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INTRODUCTION GÉNÉRALE

Il est maintenant largement admis que les changements environnementaux, dont les changements climatiques, affectent les écosystèmes lacustres. Ainsi, des modifications dans les températures et la qualité des eaux sont susceptibles d'influencer non seulement le comportement des organismes aquatiques, mais également le transfert de matière et d'énergie entre les différents niveaux trophiques (Winder & Schindler 2004). Il apparaît essentiel d'identifier et de caractériser précisément la structure et le fonctionnement des réseaux trophiques lacustres.

Le premier modèle conceptuel sur la structure trophique des écosystèmes lacustres a été publié par Lindeman en 1942 (Strayer & Likens 1986). Lindeman a montré que la chaîne alimentaire était formée de différentes étapes, appelées niveaux trophiques : Les producteurs primaires, les phytophages et les carnivores (Figure 1) (Ricklefs & Miller 2005).

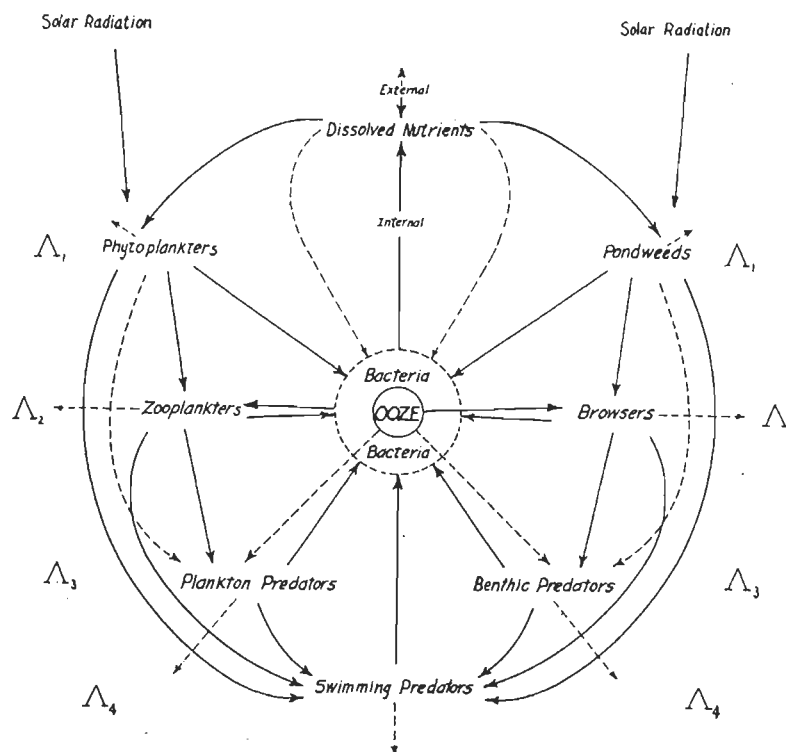


Figure 1. Diagramme de cycles alimentaires d'un lac de région tempérée (D'après Lindeman 1942).

En considérant les différents niveaux trophiques comme des étapes à un processus de transformation d'énergie, il apparaît alors clairement que le cycle de la matière de même que le flux d'énergie qui y est associé permettent de caractériser la structure de l'écosystème (Ricklefs & Miller 2005). Bien que Lindeman ait pris en compte l'habitat benthique en tant que composante à part entière du fonctionnement de l'écosystème lacustre, cet habitat est plutôt perçu comme une source ou un puits d'énergie et de nutriments pélagiques par les écologistes aquatiques (Vadeboncoeur *et al.* 2002). Les études réalisées jusqu'à nos jours en milieu lacustre ont donc majoritairement porté sur les réseaux trophiques pélagiques (Hershey *et al.* 2006), le corollaire étant qu'il y a peu de connaissances sur les habitats benthiques comparativement aux habitats pélagiques (Schindler & Scheuerell 2002). Récemment, Vadeboncoeur *et al.* (2002) ont proposé de réintégrer les processus benthiques dans les modèles de réseaux trophiques lacustres pour parvenir à une meilleure compréhension du fonctionnement des écosystèmes lacustres.

L'étude d'un réseau benthique passe notamment par l'étude des flux de matière organique particulière au travers de ses composantes. Cette matière organique particulière peut provenir de diverses sources, qu'elles soient autochtones ou allochtones (Wetzel 2001). Certaines études ont tenté d'évaluer l'importance relative des sources de carbone dans les réseaux trophiques aquatiques (Jones *et al.* 1998; Grey *et al.* 2001). Or, la multiplicité des sources de matière organique complique fortement l'analyse du fonctionnement des réseaux trophiques benthiques. Bien que les écologistes aquatiques soient conscients du rôle crucial de la composante benthique dans les systèmes lacustres, ils ont principalement concentré leurs efforts sur l'étude des réseaux

trophiques pélagiques. Ainsi, les habitats benthiques restent à ce jour peu connus comparativement aux habitats pélagiques.

Macroinvertébrés benthiques

La communauté benthique se caractérise notamment par la présence d'organismes hétérotrophes qui vivent sur le fond ou encore attachés à celui-ci (Dodson 2005). Elle est extrêmement diversifiée, pratiquement tous les phyla, allant des protozoaires aux vertébrés, y sont représentés (Wetzel 2001). Au sein de la communauté benthique, on retrouve, entre autres, des macroinvertébrés, tels des représentants des taxons Ephemeroptera, Odonata, Oligochaeta, Chironomidae, Tricoptera, Amphipoda, Coleoptera, Diptera, Hemiptera et Plecoptera, la diversité spécifique étant plus importante en milieu littoral comparativement au milieu profond (Prejs 1977). Les macroinvertébrés benthiques sont abondants dans les lacs et forment un lien entre les producteurs primaires et les niveaux trophiques supérieurs (Giani & Laville 1995) comme les poissons (Weatherhead & James 2001). En fait, selon Herwig *et al.* (2007), le transfert d'énergie aux poissons serait principalement réalisé via les macroinvertébrés benthiques. Dans certains lacs, la production benthique semble être d'importance primordiale au niveau du support de la population de poissons (Vander Zanden *et al.* 2006). Les organismes benthiques contribueraient ainsi de façon substantielle à la production totale du lac (Vadeboncoeur *et al.* 2002).

Malgré les connaissances acquises au cours des dernières années, le rôle fonctionnel (i.e., partage des ressources et transfert de la matière organique) de la faune benthique lacustre est encore peu connu. L'importance soupçonnée des macroinvertébrés benthiques pour les niveaux trophiques supérieurs souligne le besoin d'explorer davantage leur rôle fonctionnel dans les lacs.

Sources de matière organique

La matière organique particulaire (MOP), issue de la production primaire dans la colonne d'eau ou de la bande riveraine (i.e. subsidence allochtone), représente un apport de matière non négligeable pour l'habitat benthique (Strayer & Likens 1986; Olafsson *et al.* 1999). Cette matière organique, très hétérogène, peut se trouver sous forme vivante (microhétérotrophes, microalgues benthiques) ou sous forme morte (débris d'origine autochtone et allochtone à différents stades de dégradation). Elle peut par ailleurs être remise en suspension, minéralisée, incorporée au réseau trophique ou bien enfouie dans le sédiment.

La matière organique autochtone est synthétisée au sein du lac (Wetzel 2001). Les sources de matière organique autochtones utilisées par les macroinvertébrés benthiques sont les algues (phytoplancton, épilithon, périphyton) et les plantes vasculaires, tels que les macrophytes (Talbot & Ward 1987; Giani & Laville 1995; Wetzel 2001; Solomon *et al.* 2007). De plus, des tissus d'organismes vivants seraient consommés par des carnivores (Giani & Laville 1995). Des travaux récents, mettant en œuvre la technique de traçage isotopique (i.e., $\delta^{13}\text{C}$ et $\delta^{15}\text{N}$), ont montré que les subsides, tels que la matière organique provenant d'environnements terrestres, pouvaient alimenter les réseaux trophiques des lacs oligotrophes et atteindre, voire même excéder, les niveaux de production primaire autochtone (Caraco & Cole 2004; Carpenter *et al.* 2005). Les impacts des apports de subsides allochtones sur les réseaux trophiques lacustres dépendraient par ailleurs de leur forme (dissoute ou particulaire), de la voie d'entrée dans le réseau trophique et des types de consommateurs présents dans le système (Cole *et al.* 2006). En effet, les entrées de matière organique en provenance des forêts riveraines représentent une importante source d'énergie (Nakano & Murakami 2001; Wetzel 2001), puisque la matière

organique allochtone viendrait augmenter le nombre de sources pouvant être utilisées par les invertébrés (Riera *et al.* 1999) : La majeure partie de la matière organique allochtone qui se retrouve dans les écosystèmes aquatiques provient principalement des plantes terrestres (Wetzel 2001). Une modification des apports de végétation terrestre au milieu aquatique pourrait avoir comme effet potentiel d'affecter la quantité de macroinvertébrés disponibles pour les espèces de poissons résidentes (France 1995a). En effet, des résultats obtenus par France (1995a) démontrent que la communauté de macroinvertébrés littoraux est probablement plus influencée, de même que plus dépendante, de la quantité de végétation terrestre plutôt qu'aquatique. Bref, l'apport en subsides de matière organique allochtone peut être particulièrement important pour les lacs des régions tempérées, où les deux principaux déterminants de la productivité primaire, soient la température et la lumière, changent drastiquement suivant les saisons (Nakano & Murakami 2001). De plus, il semble que les lacs des régions nordiques tempérées reçoivent annuellement un apport important de carbone par le biais de contributions allochthones (France 1995a), particulièrement dans les systèmes oligotrophes où l'activité autochtone est moins importante étant donné la moins grande quantité de nutriments présents (Cole *et al.* 2006).

Couplages en milieu lacustre

Il est aujourd'hui établi qu'une description optimale du fonctionnement du réseau trophique d'un lac implique de prendre en compte le couplage entre les compartiments benthique et pélagique (Schindler & Scheuerell 2002), de même que le couplage entre les systèmes aquatiques et terrestres puisque la zone littorale est l'interface entre le lac et le milieu terrestre (James *et al.* 1998).

Couplage benthique-pélagique

Les lacs sont formés d'une mosaïque d'habitats (profond, pélagique, riparien et benthique), ce qui en fait des systèmes complexes (Figure 2) (Schindler & Sheuerell 2002). Le couplage entre habitats peut se produire de façon passive, par le biais de processus de transport, ou de façon active par le transfert d'organismes d'un habitat à l'autre (Mehner *et al.* 2005). Or, les causes et les conséquences du couplage écologique entre les habitats pélagique, benthique et riverain des lacs sont peu comprises (Schindler & Scheuerell 2002).

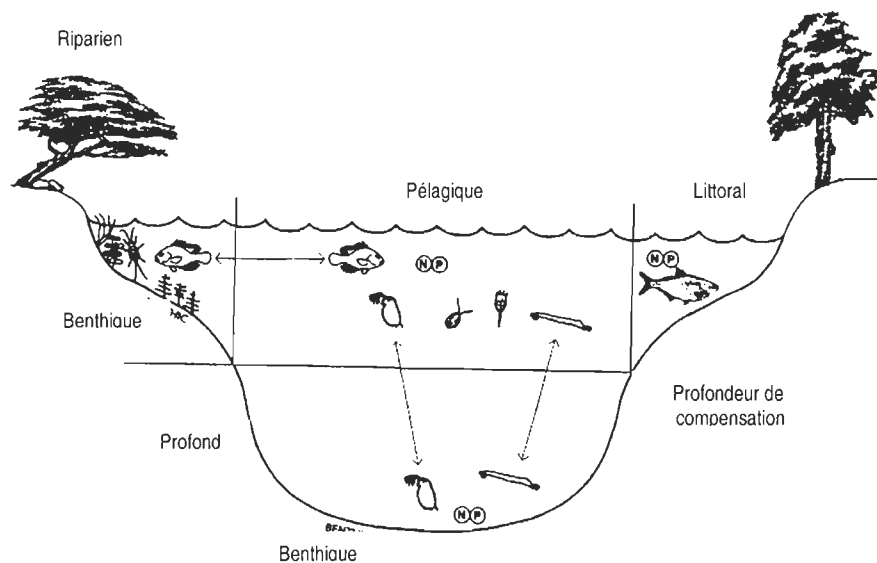


Figure 2. Schéma d'un lac comme étant un système qui intègre plusieurs habitats. Habitats benthiques : Associés au substrat de fond des lacs. Habitats pélagiques : Composantes d'eau libre des lacs. Zones littorales : Habitats peu profonds où la profondeur est inférieure à la profondeur de compensation. La profondeur de compensation est définie comme la profondeur à laquelle il y a suffisamment de lumière pour que la photosynthèse équilibre la respiration. Zones profondes : Habitats localisés profondément dans la colonne d'eau, sous la profondeur de compensation. Habitats ripariens (ou riverains) : Ils sont localisés à la limite des milieux aquatique et terrestre. Les habitats ripariens sont généralement considérés comme faisant partie du système terrestre, mais ils sont intimement liés aux habitats aquatiques par le biais du mouvement des organismes (D'après Schindler & Sheuerell 2002).

