones (Vadeboncoeur et al., 2002). The major studies of $\delta^{15}N$ in macroinvertebrate food webs have been so far mostly focussed on stream benthos (Zah et al., 2001; Anderson & Cabana, 2005) or soil invertebrates (Ponsard & Arditi, 2000). Nevertheless, a better knowledge about littoral macroinvertebrate food webs is important for whole-lake studies because it has been estimated that littoral production might be equal or greater than pelagic production, and that fish are predominantly supported by benthic secondary production (Vadeboncoeur et al., 2002; Vander Zanden et al., 2006).

supported by benthic secondary production (Vadeboncoeur et al., 2002; Vander Zanden et al., 2006).

Consequently, little information about $\delta^{15}N$ differences in littoral macroinvertebrate trophic levels is available. Nevertheless, the diversity of macroinvertebrate feeding groups is especially great in the vegetated littoral zone of lakes and in wetlands that host the most numerous invertebrate taxa and thus numerous niches (Minshall, 1984; Strayer 1985; Cyr & Downing, 1988), from grazers and detritivores to top fish-eating predators like giant water bugs (Clarke, 1981; Merrit & Cummins, 1996). Still within a given trophic level, herbivores for example can host functional groups like scrapers that eat periphyton, shredders that feed on coarse particulate matter, and collectors who generally prefer fine particulate matter or planktonic algae (Cummins, 1973; Vannote et al., 1980; Cattaneo, 1983) and thus may not be considered together as a unique baseline (i.e. primary consumer) signature of the food web.

In addition, even within a given functional group, invertebrates regroup an array of very dissimilar ingestion modes from engulfers swallowing their whole prey to fluid-feeders such as the predatory Dytiscidae (Coleoptera) larvae and Heteroptera exclusively eating pre-digested internal soft part of organisms (Polhemus, 1996). This variety of digestive modes could lead to important consequences regarding the N transfer and the ^{15}N fractionation in invertebrate food webs (McCutchan et al., 2003).

There are factors other than feeding modes that could lead to different N-isotopic signals. Differences in the origin of N-loadings from watersheds influence $\delta^{15}N$ signature of food webs (Anderson & Cabana, 2005, 2007; De Brabandere et al., 2007). Manure and fertilizer from crops are enriched in $\delta^{15}N$ while sewage water can be depleted (Van Dover et al., 1992; DeBruyn & Rasmussen, 2002) or enriched (Leavitt et al., 2006). These phenomena could affect baseline $\delta^{15}N$ signature, thus underrating the importance of $\delta^{15}N$ variability among invertebrates in food web studies and leading to errors in positioning organisms.

The purpose of the present study is to assess the influence of functional feeding group on the $\delta^{15}N$ signatures in macroinvertebrate littoral food webs taking in account the provenance of N-organic matter. More specifically, we focus on invertebrates dwelling in littoral beds of aquatic macrophytes.

3.2) MATERIALS AND METHODS

3.2.1) Study site

Our study was carried out in a fluvial lake of the St. Lawrence River, Lake St. Pierre located downstream Montréal, in Southern Québec, Canada. This lake is shallow (mean depth <4m), is extensively covered with macrophyte beds (80% of the Lake area; Vis et al., 2003) and represents 75% of the St. Lawrence marshes (Jean et al., 2000). Major macrophyte species included *Nymphea tuberosa* Paine, *Vallisneria americana* Michx., *Potamogeton* spp. and *Scirpus fluviatilis* (Torr.). The center of the lake is dredged to allow commercial boat transportation from the Great Lakes to the Atlantic Ocean. The combined effects of the St. Lawrence Seaway and water velocity prevent mixing of the water masses which originate from three main inflows. On the north part of the lake, the water rich in coloured dissolved organic matter comes from the Ottawa River and the forested Canadian Shield tributaries. In the central part flows clear water from the Great Lakes. In the southern part of the lake the water drains low lands devoted to intensive agriculture, resulting in heavy loads of manure, fertilizers, and organic matter in the tributaries. Values of nutrient loadings and concentrations in Lake St. Pierre can be found in Vis et al. (2006). We selected four sites located on both shores: on the north shore, Girodeau Island (GIR) and Maskinongé (MAS), on the south shore, Anse-du-Fort (ADF), and Baie St. François (BSF) a wetland poorly connected to the main flow of the lake (Fig. 3.1).

3.2.2) Sampling of invertebrates

Sampling was conducted in 2003 and 2004 at the four sites on a monthly basis; from early July to September in the first year and from early May to September (for the latter month only GIR and BSF were sampled) in the second year. We sampled invertebrates living in monospecific stands of the following species: *Ceratophyllum demersum* L., *Elodea canadensis* Rich., *N. tuberosa* Paine, *Potamogeton pectinatus*, L., *P. richardsonii* (A. Bennett), *P. perfoliatus*, L., *Sagittaria latifolia* Willd., *S. fluviatilis*, *Typha angustifolia* L., and *V. americana*.

Two types of samplers were used: an enlarged (13 L) Downing box (Downing and Rigler, 1984) and an aquatic hand net. The two samplers are complementary since the net permits to catch easily fast moving insects, while picking up small invertebrates attached to plants like midge larvae (Chironomidae) is easier with the box. Ten samples were collected per station between the surface to 1.5m deep: 9 samples with the Downing box and 1 with the hand net. Invertebrates were separated from plants with vigorous shaking, and predators were sorted from non predators immediately after sampling. The content of each hit was then sieved through a 500µm net.

3.2.3) Sample preparation and stable isotope analyses

Because of the great quantity of individuals, sampled invertebrates were not identified on the field but stored in a cooler prior to identification in the laboratory. Methods of gut clearance have recently been questioned (Jardine et al., 2005). Furthermore, overnight confinement to facilitate gut clearance can have potential adverse effect on isotope ratios of consumers (Kaehler & Pakhomov, 2001); we thus decided not to allow gut clearance of organisms collected. Thereafter, organisms were

kept frozen at -80°C to nullify the effects of preservation on isotopic signature (Ponsard & Amlou, 1999). Invertebrates were identified usually to the family or genus (Merrit & Cummins, 1996 for insects, Clarke, 1981 for gastropods, and Pennak, 1953 for other macroinvertebrates). Shells of gastropods were removed manually with stainless steel tweezers covered with Teflon. The organisms comprising a unique taxon were then counted and sorted in pre-cleaned vials (first rinsed with 10% HCl and then thrice with Nanopure water). Invertebrates were freeze-dried, and then ground with an acid-cleaned glass rod directly in the vial. For nitrogen stable isotope analysis, samples from vials were weighted into tin cups prior to combustion in a Carlo Erba C/N analyzer NA 1500 series 2, connected to an Isoprim Mass Spectrometer (Micromass). Isotopic results are given using standard δ notation where:

$$\delta^{15}N = [(R_{sample}/R_{reference})-1] \times 1000 \quad (1)$$

expressed in units of per mil (‰) and where $R = {}^{15}N/{}^{14}N$ (Verardo et al, 1990). Reference materials were secondary standard (N1) of known relation to the international standard of atmospheric N_2 (0.43‰ v. air). Repeated analyses of an internal standard (n=3 for each group of 20-50 samples) resulted in typical precision of ± 0.2 ‰.

3.2.4) Data treatment

Taxa were classified according to the following feeding functional groups (Pennak, 1953, Merrit & Cummins, 1996): grazers scraping live algae and epiphytes; shredders of pieces of detritus or plant material; collectors of suspended material or fine particles; omnivorous consumers relying on a mix of animal and vegetal items;

predators of other invertebrates; predators-suckers sucking other invertebrate body fluids after having dissolved them, and finally hematophagous predators that suck their blood/hemolymph.

We used JMP 5.0 for the statistical analyses. Since many taxa were not found either at all periods of time or at all the stations, we used a single linear model with factorial test effect for data analysis. Adjusted values (i.e. Least Square Means, LSM) of $\delta^{15}N$ were used as the response variable. The LSM are predicted values from the model across the level of categorical effects where the other model factors are controlled by being set to neutral values (SAS Institute Inc., 1991; Uryu et al., 2001). For example, in a model comprising four categorical factors, when comparisons are made within one factor the weights of other three factors are neutralized. Categorical explanatory factors were, temporal (year, month), spatial (station) and trophic (functional group) factors. Tukey Honestly Significantly Different (HSD) tests were then performed on the adjusted values of $\delta^{15}N$ to test inter-annual, monthly, station, and functional group differences. Simple regression analysis was performed between $\delta^{15}N$ of predators and grazers sampled within the same macrophyte species at each station and sampling period in order to determine $\delta^{15}N$ trophic fractionation factor between a grazer baseline and secondary consumers. Predators and grazers were chosen because they were the best represented groups in our samples.

3.3) RESULTS

On the 436 samples measured for $\delta^{15}N$ signature 72 were of collectors, 125 grazers, 142 omnivores, 38 predators, 16 predators-hematophagous, 33 predators-suckers, and 10 shredders. The average $\delta^{15}N$ values ranged between 6.6‰ in Limnephilidae (Trichoptera) to over 12‰ in Hirudinae, a difference of nearly two trophic levels (Table 3.1). The $\delta^{15}N$ signatures of the most abundant primary

consumers (grazers) and predators were correlated ($p<0.0001$, $r^2=0.85$, n=19) across sites and periods of sampling (Fig. 3.2). Predators were enriched of $\delta^{15}N = 1.62 \pm 0.14$ ‰ relative to grazers at the three sampled stations.

3.3.1) Temporal and spatial heterogeneity

Within the factorial test effect model, both temporal variables (year and month) were significant (Table 3.2). Macroinvertebrates in 2004 had a higher LSM $\delta^{15}N$ signature than in 2003 ($p<0.0001$; Fig. 3.3a). When the analysis was done considering only months sampled in both years (July, August, and September) the LSM $\delta^{15}N$ signatures were again higher in 2004 than in 2003 ($p<0.0001$). Seasons were significantly different, with three distinct periods: end of spring May-June, mid summer July-August, and end of summer September (Tukey HSD, $p<0.05$, $Q=2.73$). There was an increase in the macroinvertebrate average LSM $\delta^{15}N$ signatures through the summer, from an adjusted value of 7.09‰ in May to 9.95‰ in September, which corresponds to an increment roughly equivalent to one trophic level (Fig. 3.3b). For grazers in Lake St. Pierre, the $\delta^{15}N$ signature raised continuously from 7‰ to 11‰ from May to September (Fig. 3.4).

Station appeared as the variable with the highest mean square (Table 3.2). The LSM $\delta^{15}N$ value of the macroinvertebrates was higher for organisms collected on the south shore than on the north shore. Invertebrate LSM $\delta^{15}N$ ranged from 7.74‰ at the two stations of the north shore (GIR and MAS) to 8.46‰ in ADF and up to 9.79‰ in the BSF wetland. Statistically, north shore stations signatures were significantly lower than ADF ones, themselves lower than BSF ones (Tukey HSD, $p<0.05$, $Q=2.57$; Fig. 3.3c).

3.3.2) Functional feeding group

Differences among some functional groups were significant (Table 3.2). The LSM $\delta^{15}N$ increased with the trophic level, from 6.64‰ for shredders to 10.26‰ for predators-hematophagous (Fig. 3.3d). The $\delta^{15}N$ signatures of omnivores, grazers and collectors were nearly identical to that of grazers (8.15‰, 8.31‰ and 8.15‰, respectively). Predators LSM $\delta^{15}N$ were higher (9.53‰) than non predators and predators-hematophagous had the highest (10.26‰) $\delta^{15}N$. In contrast with the other predators, predators-suckers had a low $\delta^{15}N$ value (7.96‰), only superior to that of shredders. Tukey HSD test revealed differences ($p<0.05$, $Q=2.96$) between predators and predators-hematophagous on one side and all the others functional groups on the other side (Fig. 3.3d).

