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La réponse des communautés d'invertébrés benthiques sur différents substrats naturels au développement résidentiel des bassins versants des lacs des Laurentides

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La réponse des communautés d'invertébrés benthiques sur différents substrats naturels au développement résidentiel des bassins versants des lacs des Laurentides

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RÉSUMÉ

Les invertébrés benthiques sont reconnus pour être de puissants indicateurs de l'intégrité des habitats aquatiques. Beaucoup d'études portent sur l'utilisation des macroinvertébrés pour la gestion des habitats lotiques; les habitats lentiques sont quant à eux moins bien connus. Depuis deux décennies, les lacs de la région des Laurentides au Québec connaissent une croissance du développement résidentiel dans leur bassin versant. Une meilleure connaissance des communautés d'invertébrés benthiques littoraux dans cette région est importante pour établir des programmes de surveillance et de gestion écologique. Nous avons échantillonné des invertébrés benthiques sur 4 substrats naturels différents (sédiments, roches, bois et macrophytes) dans la zone littorale de 13 lacs représentant un gradient de développement résidentiel riverain. Les sédiments et les roches sont présents dans tous les lacs, tandis que le bois noyé est présent seulement dans les lacs peu développés et les macrophytes dans les lacs plus développés. Le type de substrat et le développement résidentiel se sont avérés être d'importants facteurs expliquant les variations des communautés d'invertébrés benthiques. Les invertébrés sur les roches semblent subir un effet ascendant (bottom-up) dû probablement à l'augmentation concomitante de la biomasse d'épilithon le long du gradient de développement résidentiel, alors qu'aucun changement taxinomique n'est observé. Les sédiments abritent des organismes de plus grande taille et supportent les plus fortes biomasses d'invertébrés. Toutefois, la biomasse totale des invertébrés ne change pas le long du gradient d'urbanisation. Seule la composition taxinomique varie avec le gradient de développement résidentiel. L'hétérogénéité des sédiments diminue avec les perturbations dues à la villégiature et cela influence probablement la biomasse des

Oligochètes et des Éphémères qui sont respectivement positivement et négativement reliés au gradient de perturbation. Ces taxons pourraient être utilisés dans le cadre de programmes de gestion des lacs. Les communautés d'invertébrés sur le bois noyé sont similaires à celles sur les roches, mais le bois supporte une biomasse d'invertébrés plus forte et leur retrait de la zone littorale pourrait affecter la productivité secondaire littorale à l'échelle du lac. La présence des macrophytes dans les lacs développés permet l'établissement d'invertébrés épibenthiques et contribue à augmenter l'hétérogénéité et la complexité des habitats littoraux qui sont perdues par la nature moins hétérogène des sédiments et par le retrait du bois. À l'échelle du lac, les variations de la composition en substrats de la zone littorale, qu'elles soient de source naturelle ou anthropique, peuvent avoir d'importants effets sur la productivité benthique des lacs. Pour les programmes de surveillance et de gestion, nous suggérons de se concentrer particulièrement sur les sédiments, car ce substrat est présent dans tous les lacs et s'avère être l'habitat de choix des taxons ayant une valeur potentielle comme indicateurs.

Mots-clés : invertébrés benthiques, zone littorale, lacs des Laurentides, développement résidentiel, substrats

ABSTRACT

Benthic invertebrates are known to be strong indicators of aquatic habitat integrity. Many studies concern the use of macroinvertebrates for biomonitoring lotic habitats, but less is known about lentic habitats. Previously pristine lakes of the Laurentian region of Quebec face increasing residential development on their watershed over the last two decades. A better understanding of lake littoral invertebrate communities in this region is important to establish biomonitoring surveys. We sampled benthic invertebrates on 4 different natural substrata (sediments, rocks, wood and macrophytes) in the littoral zone of 13 lakes representing a gradient of nearshore residential development. Sediments and rocks were present in all lakes, whereas submerged wood was found only in undeveloped lakes and macrophytes only in developed lakes. Substratum type and residential development were found to be important factors explaining invertebrate communities. Rock dwelling invertebrates probably underwent a bottom-up response to increasing epilithon biomass along the residential development gradient, while no taxonomic change was observed. Sediments supported the largest organisms and the highest total invertebrate biomass, but only taxonomic changes were observed along the gradient. Sediment heterogeneity decreased with residential disturbance and this possibly influenced Oligochaeta and Ephemeroptera biomass that were respectively positively and negatively related to the disturbance gradient. These taxa could be used for biomonitoring surveys. Communities on submerged wood were similar to those on rocks, but wood supported a higher invertebrate biomass and their removal from the littoral zone may affect the whole lake secondary productivity. The groth of macrophytes in developed lakes conterbalanced the losses of complexity due to less heterogeneous sediments and wood removal allowing the establishement of epibenthic invertebrates. At the lake scale, natural or human induced variations in substratum composition of the littoral zone can have profound effects on lake benthic productivity. For biomonitoring surveys, we suggest to focus on sediment because this substratum is present in all lakes and hosts potential indicator taxa.

Key-words: benthic invertebrates, littoral zone, Laurentian lakes, residential development, substratum

TABLE DES MATIÈRES

LISTE DES TABLEAUX

Chapitre 2. Response of littoral macroinvertebrate communities on rocks and sediments to lake residential development

Table 3: Adjusted coefficient of determination (R^2_{adj}) for simple regressions between several explanatory variables; TP (log_{10} total phosphorus), TN (log_{10} total nitrogen), chl-*a* (log_{10} periphyton biomass on rocks and sediments or phytoplankton), TIB (log_{10} total invertebrate biomass on rocks and sediments), D-100 (square root of dwelling density within a 100 m strip around the shore and for the whole watershed (D-ws)), CL (percentage of cleared land within a 50 m strip around the lake (CL-50) and for the whole watershed (CL-ws)). The relationship of TIB with D-50 was weaker than with D-100, so the latter is presented. Disturbances factors calculated for other riparian strips (150, 200, 250, 500, and 1000 m.) were less well related with TIB and are not presented. * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$, n=13.

Chapitre 3. Littoral invertebrates living on different natural substrata in two groups of lakes of varying anthropogenic development

Table 1: Number of dwellings along the shore, morphologic characteristics, sediment granulometry, and substratum composition for seven lakes of the Laurentian region of Quebec. Substratum composition (as % cover of lake bottom) was estimated visually by divers over 14 to 30 stations (10 m long) per lake; rocks comprise all substrata with diameter > 1 cm (Lambert, personal communication); for macrophytes, biomass (in brackets) is presented together with percentage cover.

Table 2: Water quality and algal biomass in the 7 studied lakes. TP = total phosphorus. TN = total nitrogen. DOC = dissolved organic carbon. Water quality variables and phytoplankton biomass are averaged over 6 replicates taken in summer 2003 (Gélinas and Pinel-Alloul, unpublished data). Periphyton biomasses are from Lambert (2006); they are averaged on 3 sampling stations (June 2003).

Table 3: Results of multivariate two ways ANOVA tests on taxonomic composition for a) undeveloped (19 taxa) and b) developed lakes (18 taxa). Two classification criteria were tested (lake and substratum) as well as the interaction between these criteria. Differences are significant when $P < 0.05$.

LISTE DES FIGURES

Chapitre 2. Influence of lake residential development on littoral macroinvertebrate communities

Fig.2: Total invertebrate biomass (TIB) in relation with periphyton chl-*a* biomass on a) rocks and b) sediments. Adjusted r^2 are presented for both relationships; (n = 13). Regression line is shown only for the significant relationship (a) for which the regression model is: $Log_{10}TIB = 1.031*(Log_{10}$ periphyton chl-*a*$) + 0.263$

Fig.3: Size structure of macroinvertebrate communities on a) rocks and b) sediments. Each bar (with standard error) represents the average biomass for each size class. Average biomass was calculated over 5 stations in 3 pristine lakes (n=15), 6 moderately perturbed lakes (n=30), and 4 perturbed lakes (n=20). Mean individual size (±1 standard error) is presented in the upper right corner of each graph. Lakes were grouped into 3 categories according to their level of residential development within a 100 m riparian strip: i) pristine (from 0 to 12 dwellings·km^{-2}), ii) moderately perturbed lakes (from 115 to 175 dwellings·km^{-2}), and iii) perturbed lakes (from 373 to 552 dwellings·km^{-2}).

Fig.4: Proportion of total biomass represented by dominant macroinvertebrates on a) rocks and b) sediments. Values are averages of five replicates. For each lake, only groups representing at least 10% of total biomass are shown while the other taxa are grouped as "Others". Lakes are in order of increasing residential development.

Fig.5: Redundancy analysis (RDA) performed on macroinvertebrate communities on a) rocks (19 taxa) and b) sediments (21 taxa). Area / Volume = watershed area divided by lake volume, D-100 = dwelling density within a 100 m wide riparian strip, CL-50 = percentage of cleared land within a 50 m wide riparian strip, fine particles = % of total

sediment mass represented by particles < 250μm. Adjusted R^2 are presented for each canonical analysis. The abbreviations used in the graph are: oli = Oligochaeta, gas = Gastropoda, ephe = Ephemeroptera, cera = Ceratopogonidae, clad = Cladocera, nem = Nemaatoda, col = Coleoptera, chi = Chironomidae, ani = Anisoptera, amp = Amphipoda, tri = Trichoptera, pele = Pelecypoda.

Fig.6: Biomass of a) oligochaetes and b) mayflies along the gradient of residential development. Adjusted R^2 are presented for both relationships where n=13. Regression models are: a) Log_{10} (oligochaetes biomass + 1) = $0.0927*(D-100)^{1/2} + 0.554$ and b) Log_{10} (mayflies biomass + 1) = $-0.1002*(D-100)^{1/2} + 2.382$.

Chapitre 3. Littoral invertebrates living on different natural substrata in two groups of lakes of varying anthropogenic development

Fig.1: Mean total invertebrate biomass (TIB) with standard error on different substrata in a) undeveloped and b) developed lakes. For each substratum, TIB was averaged over 12 stations (3 sites in 4 lakes) for undeveloped lakes and over 9 stations (3 sites in 3 lakes) for developed lakes. Significant differences ($P<0.05$) among substrata are represented by different letters upon bars (2 by 2 ANOVA tests).

Fig.2: Size structure of macroinvertebrate communities on different substrata in a) undeveloped and b) developed lakes. Each bar (with standard error) represents the

average biomass of organisms in each size class. Average biomass was calculated over 12 sampling stations in the 4 undeveloped lakes, and over 9 stations in the 3 developed lakes. Mean size of organisms (± 1 SE) are presented in the upper left corner.

Fig.3: Invertebrate / periphyton biomasses ratio for sediments, rocks, wood and macrophytes in the 7 studied lakes of the Laurentian region. Significant differences ($P<0.05$) among substrata are represented by different letters upon bars (2 by 2 ANOVA tests).

Fig.4: Proportion of total biomass represented by dominant macroinvertebrates on a) sediments, rocks and wood of undeveloped lakes and b) sediments, rocks and macrophytes of developed lakes. Values are averages of three replicates. For each lake, only groups representing at least 5% of total biomass are shown while the other taxa are grouped as "Others". For more details, see appendices 1 and 2.

Fig.5: Principal component analysis (PCA) performed on macroinvertebrate communities on different natural substrata for a) undeveloped lakes (19 taxa) and b) developed lakes (18 taxa) of the Laurentian region.

Fig 6: Percentage of total invertebrate biomass at the lake scale associated to different types of substratum in undeveloped and developed lakes. Values were calculated keeping in account for each substratum the invertebrate biomass (mg/m^2) weighted for the % of cover (Table 1). Values in brackets are the total areal invertebrate biomass in littoral zone at the lake scale (mg/m^2).

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Chapitre 1 :
Introduction générale

1.1 Les invertébrés benthiques

Les invertébrés benthiques sont des animaux aquatiques qui vivent, durant au moins un stade de leur vie, en association avec un substrat (Rosenberg and Resh 1993) par opposition aux invertébrés planctoniques qui vivent suspendus dans la colonne d'eau, sans association nette avec un substrat. Les invertébrés benthiques sont des organismes ayant un rôle écologique important dans les systèmes lacustres: ils accumulent le carbone en se nourrissant de matière organique particulaire ou d'algues benthiques fixées sur le substrat (périphyton) et le transfèrent vers les niveaux trophiques supérieurs comme les poissons (Eggers et al. 1978; Jònasson 1978; Wetzel 1983; Plante et Downing 1989). Ce sont donc des acteurs très importants au niveau des transferts trophiques survenant entre la zone littorale et la zone pélagique des lacs (Vadeboncoeur et al. 2002).

Les plus fortes biomasses et diversités d'invertébrés benthiques dans les lacs se retrouvent dans la zone littorale (Brinkhurst et Jamieson 1971; Johnson 1974; Tessier 2004; Tessier et al. 2007) qui leur offre une complexité et une hétérogénéité importantes d'habitats due à la présence de nombreux types de substrats (Tolonen et al 2001; Schindler et Scheuerell 2002) et de grandes quantités de nourriture, comme les débris végétaux, le périphyton et le détritus. Dans les lacs, les substrats naturels colonisés par les invertébrés benthiques sont généralement les sédiments, les roches, les troncs d'arbre submergés et les macrophytes. Cependant, tout type de surface, même artificiel, peut être colonisé par les invertébrés (quais, bouées, etc.). Les communautés d'invertébrés benthiques (ou macroinvertébrés) sont très diversifiées et composées de plusieurs taxons : larves d'insectes, crustacés, mollusques, acariens, hydres, vers. Les communautés de macroinvertébrés ne sont pas aléatoirement distribuées dans la zone littorale des lacs (Minshall et Petersen 1985; Melo et Froelich 2001). Au contraire, elles sont sensibles aux conditions de leur environnement et varient en fonction des caractéristiques du milieu, qu'elles soient naturelles, de natures abiotique et biotique, ou anthropique.

Parmi les facteurs naturels de nature abiotique, les communautés d'invertébrés répondent aux variations de la morphométrie des lacs et de la qualité physico-chimique des eaux. Ainsi, la biomasse totale d'invertébrés benthiques dans des lacs varie avec la pente du littoral, l'exposition au vent et la concentration en calcium et en chlore (Rasmussen 1988). La composition taxinomique des communautés de macroinvertébrés varie en fonction du pH de l'eau (Stephenson et al. 1994) et de sa conductivité (Pinel-Alloul et al. 1996). D'autres facteurs tels que la composition des sédiments et leur granulométrie (Robbins et al. 1989) ainsi que le statut trophique et l'abondance des nutriments sont importants pour expliquer l'abondance des invertébrés (Mundi et al. 1991; Bluemenshine et al. 1997) ainsi que leur composition taxinomique (Suren et al. 2003).

Parmi les facteurs naturels de nature biotique, l'importance des herbiers en zone littorale des lacs (Cyr et Downing 1988) et la présence de troncs d'arbres submergés (Benke et Wallace 2003) influencent les communautés d'invertébrés benthiques. Notons également l'effet important de la prédation par les vertébrés : plusieurs poissons se nourrissent en sélectionnant les plus gros invertébrés et affecte les communautés benthiques en réduisant leur spectre de taille (Tolonen et al. 2003).

Le type de substrat est aussi un des facteurs les plus important structurant les communautés d'invertébrés benthiques (Brown et Brussock 1991; Tolonen et al. 2001, Buss et al. 2004). Plusieurs espèces peuvent coloniser plus d'un type de substrat (Hynes 1970). Cependant, beaucoup d'entre elles ont des préférences et choisissent de vivre en association avec le substrat qui leur convient mieux. Par exemple, des espèces de macrophytes différentes supportent des communautés d'invertébrés différentes (Hanson 1990; Feldman 2001). Certains organismes sont xylophages obligatoires ou facultatifs et ont donc des préférences pour les substrats ligneux (Hoffmann et Hering 2000). Les organismes endobenthiques vont préférer les substrats mous (comme les sédiments) pour pouvoir s'y enfouir plutôt que les substrats durs comme les roches. Comme les communautés d'invertébrés varient d'un type de substrat à l'autre, il est important de considérer ce facteur dans l'évaluation des effets des facteurs naturels et/ou des perturbations anthropiques sur ces communautés.

Parmi les facteurs anthropiques et toxicologiques, la concentration des métaux lourds dans l'eau et les sédiments (Newell et al. 1990; Rosenberg et Resh 1993; Pinel-Alloul et al. 1996; Courtney et Clements 2002), de même que la présence dans l'eau de traces de polluants organiques comme les pesticides (Woin 1998; Berenzen et al. 2005), influencent la composition des communautés d'invertébrés benthiques le plus souvent en diminuant leur diversité suite à la disparition d'espèces non tolérantes à ces sources de pollution.

Les invertébrés benthiques sont des organismes idéaux pouvant servir d'indicateurs de l'intensité des perturbations anthropiques (Pratt et Coler 1981): ils ont une courte durée de vie, ce qui permet aux communautés de se modifier rapidement avec les changements de la qualité de l'eau et des ressources; ils sont peu mobiles et donc représentatifs des conditions locales; ils sont faciles à échantillonner à partir des berges et requièrent un minimum de matériel pour l'échantillonnage et l'analyse en laboratoire. Comptant à la fois des organismes sensibles et d'autres tolérants à des polluants spécifiques ou à des perturbations générales de nature anthropique, les communautés de macroinvertébrés benthiques représentent de puissants outils largement utilisés et mondialement reconnus dans la gestion des lacs et surtout des cours d'eau (Hynes 1966; Pratt et Coler 1981; Milbrink 1983; Schindler 1987; Rosenberg et Resh 1993; Blocksom et al. 2002; Haase et al. 2004). Par exemple, la métrique EPT (Éphémères, Plécoptères, Trichoptères) est couramment utilisée pour évaluer la qualité des cours d'eau (Lenat 1988; Klemm et al. 2001; Bednarek et Hart 2005). Ces organismes sont typiques des milieux propres et naturels et sont sensibles à la pollution et aux perturbations de leur environnement; ainsi la richesse en taxons d'insectes appartenant à la métrique EPT est fortement corrélée à la qualité de l'eau de l'environnement aquatique et constitue un outil diagnostique efficace pour déterminer l'intégrité d'un système (Kirsh 1999). D'autres organismes tels les oligochètes et les nématodes sont utilisés comme sentinelles pour la gestion de la pollution par les métaux traces qui sont présents dans les sédiments et les sols (Hart et al. 1986; Monserrat et al. 2003). La présence ainsi que l'abondance des oligochètes sont souvent utilisées comme indicateurs du statut trophique des systèmes lacustres ou ripicoles, car ce sont des organismes typiquement retrouvés dans les milieux enrichis et productifs (Wiederholm 1980).

1.2 Les perturbations anthropiques

La zone littorale est la partie des lacs la plus influencée par les changements dans les conditions environnementales du bassin versant : c'est elle qui reçoit en premier, avant la zone pélagique, les nutriments et le matériel détritique provenant du bassin versant par les eaux de ruissellement et de percolation ainsi que les débris végétaux allochtones venant de la zone riveraine (Wetzel et Allen 1972; Christensen et al. 1996). Elle est donc un milieu très sensible aux changements naturels et aux perturbations des rives et du bassin versant. Les perturbations anthropiques autour des petits lacs (déboisement, épandage d'engrais, déchets domestiques, fosses septiques défectueuses, enlèvement des macrophytes et du bois mort de la zone littorale, activités de pêche, utilisation des bateaux de plaisance…) affectent l'intégrité et la qualité de la zone littorale principalement en réduisant la diversité des habitats littoraux et en stimulant la productivité primaire des macrophytes et du périphyton (Lambert 2006; Lambert et al. 2007).

La réduction de la diversité des habitats littoraux est souvent une conséquence de la diminution de l'introduction naturelle dans la zone littorale de troncs d'arbres morts, de branches, de feuilles et de débris ligneux venant des rives, principalement causée par le déboisement riverain (Christensen et al. 1996; Jennings et al. 2003; Francis et Schindler 2006). La disponibilité de substrat ligneux en zone littorale change donc avec le niveau de perturbation des rives. De plus, l'érosion du bassin versant générée par les perturbations anthropiques (dans le cas qui nous intéresse, la construction de résidences) est causée par le déboisement non seulement des rives mais également sur tout le bassin versant. Cela crée un enlisement au cours duquel les particules fines exportées du bassin versant sédimentent en zone littorale, remplissent et colmatent les espaces vides autour des particules grossières dans les sédiments, ce qui contribue à diminuer l'hétérogénéité des habitats et a réduire les refuges pour certains organismes (Jennings et al. 2003). Les perturbations anthropiques augmentent la disponibilité des nutriments comme le phosphore et l'azote qui sont alors introduits dans le système lacustre (Frink 1991), ce qui provoque l'augmentation de la productivité primaire littorale. Il a été depuis longtemps prouvé que le phosphore est le nutriment qui limite la croissance des algues planctoniques dans la zone pélagique des lacs canadiens (Sakamoto 1971; Schindler et al. 1971). Cependant, puisque le phosphore venant du bassin versant atteint la zone littorale avant la zone pélagique, l'enrichissement ponctuel en nutriments a pour effet d'augmenter la productivité du périphyton et des macrophytes dans la zone littorale avant celle du plancton pélagique. Les macrophytes et le périphyton constituent alors un puits important pour le phosphore nouvellement introduit dans le système lacustre qui n'est pas directement transféré dans la zone pélagique (Peterson et al. 1983; Havens et al. 2004; Lambert 2006). L'augmentation de la productivité primaire dans la zone littorale, notamment l'accroissement de la biomasse du périphyton, représente une plus grande quantité de ressources nutritives pour les invertébrés benthiques qui peuvent ainsi augmenter leur biomasse (Mundi et al. 1991; Perrin et Richardson 1997; Bourassa et Cattaneo 1998). C'est ce qu'on appelle l'effet ascendant (bottom-up).

Tous ces changements dans la zone littorale induits par les perturbations anthropiques sont susceptibles d'affecter les communautés d'invertébrés benthiques.

1.3 Les lacs de villégiature des Laurentides

Les Laurentides sont une région de plus de 20 000 km^2 située au nord de Montréal et qui compte près de 10 000 lacs. Ces lacs sont d'origine glaciaire et la plupart d'entre eux sont oligotrophes et possèdent des eaux claires. Cependant, de plus en plus de ces lacs démontrent des indices d'eutrophisation, surtout observés en zone littorale (Lambert 2006) ; les perturbations anthropiques pourraient certainement en être la cause. Entre 1971 et 2003, la région a connu une hausse de 98.4% de sa population, la deuxième plus importante hausse démographique au Québec (après celle de la région de Lanaudière), ce qui correspond à une hausse brute de 241 615 personnes (Institut de la statistique du Québec). Une des conséquences de cette hausse est la conversion de chalets saisonniers en résidences permanentes et la construction de nouvelles habitations (Laurin 2000). On observe généralement une forte concentration d'habitations près des berges des lacs laissant le reste du bassin versant souvent presque intact. L'intensification de la villégiature et le développement de l'industrie touristique affectent aussi les bassins versants des lacs (parcours de golf, pistes de ski, terrains de camping, etc.).

De plus en plus de riverains se plaignent des changements qui surviennent dans l'apparence de leur lac : la prolifération des algues et des macrophytes dans la zone littorale rend les activités nautiques désagréables. Plusieurs se regroupent au sein d'associations pour la préservation de leur lac et sont prêts à faire des efforts pour contrer son eutrophisation. Il est donc très important de bien comprendre les effets des perturbations anthropiques sur la zone littorale de ces lacs, notamment en étudiant la réponse des invertébrés benthiques qui sont susceptibles de constituer de bons outils pour la gestion de ces lacs.

1.4 Objectifs et hypothèses de recherche

Le but principal de cette étude est de vérifier si les communautés d'invertébrés benthiques varient selon le type de substrat et si elles sont affectées par le développement résidentiel dans les bassins versants des lacs des Laurentides. Pour ce faire, nous avons échantillonné des invertébrés benthiques, au cours de l'été 2003, dans la zone littorale de treize lacs représentant un gradient de développement résidentiel des bassins versants et ce, sur différents substrats naturels. Les sédiments et les roches sont présents dans tous les lacs alors que les bois submergés se retrouvent en quantité suffisante seulement dans les lacs les moins perturbés et les macrophytes constituent des habitats importants seulement dans les lacs les plus perturbés.

Au Chapitre 2, les communautés d'invertébrés des sédiments et des roches ont été comparées pour l'ensemble des treize lacs sur la base de la biomasse totale, la structure en taille et la composition taxinomique. Les objectifs étaient de trouver le substrat sur lequel les communautés d'invertébrés répondaient le mieux aux perturbations et d'identifier les organismes pouvant être indicateurs de la bonne et de la mauvaise qualité du milieu littoral. Il est attendu, selon l'hypothèse de l'effet ascendant, que la biomasse totale d'invertébrés augmente le long du gradient de perturbation en réponse à l'augmentation de la biomasse de périphyton, tel qu'observé par Lambert (2006) dans les mêmes lacs. Nous anticipions également des changements dans la structure en taille et surtout dans la composition taxinomique des communautés d'invertébrés en réponse aux possibles altérations des substrats pouvant être provoquées par les perturbations anthropiques. Afin de tester la signification des relations pouvant exister entre la biomasse totale d'invertébrés et l'intensité des perturbations anthropiques ou la biomasse du périphyton, des régressions simples ont été utilisées. La structure en taille a été comparée par observation des graphiques représentant la distribution de la biomasse d'invertébrés dans chacune des classes de taille pour 3 groupes de lacs (non-perturbés, modérément perturbés et perturbés) séparément sur les sédiments et sur les roches. Enfin, pour déterminer si la composition taxinomique des communautés variait significativement le long du gradient de perturbation, nous avons eu recours à des Analyses Canoniques de Redondance (ACR) testant les relations existant entre les abondances d'espèces et les variables environnementales constituées de facteurs naturels et de facteurs décrivant les perturbations.

Au Chapitre 3, sept des treize lacs regroupés en deux catégories (4 lacs peu perturbés et 3 lacs perturbés) ont été étudiés dans le but de comparer les communautés d'invertébrés sur des substrats naturels différents (sédiments, roches, bois et macrophytes). Puisque les types d'habitats varient entre les deux groupes de lacs (absence de macrophytes dans les lacs peu perturbés, absence de bois submergés dans les lacs perturbés) et que les substrats de roches et de sédiments présents dans tous les lacs peuvent être altérés par les perturbations anthropiques, il était attendu que les communautés d'invertébrés benthiques soient différentes entre les deux groupes de lacs. De plus, comme le type substrat est un facteur important influençant les communautés d'invertébrés, nous nous attendions à observer des différences significatives au niveau de la biomasse totale, de la structure en taille et de la composition taxinomique entre les substrats. Nous avons utilisé l'ANOVA simple pour tester la signification des différences entre les substrats concernant la biomasse totale des invertébrés. L'ANOVA factorielle à deux critères de classification en mode multivariable a été utilisée pour tester les différences de composition taxinomique des communautés d'invertébrés entre les substrats et les lacs (l'interaction entre ces deux critères a aussi pu être testée). La taille des organismes a été comparée visuellement entre les substrats d'après les spectres de taille et d'après les valeurs de taille moyenne calculée pour chaque type de substrat.