L'habitat benthique participe au bon fonctionnement de l'écosystème lacustre, ce qui signifie qu'il fait parti intégrante de celui-ci, suivant le paradigme qui stipule que la production secondaire benthique est fortement liée à la production primaire pélagique (Hershey *et al.* 2006). La production secondaire benthique aurait un rôle central au niveau du support des niveaux trophiques supérieurs (Vander Zanden & Vadeboncoeur 2002). En effet, Vizzini & Mazzola (2003) ont démontré que, bien que les organismes pélagiques (poissons) se nourrissent principalement de phytoplancton et les organismes benthiques de sources provenant du benthos, il y aurait tout de même un échange entre les deux habitats puisque des organismes pélagiques (poissons) s'alimentent d'organismes benthiques. Ainsi, l'existence d'un couplage benthique-pélagique est bien démontrée par l'alimentation des poissons : Bien qu'il s'agit d'organismes pélagiques, ceux-ci utiliseraient les ressources benthiques de façon importante (Hecky & Hesslein 1995; Schindler & Scheuerell 2002; Vadeboncoeur *et al.* 2002; Vander Zanden & Vadeboncoeur 2002; Vander Zanden *et al.* 2005; Vander Zanden *et al.* 2006).

Couplage aquatique-terrestre

L'environnement terrestre peut contribuer à un important apport de matière organique (dissoute et particulaire) aux habitats benthique et pélagique (Schindler & Scheuerell 2002). Le flux d'énergie et de nutriments entre les limites des écosystèmes peut avoir un impact majeur sur la dynamique des niveaux trophiques (Huxel *et al.* 2002). En fait, les ressources allochtones (i.e sources provenant de l'extérieur de l'environnement aquatique) influencent la dynamique des populations, les interactions des communautés et les multiples processus de l'écosystème receveur (Polis *et al.* 1997). Ainsi, il semble que l'apport de matière organique allochtone peut subvenir au métabolisme de l'écosystème tout comme supporter la production des

consommateurs (Vanni & Headworth 2004). Selon Carpenter *et al.* (2005), les différents consommateurs de types animal et microbien consommeraient fréquemment des sources de nourriture qui proviennent d'habitats extérieurs. La forme la plus importante de subsidence allochtone qui devient disponible pour les communautés hétérotrophes d'un écosystème est la matière organique détritique, tant sous sa forme particulaire que dissoute (Polis *et al.* 1997) : Elle peut être utilisée directement ou encore être transformée par des microorganismes (Cole *et al.* 2006). Finalement, le carbone organique d'origine terrestre contribue à modifier les paramètres physiques et chimiques du lac, tels que la lumière, le pH, la profondeur de la thermocline, le stress causé par les rayons UV puis la quantité de nutriments (Williamson *et al.* 1999).

Hétérogénéité au sein des systèmes lacustres

Les systèmes d'eau douce sont hétérogènes (Shumway *et al.* 2007) et cela s'explique en partie par le fait que les zones littorales des lacs, dont le degré d'influence sur l'ensemble de l'écosystème varie suivant la taille d'un lac, sont fortement hétérogènes (Downing & Rath 1988; Hecky & Hesslein 1995; Harrison & Hildrew 2001; Stoffels *et al.* 2003; Stoffels *et al.* 2005). Par ailleurs, un lac n'étant pas un système isolé (Johnson *et al.* 2004), il peut recevoir des apports variables de matériel organique qui contribuent à modifier la nature de l'habitat et dans certains cas son homogénéité.

La distribution spatiale de la faune benthique est extrêmement hétérogène étant donné les exigences variables des organismes en termes d'alimentation, de croissance et de reproduction. La distribution spatiale des macroinvertébrés benthiques serait donc fortement contrôlée par les changements au niveau du substrat et ceux des eaux environnantes, soient des facteurs à l'échelle locale (Johnson *et al.* 2004), et ce suivant une base saisonnière (Wetzel 2001).

Approche de l'analyse en isotopes stables (AIS)

L'analyse des contenus stomacaux de même que les mesures de taux d'ingestion par utilisation d'isotopes radioactifs sont deux méthodes couramment utilisées pour caractériser les sources de nourriture utilisées par les organismes et donc pour identifier les transferts de la matière organique particulière au sein des réseaux trophiques. Or, une des limitations de ces méthodes tient à la relative incertitude de faire la part entre ce qui a été simplement ingéré et ce qui a été effectivement assimilé par l'animal. L'une des façons d'identifier le type de nourriture assimilée consiste à analyser la composition en isotopes stables naturels des différentes composantes étudiées (James *et al.* 2000). En effet, les isotopes stables témoignent de l'assimilation intégrée sur une certaine période de temps, celle-ci correspondant au taux de renouvellement du tissu d'un organisme (Kling *et al.* 1992). Cette approche est basée sur l'existence d'une relation étroite entre les compositions isotopiques du consommateur et celles des sources qui composent sa diète (Eggers & Jones 2000). Les rapports d'isotopes stables du carbone ($\delta^{13}\text{C}$) et de l'azote ($\delta^{15}\text{N}$) fournissent ainsi des informations sur l'origine et la transformation de la matière (Eggers & Jones 2000). Alors que le ratio $^{13}\text{C}/^{12}\text{C}$ donne une idée du type de nourriture assimilé par un organisme, le ratio $^{15}\text{N}/^{14}\text{N}$ permet l'évaluation du niveau trophique d'un organisme (Peterson & Fry 1987). C'est ainsi que cette technique permet, d'une part, d'évaluer les sources et les flux de matière organique dans les écosystèmes et, d'autre part, d'identifier la composition du régime alimentaire d'un consommateur donné. En comparant les variations spatiales et temporelles des signatures isotopiques des sources de matière organique avec celles des macroinvertébrés benthiques, il est possible d'identifier les sources de nourriture utilisées par les organismes (James *et al.* 2000). Puisque les lacs sont des écosystèmes complexes, les mesures d'abondances naturelles d'isotopes stables ont grandement contribué à la

compréhension des réseaux trophiques et des flux d'énergie dans ces systèmes (Schindler & Scheuerell 2002). L'analyse d'isotopes stables (AIS) est devenue au cours des 25 dernières années une technique privilégiée pour examiner les relations trophiques et élucider les flux d'énergie au sein des écosystèmes (Sarakinos *et al.* 2002). L'utilisation d'isotopes stables a permis de mieux percevoir le rôle des productions de matière organique allochtone (production terrestre) et de la production primaire autochtone (production benthique) dans les réseaux trophiques lacustres (Hershey *et al.* 2006).

L'analyse en isotopes stables a été utilisée à quelques reprises dans le cadre d'études portant sur des macroinvertébrés benthiques afin d'évaluer les variations spatiales des signatures isotopiques en carbone (^{13}C) et en azote (^{15}N). De la variation spatiale a été observée au niveau des signatures isotopiques de macroinvertébrés benthiques présents dans différents habitats (i.e littoral, pélagique et/ou profond), pour les isotopes stables de carbone et/ou d'azote (France 1995b, Vander Zanden & Rasmussen 1999, James *et al.* 2000, Beaudoin *et al.* 2001, Hershey *et al.* 2006). D'autres études ont observé de la variation temporelle au niveau des signatures isotopiques, mais seulement pour certains types de macroinvertébrés benthiques, tels les oligochètes (Yoshioka *et al.* 1994), les larves de chironomides (Grey *et al.* 2004), ou encore les différents stades de développement d'insectes lacustres (Solomon *et al.* 2007).

Dans une étude récente, Syväranta *et al.* (2006) se sont intéressés aux variations spatio-temporelles des signatures isotopiques en carbone (^{13}C) et en azote (^{15}N) de macroinvertébrés benthiques de même que de certaines autres composantes, telles que la matière organique particulaire (MOP), le zooplancton, le périphyton, les macrophytes et les poissons en milieu littoral. Cependant, tous les sites littoraux étudiés ne possèdent pas des caractéristiques similaires,

certaines subissant une pression anthropique plus importante que d'autres, ce qui fait que la variabilité observée au sein du lac étudié pouvait être attendue. Dans le cadre de la présente étude, le lac Des Baies, situé au sein d'une réserve faunique, est un lac qui subit peu de pression anthropique.

Projet à l'étude

Cette étude, réalisée suivant une approche faisant intervenir des traceurs d'origine de la matière organique que sont les rapports d'isotopes stables naturels du carbone (^{13}C) et de l'azote (^{15}N), vise donc à améliorer notre compréhension des transferts de matière et d'énergie au sein des réseaux trophiques benthiques littoraux et profonds lacustres, en considérant la dimension temporelle, puisque les habitats benthiques restent à ce jour peu connus comparativement aux habitats pélagiques.

Le lac Des Baies ($48^{\circ}10'$ N, $68^{\circ}40'$ W) est un lac oligotrophe situé en région Appalachienne au sein de la réserve Duchénier (Est du Québec, Canada). Ce lac a une aire de $6,14 \text{ km}^2$, une profondeur moyenne de 20 m et une profondeur maximale de 48 m. Un premier objectif à l'étude est de mesurer les différentes signatures isotopiques en $\delta^{13}\text{C}$ et $\delta^{15}\text{N}$ des macroinvertébrés benthiques et de sources de nourriture potentielles pour ces organismes. Suivant la théorie de l'analyse en isotopes stables, il est possible de croire qu'une similarité au niveau des signatures isotopiques pourra être observée entre un macroinvertébré benthique et sa principale source de nourriture. Ensuite, il s'agit de documenter la variabilité au niveau des signatures isotopiques entre les habitats littoral et profond (découplage) et entre les sites. Selon plusieurs auteurs (France 1995*b*; Vander Zanden & Rasmussen 1999; James *et al.* 2000; Post *et al.* 2000; Beaudoin *et al.* 2001; Syväranta *et al.* 2006), des différences au niveau des signatures

isotopiques devraient être observées entre les habitats littoral et profond. De plus, comme le système lacustre est un système hétérogène (Shumway *et al.* 2007), des variations entre les signatures isotopiques rencontrées entre les sites devraient être notées. Finalement, il serait intéressant d'évaluer les changements de flux de matière organique au cours du temps, en utilisant les macroinvertébrés benthiques. Puisque le lac à l'étude est un lac oligotrophe situé en région tempérée, le régime de lumière varie probablement au cours du temps et donc la disponibilité de sources de nourriture autochtones pourrait varier : Un changement dans la source de nourriture principale des macroinvertébrés benthiques pourrait être observé.

SPATIAL AND TEMPORAL VARIABILITY IN ISOTOPIC SIGNATURES OF BENTHIC MACROINVERTEBRATES OF A BOREAL LAKE: INFERENCES FROM CARBON ($\delta^{13}\text{C}$) AND NITROGEN ($\delta^{15}\text{N}$) STABLE ISOTOPES

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Summary

1. The spatio-temporal variability in the natural abundance of stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) was determined for components of the benthic food web in the oligotrophic boreal Lake des Baies. Measurements were made on benthic macroinvertebrates, terrestrial detritus (e.g., leaf litter), epilithon, pollen, particulate organic matter (POM), sediments, and the cladoceran *Daphnia* sp. The sampling occurred five times between May and September 2006.
2. Spatial variation was studied at two scales, within and between sites. A significant decoupling (i.e. variation within sites) between littoral and profundal habitats was observed in the benthic macroinvertebrates, for each sampling period and for both isotopes (Conover approach, $p < 0.001$). A significant decoupling was also observed in their food sources (Conover approach, $p < 0.001$), but this did not apply to each sampling period for the $\delta^{15}\text{N}$ values. Looking at a larger scale, variability existed between sampling sites (Conover approach, $p < 0.001$). For food source samples, no significant differences were found between sites, either in $\delta^{13}\text{C}$ (Conover approach, $p > 0.05$), or $\delta^{15}\text{N}$ (Conover approach, $p > 0.05$) values.
3. Temporal changes in food source contribution to the diet of benthic macroinvertebrates were estimated using linear mixing models. Terrestrial detritus appeared to exert a major influence on the diet of the littoral benthic macroinvertebrate community, with contributions of 13% in May to 90% in August. In littoral habitats, also played a significant role in the supply of food to benthic macroinvertebrates, with results of mixing model showing contributions ranging between 6% (July) and 26% (May), depending on the sampling period. For profundal habitats, no similar conclusions could be drawn because of the limitations in potential food sources sampled.

4. Results obtained from this study confirm the existence of marked spatial and temporal variability in isotopic signatures of benthic macroinvertebrates in lakes. The importance of terrestrial detritus for the littoral benthic food web highlights the tight nature of the coupling between lakes and their surrounding terrestrial habitats. Therefore, studies on lakes with low lakeshore development contribute valuable knowledge of the coupling existing between habitats under natural conditions.

Key words: Lake ecosystem, stable isotopes, mixing models, benthic macroinvertebrates, allochthonous subsidies

Introduction

Understanding the structure and functioning of a food web requires: 1) to know its biological diversity; 2) to identify and measure trophic interactions; and 3) to define trophic levels associated with the different biological components of the ecosystem. Use of naturally occurring stable isotopes contributes to resolve the two last points. While the $^{13}\text{C}/^{12}\text{C}$ ratio gives an idea of the type of food source assimilated by an organism, the $^{15}\text{N}/^{14}\text{N}$ ratio allows an evaluation of the trophic level of the organism (Peterson & Fry 1987). Stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are frequently used in aquatic ecological research (Grey 2006) and have enhanced our understanding of food webs and energy flows in lakes (Schindler & Scheuerell 2002). Although aquatic ecologists are aware of the crucial role of the benthic biotic components in these systems, because of their substantial contribution to whole-lake productivity (Vadeboncoeur *et al.* 2002), they have mainly concentrated their efforts on the study of pelagic food webs (Hershey *et al.* 2006). Moreover, studying benthic ecosystems involves dealing with

many problems at the levels of sampling, identification and sorting of benthic organisms (Strayer & Likens 1986; Giani & Laville 1995). Therefore, little is known about benthic habitats, relative to their pelagic counterparts (Schindler & Scheuerell 2002).