3.4) DISCUSSION

3.4.1) Functional feeding groups differences in $\delta^{15}N$

As it has had been documented by many authors (e.g. Minagawa & Wada, 1984; Cabana & Rasmussen, 1994; Ponsard & Arditi, 2000; Hart & Lovvorn, 2002) the majority of the predatory taxa presented higher $\delta^{15}N$ signatures than non predatory taxa; the exception being the predators-suckers. Shredders like the Trichoptera taxa had the lowest $\delta^{15}N$ signatures, even compared to other primary consumers like grazers. A non negligible reliance on terrestrial vegetation is expected in the shredders diet since these insects serve as integrators of terrestrial coarse particulate matter (mostly leaves) to aquatic systems (Vannote et al., 1980). Terrestrial leaves are indeed depleted in ^{15}N compared to aquatic plant, especially in temperate systems (Peterson and Fry, 1987; Martinelli et al., 1999; Herwig et al., 2007).

The almost identical $\delta^{15}N$ values for grazers and omnivores are unexpected, because omnivores usually have a substantial amount of animal tissue to their diet and thus are supposed to be enriched in ^{15}N compared to the mostly phytophageous grazers. In our study, Amphipods (*Gammarus fasciatus* Say and *Hyalella azteca* Saussure) were the most abundant omnivore taxa, as they had often been observed feeding on other organisms or individuals of their own species in times of starvation (Pennak, 1953; Tate & Hershey, 2003). Though, in a very productive system like Lake St. Pierre where epiphytes and macrophytes constitute the greatest part of the production (Vis, 2004) *Gammarus* and *Hyalella* might rely on herbivory, and thus their $\delta^{15}N$ signature become undistinguishable to that of grazers. Furthermore, it has been demonstrated (Chapter II) that *Gammarus* and *Hyalella* organic matter sources are mostly autochthonous aquatic vascular plants and epiphytes during some parts of year. Another factor that could contribute to the low $\delta^{15}N$ in these amphipods is their excretion of ammonia, compared to uric acid for insects. It has been shown that ammonia excretors exhibited a less enriched $\delta^{15}N$ signature than uric acid excretors (Vanderklift & Ponsard, 2003).

The mean $\delta^{15}N$ enrichment that we measured from grazers to predators (1.6‰) was inferior to the 3.4‰ factor generally reported between two trophic levels (Minagawa & Wada, 1984; Post, 2002) and to that reported by Zah et al. (2.25‰, 2001). However, our lower enrichment value was comparable to that measured by Anderson and Cabana (1.8‰; 2005) between invertebrate primary consumers and predators in Southern Québec streams. Low enrichment values may indicate omnivory in the macroinvertebrate food web, i.e. feeding on more than one trophic level (Anderson and Cabana, 2005). McCutchan et al. (2003) noticed in their literature review that the 3.4‰ enrichment factor seems to occur in organisms that rely on a protein-rich diet like fish, and that the mean $\delta^{15}N$ enrichment for the average consumer was close to 2.2‰ in literature data. This observation would underpin the 1.5-2‰ $\delta^{15}N$ fractionation for invertebrates alone.

In food web studies the influence of the feeding mode on $\delta^{15}N$ signatures is yet to be determined. Two interesting, but poorly documented macroinvertebrate feeding groups were the predators-hematophagous and predators-suckers which presented very different trophic enrichment in our study. In our communities, predators-hematophagous comprised leeches (Annelida: Hirudinae) and water mites (Arachnidia: Hydracarina) that both had the highest N isotopic ratio of the whole sampled macroinvertebrates. The early larval stages of water mites are predominantly ectoparasites of bigger invertebrates like water boatmen (Corixidae) or damselfly (Pennak, 1953; Proctor & Pritchard, 1989) and are free living predators in the latter stages. Thus, adult water mites might exhibit high $\delta^{15}N$ reflecting the isotopic composition of their former host/prey. Similarly, leeches can attack fish that are generally of higher trophic level in the food webs than invertebrates and thus get the enriched $\delta^{15}N$ signature of the blood of the fish (Miller, 2000).

In contrast with predators-hematophagous, predators-suckers had average $\delta^{15}N$ signatures significantly lower than that of the other predators, and close to that of macroinvertebrate primary consumers. These findings are astonishing because many taxa of the top end invertebrate food web are predators-suckers like backswimmers (Heteroptera: Notonectidae), giant water bugs (Heteroptera: Belostomatidae) or predaceous diving beetle larvae (Coleoptera: Dytiscidae). Individuals of those taxa are even able to capture, handle and eat fish (Le Louarn & Cloarec, 1997; Tate & Hershey, 2003). Their top-predator status is clearly reflected by their greater concentrations of biomagnified contaminants such as methylmercury in their tissues (Cleckner et al., 1998; Allen et al., 2005; Chapter I). The particular feeding mode of predators-suckers may explain their low N isotopic ratios since predators-suckers feed only on the internal tissues of their prey, and that soft body parts are depleted in ^{15}N compared to the cuticle in invertebrates (Lancaster & Waldron, 2001). Between-tissue differential nitrogen fractionation of the prey must then influence their $\delta^{15}N$. Indeed, McCutchan et al. (2003) has shown that fluid feeders have a lower, negative and very variable fractionation of ^{15}N of about $-0.4 \pm 0.57‰$. Other factors could

explain the lower trophic position of this group such as the heterogeneity in size distribution of individuals in a given taxa. In our samples, predators-suckers were dominated by the numerous minute individuals of the pigmy backswimmers *Neoplea* (Heteroptera: Pleidae). *Neoplea*, that prey on microinvertebrates were the smallest predators we collected in our study sites (size ~1-2 mm). After excluding this taxon from the predators-sucker group the mean adjusted $\delta^{15}N$ signatures increased from 7.96 ‰ to 8.9‰. This average $\delta^{15}N$ signature is comparable to that of other predators that we collected in this study.

3.4.2) Temporal and spatial variables

We observed significant differences between years in the $\delta^{15}N$ signal of invertebrates collected in Lake St. Pierre. The organisms were more enriched in ^{15}N in 2004 than in 2003. Several concurrent environmental factors that influence the isotopic signal of inorganic nitrogen could explain these differences. Annual lake productivity changes in macrophytes-epiphytes could affect the nitrogen signal. Greater productivity reduces the amount of inorganic N available in the milieu, and if N becomes scarce, less discrimination against the heavier isotope will occur in organisms (Peterson & Fry, 1987; Kendall, 1998). This hypothesis appears however not applicable in the case of Lake St. Pierre since this lake primary production might not be limited by N because of the continuous nutrient inflow from the tributaries (15.10^3 NO_3 tons a year, R. Carignan, Université de Montréal, personal communication). On the other hand, greater biomass production in a given year may increase the duration of anoxia events in the macrophyte beds and hence denitrification rates. Greater denitrification also enriches $\delta^{15}N$ of the remaining inorganic nitrogen pool (De Brabandere et al., 2007).

Changes in the nitrogen signal could also be due to differences in runoff particularly over agricultural land. Mean water level recorded in Lake St-Pierre was greater in 2004 than in 2003 (0.85 Sea Level Elevation compared to 0.55 in the period June to October; Vis, 2004). Increases in runoff should discharge more manure (enriched in ^{15}N) and fertilizers (volatilization of lighter ^{14}N in artificial ammonia fertilizer; Kendall, 1998) from the surroundings fields to the lake. The ^{15}N enriched N assimilated by primary producers would thus propagate along the food webs (Högberg, 1990; Peterson, 1999).

Within years, month appeared to have a greater importance in explaining $\delta^{15}N$ variability. Through the summer, macroinvertebrates increased their $\delta^{15}N$ signature of ~3‰. This increase occurred at three distinct periods (May-June, July-August, and September). This augmentation, from May to September, corresponds to the equivalent of one trophic level (Vander Zanden & Rasmussen, 2001; Post, 2002). Previous studies are inconsistent about temporal variability of macroinvertebrate $\delta^{15}N$ (Yoshioka et al., 1994; Stenroth et al., 2006 *but see* Syväranta et al., 2006). The $\delta^{15}N$ enrichment through the season could be explained by ontogeny in predatory macroinvertebrates. This explanation is nevertheless unlikely for grazers of algal epiphytes that constitute the majority of the invertebrates in our study. The $\delta^{15}N$ shift is thus likely to reflect changes in periphyton algal composition and/or in nitrogen availability through the summer. In our case, the most probable explanation is that this steady seasonal enrichment might reflect a continuous loading of heavier nitrogen isotope that supersedes fractionation effects by primary consumers (Savage & Elmgren, 2004). This may elucidate why the invertebrates of the heavily agricultural south shore (ADF, BSF) stations present higher $\delta^{15}N$ signatures than those of the north shore stations. Macroinvertebrate fauna in BSF exhibits consistently higher $\delta^{15}N$ than in any other station. This station is located in a semi-closed wetland on the south shore between the intensive agriculture impacted Yamaska and St. François Rivers and has the highest ratio of agricultural development by unit of watershed area, responsible for NO_3 concentrations reaching up to 1900 $\mu g.L^{-1}$ (R. Carignan,

Université de Montréal, personal communication). Strong temporal and spatial variations of $\delta^{15}N$ in littoral macroinvertebrates within the same site demonstrate the importance of considering these variation factors in any sampling design of littoral food webs in order to get an accurate figure of the isotopic ratio of an organism.

3.5) CONCLUSION

Our results have shown the influence of functional feeding group on the $\delta^{15}N$ variability of littoral macroinvertebrates within and between trophic levels. According to our results, and previous studies on littoral food webs, the generally accepted 3.4‰ enrichment value per trophic level could not be taken as a general rule. For aquatic invertebrate food webs, an average $\delta^{15}N$ enrichment factor of 1.6‰ appears indeed more realistic. We recommend better considering temporal and spatial factors as well. For example, in Lake St. Pierre during our sampling period the $\delta^{15}N$ signatures of invertebrates rose of about 0.6‰ per month, for a total of 3‰ for the entire sampling period. Thus ignoring temporal and spatial variability in $\delta^{15}N$ studies in aquatic systems may induce an error in $\delta^{15}N$ signatures equivalent to one trophic level. A more detailed approach backed with knowledge of invertebrate feeding modes as well as temporal and spatial characterization is critical in order to better understand food web structures and energy fluxes in the littoral ecosystems.

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Table 3.1
Non-adjusted nitrogen isotope ratios ($\delta^{15}N$, ‰) values for major taxa sampled in 2003 and 2004 in Lake St. Pierre and their functional group.

Taxon	Functional group*	$\delta^{15}N$ (‰)	n
Annelida			
Hirudinae	PH	12.68±0.35	11
Mollusca	G		
Prosobranchia		9.36±0.22	47
Pulmonata		8.70±0.18	78
Arachnidia			
Hydracarina	PH	9.48±0.43	5
Crustacea	O		
Gammarus fasciatus Say		8.62±0.14	86
Hyalella azteca Saussure		9.95±0.62	11
Asellus sp.		9.16±0.49	13
Insecta			
Ephemeroptera			
Baetidae	C	8.9±0.41	10
Odonata	P		
Coenagrion sp.		10.27±0.28	29
Libellula sp.		11	1
Aeschnidae		9.8±1.57	4
Heteroptera			
Belostoma sp.	PS	11.12±0.79	4
Callicorixa sp.	O	9.95±0.23	32
Gerris sp.	PS	8.9	1
Ranatra sp.	PS	11.6	1

Taxon	Functional group*	$\delta^{15}N$ (‰)	n
Notonecta sp.	PS	10.64±0.69	7
Neoplea sp.	PS	7.94±0.43	15
Mesoveliidae	PS	9.65±0.15	2
Trichoptera	S		
Leptoceridae		9.12±0.13	7
Limnephilidae		6.6	1
Phryganeidae		8.5±0.2	2
Coleoptera			
Dytiscidae	PS (L), P (I)	9.6 (L), 10.75±1.85 (I)	1 (L), 2 (I)
Gyrinidae	PS (L), P (I)	8.06±0.49 (L), 7.7±0.36 (I)	2 (L), 2 (I)
Diptera			
Odontomyia sp.	C	10.5 ±1.7	2
Chironominae	C	8.76±0.21	23
Orthocladiinae	C	8.85±0.21	34
Simuliidae	C	7.85±1.95	2
Tipulidae	C	7.4	1

Note: * C=collector, G=grazer, O=omnivore, P=predator, PH=predator-hematophagous, PS=predator-sucker, S=shredder, L=larvae, I=imago

Table 3.2
Analysis of variance for the test effect model of $\delta^{15}N$ of invertebrates with temporal, spatial, and trophic categorical variables

Model and variables	Sum of squares	*df*	Mean square	F ratio	*p*	r^2
Model						0.63
[a]Year	73.39	1	73.39	68.29	<0.0001	
[b]Month	237.08	4	59.27	55.15	<0.0001	
[c]Station	379.07	3	126.36	117.57	<0.0001	
[d]functional group	132.95	6	22.16	20.62	<0.0001	

a:Year 2003, 2004; b:month May, June, July, August, September; c station: ADF, BSF, GIR, MAS; d functional group: collectors, grazers, , omnivores, predators, predators-hematophagous, predators-suckers, shredders.