La recherche apporte une contribution significative aux domaines de la limnologie, de l'écologie du benthos et de la gestion des lacs. Bien que les invertébrés benthiques soient couramment utilisés pour la gestion des cours d'eau, très peu d'études se sont consacrées à l'influence des perturbations anthropiques sur les invertébrés benthiques de la zone littorale des lacs (Schindler et Scheuerell 2002). Peu d'études ont comparé les communautés de macroinvertébrés benthiques sur différents substrats dans la zone littorale des lacs et aucune, à notre connaissance, n'a directement comparé les sédiments, les roches, les bois et les macrophytes. Il serait donc utile de déterminer 1) quels taxons pourraient être utilisés comme indicateurs de la qualité de la zone littorale des lacs, et 2) sur quel substrat il serait plus efficace d'échantillonner les invertébrés dans une perspective de gestion des lacs de villégiature de la région des Laurentides.

De plus, nous remarquons que l'effet ascendant a souvent été mis en évidence lors d'expériences d'enrichissements ponctuels en nutriments dans des études utilisant des mésocosmes en rivières et en lacs. Dans notre étude, nous avons testé pour la première fois l'hypothèse de l'effet ascendant dans des lacs non manipulés et ayant subi des perturbations anthropiques qui ont engendré une augmentation de la production de périphyton dans la zone littorale, un indice précoce de l'eutrophisation anthropique des lacs de villégiature des Laurentides (Lambert 2006).

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Chapitre 2:

Response of littoral macroinvertebrate communities on rocks and sediments to lake residential development

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Abstract

Previously pristine lakes of the Laurentian region of Quebec face increasing residential development of their watershed. We tested whether littoral invertebrates respond to this perturbation, even though open water nutrients and chlorophyll are not yet altered. We examined changes in biomass, size structure, and taxonomic composition of macroinvertebrates living on rocks and sediments in 13 lakes representing a gradient of lakeshore residential development and watershed clearing. Littoral invertebrates provided early indication of lake perturbation but their response varied according to the substratum. On rocks, total invertebrate biomass significantly increased along the development gradient and size structure shifted towards larger organisms. These changes were likely mediated by a concomitant increase in periphyton biomass suggesting a bottom-up control of rock dwelling invertebrates. No significant change in total biomass and size structure along the gradient was observed for invertebrates in sediments. However, invertebrate taxonomic composition changed with lake development in sediments but not on rocks. Taxonomic shifts were probably related to changes in sediment heterogeneity due to decline of woody litter and increase of fine particle deposition. Oligochaetes were positively associated to the perturbation whereas mayflies were negatively correlated; these taxa could be used as indicators. Sediments were a better sentinel substratum than rocks for biomonitoring the impact of lake residential development.

Résumé

Plusieurs lacs non perturbés de la région des Laurentides au Québec connaissent une augmentation du développement résidentiel dans leur bassin versant. Nous avons testé si les invertébrés littoraux répondaient à ces perturbations malgré le fait que les concentrations en nutriments et en chlorophylle de la colonne d'eau demeurent inaltérées. Nous avons donc examiné les changements en biomasse, classes de tailles et composition taxinomique des macroinvertébrés vivant sur les roches et les sédiments dans 13 lacs représentant un gradient de développement résidentiel et de déboisement riverain. Les invertébrés littoraux constituent un indicateur précoce des perturbations, mais leur réponse varie selon le substrat. Sur les roches, la biomasse totale d'invertébrés augmente significativement le long du gradient de développement résidentiel et les organismes sont plus gros. Ces changements sont vraisemblablement induits par l'augmentation concomitante de la biomasse du périphyton, suggérant un effet ascendant (bottom-up) sur les invertébrés des roches. Aucun changement significatif concernant la biomasse totale ou la grosseur des organismes n'est observé le long du gradient pour les invertébrés des sédiments. Par contre, contrairement aux communautés des roches, la composition taxinomique des invertébrés des sédiments change avec les perturbations. Ces changements sont probablement reliés à la diminution de l'hétérogénéité des sédiments due à la rareté de la litière ligneuse et à l'augmentation de la sédimentation de particules fines. Les oligochètes sont positivement associés aux perturbations contrairement aux éphémères qui le sont négativement. Ces taxons pourraient donc être utilisés comme indicateurs. Les sédiments sont donc considérés comme le meilleur substrat à échantillonner pour les programmes de gestion des impacts du développement résidentiel près des lacs.

Introduction

The littoral zone of lakes presents a variety of aquatic habitats that support high biomass and diversity of benthic algae and invertebrates (Wetzel 1996). Residential development of shore and watershed may directly affect littoral habitats, which are the first to receive the inputs of terrestrial nutrients and detritus (Wetzel and Allen 1972; Christensen et al. 1996). Forest clearing, shore erosion, discharge of domestic waste and fertilisers and harvesting of submerged wood and macrophytes may increase nutrient availability (Frink 1991) but reduce habitat diversity through loss of woody debris and accumulation of fine particles transported from the disturbed watershed (Christensen et al. 1996; Jennings et al. 2003).

The Laurentian region of Quebec is rich in thousands of lakes, which are still mostly oligotrophic. In the last few decades, this region sustained a remarkable demographic development due to a 98.4% rise in population between 1971 and 2003 (Institut de la statistique du Québec: http://www.stat.gouv.qc.ca; Laurin 2000). As a consequence, previously pristine lakes are experiencing increased disruption of their watershed that is concentrated along the shore where cottages are preferentially built. The littoral zone of several of these lakes is already showing increased abundance of periphyton and macrophytes (Lambert 2006).

The aim of this study is to determine the effects of lake recreational development on littoral macroinvertebrate communities in the Laurentian lakes of Québec. We examined changes in biomass, size structure, and taxonomic composition of macroinvertebrate communities living on rocks and sediments in 13 lakes representing a gradient of lakeshore residential development and watershed clearing. We hypothesized that the invertebrate communities would be affected through different mechanisms whose importance might change depending on the substratum. In oligotrophic lakes, resources rather than predators are expected to control benthic invertebrates (Oksanen et al. 1981, Power 1992). Thus, an increase in periphyton biomass with lake residential development should translate into increased benthic invertebrate biomass (Mundi et al. 1991; Perrin and Richardson 1997). Because the response of periphyton to water enrichment tends to be stronger on hard than on soft substrata (Blumenshine et al. 1997; Lambert 2006), we expect a stronger increase in invertebrate biomass on rock than on sediments. On the other hand, sediments would experience a change in their heterogeneity due to decline of woody litter and increase of fine particle deposition whereas rocks would be less affected by changes in siltation. Habitat complexity may affect biomass and composition of invertebrate communities (Jenning et al. 2003).

Our results may have several implications for management of lakes undergoing recreational development. Because macroinvertebrates represent a central position in the littoral food chain, changes in their biomass and individual size would affect the lake trophic network. The study of changes in taxonomic composition along the perturbation gradient might identify the best taxa and the best substratum for establishing an effective monitoring program for these lakes.

Methods

Study site

The studied lakes are situated north of Montréal (Québec) in the Laurentian region of the eastern Canadian Shield within a 65 km radius from the "Station de Biologie des Laurentides" (SBL; 45°59'N, 73°60'W). This region of mixed forest is underlain by gneiss and granitic rocks covered by morainic soils. Thirteen small to medium size lakes (area: 0.07 – 1.24

km^2) were chosen to represent a gradient of residential development (from 0 to 340.3 dwellings/km^2) and forest clearing (0 to 53% of cleared land) on their watersheds (Table 1).

According to trophic classification (OCDE 1982), these lakes were still oligotrophic except two (lac Renée and lac Rond), which approached mesotrophy with mean summer total phosphorus exceeding 10 µg/L (14 and 13 µg/L, respectively) and mean summer total nitrogen above 400 µg/L, at least in lac Renée (486 µg/L) (Table 2). The lakes covered a wide range of dissolved organic carbon concentrations going from clear water (DOC < 3 mg/L) to humic lakes (DOC > 6 mg/L). All lakes were circumneutral or slightly acidic (Table 2). Periphyton biomass varied 12 fold on sediments and 36 fold on rocks among lakes, whereas phytoplankton biomass varied less (6.2 fold) (Table 2). According to the Canadian Soil Classification (Groupe de travail sur la classification des sols 2002), sediments were mainly composed of medium, coarse, and very coarse sand with small gravel in pristine lakes, while fine sand and clay were the most important fraction in developed lakes (Table 2). The percentage of fine particles (< 250 µm) varied from 13 to 84% of total sediments mass among lakes.

Table 1: Watershed and lake morphological characteristics. calculated morphological indices. and watershed human-induced disturbance factors for the 13 studied lakes of the Laurentian region of Quebec. D-100 = dwelling density within 100 m wide riparian strip. D-ws = dwelling density for the whole watershed. CL-50 = % of cleared land within a 50 m wide riparian strip. CL-ws = % of cleared land for the whole watershed. Data are not shown for D- and CL- within 200. 500. and 1000 m wide riparian strips. Lakes were grouped accordingly to dwelling density on the 100-m wide riparian strip: I = 0-12.5; II = 115.3–175.5; III = 372.7-552.

	Ws area (km^2)	Lake area (km^2)	Lake volume ($10^3 \cdot m^3$)	Max Depth (m)	Mean depth (m)	Relative depth	Ws mean slope (%)	Drainage ratio	Ws area relative to lake volume (km·2·m-3)	Groups	Anthropogenic development D-100 ($nb \cdot km^{-2}$)	D-ws ($nb \cdot km^{-2}$)	CL-50 (%)	CL-ws (%)
Cabane	2.45	0.25	1836	20.8	7.6	14.7	7.5	8.8	1.34	I	0	0	0	0
Croche	0.84	0.18	877	12.9	4.9	11.5	13	3.7	0.96	I	2.7	1.5	0	0
Violon	4.41	0.38	3325	22.6	8.9	14.1	9.2	10.5	1.33	I	12.5	3.1	0	1
Gervais	8.65	0.97	23526	60	24.5	24.8	6.2	8	0.37	II	115.3	21.1	2	0
Purvis	0.60	0.19	1446	19.7	7.8	17.4	10.6	2.2	0.42	II	117.1	89.2	13	8
Blanche	3.94	0.41	4590	26	11.7	17.4	8.2	8.6	0.86	II	122.9	16.1	17	1
Morency	2.33	0.26	2246	20.3	9.1	17	14.6	8	1.04	II	151.3	57.4	31	13
Du Nord	13.94	0.87	5514	20.6	6.4	6.8	12.5	15.1	2.53	II	167	18.4	40	40
Tracy	0.24	0.08	676	22.9	8.1	28.1	8.3	1.9	0.36	II	175.5	143.8	5	4
Rond	1.50	0.17	1206	15.8	7.2	17.7	7.5	8	1.24	III	372.7	241.5	86	53
Renée	0.22	0.07	296	9.5	4.2	15.8	10.1	2.1	0.73	III	399.9	340.3	38	30
Truite	4.23	0.51	4783	22.5	9.4	13.1	5.9	7.3	0.89	III	399.9	110.7	79	30
Connelly	24.36	1.24	9561	20.8	7.7	6.9	6.2	18.6	2.55	III	552	47.9	46	7

Table 2: Water quality, proportion of fine sediment particles, periphyton, and phytoplankton biomass in 13 lakes of the Laurentian region of Québec. TP = total phosphorus, TN = total nitrogen, DOC = dissolved organic carbon. Water quality variables and phytoplankton biomass are averaged over replicates taken at 6 dates in summer 2003 (Gélinas and Pinel-Alloul unpublished data, 2006). Periphyton biomasses are averaged over 5 stations sampled in June 2003 (Lambert, 2006). Proportion of fine sediment particles is the percentage of total sediment mass represented by particles < 250µm (De Sousa, unpublished data).

	Water quality				Proportion of fine sediment particles (%)	Periphyton Chl*a* (mg·m²)		Phytoplankton Chl-*a* (µg·L⁻¹)
	TP (µg·L⁻¹)	TN (µg·L⁻¹)	DOC (mg·L⁻¹)	pH		sedim.	rocks	
Cabane	8.2	259.8	3.6	6.2	12.9	97.9	33.2	3.01
Croche	5	256.9	4.1	6.2	14.6	165	46.7	1.26
Violon	5.7	215.1	3.5	6.6	14.6	21.3	5.7	1.23
Gervais	4.6	190.4	2.7	7	37.9	102.3	45.7	0.74
Purvis	10.3	272.7	3.1	7.2	48.4	94.5	82.5	2.73
Blanche	4.9	258	2.8	6.4	32.4	85.5	16.4	2.64
Morency	10.4	313.6	3.3	7.8	72.6	139.3	66.5	2.3
duNord	10	329.2	6.2	6.7	67.2	191.2	144.2	1.53
Tracy	6.2	266.5	2.9	7	50.4	35.7	19.4	1.34
Rond	13	384.6	3.6	8.1	55.6	208.8	119.6	4.61
René	14.2	485.6	4.2	6.1	72.3	104.9	64.5	3.85
Truite	6.5	290.5	3	7.7	84.1	217.4	118.3	1.72
Connelly	8	340	4.6	7.4	47.6	256.8	216.6	4.42

Macroinvertebrate sampling and analysis

Benthic macroinvertebrates were collected on rocks and sediments in July 2003. On each lake, we sampled five stations distributed regularly around its perimeter. All samples were collected at ~1m depth because this zone is rich in benthic invertenrates, not affected by waves and easily accessible; these considerations are important for future biomonitoring surveys. Invertebrates on rocks were sampled with a sampling device consisting in a Plexiglas cylinder (7.6 cm diameter) provided with a brush. This device was pressed against the rock by a diver and all the material dislodged by brushing (including invertebrates) was pumped into a Mason jar (Vis et al. 1998). Three replicates were combined together for a total sampling area of 136.09 cm^2. Invertebrates on sediments were sampled with a plastic core (area = 46.57cm^2) that was pushed down 10cm into the sediments. For rocks and sediments, the macroinvertebrates were concentrated by passing all the collected material through two successive sieves of 1mm and 500µm mesh size. Macroinvertebrates were preserved in 95% ethanol with addition of rose Bengal dye to stain the organisms and facilitate their sorting.

In the laboratory, invertebrates were sorted under a dissecting microscope (25X) and identified to order or class level (Edmondson 1959; Tachet et al. 1980; Merritt and Cummins 1996). Invertebrate body length was measured with an image analyser system (Image Pro-Plus) connected to a dissecting microscope. Dry mass of each organism was estimated using published length-mass relationships (Eckblad 1971; Dumont et al. 1975; Mason 1977; Roger et al. 1977; Tudorancea et al. 1979; Smock 1980; Peters and Downing 1984; Burgherr and Meyer 1997; Benke et al. 1999; Stoffels et al. 2003). Invertebrate biomass was expressed per surface unit ($mg \cdot m^{-2}$) by dividing the total biomass by the sampling area. To examine the community size structure, we grouped the invertebrates in log_2 increasing size classes: the size classes ranged from 4-8 μg to 4000-8000 μg.

Environmental variables

Watershed (area, mean slope) and lake morphological characteristics (area, volume, maximum and mean depth) were measured (MapInfo, V 6.5) from topographic and bathymetric maps. We also calculated some morphological indices: relative depth (1000 * average depth * lake area$^{1/2}$), drainage ratio (watershed area / lake area), and watershed area relative to lake volume (Table 1).

Total phosphorus (TP), total nitrogen (TN), dissolved organic carbon (DOC), pH, and phytoplankton biomass were measured in samples collected over the entire euphotic zone (defined as 1.7 times the Secchi depth) at the deepest site of the each lake six times during the growing season. Periphyton on rocks and sediments was collected four weeks before the invertebrate sampling (June 2003) at the same sites (Lambert 2006). Periphyton and phytoplankton biomass were estimated as chlorophyll *a* concentrations (Chl *a*). Analyses for water nutrients, periphyton and, phytoplankton are detailed in Lambert (2006).

To evaluate lake disturbance by residential development, dwelling density per km^2 and percentage of cleared land were measured (MapInfo, V. 6.5) on orthorectified aerial photographs (1:30 000 and 1:10 000) acquired in 2002 and 2004 (Lambert 2006). Because watershed development in the Laurentian region is usually concentrated around the lake shores, disturbance variables were estimated within riparian strips of increasing width (50, 100, 200, 500, 1000 m) and within the whole watershed (Table 1).

Statistical analyses

We used univariate and multivariate statistical analyses to evaluate the response of littoral invertebrate communities to anthropogenic disturbances keeping in account the natural environmental characteristics of the lakes. Regression models were developed to assess the response in terms of biomass, whereas redundancy analysis with forward selection (RDA) was used for assessing changes in taxonomic composition. We performed regression and redundancy analyses separately for rocks and sediments. Total invertebrate biomass was averaged over the 5 sampling sites in each lake in the regression analysis (n=13). In the RDA analysis, we used individual replicates (n=65) as number of sampling sites should be higher than number of explicative variables (Legendre and Legendre 1998). Prior to regression analysis, some variables were transformed to stabilize the variance and linearize the relationships. We used log transformation for invertebrate and periphyton biomasses as well as for water quality data and for watershed and lake morphological characteristics and indices; dwelling density was square-root-transformed and percent of cleared land was arcsine-transformed. For the multivariate analyses, explicative variables were not transformed but Hellinger's transformation was applied to the macroinvertebrates data (Legendre and Gallagher 2001).

We classified the environmental variables in two categories: i) natural watershed and lake characteristics (including morphometric variables and indices as well as pH that is not affected by lake development in this region, Tables 1 and 2), ii) human-induced disturbance factors included dwelling density and percentage of cleared land within the watershed and within riparian strips of different size (Table 1) together with environmental variables that may be influenced by lake development like periphyton and phytoplankton biomass, water nutrients, and percentage of fine sediments (Table 2). To compare the relative importance of natural versus disturbance variables in explaining the variation in taxonomic composition of macroinvertebrate communities, we used multivariate variance partitioning tests with adjusted R^2 (Legendre and Legendre 1998). All the analyses were performed using CANOCO (ter Braak 1990) and the Langage R package (Ihaka and Gentleman 1996), with a special function for RDA created by Pierre Legendre (Université de Montréal).

Results

Macroinvertebrate biomass and size structure

Total invertebrate biomass (TIB) was on average higher on sediments (1257 $mg \cdot m^{-2}$) than on rocks (195 $mg \cdot m^{-2}$) (ANOVA, $F = 139.3$, $P = 0.001$). TIB was not related to natural morphometric variables or indices both on sediments and rocks. The response to disturbance factors was different for the two substrata. Total invertebrate biomass on rocks increased significantly along the gradient of residential development (Fig. 1a, Table 3). TIB variation on rocks was better explained when disturbance descriptors were estimated within narrow riparian strip (100 m for dwelling density and 50 m for percentage of cleared land) rather than within wider strips (200, 500, and 1000 m) or within the whole watershed. In addition, TIB on rocks was significantly related to epilithon biomass (r^2 = 0.65, P =0.001, Fig.2a) but not to phytoplankton (Table 3). No relation was observed for TIB on rocks and water TP but there was a significant, albeit slight, relationship with TN (Table 3).

TIB in sediments remained largely unchanged among lakes and was not related to variables describing recreational development (Fig. 1b, Table 3). The only exception was a significant but weak relationship with percentage of cleared land within a 50 m riparian strip (Table 3). TIB in sediments was not related to epipelon biomass (Fig. 2b), and water nutrient, but was weakly related to phytoplankton biomass (Table 3).

To compare the size structure of macroinvertebrate communities along the development gradient, we grouped the lakes into three categories according to their level of residential development expressed as dwelling density within the first 100 m of shore: 3 pristine lakes (from 0 to 12 dwellings·km^{-2}), 6 moderately perturbed lakes (from 115 to 175 dwellings·km^{-2}), and 4 highly perturbed lakes (from 373 to 552 dwellings·km^{-2}) (Table 1). Macroinvertebrate size distributions were unimodal for both rocks and sediments and this could probably reflect the use of the 500 µm mesh size sieve that retained only large organisms (Fig. 3). Residential development affected macroinvertebrate size structure on rocks. In pristine lakes, macroinvertebrates on rocks were small (all < 125 µg) but their size range progressively increased with the perturbation level. Invertebrates larger than 125 µg constituted 17% of total biomass in moderately perturbed lakes and 29% in the most developed lakes. Mean individual size increased accordingly from pristine (10.5 µg) to highly perturbed lakes (37.5 µg) (Fig. 3a). In contrast, macroinvertebrate size structure on sediments did not vary greatly with the perturbation level. Invertebrates larger than 125 µg constituted 44% of total biomass in pristine lakes, 34% in moderately perturbed lakes, and 41% in the most developed lakes. The smallest mean individual size was observed in the moderately perturbed lakes (Fig. 3b). In all lakes, invertebrates in sediments were on average larger than on rocks, but this difference decreased from 10-fold to 3-fold with lake residential development.

Fig.1: Total invertebrate biomass (TIB) along the gradient of shore residential development for a) rocks and b) sediments. Adjusted r^2 are presented for both relationships; (n = 13). Regression line is shown only for the significant relationship (a) for which the regression model is: $Log_{10}TIB = 0.060*(D-100)^{1/2} + 1.301$

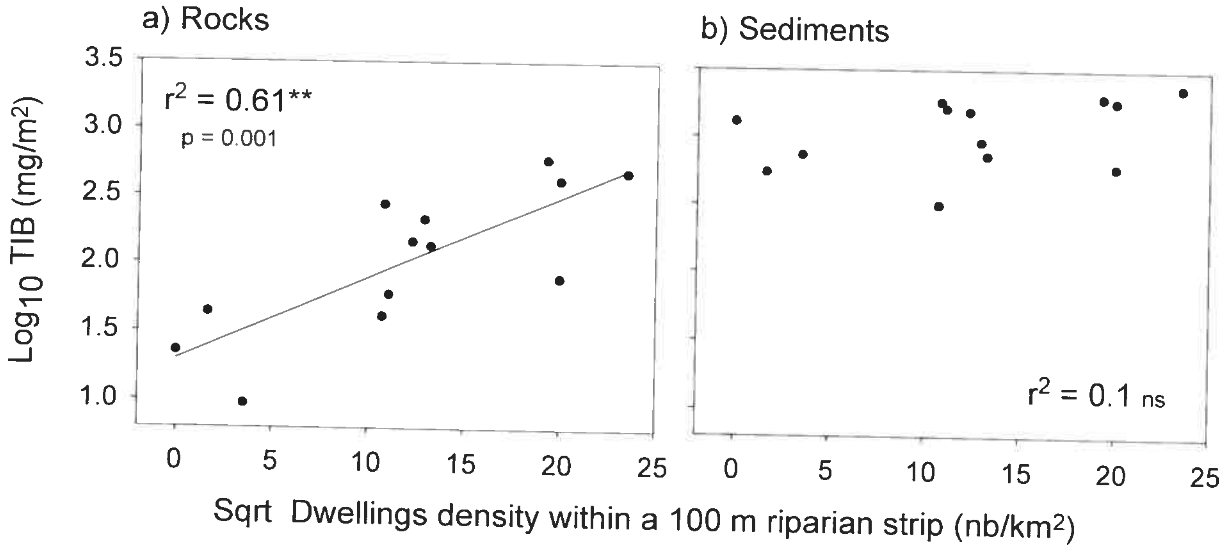

a) Rocks
b) Sediments
$r^2 = 0.61^{**}$
p = 0.001
$r^2 = 0.1$ ns
Log10 TIB (mg/m2)
3.5
3.0
2.5
2.0
1.5
1.0
0
5
10
15
20
25
Sqrt Dwellings density within a 100 m riparian strip (nb/km2)

Fig.2: Total invertebrate biomass (TIB) in relation with periphyton chl-*a* biomass on a) rocks and b) sediments. Adjusted r^2 are presented for both relationships: ($n = 13$). Regression line is shown only for the significant relationship (a) for which the regression model is: $Log_{10}TIB = 1.031*(Log_{10}\,periphyton\ chl\text{-}a) + 0.263$