Benthic macroinvertebrates form an important heterotrophic component of lake ecosystems and constitute a link between primary producers and upper trophic levels (Giani & Laville 1995), such as fishes (Weatherhead & James 2001). For instance, there is both direct (50%) and indirect (i.e., feeding on zoobenthos-supported fishes) (15%) consumption of zoobenthos by certain fishes (Vander Zanden & Vadeboncoeur 2002). Even species of fishes that are piscivorous specialists tend to consume a significant amount of benthic macroinvertebrates (Beaudoin *et al.* 2001; Schindler & Scheuerell 2002). Therefore, benthic secondary production plays a major role in sustaining higher trophic levels in lakes (Vander Zanden & Vadeboncoeur 2002). The importance of benthic macroinvertebrates for upper trophic levels highlights the need to further explore their functional role (i.e., resource partitioning and transfer of organic matter) in lakes.

Autochthonous organic matter sources in lakes, such as epilithon and phytoplankton, are known to have different carbon isotopic signatures. Indeed, the fractionation of ^{13}C is less important for benthic algae (France 1995*b, c*; Hecky & Hesslein 1995), which results in depleted $\delta^{13}\text{C}$ values for phytoplankton, compared to periphyton. In fact, reduced fractionation would be induced by the exposition to different levels of turbulence (France 1995*b*). Allochthonous organic matter sources, such as leaf litter, have different carbon and nitrogen isotopic signatures (Beaudoin *et al.* 2001). Moreover, a variety of microbial processes affect the decomposition of organic matter in aquatic systems. Hence, changes in the carbon and nitrogen isotope signals are

expected (Lehmann *et al.* 2002). It is possible to have an idea of the variability of organic source utilization by these organisms, since isotopic signatures contribute to identify the main food sources assimilated (James *et al.* 2000), by looking at spatial and temporal variations in isotopic signatures of the organic food sources and of the benthic macroinvertebrates themselves.

Spatial variations in isotopic signatures of organisms from different habitats have been observed in past studies. France (1995b) reported a small overlap in stable isotope carbon and nitrogen signatures for littoral and pelagic consumers, which is a sign of decoupling between habitats. By sampling 14 oligotrophic Canadian Shield lakes, Vander Zanden & Rasmussen (1999) showed important variations in stable carbon and nitrogen isotope ratios of primary consumers among the different types of habitats, i.e. littoral, pelagic and profundal. Indeed, for $\delta^{15}\text{N}$ the lowest values were found in the littoral habitat, while the highest values were found in the profundal habitat. $\delta^{13}\text{C}$ values decreased along the same trophic gradient, littoral-pelagic-profundal. In other studies, it was observed that $\delta^{13}\text{C}$ values of certain benthic macroinvertebrates exhibit a significant variation among different littoral sites (James *et al.* 2000) and are less depleted in littoral, compared to pelagic (Beaudoin *et al.* 2001) or profundal habitats (Syväranta *et al.* 2006; Hershey *et al.* 2006). Because of the heterogeneous nature of littoral habitats (Harrison & Hildrew 2001; Stoffels *et al.* 2003) and the heterogeneity in lake sediments (Downing & Rath 1988), data on benthic organisms from various habitats might show highly variable stable isotope signatures, since communities appear to be strongly influenced by environmental heterogeneity. Indeed, these spatial differences can be explained by different environmental conditions within littoral habitats as well as between littoral and profundal habitats, such as water turbulence, which influences ^{13}C values (France 1995c), as well as denitrification and nitrification processes, which influence ^{15}N values (Rysgaard *et al.* 1994).

These environmental conditions imply changes in the isotopic signatures of primary producers, which are then transmitted along the trophic food web. The use of various types of food sources, as well as their different origin, which can be allochthonous or autochthonous, can also have an influence on the isotopic signatures of the local benthic macroinvertebrates.

Besides spatial variations, temporal fluctuations in isotopic signatures of biotic components of lakes have also been observed in past studies. So far, however, most of the studies on this aspect have concerned mainly phytoplankton and zooplankton communities (Yoshioka *et al.* 1994). Some studies have looked at temporal variability in the isotopic signatures of selected benthic macroinvertebrates. For instance, Yoshioka *et al.* (1994) worked on a single eutrophic lake and found that temporal variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were relatively stable for oligochaetes and two species of midges. Conversely, Grey *et al.* (2004) reported pronounced seasonal changes in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of chironomid larvae in two eutrophic lakes, which may be largely explained by variations in emergence patterns between species and between lakes. Finally, Solomon *et al.* (2007) observed that variation in lake insect $\delta^{13}\text{C}$ time series relies on varying relative abundance of the different species as well as their development stages. Variation in diet preferences between species was also pointed out as a possible factor of the variation observed.

So far, only one study has assessed both spatial and temporal heterogeneity of isotope ratios of carbon and nitrogen. By sampling seven littoral sites in the urban lake Jyväskylä, Syväranta *et al.* (2006) measured both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in different compartments (particulate organic matter (POM), zooplankton, periphyton, macrophytes, macroinvertebrates and fishes) and reported spatial variation in isotopic signatures in communities. However, these

sites did not have all the same characteristics, with some exhibiting higher anthropic pressure than others. Within-lake variability was then expected.

Our study aimed at exploring the spatial and temporal variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of benthic macroinvertebrates in a lake with a low lakeshore development. This was achieved by sampling monthly benthic macroinvertebrates from littoral and profundal habitats, as well as their potential food sources at three sites. Specific objectives of this study were to: (1) estimate the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of benthic macroinvertebrates and their possible food sources; (2) investigate the variability in carbon and nitrogen stable isotope signatures within sites, between littoral and profundal habitats (decoupling), and between sites; and (3) evaluate the changes in organic matter transfer with time in benthic food webs.

Methods

Study area

This study was conducted in Spring-Summer 2006 in the littoral and profundal habitats of the Appalachian Lake des Baies (48°10' N, 68°40' W), located in the Duchénier Reserve in Eastern Quebec, Canada (Fig. 3). This oligotrophic lake covers an area of 6.14 km², with a mean depth of 20 m and a maximum depth of 48 m. It is surrounded mainly by coniferous tree species, such as Balsam Fir (*Abies balsamea*), White Cedar (*Thuja occidentalis*), Eastern White Pine (*Pinus strobes*), White Spruce (*Picea glauca*), and some hardwood species, such as Sugar Maple (*Acer saccharum*), Yellow Birch (*Betula lutea*), and White Birch (*Betula papyrifera*). It is thermally stratified in summer.

Sampling

Three sites were visited once a month, from May to September 2006. Sites 1 and 3 were positioned on the eastern side of the lake, while site 2 was on its western shores (Fig. 3). Three stations were occupied at each site, and at each station both littoral (< 1 m) and profundal (depth of c.a. 13 m) habitats were sampled. The nature of the substrate was the same for littoral habitats of sites 1 and 3, where small rocks and sand were predominant, while the littoral habitat of site 2 exhibited mainly large flat rocks. The nature of the substrate of profundal habitats at all sites was about the same. Dissolved O₂, pH, conductivity, and water temperature were measured *in situ* at each sampling site, in the profundal habitat, using a YSI 556 MPS probe. At the same time, water transparency was estimated using a Secchi disc. Water samples were collected at each sampling station (prefiltered through 300 μm to remove large zooplankton) for the determination of dissolved organic carbon (DOC), chlorophyll *a* (chl *a*) concentrations and isotopic analyses of POM. Terrestrial detritus (e.g., leaf litter), epilithon, and sediments were sampled monthly at littoral and/or profundal stations. Terrestrial detritus as well as rocks with epilithon were sampled by hand in the littoral habitat, while sediments from the superficial layers of the profundal habitat were collected using an Ekman grab. Pollen was also collected by hand in May. Zooplankton samples were obtained from June to September by horizontal trawls in the epilimnion, using a Wisconsin net with mesh size of 333 μm (Anderson 1990). The primary consumer cladoceran *Daphnia* sp. was used as baseline organism, in order to obtain information on isotopic signatures of phytoplankton food sources (Del Giorgio & France 1996; Perga 2004), even though in some cases it seems that material other than phytoplankton can contribute significantly to the stable isotope values of zooplankton (Jones *et al.* 1998; Perga 2004). Indeed, using the δ¹³C signatures of a primary consumer, such as *Daphnia* sp., has been recognized to be an alternative approach that provides reliable estimates of algal signatures, since isolating algal material from POM

appears to be a difficult method (Marty and Planas 2008). Benthic macroinvertebrates were collected on each sampling occasion both in littoral and profundal habitats. At littoral stations, benthic macroinvertebrates were sampled using a Turtox D-net with mesh size of 500 μm , while an Ekman grab was used to collect organisms from the profundal habitats. All samples were placed in cooler boxes and transported to the laboratory for processing.

Sample preparation and analysis

Water subsamples were filtered through precombusted (500°C, 5 h) Whatman GF/F filters for the determination of DOC. The filtrate was placed in glass vials with teflon-lined caps and acidified with 25% v/v H_3PO_4 (10 $\mu\text{L mL}^{-1}$). Determination of DOC levels was made with a TOC-5000A analyzer (Shimadzu, Kyoto, Japan), following the protocol of Whitehead *et al.* (2000). DOC reference standards were produced by the Hansell's Certified Reference Materials (CRM) program. Water samples for the determination of phytoplankton biomass were filtered (200 ml or more) onto Whatman GF/F filters. Chl *a* and phaeopigment concentrations were calculated using equations of Holm-Hansen *et al.* (1965), after measuring fluorescence before and after acidification (HCl 1M) in a 10-AU Turner Designs fluorometer. Prior to this, samples were extracted for 24 h in 90% acetone, at 5°C in the dark without grinding. For the determination of isotopic signatures of POM, subsamples of water were filtered through precombusted (500°C, 5 h) Whatman GF/F filters and stored frozen at -20°C until analysis.

Benthic macroinvertebrates and zooplankton were left overnight in clean water to allow for gut evacuation. Samples were sorted the following day and taxa were identified at the family level, when possible, using McCafferty (1998) and Merrit & Cummins (1998). Epilithon was scraped off rocks and all non-epilithon particles, such as small rocks or sediment and detritus, were carefully removed from samples under a microscope. All samples, including terrestrial

detritus and sediments, were kept frozen at -20°C in scintillation vials until analysis. Benthic macroinvertebrates, terrestrial detritus, sediments, epilithon, *Daphnia* sp., and POM filters were acidified using 10% HCl (Hamilton *et al.* 2005) to remove carbonates and then dried at 60°C for 24 h. Mortar and pestle were thereafter used to grind samples of benthic macroinvertebrates, sediments, epilithon, and *Daphnia* sp. into a fine powder, while an electric grinder was used for the terrestrial detritus. Powder and filter samples were then encapsulated in pressed tin capsules (5 x 9 mm) and tin foil cups (Costech Analytical Technology), respectively.

Analyses of stable isotope ratios of C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) for benthic macroinvertebrates, terrestrial detritus, sediment, epilithon, pollen, *Daphnia* sp. and POM were carried out at the Institut des Sciences de la Mer (ISMER, Rimouski, Quebec, Canada) using a COSTECH ECS 4010 Elemental Analyser coupled with a DeltaPlus XP Isotope Ratio Mass Spectrometer (IRMS, Thermo Electron Co). System control as well as acquisition and treatment of the data were carried out using the Isodat 2 software. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) according to the equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratios.

Standards used for the measurement of ^{13}C and ^{15}N were anhydrous caffeine (Sigma Chemical Co., St-Louis, USA), Mueller Hinton Broth (Becton Dickinson, USA) and *Nannochloropsis*. These homemade standards were calibrated using standards from the National

Institute of Standards and Technology (NIST, USA). Replicate analyses of standards gave analytical errors (SD) of $\pm 0.30 \text{ ‰}$ for C and $\pm 0.18 \text{ ‰}$ for N.

Statistical analyses and linear mixing models

Using the benthic macroinvertebrate isotopic signatures, a non-parametric general rank approach (Conover approach) was used to test for possible decoupling between littoral and profundal habitats at the three sites (1, 2 and 3), as well as between the five sampling periods (May, June, July, August and September). A multiple comparison test of Dunn was applied, in order to assess differences in decoupling between sampling periods. The same approach was used to test for potential differences between the signatures of the different food sources of the various benthic macroinvertebrate taxa. Pearson rank correlations were also performed between benthic macroinvertebrate and food sources, for both stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), in order to test for potential relations between isotopic signatures of food sources and benthic macroinvertebrates. All statistical analyses were performed with SYSTAT Version 11. Finally, Philipps' (2001) linear mixing models of both carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes were used for each taxon of benthic macroinvertebrates and their potential food sources, for each site at each sampling period. These allowed the conversion of isotope ratios to diet composition, since the isotopic signature of a consumer reflects the signature of its food sources in proportion to dietary contribution. These models were then used to establish the proportional contribution of different food sources to the diet of each taxon. In this study, IsoError 1.4 software was used in order to assess the relative contribution of the different food sources to the diet of benthic macroinvertebrates at each site and during each sampling month.

Results

Concerning environmental parameters, temperature was similar between the three sites for all sampling periods, with an increase in values at the three depths observed in June 2006. Dissolved O₂ and pH values were similar for the three depths, from May to September 2006, while an increase in chl *a* and a decrease in DOC were noted with increasing depth (Table 1).