3.7) FIGURE CAPTIONS

Fig. 3.1: Maps of Quebec (upper left corner) and of Lake St. Pierre. The sampled stations are in alphabetical order: Anse-du-Fort (ADF), Baie St-François (BSF), Girodeau (GIR), and Maskinongé (MAS).

Fig. 3.2: Relationships between mean $\delta^{15}N$ values of predator functional group and grazer functional group in communities sampled in Lake St. Pierre in 2003 and 2004. Only communities containing both groups were retained for this analysis. Symbols represent communities collected in the different sampling stations. Squares (■): BSF; circles (●): GIR; triangles (▲): MAS. Regression line: $y = 3.11 + 0.84x$; $r^2 = 0.85$, $p < 0.0001$, $n = 19$.

Fig. 3.3: Comparison of Lake St. Pierre macroinvertebrate $\delta^{15}N$ (mean ± SE) between years (a), months (b) of sampling, stations (c) and functional groups (d).$\delta^{15}N$ are adjusted values calculated by the test effect model. Bars not connected by the same letter are significantly different ($p<0.0001$ for year; Tukey HSD test, $p<0.05$, $Q=2.73$ for month, $Q=2.57$ for station, $Q=2.96$ for functional group).

Fig. 3.4: Monthly variations of N isotopic ratios (±SE) of Lake St. Pierre macroinvertebrate grazers in 2003 (white symbols, dotted line) and 2004 (black symbols, solid line).

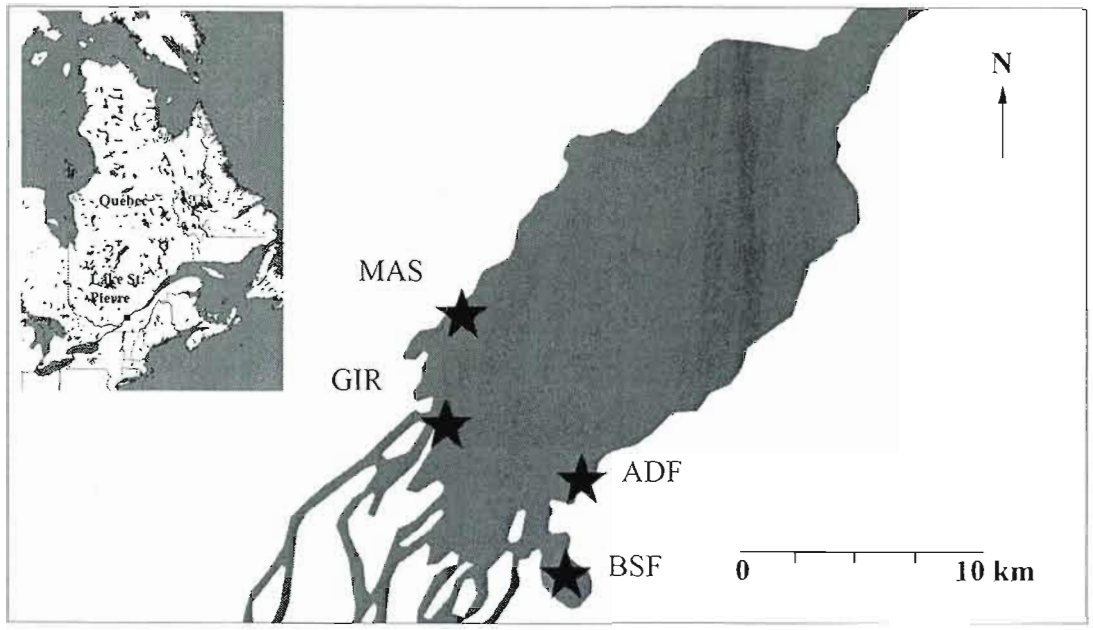

Fig. 3.1

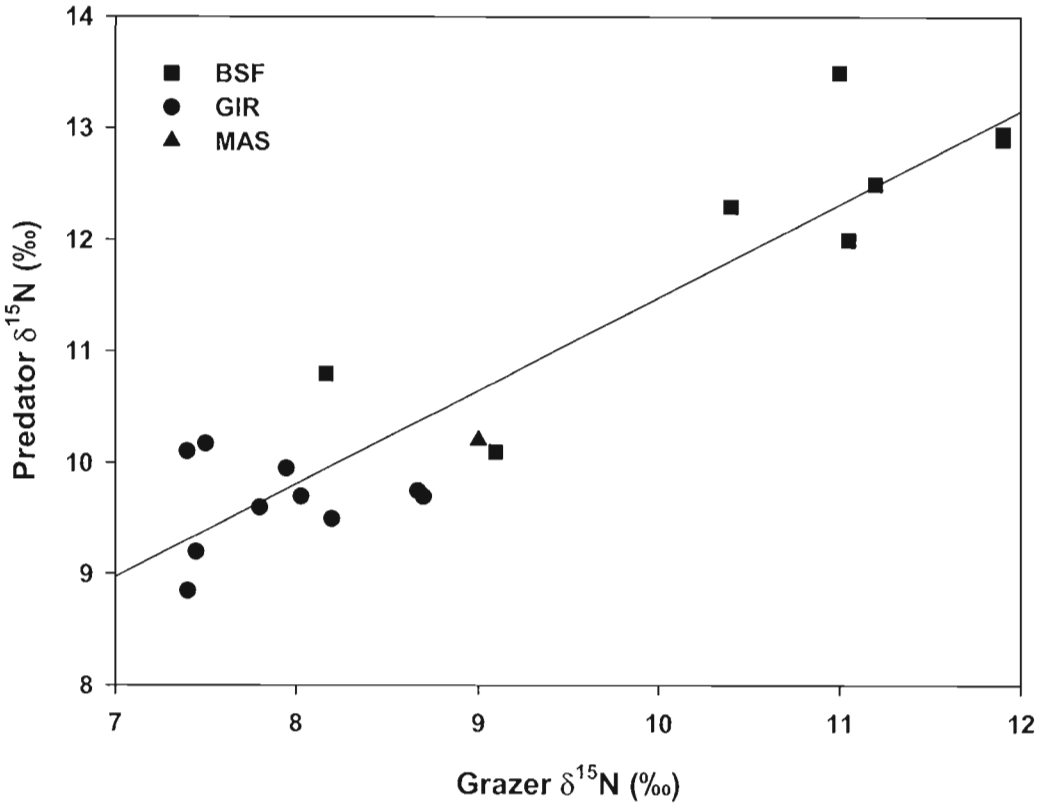
BSF
GIR
MAS
Predator δ^{15}N (‰)
Grazer δ^{15}N (‰)
14
13
12
11
10
9
8
7
8
9
10
11
12

Fig. 3.2

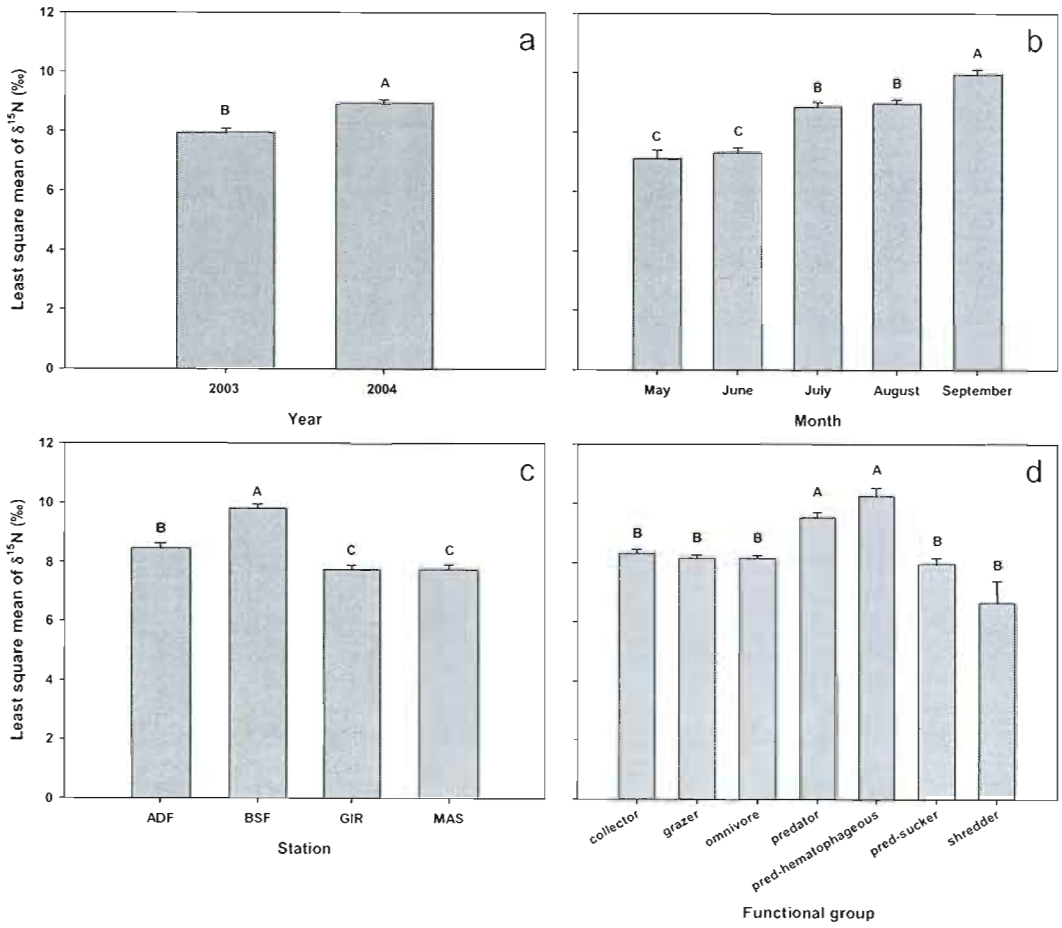
a
b
c
d
Least square mean of δ15N (‰)
Year
2003
2004
Month
May
June
July
August
September
Station
ADF
BSF
GIR
MAS
Functional group
collector
grazer
omnivore
predator
pred-hematophageous
pred-sucker
shredder

Fig. 3.3

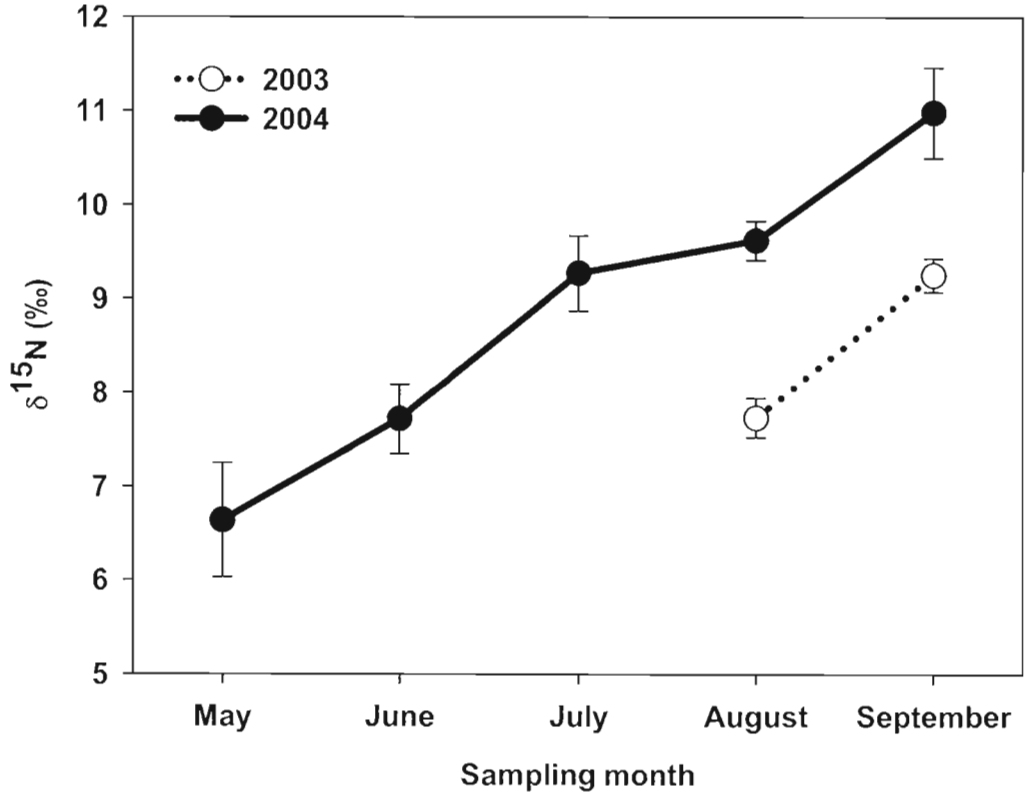
12
11
10
9
8
7
6
5
2003
2004
$\delta^{15}N$ (‰)
May
June
July
August
September
Sampling month