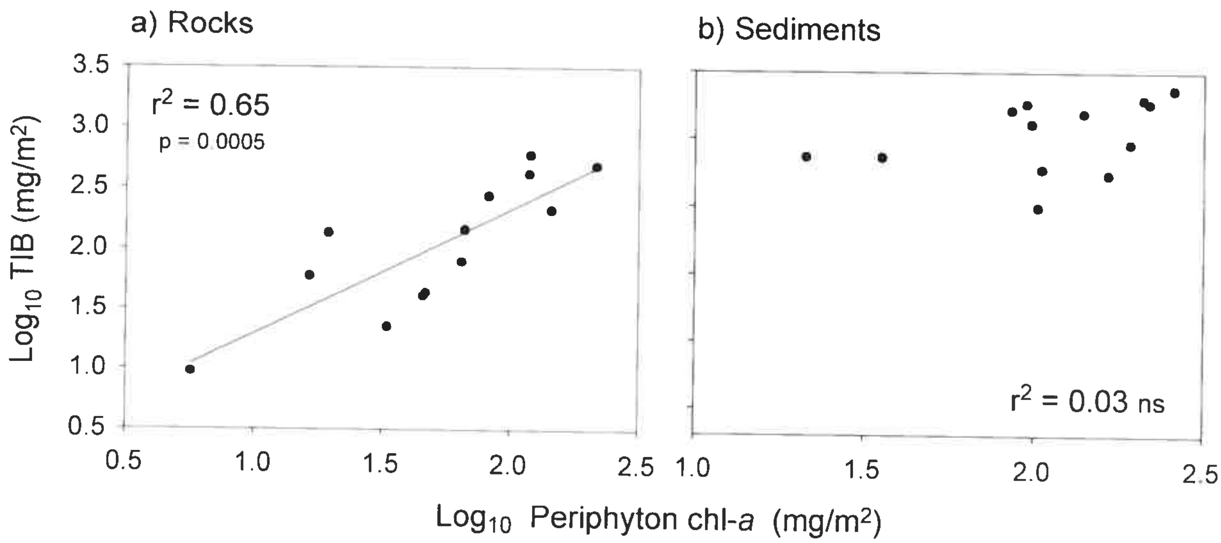
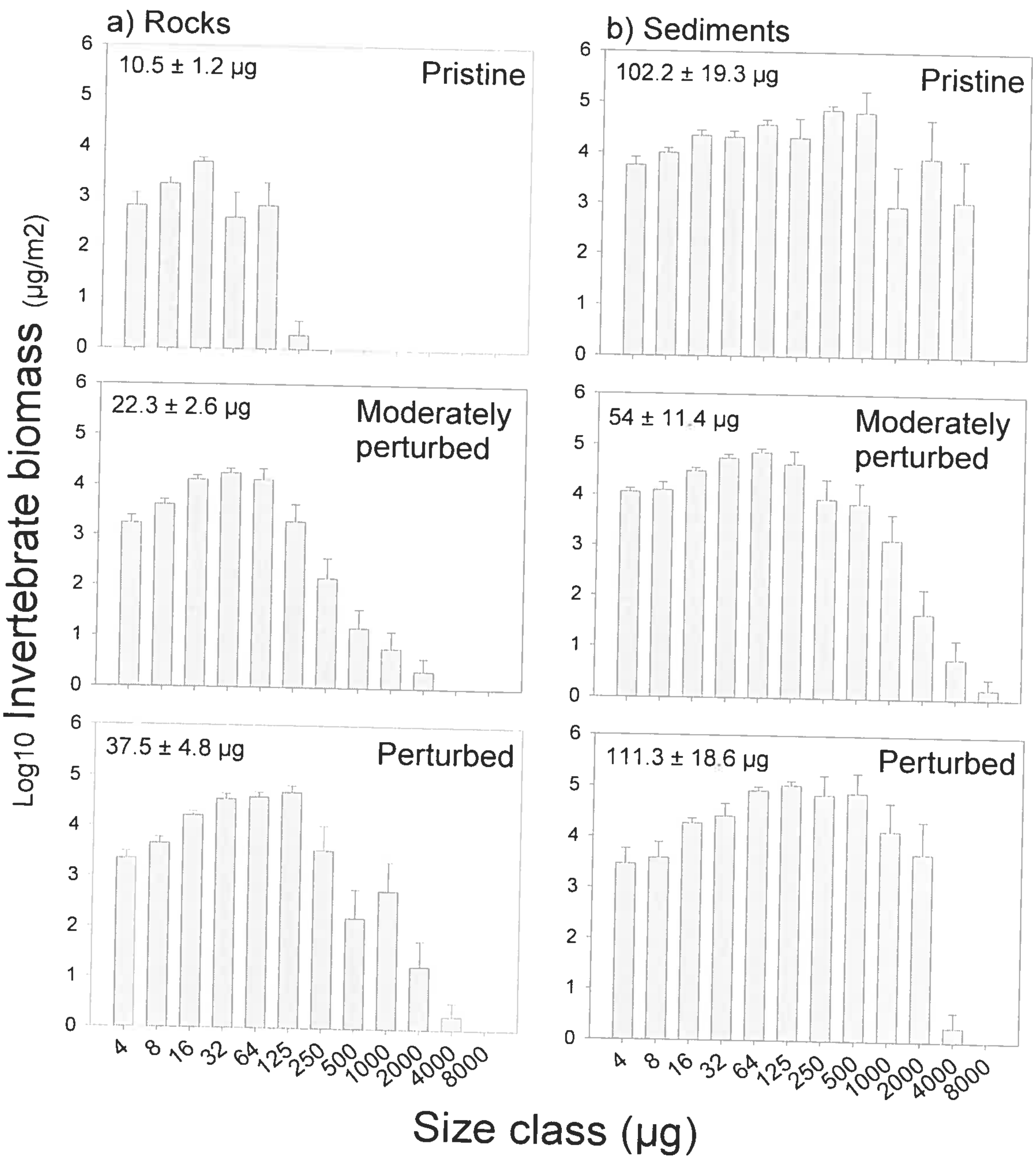

a) Rocks
b) Sediments
r² = 0.65
p = 0.0005
r² = 0.03 ns
Log10 TIB (mg/m²)
Log10 Periphyton chl-a (mg/m²)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.5
1.0
1.5
2.0
2.5
1.0
1.5
2.0
2.5

Table 3. Adjusted coefficient of determination (R^2_{adj}) for simple regressions between several explanatory variables; TP (log_{10} total phosphorus), TN (log_{10} total nitrogen), chl-*a* (log_{10} periphyton biomass on rocks and sediments or phytoplankton), TIB (log_{10} total invertebrate biomass on rocks and sediments), D-100 (square root of dwelling density within a 100 m strip around the shore and for the whole watershed (D-ws)), CL (percentage of cleared land within a 50 m strip around the lake (CL-50) and for the whole watershed (CL-ws)). The relationship of TIB with D-50 was weaker than with D-100, so the latter is presented. Disturbances factors calculated for other riparian strips (150, 200, 250, 500, and 1000 m.) were less well related with TIB and are not presented. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, n=13.

	TP	TN	Chl-*a* Phyto	Chl-*a* Rocks	Chl-*a* Sed.	D-100	D-ws	CL-50	CL-ws
TIB rocks	0.16	0.26*	0.16	0.65***	-	0.61**	0.30*	0.56**	0.34*
TIB sed.	0.07	0.06	0.34*	-	0.03	0.10	0.005	0.25*	0.04

Fig.3: Size structure of macroinvertebrate communities on a) rocks and b) sediments. Each bar (with standard error) represents the average biomass for each size class. Average biomass was calculated over 5 stations in 3 pristine lakes (n=15), 6 moderately perturbed lakes (n=30), and 4 perturbed lakes (n=20). Mean individual size (±1 standard error) is presented in the upper right corner of each graph. Lakes were grouped into 3 categories according to their level of residential development within a 100 m riparian strip: i) pristine (from 0 to 12 dwellings·km^{-2}), ii) moderately perturbed lakes (from 115 to 175 dwellings·km^{-2}), and iii) perturbed lakes (from 373 to 552 dwellings·km^{-2}).



a) Rocks
b) Sediments
10.5 ± 1.2 µg
Pristine
102.2 ± 19.3 µg
Pristine
22.3 ± 2.6 µg
Moderately perturbed
54 ± 11.4 µg
Moderately perturbed
37.5 ± 4.8 µg
Perturbed
111.3 ± 18.6 µg
Perturbed
Log10 Invertebrate biomass (µg/m2)
4 8 16 32 64 125 250 500 1000 2000 4000 8000
Size class (µg)

Macroinvertebrate taxonomic composition and indicator taxa

Taxonomic composition of macroinvertebrate communities was different on rocks and sediments. Dipterans chironomid were dominant on rocks in most of the 13 lakes (Fig. 4a, Appendix 1). In sediments, we observed a co-dominance of large insect larvae of Anisoptera, Ephemeroptera and Trichoptera in the less perturbed lakes, while Chironomidae and Oligochaeta were co-dominant in the most perturbed lakes (Fig. 4b, Appendix 2). Lake Tracy had a peculiar community dominated by Amphipoda both on rocks and sediments.

Macroinvertebrate taxonomic composition on rocks was primarily influenced by natural environmental variables: relative depth, watershed area divided by lake volume, and pH (Fig. 5a). However, these natural variables explained only 12% of among-lake variation in macroinvertebrate composition on rocks. Relative depth, a proxy of lake steepness, was the best explanatory variable indicating a dominance of amphipods in steeper lakes in one hand, and of oligochaetes and chironomids in shallower lakes. Taxonomic composition of macroinvertebrates on rocks was not influenced by any variables related to lake residential development.

In sediments, natural and disturbance variables together explained 23% of among-lake variation in macroinvertebrate taxonomic composition (Fig. 5b); this is almost twice the variation explained for communities on rocks (Fig. 5a). Macroinvertebrate composition in sediments was more influenced by disturbance variables than by natural environmental variables. The first axis of the RDA represented the residential development gradient. Dwelling density (D-100), percentage of cleared land (CL-50), TP concentration, and percentage of fine particles in sediments were the best explanatory variables. Anthropogenic variables calculated for wider riparian strips (D and CL 200, 500, and 1000 m) did not explain well taxonomic composition. A natural morphometric variable (relative depth) was associated with the second axis of the RDA. Variance partitioning test showed that disturbance variables (D-100, CL-50, TP, fine particles) explained together 21.3% of the among-lake variation in macroinvertebrate composition in sediments, whereas only 3% was explained by natural variables (relative depth). Oligochaetes and chironomids were associated to the disturbance variables whereas dragonflies, caddisflies, and especially mayflies were positioned at the other end of the axis, indicating an association with pristine conditions. The second axis represented a gradient of lake steepness indicated by relative depth that was associated to dominance of amphipods, as seen for the analysis of macroinvertebrates on rocks.

The clear opposition observed between oligochaetes and chironomids on one side and mayflies, dragonflies, and caddisflies on the other side in the RDA analysis of macroinvertebrate communities in sediments suggested a potential use of these taxonomic groups as metrics to evaluate the quality of littoral communities in residential lakes. The combined biomass of oligochaetes and chironomids was positively correlated with dwelling density (D-100) ($r^2 = 0.62$, $p = 0.00081$) but the relationship was stronger when oligochaetes biomass alone was considered ($r^2 = 0.77$, $p = 0.000051$; Fig. 6a). On the other hand, the combined biomass of mayflies, dragonflies and caddisflies was negatively correlated with near shore development ($r^2 = 0.27$, $p = 0.04$) but the relationship with D-100 improved when only mayfly biomass was considered ($r^2 = 0.73$, $p = 0.00012$; Fig. 6b).

Fig.4: Proportion of total biomass represented by dominant macroinvertebrates on a) rocks and b) sediments. Values are averages of five replicates. For each lake, only groups representing at least 10% of total biomass are shown while the other taxa are grouped as "Others". Lakes are in order of increasing residential development.

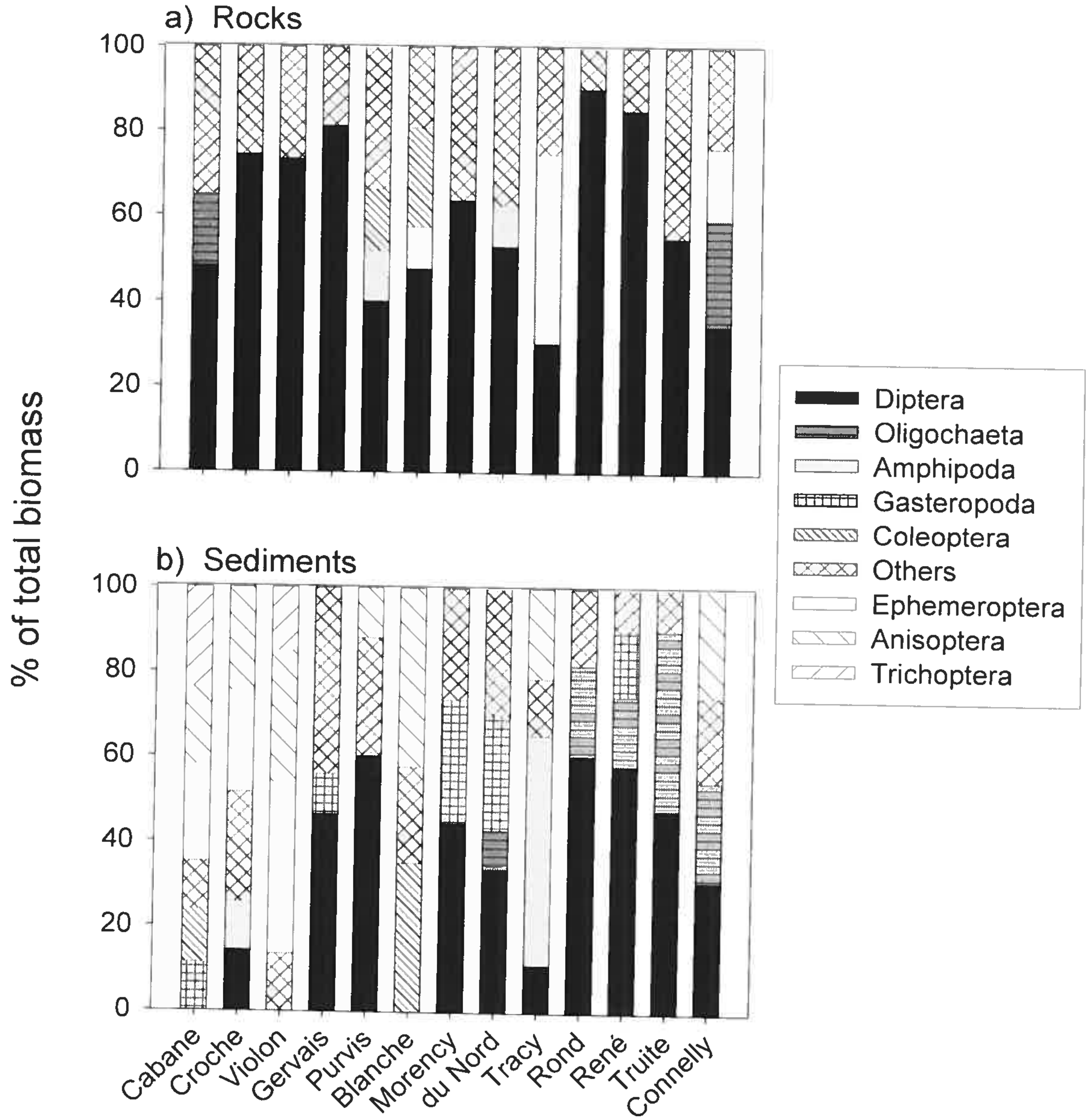
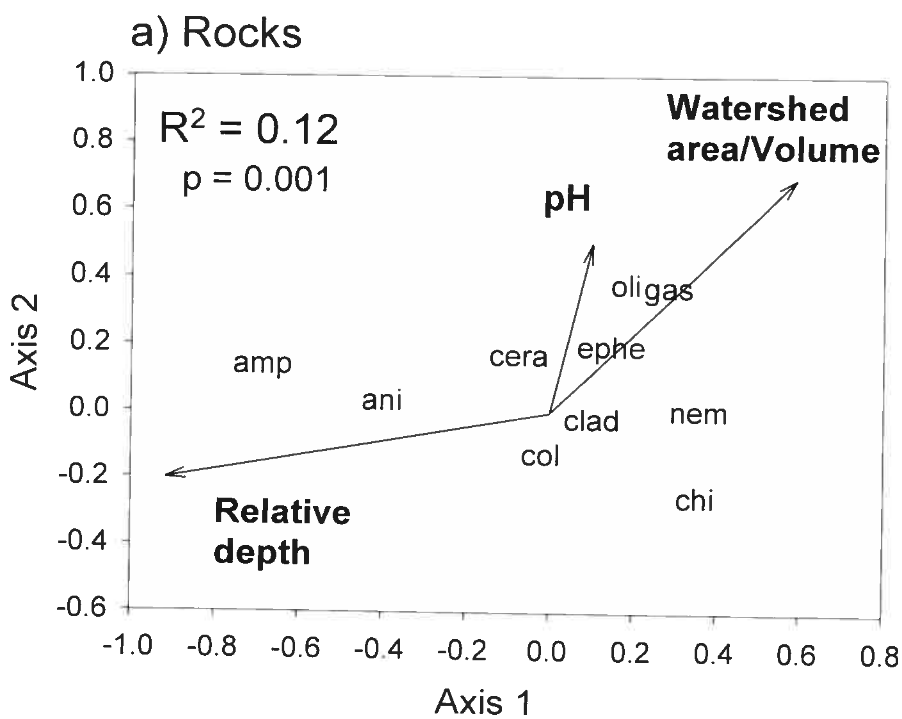
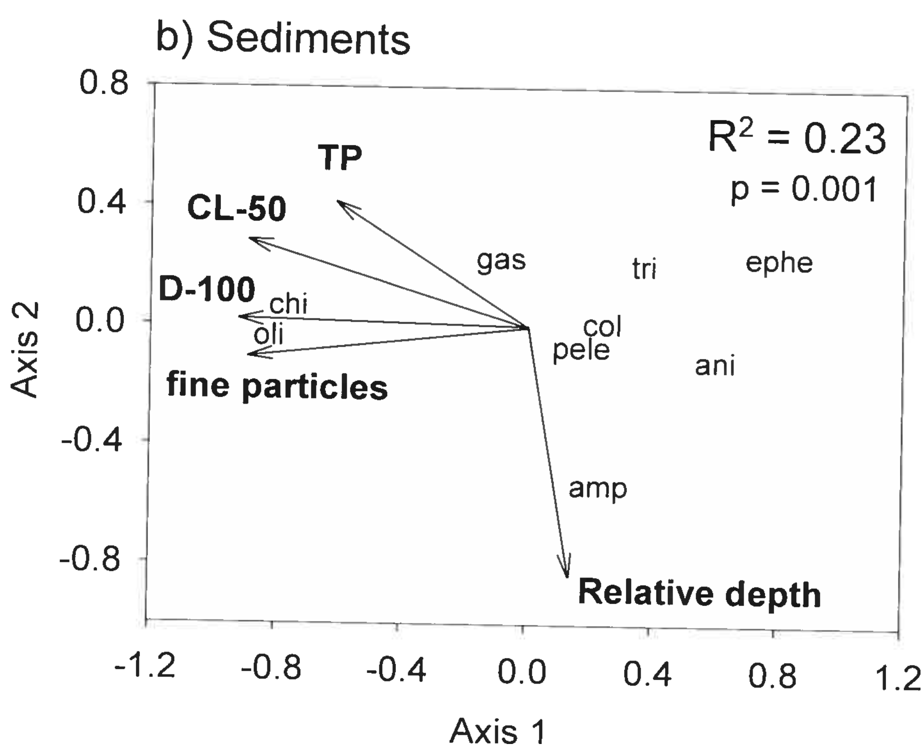

a) Rocks
b) Sediments
% of total biomass
100
80
60
40
20
0
Diptera
Oligochaeta
Amphipoda
Gasteropoda
Coleoptera
Others
Ephemeroptera
Anisoptera
Trichoptera
Cabane
Croche
Violon
Gervais
Purvis
Blanche
Morency
du Nord
Tracy
Rond
René
Truite
Connelly

Fig.5: Redundancy analysis (RDA) performed on macroinvertebrate communities on a) rocks (19 taxa) and b) sediments (21 taxa). Area / Volume = watershed area divided by lake volume, D-100 = dwelling density within a 100 m wide riparian strip, CL-50 = percentage of cleared land within a 50 m wide riparian strip, fine particles = % of total sediment mass represented by particles < 250µm. Adjusted R^2 are presented for each canonical analysis. The abbreviations used in the graph are: oli = Oligochaeta, gas = Gastropoda, ephe = Ephemeroptera, cera = Ceratopogonidae, clad = Cladocera, nem = Nemaatoda, col = Coleoptera, chi = Chironomidae, ani = Anisoptera, amp = Amphipoda, tri = Trichoptera, pele = Pelecypoda.

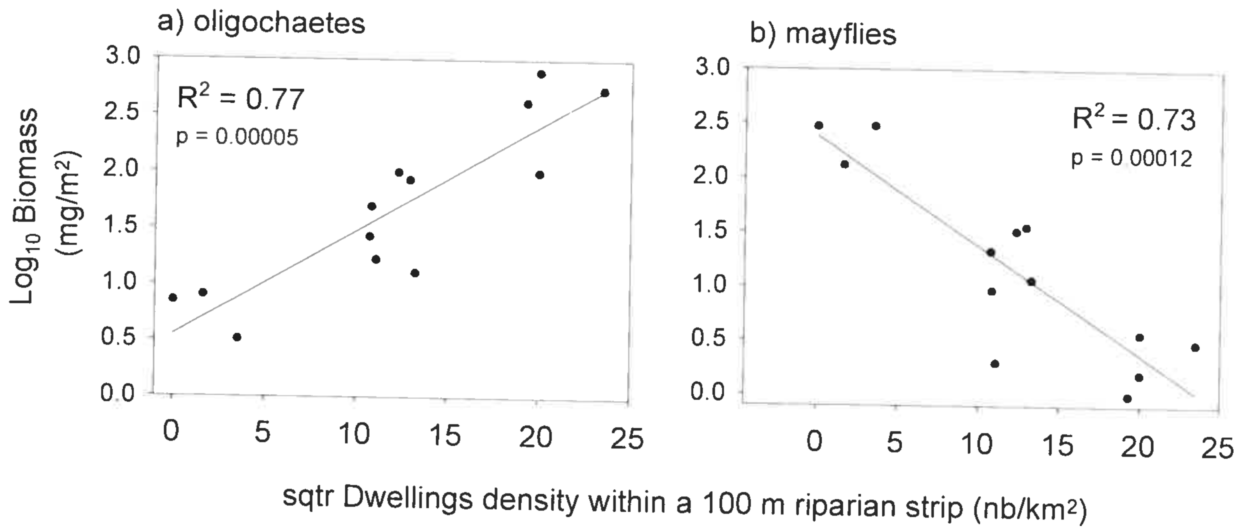


a) Rocks
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
Axis 2
R2 = 0.12
p = 0.001
Watershed
area/Volume
pH
oli
gas
amp
cera
ephe
ani
clad
nem
col
Relative
depth
chi
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
Axis 1



b) Sediments
0.8
0.4
0.0
-0.4
-0.8
Axis 2
R2 = 0.23
p = 0.001
TP
CL-50
gas
tri
ephe
D-100
chi
oli
col
pele
ani
fine particles
amp
Relative depth
-1.2
-0.8
-0.4
0.0
0.4
0.8
1.2
Axis 1

Fig.6: Biomass of a) oligochaetes and b) mayflies along the gradient of residential development. Adjusted R^2 are presented for both relationships where n=13. Regression models are: a) Log_{10} (oligochaetes biomass + 1) = $0.0927*(D-100)^{1/2} + 0.554$ and b) Log_{10} (mayflies biomass + 1) = $-0.1002*(D-100)^{1/2} + 2.382$.


a) oligochaetes
b) mayflies
Log10 Biomass (mg/m2)
R2 = 0.77
p = 0.00005
R2 = 0.73
p = 0.00012
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
5
10
15
20
25
sqtr Dwellings density within a 100 m riparian strip (nb/km2)

Discussion

The hypothesis of a bottom-up control of macroinvertebrate communities is a possible mecanism that could explain variations of rocks dwelling invertebrate biomass in Laurentian lakes. Their biomass increased significantly together with epilithon biomass (Lambert 2006) along the gradient of residential development. Changes in invertebrate biomass were largely a result of a significant rise in mean individual size whereas density increase was weak (data not shown) along the gradient. Rocks dwelling invertebrates were probably food-limited in pristine lakes. With increasing development, epilithon provided a resource not only more abundant but also of superior quality due to its increased nitrogen and phosphorus content (Lambert 2006). Taxonomic composition of the rock-dwelling fauna did not change with lake development, at least at the level we considered. Dipteran chironomids, which were dominant in all lakes, are mostly grazers and collector feeders and thus advantaged by enhanced epilithon resources. Bottom-up control of periphyton and macroinvertebrates was previously observed in nutrient enrichment experiments in streams (Mundi et al. 1991, Perrin and Richardson 1997) and lakes (Bluemenshine et al. 1997). Bourassa and Cattaneo (1998) found a significant increase of invertebrate grazers along a natural nutrient gradient in Laurentian streams. In the present study, we suggest a bottom-up effect for rock-dwelling invertebrates in unmanipulated lakes.

In contrast to the communities on rocks, the biomass of sediment-dwelling invertebrates did not increase with residential development despite a significant increase in epipelon biomass and nutrient content along the gradient (Lambert 2006). Several mechanisms could explain the lack of relationship of invertebrate biomass on sediments with residential development and with epipelon biomass. Fish predation can limit increases in macroinvertebrate abundance despite a stimulation of periphyton production by nutrients (Hershey 1992). Sediment-dwelling invertebrates may become more vulnerable to fish predation in developed lakes because decreasingly heterogeneous sediments provide fewer refuges.

Changes in sediment heterogeneity may be related with variations in macroinvertebrate taxonomic composition along the residential gradient. Percentage of fine sediment particles increased with dwelling densities within a 100 m riparian strip (% fine particles = $0.026*(D-100)^{1/2} + 0.157$; $r^2 = 0.59$**; De Sousa 2007, unpublished data). Qualitative observations of sediment samples indicated a decrease of woody debris in the developed lakes. These observations agree with changes in littoral sediment quality observed in Wisconsin lakes along a gradient of residential development (Jennings et al. 2003, Francis and Schindler 2006). The presence of woody debris and coarse particles enhances living space and refuge for macroinvertebrates (Hynes 1970). Invertebrates may also use woody debris directly as a food source (Benke and Wallace 2003). Heterogeneous sediments tend to host a diverse insect fauna and favour mayflies in particular (Buss et al 2004). On the other hand, Oligochaeta are typically found in nutrient enriched and productive systems where they profit of the high availability of organic matter (Wiederholm 1980, Quinn and Hickey 1990, Verdonschot 1996). Chironomids are often the dominant order of insect in the freshwater environments (Thorp and Kovich 1991); we observed their dominance on rocks along the perturbation gradient and on sediments in the most perturbed lakes. Food resource seemed to be an important factor controlling abundance of Chironomidae; we observed an increase in

Chironomidae biomass, for both rocks and sediments, along the perturbation gradient (data not shown).

The only non-anthropogenic variable that explained a significant proportion of the variation in invertebrate taxonomic composition on rocks and sediments was relative depth, a proxy of lake steepness. This was due to the high biomass of Amphipoda observed in Lake Tracy, which was the steepest lake. This association between Amphipoda and lake relative depth is probably mediated by the absence in Lake Tracy of benthivorous fishes (white suckers, golden shiner, and pumpkinseed) common in the other lakes (Pascale Gibeau, Université de Momtréal, personnal communication).

In the Laurentian lakes, water nutrient concentrations and phytoplankton Chl-*a* remained low throughout a large range of recreational development with values slightly exceeding those typical of oligotrophic lakes (OCDE 1982) in only 2 instances. In contrast, littoral macroinvertebrates seemed to be affected by dwelling density and forest clearing along the lake shore. The response of macroinvertebrates to developments is dependent on the substratum: changes in biomass were evident on rocks whereas shifts in community composition were important only on sediments. The increase in invertebrate total biomass and individual size on rocks could propagate along the food chain because these organisms are consumed by planktonic and benthic fish (Vadeboncoeur et al. 2002).