In total, 263 benthic macroinvertebrate samples were analysed in this study: 225 littoral and 38 profundal. Moreover, 123 samples of food sources were also processed. In May, six taxa were common to the three sites: Ephemeroptera Ephemeraeidae, Heptageniidae and Ephemerellidae, Amphipoda, Oligochaeta, and Plecoptera Perlidae. The occurrence of six common taxa was also observed in June: Ephemeroptera Heptageniidae, Amphipoda, Oligochaeta, Plecoptera Perlidae, Coleoptera Elmidae, and profundal Amphipoda. Common taxa between all sites became less frequent in July (4 common taxa), August (2 common taxa), and September (4 common taxa). Common taxa in July were Ephemeroptera Heptageniidae, Oligochaeta, Plecoptera Perlidae, and Coleoptera Elmidae. Common taxa in August were Ephemeroptera Heptageniidae and Plecoptera Perlidae. Common taxa in September were Ephemeroptera Ephemeraeidae and Heptageniidae, Oligochaeta, and Plecoptera Perlidae. In order to evaluate the decoupling between littoral and profundal habitats, Plecoptera Perlidae and Odonata Libellulidae, some littoral organisms, were removed from the data set, since these benthic macroinvertebrates are known as predators, so their isotopic signatures are probably different from the one of the littoral-pelagic benthic macroinvertebrates.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of benthic macroinvertebrates and of their potential food sources changed at Lake des Baies from May to September 2006 (Figs 4, 5 & 6; Tables 2 & 3). For each

site, changes were observed in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ combination of benthic macroinvertebrates and of food sources available from May to September 2006. Some variations were also observed between the three sites of a given sampling period. Looking at $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values obtained for food sources (Tables 2 & 3), overlap between isotopic signatures is apparent. The intervals for values of samples varied for carbon and nitrogen stable isotopes, respectively: littoral benthic macroinvertebrates (-22.53 ‰ to -40.70 ‰ $\delta^{13}\text{C}$ and -1.51 ‰ to 6.38 ‰ $\delta^{15}\text{N}$), profundal benthic macroinvertebrates (-25.56 ‰ to -40.05 ‰ $\delta^{13}\text{C}$ and 1.08 ‰ to 8.20 ‰ $\delta^{15}\text{N}$), epilithon (-18.13 ‰ to -23.65 ‰ $\delta^{13}\text{C}$ and -3.56 ‰ to 2.21 ‰ $\delta^{15}\text{N}$), pollen (-28.18 ‰ to -28.72 ‰ $\delta^{13}\text{C}$ and -6.18 ‰ to -4.53 ‰ $\delta^{15}\text{N}$), terrestrial detritus (-21.59 ‰ to -29.66 ‰ $\delta^{13}\text{C}$ and -3.53 ‰ to 2.99 ‰), sediments (-20.92 ‰ to -30.16 ‰ $\delta^{13}\text{C}$ and 0.07 ‰ to 7.26 ‰ $\delta^{15}\text{N}$), *Daphnia* sp. (-24.32 ‰ to -34.09 ‰ $\delta^{13}\text{C}$ and -2.27 ‰ to 1.59 ‰ $\delta^{15}\text{N}$), littoral POM (-30.07 ‰ to -32.04 ‰ and -6.63 ‰ to 1.96 ‰), and profundal POM (-30.92 ‰ to -33.61 ‰ and -5.91 ‰ to 4.76 ‰) showed important variations in their isotopic signatures. These represent pooled values from the three sites. However, in some cases different types of food sources from the same site and sampling period exhibited similar isotopic values for one of the two stable isotopes used. Particulate organic matter was not considered as a food source in the use of mixing models since it represents a mix of various components.

Between habitat variability in isotopic signatures

Benthic macroinvertebrates

For all sampling periods, a significant decoupling was observed in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between littoral and profundal habitats (Conover approach, $p < 0.001$) (Fig. 7). Overtime, mean littoral $\delta^{13}\text{C}$ values varied from -25.14 ‰ to -29.25 ‰, while mean profundal values varied from -33.52 ‰ to -35.41 ‰. Concerning $\delta^{15}\text{N}$, mean littoral values varied from 0.19 ‰ to 1.55 ‰,

while mean profundal values varied from 2.10 ‰ to 4.17 ‰. The range of $\delta^{13}\text{C}$ (Fig. 8) and $\delta^{15}\text{N}$ (Fig. 9) values varied monthly in both littoral and profundal benthic macroinvertebrate samples. Generally, profundal $\delta^{13}\text{C}$ values were more depleted compared to littoral ones, while profundal $\delta^{15}\text{N}$ values were higher than littoral ones. Indeed, the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of littoral samples were $-27.41 \text{ ‰} \pm 0.18$ and $0.85 \text{ ‰} \pm 0.09$, respectively, while for profundal samples they were $-34.41 \text{ ‰} \pm 0.43$ and $3.43 \text{ ‰} \pm 0.22$, respectively. The degree to which the decoupling between the littoral and the profundal habitats occurred varied between sampling periods. For $\delta^{13}\text{C}$ values, minimum decoupling appeared in May (Dunn, $q = 3.35$; $Q(0.05;10)$), while maxima occurred in August (Dunn, $q = 5.91$; $Q(0.05;10)$) and September (Dunn, $q = 5.90$; $Q(0.05;10)$). For $\delta^{15}\text{N}$ values, the only decoupling present between littoral and profundal habitats occurred in July (Dunn, $q = 3.58$; $Q(0.05;10)$).

Food sources

$\delta^{13}\text{C}$ values differed significantly between the littoral and profundal habitats (Conover approach, $p < 0.001$). A decoupling generally occurred at every site for each sampling period, except for site 1 in May, June and September. For $\delta^{15}\text{N}$ values, significant decoupling was also observed between littoral and profundal habitats (Conover approach, $p < 0.001$). However, this did not apply to each site during every sampling period, as no decoupling was observed at site 2 in May, at sites 1 and 2 in June, at site 1 in August and at sites 1, 2, and 3 in September.

Link between isotopic signatures of benthic macroinvertebrates and food sources

For $\delta^{13}\text{C}$ values, no significant relation was found between either littoral (Pearson's rank correlation, $r = 0.13$; $p > 0.05$) or profundal (Pearson's rank correlation, $r = 0.10$; $p > 0.05$) values of benthic macroinvertebrates and their food sources. The absence of significant relations was

also noted for the $\delta^{15}\text{N}$ values of littoral (Pearson's rank correlation, $r = 0.18$; $p > 0.05$) and profundal (Pearson's rank correlation, $r = 0.07$; $p > 0.05$) samples.

Between sites variability in isotopic signatures

Benthic macroinvertebrates

Looking at a larger spatial scale, variability existed between sampling sites. For each sampling period, $\delta^{13}\text{C}$ values of benthic macroinvertebrates were significantly different at the three sites (Conover approach, $p < 0.001$). Variability was maximal between sites 1 and 3 in May (Dunn, $q = 7.85$; $Q(0.05; 3)$), June (Dunn, $q = 8.43$; $Q(0.05; 3)$), August (Dunn, $q = 30.32$; $Q(0.05; 3)$), and September (Dunn, $q = 16.01$; $Q(0.05; 3)$). For $\delta^{15}\text{N}$ values, variability between sites also occurred, but not systematically for each sampling period. Also, contrary to $\delta^{13}\text{C}$ values, maximum variability was not between sites 1 and 3, but rather between sites 2 and 3 in May (4.40; $Q(0.05; 3)$), August (24.65; $Q(0.05; 3)$), and September (12.19; $Q(0.05; 3)$), and between sites 1 and 2 in June (6.71; $Q(0.05; 3)$) and July (6.82; $Q(0.05; 3)$). Some sites also exhibited similar values at times, like sites 1 and 2 in May (0.44; $Q(0.05; 3)$), and sites 1 and 3 in June (1.65; $Q(0.05; 3)$) and July (1.88; $Q(0.05; 3)$).

Food sources

No significant differences in food source values were obtained between the three sampling sites, for either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (Conover approach, $p > 0.05$).

Organic matter fluxes and temporal variability

According to the mixing model of Philipps (2001), variable contributions of the different available food sources to the diet of littoral benthic macroinvertebrates were observed from May

to September 2006 (Table 4). Four potential food sources were available in littoral habitats, i.e. pollen, epilithon, terrestrial detritus, and phytoplankton (obtained from isotopic signatures of *Daphnia* sp. collected *in situ*). Pollen was available only in May but did not seem to contribute to the diet of benthic macroinvertebrates. Epilithon was collected during each sampling period, and contributed to the total diet as follows: May, $24.09 \pm 4.74\%$; June, $19.49 \pm 4.02\%$; July, 10.72% ; August, 21.43% ; September, 11.11% . Terrestrial detritus represented an important food source, used in various contributions, except in September: May, $17.65 \pm 5.11\%$; June, $27.69 \pm 12.02\%$; July, 32.14% ; August, $78.57 \pm 4.81\%$. Finally, phytoplankton was used in June ($12.83 \pm 0.90\%$), July (10.72%) and September (33.33%), but could not be evaluated for May or August since data were not available. Two potential food sources were available in profundal habitats, i.e. sediments and phytoplankton. Sediment was sampled from May to September, but it was apparently used as food source by benthic macroinvertebrates only in July, making a contribution of $25.00 \pm 35.36\%$ to their total diet. *Daphnia* sp. was not sampled in May and in August, so phytoplankton was used in June ($25.00 \pm 35.46\%$) and September ($16.67 \pm 23.57\%$). The category “no solution to the mixing model” formed an important proportion of the total diet from May to September.

Discussion

This study looked at spatial and temporal variability in stable isotope signatures of lake benthic macroinvertebrates and their potential food sources, based on the sampling of three sites. The lake under study has a low lakeshore development, thereby providing a suitable situation for the assessment of the coupling that exists at the natural state between aquatic and terrestrial habitats.

Spatial variability: Decoupling between littoral and profundal habitats

The occurrence of a significant decoupling between littoral and profundal habitats for benthic organisms is in agreement with findings from previous studies. According to Vander Zanden & Rasmussen (1999), important variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures of primary consumers occur along a gradient of habitats, i.e. littoral, pelagic, and profundal. Indeed, $\delta^{13}\text{C}$ isotopic signatures of benthic macroinvertebrates between nearshore and offshore habitats of small oligotrophic Arctic lakes differed, with depleted ^{13}C values observed in offshore habitats (Hershey *et al.* 2006). In our study, benthic macroinvertebrates from profundal habitats were depleted in $\delta^{13}\text{C}$ and enriched in $\delta^{15}\text{N}$ values, compared to those of their littoral counterparts. Various environmental processes may influence isotopic ratios (Rau 1980). For instance, thermal stratification in lakes creates an effective barrier that separates different water masses, thereby also limiting the water exchange between littoral and profundal habitats. Also, it seems that fixation of respired CO_2 in profundal habitats may contribute to depleted $\delta^{13}\text{C}$ values (Rau 1980). The fact that profundal $\delta^{15}\text{N}$ values are enriched compared to those of littoral habitats depends on rates of nitrification that are influenced by temperature (Henriksen *et al.* 1981). In our study, carbon and nitrogen isotope signatures of benthic macroinvertebrates may have been influenced by the differential use of food sources in the two habitats, since the isotopic signatures of food sources also varied between littoral and profundal habitats. However, the expected influence of food sources on the isotopic signatures of benthic macroinvertebrates was not conclusive, since no significant linear relations were observed between the isotopic signatures of benthic macroinvertebrates and those of their food sources analyzed. Average $\delta^{13}\text{C}$ values for littoral benthic macroinvertebrates measured in this study are similar to those reported by Syväranta *et al.* (2006). On the other hand, the $\delta^{15}\text{N}$ values obtained in our study are lower than those recorded

by these authors. This can be explained by the low lakeshore development that Lake des Baies exhibits, probably resulting in low nitrogen input into the lake ecosystem and, therefore, lower overall $\delta^{15}\text{N}$ values. Indeed, human activities contribute to raise the export of nitrogen from land to water systems (Lake *et al.* 2001; Kalff 2002).

In this study, the intensity of decoupling between littoral and profundal habitats varied through time, being more important in August and September and less important in May. Biological activity within the lake could partly explain the changes in intensity of decoupling for $\delta^{13}\text{C}$. At the beginning of the warm season (May), the biological activity in the lake was probably low, since the ice had just recently disappeared and the water was still cold. The maximum decoupling observed in August and September 2006 could be a direct result of the maximal biological activity that occurs in the area during this part of the year. Maximum decoupling indicates that littoral and profundal benthic macroinvertebrates probably assimilated different food sources. Temporal variation in decoupling for $\delta^{15}\text{N}$ values probably relies on processes of denitrification and nitrification, with availability of dissolved oxygen having a major influence on these processes (Rysgaard *et al.* 1994).

Spatial variability: Variations of isotopic signatures at a larger scale

Variability in $\delta^{13}\text{C}$ values of benthic macroinvertebrates was also observed between the three sites, from May to September 2006. Since littoral habitats are regarded as highly heterogeneous environments (Hecky & Hesslein 1995; Harrison & Hildrew 2001; Stoffels *et al.* 2003; Stoffels *et al.* 2005), some variability in isotopic signatures within a lake is expected. Syväranta *et al.* (2006) suggested that the presence of variable isotopic compositions in

heterogeneous littoral areas of lakes would be transferred to higher trophic levels. This in turn would contribute to the variable isotopic signatures, according to the different feeding areas. On the other hand, as profundal habitats appear to be rather homogeneous (Wetzel 2001), the observed variation in isotopic signatures of benthic macroinvertebrates from these habitats might be less important. Since habitats are heterogeneous in lakes (Schindler & Sheuerell 2002), various factors could contribute to this variability in isotopic signatures, such as water temperature (Henriksen *et al.* 1981), nature of substrate and geographic position. During this study, water temperature was very similar at the different sites during each sampling period. Also, the nature of the substrate was about the same for sites 1 and 3. Regarding geographic position, sites 1 and 3 were located on the eastern side of the lake, while site 2 was on its western shore. Despite the similarities between sites 1 and 3, compared to site 2, the highest spatial variability in $\delta^{13}\text{C}$ values of benthic macroinvertebrates was actually observed between these two sites, except in May. Finally, contrary to the variation observed in isotopic signatures within sites, the differences in benthic macroinvertebrate samples were clearly less influenced by their food sources, since the isotopic signature of each type of food source was quite similar at each site across sampling periods. Since environmental factors and food sources could not explain all the variability observed, the composition of the benthic macroinvertebrate communities was also investigated. These communities are known to be highly heterogeneous in lakes. According to Stoffels *et al.* (2005), the variation in spatial patterns of benthic invertebrate communities is linked to the habitat characteristics of each site. Generally, the highest variability in stable isotope values observed between two sites in this study reflected the largest difference of composition in the respective macroinvertebrate communities. Sites 1 and 3 exhibited the largest differences in the taxa composition of their benthic macroinvertebrate communities. An exception to this was

observed in July, when sites 1 and 3 appeared less distinct, despite having a similar composition in their communities.

