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CHAPITRE 1

INTRODUCTION GÉNÉRALE

Influences de l'utilisation du sol sur les milieux aquatiques

La nature de l'utilisation des bassins versants[1] est de plus en plus prise en compte dans les études portant sur les écosystèmes aquatiques. Il y a plus de 30 ans, Hynes (1975; tel que cité par Allan et Johnson, 1997) écrivait déjà que « in every aspect, the valley rules the stream » (sur tous les aspects, la vallée mène la rivière). Bien qu'à l'époque, et jusqu'à tout récemment, l'utilisation du territoire ne constituait qu'une information parmi tant d'autres, ce champ de connaissances progresse aujourd'hui rapidement. De nos jours, les perturbations humaines du paysage sont reconnues comme ayant des impacts étendus et généralement négatifs sur la santé des écosystèmes aquatiques (e.g. Burt *et al.*, 1991; Casper, 1994; Allan et Johnson, 1997; Cooke et Prepas, 1998; Johnson, 1998; Johnson *et al.*, 2004; Cuffney *et al.*, 2005). Par exemple, l'augmentation des aires urbanisées favorise l'érosion des berges, pouvant conduire ultimement à la destruction des habitats aquatiques (Gresens *et al.*, 2007). L'artificialisation des bandes riveraines, résultat fréquent de l'urbanisation, réduit la capacité des sols et de la végétation à filtrer les sources diffuses de pollution avant qu'elles n'entrent dans les cours d'eau (Cuffney *et al.*, 2005). De plus, les eaux usées urbaines, injectées en milieu aquatique, entraînent des apports élevées de sels, de métaux et d'hydrocarbures qui peuvent limiter la reproduction et la croissance des organismes aquatiques (Brodersen *et al.*, 1998; Paul et Meyer, 2001). Certaines activités

[1] Portion de territoire délimitée par des lignes de crête dont les eaux alimentent un exutoire commun (MDDEP, 2002)

telles que l'agriculture amplifient les apports de nutriments tels que le phosphore et l'azote dans le milieu aquatique. Ces derniers stimulent la production primaire et accélèrent ainsi l'eutrophisation des eaux de surface (Johnson et Gage, 1997; Cooke et Prepas, 1998).

Au-delà de la prise en compte des effets des perturbations anthropiques sur les propriétés physiques et chimiques des écosystèmes aquatiques, plusieurs études tentent désormais de montrer l'influence des attributs du paysage sur les caractéristiques biologiques de ces systèmes (Kratz *et al.,* 1997). La classification de l'état de santé des plans d'eau, autrefois basée uniquement sur la physico-chimie, semble maintenant vouloir s'appuyer de plus en plus sur des caractéristiques biologiques telles que la composition spécifique des communautés animales (Brodersen *et al.*, 1998; White et Irvine, 2003). Des études sur les communautés ichthyennes ont ainsi révélé que plusieurs facteurs environnementaux expliqueraient les différences inter-lacs en termes de composition et de diversité spécifique à l'intérieur d'une même région (Rodriguez et Lewis, 1997; Heino, 2000). La caractérisation et la compréhension de la réponse des communautés aquatiques aux changements de structure du paysage sont donc importantes pour l'élaboration de méthodes biologiques d'évaluation de la qualité de l'eau.

Les macro-invertébrés benthiques, composantes biologiques clés des écosystèmes aquatiques

Du fait de leur mobilité relativement limitée, de leur durée de vie suffisamment longue et de la sensibilité de certains d'entre eux aux perturbations de leur environnement (Casper, 1994; Jackson, 1993; Rosenberg et Resh, 1993; Pinel-Alloul, 1995), les macro-invertébrés benthiques représentent des indicateurs biologiques de pollution diffuse fréquemment utilisés (Metcalfe, 1989; Rosenberg et Resh, 1993). Bien que plusieurs études aient été menées sur les communautés de macro-invertébrés des eaux courantes (e.g. Griffiths, 1991; Cao *et al.*, 1996; Allan *et al.*, 1997; Lammert et Allan, 1999; Sponseller *et al.*, 2001; Townsend *et al.*, 2004), peu d'entre elles décrivent les répercussions des modifications de structure du paysage sur les communautés de macro-invertébrés benthiques des écosystèmes lacustres (Brodersen *et al.*, 1998; Cheal *et al.*, 1993; Weatherhead et James, 2001).

Lund (1908, tel que cité par Brodersen *et al.*, 1998) fut l'un des premiers à mettre en lumière la très grande diversité des communautés d'invertébrés dans la zone littorale des lacs. Ces derniers jouent un rôle clé dans cette zone car ils peuvent potentiellement contrôler la production primaire benthique (James *et al.*, 2000), recycler les détritus (Weatherhead et James, 2001) et jouer un rôle intermédiaire entre les producteurs primaires et des espèces exploitées, puisqu'ils constituent notamment la source de nourriture de nombreux poissons (Pinel-Alloul., 1995; Weatherhead et James, 2001). Alors que les premières recherches effectuées dans le domaine de l'écologie des macro-invertébrés benthiques suggéraient que les communautés biologiques lacustres étaient uniquement le produit d'interactions entre les espèces, des recherches plus récentes tendent à montrer aussi l'importance de facteurs régionaux dans la régulation de l'organisation des communautés benthiques (Allan et Johnson, 1997; Huryn *et al.*, 2002; Johnson *et al.*, 2004). Les macro-invertébrés benthiques utilisent différents types de nourriture, allant de la nourriture vivante, animale ou végétale, aux innombrables formes de détritus (Rosenberg et Resh, 1993). Chacun de ces types de nourriture dépendent, de par leur origine et leur devenir, de la productivité du lac et de son bassin versant.

Facteurs influençant la distribution des macro-invertébrés benthiques

Les macro-invertébrés littoraux lacustres suivent des patrons de distribution spatiale hétérogènes qui coïncident avec l'hétérogénéité tant des facteurs biotiques qu'abiotiques (Heino, 2000). La complexité des habitats littoraux semble avoir des conséquences importantes pour la structure des communautés d'invertébrés (Heino, 2000; Weatherhead et James, 2001; White et Irvine, 2003; Johnson *et al.*, 2004). La présence de macrophytes (Heino, 2000; Della Bella *et al.*, 2005; Garcia-Criado et Trigal., 2005), le type de substrat (Weatherhead et James, 2001; White et Irvine, 2003; Johnson *et al.*, 2004), la production primaire (Brodersen *et al.*, 1998), les apports de matière allochtone (Beaty *et al.*, 2006), l'action des vagues, la taille et la profondeur moyenne des lacs (Brodersen *et al.*, 1998; Weatherhead et James, 2001; Johnson *et al.*, 2004; Beaty *et al.*, 2006) et la concentration en oxygène dissous (Dinsmore *et al.*, 1999) ne sont que quelques-uns des facteurs qui peuvent influencer les patrons de distribution spatiale des macro-invertébrés littoraux. Le couplage entre les habitats terrestres et aquatiques suggère que les macro-invertébrés benthiques devraient aussi être influencés par les caractéristiques du territoire, ne serait-ce que par les modifications à l'échelle de leurs habitats.

Les macro-invertébrés benthiques comme indicateurs de l'intégrité biotique

L'idée que certains organismes puissent témoigner de la qualité du milieu est bien établie. En effet, la présence d'une espèce dans un habitat donné suggère que cet habitat présente les caractéristiques nécessaires à la survie de cette espèce (e.g. Cao *et al.*, 1996 ; Royer *et al.*, 2001 ; Wetzel, 2001 ; Blocksom *et al.*, 2002). En connaissant les préférences quant à l'alimentation et aux variables d'habitat d'une espèce, et, par le fait même, sa tolérance aux perturbations environnementales, il devient possible de faire des liens entre la présence de cette espèce et les conditions de son environnement. En milieu aquatique, les microalgues et les macro-invertébrés sont les deux groupes d'organismes sentinelles utilisés pour évaluer la qualité de l'eau (Rosenberg et Resh, 1993). En pratique, cependant, les macro-invertébrés sont de loin le groupe d'organismes le plus fréquemment utilisé pour ce type d'évaluation (Royer *et al.*, 2001; Klemm *et al.*, 2003). Tel que cité précédemment, ces derniers présentent plusieurs avantages qui expliquent leur popularité : 1) ils sont sensibles à divers types de polluants et à un large éventail de types et de niveaux de stress; 2) ils sont omniprésents, abondants, relativement faciles à récolter et leur identification n'est pas aussi ardue que celle des microorganismes autotrophes; 3) leur mobilité est réduite, ce qui en fait des bons témoins des conditions locales de l'environnement et 4) leur durée de vie, suffisamment longue, en fait de bons intégrateurs des variations de l'environnement pour procurer une information sur la qualité de l'environnement (Metcalfe, 1989; Rosenberg et Resh, 1993; Klemm *et al.*, 2003).