Our study emphasises the importance of choosing the appropriate substratum when sampling macroinvertebrates for biomonitoring. Sediments represented a good sentinel substratum (sensus Piscart et al. 2006) since they were present in all lakes and supported very different macroinvertebrate assemblages along the development gradient. Simple measurements such as total biomass of oligochaetes and mayflies could provide easy indicators of impaired and natural littoral habitats, respectively in the Laurentian lakes subjected to residential development, at least for the period covered by the sampling protocol (july). Further studies should be conducted to beter understand the effect of sampling period on macroinvertebrate communities.

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Appendix 1. Proportion of total biomass represented by macroinvertebrate taxa on rocks. Values are averages of five replicates.

	Cabane	Croche	Violon	Gervais	Purvis	Blanche	Morency	duNord	Tracy	Rond	René	Truite	Connelly
Hydra	4.1	0.1	0.7	-	0.4	0.7	2.3	0.4	-	0.3	1.3	0.5	-
Turbellaria	-	2.4	-	-	3.5	0.9	0.8	0.4	11.5	-	-	0.1	0.2
Nematoda	0.4	1.8	1.7	-	11.4	2.2	4.9	2.4	0.2	2.2	1.2	17.0	7.9
Oligoghaeta	16.9	2.8	4.0	5.7	1.9	0.2	3.7	5.4	1.1	2.8	2.2	4.6	24.7
Cladocera	3.1	6.0	4.2	1.8	1.6	4.2	0.6	5.9	0.5	0.9	0.6	1.0	1.2
Ostracoda	-	-	2.4	-	-	0.3	0.2	0.3	-	0.1	0.7	1.5	1.1
Cyclopoïda	0.6	2.1	1.3	0.2	1.8	0.7	0.9	0.6	1.1	0.1	0.2	0.1	0.1
Amphipoda	-	-	-	4.7	11.7	9.8	4.2	9.7	44.2	-	-	-	-
Ephemeroptera													
Caenidae	0.8	-	-	-	-	-	-	1.7	-	-	-	3.2	4.4
Baetidae	-	-	-	-	0.3	0.2	1.4	-	-	1.6	-	-	-

	Cabane	**Croche**	**Violon**	**Gervais**	**Purvis**	**Blanche**	**Morency**	**duNord**	**Tracy**	**Rond**	**René**	**Truite**	**Connelly**
Odonata													
Anisoptera	8.1	6.2	7.0	4.1	-	4.8	6.4	1.5	10.1	0.3	-	-	0.1
Coleoptera	7.5	-	-	-	14.5	23.4	-	-	-	-	-	-	-
Trichoptera													
Leptoceridae	0.8	0.1	-	-	3.2	-	-	-	0.2	-	-	-	-
Polycentropodidae	-	-	-	-	-	0.6	3.3	0.4	-	-	7.5	-	-
Hydropsychidae	-	-	-	-	-	-	-	-	-	-	0.3	-	-
Diptera													
Chironomidae	48.2	74.4	73.4	64.5	40.2	47.7	53.2	53.0	15.6	73.4	73.6	55.1	34.8
Ceratopogonidae	0.7	3.0	3.0	16.7	5.8	2.1	10.7	7.9	14.9	16.9	11.5	9.5	7.9
Plecoptera	-	-	-	-	-	0.2	-	-	-	-	-	-	-
Megaloptera	-	-	-	-	-	-	-	-	0.1	-	-	1.0	-

	Cabane	Croche	Violon	Gervais	Purvis	Blanche	Morency	duNord	Tracy	Rond	René	Truite	Connelly
Hydracarina	0.7	1.2	2.1	1.1	0.9	0.7	1.7	1.2	-	1.0	0.4	0.1	0.5
Gastropoda													
Physidae	8.0	-	-	-	1.1	-	-	-	-	-	-	-	12.6
Planorbidae	-	-	-	1.1	1.6	1.4	5.8	8.8	0.5	0.5	0.5	6.1	4.3
Pelecypoda	-	-	-	-	0.1	-	-	0.4	-	-	-	0.2	0.2

Appendix 2. Proportion of total biomass represented by macroinvertebrate taxa on sediments. Values are averages of five replicates.

	Cabane	Croche	Violon	Gervais	Purvis	Blanche	Morency	duNord	Tracy	Rond	René	Truite	Connelly
Hydra	0.2	0.4	-	0.4	-	-	-	0.3	-	-	0.1	-	-
Turbellaria	-	-	-	-	0.5	0.2	-	-	-	-	-	0.2	-
Nematoda	2.9	2.4	2.4	5.2	5.4	2.6	3.7	3.0	0.2	13.0	0.2	2.4	6.3
Oligochaeta	0.5	1.3	0.3	8.3	2.7	1.0	6.3	9.2	1.6	21.3	16.6	42.2	23.5
Hirudinea	-	-	-	-	-	-	0.3	3.5	-	-	-	-	-
Cladocera	0.8	2.5	0.1	2.7	1.9	0.6	0.2	1.2	0.7	-	0.2	-	0.5
Ostracoda	-	0.1	0.4	0.4	1.5	0.1	0.8	0.6	1.2	0.3	4.2	0.2	0.4
Cyclopoïda	0.3	0.6	0.3	1.2	0.8	0.4	0.5	0.5	0.6	-	0.4	-	0.1
Harpacticoïda	0.3	0.3	-	0.9	-	-	0.5	1.0	-	2.2	1.7	-	0.4
Amphipoda	-	11.4	-	2.6	3.5	2.5	0.7	3.9	54.1	-	0.2	-	-
Isopoda	-	-	-	-	0.2	-	1.7	-	-	-	-	-	-

	Cabane	Croche	Violon	Gervais	Purvis	Blanche	Morency	duNord	Tracy	Rond	René	Truite	Connelly
Ephemeroptera													
Caenidae	10.2	17.7	22.2	4.2	0.2	-	0.5	3.5	-	-	0.1	-	-
Ephemeridae	11.9	4.9	18.0	-	0.3	-	0.2	0.3	-	-	-	-	-
Leptophlebiidae	0.5	1.2	-	2.3	-	0.1	1.3	-	1.5	-	0.3	-	0.1
Odonata													
Anisoptera	18.5	24.5	31.1	3.2	11.6	42.1	1.6	2.8	21.1	-	-	-	25.4
Zygoptera	-	-	-	-	-	-	-	-	-	-	-	-	-
Coleoptera	12.6	9.8	-	-	1.7	35.2	-	2.4	3.1	-	-	-	3.2
Trichoptera													
Leptoceridae	22.1	-	7.9	2.1	-	0.2	0.1	0.1	-	-	1.1	0.2	-
Polycentropodidae	-	-	7.0	-	-	-	-	1.9	-	-	-	-	-
Hydroptilidae	1.3	-	-	-	0.2	-	-	-	-	-	0.6	-	-

	Cabane	Croche	Violon	Gervais	Purvis	Blanche	Morency	duNord	Tracy	Rond	René	Truite	Connelly
Diptera													
Chironomidae	5.8	14.4	6.5	46.7	45.2	9.1	44.7	33.9	11.3	60.7	58.2	48.0	31.2
Ceratopogonidae	-	1.4	2.1	4.1	15.2	2.1	3.5	1.1	1.2	-	0.2	1.9	4.5
Megaloptera	-	-	0.1	-	3.9	-	-	-	-	-	-	-	-
Hydracarina	-	0.2	0.1	0.2	0.1	0.1	0.1	0.1	-	-	0.3	-	-
Gastropoda													
Physidae	11.4	3.3	-	5.7	2.9	1.1	18.1	15.4	-	-	12.4	4.6	3.6
Planorbidae	-	0.5	0.2	3.7	1.0	0.1	10.9	11.6	1.1	1.8	3.0	-	0.7
Pelecypoda	0.5	3.3	1.4	6.1	1.0	2.8	4.2	3.9	2.4	0.5	-	0.3	0.1

Accord des coauteurs

Simon De Sousa

M. Sc. En sciences biologiques

Simon de Sousa, Bernadette Pinel-Alloul et Antonella Cattaneo. Response of littoral macroinvertebrate communities on rocks and sediments to lake residential development. À soumettre à *Canadian Journal of Fisheries and Aquatic Sciences*

À titre de coauteur de l'article identifié ci-dessus, je suis d'accord pour que **Simon De Sousa** inclue cet article dans son **mémoire de maîtrise** qui a pour titre : « **La réponse des communautés d'invertébrés benthiques sur différents substrats naturels au développement résidentiel des bassins versants des lacs des Laurentides** ».

[redacted]

Coauteur : BernadettePinel-Alloul Date

[redacted]

Coauteur : Antonella Cattaneo Date

Chapitre 3:

Littoral invertebrates living on different natural substrata in two groups of lakes of varying anthropogenic development

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Abstract

We compared total biomass, size structure, and taxonomic composition of macroinvertebrate communities associated with 4 different natural substrata (sediments, rocks, submerged wood, and macrophytes) in the littoral zone of 7 lakes of the Laurentian region of Quebec. Four of the lakes were relatively undeveloped while 3 were experiencing intense recreational development. Sediments and rocks were present everywhere whereas wood was frequent only in the undeveloped lakes and macrophytes only in the developed lakes. In undeveloped lakes, total biomass and individual size were greatest on sediments, lowest on rocks, and somewhat intermediate on wood. Invertebrate taxonomic composition was similar on rocks and wood with a clear dominance of Chironomidae. Sediments dwelling invertebrates were more diverse and represented by Anisoptera, Coleoptera, Ephemeroptera, and Gastropoda. In developed lakes, total biomass and individual size were again highest in sediments followed by rocks and macrophytes. Taxonomic composition clearly varied among substrata. Sediments of developed lakes lost some complexity and hosted a mainly endobenthic fauna (Oligochaeta and Nematoda). The presence of macrophytes conterbalanced some of the habitat heterogeneity lost in the sediments and with wood removal and allowed the establishment of epibenthic invertebrates (Gastropoda, *Hydra*, Ephemeroptera and Ceratopogonidae). Rocks remained dominated by Chironomidae but total invertebrate biomass increased with perturbations suggesting a bottom-up response of invertebrates to the concomitant increasing epilithon biomass.

Résumé

Nous avons comparé la biomasse totale, les classes de tailles ainsi que la composition taxinomique des communautés de macroinvertébrés benthiques associées à 4 différents substrats naturels (sédiments, roches, bois submergés et macrophytes) dans la zone littorale de 7 lacs de la région des Laurentides au Québec. Quatre lacs sont relativement peu développés, alors que trois lacs subissent d'intenses développements résidentiels. Les sédiments et les roches sont présents dans tous les lacs tandis que le bois est présent seulement dans les lacs peu développés et les macrophytes dans les lacs développés. Dans les lacs peu développés, la biomasse totale et la taille des invertébrés sont plus élevées sur les sédiments, plus faibles sur les roches et intermédiaires sur le bois. La composition taxinomique est similaire sur les roches et le bois avec une dominance des Chironomides. Les invertébrés des sédiments sont plus diversifiés (Anisoptères, Coléoptères, Éphémères et Gastéropodes). Dans les lacs développés, la biomasse totale et la taille des invertébrés sont encore une fois plus élevées sur les sédiments, suivi par les roches et les macrophytes. La composition taxinomique varie clairement entre les substrats. Les sédiments des lacs développés ont perdu de leur complexité et supportent une faune endobenthique (Oligochètes, Nématodes). La présence des macrophytes contribue à augmenter l'hétérogénéité des habitats qui avait été perdue dans les sédiments fins et par l'enlèvement du bois submergé et permet l'établissement d'invertébrés épibenthiques (Gastéropodes, Hydres, Éphémères et Cératopogonidés). Les roches demeurent dominés par les Chironomides, mais la biomasse d'invertébrés augmente avec les perturbations, en concomitance avec la biomasse d'épilithon, suggérant un effet ascendant.

Introduction

Lake and shore morphology mainly dictate the substratum composition of littoral habitats (Hakanson and Jansson 1983, Cyr 1998). Stony substrata are prevalent on steep shores exposed to strong winds while sheltered shores typically have soft bottoms with macrophytes. Habitat complexity in the littoral zone of lakes spatially structures benthic invertebrates and may lead to high benthic fauna diversity (Minshall 1984, Tolonen et al. 2001, Taniguchi and Tokeshi 2004). Benthic invertebrate communities are affected by substratum type in rivers (Brown and Brussock 1991, Buss et al. 2004) and in lakes (Tolonen et al. 2001).

Anthropogenic development of lake shores can directly affect the heterogeneity and quality of the littoral substrata. Residential development may decrease sediments complexity by reducing litter and woody debris accumulation (Christensen et al. 1996, Jennings et al. 2003, Francis and Schindler 2006, De Sousa 2007); it also increases the thickness of periphyton cover through a rise in nutrient inputs (Lambert 2006). With increasing lake development, macrophytes increase whereas submerged wood becomes rare as a result of clearing of riparian vegetation (Christensen et al. 1996). Therefore, residential development through changes in littoral habitat complexity and substrate type availability may alter the macroinvertebrate communities.

Thousands of lakes are found in the Laurentian region of Quebec and the majority of them are still relatively clean. Since the seventies, this region has supported an important demographic development: it underwent a 98.4% rise of its population between 1971 and 2003 (Institut de la statistique du Québec: http://www.stat.gouv.qc.ca).

Consequently, previously pristine lakes are experiencing increasing residential development that is concentrated along the shores.

The goal of this study is to examine how macroinvertebrate communities vary between substratum types in two groups of lakes experiencing different levels of residential development. We test if natural availability of different substrata (sediments, rocks, wood and macrophytes) in the littoral zone and its possible alteration by anthropogenic development affect total biomass, size structure and taxonomic composition of invertebrate communities. We anticipated that alteration of substratum texture (sediments and rocks common in all lakes) and changes in availability of different substratum types (macrophytes in developed lakes vs. submerged wood in undeveloped lakes) would have an impact on macroinvertebrate communities at the lake scale. As benthic macroinvertebrates are major players in the trophic transfer between littoral and pelagic habitats (Vadeboncoeur et al. 2002), any change induced by residential development may have profound influence on whole-lake food webs and productivity.

Methods

Study site

The studied lakes are situated in the Laurentian region of the eastern Canadian Shield (45°59'N, 73°60'W), about 80 kilometres north of Montreal, Quebec. This region of mixed forest is underlain by gneiss and granitic rocks covered by morainic soils. In July 2003, we sampled benthic invertebrates in lakes differing by their level of residential development, which was estimated as number of dwellings km^{-1} counted within a 100 m wide strip around the lake (on orthorectified 1:30 000 and 1:10 000 aerial photographs acquired in 2002 and 2004; Lambert 2006). We grouped the lakes in: i) undeveloped (from 0 to 10 dwellings per km of shore) represented by four lakes (De la Cabane, Croche, Gervais, and De la Blanche) and ii) developed (from 39 to 50 dwellings per km of shore) represented by three lakes (Rond, Connelly, and À la Truite) (Table 1). These seven lakes are of small to medium size (lake area: 0.17 – 1.24 km^2, Table 1) and still on the low range of trophy according to trophic classification (OECD 1982) based on total phosphorus (TP) concentrations and phytoplankton chlorophyll *a* biomass (Table 2). Only Lac Rond can be considered mesotrophic with mean summer TP and TN reaching 13 $\mu g \cdot L^{-1}$ and 385 $\mu g \cdot L^{-1}$ respectively. These lakes have relatively clear waters (DOC < 4.6 $mg \cdot L^{-1}$). The less developed lakes are circumneutral or slightly acid (6.2-7.0) whereas the more developed lakes are more alkaline (7.4-8.1) (Table 2).

Periphyton biomass varied greatly among lakes and substrata, ranging from 89 to 246 $mg \cdot m^2$ of Chl-*a* on sediments and 21 to 221 $mg \cdot m^2$ of Chl-*a* on rocks. It was generally lower and varied less on wood (28 to 41 $mg \cdot m^2$) and macrophytes (3 to 66 $mg \cdot m^2$); data are from Lambert (2006). Phytoplankton biomass also varied among lakes (0.7 to 4.6 $\mu g \cdot L^{-1}$ of Chl-*a*; Gélinas and Pinel-Alloul, unpublished data; Table 2). According to the « Système canadien de classification des sols » (Groupe de travail sur la classification des sols 2002), sediments were mainly composed of medium, coarse and very coarse sand with small stones in less developed lakes, while there were more fine sand and clay in more developed lakes. The percentage of fine particles (< 250 µm) varied from 12.9 to 84.1 % of total sediment mass among lakes (Table 1). Qualitative observations of sediments samples also showed more plant detritus in more developed lakes, and more litter (leaves, woody debris and branches) in less developed lakes.

Macroinvertebrate sampling and analysis

We sampled benthic invertebrates on four substrata: sediments, rocks, submerged wood, and macrophytes. Sediments and rocks were present in all lakes while wood was frequent only in undeveloped lakes and macrophytes only in developed lakes. We established three sampling stations in each lake distributed regularly around its perimeter. All samples were collected at 1m depth. Invertebrates on rocks and wood (hard substrata) were sampled with a brush-syringe sampling device that consisted in a plexiglass cylinder (7.6 cm diameter) provided with a brush. This device was pressed against the rock or wood by a diver and all the dislodged material (including invertebrates) was pumped it into a Mason jar (Vis et al. 1998). Three replicates were combined together for a total sampling area of 136.09 cm^2. Invertebrates on sediments were sampled with a plastic corer (area = 46.57cm^2) that was embedded down 10cm into the sediments. Macrophyte dwelling invertebrates were collected by a diver closing a Plexiglas box (5.7 L) around the vegetation (Downing and Cyr, 1985). This device allowed quantitative sampling of all invertebrates including those only loosely associated with the vegetation. The water was filtered through a 500 μm mesh sieve to collect floating invertebrates. Macrophytes were transferred to a plastic container half-filled with tap water and invertebrates were detached from the vegetation by vigorous manual agitation. The suspension was filtered through the same 500 μm mesh sieve. Invertebrates were preserved in 70% ethanol and stored until analysis. Macrophytes were visually inspected to ensure total invertebrate removal and then dried at ~ 40 °C for 4 d to allow determination of dry mass. To estimate areal macrophyte biomass, we collected all the vegetation in two quadrats (30cm * 30cm) positioned haphazardly at each site. This estimate allowed conversion of invertebrate biomass per dry mass of macrophyte into invertebrate biomass per m^2 of lake bottom to compare communities on macrophytes with those on rocks, wood, and sediments. For each substratum, all the collected material was passed through two successive sieves of 1mm and 500μm mesh size to concentrate the macroinvertebrates, which were preserved in 95% ethanol with addition of rose Bengal dye to stain the organisms and facilitate their sorting.

In the laboratory, invertebrates were sorted under a dissecting microscope (25X) and identified to order or class level (Edmondson 1959; Tachet et al. 1980; Merritt and Cummins 1996). Invertebrate body length was measured with an image analyser system (Image Pro-Plus) connected to a dissecting microscope. Dry mass of each organism was estimated using published length-mass relationships (Eckblad 1971; Dumont et al. 1975; Mason 1977; Rogers et al. 1977; Tudorancea et al. 1979; Smock 1980; Peters and Downing 1984; Burgherr and Meyer 1997; Benke et al. 1999; Stoffels et al. 2003). Invertebrate biomass was expressed per surface unit ($mg \cdot m^{-2}$) by dividing total biomass by the sampling area. To examine the size structure of the communities, we grouped the invertebrates in $\log_2$ increasing size classes: the first class was 4 to 8μg, the last one 4000 to 8000μg.

Statistical analyses

Differences in total invertebrate biomass (TIB) and periphyton biomass among substrata were tested using simple ANOVA. Analyses were performed separately for undeveloped and developed lakes. We used log transformation for TIB and periphyton biomass. To investigate differences in taxonomic composition of macroinvertebrate communities among substrata, principal component analysis (PCA) was used for each group of lakes (undeveloped and developed) separately. To test the significance of these differences in taxonomic composition, we used multi-dimensional ANOVA tests performed as a multiple-regression linear model (RDA) using macroinvertebrate biomass and orthogonal dummy variables (Legendre and Anderson 1999). Prior to multi-dimensional analysis, Hellinger's transformation was applied to the macroinvertebrates data (Legendre and Gallagher 2001). All of the analyses were performed using the Language R package (Ihaka and Gentleman 1996).

Table 1: Number of dwellings along the shore. morphologic characteristics. sediment granulometry. and substratum composition for seven lakes of the Laurentian region of Quebec. Substratum composition (as % cover of lake bottom) was estimated visually by divers over 14 to 30 stations (10 m long) per lake: rocks comprise all substrata with diameter > 1 cm (Lambert. personal communication): macrophyte biomass (in brackets) is presented together with percentage cover.

	Dwellings	**Lake Area**	**Max Depth**	**Mean depth**	**Granulometry particles < 250 μm**	**Substratum composition**			
						Sed.	**Rocks**	**Wood**	**Macrophyte**
	nb·km^{-1}	km^2	m	m	%	%	%	%	% (g·m^{-2})
Undeveloped									
De la Cabane	0	0.25	20.8	7.6	12.9	48	25	25	2 (<1)
Croche	0.2	0.18	12.9	4.9	14.6	34	52	13	2 (<1)
Gervais	10.2	0.97	60.0	24.5	37.9	38	37	17	8 (<1)
De la Blanche	12.0	0.41	26.0	11.7	32.4	52	28	13	7 (<1)
Developed									
Rond	39.0	0.17	15.8	7.2	55.6	27	20	0	53 (24)
À la Truite	41.8	0.51	22.5	9.4	84.1	52	3	1	44 (11)
Connelly	49.6	1.24	20.8	7.7	47.6	26	19	3	52 (25)

Table 2: Water quality and algal biomass in the 7 studied lakes. TP = total phosphorus. TN = total nitrogen. DOC = dissolved organic carbon. Water quality variables and phytoplankton biomass are averaged over 6 replicates taken in summer 2003 (Gélinas and Pinel-Alloul. unpublished data). Periphyton biomasses are from Lambert (2006): they are averaged on 3 sampling stations (June 2003).

	Water quality				Phytoplankton	Periphyton biomass			
	TP ($\mu g \cdot L^{-1}$)	TN ($\mu g \cdot L^{-1}$)	DOC ($mg \cdot L^{-1}$)	pH	biomass ($\mu g \cdot L^{-1}$)	sed ($mg \cdot m^{-2}$ Chl-*a*)	rock	wood	mac
Undeveloped									
De la Cabane	8.2	259.8	3.6	6.2	3.01	89.2	20.6	31.3	-
Croche	5	256.9	4.1	6.2	1.26	156.2	50.9	39.8	-
Gervais	4.6	190.4	2.7	7	0.74	113.8	57.4	27.8	-
De la Blanche	4.9	258	2.8	6.4	2.64	73.2	21.6	40.9	-
Developed									
Rond	13	384.6	3.6	8.1	4.61	215.7	82.6	-	28.3
À la Truite	6.5	290.5	3	7.7	1.72	194.2	115.6	-	2.5
Connelly	8	340	4.6	7.4	4.42	245.7	220.7	-	65.8

Results

Macroinvertebrate total biomass and size structure

Total invertebrate biomass (TIB) was significantly different between the three substrata in the undeveloped lakes (ANOVA, F=39.9, *P*=0.001). 2 by 2 ANOVA tests showed that all differences were significant (sediments-wood, *P*=0.001; sediments-rocks, *P*=0.001; wood-rocks, *P*=0.003). TIB was greatest on sediments (mean = 1116 ± 238 mg/m^2), lowest on rocks (mean = 48 ± 10 mg/m^2), and somewhat intermediate on wood (mean = 153 ± 37 mg/m^2) (Fig. 1a). All macroinvertebrate size distributions in undeveloped lakes (Fig.2a) were unimodal due to the use of the 500µm mesh size sieve that retained only large organisms. Invertebrates were largest on sediments (mean size = 68 ± 14 µg), intermediate on wood (mean size = 25 ± 3 µg) and smallest on rocks (mean size = 16 ± 3 µg) (Fig. 2a).

TIB was significantly different between the three substrata (ANOVA, F=28.7, *P*=0.001) also in developed lakes,. 2 by 2 ANOVA tests showed that all differences were significant (sediments-macrophytes, *P*=0.001; sediments-rocks, *P*=0.001; macrophytes-rocks, *P*=0.041); TIB was the greatest on sediments (mean = 2189 ± 269 mg/m^2), intermediate on rocks (mean = 438 ± 57 mg/m^2), and the smallest on macrophytes (mean = 267 ± 67 mg/m^2) (Fig. 1b). Size structure revealed that invertebrates on sediments were larger (mean size = 110 ± 19 µg) than those on rocks (mean size = 42 ± 7 µg) and macrophytes (mean size = 39 ± 4 µg). The size structure and mean size of rock and macrophyte dwelling invertebrates were apparently not different (Fig. 2a).

Fig.1: Mean total invertebrate biomass (TIB) with standard error on different substrata in a) undeveloped and b) developed lakes. For each substratum, TIB was averaged over 12 stations (3 sites in 4 lakes) for undeveloped lakes and over 9 stations (3 sites in 3 lakes) for developed lakes. Significant differences ($P<0.05$) among substrata are represented by different letters upon bars (2 by 2 ANOVA tests).