The use of linear mixing models

According to Beaudoin *et al.* (2001), the presence of an overlap in $\delta^{13}\text{C}$ isotopic signatures of different potential food sources makes the identification of the contribution of food sources to diet of an invertebrate ambiguous. However, these authors did not mention how the determination of the contribution of food sources was made. In the present study, overlap occurred in some occasions for one of the stable isotopes of certain food sources. The use of linear mixing models allowed us, however, to determine the contribution of multiple food sources available by using both stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) at the same time. The combination of information from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can provide more accurate information on the food sources assimilated, thereby reducing the ambiguity highlighted by Beaudoin *et al.* (2001).

Mixing models are based on the observation that the total isotopic signature of a consumer reflects the signature of its food sources, in proportion to the dietary contribution of each source (Philipps 2001). These models are more accurate than others models that use Euclidean distances, such as the Ben-David equations (Ben-David & Schell 2001; Philipps 2001). Such models are known to underestimate the contribution of the most commonly used food sources, while overestimating those that are rarely consumed. Also, these models implicitly assume that partitioning of food sources from different types of tissue is the same for both carbon and nitrogen (Philipps, *pers. comm.*). In fact, there is evidence suggesting that only linear mixing models may provide quantitatively unbiased values (Philipps 2001). However, it has to be kept in

mind that mixing models are also not ideal, but they nevertheless provide the best available tool to investigate multi-sourced, proportional dietary contributions in organisms.

In this study, values in the range of 0 to 100%, obtained using the IsoError 1.4 software, allowed the identification of a major food source within a complex diet. Indeed, these values represent estimates of proportional contributions of sources to a mixture. However, in some cases no such resolution was possible, as values obtained were < 0 or $> 100\%$. In those cases, the major food source couldn't be identified and was then classified as "no solution to the mixing model". Furthermore, cases of missing data for some sampling periods also hindered the identification of potential food sources. Sources not sampled, such as bacteria, that could also represent possible dietary items, were not considered in this study. Aquatic macrophytes, which contributed to the diet of benthic macroinvertebrates in other studies, were not present in Lake des Baies. So, among the food sources available and used in the mixing models, terrestrial detritus (e.g., leaf litter) was actually an important contributor of food to the benthic macroinvertebrates in littoral habitats, from May to August 2006. The high values of standard errors can be explained by the variation in isotopic signatures of benthic macroinvertebrates that existed between the three sampled sites. Mixing models were also performed on data of benthic macroinvertebrates and their food sources from the profundal habitats. The results were, unfortunately, inconclusive, since the percentages of the category "no solution to the mixing model" were important in virtually all sampling periods.

Temporal variability: looking at organic matter fluxes

$\delta^{13}\text{C}$ values give an indication of the type of food source assimilated by an organism. In this study, since benthic macroinvertebrate values changed with sampling period both in the

littoral and profundal habitats, it can be assumed that assimilation of food sources changed accordingly, with time. However, since the carbon and nitrogen isotope signatures of the food sources also changed, it would be more appropriate to say that the proportional contribution of various food sources to the total diet of benthic macroinvertebrates changed. Looking at the utilisation of the different potential food sources sampled, it appears that terrestrial detritus was a component of the diet of the benthic macroinvertebrate community in littoral habitats, more or less important according to the sampling season. According to previous studies, the importance of allochthonous inputs of organic matter is often important in lacustrine environments. Carbon budgets of aquatic systems happen to be often dominated by important inputs of carbon (dissolved and particulate) from terrestrial habitats (Pace *et al.* 2007). According to Jansson *et al.* (2007), not only allochthonous organic carbon dominates quantitatively the trophic budget of lakes, but it would also affect some fundamental functions of the lake ecosystem such as changes on the role of bacteria for carbon fluxes. This is particularly the case in oligotrophic systems (France 1995a; Jones *et al.* 2001; Stoffels *et al.* 2005; Jansson *et al.* 2007), where autochthonous activity is less important because of low nutrient availability (Cole *et al.* 2006). Thus, the importance of allochthonous inputs would decrease with increasing lake trophism (Jones 1992). Moreover, past studies undertaken on large lakes have demonstrated the necessity of allochthonous inputs for benthic invertebrates, as a potential food source structuring communities. Indeed, there seems to be a larger dependence of littoral benthic macroinvertebrates on terrestrial, rather than aquatic, vegetation (France 1995a). Thus, allochthonous organic matter could not only be used as a food source when the biological activity of the lake is low, but also during the other seasons, when there is no ice cover. For instance, lakes of north-temperate regions receive an important proportion of their total annual carbon budget through allochthonous contributions (France 1995a). According to France (1995a), dense growths of macrophytes in

Canadian Shield lakes only occupy 40%, the major component being allochthonous detritus, so these detritus might contribute more toward the macroinvertebrate community. In large oligotrophic lakes, riparian inputs of POM may be important in structuring invertebrate communities (Stoffels *et al.* 2005). Finally, France (1995a) compared macroinvertebrate densities from both macrophytic and detrital dominated habitats and concluded that allochthonous detritus made an important contribution to lake standing crop (density x habitat area). Even though Lake des Baies is a rather small lake, allochthonous inputs definitely play a role as a food supply to benthic macroinvertebrates. In this study, there was also another category called “no solution to the mixing model”, present at every sampling period. One of the possible explanations that can justify the absence of solutions with the linear mixing models is the presence of other food sources that were not sampled (Philipps *pers. comm.*). Other reasons, such as possible metabolic routine effects, or a significant variation in the relative concentrations of C and N in the various sources could also be considered (Philipps *pers.comm.*). As for littoral habitats, the use of food sources in profundal habitats also seemed to change through time. However, it was not possible to determine what food source was preferentially used in May and August. Key food sources were probably missed on those occasions, since it was not possible to attain a biological resolution with the linear mixing models.

Conclusions

Clear spatial and temporal variations in isotopic signatures of benthic macroinvertebrates were observed in this study for littoral habitats. These were less obvious for the profundal habitats, since a poor availability of samples from profundal habitats constituted a limitation to a more comprehensive analysis. Spatial variability was affected by the scale of the study, with the importance of the factors affecting variability changing according to habitat type (littoral vs

profundal). Environmental parameters, food sources availability, and composition of benthic macroinvertebrate communities were some of the factors identified as having an influence on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures. Temporal variability was expressed as change with sampling periods in the relative contribution of each food source to the total diet of benthic macroinvertebrates. However, changes in the composition of benthic macroinvertebrate communities, as well as the variation in diet preferences in some taxa could also have contributed to the spatial and temporal variations in isotopic signatures observed in this study (Syväranta *et al.* 2006; Solomon *et al.* 2007). Finally, among the food sources used in the mixing models, terrestrial detritus such as leaf litter seemed to exert an important influence on littoral food webs. The importance of terrestrial detritus is evidence that a close coupling between aquatic and terrestrial systems exists in Lake des Baies. Studying lakes with low lakeshore development provides an opportunity to understand the coupling that occurs in a natural state between ecosystems. This is a first essential step in order to understand the consequences of human disturbances on the shores of aquatic systems. By avoiding the noise of human impacts on aquatic ecosystem functioning, it becomes possible to see how aquatic and terrestrial systems are linked. This is currently a necessary research objective, as it allows an understanding of benchmark limnological processes that can be used towards the implementation of improved strategies of lake management.

Acknowledgments

This research was supported by grants from the Natural Sciences and Engineering Research Council (NSERC) of Canada to C.N. We wish to thank Alain Langlais and staff of the Duchénier Reserve for allowing the use of facilities during the field surveys. We are grateful to Alain Caron for helping with the statistical analyses, Richard St-Louis with the stable isotopes measurements,

Donald Philipps with the use of mixing models, Claude Normand with the ArcGis software and Pierre Simard with field assistance. This is a contribution to BioNord and the Centre d'études nordiques (CEN) research programs.

Table 1. Environmental characteristics of sampling sites. Temperature (°C), dissolved oxygen (mg/L), pH, Chl *a* (µg/L), DOC (mg/L), and Secchi depth (m) values measured at each site for surface and bottom waters, from May to September 2006.

Sites	May			June			July			August			September		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
<i>Epilimnion</i>															
Temperature	10.0	10.6	12.7	18.5	19.9	19.9	22.2	22.1	22.0	19.3	19.4	19.7	15.2	16.3	14.0
Dissolved O ₂	9.4	9.5	9.5	7.9	9.1	8.4	9.0	8.4	8.1	7.9	8.7	9.0	8.9	9.0	8.9
pH	7.5	7.7	7.0	7.7	7.9	7.6	7.7	7.6	7.5	6.9	7.5	7.7	7.0	6.8	7.0
chl <i>a</i>	1.5	1.5	1.0	0.7	1.0	0.8	0.9	1.0	1.3	1.1	1.2	na	1.7	1.9	1.9
DOC	4.0	3.6	6.3	3.9	4.0	5.2	na	3.7	3.7	na	3.9	na	3.7	na	na
<i>Metalimnion</i>															
Temperature	8.8	8.2	8.7	13.3	13.9	12.0	14.4	17.8	17.8	14.0	15.0	17.1	15.0	13.3	13.8
Dissolved O ₂	9.2	9.3	9.3	8.4	10.4	9.2	10.8	9.6	9.2	9.1	9.6	9.0	8.8	9.3	8.8
pH	7.4	7.7	7.3	7.9	7.9	7.8	7.6	7.6	7.4	5.6	7.1	7.7	7.1	6.9	7.1
chl <i>a</i>	2.2	2.7	2.2	1.3	1.7	1.8	1.9	1.3	1.1	1.4	2.2	na	2.0	1.8	1.8
DOC	3.8	3.7	4.0	4.8	4.3	3.9	na	3.9	3.8	na	3.6	na	3.7	na	na
<i>Hypolimnion</i>															
Temperature	6.1	5.9	5.9	6.6	7.4	7.2	7.6	8.3	8.3	8.4	11.4	10.3	14.4	12.2	13.8
Dissolved O ₂	8.5	8.3	8.4	6.7	8.8	7.9	8.8	8.5	8.0	7.5	9.0	8.7	8.7	9.5	8.8
pH	7.2	7.4	6.0	7.3	7.6	na	6.4	6.7	na	na	7.4	7.5	7.1	6.9	7.1
chl <i>a</i>	1.8	3.3	1.4	1.8	2.7	2.0	2.5	2.6	2.6	2.8	2.4	na	1.8	1.7	1.8
DOC	3.8	3.8	3.6	3.6	3.6	3.9	na	3.7	3.6	na	3.5	na	3.5	na	na
Secchi depth	5	4.5	4	7.5	6	6	7	7.5	6	5.25	5.75	na	7	7.5	na

Table 2. Range of stable isotope signatures of carbon ($\delta^{13}\text{C}$) for macroinvertebrates and food sources, pooled for all sites, available from May to September 2006. Values in parentheses refer to mean \pm SE and sample size in bold.