Plusieurs chercheurs ont tenté d'établir un lien entre la composition taxonomique au sein des communautés de macro-invertébrés benthiques et l'état trophique des milieux aquatiques d'eau douce (Kansanen *et al.*, 1990; Brodersen *et al.*, 1998; Allen *et al.*, 1999). Si la majorité des recherches ayant montré de tels liens ont porté sur les milieux lotiques (e.g. Griffiths, 1991; Cao *et al.*, 1996 ; Allan *et al.*, 1997; Lammert et Allan, 1999; Sponseller *et al.*, 2001; Townsend *et al.*, 2004) un certain nombre d'entre elles ont également été menées en milieu lacustre. Brodersen *et al.* (1998) ont, par exemple, établi une corrélation entre la distribution des taxons et le stade trophique de 39 lacs danois. Tololen *et al.* (2001) ont, pour leur part, montré que la structure d'habitat d'un lac affecte plus la distribution des communautés de macro-invertébrés que le statut trophique de ce dernier.

Au-delà de la volonté de mieux comprendre les écosystèmes aquatiques, la recherche de liens entre les organismes et leur environnement est aussi motivée par le besoin de diagnostiquer et de classer l'intégrité de ces milieux. Les indices d'intégrité biotique qui en découlent permettent donc de classer le degré de pollution d'un système aquatique en utilisant la présence d'espèces indicatrices comme déterminant de ce degré de pollution (Johnson *et al.*, 1993). La majorité des indices biotiques assument d'ailleurs que les sites perturbés contiennent généralement moins d'espèces que les sites non perturbés et que les espèces tendent à disparaître selon un gradient de sensibilité à la perturbation (Johnson, 1998; Cuffney *et al.*, 2005). Ainsi, les indices biotiques sont majoritairement basés sur l'existence d'une corrélation négative entre l'indice de diversité et les paramètres trophiques des lacs, tels que les concentrations en phosphore, en chlorophylle *a* et en oxygène dissous, s'appuyant sur l'hypothèse selon laquelle l'augmentation de la productivité primaire d'un lac entraîne une perte des espèces les moins tolérantes et une augmentation des quelques espèces plus tolérantes. Les paramètres les plus fréquemment utilisés dans la détermination de l'intégrité biotique d'un plan d'eau son l'abondance relative des taxons dits tolérants (Casper, 1994; White et Irvine, 2003) tels que les Diptères (Blocksom *et al.*, 2002), les Oligochètes (Burt *et al.*, 1991; Blocksom *et al.*, 2002), les Nématodes (Burt *et al.*, 1991) et les Chironomides (Burt *et al.*, 1991; Cuffney *et al.*, 2005; Garcia Criado et Trigal., 2005; Beaty *et al.*, 2006). La présence de taxons généralement considérés comme peu tolérants à la pollution organique et aux faibles concentrations en oxygène dissous, tels que les Ephéméroptères, peut aussi être considérée comme indicateur d'une eau de bonne qualité (Roback, 1974, tel que cité par Burt *et al.*, 1991; Cuffney *et al.*, 2005; Garcia Criado et Trigal, 2005).

Problématique générale

Dans une perspective de gestion du territoire, la caractérisation et la compréhension de la réponse des communautés aquatiques aux changements de structure du paysage sont donc importantes pour l'évaluation des impacts de l'utilisation du paysage sur l'intégrité des systèmes aquatiques. À ce sujet, bien que les connaissances concernant les eaux courantes soient de plus en plus nombreuses, peu d'études ont été effectuées en milieu lacustre. La variabilité inter-habitats des lacs explique en partie cette lacune puisqu'elle rend la comparaison inter-lacs plus difficile (Rasmussen, 1988; Johnson, 1998; Tolonen *et al.*, 2001; White et Irvine, 2003). Un suivi biologique considérant cette variabilité exige effectivement une acquisition de données à partir d'un nombre élevé de variables sur plusieurs lacs et sur leur bassin versant. Ainsi, la plupart des études publiées tendent à porter leur attention sur un seul type d'utilisation du sol (e.g. James *et al.*, 1998, 2000; Cuffney *et al.*, 2005; DeSousa *et al.*, 2008), à une seule échelle spatiale (Weatherhead et James, 2001; White et Irvine, 2003; Beaty *et al.*, 2006) ou encore sur un ou quelques lacs présentant un gradient limité d'état trophique (e.g. Burton *et al.*, 1999; Stoffels *et al.*, 2005). Très peu d'études ont tenté de relier l'utilisation du territoire, à de multiples échelles spatiales, avec les communautés de macro-invertébrés benthiques et ce, en utilisant plusieurs lacs répartis le long d'un gradient d'état trophique et exposés à différents types d'occupation du sol (agricole, forestière, urbaine, etc.).

Le présent projet vise donc à caractériser les impacts des activités humaines et des paramètres généraux du territoire (pente, superficie, hydrologie, etc.) sur vingt lacs habités de la région du Bas-St-Laurent, par l'étude des communautés de macro-invertébrés benthiques, groupe d'organismes sentinelles dans l'évaluation de l'intégrité du milieu aquatique. Il s'agit d'une approche comparative par bassin versant, visant à étudier non seulement l'impact de l'utilisation immédiate du pourtour des lacs mais également l'impact de l'utilisation du territoire drainé par ces lacs, qu'elle soit agricole, forestière, urbaine ou naturelle. En considérant le bassin versant comme étant la portion de territoire délimitée par des lignes de crête, dont les eaux qui parcourent cette portion de territoire alimentent un exutoire, par exemple, un lac, il apparaît évident que la prise en compte de cette échelle semble la plus appropriée à une étude portant sur les impacts de l'utilisation du sol sur le milieu lacustre (Allan et Johnson, 1997; Allan *et al.*, 1997; D'Arcy et Carignan, 1997; Hawkins *et al.*, 2000; Huryn *et al.*, 2002).

Objectifs du projet de recherche et hypothèses associées

L'objectif général de ce projet de recherche est de caractériser les liens entre les communautés de macro-invertébrés benthiques et les variables environnementales à l'échelle du paysage. Cet objectif est ensuite subdivisé en trois niveaux :
1) caractériser les assemblages de macro-invertébrés colonisant la première portion du littoral des lacs sélectionnés; 2) quantifier les corrélations entre les macro-invertébrés benthiques et les attributs du paysage à différentes échelles géographiques (bassin versant, bande riveraine, lac, site d'échantillonnage) et 3) identifier les attributs du paysage les plus influents sur les vingt lacs, tels qu'indiqué par les communautés de macro-invertébrés benthiques.

Tel qu'exposé précédemment, plusieurs études tendent à montrer que les variables physiques et chimiques à petite échelle spatiale, par exemple à l'échelle du lac, sont influencées par d'autres variables à une plus grande échelle spatiale (Allan *et al.*, 1999 ; Johnson *et al.*, 2004). Ainsi, il est supposé que, par exemple, un lac dont le bassin versant présente une forte proportion de terres agricoles et/ou d'urbanisation devrait présenter une eau plus enrichie et un stade trophique plus eutrophié. Des concentrations plus élevées en nutriments et une production primaire élevée devraient donc être observées en même temps qu'une plus grande présence de matière organique, de sédiment meuble et de plantes aquatiques. Puisque les communautés macrobenthiques sont influencées par les variables de leur habitat (e.g. Heino, 2000; Weatherhead et James, 2001; White et Irvine, 2003; Johnson *et al.*, 2004), et en assumant que ces variables sont directement reliées aux apports provenant des activités en amont des lacs, certaines caractéristiques du territoire devraient influencer les communautés benthiques lacustres.