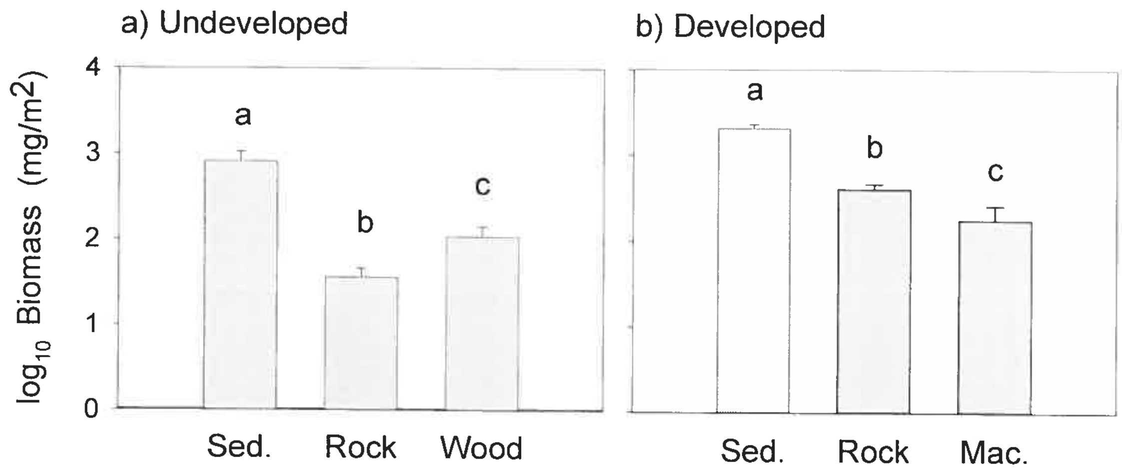
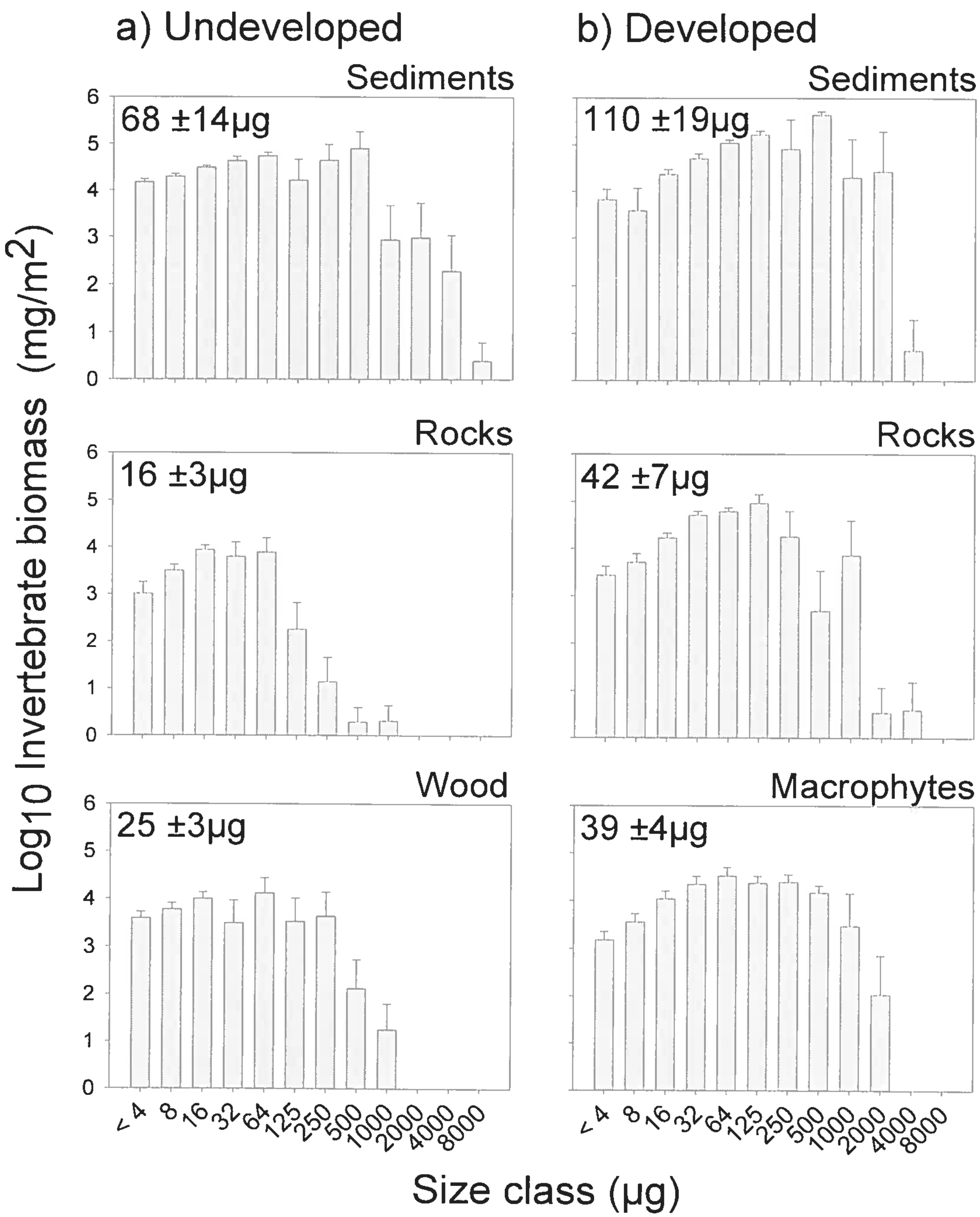
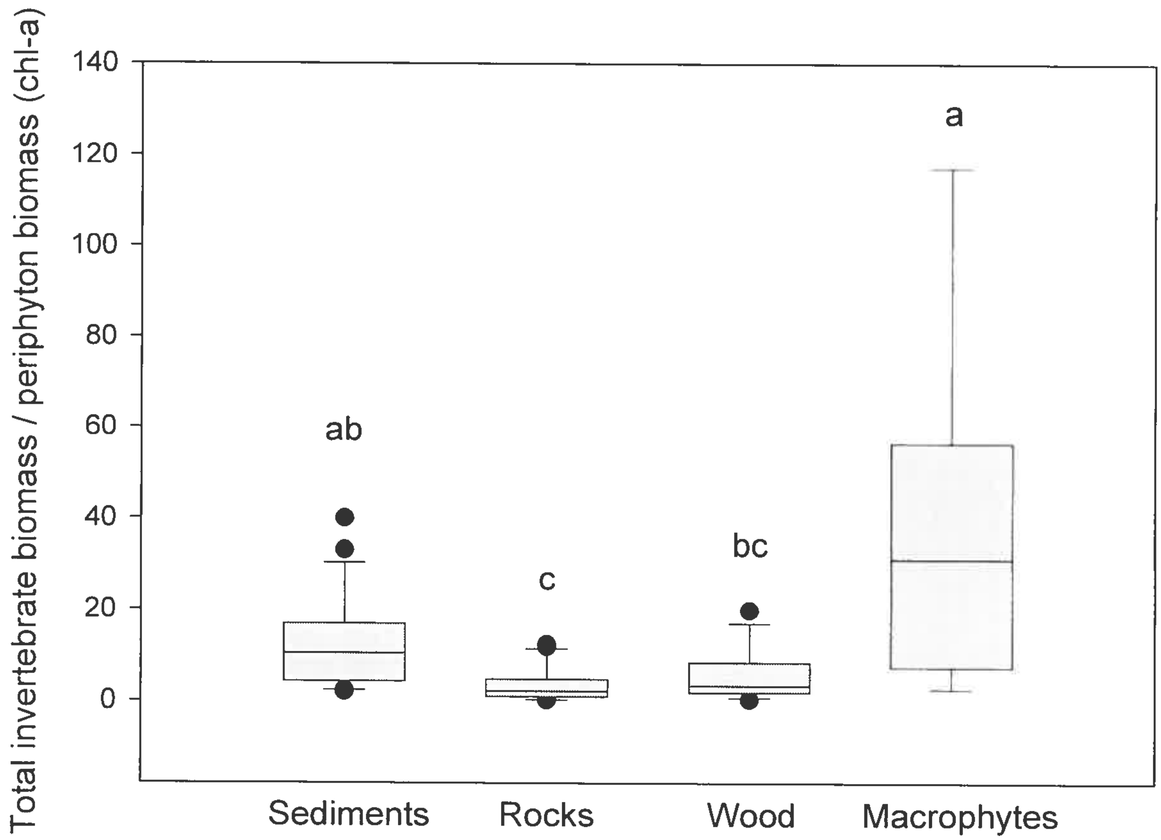

a) Undeveloped
b) Developed
log10 Biomass (mg/m2)
4
3
2
1
0
a
b
c
a
b
c
Sed.
Rock
Wood
Sed.
Rock
Mac.

Fig.2: Size structure of macroinvertebrate communities on different substrata in a) undeveloped and b) developed lakes. Each bar (with standard error) represents the average biomass of organisms in each size class. Average biomass was calculated over 12 sampling stations in the 4 undeveloped lakes, and over 9 stations in the 3 developed lakes. Mean size of organisms (± 1 SE) are presented in the upper left corner.


a) Undeveloped
b) Developed
Sediments
68 ±14μg
Sediments
110 ±19μg
Rocks
16 ±3μg
Rocks
42 ±7μg
Wood
25 ±3μg
Macrophytes
39 ±4μg
Log10 Invertebrate biomass (mg/m2)
0
1
2
3
4
5
6
< 4
8
16
32
64
125
250
500
1000
2000
4000
8000
Size class (μg)

TIB on sediments was 2 fold higher in developed than in undeveloped lakes whereas the increase between groups of lakes was 9 fold on rocks. The ratio between invertebrate and periphyton biomass (as Chl-*a*) was different among substrata. Macrophytes (39 ± 11.9) and sediments (12.3 ± 2.2) tended to have more invertebrate biomass per unit of periphyton Chl-*a* than wood (5.6 ± 1.6) and rocks (3.6 ± 0.8) (Fig. 3; Kruskal-Wallis statistic = 24.5, $P < 0.05$).

Fig.3: Box plots of the ratio of invertebrate (mg dry mass m^{-2}) to periphyton biomass (mg Chla m^{-2}) observed on sediments (n = 21), rocks (n =21), wood (n = 12), and macrophytes (n = 9) collected in 7 lakes of the Laurentian region. Boxes indicate the quartiles, lines inside boxes indicate medians, whiskers indicate the 95th percentiles, and dots outside the whiskers indicate extreme outliers. Significant differences ($P<0.05$) among substrata are indicated by different letters upon bars (2 by 2 ANOVA tests).

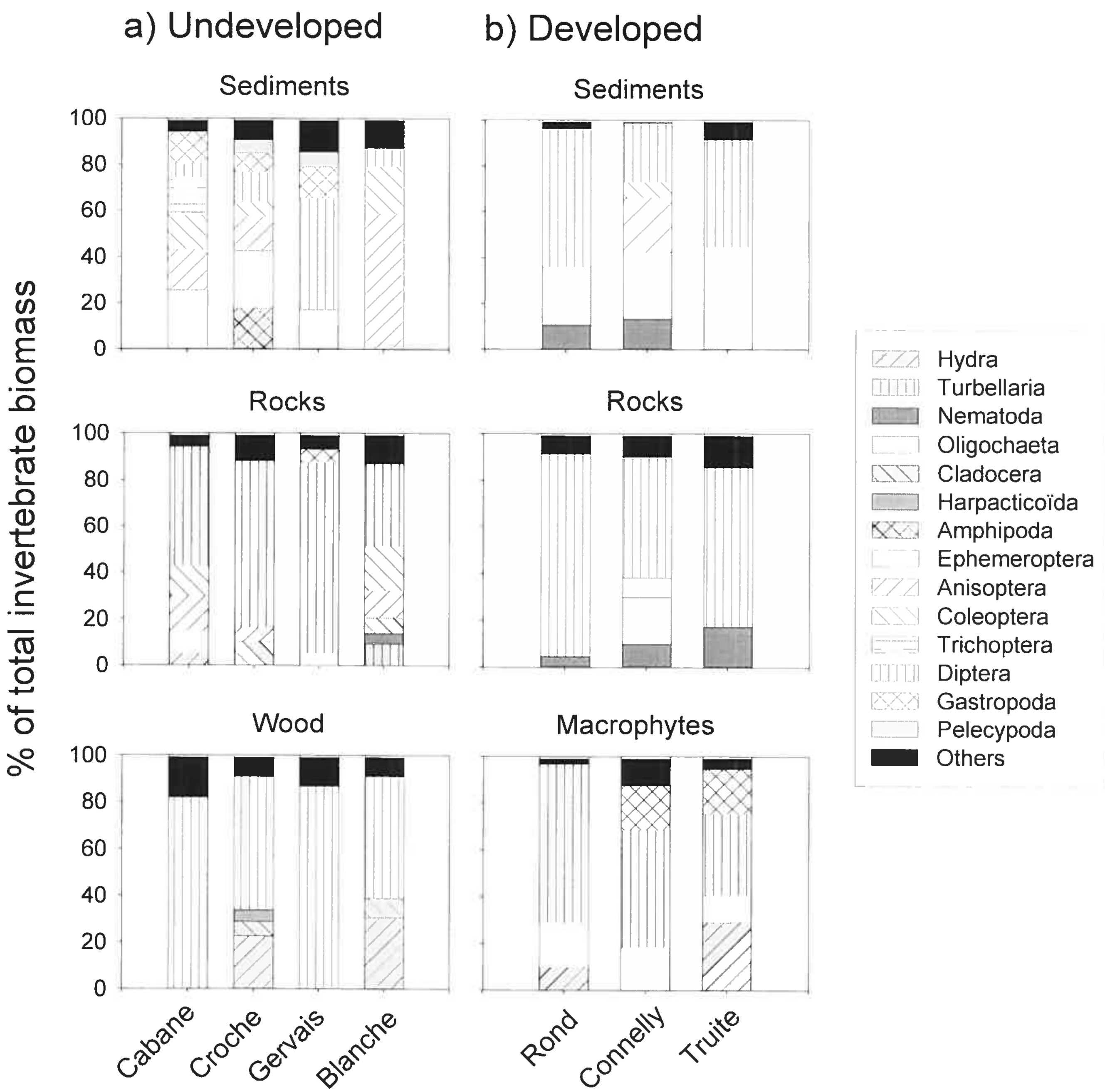

Total invertebrate biomass / periphyton biomass (chl-a)
140
120
100
80
60
40
20
0
a
ab
c
bc
Sediments
Rocks
Wood
Macrophytes

Macroinvertebrate taxonomic composition

In the undeveloped lakes, sediment dwelling invertebrates were mainly insects (Ephemeropteran Caenidae and Ephemeridae, Anisoptera, Coleoptera, Diptera), Amphipoda, and Gastropoda (Physidae). These communities were highly diversified and varied greatly among lakes (Fig. 4a). On rocks, dipteran Chironomidae were dominating but Anisoptera and Coleoptera were also important. Wood too was clearly dominated by Chironomidae with a non negligible presence of *Hydra*.). PCA analysis confirmed that sediments differed from other substrata: Ephemeroptera, Anisoptera, Coleoptera, and Gastropoda were associated with sediments whereas Chironomidae were associated with rocks and wood (Fig. 5a). Overall, taxonomic composition did not vary significantly among lakes but was different between substrate types (ANOVA test; no interaction between lake and substrate type, Table 3a). 2 by 2 ANOVA tests showed that composition of invertebrate communities on sediments was significantly different from those on rocks (P=0.001) and wood (P=0.001) substrata. Rock and wood dwelling invertebrates were not significantly different (P=0.32).

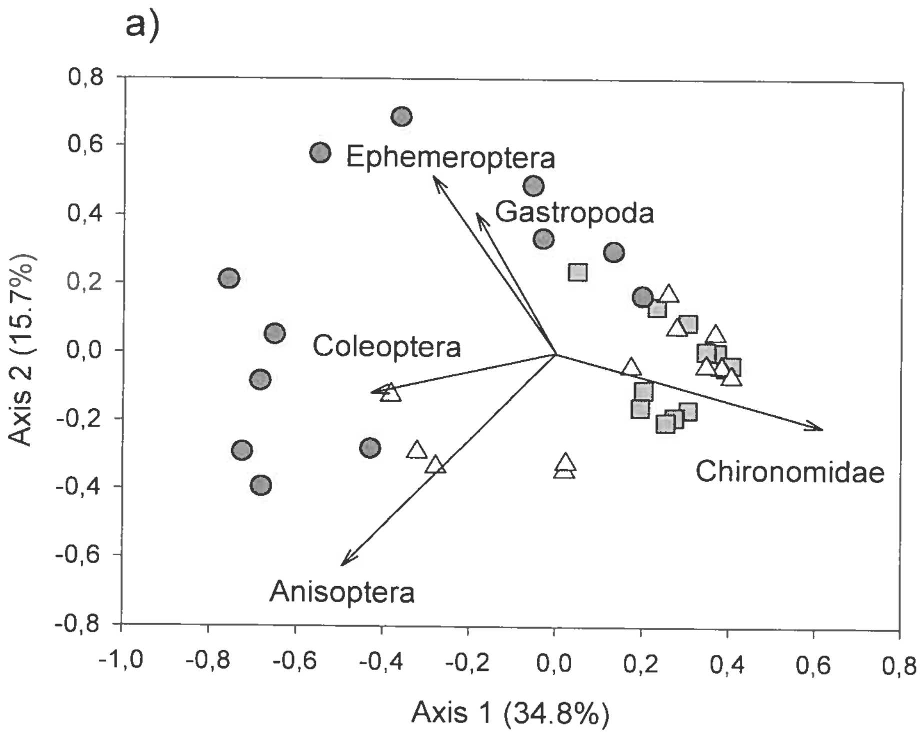
Sediments of developed lakes supported communities dominated by Oligochaeta and Diptera (mostly Chironomidae) with a non negligible presence of Nematoda (Fig. 4b). Invertebrate communities on rocks were again dominated by dipteran Chironomidae with some Nematoda and Oligochaeta. On macrophytes, small sized crustaceans like Copepoda and Cladocera were numerically dominants (data not shown) but accounted for a small fraction of total invertebrate biomass. Macrophyte dwelling invertebrates were mainly composed of dipteran Ceratopogonidae, Gastropoda (Physidae, Planorbidae), *Hydra*, ephemeropteran Baetidae (Fig. 4b). More details on taxonomic composition are presented in appendices 1 and 2. PCA analysis showed that sediments Oligochaeta and Nematoda were associated with sediments, Chironomidae with rocks, and Gastropoda, *Hydra*, Ceratopogonidae, and Ephemeroptera with macrophytes (Fig. 5b). Taxonomic composition varied among lakes and substratum type (no interaction between lake and substratum type, Table 3b). However, substratum type was more important than lake to explain variations in taxonomic composition (R^2=0.31 for substratum; R^2=0.14 for lake; Table 3b). When compared two by two with ANOVA tests, communities on all substrata were different from each other (data not shown).

Fig.4: Proportion of total biomass represented by dominant macroinvertebrates on a) sediments, rocks and wood of undeveloped lakes and b) sediments, rocks and macrophytes of developed lakes. Values are averages of three replicates. For each lake, only groups representing at least 5% of total biomass are shown while the other taxa are grouped as "Others". For more details, see appendices 1 and 2.



a) Undeveloped
b) Developed
Sediments
Rocks
Wood
Sediments
Rocks
Macrophytes
% of total invertebrate biomass
0
20
40
60
80
100
Cabane
Croche
Gervais
Blanche
Rond
Connelly
Truite
Hydra
Turbellaria
Nematoda
Oligochaeta
Cladocera
Harpacticoïda
Amphipoda
Ephemeroptera
Anisoptera
Coleoptera
Trichoptera
Diptera
Gastropoda
Pelecypoda
Others

Fig.5: Principal component analysis (PCA) performed on macroinvertebrate communities on different natural substrata for a) undeveloped lakes (19 taxa) and b) developed lakes (18 taxa) of the Laurentian region.


a)
0,8
0,6
0,4
0,2
0,0
-0,2
-0,4
-0,6
-0,8
Axis 2 (15.7%)
Ephemeroptera
Gastropoda
Coleoptera
Chironomidae
Anisoptera
-1,0
-0,8
-0,6
-0,4
-0,2
0,0
0,2
0,4
0,6
0,8
Axis 1 (34.8%)

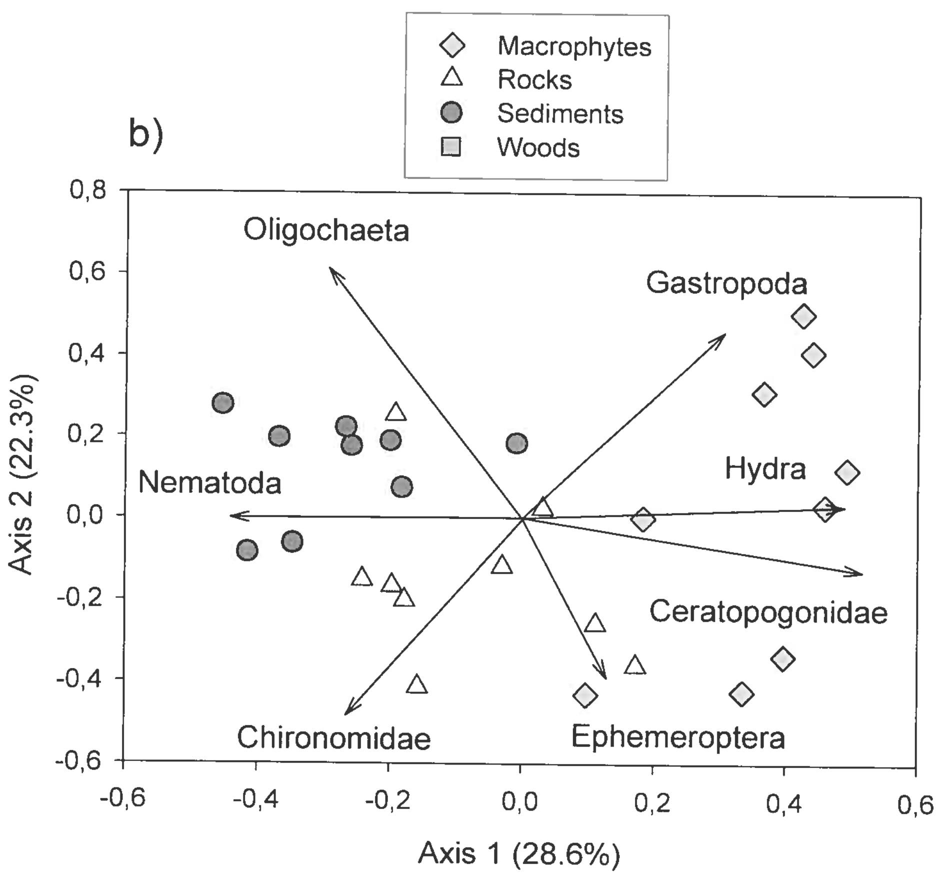

Macrophytes
Rocks
Sediments
Woods
b)
0,8
0,6
0,4
0,2
0,0
-0,2
-0,4
-0,6
Axis 2 (22.3%)
Oligochaeta
Gastropoda
Hydra
Nematoda
Ceratopogonidae
Chironomidae
Ephemeroptera
-0,6
-0,4
-0,2
0,0
0,2
0,4
0,6
Axis 1 (28.6%)

Table 3: Results of multivariate two ways ANOVA tests on taxonomic composition for a) undeveloped (19 taxa) and b) developed lakes (18 taxa). Two classification criteria were tested (lake and substratum) as well as the interaction between these criteria. Differences are significant when $P < 0.05$.

a) Undeveloped

	R^2	F	*P*
Lake	0.012	0.532	0.827
Substratum	0.241	5.319	0.001
Interaction	0.067	1.489	0.125

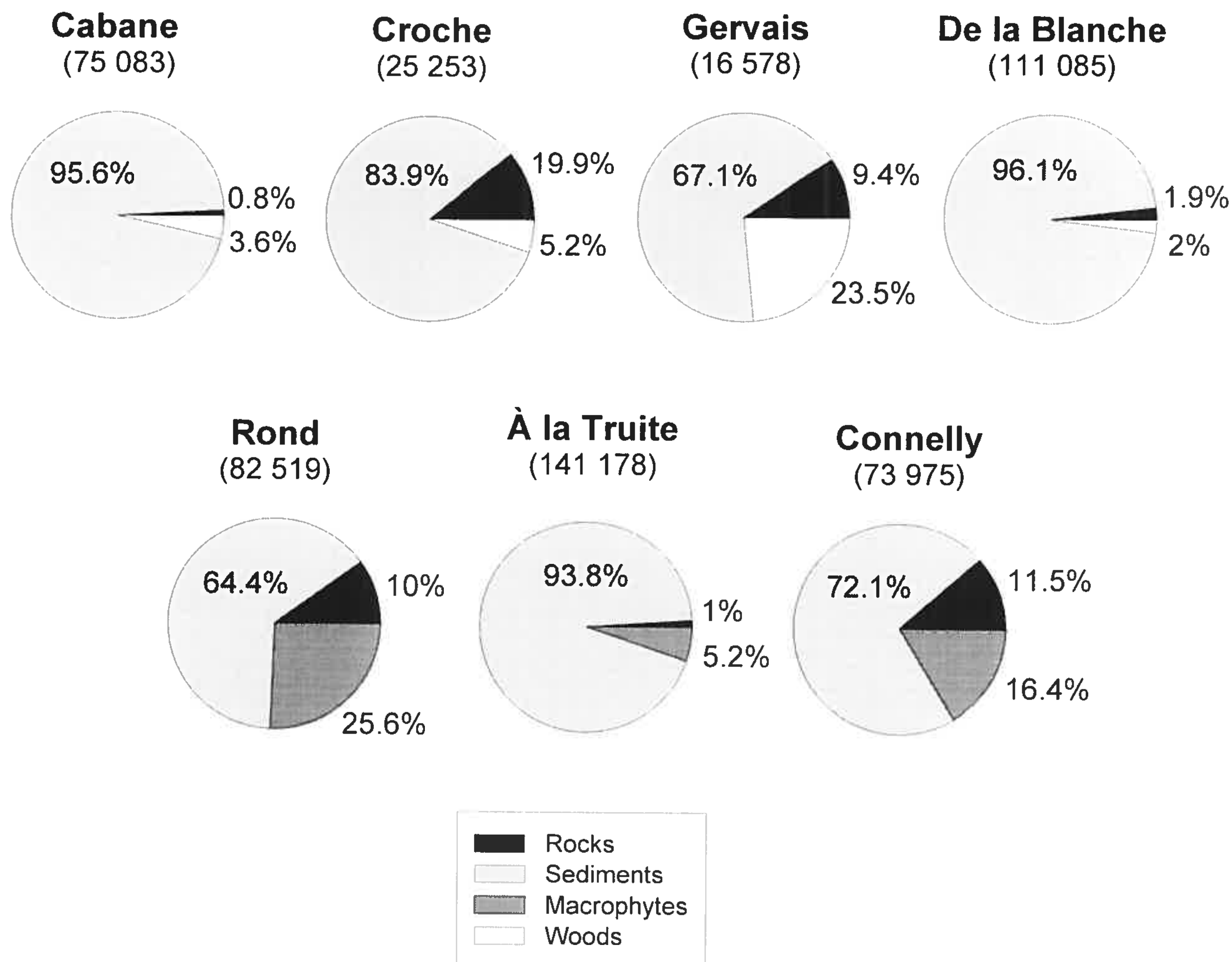
b) Developed

	R^2	F	*P*
Lake	0.136	2.889	0.001
Substratum	0.307	6.539	0.001
Interaction	0.136	1.445	0.06

Substrata composition and total invertebrate biomass at the lake scale

The relative contribution of each substratum to the whole lake macroinvertebrate biomass was estimated keeping in account the mean biomass on each substratum and the areal percentage of each substratum in the littoral zone. In all lakes, sediments supported the largest proportion of the whole lake TIB (64 – 96 %) as this substratum covered a large proportion of the littoral area and was the most productive (Fig. 6). In undeveloped lakes, wood supported on average higher invertebrate biomass at the lake scale than rocks (Fig. 6) despite covering a smaller percentage of lake bottom (Table 1). Wood was particularly important in Lac Gervais where it supported 24% of total invertebrate biomass at the lake scale. In developed lakes, macrophytes supported always more invertebrates than rocks at the lake scale (Fig. 6) because of the importance of their cover (Table 1). Generally, undeveloped lakes had lower total areal invertebrate biomass in the littoral zone at the lake scale than developed lakes (Fig. 6), except for Lac de la Blanche where sediments was almost the major substratum (Table 1).