Fig. 3.4

3.8) REFERENCES

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CHAPITRE IV

BIOMASS AND COMPOSITION OF MACROINVERTEBRATE COMMUNITIES ASSOCIATED WITH DIFFERENT TYPES OF MACROPHYTE ARCHITECTURES AND HABITATS IN A LARGE FLUVIAL LAKE

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Résumé: L'influence de l'habitat et de l'architecture des macrophytes sur la biomasse, l'abondance et la richesse des macroinvertébrés fut étudiée au lac St Pierre, un grand lac fluvial du St Laurent (Québec, Canada). Une estimation à l'échelle du lac de la biomasse de macroinvertébrés associée aux différents types d'habitats macrophytiques fut aussi calculée afin d'estimer les effets quantitatifs de changements de végétation sur les communautés de macroinvertébrés. Les macroinvertébrés phytophiles furent échantillonnés dans des lits de macrophytes comprenant plus de dix espèces de plantes et trois habitats (émergent, flottant, submergé), et dans trois architectures de macrophytes (simple, intermédiaire, complexe) durant la période libre de glace pendant deux ans. Les sous-échantillons d'invertébrés furent classés en quatre groupes fonctionnels (détritivores, brouteurs, prédateurs rampants, prédateurs nageurs). La biomasse et la densité d'invertébrés furent exprimées par unité de poids sec de plante. La biomasse, l'abondance et la richesse des communautés de macroinvertébrés étaient significativement plus grandes dans les habitats submergés que dans les habitats émergents et flottants. Cependant, les macrophytes avec une architecture complexe n'hébergeaient pas significativement de plus forte biomasse de macroinvertébrés que les plantes avec une architecture plus simple. Ceci pourrait être relié aux préférences de substrat des herbivores (surtout des gastéropodes) envers *Vallisneria americana*. Des différences de biomasse et d'abondance de macroinvertébrés furent trouvées entre les deux années de variations de niveaux d'eau. Durant l'année avec un niveau d'eau normal la biomasse lacustre de macroinvertébrés était 16% plus élevée que durant l'année de bas niveau d'eau. En conclusion, la baisse de niveau d'eau attendue au lac St Pierre pourrait mener à une diminution de la biomasse benthique qui constitue un élément d'alimentation crucial pour les poissons.

Mots clés: macroinvertébrés, groupe fonctionnel, habitats de macrophytes, architecture des plantes, zones humides, lac St. Pierre

Abstract: The influence of macrophyte habitat and architecture on macroinvertebrate biomass, abundance, and richness was investigated in Lake St. Pierre, a large fluvial lake of the St. Lawrence River (Quebec, Canada). A lake-wide estimate of macroinvertebrate biomass associated with different macrophyte habitats was also calculated in order to assess the quantitative effects of vegetation changes on macroinvertebrate communities. For two years during the ice-free period, phytophilous macroinvertebrates were sampled in macrophyte beds comprising more than ten species of plants and three habitats (emergent, floating-leaved, submerged), and in three submerged macrophyte architectures based on plant morphology (simple, intermediate, and complex). Invertebrate sub-samples were classified into four functional groups (detritivore, grazer, crawling predator, diving predator). Biomass and density of invertebrates were expressed per unit of plant dry weight. The main findings are that macroinvertebrate biomass, abundance and richness were

related to substrate preferences of herbivores (mostly Gastropoda) toward the tape grass *Vallisneria americana*. Differences in macroinvertebrate abundance and biomass were found between the two years associated with variations in the river water level. During the year with average water level, total macroinvertebrate biomass was 16% greater than in the year with a lower water level. We conclude that a reduction in the water level of Lake St. Pierre, predicted to occur with climate change, could lead to a decrease in benthos biomass which constitutes a crucial food source for fish.

Keywords: macroinvertebrates, functional group, macrophyte habitats, plant architecture, wetlands, Lake St. Pierre.

4.1) INTRODUCTION

The littoral zone is of critical ecological importance since it is considered the main site of secondary production in lakes (Brinkhurst 1974, Vadeboncoeur et al. 2002). It is also within the littoral zone that macroinvertebrate richness and density are greatest (Strayer 1985). Generally, macroinvertebrate biomass per unit of surface area is greater on vegetated than on non-vegetated substrates (Rasmussen & Rowan 1997). A decline in macrophyte cover is thus often followed by a decline in zoobenthic biomass (Davies 1982). Macrophytes provide more surface area attachment for periphyton (Cattaneo 1983, Gosselain et al. 2005), a major component in the diet of macroinvertebrate primary consumers (Campeau et al. 1993). Macrophyte beds also offer protection against visual predators and are suitable sites for insect egg deposition.

Three types of habitats can be defined in the littoral zone according to the specific composition of their macrophytes: marshes dominated by emergent plants species, low turbulence areas populated by floating-leaved macrophytes, and aquatic meadows where the main habitat consists of species of submerged macrophytes. Several studies have shown that macrophyte species have an influence on the richness and the abundance of littoral insect communities (Gerrish & Bristow 1979, Cyr & Downing 1988a, b, Hanson 1990, Feldman 2001). The more diversified substrates provided in the submerged macrophyte environment contain more ecological niches than homogeneous systems such as the underwater portion of emergent macrophytes (Mackay & Kalff 1969, Tessier et al. 2004). Moreover, submerged macrophyte assemblages offer larger surfaces for periphyton growth, especially in the canopy (Vis et al. 2006). On the other hand, bare stems of emergent plants offer less substratum for periphyton growth, less protection against turbulence, and higher exposure to visual predators (Gosselain et al. 2005). Similarly, floating-leaved

macrophytes provide little habitat in the vertical dimension compared to emergent plants and reduce light penetration into the water column, thus limiting the growth of periphyton.

Submerged macrophyte architecture can be defined as the fractal dimension of the leaves of a macrophyte species (Jeffries 1993). Differences in architecture between macrophyte species are striking, ranging from species with bare stems (simplest architecture) to species with very delineated and dissected leaves that form complex canopies (most complex architecture). Macrophyte architecture is believed to structure macroinvertebrate communities because architecture influences a plant's surface-to-biomass ratio (Lalonde & Downing 1992). Greater surface area is favourable for periphyton colonisation and may harbour more macroinvertebrates as there is literally more habitat to use (Krecker 1939, Rosine 1955, Dvorak & Best 1982, McAbendroth et al. 2005). Changes in macrophyte specific composition could then indirectly modify phytophilous macroinvertebrate community composition and biomass.

In the context of global climate changes, modifications of lake and wetland water level on macrophyte habitat are a growing concern (Coops et al. 2002; Wright et al. 2002). Climate changes, combined with land-use and other anthropogenic disturbances could dramatically alter macrophyte cover, especially in shallow lakes because of their large littoral zone (Hudon 1997, 2004). As macrophyte-epiphyte complexes are the most important primary producers in the littoral zone (Vis 2004), large-scale modifications of these plant assemblages could cause trophic cascades in higher trophic levels of the food web by altering phytophilous macroinvertebrate communities and the fish populations that feed on them (Healey 1984, Bertolo et al. 2005). The first two goals of this study were to assess the influence of habitat and macrophyte architecture on macroinvertebrate richness and biomass in a large and

shallow fluvial lake of the St. Lawrence River, Lake St. Pierre (Quebec, Canada). The third goal was to estimate the lake-wide biomass of macroinvertebrates associated with emergent and submerged macrophyte habitats in order to assess the quantitative effects of vegetation changes on macroinvertebrate communities. This particular study site was chosen because of its extensive wetlands (20% of the St. Lawrence wetlands, Langlois et al. 1992) that harbour a considerable macroinvertebrate fauna and because two-thirds of lake productivity is constituted by macrophytes and their attached epiphytes (Vis 2004). Water level fluctuations in the lake have a strong influence on plant biomass in relation to the plant habitat (Hudon 1997). High waters favour an open water body with an increase in submerged macrophyte habitat but with a lower biomass per unit surface area while low waters turn the lake into a large marshland that could support twice the macrophyte biomass (Hudon 1997, 2004). Currently, the water column depth of Lake St. Pierre is decreasing because of two synergistic phenomena: filling-up with particulate matter brought in by tributaries coming from agricultural land within the watershed and sediment retention by the macrophyte beds covering a large part of the lake benthic zone (Morin & Côté 2003, Carignan 2004).

4.2) METHODS

4.2.1) Study site and sampling design

More than half (6,200 ha out of 11,952) of the Lake St. Pierre area is covered by aquatic plants[‡], representing one fifth of all freshwater wetlands on the St. Lawrence River (Langlois et al. 1992). This wetland is highly productive, and macrophytes and attached epiphytes contribute up to 70% of lake productivity

[‡] Lac Saint-Pierre, Québec. Information Sheet on Ramsar Wetlands. http://www.wetlands.org

(Tessier et al. 1984, Vis 2004). Lake water originates from three major sources. Brown waters rich in dissolved organic carbon (DOC) from the Ottawa River and other tributaries on the Canadian Shield flow along the north shore (mean annual flow 1500 m3 s-1, Vis et al. 2003). The green waters from Lake Ontario flow in the central channel (mean annual flow 9300 m3 s-1). Finally, tributaries draining extensively farmed lands bring turbid, nutrient-rich water along the south shore of Lake St. Pierre (mean annual flow 700 m3 s-1). Sampling was conducted during the ice-free period at 4 stations in the littoral zone of Lake St. Pierre, three times from early July to September in 2003 and during the first week of each month from May to September 2004 (Fig. 1). Two stations were situated near the north shore: the first one close to the Maskinongé River (MAS) and the second one near Girodeau Island at the eastern part of Sorel archipelago (GIR). The other two stations were located near the south shore: the Anse-du-Fort (ADF) and the Baie St. François (BSF) wetland. All stations were shallow (depth <1.5 m) and extensively covered with macrophytes.

4.2.2) Sampling of macroinvertebrates and macrophytes

At each station, macroinvertebrate samples were collected within the dominant macrophyte species (six in May and June and nine in July through to September), with three samples per species. For this purpose, terrestrial plant remains were treated as a single species. The sampler, a Plexiglas Downing box (13 L volume; Downing & Rigler 1984) was slowly immersed in the water between the water surface to 1 m deep and then gently closed, capturing invertebrates and macrophytes alike. The content of the box was sieved through a 500-µm mesh net, and macroinvertebrates were separated from macrophytes by vigorous hand shaking in a plastic container. In the field, macroinvertebrates were pre-sorted in order to isolate predators and prey,

and kept in Nalgene™ jars filled with lake water. Macroinvertebrate samples were stored at −80°C. Thawed macroinvertebrates were identified and sorted by family or genus with the exception of gastropods that were sorted by sub-class (i.e., Prosobranchia, Pulmonata). Gastropods were manually removed from their shell. Within each Downing box sample, all individuals of the same taxon were grouped into a sub-sample. The following keys were used: Merrit & Cummins (1996) for insects, Clarke (1981) for gastropods and Pennak (1953) for other organisms. We classified the macroinvertebrate sub-samples into 4 functional groups: grazers/herbivores (called grazers hereafter), detritivores/collectors/scavengers (called detritivores hereafter), crawling predators (e.g. odonates, and other poor swimmers) and diving predators (i.e., vagile insects that actively swim and go to the surface to breathe aerial oxygen, like dytiscids and notonectids). Invertebrates were freeze-dried for 24h. Samples were weighed on a high precision AT201 Mettler Toledo™ electrobalance (Mettler Toledo Canada).