Les objectifs du projet de recherche permettent ainsi de tester les hypothèses suivantes :

1) Les variables environnementales associées au lac, telles que les propriétés physico-chimique de l'eau, sa teneur en éléments nutritifs et la biomasse algale, sont influencées par les caractéristiques de leur bassin versant (ex. : occupation du sol);
2) La composition des communautés macrobenthiques est influencée par les caractéristiques des bassins versants telles que l'occupation et l'utilisation du sol;
3) Les variables montrant les plus grandes corrélations avec la composition des communautés macrobenthiques sont celles associées à l'enrichissement des lacs en éléments nutritifs.

CHAPITRE 2

BENTHIC MACROINVERTEBRATES AS INDICATORS OF HUMAN IMPACTS ON INTEGRITY OF 20 LAKES IN EASTERN QUÉBEC: A COMPARATIVE CATCHMENT APPROACH.

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Abstract

1. In landscape management, understanding how human land-use and natural parameters interact, and at which scale, is essential for predicting how human perturbations will affect lakes processes and ecological integrity.

2. Using a multivariate data set covering twenty (20) inhabited lakes, showing a trophic state gradient, the purpose of this study was to quantify relationships between macroinvertebrate assemblage attributes and catchment land cover at different geographic spatial scales (catchment, riparian, habitat) and investigate which of all the landscape characteristics are the most influential on the composition of macroinvertebrate communities.

3. At geographic scale lever, our results indicate that catchment variables showed the same importance as water characteristics variables in explaining the composition of benthic invertebrate communities.

4. At multi-scale level, communities were significantly correlated to nutrient input and to chlorophyll *a*. Lake area, agriculture cover and forest cover at catchment scale have also been showed to have impact on the communities, probably by inferring in those water characteristics parameters as well as having impacts on habitat heterogeneity.

5. This study however demonstrates that urbanisation and slope have important hidden influence on lakes, most likely by amplifying impacts of the other parameters. It suggests that managers must continue their efforts in a catchment approach, paying especially attention to those confounding factors.

6. Moreover, our results indicate that benthic macroinvertebrate communities can be indicator of oligotrophic lake but cannot individually discriminate other trophic states. They may be useful for comparative studies on long time scale to detect degradation in their communities composition and/or for confirming water characteristics diagnostic.

Key words: lakes, macroinvertebrates, catchment, land-use, spatial scale

Introduction

During the last decades, there has been an intensification of human pressure on rivers and lakes, which were already impacted by human activities on their surrounding territory. For instance, human activities such as logging, agriculture and urbanization, have been shown to negatively affect aquatic ecosystems (e.g. Burt *et al.*, 1991; Casper, 1994; Allan & Johnson, 1997; Cooke & Prepas, 1998; Johnson, 1998; Johnson *et al.*, 2004; Cuffney *et al.*, 2005). Specifically, some of these activities have lead to an increase of the amount of nutrients exported from the terrestrial to the aquatic environment (D'Arcy & Carignan, 1997; Knoll, *et al.*, 2003), which stimulates primary production and accelerate eutrophication (Johnson & Gage, 1997; Cooke & Prepas, 1998). However, lakes are responding in different ways to human disturbance. Little is known about the factors driving the differences observed between the responses of aquatic systems (Brodersen *et al.*, 1998; Cuffney *et al.*, 2005) like, for example, the spatial scale at which the correlations are greater (catchment, riparian, lake) and how natural characteristics of the landscape interact with human activities.

In landscape management, understanding how, and at which spatial scale, human land-use and natural parameters interact and affect water characteristics and lake processes, is essential for predicting how human perturbations (e.g. forestry, agriculture and recreation) influence the ecological integrity of aquatic systems (Johnson & Goedkoop, 2002). With the growing interest in catchment-scale management, that knowledge could provide the opportunity for humans to minimise their impacts on aquatic ecosystems by making appropriate choices in their land-use development.

Environmental studies that were, in the past, based uniquely on water chemistry (Allan & Johnson, 1997; D'Arcy & Carignan, 1997; Dinsmore *et al.*, 1999; Hawkins *et al.*, 2000), now tend to lead toward biological indicators (Rodriguez & Lewis, 1997; Heino, 2000), increasing our understanding of ecosystem response to disturbances. Benthic macroinverterates are the most used organisms in environmental evaluation (e.g. Bendell & McNicol, 1987, 1995; Wellborn *et al.*, 1996; Brodersen *et al.*, 1998; Heino, 2000; Royer *et al.*, 2001; Klemm *et al.*, 2003; DeSousa *et al.*, 2008). This is due to their limited mobility, their short average life duration, their relative sensitivity to environmental changes (Casper, 1994; Jackson, 1993; Rosenberg & Resh, 1993; Weatherhead & James, 2001) and their important role in aquatic food webs, by linking primary producers and upper trophic levels (Pinel-Alloul, 1995; Vadeboncoeur *et al.*, 2002). So far, they have been successfully used as ecological indicators of disturbances on lotic ecosystems (e.g. Richards & Host, 1994; Cao *et al.*, 1996; Allan *et al.*, 1997; Allen *et al.*, 1999; Edwards *et al.*, 2000; Cresser *et al.*, 2000; Sponseller *et al.*, 2001; Roy *et al.*, 2003; Huryn *et al.*, 2002 Townsend *et al.*, 2004) but rarely used to study lake ecosystem integrity. Of the few of them, Brodersen *et al.* (1998) related macroinvertebrate communities of 39 Danish lakes to their trophic state, while Tolonen *et al.* (2001) found that benthic macroinvertebrates were affected by habitat characteristics. DeSousa *et al.* (2008) observed changes in benthic macroinvertebrates communities along a gradient of lakeshore residential development and catchment deforestation. The small number of studies that have focussed on macroinvertebrate in lake ecosystems can be explained by the heterogeneity characterizing their habitats which makes comparisons and generalisation between lakes harder than for river ecosystems (Rasmussen, 1988; Johnson, 1998; Tolonen *et al.*, 2001; White & Irvine, 2003). Moreover, since acquiring environmental and biological data on multiple lakes and related landscape is time and resource consuming, most studies have focused on one type of land-use (e.g. James *et al.*, 1998, 2000; Cuffney *et al.*, 2005; DeSousa *et al.*, 2008) and/or at one spatial scale (Weatherhead & James, 2001; White & Irvine, 2003; Beaty *et al.*, 2006) and/or on one or few lakes presenting limited range of trophic states (e.g. Burton *et al.*, 1999; Stoffels *et al.*, 2005). To our knowledge, few studies have tried to relate land-use, at multiple scales (lake, riparian zone, catchment), with benthic macroinvertebrates communities, using lakes spanning a large gradient of trophic states and land-use types (e.g. Johnson & Goedkoop, 2002; Brauns *et al.*, 2007).

In this study, a multivariate data set covering twenty inhabited lakes, showing a trophic state gradient, and all their catchment land-use, was used to: (1) quantify relationships between benthic macroinvertebrate communities attributes and catchment land cover at different spatial scales (catchment, riparian, habitat) and (2) investigate which of the landscape characteristics are the most influential on the composition and abundance of benthic macroinvertebrate communities.

Methods

Study site

This study took place in the Bas-Saint-Laurent region (eastern Quebec, Canada) (Figure 1). This region is characterized by a subpolar-subhumic and continental climate. The mean annual air temperature is around 3.6°C and the total annual precipitation is about 913 mm (Environment Canada, 2008). The bedrock is composed of sedimentary rocks, mainly shale, sandstone, limestone and conglomerate (Robitaille & Saucier 1998). In a north-south gradient, the soil deposit is going from marine origin to alteration and till origin. Forests are mainly composed of yellow birch (*Betula alleghaniensis*), balsam fir (*Abies balsamea*), maple sugar (*Acer saccharum*), white birch (*Betula papyrifera*), white cedar (*Thuja occidentalis)* and aspen (*Populus tremuloides*) (Robitaille & Saucier 1998). The urbanized part of the land represents less than 3%, while forest covers 85%, agriculture 9%, and water 3% (MRC Rimouski-Neigette 2005).