Fig. 6: Percentage of total invertebrate biomass at the lake scale associated to different types of substratum in undeveloped and developed lakes. Values were calculated keeping in account for each substratum the invertebrate biomass (mg/m^2) weighted for the % of cover (Table 1). Values in brackets are the total areal invertebrate biomass in littoral zone at the lake scale (mg/m^2).


Cabane
(75 083)
95.6%
0.8%
3.6%
Croche
(25 253)
83.9%
19.9%
5.2%
Gervais
(16 578)
67.1%
9.4%
23.5%
De la Blanche
(111 085)
96.1%
1.9%
2%
Rond
(82 519)
64.4%
10%
25.6%
À la Truite
(141 178)
93.8%
1%
5.2%
Connelly
(73 975)
72.1%
11.5%
16.4%
Rocks
Sediments
Macrophytes
Woods

Discussion

Several studies have adressed the importance of habitat complexity in lotic systems (Tanigushi and Tokeshi 2004, Scealy et al. 2007) but less is known about the littoral zone of lakes (Tolonen et al. 2001). In the present study, biomass, size structure, and taxonomic composition of macroinvertebrate communities varied among the different substrata encountered in the lake littoral zone. The availability of these substrata in undeveloped and developed lakes may affect the quantity and quality of littoral fauna.

Undeveloped lakes

Invertebrate biomass was 23 times higher and organisms were on average twice larger on sediments than on rocks. This disproportion can be partly related to higher resources, periphyton and detritus, in sediments than on rocks. Higher TIB / Chl-*a* ratio on sediments compared with rocks suggested that sediments offered advantages other than periphyton to invertebrates. Moreover, sediments of these undeveloped lakes were composed of large particles, including coarse woody debris, leaf litter, and gravel (De Sousa 2007, Chapter 2). Invertebrates, especially the large ones, may benefit of the high amount of interstitial spaces and refuges offered by such heterogeneous sediments, as previously observed in rivers (Flecker and Allan 1984). Invertebrate biomass and composition would vary greatly among lakes or different zones within the same lake simply in relation to the natural prevalence of sediments versus rocks.

Submerged wood provides an important addition to the mineral substrata. Like rocks, it is a stable, hard substratum. In our study, despite similar periphyton biomass, invertebrate biomass and average size were higher on wood than on rocks. Wood itself can be a source of food for some xylophagous invertebrates, including Chironomidae (Hoffmann and Hering 2000). Moreover, wood is soft enough to be gouged by invertebrates to create refuges (Benke and Wallace 2003). At the lake scale, wood supported more invertebrate biomass than rocks, even if it accounted for a smaller proportion of the littoral zone cover. Submerged wood is usually abundant in the littoral zone of undeveloped lakes (Christensen et al.1996) and its removal would reduce invertebrate biomass on rocky littoral zones even if it would not affect taxonomic composition, at least at the order or family level. Smokorowski et al. (2006) studying the effect of wood removal on periphyton and invertebrates in Ontario lakes concluded that this removal would not affect the whole-lake invertebrate community because of the small proportion of wood cover in littoral zone. In contrast, our findings show that wood can support as much as 24% of total littoral invertebrate biomass at the lake scale. Decreasing submerged wood in littoral zone would also contribute to the loss of habitat heterogeneity and the simplification of nearshore structures which is detrimental to fish communities (Christensen et al. 1996, Schindler et al. 2000, Jennings et al. 2003). In another hand, wood removal in sediment areas might increase the percentage of sediments in the littoral zone, a substratum which supported higher invertebrate biomass, and finally enhance benthic production.

Developed lakes

In the same region, lakes experiencing residential development underwent changes in their littoral zone. Riparian clearing led to increased siltation and decreased input of woody debris. In consequence, sediments lost some of their complexity (De Sousa 2007, Chapter 2). Similar changes in sediment heterogeneity were reported in Wisconsin lakes along a gradient of residential development (Jennings et al. 2003; Francis and Schindler 2006). Rock texture also changed in developed lakes because they were covered by thicker periphyton mats (Lambert 2006). Submerged wood dramatically decreased and macrophytes became more abundant and contributed to increase the habitat complexity (Benson and Magnuson 1992; Tolonen et al. 2003) that was lost on sediments and by wood removal. These changes in the littoral zone may have induced modifications of littoral invertebrate communities.

On sediments, invertebrate biomass increased 2-fold compared with undeveloped lakes and was higher than on the other substrata. The mostly epibenthic fauna observed in the undeveloped lakes was replaced by mainly endobenthic taxa such as Oligochaeta and Nematoda, for which fine sediments rich in organic matter are the preferred substratum (Quinn and Hickey 1990; Thorp and Kovich 1991; Verdonschot 1996). Invertebrate biomass increased 9-fold on rocks between undeveloped and developed lakes. Rock dwelling invertebrates are mostly Chironomidae that are grazers and collectors and thus probably tightly linked to periphyton availability. The ratio of invertebrate biomass to periphyton Chl-*a* was the lowest on rocks suggesting that alternative food sources were less available than on the other substrata. Residential development may have greatly stimulated invertebrate biomass on rocks probably through their bottom-up response to increasing periphyton (De Sousa 2007, Chapter 2).

Surprisingly, invertebrate biomass was lower on macrophytes compared with rocks and sediments. Several studies suggest that macrophyte stands support higher abundance of benthic invertebrates than nearby mineral substrata (Sozka 1975; Cyr and Downing 1988;

Beckett et al. 1992; Velasquez and Miserendino 2003; Uvira et al. 2005). Lalonde and Downing (1992) showed that phytofaunal biomass was positively correlated with macrophyte biomass. In the Laurentian lakes, macrophytes areal biomass was still small (11-25 g/m^2) compared with those reported in other studies (e. g. 34-500 g/m^2; Lalonde and Downing 1992). The absence of dense macrophyte beds may explain their low areal invertebrate biomass. The high TIB / Chl-*a* ratio observed on macrophytes could be explained by an underestimation of periphyton biomass due to the difficulty of detaching epiphyton from macrophytes.

Rasmussen (1988) invoked the difficulty of partitioning the fauna associated to sediments and macrophytes. Because this partition is highly variable in time and space, he proposed to consider the littoral zoobenthos as a single vertically integrated community. In that perspective, sediment and macrophyte dwelling invertebrates should be probably combined into a single community. Macrophytes were characterized by Gastropoda, *Hydra*, Ceratopogonidae and ephemeropteran Baetidae (that are active swimmers). Many authors have reported the dominance of Gastropoda in the phytofauna of some lakes (Biggs and Malthus 1982; Vincent et al. 1982; Talbot and Ward 1987). Gastropoda could have switched from sediments to macrophytes with increasing development. *Hydra* are typical representatives of lakes littoral fauna and they are currently found attached on macrophytes, stones, wood or debris but they never occur on soft bottoms (Pennak 1978). No surprisingly, they were abundant on macrophytes in undeveloped lakes and, to a lesser extent, on wood in the undeveloped lakes.

Important differences in invertebrate biomass and taxonomy can exist between lakes having naturally a different substratum composition. Residential development can also alter substrata occurrence or texture and so influence invertebrate communities. A lake having littoral zone mostly composed of sediments may support more invertebrate biomass and insects than a lake rich in rocks or wood. However, a lake rich in rocks may undergo important increase of invertebrate biomass with increasing residential development.

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Appendix 1: Proportion of total biomass represented by macroinvertebrate taxa on sediments, rocks and wood in less developed lakes. Values are averages of 12 replicates (3 sampling stations in 4 lakes).

	% of total biomass		
	Sediments	Rocks	Wood
Hydra	0.2	1.2	3.7
Turbellaria	0.1	1.4	0.1
Nematoda	2.9	1.3	0.2
Oligochaeta	1.6	2.9	3.9
Cladocera	1.2	4.9	7.7
Ostracoda	0.1	0.2	0.5
Cyclopoïda	0.5	1.0	0.5
Harpacticoïda	0.2	0.0	2.1
Amphipoda	3.2	3.6	1.2
Ephemeroptera Caenidae	6.5	0.0	0.0
Ephemeroptera Ephemeridae	4.7	0.0	0.0
Ephemeroptera Leptophlebiidae	0.4	0.0	0.0
Ephemeroptera Baetidae	0.0	0.1	0.0
Anisoptera	36.3	6.0	2.6
Coleoptera	18.2	13.5	0.0
Trichoptera Leptoceridae	4.9	0.1	0.0
Trichoptera Polycentropodidae	0.0	0.3	0.1
Trichoptera Hydroptilidae	0.5	0.0	0.1
Chironomidae	9.7	54.7	75.8
Ceratopogonidae	0.5	6.8	1.4
Plecoptera	0.0	0.1	0.0
Hydracarina	0.1	0.8	0.1
Gastropoda Limnaeidae Physidae	6.1	0.0	0.0
Gastropoda Planorbidae	0.5	1.1	0.0
Pelecypoda	1.7	0.0	0.0

Appendix 2: Proportion of total biomass represented by macroinvertebrate taxa on sediments, rocks and macrophytes in more developed lakes. Values are averages of 9 replicates (3 sampling stations in 3 lakes).

	% of total biomass		
	Sediments	Rocks	Macrophytes
Hydra	0.0	0.4	15.4
Turbellaria	0.0	0.1	0.0
Nematoda	9.0	14.4	0.0
Oligochaeta	28.4	9.6	8.0
Cladocera	0.2	1.2	1.4
Ostracoda	0.2	1.2	0.0
Cyclopoïda	0.0	0.1	0.2
Harpacticoïda	1.2	0.0	0.0
Ephemeroptera Caenidae	0.0	3.9	0.0
Ephemeroptera Leptophlebiidae	0.1	0.0	0.0
Ephemeroptera Baetidae	0.0	1.3	12.6
Anisoptera	15.2	0.3	0.7
Coleoptera	1.9	0.0	0.0
Trichoptera Leptoceridae	0.0	0.0	0.5
Trichoptera Polycentropodidae	0.0	0.0	0.1
Trichoptera Hydroptilidae	0.0	0.0	0.2
Chironomidae	42.0	52.9	32.2
Ceratopogonidae	0.4	11.7	17.5
Megaloptera	0.0	0.5	0.0
Hydracarina	0.0	0.5	0.1
Gastropoda Limnaeidae Physidae	1.0	0.0	6.8
Gastropoda Planorbidae	0.2	1.7	4.4
Pelecypoda	0.3	0.2	0.0

Accord des coauteurs

Simon De Sousa

M. Sc. En sciences biologiques

Simon de Sousa, Antonella Cattaneo et Bernadette Pinel-Alloul. Littoral invertebrates living on different natural substrata in two groups of lakes of varying anthropogenic development. À soumettre à *Freshwater Biology*.

À titre de coauteur de l'article identifié ci-dessus, je suis d'accord pour que **Simon De Sousa** inclue cet article dans son **mémoire de maîtrise** qui a pour titre : « **La réponse des communautés d'invertébrés benthiques sur différents substrats naturels au développement résidentiel des bassins versants des lacs des Laurentides** ».

[redacted]

Coauteur : Antonella Cattaneo Date

[redacted]

Coauteur : BernadettePinel-Alloul Date

Conclusions générales

La recherche met en évidence que les invertébrés benthiques de la zone littorale peuvent être des indicateurs précoces de l'urbanisation des lacs de villégiature des Basses Laurentides. Les communautés de macroinvertébrés benthiques répondent apparement au gradient de perturbation de la zone riveraine par le développement résidentiel, via les changements induits dans les types et l'hétérogénéité des substrats (sédiments, roches, bois submergé, macrophytes) et l'enrichissement en algues benthiques sur les substrats rocheux (épilithon). Dans le Chapitre 2, on montre que les communautés de macroinvertébrés des sédiments et des roches répondent de façon différente au gradient de développement résidentiel sur les berges des lacs. Sur les roches, la biomasse totale d'invertébrés est positivement et fortement corrélée à l'intensité du développement résidentiel sur les berges des lacs et à la biomasse d'épilithon, suggérant un certain effet ascendant. Par contre, la composition taxinomique ne change pas le long du gradient de perturbation, les communautés des roches étant toujours largement dominées par les Diptères chironomides. Sur les sédiments, la biomasse totale d'invertébrés ne varie pas significativement le long du gradient de perturbation, malgré une faible augmentation de la biomasse des algues benthiques (épipelon). Cependant, la composition taxinomique des invertébrés sur les sédiments est significativement associée au développement résidentiel sur les rives des lacs. Les Éphémères sont caractéristiques des lacs ayant un faible développement résidentiel, alors que les Oligochètes sont associés aux lacs ayant un fort développement résidentiel. Des changements dans l'hétérogénéité des sédiments pourraient avoir influencé la composition des communautés d'invertébrés. Dans les lacs peu développés, les sédiments contiennent plus de litière ligneuse (débris de bois, feuilles d'arbre) et de cailloux, alors que dans les lacs développés, beaucoup moins de litière est présente et les sédiments contiennent plus de particules fines. Les communautés d'invertébrés des sédiments pourraient donc avoir répondu à un changement au niveau de la complexité et de l'hétérogénéité de leur habitat. Les sédiments plus hétérogènes des lacs peu perturbés offriraient plus de refuge aux organismes de grande taille tels que les insectes Éphémères, tandis que les sédiments plus fins et plus riches en matière organique des lacs perturbés seraient favorables aux organismes endobenthiques tels que les Oligochètes. Les sédiments seraient le meilleur substrat pour un suivi écologique et ces deux taxons (Éphémères et Oligochètes) pourraient être utilisés respectivement comme indicateurs de la bonne et mauvaise qualité des sédiments dans la zone littorale des lacs des Laurentides. Dans une perspective d'utilisation des macroinvertébrés pour la gestion écologique des lacs, nous suggérons donc de concentrer les efforts d'échantillonnage sur les sédiments puisqu'ils sont toujours largement présents dans les lacs et qu'ils contiennent des organismes sensibles aux perturbations causées par le développement résidentiel riverain. Notre étude montre que même dans un contexte géographique où les perturbations anthropiques sont encore récentes (deux décennies) et relativement faibles comparé aux perturbations par des activités de type agricole, les communautés d'invertébrés benthiques des sédiments représentent un outil de gestion sensible pouvant détecter les indices précoces de la perturbation de la zone littorale causée par le développement résidentiel.

Puisque l'hétérogénéité des substrats de la zone littorale des lacs est très importante en termes de types de substrat (sédiments, roches, bois submergé, macrophytes) et de leur importance le long du gradient de perturbation résidentielle, il était nécessaire de mieux comprendre les associations invertébrés-substrats. Au Chapitre 3, l'importance du type de substrat pour expliquer la distribution des communautés d'invertébrés le long du gradient de perturbation a été particulièrement mise en évidence. Les sédiments et les roches sont toujours présents tandis que le bois submergé se retrouve surtout dans les lacs peu perturbés et les macrophytes dans les lacs perturbés par le développement résidentiel. Les sédiments supportent toujours une plus grande biomasse totale et de plus gros invertébrés que les roches, le bois ou les macrophytes. Le développement résidentiel semble avoir provoqué, dans les sédiments, une transition d'invertébrés plutôt épibenthiques dans les lacs peu développés vers des invertébrés plutôt endobenthiques dans les lacs perturbés. A l'échelle globale de la zone littorale des lacs et le long du gradient de perturbation, les sédiments sont toujours le type de substrat le plus important et le plus riche en invertébrés benthiques. Les roches et le bois supportent des communautés moins riches et plutôt semblables du point de vue taxinomique (prédominance des Diptères chironomides). Le bois supporte cependant une plus grande biomasse d'invertébrés par unité de surface que les roches. À l'échelle globale de la zone littorale, le bois submergé supporte une plus grande proportion de la biomasse totale d'invertébrés que les roches. L'enlèvement du bois submergé de la zone littorale priverait donc les lacs d'une biomasse d'invertébrés non négligeable. La croissance importante des algues benthiques (épilithon) associée au développement résidentiel est accompagnée par une forte hausse de la biomasse d'invertébrés benthiques, particulièrement sur les roches, suggérant ainsi un effet ascendant. Les macrophytes représentent, dans les lacs ayant un fort développement résidentiel, un habitat important car ils contribuent à augmenter l'hétérogénéité et la complexité des habitats littoraux qui sont perdues dans les sédiments fins et par l'enlèvement du bois submergé. La présence des macrophytes permet donc l'établissement d'une diversité d'invertébrés épibenthiques qui ont disparus des sédiments.

En conclusion, la recherche montre que les invertébrés benthiques sont de bons indicateurs des perturbations des substrats et de l'enrichissement en algues dans la zone littorale des lacs des Laurentides affectés par le développement résidentiel riverain. Toutefois, l'occurrence et l'importance des différents types de substrat le long du gradient de perturbation sont très importantes pour expliquer la distribution des communautés d'invertébrés benthiques dans la zone littorale des lacs. Dans une perspective d'utilisation des macroinvertébrés pour la gestion des lacs, il est important de choisir le bon substrat à échantillonner afin de minimiser les coûts et le temps reliés à l'analyse des échantillons en laboratoire. Cette étude démontre que les sédiments sont le substrat de choix et que l'utilisation d'une échelle taxinomique grossière (classe, ordre ou famille) est apparemment suffisante pour détecter l'influence du développement résidentiel riverain sur les communautés d'invertébrés. L'utilisation des taxons (Éphémères et Oligochètes) identifiés comme étant les meilleurs bioindicateurs de qualité de la zone littorale des lacs serait relativement aisée pour un non spécialiste. De plus, la faible profondeur d'échantillonnage (1 mètre) rend facile la collecte des échantillons. Ceci pourrait faciliter l'utilisation des invertébrés benthiques des sédiments par les associations de riverains des lacs dans un but de surveillance écologique de la qualité de la zone littorale qui reflète de façon précoce les effets du développement résidentiel récent mais accéléré des lacs des Basses Laurentides. Nous tenons également à souligner que puisque l'échantillonnage s'est déroulé en juillet et que les communautés de macroinvertébrés sont influencés par le facteur temporel (certaines larves d'insectes émergent à différents moment durant la période estivale), il serait prudent de respecter la période d'échantillonnage utilisée dans cette étude pour établir des programmes de suivi écologique utilisant les conclusions que nous avons présentées. D'éventuelles études devront être menées afin de vérifier si nos conclusions sont toujours valides pour des pédriodes différentes durant l'été, voire même durant le printemps et l'automne.

ANNEXE 1 : Relations longueur masse

L = longueur en mm
DM = masse sèche en mg

Taxon	Équation (DM =)	Source
Chironomides	$0,0018 * L^{(2.617)}$	Benke et al 1999
Ceratopogonidés	$0,0025 * L^{(2.469)}$	Benke et al 1999
Mégaloptères	$0,00290013 * L^{(2.75)}$	Smock 1980
Odonates	$0,013996 * L^{(2.78)}$	Smock 1980
Coléoptères (Elmidae)	$0,00737 * L^{(2.879)}$	Benke et al 1999
Éphémères	$0,0065979 * L^{(2.88)}$	Smock 1980
Trichoptères	$0,0018998 * L^{(3.12)}$	Smock 1980
Plécoptères	$0,0022996 * L^{(3.39)}$	Smock 1980
Acariens	$0,0033682 * L^{(2.761)}$	Roger et al 1977
Tardigrades	$0,0033682 * L^{(2.761)}$	idem Acarien
Plathelminthes	$0,0095 * L^{(2.154)}$	Benke et al 1999
Nématodes	$0,001 * L^{(3)}$	communication avec A. Cattaneo
Oligochètes	$0,00241 * L^{(1.875)}$	Stoffels et al. 2003
Hirudinés	$10^{(0.1972*L - 1.0646)}$	Mason 1977
Ostracodes	$0.041007 * L^{(2.76063)}$	Tudorancea et al. 1979
Cladocères (Chydoridae)	$0,0098749 * L^{(2.1)}$	Peters and Downing 1984
Harpacticoïdes	$0,01251 * L^{(4.4)}$	Dumont et al. 1975
Cyclopoïdes	$0.00647724 * L^{(2.59)}$	Dumont et al. 1975
Amphipodes	$0.007083 * L^{(2.83)}$	Burgherr and Meyer 1997
Isopodes	$0,0054 * L^{(2.948)}$	Benke et al 1999
Gastéropodes		
Physidae	$e^{(-3.664+0.867*L)}$	Eckblad 1971
Planorbidae	$e^{(-4.321+0.962*L)}$	Eckblad 1971
Pélécypodes (Sphaeriidae)	$0,0163 * L^{(2.477)}$	Benke et al 1999
Hydres	$0,03125 * L^{(3)}$	communication avec A. Cattaneo

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ANNEXE 2: Description des lacs

Lac De la Cabane

Aire du lac : 0,2503 km^2

Volume : 1 836 000 m^3

Périmètre : 3,79 km

Profondeur moyenne : 7,6 m

Profondeur maximum : 20,8 m

Aire du bassin versant : 2,457 km^2

Pente moyenne du bassin versant : 7,46 %

Indice de creux : 14,7

Ratio de drainage : 8,8

Aire du bassin versant relatif au volume : 1,34 $km^2 \cdot m^{-3}$

PT : 8,2 $\mu g \cdot L^{-1}$

PTD : 2,6 $\mu g \cdot L^{-1}$

NT : 259,8 $\mu g \cdot L^{-1}$

NO_3 : 40,3 $\mu g \cdot L^{-1}$

COD: 3,6 $mg \cdot L^{-1}$

pH : 6,2

Proportion de particules fines (<250µm) dans les sédiments: 12,9 %

Secchi : 3,3 m

Phytoplancton: 3,01 $\mu g \cdot L^{-1}$

Épilithon : 33,2 $mg \cdot m^{-2}$

Épipelon : 97,9 $mg \cdot m^{-2}$

Bande riveraine

	50 m	100 m	150 m	200 m	250 m	500 m	1000 m	B.V.
Nb. d'habitations	0	0	0	0	0	0	0	0
Habitations/km²	0	0	0	0	0	0	0	0
% zone ouverte	0	0	0	0	0	0	0	0
% zone humide	0	0	0	0	0	0	1	1

Lac Violon

Aire du lac : 0,3824 km^2

Volume : 3 325 000 m^3

Périmètre : 2,45 km

Profondeur moyenne : 8,9 m

Profondeur maximum : 22,6 m

Aire du bassin versant : 4,4145 km^2

Pente moyenne du bassin versant : 9,2 %

Indice de creux : 14,1

Ratio de drainage : 10,5

Aire du bassin versant relatif au volume : 1,33 $km^2 \cdot m^{-3}$

PT : 5,7 $\mu g \cdot L^{-1}$

PTD : 3,1 $\mu g \cdot L^{-1}$

NT : 215,1 $\mu g \cdot L^{-1}$

NO_3 : 1,4 $\mu g \cdot L^{-1}$

COD : 3,5 $mg \cdot L^{-1}$

pH : 6.6

Proportion de particules fines (<250µm) dans les sédiments: 14,6 %

Secchi : 5,3 m

Phytoplancton: 1,23 $\mu g \cdot L^{-1}$

Épilithon : 5,7 $mg \cdot m^{-2}$

Épipelon : 21,3 $mg \cdot m^{-2}$

Bande riveraine

	50 m	100 m	150 m	200 m	250 m	500 m	1000 m	B.V.
Nb. d'habitations	1	3	3	3	3	5	5	5
Habitations/km^2	8	13	9	7	5	5	3	3
% zone ouverte	0	0	0	0	0	0	0	0
% zone humide	0	0	0	0	0	0	0	0

Lac Croche

Aire du lac : 0,18 km^2

Volume : 877 000 m^3

Périmètre : 4,31 km

Profondeur moyenne : 4,9 m

Profondeur maximum : 12,9 m

Aire du bassin versant : 0,84 km^2

Pente moyenne du bassin versant : 13,0 %

Indice de creux : 11,5

Ratio de drainage : 3,7

Aire du bassin versant relatif au volume : 0,96 $km^2 \cdot m^{-3}$

PT : 5,0 $\mu g \cdot L^{-1}$

PTD : 2,0 $\mu g \cdot L^{-1}$

NT : 256,9 $\mu g \cdot L^{-1}$

NO_3 : 27,9 $\mu g \cdot L^{-1}$

COD : 4,1 $mg \cdot L^{-1}$

pH : 6,2

Proportion de particules fines (<250µm) dans les sédiments: 14,6 %

Secchi : 4,0 m

Phytoplancton: 1,26 $\mu g \cdot L^{-1}$

Épilithon : 46,7 $mg \cdot m^{-2}$

Épipelon : 165,0 $mg \cdot m^{-2}$

Bande riveraine

	50 m	100 m	150 m	200 m	250 m	500 m	1000 m	B.V.
Nb. d'habitations	1	1	1	1	1	1	1	1
Habitations/km^2	5	3	2	2	2	2	2	2
% zone ouverte	0	0	0	0	0	0	0	0
% zone humide	0	0	0	0	0	0	0	0

Lac Tracy

Aire du lac : 0,0833 km^2

Volume : 676 000 m^3

Périmètre : 1,38 km

Profondeur moyenne : 8,1 m

Profondeur maximum : 22,9 m

Aire du bassin versant : 0,2432 km^2

Pente moyenne du bassin versant : 8,3 %

Indice de creux : 28,1

Ratio de drainage : 1,9

Aire du bassin versant relatif au volume : 0,36 $km^2 \cdot m^{-3}$

PT : 6,2 $\mu g \cdot L^{-1}$

PTD : 2,5 $\mu g \cdot L^{-1}$

NT : 266,5 $\mu g \cdot L^{-1}$

NO_3 : 17,4 $\mu g \cdot L^{-1}$

COD : 2,9 $mg \cdot L^{-1}$

pH : 7,0

Proportion de particules fines (<250µm) dans les sédiments: 50,4 %

Secchi : 5,3 m

Phytoplancton: 1,34 $\mu g \cdot L^{-1}$

Épilithon : 19,4 $mg \cdot m^{-2}$

Épipelon : 35,7 $mg \cdot m^{-2}$

	Bande riveraine							
	50 m	**100 m**	**150 m**	**200 m**	**250 m**	**500 m**	**1000 m**	**B.V.**
Nb. d'habitations	20	21	23	23	23	23	23	23
Habitations/km^2	289	176	157	144	144	144	144	144
% zone ouverte	5	6	5	4	4	4	4	4
% zone humide	0	0	0	0	0	0	0	0