Macrophytes were collected simultaneously with macroinvertebrates. Plants were identified in the field and classified into four habitat types: spring terrestrial plant remains washed-out by spring floods, and emergent, floating-leaved, and submerged macrophytes. Within the submerged macrophytes, three groups of species were obtained relative to their architecture: simple (plants with bare stems, i.e. *Vallisneria americana*), intermediate (plants with long, entangled stems and leaves e.g. *Potamogeton perfoliatus* L.), and complex (i.e., plants with highly dissected leaves like Myriophyllum spicatum, Gosselain et al. 2005). Macrophyte samples were kept frozen at −80°C. Plant dry weight per unit area was determined following desiccation in an oven at 50°C until a constant weight was obtained.

4.2.3) Data treatment

The invertebrate communities were quantified both as abundance (n individuals per g DW or kg of macrophyte ±1 SE) and as biomass (mg of invertebrates per g DW or kg of macrophyte ±1 SE). Since species representative of all 3 types of macrophyte architecture were only found among submerged plants, comparisons for architecture effects on macroinvertebrate biomass were only carried out among plants within this habitat. Statistical analyses were performed by JMP (version 5.0, SAS Institute Cary, North Carolina).Animal biomass (mg kg-1) was log10 transformed to meet the requirements of normality. We used a factorial test effect model (SAS Institute Inc. 1991) to disentangle the different categorical parameters (year, month, station, functional group, habitat, architecture) influence on invertebrate biomass (Uryu et al. 2001). The output values are adjusted values or least squares means (LSMs) that were tested with mean comparisons tests (Tukey-Kramer Honestly Significantly Different (HSD) test or ANOVA). The LSMs are predicted values from the model across the level of categorical effects where the other model factors are controlled by being set to neutral values (SAS Institute Inc. 1991, Uryu et al. 2001). The categorical variables were year (n=2), month (n=5), station (n=4), feeding functional group (n=4), habitat (n=4), and architecture (n=3).

4.2.4) Lake-wide estimate of macroinvertebrate biomass

In order to forecast the influence of climate change on invertebrate communities, we used the mean macroinvertebrate biomass per unit of plant we measured in year 2003 and 2004 and estimates of macrophyte dry mass that Hudon (1997) calculated using hydrology data from 1912-1994 and macrophyte biomass measured during the 1990-1996 period. Year 2003 was considered a low water-level

year and 2004 an average water-level year (Vis 2004). Lake-wide estimates of macrophyte biomass obtained from Hudon (1997) were:

-emergent macrophyte dry mass in low water-level year: 94.4 .103 t,

-submerged macrophyte dry mass in low water-level year: 50.9 .103 t,

-emergent macrophyte dry mass in average water-level year: 47.8 .103 t,

-submerged macrophyte dry mass in average water-level year: 75.9 .103 t

(Hudon 1997). Macrophyte dry mass values were then multiplied by our macroinvertebrate biomass measurements for 2003 and 2004 in order to obtain a lake-wide estimate of macroinvertebrate biomass associated with macrophytes for each year. This information was used to assess which year (dry year 2003, average year 2004) supported the greatest total macroinvertebrate biomass. Because whole lake estimates of the biomass of floating-leaved plants were not available, only emergent and submerged macrophyte beds were considered in our analysis.

4.3) RESULTS

4.3.1) Characteristics of the sampled communities

From early May to early June, meadows and wetlands included remains from the former season (senescent macrophytes, mostly *Potamogeton* spp.), young stems of emergent macrophytes as well as terrestrial plant material (up to 1 m thick) washed out during spring floods. At this time, periphyton was abundant on macrophyte remains allowing the sustenance of grazing organisms like *Gammarus fasciatus* Say and Chironomidae of the Orthocladiinae sub-family. In July, growing macrophytes were dominated by submerged *Potamogeton* spp. and by emergent Typha and Scirpus spp. In August, submerged *V. americana* with simple architecture and the more complex *Elodea canadensis*, *M. spicatum* and *Ceratophyllum demersum* were well

established. In September, a decline in macrophyte cover was observed; many decaying plants had been removed from their substratum by late summer storms and were floating in assemblages of different species (Table 1).

Annual average macroinvertebrate abundance ranged between 11.4 ind g^{-1} DW in 2003 to 5.7 ind g^{-1} DW in 2004. Abundance and biomass were correlated ($p < 0.0001$, $r^2 = 0.44$, $n = 691$; Fig. 2). A large majority (up to 80%) of the sampled organisms belonged to the grazer functional group (Table 2) with gastropods and amphipods being the dominant taxa. The abundance of detritivores, constituted mostly by *Asellus* sp. (Isopoda), was highly variable depending on the year, low (2 to 2.5%) in 2003 and higher (around 15%) in 2004. Crawling predator contribution to total community density varied from 6 to 20%, with damselfly larvae *Coenagrion* sp. (Zygoptera) being the most abundant taxa of this group. Diving predator biomass was the lowest (< 7%) among functional groups and it was predominantly represented by *Neoplea* sp. (Heteroptera: Pleidae).

Sixty taxa, mostly insects, were collected in Lake St-Pierre in 2003 and 2004. Total richness varied according to season, with higher values in mid-summer than in spring and in late summer (Fig. 3A). The four functional groups were in general evenly represented on all sampling dates. Grazer richness peaked in August (14 taxa) when macrophytes and their epiphytes were fully grown and thus more resources and niches available, then dropped in September (5 taxa) when macrophyte assemblages began to decay. Conversely, detritivore richness was the highest (9 taxa) in early June when new growing macrophyte beds were still scarce but old macrophyte remains and terrestrial detritus were abundant. The trends were less clear for the other functional groups although crawling predators and diving predators were more diversified in June and in July, respectively.

4.3.2) Macrophyte habitat and plant architecture vs. macroinvertebrate richness

Macroinvertebrate taxonomic richness was influenced by the type of habitat (Fig. 3B). Terrestrial plant remains hosted the least number of taxa (7) and submerged macrophytes the most (25 taxa). Richness on emergent macrophytes (21) was slightly lower than on submerged macrophytes while floating-leaved plants hosted even less taxa (15). Only minor differences were observed in the contribution of each functional group to total richness in each habitat. Nevertheless, there were more grazer and diving predator taxa and less detritivore and crawling predator taxa in submerged macrophytes compared to emergent plants.

Macroinvertebrate taxa richness varied in relation to plant architecture. Within the submerged macrophytes, the richest communities were found in plants with an intermediate complexity (Fig. 3C) such as pondweeds (i.e., two species of *P. richardsonii* and *P. perfoliatus*). Complex plants supported a macroinvertebrate community nearly as rich as the intermediate architecture species while simple plants (i.e., tape grass *V. Americana*) harboured the poorest communities. Richness within functional groups was not evenly distributed, the largest array of grazer species being found in pondweeds while complex plants hosted most of the predator species. *V. americana* (simple architecture) beds supported all functional groups except diving predators (Fig. 3C).

4.3.3) Year, habitat and plant architecture vs. macroinvertebrate biomass

Macroinvertebrate biomass in Lake St. Pierre tended to be greater for organisms dwelling in the submerged macrophyte habitats (Table 3). Mean macroinvertebrate biomass was roughly 2-fold in submerged compared to emergent and floating-leaved habitats and 40-fold greater compared to terrestrial plant remains.

Mean annual values were: 1.55 mg g^{-1} DW for invertebrates collected in emergent habitats, 4.66 mg g^{-1} DW for those from submerged habitats in 2003. In 2004, for the same months sampled as in 2003, they were 3.21 and 3.97 mg g^{-1} DW respectively. When the 2004 values from May and June were included, biomass was 2.61 and 3.12 mg g^{-1} for emergent and submerged habitats.

All variables entered in the test effect model were significant ($p < 0.05$, Table 4). In model 1, where only temporal and spatial variables were used, mean squares indicated that month explained the most variation followed by year and station. Biomass LSMs of invertebrates were significantly greater in August and September than in previous months (Tukey HSD test, $p < 0.05$, $Q = 2.73$). In model 2, habitat was entered and was highly significant, but it added little information to explain the variation in biomass (Table 4). Month and year variables were significant and their mean squares were nearly equal. When functional feeding group was entered in model 3, all variables became highly significant and the model explained a larger part of the variation in biomass (Table 4). The functional group mean square value was higher than that of all the other variables combined. The mean biomass of macroinvertebrates was significantly lower in 2003 than in 2004 (26.9 and 42.6 mg kg^{-1} DW respectively, ANOVA model 3, Tukey HSD test, $p < 0.001$). Submerged macrophyte habitats supported significantly higher biomass than emergent and floating-leaved macrophyte habitats, with terrestrial plant remains being intermediate (Fig. 4A, Tukey HSD test, $p < 0.05$, $Q = 2.57$).

With only data collected from submerged habitats, a test effect model was entered with the variables year, month, station, and macrophyte architecture (model 4). All variables were significant; with month as the strongest variable. With the addition of functional group in model 5, station became non significant. The latter model explained nearly half of the total variation in macroinvertebrate biomass (r^2 =

0.42). Submerged complex and simple plants harboured more invertebrate biomass than intermediate plants shown by Tukey HSD test for LSMs of macroinvertebrate functional groups biomass extracted from model 5 (Fig. 4B). Considering comparisons between grazers only (which are supposedly the group the most dependent on periphyton colonization and thus macrophyte architecture), it appeared that plants with a simple architecture hosted significantly more organisms than plants with an intermediate architecture while complex plants were intermediate (Fig. 4C). In contrast, all non-grazer taxa (detritivores, crawling, and diving predators) had significantly higher biomass on complex plants than on intermediate ones but were not significantly higher than on simple architecture plants (Fig. 4D, Tukey HSD, $p < 0.05$, $Q = 2.36$).

4.3.4) Lake-wide macroinvertebrate biomass and habitats in low and normal water-level years

Lake-wide estimates of total macroinvertebrate biomass differed between low and average water-level years, with average the water-level year having more invertebrate biomass than low water-level year. In the low water-level year, an estimated 383 t of invertebrates were associated with macrophytes. Of this biomass, 237 t (62%) were associated with submerged macrophyte habitats and 146 t were living in emergent habitats. For the average water-level year, total invertebrate biomass was estimated at 456 t, with 301 t (66%) associated with submerged plant habitat and 155 t associated with emergent plant beds.

4.4) DISCUSSION

4.4.1) Habitat and architecture influence on macroinvertebrate richness and biomass

We have shown that aquatic macroinvertebrate biomass in Lake St. Pierre was greater in submerged habitats than in emergent and floating-leaved habitats or in terrestrial plant remains. These findings are in agreement with the majority of previous studies where the influence of substratum was examined and it was found that submerged macrophytes hosted more phytophilous invertebrates than the other aquatic plants habitats (Dvorak & Best 1982, Cattaneo et al. 1998, Feldman 2001, Tessier et al. 2004, *but see* Hanson 1990, Strayer et al. 2003). In our study, stronger correlations were found between invertebrate abundance and biomass than in previous research (e.g., Lalonde & Downing 1992) probably because we only considered macrobenthos, defined roughly as organisms retained by nets larger than 250 μm (Kalff 2002). This resulted in less than two orders of magnitude in size differences of macroinvertebrates (max: Zygoptera larvae, 4.0 mg; min: *Daphnia* sp, 0.042 mg).

In contrast to literature data, we found macroinvertebrate taxonomic richness was greater in beds of submerged macrophytes that in the other aquatic plant habitats in Lake St. Pierre. Results of previous research are inconsistent on this topic (Cattaneo et al. 1998, Feldman 2001, McAbendroth et al. 2005 *but see* Mackay & Kalff 1969, Tessier et al. 2004). Terrestrial plant remains hosted very poor communities (between 1/3 to 1/5 as many taxa as the other substrates) and the most prominent taxon in this habitat was an isopod of the genus *Asellus*. However, since terrestrial plant remains were only sampled in May, it is difficult to definitively

conclude whether sampling period or habitat was responsible for the low richness observed.