Sampling lakes (20) were first selected based on the occurrence of human development along their shores in order to measure its impact at the catchment scale. The lakes were also chosen to ensure a large gradient of trophic state and a wide diversity of watershed morphometry and land-use (Table 1). Comparative approach was privileged, taking into account the impossibility to obtain a control lake under the same environmental conditions. Thirteen lakes were located in the Rimouski river drainage basin, two in the Sud-Ouest river drainage basin, two in the Germain-Roy river drainage basin and two in the Mitis river drainage basin and one in the Bic river drainage basin (Figure 1).

Data acquisition

Assessment of catchment land-use and spatial analysis treatment

Catchments were delimitated from Quebec topographic database (BDTQ 1:20000) using ArcGIS (version 9.1; ESRI inc., 2007). Land cover was quantified by matching boundaries with cover classification obtained from ecoforestry information

System (Quebec) (SIEF; Ministère des Ressources naturelles, 2004). This produces a GIS that provides proportional cover of different land cover types in each watershed. Morphometric characteristics (e.g. slope, lake area, catchment area; Table 2) and other information (e.g. hydrology, buildings, roads) were also estimated using this GIS. Land cover types were categorized into: agriculture, forest, wetland, urban and other. All information regarding human disturbance and land-use was analyzed for two spatial scales; catchment surface and riparian zone, i.e. 30 meters around each lake. The 30-meter strip was selected according to several studies reporting the effectiveness of natural buffer lengths (e.g. Erman *et al.*, 1977; Graynoth, 1979; Davies & Neilson, 1994). Several indices such as the density of building per area were derived from those measures (Table 2).

Macroinvertebrates sampling and treatment

Lakes were randomly visited between 3 and 28 of July 2006 and benthic macroinvertebrate samples were systematically collected from 5 sites distributed at equal intervals along the margins of the water body of each lake. Sampling was carried out with a 500 μm D-net using a 5-minute time-limited kick-sample method along a 1-m stretch (Rosenberg *et al.,* 1997). Benthic samples were preserved in 5% formalin solution and rose Bengal stain was added in laboratory to facilitate sorting and identification of organisms. Macroinvertebrates were identified to family, and rarely at higher taxonomic level (i.e. Oligochaeta and Bivalva). According to Pedersen and Perkins (1986), taxonomic level of family is an appropriate and sensitive indicator of benthic macroinvertebrate response to system disturbance. The identification was made using a dissecting microscope (10 x power) and classification keys provided by McCafferty (1998) and Merritt and Cummins (1998).

Sampling site characterization and water sampling

During benthic macroinvertebrate sampling, sites were classified according to the percentage of each type of substratum (block, rock and pebble; pebble and coarse; coarse and sand; sand clay and silt), the occurrence of macrophytes (presence vs absence) and human disturbance in the near-shore riparian zone (0-10%; 11-35%; 36-60% 65-85% and 86-100% disturbed). Water samples were collected for the determination of chlorophyll *a* (µg L-1) concentrations in the littoral zone. Dissolved oxygen (DO; mg/l) concentration, water temperature (°C), conductivity (µS cm^{-1} @25°C) and pH were also measured *in situ* with an YSI 556MPS probe held in the water column. These water caracteristics parameters were also measured for water samples taken at the deepest point of the lake. In addition to chlorophyll *a* concentration, dissolved organic carbon (DOC; µg L^{-1}) and total phosphorus (TP; µg L^{-1}) concentration was measured from those water samples. TP was measured by colorimetric determination (Centre d'expertise en analyse environnementale du Québec, 2007), while determination of DOC concentration was made with a TOC-5000A analyzer (Shimadzu, Kyoto, Japan), following the protocol of Whitehead *et al.* (2000). DOC reference standards were produced by the Hansell's Certified Reference Materials (CRM) program.

Statistical analyses

Environmental and water characteristics

All variables retained for the analyses were also associated to specific spatial scales (catchement, riparian zone, lake or sampling site) and type (environmental or water characteristics variables, see Table 2). Statistical analyses were performs using PRIMER (version 6, PRIMER-E, Plymouth, UK, 2006) and CANOCO (Version 4.5, Ter Braak & Smilaeur, 1998) software packages

Clustering analysis

Two agglomerative hierarchical cluster analyses were first performed on the 20 lakes. The first cluster analysis was realized using water characteristics variables to identify clusters associated to the trophic states of the lakes. A second cluster analysis was then performed on environmental variables, to regroup lakes according to their land-use characteristics. Euclidian distances was used on samples as a dissimilarity measure for the cluster and complete linkages have been used to perform the analyses. For all analyses, data were first standardized (z-score transformation) to remove the influence of magnitude between scales or units of different variables (Ramette, 2007) (PRIMER; Clarke and Gorley, 2006).

Macroinvertebrates assemblages characteristics

Analysis of similarity (ANOSIM; Clarke and Gorley, 2006) was used to test differences in the benthic communities between lake clusters. Taxa occurring only at a single sampling site (1/100 sampling sites) have been omitted from all analyses. Moreover, data of taxa abundances were also transformed using Hellinger transformation giving low weights to rare families (Legendre & Gallagher, 2001). Finally, a SIMPER test (species contributions to similarity; Clarke, 1993) was performed to determine the families that contributed the most to differentiating between those same trophic state groups. Those families were then used as indicators for further analysis.

Macroinvertebrate assemblages vs environmental and water characteristics variables

Canonical analyses were carried out to develop the knowledge on the relationship between benthic data and water characteristics and environmental variables (ter Braak, 1986; ter Braak & Verdonschot, 1995).

Redundancy analyses (RDA) was chosen based on a preliminary detrended correspondence analysis (DCA) of Hellinger transformed species abundance, detrending by segments, which gave relatively small gradient lengths (1.215 for axis1 and 0.085 for axis 2), indicating that a linear model was more appropriate (Leps & Smilauer, 2003). Individual replicates (n=100) were used in the RDA analyses so that the number of sampling sites would be higher than the number of independent variables (Legendre & Legendre, 1998).

Land-use pattern

A first RDA was performed using the cluster previously identified as explanatory variables to measure and visualise how macroinvertebrates communities can be related to land-use pattern. Indicator families identified in previous analyses, as well as those sorted using CANOCO software package (Version 4.5, Ter Braak & Smilaeur, 1998), were used to bring attention to the families that were associated with particular environmental characteristics

Forward selection

Another RDA analysis, using forward selection procedure, was run on all variables to explore the proportion of explanation brought in by each environmental variable independently of the other (marginal effect) and also conditionally to other ones already selected (conditional effect). This last RDA analysis allowed reducing the amount of potential explanatory variables use in subsequent analyses. Non-significant variables ($p>0.05$) were excluded and RDA was run again until all remaining variables showed significant relationships with macroinvertebrates data.

Partitioning the variance

Series of partial RDA were realised to partition the variance according to the type (environmental or water characteristics factors) and spatial scale (catchment, riparian zone, lake, sampling site) of variables. The partitioning was done by entering some variables as covariables, eliminating the "noise" attributed by those variables and to the co-effects of variables together (Anderson, 2004). Those three series of RDA will subsequently be referred as variable type series, spatial scale series and individual series.

The first series of RDA (variable type series), was done using all variables together, and then, separating the effect of environmental variables alone versus water characteristics variables. The second series of RDA analyses (spatial scale series) was performed to establish which spatial scale (catchment surface, riparian zone, lake and sampling site) was most correlated to macroinvertebrates communities. Finally, the third series of RDA (individual series) analyses was done on individual variables one by one, using all the others as covariables, to point out their own relationship with the macroinvertebrate data, when removing the possible interaction with other variables. Partial RDA yielded ordinations of the residual variation in the invertebrate data after the covariables were factored out by multivariate linear regression (Borcard *et al.* 1992; ter Braak, 1995). Monte Carlo permutation test (n=999) was performed to assess the significance of the relationships between environmental variables and species composition among study sites.

Results

Environmental and water characteristics

Catchment scale characteristics

The catchment surface of studied lakes averaged 20.37 km^2 (SE: ± 7.69), while the mean lake area was 0.54 (± 0.12) km^2 (Table 1). Mean slope in catchment surface was generally lower than 10°, with a mean slope maximum of 11.4° (± 0.67) (Table 2).