Lac Gervais

Aire du lac : 0,9656 km^2

Volume : 23 530 000 m^3

Périmètre : 7,08 km

Profondeur moyenne : 24,5 m

Profondeur maximum : 60 m

Aire du bassin versant : 8,6510 km^2

Pente moyenne du bassin versant : 6,2 %

Indice de creux : 24,8

Ratio de drainage : 8,0

Aire du bassin versant relatif au volume : 0,37 $km^2 \cdot m^{-3}$

PT : 4,6 $\mu g \cdot L^{-1}$

PTD : 1,7 $\mu g \cdot L^{-1}$

NT : 190,4 $\mu g \cdot L^{-1}$

NO_3 : 2,0 $\mu g \cdot L^{-1}$

COD : 2,7 $mg \cdot L^{-1}$

pH : 7,0

Proportion de particules fines (<250µm) dans les sédiments: 37,9 %

Secchi : 7,7 m

Phytoplancton: 0,74 $\mu g \cdot L^{-1}$

Épilithon : 45,7 $mg \cdot m^{-2}$

Épipelon : 102,3 $mg \cdot m^{-2}$

	Bande riveraine							
	50 m	**100 m**	**150 m**	**200 m**	**250 m**	**500 m**	**1000 m**	**B.V.**
Nb. d'habitations	69	72	75	77	79	86	108	162
Habitations/km²	212	115	82	66	56	33	27	21
% zone ouverte	2	1	1	1	1	1	1	1
% zone humide	0	0	0	0	0	0	0	0

Lac De la Blanche

Aire du lac : 0,4107 km^2

Volume : 4 590 000 m^3

Périmètre : 3,82 km

Profondeur moyenne : 11,7 m

Profondeur maximum : 26 m

Aire du bassin versant : 3,945 km^2

Pente moyenne du bassin versant : 8,19 %

Indice de creux : 17,4

Ratio de drainage : 8,6

Aire du bassin versant relatif au volume : 0,86 $km^2 \cdot m^{-3}$

PT : 4,9 $\mu g \cdot L^{-1}$

PTD : 1,7 $\mu g \cdot L^{-1}$

NT : 258,0 $\mu g \cdot L^{-1}$

NO_3 : 65,1 $\mu g \cdot L^{-1}$

COD : 2,8 $mg \cdot L^{-1}$

pH : 6,4

Proportion de particules fines (<250µm) dans les sédiments: 32,4 %

Secchi : 5,3 m

Phytoplancton: 2,64 $\mu g \cdot L^{-1}$

Épilithon : 16,4 $mg \cdot m^{-2}$

Épipelon : 85,5 $mg \cdot m^{-2}$

Bande riveraine

	50 m	100 m	150 m	200 m	250 m	500 m	1000 m	B.V.
Nb. d'habitations	42	46	47	48	48	53	57	57
Habitations/km^2	219	123	89	73	63	47	26	16
% zone ouverte	17	9	7	6	5	4	2	1
% zone humide	0	0	0	0	1	1	3	2

Lac Purvis

Aire du lac : 0,1901km^2

Volume : 1 446 000 m^3

Périmètre : 2,62 km

Profondeur moyenne : 7,8 m

Profondeur maximum : 19,7 m

Aire du bassin versant : 0,6048 km^2

Pente moyenne du bassin versant : 10,6 %

Indice de creux : 17,4

Ratio de drainage : 2,2

Aire du bassin versant relatif au volume : 0,42 km^2·m^{-3}

PT : 10,3 µg·L^{-1}

PTD : 3,8 µg·L^{-1}

NT : 272,7 µg·L^{-1}

NO_3 : 1,5 µg·L^{-1}

COD : 3,1 mg·L^{-1}

pH : 7,2

Proportion de particules fines (<250µm) dans les sédiments: 48,4 %

Secchi : 6,2 m

Phytoplancton: 2,73 µg·L^{-1}

Épilithon : 82,5 mg·m^{-2}

Épipelon : 94,5 mg·m^{-2}

Bande riveraine

	50 m	100 m	150 m	200 m	250 m	500 m	1000 m	B.V.
Nb. d'habitations	13	27	31	37	37	37	37	37
Habitations/km^2	106	117	100	101	94	89	89	89
% zone ouverte	13	9	10	9	9	8	8	8
% zone humide	0	0	0	0	0	0	0	0

Lac Morency

Aire du lac : 0,2593 km^2

Volume : 2 246 000 m^3

Périmètre : 2,99 km

Profondeur moyenne : 9,1 m

Profondeur maximum : 20,3 m

Aire du bassin versant : 2,3340 km^2

Pente moyenne du bassin versant : 14,6 %

Indice de creux : 17,0

Ratio de drainage : 8,0

Aire du bassin versant relatif au volume : 1,04 $km^2 \cdot m^{-3}$

PT : 10,4 $\mu g \cdot L^{-1}$

PTD : 2,9 $\mu g \cdot L^{-1}$

NT : 313,6 $\mu g \cdot L^{-1}$

NO_3 : 54,8 $\mu g \cdot L^{-1}$

COD : 3,3 $mg \cdot L^{-1}$

pH : 7,8

Proportion de particules fines (<250µm) dans les sédiments: 72,6 %

Secchi : 6,0 m

Phytoplancton: 2,30 $\mu g \cdot L^{-1}$

Épilithon : 66,5 $mg \cdot m^{-2}$

Épipelon : 139,3 $mg \cdot m^{-2}$

	Bande riveraine							
	50 m	**100 m**	**150 m**	**200 m**	**250 m**	**500 m**	**1000 m**	**B.V.**
Nb. d'habitations	23	46	58	72	81	114	119	119
Habitations/km²	152	151	126	116	103	69	57	57
% zone ouverte	31	28	24	22	21	15	13	13
% zone humide	0	0	0	0	0	0	0	0

Lac Baie du Nord

Aire du lac : 0,8670 km^2

Volume : 5 514 000 m^3

Périmètre : 6,39 km

Profondeur moyenne : 6.4 m

Profondeur maximum : 20,6 m

Aire du bassin versant : 13,950 km^2

Pente moyenne du bassin versant : 12.5 %

Indice de creux : 6,8

Ratio de drainage : 15,1

Aire du bassin versant relatif au volume : 2.53 $km^2 \cdot m^{-3}$

PT : 10,0 $\mu g \cdot L^{-1}$

PTD : 3.4 $\mu g \cdot L^{-1}$

NT : 329,2 $\mu g \cdot L^{-1}$

NO_3 : 5.3 $\mu g \cdot L^{-1}$

COD : 6.2 $mg \cdot L^{-1}$

pH : 6,7

Proportion de particules fines (<250µm) dans les sédiments: 67.2 %

Secchi : 3.2 m

Phytoplancton: 1,53 $\mu g \cdot L^{-1}$

Épilithon : 144.2 $mg \cdot m^{-2}$

Épipelon : 191,2 $mg \cdot m^{-2}$

Bande riveraine

	50 m	100 m	150 m	200 m	250 m	500 m	1000 m	B.V.
Nb. d'habitations	78	95	102	102	102	105	119	241
Habitations/km²	261	167	127	100	82	44	23	18
% zone ouverte	40	26	19	15	13	7	3	3
% zone humide	0	0	0	0	0	0	1	2

Lac Renée

Aire du lac : 0,0705 km^2

Volume : 296 000 m^3

Périmètre : 1,21 km

Profondeur moyenne : 4,2 m

Profondeur maximum : 9,5 m

Aire du bassin versant : 0,2174 km^2

Pente moyenne du bassin versant : 10 %

Indice de creux : 15,8

Ratio de drainage : 2,1

Aire du bassin versant relatif au volume : 0,73 $km^2 \cdot m^{-3}$

PT : 14,2 $\mu g \cdot L^{-1}$

PTD : 4,5 $\mu g \cdot L^{-1}$

NT : 485,6 $\mu g \cdot L^{-1}$

NO_3 : 32,3 $\mu g \cdot L^{-1}$

COD : 4,2 $mg \cdot L^{-1}$

pH : 6,1

Proportion de particules fines (<250µm) dans les sédiments: 72,3 %

Secchi : 4 m

Phytoplancton: 3,85 $\mu g \cdot L^{-1}$

Épilithon : 64,5 $mg \cdot m^{-2}$

Épipelon : 104,9 $mg \cdot m^{-2}$

	Bande riveraine							
	50 m	**100 m**	**150 m**	**200 m**	**250 m**	**500 m**	**1000 m**	**B.V.**
Nb. d'habitations	21	37	45	48	50	50	50	50
Habitations/km²	388	400	406	393	381	340	340	340
% zone ouverte	38	43	40	36	34	30	30	30
% zone humide	0	0	0	0	0	0	0	0

Lac Rond (Sainte-Adèle)

Aire du lac : 0,1668 km^2

Volume : 1 206 000 m^3

Périmètre : 1,64 km

Profondeur moyenne : 7,2 m

Profondeur maximum : 15,8 m

Aire du bassin versant : 1,500 km^2

Pente moyenne du bassin versant : 7,5 %

Indice de creux : 17,7

Ratio de drainage : 8,0

Aire du bassin versant relatif au volume : 1,24 $km^2 \cdot m^{-3}$

PT : 13,0 $\mu g \cdot L^{-1}$

PTD : 4,0 $\mu g \cdot L^{-1}$

NT : 384,6 $\mu g \cdot L^{-1}$

NO_3 : 4,8 $\mu g \cdot L^{-1}$

COD : 3,6 $mg \cdot L^{-1}$

pH : 8,1

Proportion de particules fines (<250µm) dans les sédiments: 55,6 %

Secchi : 5,5 m

Phytoplancton: 4,61 $\mu g \cdot L^{-1}$

Épilithon : 119,6 $mg \cdot m^{-2}$

Épipelon : 208,8 $mg \cdot m^{-2}$

	Bande riveraine							
	50 m	**100 m**	**150 m**	**200 m**	**250 m**	**500 m**	**1000 m**	**B.V.**
Nb. d'habitations	27	64	111	146	183	279	320	322
Habitations/km^2	323	373	417	400	391	330	255	242
% zone ouverte	86	90	91	90	86	74	54	53
% zone humide	0	0	0	0	0	0	0	0

Lac Connelly

Aire du lac : 1,240 km^2

Volume : 9 561 000 m^3

Périmètre : 7,28 km

Profondeur moyenne : 7,7 m

Profondeur maximum : 20,8 m

Aire du bassin versant : 24,360 km^2

Pente moyenne du bassin versant : 6,15 %

Indice de creux : 6,9

Ratio de drainage : 18,6

Aire du bassin versant relatif au volume : 2,55 $km^2 \cdot m^{-3}$

PT : 8,0 $\mu g \cdot L^{-1}$

PTD : 3,0 $\mu g \cdot L^{-1}$

NT : 340,0 $\mu g \cdot L^{-1}$

NO_3 : 44,1 $\mu g \cdot L^{-1}$

COD : 4,6 $mg \cdot L^{-1}$

pH : 7,4

Proportion de particules fines (<250μm) dans les sédiments: 47,6 %

Secchi : 3,5 m

Phytoplancton: 4,42 $\mu g \cdot L^{-1}$

Épilithon : 216,6 $mg \cdot m^{-2}$

Épipelon : 256,8 $mg \cdot m^{-2}$

Bande riveraine

	50 m	100 m	150 m	200 m	250 m	500 m	1000 m	B.V.
Nb. d'habitations	234	361	423	469	498	595	803	1107
Habitations/km^2	686	552	448	389	339	217	157	48
% zone ouverte	46	39	33	28	26	17	16	7
% zone humide	0	0	0	0	0	0	1	2

Lac À la Truite

Aire du lac : 0,5121 km^2

Volume : 4 783 000 m^3

Périmètre : 3,54 km

Profondeur moyenne : 9,4 m

Profondeur maximum : 22,5 m

Aire du bassin versant : 4,2350 km^2

Pente moyenne du bassin versant : 5,9 %

Indice de creux : 13,1

Ratio de drainage : 7,3

Aire du bassin versant relatif au volume : 0,89 $km^2 \cdot m^{-3}$

PT : 6,5 $\mu g \cdot L^{-1}$

PTD : 2,0 $\mu g \cdot L^{-1}$

NT : 290,5 $\mu g \cdot L^{-1}$

NO_3 : 87,3 $\mu g \cdot L^{-1}$

COD : 3,0 $mg \cdot L^{-1}$

pH : 7,7

Proportion de particules fines (<250µm) dans les sédiments: 84,1 %

Secchi : 5,2 m

Phytoplancton: 1,72 $\mu g \cdot L^{-1}$

Épilithon : 118,3 $mg \cdot m^{-2}$

Épipelon : 217,4 $mg \cdot m^{-2}$

Bande riveraine

	50 m	100 m	150 m	200 m	250 m	500 m	1000 m	B.V.
Nb. d'habitations	78	148	227	277	302	384	412	412
Habitations/km^2	430	400	404	368	322	202	123	111
% zone ouverte	79	71	64	60	58	50	34	30
% zone humide	0	0	0	0	0	0	0	0

ANNEXE 3 : Tableaux de données

Tableau I: Biomasse par unité de surface (mg•m^{-2}) de 24 grands groupes d'invertébrés dans les stations échantillonnées de sédiments, roches, bois et macrophytes. L'identification des échantillons se fait comme suit : substrat-lac-numéro de station (exemple : SCa3 → S = sédiments, Ca = lac De la Cabane, 3 = station 3). Les abréviations suivantes sont utilisées dans l'identification des stations : S = sédiments, R = roches, B = bois, M = macrophytes, Ca = lac De la Cabane, Vi = lac Violon, Cr = lac Croche, Ty = lac Tracy, Ge = lac Gervais, Bl = lac De la Blanche, Pu = lac Purvis, Mo = lac Morency, Bn = lac Baie du Nord, Re = lac Renée, Sa = lac Rond (Sainte-Adèle), Co = lac Connely, Tr = lac Truite.

Biomasse par unité de surface (mg•m^{-2}) (*Grands groupes*)																								
Sites	Hydres	Plathelminthes	Nématodes	Oligochètes	Hirudinés	Cladocères	Ostracodes	Cyclopoïdes	Harpacticoïdes	Amphipodes	Isopodes	Éphémères	Anisoptères	Zygoptères	Coléoptères	Trichoptères	Chironomides	Cératopogonidés	Plécoptères	Mégaloptères	Tardigrades	Hydracariens	Gastéropodes	Pélécypodes
Sédiments																								
SCa3	0	0	34,8	5,7	0	7,52	0	2,35	0,72	0	0	278	0	0	163	149	58,8	0	0	0	0	0,19	199	1,08
SCa4	11,2	0	59	12,3	0	8,36	0	1,95	11,1	0	0	384	492	0	120	457	98,5	0	0	0	0	0,24	0	0
SCa14	0	0	57,7	5,88	0	16,3	1,25	12,2	1,51	0	0	441	432	0	367	102	99,6	0	0	0	0	0,27	390	0
SCa7	0	0	0	0,79	0	10	0	0	0	0	0	67,1	33,9	0	0	505	45,2	0	0	2,12	0	0,26	0	25,4
SVi3	0	0	86,8	3,02	0	1,46	0	1,19	0	0	0	246	0	0	0	249	51	65,7	0	2,02	0,15	0,85	0	23,1

SVi7	0	0	0	0	0	0	1,63	4,22	0	0	0	165	643	0	0	142	78,4	0	0	0	0	0	0	1,19
SVi12	0	0	0	0	0	0	8,6	2,86	0	0	0	75,6	72	0	0	38,9	0	10,4	0	0	0	0,63	5,81	0
SVi10	0	0	1,16	8,21	0	1,88	3,23	2,84	0	0	0	415	359	0	0	0	57,3	0	0	0	0	0,83	0	2,02
SVi9	0	0	0,32	0	0	0	0	1,22	0	0	0	574	68,1	0	0	117	50	0	0	0	0	0,1	0	24
SCr4	0	0	0,8	9,5	0	22,2	0	4,14	0	0	0	134	0	0	0	0	16,7	0	0	0	0,06	0,11	71,4	48,7
SCr8	7,73	0	24,5	10,9	0	16,6	1,28	3,25	4,33	3,17	0	184	492	0	213	0	93,6	14,4	0	0	0,12	2,25	11,5	23,8
SCr14	0	0	14,9	2,94	0	15,6	0	5,95	1,56	244	0	60,8	0	0	0	0	95	12,7	0	0	0,43	0,86	0	0
SCr12	0	0	11,2	5,06	0	0,94	0	0	0	0	0	139	41,8	0	0	0	109	2,6	0	0	0	0,44	0	0
STy1	0	0,52	0	15,5	0	3,83	29,6	7,85	0	717	0	0	0	0	0	0	144	24,3	0	0	0	0,09	0	77,7
STy8	0	0	3,56	19,2	0	12,1	0	0	0	650	0	4,08	54,2	0	0	0	76	1,53	0	0	0	0	0	0
STy12	0	0	2,76	10,8	0	0	0	4,83	0	543	0	30,1	74,4	0	114	0	97,8	17,9	0	0	0	0,07	0	0
STy5	0	0	0	6,45	0	0	0	1,88	0	37,4	0	4,21	642	0	0	0	0	0	0	0	0	0	0	0
STy14	0	0	0,22	7,77	0	8,88	14,7	6,55	0	25,6	0	14,9	0	0	0	0	93,4	0	0	0	0,06	0,03	39,5	8,2
SGe6	2,41	0	6,16	36	0	14,9	0	6,31	6,81	0	0	4,3	0	0	0	0	144	0	0	0	0	0,74	71,1	0
SGe14	0	0	13	29	0	5,84	1,64	2,15	1,15	29,2	0	50,5	0	0	0	0	101	0	0	0	0	0,44	46,3	12,9
SGe23	0	0	19,1	26,5	0	4,12	3,96	3,44	2,22	2,98	0	5,46	0	0	0	0	150	30	0	0	0	0,6	0	44,7
SGe8	1,99	0	26,7	12,8	0	8,77	0	2,94	1,71	0	0	21,8	40,1	0	0	26,5	193	22	0	0	0,01	0,97	0	19
SBl3	0	0	3,82	0	0	0	5,62	0	0	0	0	0	0	0	1300	2,48	257	165	0	0	0	0	0	122
SBl5	0,61	0	14,4	13,9	0	7,41	0	4,83	0,1	0	0	4,99	1692	0	161	4,27	131	0	0	0	0,05	4,87	38,3	27,6
SBl9	0	0	73,6	56,4	0	25,8	0	12,9	0	104	0	0	884	0	0	0,5	182	7,77	0	0	0,05	1,3	47,8	20,9
SBl11	0	12,7	73,7	7,74	0	12,3	0	9,56	1,69	44,4	0	0	875	0	1419	6,48	124	0	0	0	0	1,69	5,86	42,7
SBl13	0	0	46,2	1,64	0	0,73	0	1,9	0,02	59,1	0	0	0	0	0	0,86	46,3	0	0	0	0	1,04	0	13,9
SPu1	0	0	4,26	0	0	9,05	53,1	13,3	1,04	35,9	21,8	22,8	1067	0	0	0	268	29,6	0	0	0	0,83	91,6	0
SPu4	0	0	8,54	13,5	0	34,4	27,8	15,5	3,53	32,9	0	5,15	0	0	156	2,69	283	474	2,36	352	0	2,3	229	5,84
SPu8	0	0	61,1	11,6	0	28,6	17,9	19,4	0	236	0	0	0	0	0	0	456	149	0,75	0	0,01	0,66	0	83,9

SPu12	0	0	52,7	88,4	0	51,8	6,28	9,73	0	20,5	0	0	0	0	0	10,8	909	242	0,92	0	0	1,44	31,7	0
SPu14	0	47,2	371	131	0	53,8	35,8	19,7	0	0	0	13,7	0	0	0	3,94	2221	496	0	3,32	0	2,78	5,42	0
SMo3	0	0	2,39	5,01	0	0	3,52	1,05	14,7	0	0	0	0	0	0	6,6	908	23,8	0	0	0,05	0,98	188	7,92
SMo7	0	0	3	47,6	0	4,17	13,4	14,5	12,4	0	0	116	42,4	0	0	0	801	0	0	0	0	0,49	0	247
SMo10	0	0	54,9	383	0	0	4,25	2,31	13,5	0	0	0	0	0	0	0	184	24	0	0	0	4,9	38,2	0
SMo12	0	0	0	9,6	0	3,27	0	7,73	0	0	131	6,04	82,1	0	0	0	647	10,1	0	0	0	0,82	955	18
SMo14	3,1	0	226	49,7	26,2	10,3	39	10,2	1,52	50,8	0	36,3	0	0	0	0	950	217	0	0	0	0,98	1087	55,5
SBn4	0	0	8,21	63,6	0	7,62	0	11,2	0,69	180	0	0	7,92	0	0	2,12	608	0	0	0	0,04	0	45,2	129
SBn10	0	0	78,4	4,52	0	1,73	11,7	4,97	0,67	0	0	139	0	0	109	90	388	0	0	0	0	0,73	102	53,1
SBn16	0	0	12	24,4	161	17,2	6,53	0,13	13,8	0	0	13,5	0	0	0	0	96,4	4,15	0	0	0	1,17	0	0
SBn20	0	0	28,8	323	0	5,05	0,82	4,45	23	0	0	14,4	0	0	0	0	177	44,5	0	0	0,06	0,4	475	0
SBn23	13,1	0	12,7	9,46	0	22	7,84	0,45	6,26	0	0	7,69	121	0	0	2,47	296	0,96	0	0	0,01	1,32	625	0
SRe3	3,22	0,74	0,56	261	0	4,67	9,63	0,9	5,28	6,51	0	0	0	0	0	0,15	127	0	0	0	0	0,16	372	0
SRe5	0	0	3,27	49,5	0	0	57,4	4,28	2,33	0	0	4,42	0	0	0	31,1	534	2,98	0	0	0	4,75	81,5	0
SRe7	0	0	2,59	143	0	1,07	0	5,3	7,19	0	0	0	0	0	0	0,61	305	4,21	0	0	0	0,11	8,39	0
SRe10	0	0	0,41	44	0	0,31	0	0,76	35,8	0	0	0	0	0	0	19,6	246	0	0	0	0	0,76	0	0
SRe11	0	0	0	0	0	0	58	0	1,64	0	0	8,91	0	0	0	0	529	0	0	0	0	1,93	0	0
SSa7	0	0	94,6	349	0	0	0	0,79	10,1	0	0	0	0	0	0	0	1458	0	0	0	0	0,25	0	17,3
SSa8	0	0	87,3	1006	0	0	0	0	0	0	2,51	0	0	0	0	0	958	0	0	0	0	0	0	32,1
SSa10	0	0	426	223	0	0	4,83	0	0,32	0	0	0	0	0	0	0	1237	0	0	0	0	0,37	0	0
SSa13	0	0	682	241	0	0	22,3	1,49	211	0	0	0	0	0	0	0	1699	3,82	0	0	0,01	1,27	0	0
SSa15	0	0	0	289	0	0	7,35	0	0,17	0	0	0	0	0	0	0	658	0	0	0	0	0,49	179	0
SCo1	0	0	12,8	556	0	0,84	3,61	0,85	18,6	0	0	0	0	0	379	0	858	0	0	0	0	0,28	21,3	0
SCo12	0	0	649	726	0	0	0	0,73	0	0	0	10,1	0	0	0	0	263	0	0	0	0	0,36	0	0
SCo15	0	0	27,9	518	0	0	18,3	2,44	11,1	0	0	0	0	0	0	0	1290	520	0	0	0,17	2,6	456	8,82

SCo19	0	0	15	498	0	28,6	2,48	1,58	1,71	0	0	0	2976	0	0	0	595	8,41	0	0	0,05	2,29	8,83	0
SCo27	0	0	38,1	457	0	29,8	21,6	2,29	9,87	0	0	0	0	0	0	0	659	0	0	0	0,1	0,13	19,2	0
STr3	0	17,5	0	856	0	2,12	0	0	0	0	0	0	0	0	0	15,1	695	0	0	0	0	0	236	0
STr5	0	0	135	407	0	0	14,9	0	0	0	0	0	0	0	0	0	644	56,2	0	0	0,02	0	81,6	0
STr8	0	0	80,7	993	0	0,4	0	0,13	0	0	0	2,83	0	0	0	0	1255	1,12	0	0	0	0	105	3,82
STr10	0	0	0	791	0	0	0	0	0	0	0	0	0	0	0	0	486	0	0	0	0	0	0	0
STr12	0	0	7,14	859	0	0	7,78	0	0	0	0	0	0	0	0	0	1360	122	0	0	0	0	0	21,3
Roches																								
RCa7	4,7	0	0,04	3,7	0	0,86	0	0	0,03	0	0	0	0	0	0	0,32	21,2	0,45	0	0	0	0,11	0	0
RCa11	0	0	0	2,52	0	1,61	0	0	0	0	0	0	3,62	0	8,59	0	6,04	0	0	0	0	0	0	0
RCa4	0	0	0,38	8,7	0	0,36	0	0,65	0	0	0	0	0	0	0	0,46	11,7	0,32	0	0	0	0,15	9,17	0
RCa14	0	0	0,02	3,09	0	0	0	0	0	0	0	0,97	0	0	0	0	4,25	0	0	0	0	0,38	0	0
RCa3	0	0	0	1,31	0	0,73	0	0	0	0	0	0	5,6	0	0	0,11	11,8	0	0	0	0	0,18	0	0
RVi3	0	0	0,32	1,72	0	0	1,16	0	0	0	0	0	3,34	0	0	0	12,6	0	0	0	0	0,46	0	0
RVi7	0,35	0	0,1	0	0	2,01	0	0,07	0	0	0	0	0	0	0	0	6,98	1,42	0	0	0	0,06	0	0
RVi12	0	0	0,35	0,17	0	0	0	0	0	0	0	0	0	0	0	0	4,65	0	0	0	0	0,04	0	0
RVi10	0	0	0	0	0	0	0	0,54	0	0	0	0	0	0	0	0	5,62	0	0	0	0	0,31	0	0
RVi9	0	0	0,05	0	0	0	0	0	0	0	0	0	0	0	0	0	4,96	0	0	0	0	0,15	0	0
RCr4	0,13	0	1,21	2,67	0	0	0	0	0	0	0	0	0	0	0	0	25,6	0	0	0	0	0,52	0	0
RCr8	0	0	1,01	0,21	0	1,09	0	1,68	0	0	0	0	0	0	0	0,15	64,4	2,71	0	0	0	1,32	0	0
RCr12	0	0	0,23	2,07	0	3,93	0	0,29	0	0	0	0	0	0	0	0	16,8	0	0	0	0	0,13	0	0
RCr14	0	5,34	1,55	1,2	0	8,15	0	2,58	0	0	0	0	11,6	0	0	0	32,6	0	0	0	0	0,16	0	0
RCr16	0	0	0	0	0	0	0	0	0	0	0	0	2,01	0	0	0	23,8	3,78	0	0	0	0,57	0	0
RTy5	0	0	0	1,77	0	0,71	0	1,95	0	42,2	0	0	5,07	0	0	0	17,3	0	0	0,57	0	0	3,14	0
RTy12	0	72,5	0,57	0	0	0	0	2,86	0	107	0	0	13	0	0	0	23,2	14,2	0	0	0	0,02	0	0