Plants with a complex architecture did not host significantly greater biomass than simpler plants, which is inconsistent with the generally accepted hypothesis that complex plant assemblages constitute more favourable conditions for macroinvertebrates (Krecker 1939, Cyr & Downing 1988b, Jeffries 1993, Cheruvelil et al. 2002, McAbendroth et al. 2005, Xie et al. 2006, *but see* Cyr and Downing 1988a). One of the reasons for this observation is that more complex environments support a greater number of individuals, but of smaller body-size compared to simpler environments (Jeffries 1993). However, this explanation is unlikely in this study because macroinvertebrate abundance and biomass were correlated. Herbivores were more abundant on the macrophyte species with the simplest architecture such as the tape grasses *V. americana*. It has been shown that *V. americana* beds can sometimes support large communities of gastropods (Lalonde & Downing 1992) which constituted the majority of the grazers at our study sites. This macrophyte species, with its long and narrow, tape-shaped leaves, allow more light penetration and nutrient exchange than beds of denser plants like *Potamogeton* spp., thus favouring periphyton growth (Kairesalo 1983). Furthermore, greater water circulation in *V. americana* stands can favour other critical conditions for macroinvertebrate distributions like dissolved O_2 (Caraco & Cole 2002) which is especially important for macroinvertebrates that obtain their oxygen from water such as amphipods and Prosobranchia. In the case of herbivores, our results do not support our hypothesis that architecture complexity sustains higher biomass, indicating that architecture alone may not be a good predictor of invertebrate distribution. We found that *Vallisneria* not only supported greater grazer biomass but was also a good habitat for clinging predators like damselfly larvae (*Coenagrion* sp.). However, *Vallisneria* hosted comparatively poorer phytomacrofauna communities than the more complex

submerged macrophyte species. The diving predators in particular, which were mostly hemipterans in our study, were absent in the *Vallisneria* beds. These insects breathe oxygen from air (Merrit & Cummins 1996) and could exploit less oxygenated waters where competition for food is lower.

4.4.2) Implications of water level changes on invertebrate biomass distribution

In our two-year study, annual differences affected the distribution of macroinvertebrates in Lake St. Pierre. During the low water-level year, our model predicted a mean invertebrate biomass per plant unit nearly half the value of the average water-level year. In addition to a decrease in the availability of substrates and submerged habitats, low water-level episodes may result in an increase in water temperature that can reduce dramatically the O_2 solubility and lead to hypoxia. The majority of invertebrates that were sampled, with the exception of some diving predators and Pulmonata, breathe dissolved O_2. Low water-level episodes could thus result in benthos flight or even benthos kills (Rahel & Kolar 1990, Hogg & Dudley-Williams 1996). Furthermore, in these nearly treeless marshes with few physical refuges, lower water levels result in increasing exposure of benthos to UV penetration into the water column. UV-B especially can penetrate up to a half meter in eutrophic ponds and have lethal effects on individuals of aquatic invertebrate populations (Hurtubise et al. 1998).

Based on lake-wide estimates, a water level reduction appeared to have an adverse effect on macroinvertebrate biomass in Lake St. Pierre. Though the proportions of macroinvertebrates dwelling in submerged relative to emergent habitats remained more or less the same (2/3 of the biomass) in the two scenarios, the total macroinvertebrate biomass rose 16% between a low and an average water-level

year, which corresponds to 73 t of invertebrates. Biomass estimates were conservative because organisms living in sediments were not sampled, individuals smaller than 500 μm were not retained, and macroinvertebrates associated with floating-leaved plants or macroalgae were not considered. The decrease in macroinvertebrate biomass may have a bottom-up effect by reducing food availability to fish species and consequently reduce their population sizes. Recurrent low water-levels over multiple years could thus have severe consequences for local fisheries and the community economy.

4.5) CONCLUSION

In this study of Lake St. Pierre, we demonstrated that macroinvertebrate distribution differed between aquatic plant habitats, and submerged macrophytes hosted greater biomass, abundance and richness than emergent and floating-leaved plants. The architecture of submerged stands did not have a significant influence since plants with finely dissected leaves did not bear a greater invertebrate biomass than simpler forms. In the case of grazers, architecture alone may not predict biomass as illustrated by the high densities of organisms on simple tape grass *V. Americana*. If Lake St. Pierre evolves from an open-water system towards a large wetland as a result of climate changes, macroinvertebrate density should decrease, thus causing a reduction in prey items for fish, and potentially decreasing fisheries yields.

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Table 4.1
Spatial and temporal composition of the sampled macrophyte beds, and other substrates in Lake St. Pierre during the ice-free season in 2003 and 2004

Habitat	Species	Architecture	Sampling month	Station
Terrestrial plant	Dead terrestrial plants	–	May	MAS
Submerged	Diverse macrophyte species	Complex	September	GIR
	Ceratophyllum demersum L.	Complex	September	BSF
	Elodea canadensis Rich.	Complex	August	GIR
	Potamogeton pectinatus, L.	Complex	June	ADF
	P. richardsonii (A. Bennett)	Intermediate	May, June	ADF, BSF, GIR, MAS
	P. perfoliatus, L.	Intermediate	July, August	ADF, BSF, GIR, MAS
	Vallisneria americana Michx.	Simple	June, July, August	ADF, BSF, MAS
Floating-leaved	*Nymphea tuberosa* Paine	–	July	BSF
Emergent	*Sagittaria latifolia* Willd.	–	July, August, September	ADF, GIR
	Scirpus fluviatilis (Torr.)	–	June, July, August	ADF, GIR, MAS
	Typha angustifolia L.	–	May, June, July, August, September	ADF, BSF, GIR

Table 4.2
Total macroinvertebrate abundance (n. individuals $g.^{-1}$ DW) and biomass (mg g^{-1} DW) of the 4 functional groups collected in 2003 and 2004 in Lake St. Pierre (percentages of total community abundance or biomass are in brackets)

Functional group	Abundance		Biomass	
	2003	2004	2003	2004
Grazers	18749 (87.18)	8533 (73.84)	6441 (82)	5733 (61.26)
Detritivores	472 (2.19)	1902 (16.45)	192 (2.44)	1023 (10.93)
Crawling predators	1817 (8.45)	717 (6.20)	795 (10.12)	1988 (21.24)
Diving predators	467 (2.17)	404 (3.50)	426 (5.42)	614 (6.56)

Table 4.3
Mean biomass (mg g^{-1} DW ±1 SE) of the macroinvertebrate sub-samples classified into four functional groups and sampled in Lake St. Pierre, as a function of habitat and submerged macrophyte architecture (number of sub-samples given in brackets)

Habitat	Architecture	Sub-sample mean biomass				
		All groups average	Grazers	Detritivores	Crawling predators	Diving predators
Emergent		2.38 ± 0.81 (155)	1.94± 0.49 (81)	4.26 ± 3.50 (34)	1.86 ± 0.53 (26)	1.30 ± 0.41 (14)
Floating-leaved		1.86 ± 0.27 (97)	2.58 ± 0.48 (43)	1.68 ± 0.52 (14)	0.68 ± 0.16 (26)	2.05 ± 0.84 (14)
Submerged		4 ± 0.35 (434)	6.34 ± 0.57 (237)	1.66 ± 0.61 (72)	0.89 ± 0.12 (106)	0.93 ± 0.25 (19)
	Simple	6.38 ± 0.91 (95)	10.06 ± 1.27 (58)	0.74 ± 0.14 (16)	0.52 ± 0.11 (21)	–
	Intermediate	2.25 ± 0.24 (207)	3.65 ± 0.39 (114)	0.39 ± 0.06 (34)	0.55 ± 0.1 (47)	0.86 ± 0.32 (12)
	Complex	5.02 ± 0.83 (132)	7.74± 1.46 (65)	4.30 ± 1.91 (22)	1.52 ± 0.28 (38)	1.05 ± 0.40 (7)
Terrestrial plant remains		0.24 ± 0.10 (12)	0.15± 0.05 (5)	0.31± 0.20 (6)	–	0.24 (1)

Table 4.4
Test effect model of $\log_{10}$(biomass+1 mg kg^{-1}) of invertebrates collected in Lake St. Pierre with selected variables

Model and source	Sum of squares	df	Mean square	F ratio	*P*	r^2
Model 1						0.13
Year	5.86	1	5.86	12.61	0.0004	
Month	36.49	4	8.62	18.55	<0.0001	
Station	7.18	3	2.39	5.15	0.0016	
Model 2						0.15
Year	6.49	1	6.49	14.34	0.0002	
Month	25.68	4	6.42	14.17	<0.0001	
Station	7.11	3	2.37	5.23	0.0014	
Habitat	9.47	3	3.15	6.97	0.0001	
Model 3						0.30
Year	4.81	1	4.81	12.87	0.0003	
Month	20.62	4	5.15	13.77	<0.0001	
Station	9.91	3	3.30	8.83	<0.0001	
Habitat	11.67	3	3.89	10.4	<0.0001	
Functional group	55.16	3	18.38	49.14	<0.0001	
Model 4*						0.16
Year	4.32	1	4.32	9.17	0.0026	
Month	16.39	4	4.09	8.69	<0.0001	
Station	5.86	3	1.95	4.14	0.0065	
Plant architecture	5.35	2	2.67	5.67	0.0037	
Model 5*						0.42
Year	3.23	1	3.23	9.98	0.0017	
Month	11.13	4	2.78	8.59	<0.0001	
Station	1.34	3	0.44	1.38	0.2478	
Plant architecture	4.28	2	2.14	6.61	0.0015	
Functional group	63.43	3	21.14	65.28	<0.0001	

Table 4.4
Continued

*samples collected in submerged habitats. Year: 2003, 2004; Month: May, June, July, August, September; Station: ADF, BSF, GIR, MAS; Habitat: emergent, floating-leaved, submerged, terrestrial plant remains; Architecture: simple, intermediate, complex; Functional group: detritivores, grazer, diving predator, predator.

4.7) FIGURE CAPTIONS

Fig. 4.1: Maps of Quebec (upper left corner) and Lake St. Pierre (St. Lawrence River, QC, Canada). The sampled stations are in alphabetical order: Anse-du-Fort (ADF), Baie St-François (BSF), Girodeau (GIR), and Maskinongé (MAS).

Fig. 4.2: Relationship between abundance and biomass of macroinvertebrates sampled in 2003 and 2004. Log (biomass) = -0.598979 + 0.6557123 log (abundance); $r^2 = 0.44$; F ratio = 556.9; $p < 0.0001$; $n = 691$. Each point represents all the individuals of the same taxa collected with a Downing box.

Fig. 4.3: Richness of macroinvertebrate functional groups sampled in Lake St. Pierre in 2003 and 2004, in relation to month (A), habitat (B) and macrophyte architecture (C). Richness represents the cumulative number of taxa of the four functional groups.

Fig. 4.4: Comparisons of adjusted biomasses (Least square means, LSM) of invertebrates in differing habitats (A) and plant architectures (B, C, D). Bars represent the mean value with 1 standard error. Bars not connected by the same letter are significantly different (Tukey HSD test, $p < 0.05$). Functional groups tested: all (A, B), grazers only (C), all but grazers (D). LSM are extracted from model 3 (A), and model 5 (B, C, D). TPR = terrestrial plant remains.