Forest was the dominant land-use observed at catchment scale for 18 of the 20 lakes and all catchment had > 40% forest. Agricultural land-use ranged from 0 to 48% and half of the catchment presented less than 10% of this type of land cover. Urbanisation was present at low proportion (<10%) in all catchments but one, which showed 37.8% urban land-use. The density of buildings in catchment surface varied between 1.3 and 423.8 per km^2 (mean= 35.71 ±20.08 per km^2).

Riparian scale characteristics

Lakes riparian zone were characterized by a stronger urbanisation land-use than their catchment surface (Table 2) and varied between 0 and 99.99%, being the dominant land cover type for five of the lakes (>50%). Additionally, building density around lakes ranged from 39.6 to 984.8 km^{-2}. Forest was the dominant land-use type for 13 lakes, with proportion varying between 0 and 94.4% (mean= 48.76 ± 6.12%). Agricultural land-use was absent of the riparian zone for 12 of the 20 lakes, was of less then 10% for 5 others, but reached 60.9%, 47.7% and 30.9% for the three remaining ones (respectively lakes Station, Passetout & Guimond). Mean slope in riparian zone reached 13.07° (mean for all lakes= 5.72 ± 0.75°).

Sampling scale characteristics

The sampling sites showed various habitat patterns (Table 2). Substrate with small particles, like sand, clay and silt, was dominating more than 55% of the sites, while block, rock and pebble were characterising 12% of the others. Macrophytes occurred in 58% of the sampling sites. Human artificialisation in near shore riparian zone was observed at 43% of the sites, while the remaining 57% was natural or only weakly modified.

Clustering environmental and water characteristics data

The clustering of lakes according to water characteristics variables divided lakes into five distinct groups according to their trophic states (Figure 2a). A first group including lakes showing the lowest concentrations in TP (mean=4 μgL^{-1}) and chlorophyll *a* (mean=1.22 $\mu g\ L^{-1}$) and the highest secchi depths (mean= 5.25 m) composed the oligotrophic lakes group (G_{Oligo}), whereas a second group including lakes showing the highest concentrations in phosphorus (mean= 33.5 $\mu g\ L^{-1}$) and chlorophyll *a* (mean= 9.25 $\mu g\ L^{-1}$) and the lowest secchi depths (mean= 1.40 m) composed eutrophic lakes group (G_{Eutro}). The remaining groups, including lakes with intermediate ranges of nutrients and chlorophyll *a* concentrations and secchi depths, composed the oligo-mesotrophic lakes group ($G_{OligoMeso}$), mesotrophic lakes group (G_{Meso}) and meso-eutrophic lakes group ($G_{MesoEutro}$) respectively.

The second clustering based on environmental variables, allowed the identification of four lakes groups based on their land-use patterns (Figure 2b). Accordingly, the first group, including medium to small lakes showing an important human development in lakeshore, composed the human developed lakes group (G_{Hdev}) whereas natural lakes group ($G_{Natural}$) assembles the lakes which shows the most natural catchment land-use. Agricultural lakes group (G_{Agri}) puts together lakes showing a medium size catchment area associated with dominance of agricultural activities and, finally, large catchment lakes group (G_{Large}) is composed of lakes associated with large and disturbed catchment surfaces.

Comparing lake groups formed by the two clusters show that oligotrophic lakes group (G_{Oligo}) from the first cluster analysis is composed by the same lakes as the natural lakes group ($G_{Natural}$) from second cluster analysis (Figure 2). However, no other obvious similarities could be distinguished.

Macroinvertebrate assemblages characteristics

A total of 43 771 invertebrates and 52 taxa were collected and retained for further analyses. Benthic samples were numerically dominated by amphipoda (indeterminate family), chironomidae larvae, oligochaeta (indeterminate family) and caenidae (Table 3).

ANOSIM and SIMPER analyses- Similarity test indicated that benthic invertebrate assemblages were able to distinguish the groups of lakes previously discriminated by water characteristics variables. There was a significant difference between G_{Oligo} and $G_{MesoEutro}$ (ANOSIM, R=0.61, p=0.001). Notable differences were however observed between communities of groups $G_{MesoEutro}$ and G_{Eutro} (ANOSIM, R=0.46, p=0.001), G_{Oligo} and G_{Meso} (ANOSIM, R=0.39, p=0.001), G_{Oligo} and G_{Eutro} (ANOSIM, R=0.26, p=0.008) and G_{Oligo} and $G_{OligoMeso}$ (ANOSIM, R=0.29, p=0.01). Taxa that contributed mostly to those differences were heptageniidae, psephenidea, elmidae larvae, amphipoda (indeterminate family), oligochaeta and chironomidae larvae (SIMPER, table 4). Amphipoda, oligochaeta and chironomidae were present in all groups but also contributed to differentiate between the trophic groups. However, heptageniidae and psephenidae were more abundant in oligotrophic lakes and elmidae larvae were abundant in oligo-mesotrophic lakes. These three taxa were the ones which discriminated best oligotrophic lakes.

Macroinvertebrate assemblages vs environmental and water characteristics variables

Land-use pattern

The first redundancy analysis identified how the macroinvertebrate communities were related to general catchment land-use pattern, as defined by cluster previously made (Figure 3). Attention was particularly put on taxa that were designed by SIMPER analysis to contribute the most to the differentiations of lakes according to their trophic state and on taxa which showed the highest range of percentage of explained variance. The four land-use groups explained 12.4% of total macroinvertebrates data variations and the first two RDA axes accounted for 88.3% of that variation (F= 4.525; p=0.0010; Monte Carlo test, perm. =999). Heptageniidae, psephenidae and elmidae larvae showed great positive relation with land-use group $G_{Natural}$, forming the lakes that showed the most natural catchment land-use. Cumulative fit per species also pointed out these taxa. According to this analysis, ephemeridae and ephemerellidae also seemed to be closely linked to this type of land-use pattern. These results can be compared to previous analyses, where those same taxa were associated with oligotrophic and oligo-mesotrophic lakes.

In the opposite direction on the first RDA axis, the land-use groups G_{Hdev} and G_{Large} were respectively positively associated with oligochaeta and amphipoda. On

RDA second axis, land-use group G_{Agri} was positively correlated to caenidae and chironomidae taxa.

Forward selection

The first RDA analysis of the relation between all 27 variables and the macroinvertebrates data set gave an explained variation of 57.5% (F=3.804; p=0.0010; Monte Carlo test, perm. =999). When taken individually, the variables that explained the greatest amount of variations were lake area (9.5%), DOC (5.9%), road density in the riparian zone (5.3%), DO (4.8%), proportion of agriculture in catchment surface (4.4%) and mean ground slope in catchment surface (4.3%) (Table 5; marginal effect). When running a forward-selection, where proportion explained by each variable added to the model is conditional on variables already there, the relative importance of few variables changed (Table 5; conditional effect). The most important variables were lake area (9.5%), followed by DOC (4.1%), proportion of forest in catchment surface (3.8%), chlorophyll *a* concentration (3.5%) and proportion of agriculture in catchment surface (3.4%). Figure 4 illustrates how those variables are linked to macroinvertebrate taxa.

Here again, attention was particularly put on taxa that were designed by SIMPER analysis to contribute the most to the differentiations of lakes according to their trophic state and on taxa which fit in the highest range of percentage of explained variability. As shown on Figure 4, taxa previously associated with oligotrophic and oligo-mesotrophic lakes (heptageniidae, psephenidae and elmidae larvae), as well as leptophebiidae and ephemeridae, showed positive relationships with lake area and proportion of forest in catchment surface, and an inverse relationship with the proportion of agriculture in catchment surface and chlorophyll *a* concentration. Furthermore, this last variable showed a strong positive relationship with chironomidae larvae, cladocera, caenidae and oligochaeta taxa. A positive relationship can also be observed between the abundance of amphipoda and DOC. Finally, the stepwise forward procedures associated with this RDA routine retained 17 of the 27 variables ($p<0.05$), excluding proportion of wetland in catchment surface and in riparian zone, proportion of catchment area versus lake area, road density in catchment surface, DO at the center of the lake and parameters relied to sampling site scale (macrophyte, human disturbance, chlorophyll *a*, DO and pH).