Samples	May	June	July	August	September
Macroinvertebrates					
Littoral habitat					
Ephemeroptera Ephemeriidae	-25.96 to -30.49	-25.79 to -29.01	-25.46 to -27.75		-22.64 to -27.33
<i>Ephemera</i>	(-27.27 \pm 0.57) (8)	(-27.61 \pm 0.63) (5)	(-26.54 \pm 0.50) (4)		(-25.29 \pm 0.55) (9)
Odonata Libellulidae	-26.89 to -40.70				
	(33.95 \pm 2.53) (5)				
Ephemeroptera EphemereIIDae	-25.57 to -32.99	-24.77 to -30.97			
<i>Eurylophella</i>	(-30.14 \pm 0.73) (9)	(-27.88 \pm 1.28) (4)			
Plecoptera Perlidae	-26.03 to -29.82	-26.81 to -30.33	-24.89 to -28.21	-24.77 to -26.84	-25.82 to -28.10
<i>Acroneuriinae</i>	(-27.43 \pm 0.43) (9)	(-28.61 \pm 0.52) (7)	(-26.68 \pm 0.42) (7)	(-26.01 \pm 0.39) (5)	(-27.06 \pm 0.28) (9)
Hemiptera Corixidae <i>Sigara</i>	-26.48 to -30.85	-25.67 to -27.01	-23.17 to -25.31		
	(-28.12 \pm 0.95) (4)	(-26.34 \pm 0.67) (2)	(-24.13 \pm 0.40) (5)		
Amphipoda	-29.79 to -33.37	-25.39 to -30.35	-23.56 to -27.26	-22.53 (1)	-25.02 (1)
	(-31.19 \pm 0.50) (7)	(-28.28 \pm 0.53) (9)	(-25.62 \pm 0.62) (5)		
Ephemeroptera Heptageniidae	-28.77 to -34.56	-26.93 to -30.63	-25.61 to -33.51	-25.17 to -29.19	-27.33 to -29.85
<i>Heptageninae</i>	(-30.58 \pm 1.06) (5)	(-28.53 \pm 0.42) (8)	(-28.66 \pm 1.24) (8)	(-26.58 \pm 0.58) (6)	(-28.60 \pm 0.30) (9)
Diptera Chironomidae					-24.66 (1)
Colcoptera Elmidae <i>Stenelmis</i>	-25.45 (1)	-25.05 to -28.85	-25.34 to -28.05	-23.76 to -25.91	-24.76 to -28.69
		(-27.02 \pm 0.52) (8)	(-27.35 \pm 0.37) (7)	(-24.72 \pm 0.45) (4)	(-26.98 \pm 0.62) (6)
Oligochaeta	-26.99 to -31.48	-27.02 to -29.55	-25.08 to -28.08	-22.92 to -25.24	-25.25 to -26.52
	(-28.48 \pm 0.89) (5)	(-28.12 \pm 0.30) (8)	(-25.98 \pm 0.46) (6)	(-24.06 \pm 0.48) (4)	(-25.79 \pm 0.30) (4)
Profundal habitat					
Ephemeroptera Ephemeriidae					-29.00 to -31.94
<i>Ephemera</i>					(-30.47 \pm 1.47) (2)
Amphipoda	-32.80 to -36.60	-32.91 to -39.01		-33.65 (1)	-32.51 to -39.61
	(-34.83 \pm 1.11) (3)	(-35.65 \pm 0.76) (5)			(-36.04 \pm 1.46) (4)
Diptera Chironomidae	-33.52 to -34.44	-34.38 to -35.27	-25.56 to -35.50	-33.39 (1)	-34.56 to -40.05
	(-33.98 \pm 0.46) (2)	(-34.83 \pm 0.45) (2)	(-32.40 \pm 1.52) (5)		(-37.31 \pm 2.75) (2)
Oligochaeta	-32.34 (1)		-32.11 (1)		-32.88 to -34.28
					(-33.77 \pm 0.45) (3)
Epilithon	-23.65 to -30.03	-22.58 to -35.39	-18.13 to -34.38	-19.08 to -23.26	-18.80 to -23.83
	(-27.61 \pm 0.87) (9)	(-23.51 \pm 1.50) (8)	(-24.19 \pm 2.14) (7)	(-21.46 \pm 0.92) (4)	(-21.32 \pm 2.52) (2)
Pollen	-28.18 to -28.72				
	(-28.38 \pm 0.07) (6)				
Terrestrial detritus	-27.20 to -30.99	-26.93 to -31.95	-21.59 to -30.34	-25.61 to -30.46	-29.66 to -30.90
	(-29.68 \pm 1.27) (3)	(-28.86 \pm 1.56) (3)	(-27.28 \pm 1.09) (9)	(-29.31 \pm 0.50) (9)	(-30.34 \pm 0.20) (6)
Sediment	-30.16 to -31.79	-28.67 to -31.14	-30.16 to -31.51	-28.28 to -30.92	-20.92 to -36.40
	(-31.02 \pm 0.19) (9)	(-30.03 \pm 0.11) (9)	(-31.09 \pm 0.06) (9)	(-29.99 \pm 0.41) (6)	(-31.89 \pm 1.96) (7)
Littoral POM	-31.63 to -33.20	-30.16 to -30.37	-30.07 to -32.17	-30.82 to -32.08	-32.04 to -33.48
	(-32.43 \pm 0.22) (6)	(-30.27 \pm 0.11) (2)	(-31.32 \pm 0.25) (9)	(-31.26 \pm 0.22) (5)	(-32.67 \pm 0.14) (9)
Profundal POM	-33.60 to -37.76	-32.96 to -34.33	-33.61 to -34.95	-30.92 to -36.94	-32.96 to -34.87
	(-35.19 \pm 0.80) (6)	(-33.64 \pm 0.43) (4)	(-34.23 \pm 0.12) (9)	(-33.33 \pm 0.22) (5)	(-33.71 \pm 0.27) (8)
Daphnia		-34.09 to -37.02	-32.37 to -33.45		-24.32 to -34.43
		(-35.15 \pm 0.65) (4)	(-33.00 \pm 0.15) (6)		(-28.19 \pm 0.19) (6)

Table 3. Range of stable isotope signatures of nitrogen ($\delta^{15}\text{N}$) for macroinvertebrates and food sources, pooled for all the sites, available from May to September 2006. Values in parentheses refer to mean \pm SE and sample size in bold.

Samples	May	June	July	August	September
Macroinvertebrates					
Littoral habitat					
Ephemeroptera Ephemerae <i>Ephemera</i>	1.29 to 2.08 (1.67 \pm 0.11) (7)	1.38 to 2.40 (1.94 \pm 0.17) (5)	1.13 to 1.53 (1.35 \pm 0.10) (4)		-1.12 to 3.63 (-0.23 \pm 0.49) (9)
Odonata Libellulidae	2.09 to 3.07 (2.56 \pm 0.19) (5)				
Ephemeroptera Ephemerae <i>Eurylophella</i>	0.23 to 2.13 (0.88 \pm 0.23) (9)	-0.69 to 0.07 (-0.20 \pm 0.18) (4)			
Plecoptera Perlidae <i>Acroneurinae</i>	2.94 to 4.43 (3.84 \pm 0.16) (9)	0.95 to 3.63 (2.93 \pm 0.37) (7)	1.94 to 4.10 (2.70 \pm 0.28) (7)	2.73 to 3.67 (3.12 \pm 0.21) (5)	1.11 to 6.38 (4.55 \pm 0.47) (9)
Hemiptera Corixidae <i>Sigara</i>	1.64 to 2.42 (1.93 \pm 0.18) (4)	0.71 to 2.99 (1.85 \pm 1.14) (2)	-0.26 to 1.33 (0.80 \pm 0.27) (5)		
Amphipoda	1.65 to 4.14 (2.48 \pm 0.35) (7)	-0.06 to 1.25 (0.59 \pm 0.16) (7)	-0.11 to 0.55 (0.01 \pm 0.23) (5)	-0.36 (1)	-1.46 (1)
Ephemeroptera Heptageniidae <i>Heptageniinae</i>	1.07 to 2.40 (1.91 \pm 0.23) (5)	-0.19 to 0.90 (0.43 \pm 0.15) (8)	0.39 to 2.56 (1.04 \pm 0.31) (7)	-0.08 to 2.14 (0.85 \pm 0.30) (6)	0.46 to 4.44 (2.45 \pm 0.51) (9)
Diptera Chironomidae					2.80 (1)
Coleoptera Elmidae <i>Stenelmis</i>	0.54 (1)	-0.11 to 5.86 (2.93 \pm 0.87) (8)	-0.57 to 1.30 (0.56 \pm 0.26) (7)	0.19 to 2.25 (0.88 \pm 0.47) (4)	-1.51 to 4.60 (1.52 \pm 1.00) (6)
Oligochaeta	-1.36 to 1.42 (0.25 \pm 0.58) (4)	-0.44 to 1.77 (0.77 \pm 2.65) (7)	-0.07 to 1.39 (0.54 \pm 0.22) (6)	0.16 to 0.38 (0.28 \pm 0.05) (4)	-0.39 to 4.52 (2.34 \pm 1.04) (4)
Profundal habitat					
Ephemeroptera Ephemerae <i>Ephemera</i>					3.29 to 5.80 (4.55 \pm 1.26) (2)
Amphipoda	2.81 to 3.73 (3.27 \pm 0.38) (3)	3.30 to 4.35 (3.76 \pm 0.19) (5)		3.31 (1)	2.07 to 2.86 (2.47 \pm 0.40) (2)
Diptera Chironomidae	4.55 to 5.24 (4.90 \pm 0.35) (2)	4.97 to 8.20 (6.59 \pm 1.62) (2)	1.26 to 5.04 (3.92 \pm 0.71) (5)	5.03 (1)	2.80 to 6.92 (4.86 \pm 2.07) (2)
Oligochaeta	3.30 (1)		3.23 (1)		1.08 to 5.12 (3.65 \pm 1.29) (3)
Epilithon	-3.56 to 4.14 (1.21 \pm 0.81) (9)	-1.31 to -0.61 (-0.88 \pm 0.10) (8)	2.21 to 2.55 (2.38 \pm 0.09) (2)	-2.75 to 0.24 (-0.15 \pm 0.38) (3)	-0.90 to -1.49 (-1.20 \pm 0.30) (2)
Pollen	-6.18 to -4.53 (-5.33 \pm 0.07) (6)				
Terrestrial detritus	-2.63 to -1.45 (-2.09 \pm 1.27) (3)	-2.08 to -1.07 (-1.58 \pm 1.56) (3)	-2.34 to 1.26 (0.45 \pm 0.09) (5)	-3.53 to -2.47 (-2.92 \pm 0.37) (4)	2.32 to 2.99 (2.70 \pm 0.20) (3)
Littoral POM	-1.03 to 1.96 (0.35 \pm 0.44) (6)	0.01 to 0.61 (0.31 \pm 0.22) (2)	-6.63 to 0.59 (-1.62 \pm 0.69) (9)	-5.12 to -0.32 (-2.06 \pm 0.81) (5)	-3.66 to -0.87 (-1.62 \pm 0.29) (9)
Profundal POM	-0.76 to 4.76 (1.32 \pm 1.02) (6)	-4.04 to 1.19 (-1.16 \pm 1.33) (3)	-2.89 to -0.56 (-1.16 \pm 0.23) (9)	-5.72 to -1.31 (-2.80 \pm 0.83) (5)	-5.91 to 2.48 (-0.77 \pm 1.14) (8)
Daphnia		-0.22 to 0.30 (0.00 \pm 0.65) (4)	1.01 to 1.42 (1.23 \pm 0.06) (6)		-2.27 to 1.59 (0.75 \pm 0.69) (6)

Table 4. Evaluation of the proportional contribution (%) (mean \pm SE) of each food source to diet of littoral and profundal benthic macroinvertebrates from May to September 2006 (sites 1, 2, and 3 pooled), using both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the IsoError mixing model of Philipps (2000).

	May 2006	June 2006	July 2006	August 2006	September 2006
Littoral habitat					
Pollen	0	absent	absent	absent	absent
Epilithon	24.09 \pm 4.74	19.49 \pm 4.02	10.72	21.43	11.11
Terrestrial detritus	17.65 \pm 5.11	27.69 \pm 12.02	32.14	78.57 \pm 4.81	0
Phytoplankton	na*	12.83 \pm 0.90	10.72	na	33.33
No solution to the mixing model	58.26 \pm 6.45	40.00 \pm 7.09	46.43 \pm 10.44	0	55.55 \pm 15.25
Profundal habitat					
Sediment	0	0	25.00 \pm 35.36	0	0
Phytoplankton	na	25.00 \pm 35.46	0	na	16.67 \pm 23.57
No solution to the mixing model	100.00	75.00 \pm 35.46	75.00 \pm 25.07	100.00	83.34 \pm 10.52