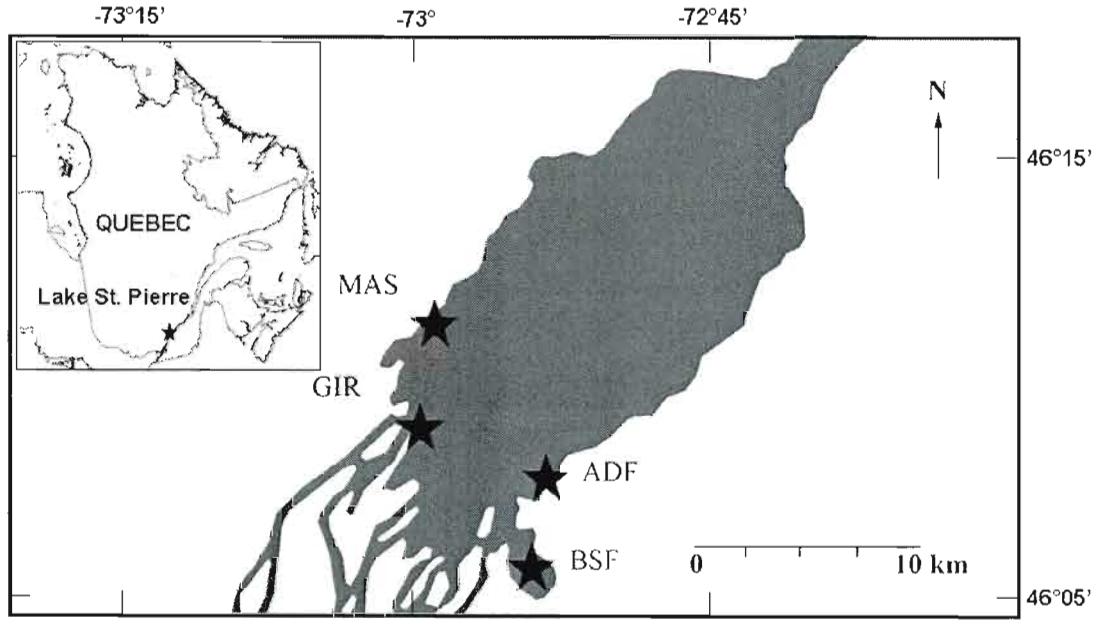
-73°15'
-73°
-72°45'
N
46°15'
QUEBEC
Lake St. Pierre
MAS
GIR
ADF
BSF
0
10 km
46°05'

Fig. 4.1

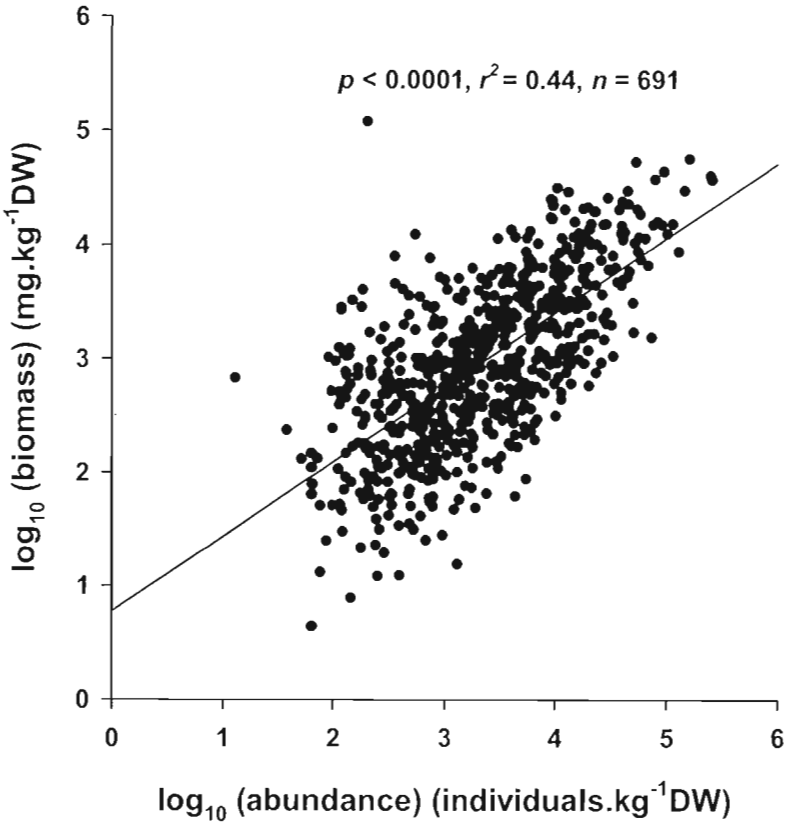
$p < 0.0001$, $r^2 = 0.44$, $n = 691$
$\log_{10}$ (biomass) (mg.kg^{-1}DW)
$\log_{10}$ (abundance) (individuals.kg^{-1}DW)
0
1
2
3
4
5
6

Fig. 4.2

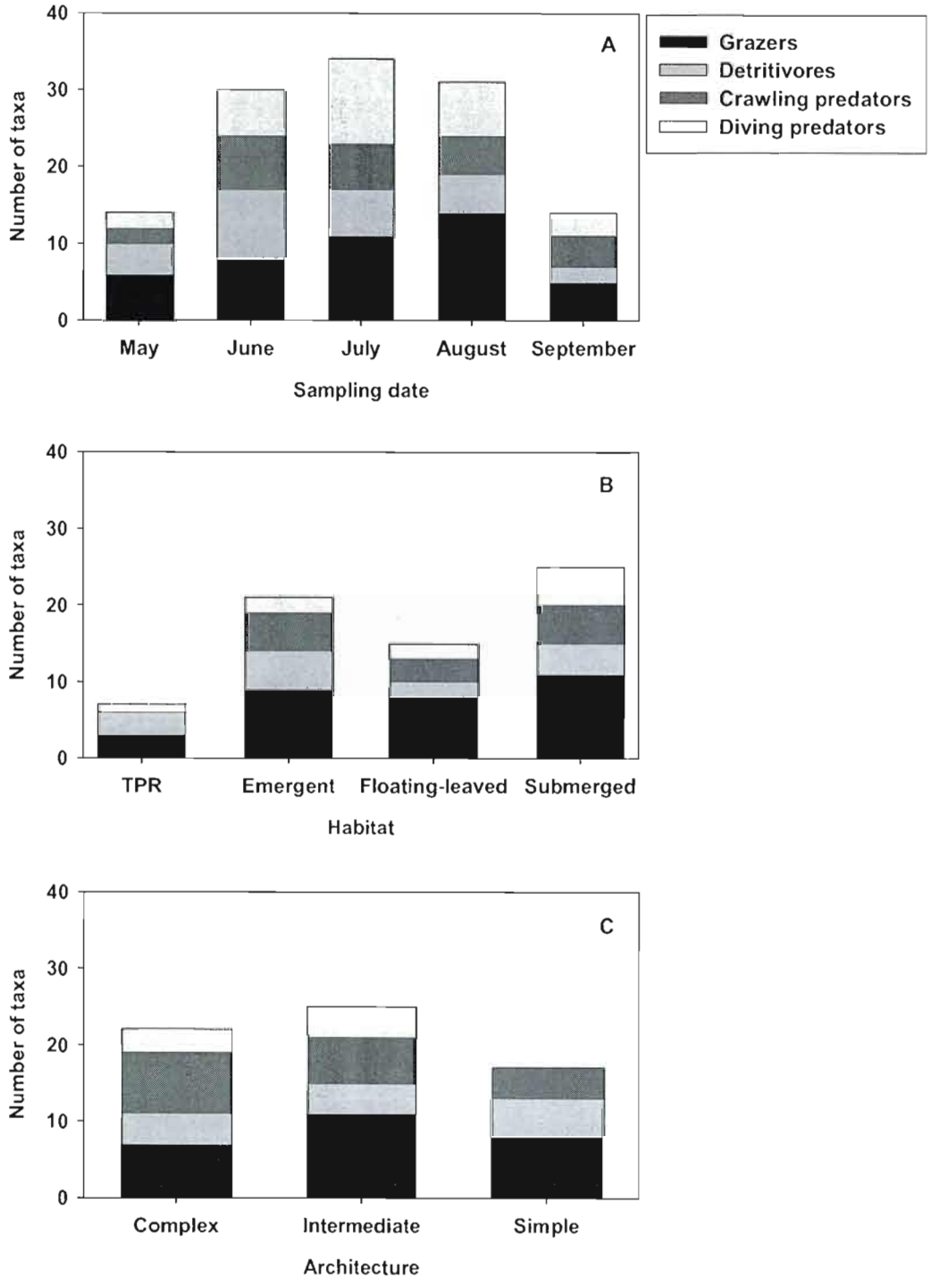
A
Grazers
Detritivores
Crawling predators
Diving predators
Number of taxa
0
10
20
30
40
May
June
July
August
September
Sampling date
B
Number of taxa
TPR
Emergent
Floating-leaved
Submerged
Habitat
C
Number of taxa
Complex
Intermediate
Simple
Architecture

Fig. 4.3

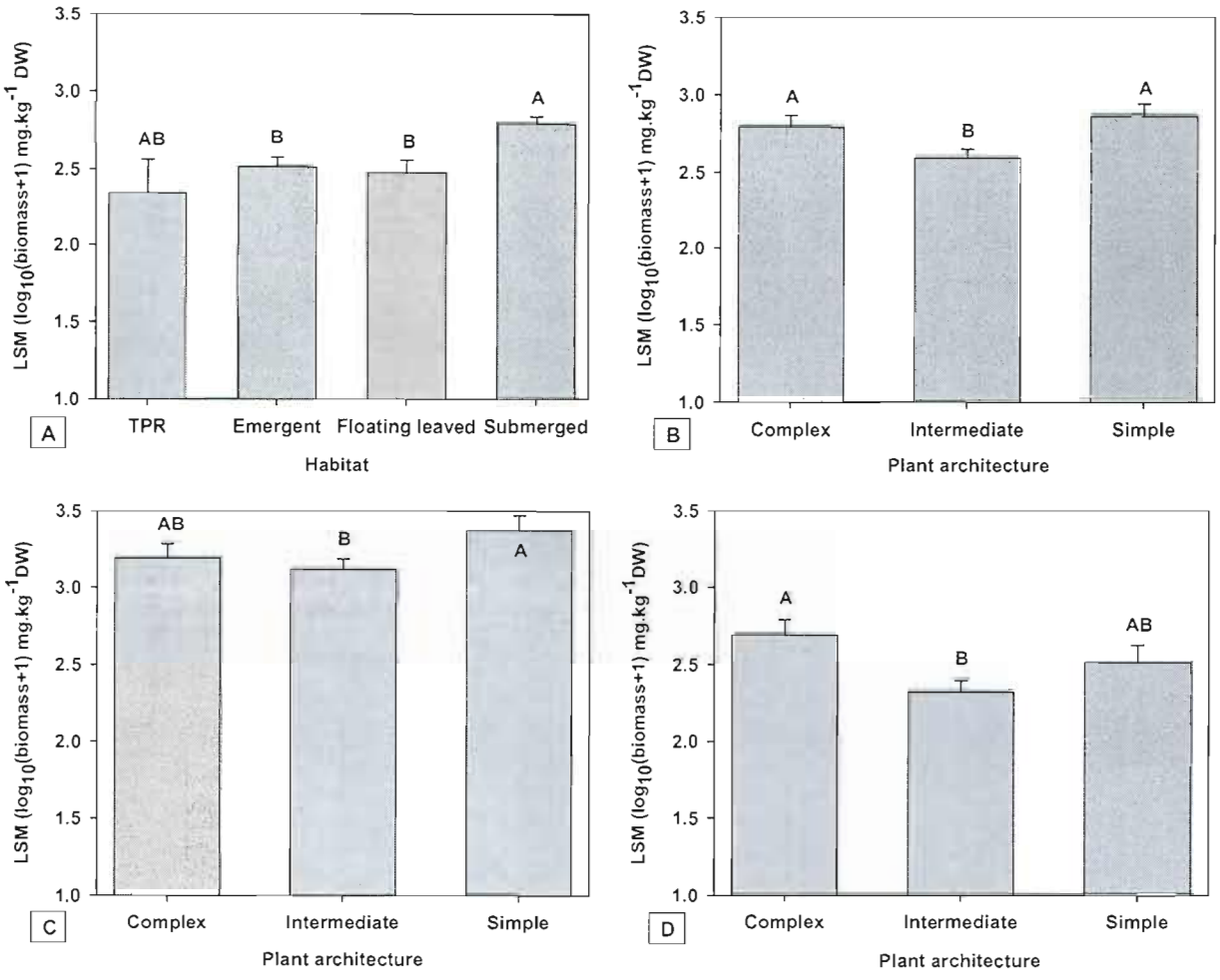
LSM (log_{10}(biomass+1) mg.kg^{-1} DW)
3.5
3.0
2.5
2.0
1.5
1.0
AB
B
B
A
TPR
Emergent
Floating leaved
Submerged
Habitat
A
LSM (log_{10}(biomass+1) mg.kg^{-1}DW)
A
B
A
Complex
Intermediate
Simple
Plant architecture
B
LSM (log_{10}(biomass+1) mg.kg^{-1} DW)
AB
B
A
Complex
Intermediate
Simple
Plant architecture
C
LSM (log_{10}(biomass+1) mg.kg^{-1}DW)
A
B
AB
Complex
Intermediate
Simple
Plant architecture
D

Fig. 4.4

4.8) REFERENCES

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CONCLUSION GÉNÉRALE

De cette thèse de doctorat, il apparaît que les macroinvertébrés jouent un rôle considérable dans le transfert de MeHg et dans plusieurs processus écologiques qui y sont liés. Tout d'abord, dans les réseaux trophiques de macroinvertébrés nous avons pu observer que certains organismes participent à une dynamique originale de *non-transfert* d'un polluant environnemental, le MeHg (impasses trophiques, chapitre I). D'autres organismes au contraire, s'avèrent de fidèles propagateurs des contaminations *bottom-up* par le MeHg (consommateurs primaires, chapitre II) et leurs valeurs de $\delta^{15}N$ indiquent probablement l'influence des engrais provenant du bassin-versant (chapitre III). Enfin, les macroinvertébrés reflètent le degré de complexité spatiale des niches écologiques qu'ils occupent (chapitre IV). Ci-dessous les conclusions principales de chaque chapitre et leurs implications scientifiques et environnementales.