Partitioning the variance

Variable type series - RDA performed on all the 17 remaining variables explained almost half of the variation (49.6%; F=4.756; p=<0.001; Monte Carlo test, perm. =999). With RDA model using water characteristics parameters as covariables, environmental variables explained 34.1% (F=4.631; p=<0.001; Monte Carlo test, perm. =999) of the variation and, at the opposite, water characteristics variables explained 13.5% (F=4.397; p=<0.001; Monte Carlo test, perm. =999) when removing the contribution of other variables (Table 6A).

Spatial scale series - According to the spatial scale analyses, the best set of explanatory variables, when respectively taking out the compositional variability explained by the variables of other spatial scale, are those ones related to water characteristics at lake scale (12.3%; F=4.994; p=<0.001; Monte Carlo test, perm. =999) and to land-use at catchment scale (12.2%; F=4.953; p=<0.001; Monte Carlo test, perm. =999), followed by information from riparian zone variables (10.5%; F=4.284; p=<0.001; Monte Carlo test, perm. =999). Remaining groups of variables, related to the lake itself and sampling site scale, were only adding, together, less than 10% (Table 6B).

<u>*Multi-scale individual series*</u> - Finally, the individual series of RDA analyses have been done by analysing the impact of each of all the selected variables, using all the others as covariables, independently of their type or spatial scale. Unlike the RDA made in forward selection, these analyses, as well as removing the possible influence of all other variables, also removes the co-effects of variables together. Table 6c shows all results associated to those analyses. According to these, three variables showed the same and highest proportion (4.9%) of correlations to macroinvertebrate communities. Those were chlorophyll *a* concentration (F=7.996; p=<0.001; Monte Carlo test, perm. =999), density of building in catchment surface (F=7.982; p=<0.001; Monte Carlo test, perm. =999) and mean slope of ground in catchment surface (F=7.969; p=<0.001; Monte Carlo test, perm. =999). Total phosphorus concentration also seems to be an important variable (4.2%; F=6.812; p=<0.001; Monte Carlo test, perm. =999).

Discussion

A better understanding of ecological linkages between lakes and their respective catchment surface is of critical importance to understand the impact of land uses on lakes ecosystems. After many years of works linking human activities with water chemistry and eutrophication process, research now tend to show that changes in trophic states also result in changes in ecosystem structure (e.g. Jeppesen *et al.*, 2000; Brauns *et al.*, 2007), using frequently benthic macroinvertebrate communities as biological indicators. Knowing that macroinvertebrate communities differ among trophic states (e.g. Tolonen *et al.*, 2001; Brauns *et al.*, 2007), this study also pointed out that there is a significant relationship between landscapes attributes and lentic system integrity.

Macroinvertebrate assemblages vs water characteristics variables

Comparisons of inter-lakes benthic macroinvertebrate composition first confirm here clear differences between oligotrophic and eutrophic lakes. Notable differences were mainly observed between communities of opposite trophic states and specific taxas were associated with particular trophic state. Ephemera (heptageniida, leptophlebiidae, ephemeridae and ephemerellidae), coleoptera (elmidae) and plecoptera (psephenidae) taxa, generally seen as sensitive (Rosenberg & Resh, 1993; Cuffney *et al.*, 2005; Garcia-Criado & Trigal, 2005), were linked to oligotrophic lakes, whereas generalist taxa like chironomidea, oligochaeta and amphipoda were dominating eutrophic systems. These results agree with those of Brodersen *et al.* (1998), who found that eutrophication causes a loss of less tolerant species and an increase in the abundance of a few tolerant ones. Also, Brauns *et al.* (2007) reported that compositions of communitie across lakes in middle trophic states was not clearly distinct. Similarly macroinvertebrate families individually could not, be used as ecological indicators in our study. However, the finding that inter-lake differences between communities can be linked to trophic state can lead to the conclusion that they can also be relay lakes ecological integrity. In that perspective, this study revealed that environmental characteristics, after removing variability due to water characteristics parameter, explained more that the third of community variability (34%). This agreed with several studies, which found that environmental factors, other than nutrient concentration, explain most of the variance in compositions of macroinvertebrate communities (e.g. Brodersen *et al.*, 1998; Johnson & Goedkoop, 2002; Brauns *et al.*, 2007).

Macroinvertebrate assemblages vs spatial scale

Macroinvertebrates are known to be link to habitat trait, particularly substratum type and presence of macrophyte (e.g. Brodersen *et al.,* 1998; Tolonen *et al.,* 2001; Weatherhead & James, 2001; Beaty *et al.*, 2006; Brauns *et al.*, 2007; Heino, 2008). When comparing different geographic scale influence, Johnson and Goedkoop (2002) found a correlation decreasing with distance i.e. that habitat-level descriptors were the best predictors of littoral macroinvertebrate communities. However, because of the funnel shape and the water residency time associated with lakes, limnologists have to face the wide interdependence between lake and regional scale (Johnson and Goedkoop, 2002).

In that perspective, it as been shown that landscape variables have generally more impact than habitat variables on macroinvertebrates communities (e.g. Ormerod & Edwards, 1987; White & Irvine, 2003). By analysing the importance of each spatial scale (catchment surface, riparian zone, sampling site) individually on the 20 studied lakes, macroinvertebrates data showed a strongest relationship with catchment scale variables than with other geographic scale. Variables associated with riparian zone showed a lower importance, while those measured at sampling site scale showed little importance in explaining macroinvertebrates communities. Similar results were also observed by Stendera and Johnson (2005), who found that the largest amount of variance in macroinvertebrate communities was explained by the effect of regional-scale alone. It can be proposed that landscape variables have impacts on habitat traits, as well as on macroinvertebrates themselves. It can also be proposed that the importance of a natural riparian zone for the integrity of lakes can largely depend on the pressure coming from catchment scale activities. In fact, assuming that different land use patterns bring different kinds and intensity of influences on lake integrity, the importance of a natural riparian zone as the last shield should then vary, depending on the type and loudness of human activities on the land behind. In a management perspective, this suggests that lakeshore development and artificialisation should be made in a landscape perspective, by taking into account catchement land-use.

Macroinverterbrates vs multi-scale individual variables

Much attention was given recently to the relationships between specific land-use types and ecological communities (e.g. Burt *et al.*, 1991; Casper, 1994; Allan and Johnson, 1997; Cooke et Prepas, 1998; Johnson, 1998; Johnson *et al.*, 2004; Cuffney *et al.*, 2005). It is now known that, for example, the increase of urbanized surfaces causes shore erosion, leading to destruction of several aquatic habitats, as well as bringing large quantity of sediment and nutrients (Gresens *et al.*, 2007). Artificialisation of riparian zone reduces the capacity of the grounds and the vegetation to filter the diffuse sources of pollution before they enter the aquatic systems (Cuffney *et al.*, 2005).

Otherwise, a great proportion of the types of catchment land use affect the amount of nutrients exported into lakes and reservoirs via stream inflows. Catchments dominated by agricultural or urban lands typically export nutrients at higher rates than undisturbed watersheds (Knoll *et al.*, 2003).

Land-use pattern

Assuming that influences of land-use on lakes integrity varies in different ways, depending on the type of activities and on interaction with natural parameters, the second objective of this study was to investigate which of the landscape characteristics are the most influential on the composition and abundance of benthic macroinvertebrate communities. First analyses showed that even wide and general groups of land-use patterns, such as natural catchment lakes group or agricultural catchment lake group, explained nevertheless more than 10% of macroinvertebrates variability. Sensitive taxa were strongly related to lakes showing natural catchment land-use pattern, which are also lakes categorized as oligotrophics. It is also interesting to notice that lakes having large catchment size were related to macroinvertebrates communities in the same way as lakes showing smaller catchment area but a high human development. This can be due to the fact that urbanisation and large catchment area have the same effect on lake by both affecting quantity and flow of water drainage. As urbanisation create multitude of impervious surfaces (Paul & Meyer, 2001) accelerating drainage and water flow, large catchment areas, with their hydrologic systems, drains a greater territory and bring a largest quantity of water. However, knowing that lakes are complex ecological systems in which biotic and abiotic parameters are interrelated, we may be interested in finding a model which would select the minimal variables explaining, together, the largest proportion of variation in the littoral macroinvertebrates composition.