*na: sources that were not sampled

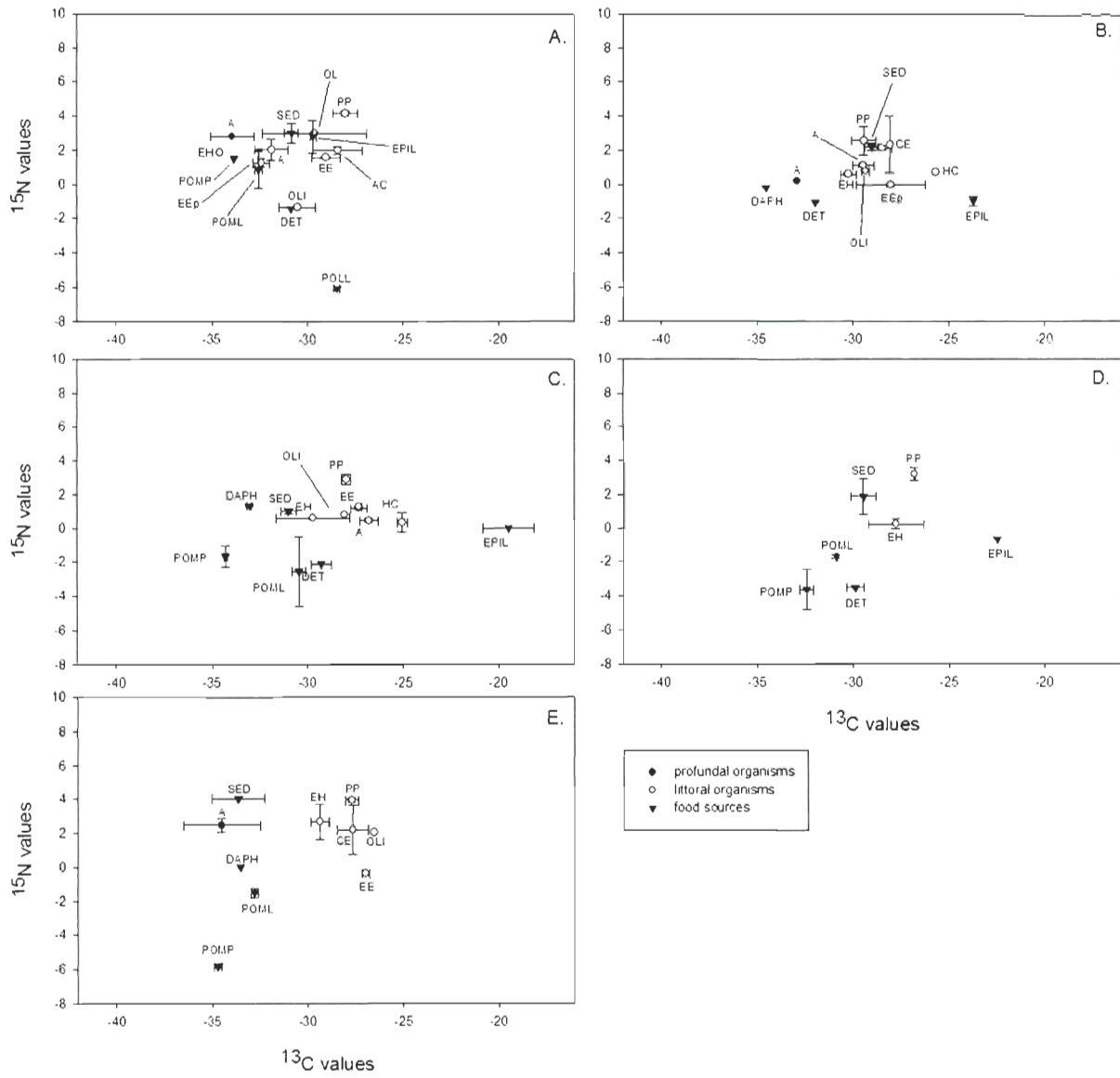
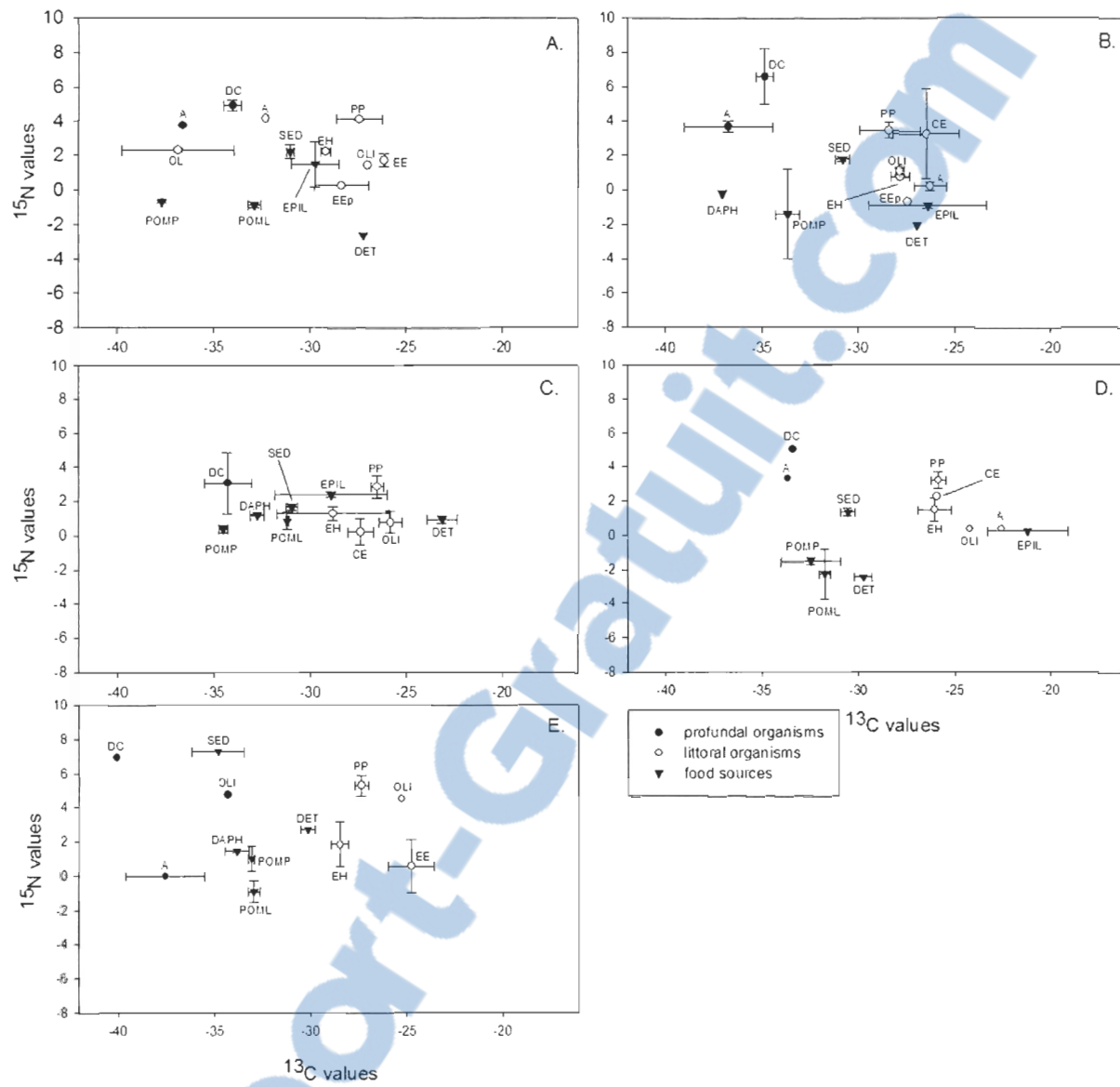
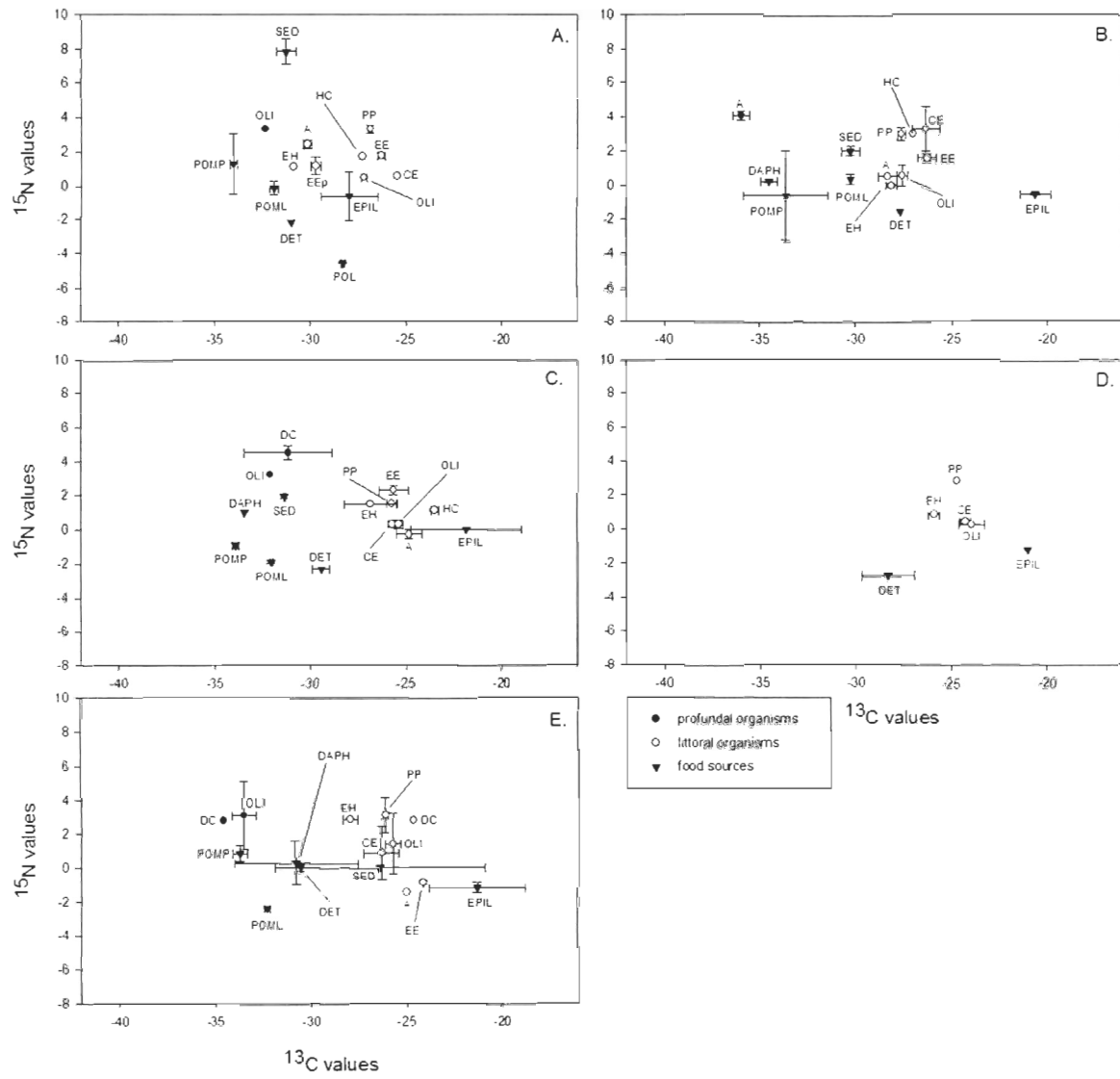