RTy14	0	5,31	0	2,59	0	1,1	0	0,61	0	32,6	0	0	10,7	0	0	1,29	47,3	41,1	0	0	0	0	0	0
RTy1	0	0	0,68	1,42	0	0	0	1,47	0	61,1	0	0	13,3	0	0	0	17,1	36,8	0	0	0	0	0	0
RTy8	0	0	0	1,81	0	1,77	0	0,48	0	56,7	0	0	26,5	0	0	0	0,62	9,05	0	0	0	0,04	0	0
RGe8	0	0	0	3,65	0	0,49	0	0	0	9,79	0	0	0	0	0	0	34,2	31,7	0	0	0	0,6	0	0
RGe20	0	0	0	0	0	0,73	0	0	0	0	0	0	0	0	0	0	30,5	1,11	0	0	0	0,73	0	0
RGe23	0	0	0	1,58	0	0	0	0	0	0	0	0	0	0	0	0	8,23	0,59	0	0	0	0,26	2,17	0
RGe5	0	0	0	0,92	0	2,48	0	0,38	0	0	0	0	1,04	0	0	0	46,7	0,99	0	0	0	0,21	0	0
RGe14	0	0	0	5,63	0	0	0	0	0,03	0	0	0	7,53	0	0	0	13,9	0,27	0	0	0	0,57	0	0
RBl3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3,98	0	0	0	0	0,15	0	0
RBl13A	0	0	1,65	0	0	1,98	0	0,72	0	18,5	0	0	0	0	0	0	47,3	3,48	0	0	0	0,75	0	0
RBl13B	2,01	0	3,75	0,61	0	8,9	0	1,45	0,07	5,91	0	0,68	3,67	0	0	1,82	57,9	1,6	0	0	0	1,11	0	0
RBl5	0	0	0	0	0	0,74	0	0	0	5,05	0	0	8,25	0	69,9	0	32,2	1,18	0	0	0	0	4,07	0
RBl9	0	2,67	1,09	0	0	0,96	0,9	0	0	0	0	0	2,33	0	0	0	1,26	0	0,67	0	0	0	0	0
RPu1	3	0,7	1,56	0,18	0	2,74	0	2,12	0	37,8	0	0	0	0	201	0	88,9	4,15	0	0	0	1,34	4,11	0
RPu4	0	14,9	2,39	0	0	1,06	0	8,04	0	67	0	0	0	0	0	0	60,9	51,7	0	0	0	1,8	13,6	2,05
RPu8	1,63	1,55	116	24,7	0	10,3	0,24	5,74	0,43	3,32	0	3,5	0	0	0	0	132	4,99	0	0	0	2,85	19,9	0
RPu12	0	24,4	2,4	1,39	0	3,09	0	3,33	0	53,6	0	0	0	0	0	44,1	182	14,5	0	0	0	3,68	0	0
RPu15	1,03	6,85	35,1	0,11	0	5,54	0	5,22	0	0	0	0	0	0	0	0	93,2	4,92	0	0	0	2,41	0	0
RMo3	0	2,14	3,53	0	0	0	0	0	0	1,75	0	0	0	0	0	0	49,2	10,6	0	0	0	2,75	1,85	0
RMo7	0	2,9	5,61	6,55	0	2,53	0	4,59	0	0	0	10,1	5,61	0	0	22,6	72	40,7	0	0	0	4,5	3,77	0
RMo11	0	0,05	8,47	2,57	0	1,04	0	0	0	0	0	0	18,2	0	0	0	55,7	4,34	0	0	0	1,09	16,8	0
RMo12	16,4	0,72	8,71	15,8	0	0,43	0	0,53	0	0	0	0	22,7	0	0	1,17	148	0	0	0	0	3,94	11,8	0
RMo14	0	0	9,17	1,61	0	0	1,24	1,4	0	28,9	0	0	0	0	0	0	60,8	22,4	0	0	0	0,32	8,16	0
RBn4	0	0	11,2	12,3	0	11,3	2,69	2,73	0,02	50,9	0	0,6	0	0	0	0	112	9,37	0	0	0	0,69	2,39	0
RBn10	1,33	2,37	0	11,3	0	2,99	0	2,15	0	0	0	0	6,82	0	0	4,19	120	0	0	0	0	7,21	32,5	0

RBn16	0	0,03	4,93	6,25	0	16,1	0	0,47	0	19,6	0	10,6	0	0	0	0	65,8	44,5	0	0	0	0,54	2,93	4,57
RBn20	0,78	2,03	0	18,3	0	14,5	0	0,98	0	0	0	6,43	9,69	0	0	0	165	6,85	0	0	0	1,52	27,1	0
RBn23	2,19	0	9,89	9,47	0	18,1	0	0	0	33,2	0	0,55	0	0	0	0,23	104	23,4	0	0	0	2,39	29	0
RRe3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	93,9	34,5	0	0	0	0,02	0	0
RRe5	0	0	1,43	0	0	0	0	0	0	0	0	0	0	0	0	0,04	26,9	0,53	0	0	0	0,05	0	0
RRe7	5,09	0	2,34	5,46	0	0	0	0,48	0	0	0	0	0	0	0	0	42,9	10,6	0	0	0	0,34	0	0
RRe10	0	0	1,08	2,86	0	1,28	1,06	0	0	0	0	0	0	0	0	0	37,3	0	0	0	0	0,4	2,02	0
RRe11	0	0	0	0,38	0	1	1,65	0,51	0	0	0	0	0	0	0	31,1	91,7	0	0	0	0	0,81	0	0
RSa7	4,15	0	46,8	5,58	0	0	0	0	0	0	0	0	8,54	0	0	0	264	173	0	0	0	4,04	0	0
RSa8	0	0	2,4	5,71	0	0	0	0,45	0	0	0	49,3	0	0	0	0	377	0	0	0	0	1,14	0	0
RSa10	0	0	0	9,92	0	23,9	0	0	0	0	0	0	0	0	0	0	670	0	0	0	0	11	9,85	0
RSa13	0,9	0	0	50,1	0	2,53	2,46	2,11	0	0	0	0	0	0	0	0	630	331	0	0	0	10,2	0	0
RSa15	3,34	0	15,5	12,2	0	1,25	0	0	0	0	0	0	0	0	0	0	253	0	0	0	0	2,1	4,43	0
RCo1	0	4,24	76,6	48,8	0	0	0	0,41	0	0	0	0	3,41	0	0	0	217	140	0	0	0,19	4,85	33,4	4,45
RCo12	0	0	9,22	49,5	0	9,41	0	0,47	0	0	0	88,5	0	0	0	0	179	7,34	0	0	0	0,74	16,7	0
RCo15	0	0	1,77	78,1	0	0	6,79	0	0	0	0	17,3	0	0	0	0	195	8,93	0	0	0	0,82	35,8	0
RCo19	0	0	62,1	179	0	17,8	20,5	1,44	0,16	0	0	0	0	0	0	0	153	27,2	0	0	0	3,68	11,2	0
RCo27	0	0	42,2	243	0	3,05	0	0	0	0	0	0	0	0	0	0	101	8,96	0	0	0	2,64	313	0
RTr5A	0,6	0	0	3,11	0	1,12	3,55	0,78	0	0	0	0	0	0	0	0	115	85,9	0	0	0	0,05	34,9	1,2
RTr5B	1,12	0	317	65,6	0	0	26,9	0,71	0	0	0	66,9	0	0	0	0	278	44,1	0	0	0	0,25	0	2,38
RTr8	3,56	0	33,1	9,9	0	18,4	0	0	0,12	0	0	0	0	0	0	0	204	2,78	0	17,4	0	0,74	0	0
RTr10	5,32	1,34	6,14	0	0	1,35	0	0	0,09	0	0	0	0	0	0	0	161	64,6	0	3,38	0	0,48	0	0
RTr12	0,37	0	0	17,8	0	0,96	1,64	1,09	0	0	0	0	0	0	0	0	395	1,68	0	0	0	0,14	92	0

Bois																								
BCa4	0	2,02	0,09	0	0	0	0	0	0	0	0	0	0,92	0	0	0	56,5	0	0	0	0	0	0	0
BCa7	5,22	0	0,04	9,81	0	4,88	0	2,14	15,4	0	0	0,35	8,84	0	0	0	92,3	0	0	0,87	0	0,04	0	0
BCa12	0	0	0,03	8,26	0	10	0	0	0	0	0	0	0	0	0	0,25	104	3,8	0	0	0	0	0	0
BCr12	11,1	0	0,07	4,99	0	16,3	0	0	19	0	0	0	0	0	0	0	137	0,19	0	0	0	0,2	0	0
BCr8	6,99	0	0,07	1,95	0	6,87	0	0,99	3,54	7,23	0	0	0	0	0	1,46	38,8	0,48	0	0	0	0,14	0	0
BCr16A	22,3	0	2,43	0,4	0	0	0	0	0	0	0	0	0	0	0	0	17,9	0	0	0	0	0,09	0	0
BGe21	0	0	0,39	1,71	0	0	0	1,4	0	0	0	0	0	0	0	2,33	37,9	2,69	0	0	0	0,01	0	0
BGe5	0	0	0,04	1,21	0	20,7	8,27	0	0	0	0	0	6,14	0	0	0	159	0,19	0	0	0	0,46	0	0
BGe23	2,13	0	0,47	30,7	0	3,49	0	0	0	0	0	0	0	0	0	0	407	0,81	0	0	0	0,37	0	0
BBl9	0	0	0,38	4,62	0	5,28	0	3,77	0	0	0	0	10,5	0	0	0	136	3,12	0	0	0	0,28	0	0
BBl3	19,1	0	0,03	0,18	0	0	0	0	0	0	0	0	0	0	0	0	1,64	0	0	0	0	0	0	0
BBl13	0,89	0	0,1	6,87	0	73,2	0	1,39	0	14,9	0	0	21	0	0	1,19	202	14,3	0	0	0	0,32	0	0
Macrophytes																								
MSa8	57,8	0	1,14	5,07	0	2,22	0	2,14	0	0	0	50,2	2,81	0	0	0,22	197	132	0	0	0	0,71	0	0
MSa10	0	0	0	0,51	0	2,62	0,1	0,45	0	0	0	14,3	2,94	0	0	0,25	101	13,1	0	0	0	0,04	0	0
MSa15	99,3	0	0	1,87	0	0	0	0	0	0	0	220	4,51	0	0	0,03	246	37,9	0	0	0	0,35	0	0
MCo12	0	0	0	4,57	0	2,83	0	0,2	0	0	0	0,86	0	0	0	2,59	19,9	6	0	0	0	0,11	2,74	0
MCo15	0	0	0	36	0	1,07	0	1,47	0	0	0	0	4,28	0	0	0	65,2	84	0	0	0	0,73	122	0
MCo27	14,9	0	0	48,5	0	6,11	0	0	0	0	0	0	1,74	0	0	4,71	14,9	42,2	0	0	0	0,09	16,8	0
MTr8	127	0	0	65,3	0	2,71	0	0,25	0	0	0	16,8	0	0	0	10	99,8	99,9	0	0	0	0,16	3,23	0
MTr10	8,01	0	0	2,04	0	0,52	0	0	0	0	0	0	0	0	0	0	7,22	4,54	0	0	0	0,04	2,16	0
MTr12	63,4	0	0	27,5	0	15	0	0,19	0	0	0	0	0	0	0	0	22,9	0	0	0	0	0,3	122	0

Biomasse par unité de surface (mg•m-2)

(Familles)

Sites	Caenidae	Ephemeridae	Leptophlebiidae	Baetidae	Leptoceridae	Polycentropodidae	Hydroptiliidae	Hydropsychidae	Limnaeidae Physidae	Planorbidae
	Éphémères				Trichoptères				Gastéropodes	
Sédiments										
SCa3	163	115	0	0	149	0	0	0	199	0
SCa4	172	187	25,3	0	390	0	67	0	0	0
SCa14	192	250	0	0	102	0	0	0	390	0
SCa7	2,24	64,9	0	0	505	0	0	0	0	0
SVi3	201	45	0	0	249	0	0	0	0	0
SVi7	118	47,5	0	0	0	142	0	0	0	0
SVi12	42,2	33,5	0	0	38,9	0	0	0	0	5,81
SVi10	344	70,3	0	0	0	0	0	0	0	0
SVi9	109	465	0	0	0	117	0	0	0	0
SCr4	104	30	0	0	0	0	0	0	71,4	0

SCr8	122	40,9	21,2	0	0	0	0	0	0	11,5
SCr14	60,8	0	0	0	0	0	0	0	0	0
SCr12	98,4	35,5	4,92	0	0	0	0	0	0	0
STy1	0	0	0	0	0	0	0	0	0	0
STy8	0	0	4,08	0	0	0	0	0	0	0
STy12	0	0	30,1	0	0	0	0	0	0	0
STy5	0	0	4,21	0	0	0	0	0	0	0
STy14	0	0	14,9	0	0	0	0	0	0	39,5
SGe6	4,3	0	0	0	0	0	0	0	71,1	0
SGe14	48,5	0	2,03	0	0	0	0	0	0	46,3
SGe23	0	0	5,46	0	0	0	0	0	0	0
SGe8	0	0	21,8	0	26,5	0	0	0	0	0
SBl3	0	0	0	0	2,48	0	0	0	0	0
SBl5	0	0	4,99	0	4,27	0	0	0	38,3	0
SBl9	0	0	0	0	0,5	0	0	0	47,8	0
SBl11	0	0	0	0	6,48	0	0	0	0	5,86
SBl13	0	0	0	0	0,86	0	0	0	0	0
SPu1	9,8	13	0	0	0	0	0	0	57,4	34,2
SPu4	5,15	0	0	0	2,69	0	0	0	208	21,1
SPu8	0	0	0	0	0	0	0	0	0	0
SPu12	0	0	0	0	0	0	10,8	0	0	31,7
SPu14	0	13,7	0	0	0	0	3,94	0	0	5,42
SMo3	0	0	0	0	6,6	0	0	0	181	7,6
SMo7	0	12	104	0	0	0	0	0	0	0

SMo10	0	0	0	0	0	0	0	0	38,2	0
SMo12	6,04	0	0	0	0	0	0	0	132	823
SMo14	36,3	0	0	0	0	0	0	0	1066	21,1
SBn4	0	0	0	0	2,12	0	0	0	0	45,2
SBn10	126	12,6	0	0	0	89,5	0,5	0	58,3	43,5
SBn16	13,5	0	0	0	0	0	0	0	0	0
SBn20	14,4	0	0	0	0	0	0	0	54,9	420
SBn23	7,69	0	0	0	2,47	0	0	0	598	27,7
SRe3	0	0	0	0	0,15	0	0	0	372	0
SRe5	3	0	1,42	0	31,1	0	0	0	0	81,5
SRe7	0	0	0	0	0,61	0	0	0	0	8,39
SRe10	0	0	0	0	1,69	0	17,9	0	0	0
SRe11	0	0	8,91	0	0	0	0	0	0	0
SSa7	0	0	0	0	0	0	0	0	0	0
SSa8	0	0	0	0	0	0	0	0	0	0
SSa10	0	0	0	0	0	0	0	0	0	0
SSa13	0	0	0	0	0	0	0	0	0	0
SSa15	0	0	0	0	0	0	0	0	0	179
SCo1	0	0	0	0	0	0	0	0	0	21,3
SCo12	0	0	10,1	0	0	0	0	0	0	0
SCo15	0	0	0	0	0	0	0	0	427	29,2
SCo19	0	0	0	0	0	0	0	0	0	8,83
SCo27	0	0	0	0	0	0	0	0	0	19,2
STr3	0	0	0	0	15,1	0	0	0	236	0

STr5	0	0	0	0	0	0	0	0	81,6	0
STr8	0	0	2,83	0	0	0	0	0	105	0
STr10	0	0	0	0	0	0	0	0	0	0
STr12	0	0	0	0	0	0	0	0	0	0
Roches										
RCa7	0	0	0	0	0,32	0	0	0	0	0
RCa11	0	0	0	0	0	0	0	0	0	0
RCa4	0	0	0	0	0,46	0	0	0	9,17	0
RCa14	0,97	0	0	0	0	0	0	0	0	0
RCa3	0	0	0	0	0,11	0	0	0	0	0
RVi3	0	0	0	0	0	0	0	0	0	0
RVi7	0	0	0	0	0	0	0	0	0	0
RVi12	0	0	0	0	0	0	0	0	0	0
RVi10	0	0	0	0	0	0	0	0	0	0
RVi9	0	0	0	0	0	0	0	0	0	0
RCr4	0	0	0	0	0	0	0	0	0	0
RCr8	0	0	0	0	0,15	0	0	0	0	0
RCr12	0	0	0	0	0	0	0	0	0	0
RCr14	0	0	0	0	0	0	0	0	0	0
RCr16	0	0	0	0	0	0	0	0	0	0
RTy5	0	0	0	0	0	0	0	0	0	3,14
RTy12	0	0	0	0	0	0	0	0	0	0
RTy14	0	0	0	0	1,29	0	0	0	0	0

RTy1	0	0	0	0	0	0	0	0	0	0
RTy8	0	0	0	0	0	0	0	0	0	0
RGe8	0	0	0	0	0	0	0	0	0	0
RGe20	0	0	0	0	0	0	0	0	0	0
RGe23	0	0	0	0	0	0	0	0	0	2,17
RGe5	0	0	0	0	0	0	0	0	0	0
RGe14	0	0	0	0	0	0	0	0	0	0
RBl3	0	0	0	0	0	0	0	0	0	0
RBl13A	0	0	0	0	0	0	0	0	0	0
RBl13B	0	0	0	0,68	0	1,82	0	0	0	0
RBl5	0	0	0	0	0	0	0	0	0	4,07
RBl9	0	0	0	0	0	0	0	0	0	0
RPu1	0	0	0	0	0	0	0	0	0	4,11
RPu4	0	0	0	0	0	0	0	0	0	13,6
RPu8	0	0	0	3,5	0	0	0	0	15,1	4,82
RPu12	0	0	0	0	44,1	0	0	0	0	0
RPu15	0	0	0	0	0	0	0	0	0	0
RMo3	0	0	0	0	0	0	0	0	0	1,85
RMo7	0	0	0	10,1	0	22,6	0	0	0	3,77
RMo11	0	0	0	0	0	0	0	0	0	16,8
RMo12	0	0	0	0	0	1,17	0	0	0	11,8
RMo14	0	0	0	0	0	0	0	0	0	8,16
RBn4	0,6	0	0	0	0	0	0	0	0	2,39
RBn10	0	0	0	0	0	4,19	0	0	0	32,5

RBn16	10,6	0	0	0	0	0	0	0	0	2,93
RBn20	6,43	0	0	0	0	0	0	0	0	27,1
RBn23	0,55	0	0	0	0	0,23	0	0	0	29
RRe3	0	0	0	0	0	0	0	0	0	0
RRe5	0	0	0	0	0,04	0	0	0	0	0
RRe7	0	0	0	0	0	0	0	0	0	0
RRe10	0	0	0	0	0	0	0	0	0	2,02
RRe11	0	0	0	0	0	29,9	0	1,12	0	0
RSa7	0	0	0	0	0	0	0	0	0	0
RSa8	0	0	0	49,3	0	0	0	0	0	0
RSa10	0	0	0	0	0	0	0	0	0	9,85
RSa13	0	0	0	0	0	0	0	0	0	0
RSa15	0	0	0	0	0	0	0	0	0	4,43
RCo1	0	0	0	0	0	0	0	0	0	33,4
RCo12	88,5	0	0	0	0	0	0	0	0	16,7
RCo15	17,3	0	0	0	0	0	0	0	0	35,8
RCo19	0	0	0	0	0	0	0	0	0	11,2
RCo27	0	0	0	0	0	0	0	0	306	7,11
RTr5A	0	0	0	0	0	0	0	0	0	34,9
RTr5B	66,9	0	0	0	0	0	0	0	0	0
RTr8	0	0	0	0	0	0	0	0	0	0
RTr10	0	0	0	0	0	0	0	0	0	0
RTr12	0	0	0	0	0	0	0	0	0	92

Bois										
BCa4	0	0	0	0	0	0	0	0	0	0
BCa7	0,35	0	0	0	0	0	0	0	0	0
BCa12	0	0	0	0	0,25	0	0	0	0	0
BCr12	0	0	0	0	0	0	0	0	0	0
BCr8	0	0	0	0	0	0	1,46	0	0	0
BCr16A	0	0	0	0	0	0	0	0	0	0
BGe21	0	0	0	0	0	2,33	0	0	0	0
BGe5	0	0	0	0	0	0	0	0	0	0
BGe23	0	0	0	0	0	0	0	0	0	0
BBl9	0	0	0	0	0	0	0	0	0	0
BBl3	0	0	0	0	0	0	0	0	0	0
BBl13	0	0	0	0	0	0	1,19	0	0	0
Macrophytes										
MSa8	0	0	0	50,2	0,11	0	0,1	0	0	0
MSa10	0	0	0	14,3	0	0	0,25	0	0	0
MSa15	0	0	0	220	0,03	0	0	0	0	0
MCo12	0	0	0	0,86	0	2,59	0	0	0	2,74
MCo15	0	0	0	0	0	0	0	0	102	20
MCo27	0	0	0	0	1	0	3,71	0	4,34	12,4
MTr8	0	0	0	16,8	10	0	0	0	0	3,23
MTr10	0	0	0	0	0	0	0	0	1,96	0,2
MTr12	0	0	0	0	0	0	0	0	53,9	68

Tableau II: Biomasse totale d'invertébrés par unité de surface ($mg \bullet m^{-2}$) dans les stations échantillonnées de a) Sédiments, b) Roches, c) Bois et d) Macrophytes. L'identification des stations se fait de la même façon que pour le tableau I.

a) Sédiments

Site	TIB
SCa3	899,72
SCa4	1656,66
SCa14	1928,52
SCa7	689,34
SVi3	730,83
SVi7	1035,18
SVi12	214,83
SVi10	850,92
SVi9	834,57
SCr4	307,77
SCr8	1106,96
SCr14	455,06
SCr12	309,94
STy1	1020,65
STy8	820,27
STy12	896,04
STy5	692,05
STy14	219,80
SGe6	292,34
SGe14	293,21
SGe23	292,96
SGe8	377,84

Site	TIB
SBl3	1855,97
SBl5	2104,78
SBl9	1417,31
SBl11	2637,46
SBl13	171,71
SPu1	1618,52
SPu4	1648,39
SPu8	1065,12
SPu12	1424,59
SPu14	3404,51
SMo3	1162,31
SMo7	1301,22
SMo10	708,35
SMo12	1870,35
SMo14	2764,51
SBn4	1063,10
SBn10	982,62
SBn16	350,02
SBn20	1096,23
SBn23	1126,97
SRe3	792,27
SRe5	775,61

Site	TIB
SRe7	477,58
SRe10	348,00
SRe11	599,84
SSa7	1929,51
SSa8	2085,26
SSa10	1891,61
SSa13	2861,39
SSa15	1134,12
SCo1	1851,98
SCo12	1648,79
SCo15	2856,49
SCo19	4138,25
SCo27	1236,99
STr3	1822,14
STr5	1338,42
STr8	2441,89
STr10	1277,03
STr12	2376,73

b) Roches

Site	TIB
RCa7	31,41
RCa11	22,37
RCa4	31,88
RCa14	8,71
RCa3	19,71
RVi3	19,60
RVi7	10,98
RVi12	5,21
RVi10	6,46
RVi9	5,16
RCr4	30,17
RCr8	72,58
RCr12	23,48
RCr14	63,09
RCr16	30,12
RTy5	72,70
RTy12	233,56
RTy14	142,55
RTy1	131,94
RTy8	96,97
RGe8	80,35
RGe20	33,07
RGe23	12,83
RGe5	52,73
RGe14	27,97

Site	TIB
RBl3	4,13
RBl13A	74,34
RBl13B	89,48
RBl5	121,42
RBl9	9,88
RPu1	347,24
RPu4	223,42
RPu8	327,63
RPu12	332,62
RPu15	154,36
RMo3	71,84
RMo7	181,32
RMo11	108,33
RMo12	230,53
RMo14	134,09
RBn4	215,69
RBn10	190,61
RBn16	176,32
RBn20	253,16
RBn23	231,99
RRe3	128,45
RRe5	28,91
RRe7	67,21
RRe10	46,05
RRe11	127,13

Site	TIB
RSa7	506,31
RSa8	435,51
RSa10	725,08
RSa13	1029,20
RSa15	292,17
RCo1	533,22
RCo12	360,62
RCo15	344,51
RCo19	476,21
RCo27	713,54
RTr5A	246,09
RTr5B	802,58
RTr8	290,26
RTr10	243,29
RTr12	510,40

c) Bois

Site	TIB
BCa4	59,53
BCa7	139,94
BCa12	126,03
BCr12	189,25
BCr8	68,47
BCr16A	43,11
BGe21	46,47
BGe5	195,82
BGe23	444,75
BBl9	163,98
BBl3	20,97
BBl13	336,20

d) Macrophytes

Site	TIB
MSa8	451,20
MSa10	135,59
MSa15	609,52
MCo12	39,78
MCo15	314,89
MCo27	149,78
MTr8	425,36
MTr10	24,52
MTr12	251,19