Forward selection

Few studies have tried to estimate the impacts of particular environmental parameter like logging and recreational activities on aquatic systems. Results are varying considerably through studies, depending on studied parameters, scale, etc. Lake area, macrophyte cover, TP, and hardness seem to be influential determinants of the taxonomic structure of littoral macroinvertebrate communities (Brönmark, 1985; Dodson, 1992; Brodersen *et al.,* 1998; Brauns *et al.,* 2007; Heino, 2008). In an other hand, macroinvertebrate communities of stony littoral regions of Danish lakes were found to be correlated with mean lake depth, Secchi depth and chlorophyll *a* concentration (Brodersen, *et al.*, 1998).

The forward selection model explaining best the difference in benthic macroinvertebrate communities compositions in the studied lakes was the one made by the interaction of lake area, dissolved organic carbon (DOC), forest and agriculture land cover in catchment surface and chlorophyll *a* concentration. The variable showing the stronger correlation was, here also, lake area. This relation can be explained by the wider habitat variability associated with larger lakes, providing more niche opportunities to taxa (Johnson & Goedkoop, 2002; Brauns *et al.*, 2007; Heino, 2000, 2008). Importance of lake area can also be correlated to wave action (Johnson & Goedkoop, 2002; Johnson *et al.*, 2004), which was showed as an important parameter for littoral organisms (James *et al.*, 1998; Johnson *et al.*, 2004; Brauns *et al.*, 2007).

Habitat heterogeneity can also explain the importance of forest land-use in catchment surface on littoral invertebrates. Forest in landscape provides shadow from canopy, coarse woody debris and root habitats (Heino, 2000; Brauns *et al.*, 2007 and Kreutzweiser *et al.*, 2008). Accumulation and decomposition of leaf litter also provide food and habitat resources for aquatic microbial and invertebrate communities (Kreutzweiser *et al.*, 2008). Forest land cover is known to have significant influences on water and ecosystem quality by maintaining cool water, limiting drainage and filtrating water from nutrient (Schauman, 2000). On the opposite, the same hypothesis may explain the importance, in our model, of agricultural land-use in catchment surface. Indeed, the deforestation associated with agriculture involves a deceleration of the infiltration of water causing an increase in the streaming, sedimentation and migration of the contaminants. Those phenomena are known to reduce macroinvertebrate species richness in streams systems (Richards & Host, 1994; Edwards *et al.*, 2000).

Relationships have also been established between agriculture and phosphorus (Carpenter *et al.*, 1998; Cooke & Prepas, 1998). Knowing that increase in phosphorus concentration is associated with an increase in the primary production and, consecutively, of chlorophyll *a* concentrations in lakes (Richards & Host, 1994), it is not surprising that chlorophyll *a* concentration, as for this study, generally appears to be an important variable in explaining macroinvertebrates composition (e.g. Brodersen *et al.*, 1998; Brodersen & Lindegaard, 1999; Langdon *et al.*, 2006).

To our knowledge, only few linkages have been made between DOC and littoral invertebrates in lakes. Schell and Kerekes (1989) found that total macroinvertebrate numbers were apparently not controlled by DOC while Pastuchová (2006) found that low DOC in summer formed, with other parameter such as temperature, limiting factor for the development of macroinvertebrate assemblages and led to the decrease in the number of invertebrate groups sensitive to pollution. However, DOC has diverse and powerful effects on lakes ecosystem metabolism (Carpenter *et al.*, 1998) by altering both primary production and chlorophyll *a* concentration (Houle *et al.*, 1995; Carpenter *et al.*,, 1998). DOC concentration is also related to lake area, as shown by Rasmussen *et al.* (1989) for a variety of lakes in the northern United States and Canada. Allochthonous DOC can enter a system through precipitation, leaching, and decomposition (Gergel *et al.,* 1999). Wetlands and wetland soils are often the source of much DOC input to lakes and streams, even though they may occupy only a small percentage of the catchment surface (Rasmussen *et al.,* 1989; Gergel *et al.*, 1999).

Partitioning the variance

Analysing data considering the interconnection between all variables, as with forward selection model, can hide some parameters that are important. This joint effect among the variables was observed by Johnson and Goedkoop (2002), who suggested that, for example, local factors, like the input and retention of organic matter, are related to the vegetation type and topographical relief but can be hidden in conventional analyses. In that perspective, this study also pointed out the pure contribution of each environmental parameter, independently of interaction with other ones. Thus, the strongest relationship were observed with chrolophyll *a* concentration, urbanisation in catchment surface (as expressed by building density), mean slope in catchment surface and in riparian zone and TP and DOC concentrations. In other words, these variables are those having, alone, the highest influence on macroinvertebrate communities and, possibly, on lake integrity.

Phosphorus is commonly regarded as the nutrient most likely to be limiting in freshwater (Edwards *et al.*, 2000) and was part of the most important environmental variables shaping the functional structure of communities (Brodersen *et al.* 1998; Jeppesen *et al.*, 2000; Knoll *et al.*, 2003; Brauns *et al.* 2007; Heino, 2000, 2008). Sources of phosphorus enrichment are multiples, explaining why it has been confounded in previous analyse where benthic macroinvertebrate communities compositions were best explained by the interaction of lake area, dissolved organic carbon (DOC), forest and agriculture land cover in catchment surface and chlorophyll *a* concentration. Mainly, link between land-use and phosphorus enrichment have previously been establish with agriculture (D'Arcy & Carignan, 1997; Carpenter *et al.*, 1998; Cooke & Prepas, 1998), particularly with intensively managed agriculture territories (Edwards *et al.*, 2000), and with industrial and domestic waste discharges (Carpenter *et al.*, 1998; Edwards *et al.*, 2000; Brauns *et al.*, 2007).

Concerning the importance, in this study, of building density in catchment surface, it as been shown that urbanisation, even at small level, directly affect benthic communities, especially in running water (Casper, 1994; Huryn *et al.* 2002; Cuffney *et al.*, 2005). Besides being important nutrient source, urbanisation creates large impervious surface cover, erosion and habitat destruction, associated with decreased diversity and overall abundance of macroinvertebrate organisms and increased relative abundance of tolerant organisms such as chironomidae and oligochaetes (Paul & Meyer 2001).

Thus, amount and flow of drainage water is a critical parameter, has pointed out by D'Arcy & Carignan (1997), who actually found that catchment slope explained a lot of the variability of chlorophyll *a,* DOC and TP in 30 Canadian lakes. The fact that catchment and riparian mean slope are also individually important parameters leads to the assumption that those variables, in the same way as impervious surfaces and wide density of roads brought by urbanisation, might have their critical importance by amplifying the impacts of other parameter such as agriculture. This can explain why they were masked by other analyses focussing on interactions.

Conclusion

In the recognition by scientists and governments of the relevancy of catchment-scale management to ensure the integrity of aquatic ecosystems, knowledge of the strength of ecological correlations between catchments and lakes is important. For that purpose, our results showed that aquatic integrity, as successfully assessed by benthic macroinvertebrate communities, appeared to be strongly influenced by nutrient input like TP and DOC. At the catchment scale, lake area, agriculture and forest cover, have also been showed to have impact on macroinvertebrate communities, potentially by influencing water characteristics parameters and habitat heterogeneity. However, this study also demonstrates that urbanisation and slope have important masked influence on lakes, most likely by amplifying impacts of other parameters. This study suggests that managers must continue their efforts in a catchment approach, paying especially attention to those confounding factors. Also, effects of other potential confounding factors, like age and historic of lakes (Blocksom *et al.*, 2002; Dodson *et al.*, 2007) and soil composition (Cresser *et al.*, 2000), could be more detailed. Moreover, our results indicate that benthic macroinvertebrate families can be indicator of oligotrophic lake but cannot, alone, discriminate other trophic states in our study area. However, they may be useful for comparative studies along time to detect degradation in communities compositions and/or confirming water characteristics diagnostic.

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Table 1. Catchment and lake morphological characteristic, watershed land-use and water characteristics parameters for the 20 studied lakes.