Figure 4. Gareau *et al.*

Figure 5. Gareau *et al.*

Figure 6. Gareau *et al.*

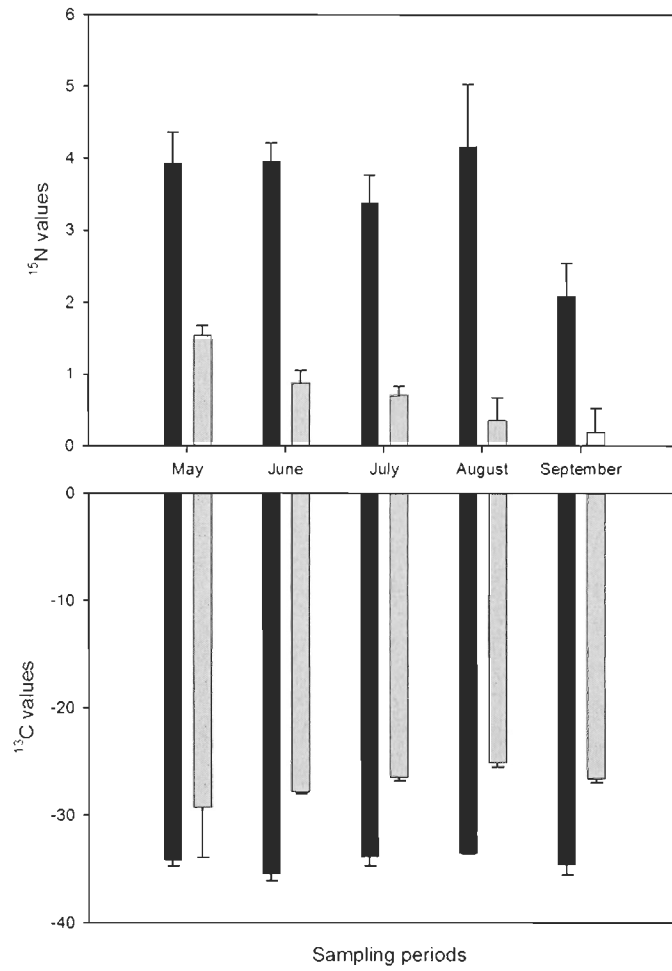


Figure 7. Gareau *et al.*

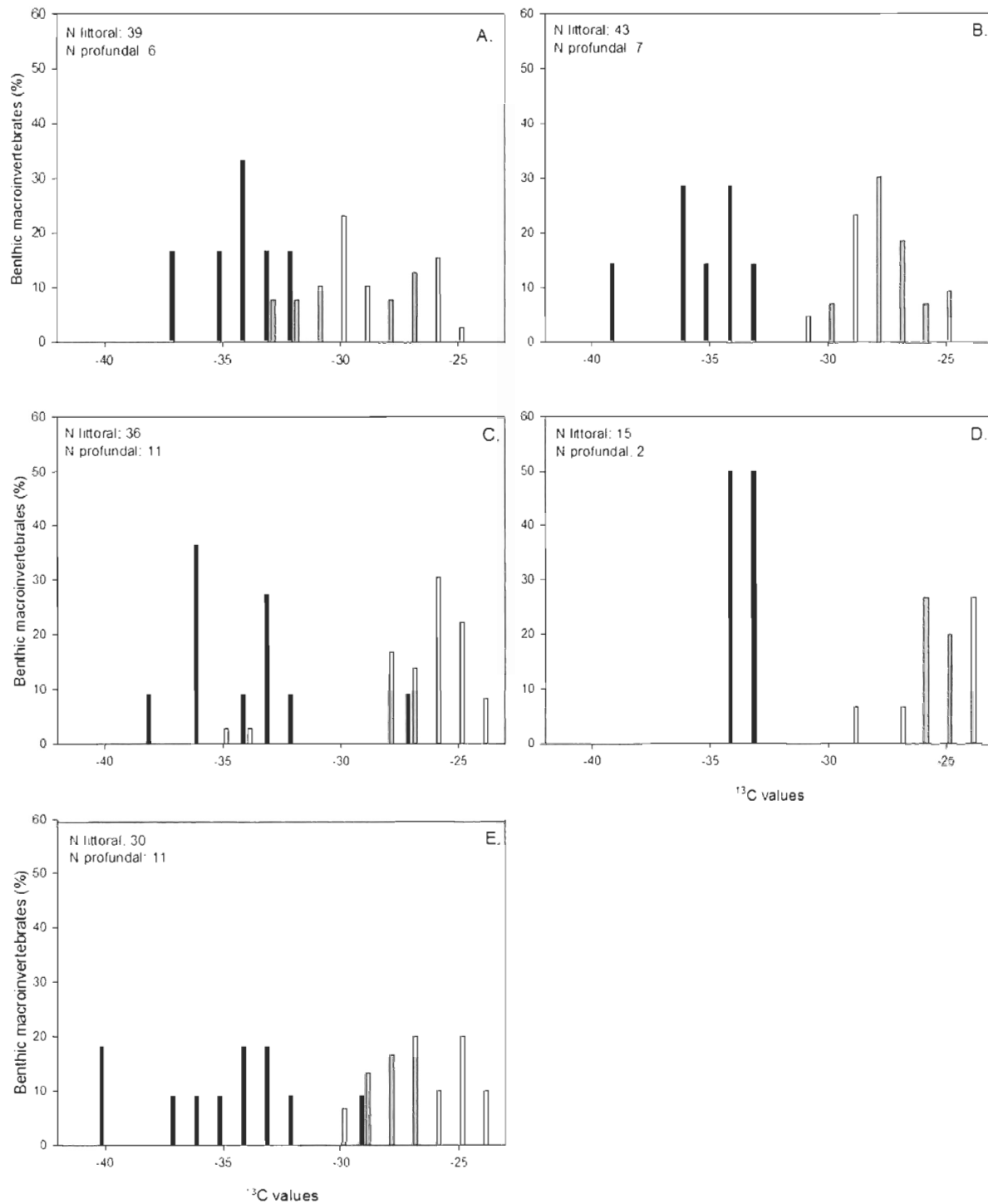
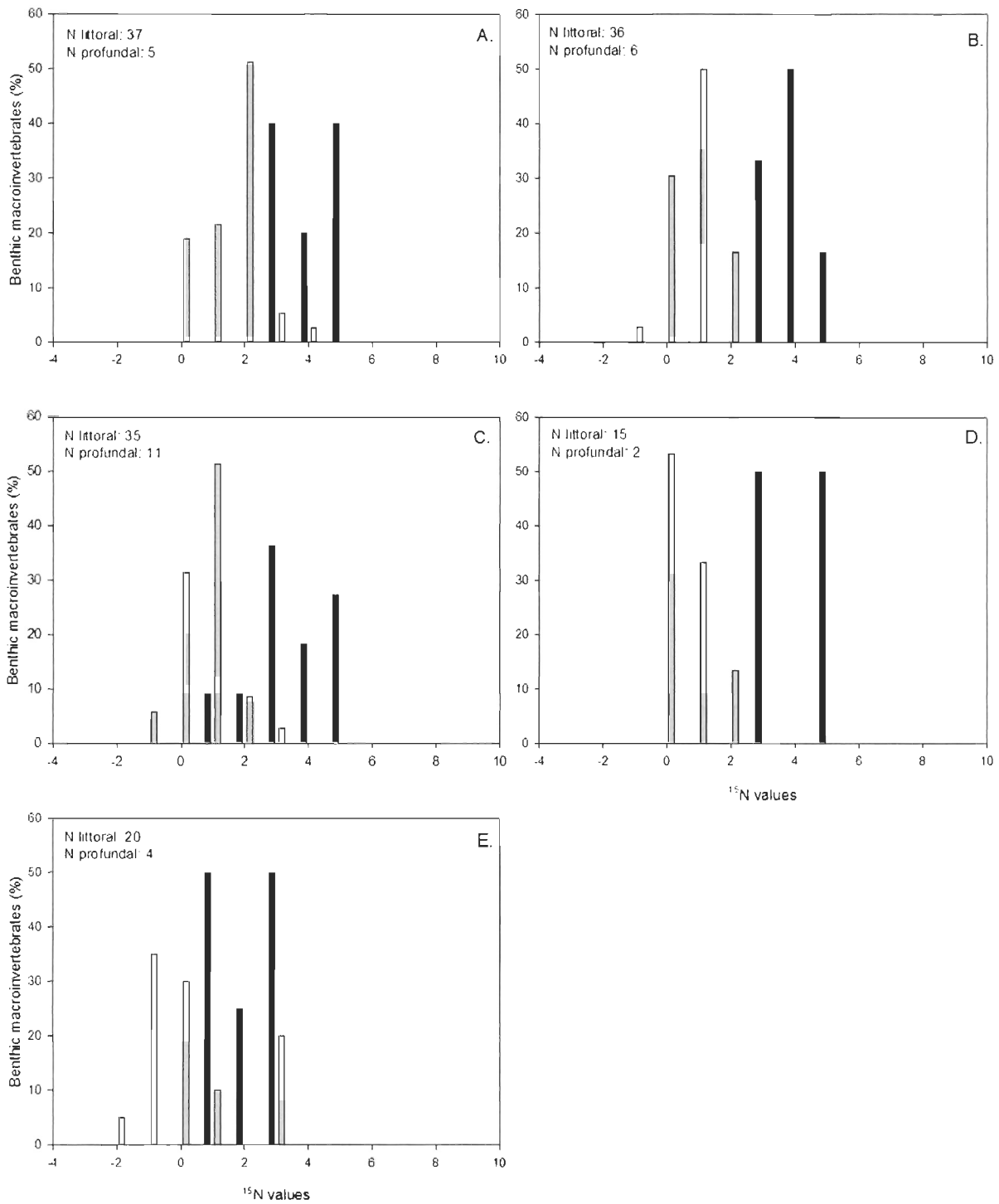


Figure 8. Gareau *et al.*

Figure 9. Gareau *et al.*

CONCLUSION GÉNÉRALE ET PERSPECTIVES

La présente étude a permis d'estimer les signatures isotopiques en $\delta^{13}\text{C}$ et $\delta^{15}\text{N}$ de macroinvertébrés benthiques d'habitats littoraux et profonds, de même que de différentes sources de nourriture potentielles utilisées par ces organismes, soient de l'épilithon, du pollen, de sédiments, de phytoplancton (*Daphnia* sp. comme organisme « ligne de base ») et de détritits de feuilles de plantes terrestres. L'obtention de valeurs isotopiques variables entre les différents habitats (littoral, profond) de même que tout au long de la saison d'échantillonnage (mai à septembre) a permis de confirmer la variabilité spatio-temporelle attendue : En ayant des signatures isotopiques différentes, il est possible de croire que les macroinvertébrés benthiques s'alimentent de sources nourritures différentes, ou encore que l'environnement influence les signatures isotopiques des sources de nourriture consommées, d'où l'observation d'une variabilité spatio-temporelle.

Un découplage au niveau des signatures isotopiques obtenues a été mis en évidence, tant au sein des sites (entre l'habitat littoral et profond d'un même site) qu'entre les différents sites à l'étude. Cette variabilité spatiale des signatures isotopiques chez les macroinvertébrés benthiques pourrait être expliquée par différents paramètres environnementaux, la disponibilité des sources de nourriture et/ou la composition des communautés de macroinvertébrés benthiques. La variabilité temporelle des signatures isotopiques observée serait reliée, quant à elle, à la contribution relative de chacune des sources de nourriture à la diète des macroinvertébrés benthiques. Cependant, il n'est pas exclu que des différences au niveau de la composition des communautés de macroinvertébrés benthiques aient également fortement contribué à la variation

temporelle observée au niveau des signatures isotopiques (Syväranta *et al.* 2006; Solomon *et al.* 2007).

Par le passé, des modèles se basant sur des calculs de distances euclidiennes (e.g., les équations de Ben-David) ont été utilisés afin de déterminer les sources de nourriture assimilées par différents types d'organismes. Or, ces modèles présentaient certaines failles qui sont résolues par l'utilisation du modèle linéaire mixte de mélange de Philipps. En effet, avec le modèle de Philipps, les problèmes de sous-estimation des principales sources de nourriture et de sur-estimation des sources de nourriture rarement utilisées sont corrigés. De plus, ce modèle tient compte du fractionnement des différents éléments (carbone et azote), étant donné que celui-ci diffère selon le type de tissu (animal, végétal) ingéré par les organismes. Cependant, le modèle de Philipps ne fonctionne pas à tout coup et certaines raisons peuvent être évoquées, telles l'existence de sources de nourriture autres, l'utilisation d'un facteur de correction du fractionnement inapproprié ou, encore, une variation significative dans les concentrations relatives de carbone et d'azote des différentes sources de nourriture (le modèle considère que le pourcentage de contribution du carbone et de l'azote est le même pour une source de nourriture donnée). Bref, il ne s'agit pas d'un modèle sans faille, mais il donne une idée de ce qui se passe et devrait toujours être utilisé afin d'estimer la contribution de sources de nourriture à la diète. Il reste que parmi les modèles qui tentent de résoudre la contribution de sources de nourritures à la diète d'un organisme, seul le modèle linéaire mixte de mélange permet l'obtention de proportions mathématiquement non-biaisées.

Ce modèle a permis d'évaluer la contribution proportionnelle de différentes sources de nourriture à la diète des macroinvertébrés benthiques littoraux. Il a été possible de démontrer que

les détritiques de feuilles de plantes terrestres ont largement contribué à la diète des macroinvertébrés benthiques des habitats littoraux de mai à septembre 2006, avec des contributions se situant entre 13 % (mai) et 90 % (août). Cela confirme la présence d'un couplage entre les systèmes terrestre et aquatique. En effet, selon plusieurs auteurs, les apports allochtones de matière organique sont souvent importants dans les environnements lacustres, particulièrement dans le cas de lacs oligotrophes (France 1995a; Jones *et al.* 2001; Stoffels *et al.* 2005; Jansson *et al.* 2007). De plus, des travaux récents, mettant en œuvre la technique de traçage isotopique (e.g. $\delta^{13}\text{C}$ et $\delta^{15}\text{N}$), ont montré que des subsides (i.e., la matière organique provenant d'environnements terrestres) pouvaient alimenter les réseaux trophiques des lacs oligotrophes et atteindre, voire même excéder, les niveaux de production primaire autochtone (Caraco & Cole 2004 ; Carpenter *et al.* 2005). Aucune conclusion n'a pu être tracée pour les macroinvertébrés benthiques profonds : N'ayant pas un nombre d'échantillons profonds suffisant ni suffisamment de sources de nourriture potentielles, le modèle n'a pas pu apporter de résultats concluants.

L'originalité de cette étude relève d'abord du fait qu'elle porte sur les habitats benthiques lacustres. En effet, puisque ces habitats, comparativement aux habitats pélagiques, restent particulièrement peu connus malgré la prise de conscience des écologistes aquatiques par rapport au rôle crucial des composantes benthiques dans les systèmes lacustres, cette étude ne peut qu'être vue comme un pas de plus vers l'amélioration des connaissances. De plus, la sélection de trois stations littorales et de trois stations profondes permet l'acquisition d'une plus grande quantité d'information sur le fonctionnement de l'écosystème lacustre, comparativement aux études passées qui ne considéraient qu'un des deux habitats (littoral ou profond) ou, encore, dont les stations échantillonnées ne possédaient pas de caractéristiques similaires. La présente étude

portant sur un lac situé dans une Réserve Faunique, les activités anthropiques y sont minimisées et donc les stations étudiées apparaissent davantage similaires entre elles. Bref, par l'analyse des signatures isotopiques de macroinvertébrés benthiques d'un lac peu anthropisé, la présente étude contribue à l'avancement des connaissances concernant la compréhension du couplage qui existe à l'état naturel entre les systèmes aquatique et terrestre en région boréale.

Perspectives

Cette étude porte sur un seul lac, de nature plutôt oligotrophe. Afin d'avoir une meilleure idée de ce qui se passe au sein des lacs en région tempérée, il serait intéressant de réaliser une étude semblable à plus grande échelle, soit en considérant un plus grand nombre de lacs, répartis le long d'un gradient de productivité. Aussi, estimer l'importance relative de l'apport du carbone allochtone (i.e., en provenance du système terrestre) et du carbone autochtone (i.e., en provenance du système aquatique) aux réseaux lacustres répartis le long de ce même gradient permettrait d'en connaître davantage sur le fonctionnement de ces réseaux. En ayant une meilleure compréhension de la connectivité (i.e., couplage) qui existe entre les systèmes aquatique et terrestre, il deviendrait alors possible de mettre en place des plans de gestion de l'habitat aquatique plus efficaces et plus appropriés. Beaucoup de connaissances restent à acquérir concernant le fonctionnement de l'écosystème lacustre boréal avant d'intégrer les conséquences d'une perturbation sur le système aquatique.

Avec le développement de l'analyse en isotopes stables (AIS), il est devenu possible de mieux comprendre les relations trophiques au sein des lacs. L'observation des variations spatiale et temporelle dans le cadre de la présente étude s'est fait par le biais de l'utilisation simultanée des isotopes stables de carbone ($\delta^{13}\text{C}$) et d'azote ($\delta^{15}\text{N}$). Dans les dernières décennies, les

isotopes stables ont été de plus en plus utilisés dans le but d'évaluer les interactions écologiques au sein des écosystèmes en permettant, entre autres, de déterminer les sources de matière organique de même que le nombre de niveaux trophiques dans les réseaux trophiques (Schindler & Lubetkin 2004), ce qui a permis de contribuer grandement à la compréhension des réseaux trophiques et des flux d'énergie dans ces systèmes, étant donné la complexité des systèmes lacustres (Schindler & Scheuerell 2002). Aussi, il semble qu'une utilisation simultanée de plusieurs isotopes stables permet une meilleure résolution (Peterson *et al.* 1985; Peterson & Howarth 1987). Ainsi, afin d'augmenter la robustesse des analyses réalisées sur les réseaux trophiques, il pourrait être intéressant, dans le cadre d'études futures, d'augmenter le nombre d'isotopes stables utilisés. En effet, les deux isotopes stables du soufre, soient ^{32}S et ^{34}S , sont largement utilisés dans le cadre d'étude sur les écosystèmes aquatiques et leur utilisation pourrait être combinée à celle des isotopes stables du carbone (^{13}C) et de l'azote (^{15}N). Par exemple, ^{34}S permettrait de distinguer les sources des systèmes aquatique et terrestre puisque de grandes variations au sein de signatures isotopiques ont été notées entre des organismes provenant de ces deux systèmes (Lott *et al.* 2003).

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