Chapitre I – Bien que des mesures des concentrations de MeHg chez les hétéroptères et coléoptères aient été effectuées par certains auteurs (Cleckner *et al.*, 1998; Allen *et al.*, 2005), c'est la première fois que la non palatabilité de ces organismes est considérée dans une étude de transfert de MeHg. Notre étude a montré que les macroinvertébrés prédateurs non consommables ont les concentrations en MeHg les plus élevées de tous les macroinvertébrés aquatiques. La quantité de MeHg séquestrée dans ces organismes peut représenter jusqu'à un tiers de la quantité totale de MeHg mesurée chez tous les macroinvertébrés. Cette observation pourrait contribuer à expliquer les faibles concentrations en MeHg des poissons du lac St Pierre (Simoneau *et al.*, 2005), car les impasses trophiques sont présentes dans la zone littorale et nulle part ailleurs, et le lac St Pierre est une immense zone littorale.

Certaines questions restent néanmoins sans réponse et appellent à des recherches futures. Par exemple, quel est le devenir *post mortem* du MeHg des

impasses trophiques ? Est-ce que le MeHg séquestré dans ces organismes de leur vivant est rendu bioaccumulable après leur mort ? Tout donne à penser que oui, puisque l'inactivité des glandes pygidiales et la dégradation subséquente des composés défensifs chez ces insectes devraient cesser de faire obstacle à leur consommation. Dans le cas contraire, les cadavres de ces organismes deviendraient des « puits » de MeHg, ce qui n'a pas été observé jusqu'à présent. Notre étude s'est cantonnée aux réseaux trophiques aquatiques, mais nous ne savons pas dans quelle mesure les prédateurs terrestres peuvent servir à l'exportation du MeHg des impasses trophiques vers les écosystèmes terrestres. Certains prédateurs potentiels comme les oiseaux sont réputés posséder des papilles gustatives en plus faible quantité que les poissons (Brower, 1969). Ils ne seraient donc pas autant rebutés par les hétéroptères et les coléoptères comme le sont les poissons. Dans le cas de cette étude, le MeHg initialement lié aux impasses trophiques pourrait donc se retrouver lié aux détritus benthiques à la mort des impasses trophiques ou à la biomasse terrestre en cas de consommation des impasses par des prédateurs terrestres. Dès ce moment, on se rend compte que l'approche écosystémique interdisciplinaire s'avère fondamentale pour mieux comprendre le cycle du Hg puisque le polluant à un moment de son cycle s'échappe du « champ de vision » disciplinaire.

Chapitre II – Notre étude a montré à l'aide des outils isotopiques que les macroinvertébrés du lac St Pierre tirent majoritairement leur matière organique de sources autochtones comme les épiphytes et, dans une moindre mesure, des macrophytes. Le débat sur l'origine de la matière organique des réseaux trophiques lacustres est connu (Meili, 1992). On a supposé que parce qu'elle était la première zone lacustre à recevoir les apports de matière organique du bassin versant, la zone littorale était majoritairement consommatrice de matière organique allochtone. D'autres chercheurs ont avancé que la zone littorale est la partie la plus productive des lacs, et qu'alors c'est surtout la matière organique autochtone qui y était

consommée. Comme dans les lacs fluviaux de faible profondeur les macroinvertébrés constituent la principale source de matière organique au cours de l'ontogénie des poissons, il serait tentant d'affirmer d'après nos résultats que la majorité de l'énergie dans les réseaux trophiques de ces écosystèmes transite depuis les complexes macrophytes-épiphytes. Une étude temporelle plus exhaustive, basée sur une année par exemple, permettrait de réduire les zones d'ombre, notamment pour déceler un changement d'alimentation, comme celui qui semble de dessiner au mois d'août, avec une part croissante des sources de matière organique allochtone. Les invertébrés pourraient ainsi se nourrir de matière organique autochtone durant la période de croissance des algues et de matière organique allochtone le reste de l'année (*diet shift*).

Les processus de méthylation au sein des épiphytes sont étudiés depuis récemment (Cleckner *et al.*, 1999; Desrosiers *et al.*, 2006). Cependant, l'importance quantitative des épiphytes dans le transfert de MeHg aux niveaux trophiques supérieurs n'a pas encore bénéficié de recherches spécifiques. Malgré l'absence de relation statistique directe entre les [MeHg] des macroinvertébrés et la proportion d'épiphytes dans leur alimentation, nous avons néanmoins observé une corrélation entre cette dernière variable et le rapport MeHg/THg. Cette observation, combinée à l'anticorrélation entre la proportion d'épiphytes dans l'alimentation des invertébrés et leurs concentrations de THg et de Hg inorganique, nous permet d'avancer que les épiphytes pourraient probablement constituer la voie privilégiée par laquelle le MeHg entrerait dans les réseaux trophiques aquatiques de macroinvertébrés littoraux. Ainsi, les processus de méthylation au sein des épiphytes seraient alors les principaux facteurs à même de moduler la quantité de MeHg disponible pour les niveaux trophiques supérieurs. Cette idée avait été exposée dans un précédent travail de synthèse environnementale (Cremona, 2005). Elle pourrait acquérir une force supplémentaire à la lumière de ces nouveaux résultats. Dans une approche

écosystémique, pour réduire quantitativement le MeHg biodisponible dans les réseaux trophiques, il faudrait alors agir sur les facteurs influençant la méthylation épiphytique (pH, O_2 dissous, etc.). Des mesures *bottom-up* de ce type permettraient de « fermer le robinet » de la méthylation et donc de diminuer en valeur absolue les quantités de MeHg qui se propageraient dans tout le réseau trophique.

Chapitre III – Les macroinvertébrés prédateurs broyeurs sont enrichis d'environ 1.6‰ par rapport à leur proie. Bien que le facteur d'enrichissement du $\delta^{15}N$ de 3.4‰ par niveau trophique a été mis en évidence depuis longtemps (Minagawa et Wada, 1984), la plupart des études subséquentes n'ont fait qu'utiliser ce facteur tel quel, sans questionner sa validité dans des conditions physiologiques et trophiques particulières. Il semble que cette valeur de 3.4‰ soit appropriée dans le cas d'animaux se nourrissant d'organismes riches en protéines (comme les poissons piscivores, McCutchan *et al.* 2003) mais ne conviendrait pas en ce qui concerne les invertébrés. McCutchan *et al.* (2003) ont montré que tous consommateurs confondus (poissons, insectes, etc.) le $\delta^{15}N$ d'un consommateur était plus élevé en moyenne de 2.2‰ par rapport à sa source de matière organique. Notre étude démontre que chez les macroinvertébrés l'enrichissement serait de 1.6‰ de consommateurs primaires aux consommateurs secondaires. Quelles pourraient être les conséquences de cette hétérogénéité des facteurs d'enrichissement du $\delta^{15}N$ dans les réseaux trophiques ? Tout d'abord, les équations de calcul de niveau trophique devraient être adaptées à cette caractéristique, en particulier dans les cas de nombreux niveaux trophiques occupés par des invertébrés. Les équations devraient employer un facteur d'enrichissement de ~1.6‰ pour les niveaux inférieurs et ~3.4‰ pour les niveaux supérieurs. Cela contribuerait à éviter des niveaux discrets trop rapprochés: dans les niveaux inférieurs, par exemple un consommateur avec un $\delta^{15}N$ de 2‰ plus élevé que sa source serait *de facto* d'au moins un niveau trophique supérieur à sa source. Si l'on

employait un facteur d'enrichissement de 3.4‰, le consommateur ne serait que d'à peu près un demi niveau trophique plus élevé que sa source.

En lien avec les chapitres I et II il apparaît que le $\delta^{15}N$ seul est un outil inadéquat pour prédire les concentrations en MeHg des organismes de la zone littorale. En effet, nous n'avons pas trouvé de relation entre signature de $\delta^{15}N$ et concentration en MeHg chez les macroinvertébrés. Les organismes les plus concentrés en MeHg (prédateurs non consommables) sont ceux présentant les valeurs de $\delta^{15}N$ parmi les plus basses, à cause notamment de certaines particularités physiologiques et écologiques. Au contraire, certains détritivores consommant de la matière allochtone enrichie en $\delta^{15}N$ ont des concentrations mercurielles très basses. Dans la zone littorale, à l'inverse de ce que l'on observe dans la zone pélagique, il apparaît donc que la variabilité isotopique la plus élevée se trouve dans la signature de $\delta^{13}C$ (source de matière organique) et non pas dans celle de $\delta^{15}N$ (niveau trophique). Et comme nous l'avons vu, c'est donc la dimension horizontale (source de matière organique) qui va déterminer les concentrations en MeHg pour tout le reste du réseau trophique littoral.

Chapitre IV – La biomasse et l'abondance des macroinvertébrés phytophiles sont plus élevées dans les habitats de plantes submergées que dans les habitats de plantes émergentes. Elles sont aussi plus fortes chez les macroinvertébrés échantillonnés dans des macrophytes à l'architecture complexe que dans les macrophytes à l'architecture plus simple. La diminution du niveau d'eau au lac St Pierre aurait pour conséquence d'abaisser également la biomasse de macroinvertébrés phytophiles. Ces résultats nous amènent à penser que le remplacement des peuplements de macrophytes submergées par des peuplements de macrophytes émergentes s'avérerait néfaste pour les communautés de macroinvertébrés aquatiques et donc par cascade trophique pour les consommateurs comme les poissons qui

dépendent de ces communautés. Le lac St Pierre jouit non seulement d'un attrait économique considérable pour sa région avec environ 500 t[§] de poissons pêchées chaque année par les pêcheries commerciales, mais il est également classé comme « réserve de biosphère » par l'UNESCO. Des modifications de sa profondeur avec les conséquences exposées plus haut pourraient considérablement altérer sa valeur économique et patrimoniale pour les populations humaines.

Pour conclure, nous pouvons dire que dans l'écosystème du lac St Pierre, il existe une double modulation des flux de MeHg. Tout d'abord, en lien avec les recherches menées sur la méthylation, il apparaît que les macroinvertébrés consommateurs primaires peuvent se nourrir de deux sortes de matière organique. Soit de la matière organique autochtone contaminée au MeHg, soit de la matière organique allochtone peu contaminée. En choisissant de se nourrir majoritairement de sources matière organique autochtone (les épiphytes) contaminée en MeHg, les consommateurs primaires modulent une première fois le transfert de MeHg vers le reste du réseau trophique. Ils constituent donc la voie d'entrée principale de bioamplification du MeHg dans le réseau trophique. Les organismes se nourrissant de ces consommateurs primaires vont par la suite soit permettre la continuation de ce transfert vers les poissons (prédateurs consommables) soit la bloquer dans le réseau trophique aquatique (prédateurs non consommables i.e., impasses trophiques), c'est donc une deuxième modulation possible. Le transfert de MeHg dans l'écosystème aquatique du lac St Pierre apparaît donc très original (forme en « X », avec deux sources à la base du réseau et deux voies possibles de transfert) comparé au modèle théorique linéaire de chaîne trophique (forme en « I », avec une source et une voie) de transfert de MeHg.

[§] http://www.mapaq.gouv.qc.ca/Fr/Peche/Profil/pecheaquaculture/pechecommerciale

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