Name	Al (m)	Catchment area (km^2)	Lake area (km^2)	Max. depth (m)	Catchment land use: wetland (%)	forest (%)	agriculture (%)	urban (%)	other (%)	Water characteristic parameter: TP $\mu g\ L^{-1}$	Chloro. *a* $\mu g\ L^{-1}$	Secchi m
Anguille	49	6.57	0.97	8.0	17.5	52.1	26.5	0.0	4.0	18	5.16	2.80
Bellavance	180	1.57	0.05	2.5	3.3	44.4	46.9	0.0	5.3	11	6.47	2.00
Chaud	130	12.29	0.06	3.5	1.8	60.4	34.3	0.9	2.6	13	3.73	3.00
Cote	330	21.45	1.24	15.0	8.5	91.0	0.0	0.0	0.4	5	1.56	5.70
Ferré	230	66.10	1.15	10.5	3.7	87.4	7.9	0.0	1.0	4	1.73	4.00
Gasse	52	1.54	0.11	1.0	6.9	58.0	28.3	0.0	6.8	27	6.12	1.00
Grand lac Shaw	200	19.57	0.23	5.0	4.1	71.0	16.9	1.8	6.3	24	5.65	2.75
Guimond	230	0.27	0.02	1.5	5.9	87.5	3.8	0.0	2.8	10	4.92	1.50
Linda	170	0.43	0.02	2.5	5.8	45.7	10.7	37.8	0.0	39	7.95	1.30
Malobès	43	20.59	1.71	4.0	9.3	56.8	28.0	0.0	5.7	17	5.00	1.70
Neigette	210	8.04	0.70	8.5	14.7	57.0	27.7	0.0	0.6	7	6.87	2.50
Noir	95	12.68	1.09	6.5	12.8	74.6	4.0	4.3	4.4	8	2.04	4.00
Passetout	170	1.31	0.04	6.0	2.8	44.0	48.2	0.0	4.9	14	4.79	3.10
Petit lac Ferré	170	58.97	0.48	6.0	2.2	87.6	8.3	0.0	2.0	12	4.60	2.25
Petit lac Lunette	150	1.37	0.02	3.0	2.6	93.3	1.8	0.0	2.3	10	3.85	3.00
Petit lac Macpès	73	15.19	1.25	10.0	17.2	79.2	1.6	0.0	2.0	6	2.58	3.80
Pointu	160	7.09	0.97	19.5	16.5	76.7	0.1	0.0	6.8	3	0.88	4.80
Station	37	148.64	0.57	3.0	5.9	72.9	18.4	0.4	2.4	26	10.54	1.50
Tonio-Cyr	58	1.20	0.04	4.5	4.5	86.0	0.8	0.0	8.6	11	1.05	4.60
Truite	55	2.56	0.15	5.0	6.0	77.9	7.9	0.0	8.3	23	3.65	2.20

Table 2. Variables selected for the 20 lakes included in the analysis.

Parameter	Units	Mean	Median	SE
Environmental variables				
Lake variables				
Lake area	km²	0.54	0.36	0.12
Sinuosity	-	1.74	1.59	0.10
Catchment variables				
Catchment area / lake area	-	51.24	17.53	14.86
Buildings / catchment area	nb/km²	35.71	11.79	20.08
Road / catchment area	km/km²	2.27	1.69	0.34
Forest / catchment area	%	68.91	70.46	3.66
Wetland / catchment area	%	7.42	5.87	1.09
Agriculture / catchment area	%	17.13	13.79	3.28
Mean slope in catchment surface	degree	6.39	5.60	0.67
Riparian zone variables				
Buildings / riparian zone area	nb/km²	387.95	265.27	60.78
Forest / riparian zone	%	48.76	51.93	6.12
Wetland / riparian zone	%	4.90	0.14	2.58
Agriculture / riparian zone	%	7.86	0.00	3.82
Road / riparian zone area	km/km²	2.54	1.60	0.78
Mean slope in riparian zone	degree	5.72	5.76	0.75
Sampling-site variables				
Substratum	Classified 1-4	3.22	4,00	0.11
Macrophyte	Dummy	0.58	1,00	0.05
Human disturbance	Classified 1-5	2.36	2,00	0.15
Water characteristics variables (lake scale)				
Dissolved organic carbon	mg/l	6.29	5.94	0.38
Secchi / lake depth	-	2.88	2.78	0.28
Total phosphorus	µg/l	14.40	11.50	2.03
Chlorophyll *a*	mg/m³	4.46	4.69	0.54
Dissolved oxygen	mg/ l	8.25	8.10	0.10
Water characteristics variables (sampling scale)				
Chlorophyll *a*	mg/m³	6.26	4.68	0.62
Temperature	°C	23.05	22.83	0.17
Dissolved oxygen	mg/l	8.18	7.93	0.16
pH		7.94	7.98	0.03

Table 3. List of macroinvertebrate taxa occurring in >1 of the 100 sampling sites and summary statistics.

Taxa	Total number	Mean number	Maximum number in sample	Sample present	Lake present	Mean when present	Median when present
Hydra	247	2	57	25	9	10	3
Oligochaeta	8061	81	761	99	20	77	33
Hirudinae	646	6	57	67	18	9	5
Gastropoda	353	4	62	44	16	7	3
Bivalvia	1847	18	304	69	17	20	8
Amphipoda	10668	107	1298	91	19	96	38
Copepoda	1806	18	469	67	17	21	4
Ostracoda	127	1	32	23	14	6	2
Cladocera	2195	22	408	77	20	22	9
Isopoda	153	2	136	4	1	38	8
Planaria	618	6	238	30	12	20	5
Acari	249	2	90	47	16	3	2
Tricorythidae	226	2	162	10	3	23	6
Heptageniidae	1442	14	309	60	20	19	4
Beatidae	778	8	233	71	17	9	3
Caenidae	2194	22	561	50	17	34	8
Ephemeridae	36	0	8	12	6	3	3
Ephemerellidae	13	0	3	8	5	2	1
Leptophlebiidae	336	3	39	37	13	8	4
Corduliidae	75	1	10	27	12	2	1
Aeshnidae	44	0	7	24	11	2	1
Gomphidae	21	0	7	9	7	2	1
Libellulidae	2	0	1	2	2	1	1
Coenagrionidae	389	4	86	26	11	14	3

Table 3. List of macroinvertebrate taxa occurring in >1 of the 100 sampling sites and summary statistics.

Taxa	Total number	Mean number	Maximum number in sample	Sample present	Lake present	Mean when present	Median when present
Policentropodidae	50	1	5	25	13	2	1
Limnephilidae	9	0	2	7	5	1	1
Leptoceridae	390	4	44	59	19	6	2
Phryganeidae	25	0	8	12	8	2	1
Helicopsychidae	4	0	2	3	3	1	1
Hydroptilidae (L)	73	1	41	12	7	6	3
Hydroptilidae (A)	2	0	1	2	2	1	1
Sialidae	6	0	2	5	4	1	1
Corydalidae	17	0	4	7	5	2	2
Elmidae (L)	727	7	118	28	12	24	10
Elmidae (A)	16	0	4	10	8	2	1
Psephenidae	220	2	71	19	7	12	7
Haliplidae (L)	23	0	11	8	5	3	2
Haliplidae (A)	7	0	4	3	2	2	2
Chrysomelidae	8	0	3	5	4	2	1
Gyrinidae	7	0	2	6	4	1	1
Dytiscidae	16	0	3	13	7	1	1
Chironomidae(L)	9213	92	808	98	20	82	45
Chironomidae(P)	138	1	20	36	15	3	2
Ceratopogonidae(L)	51	1	10	21	10	2	1
Ceratopogonidae(P)	4	0	3	2	2	2	2
Chaoboridae	10	0	8	3	2	3	1
Tipulidae	2	0	1	2	2	1	1
Noton	10	0	5	6	4	2	1

Table 3. List of macroinvertebrate taxa occurring in >1 of the 100 sampling sites and summary statistics.

Taxa	Total number	Mean number	Maximum number in sample	Sample present	Lake present	Mean when present	Median when present
Corixi	207	2	157	17	10	12	1
Gerridae	3	0	1	3	3	1	1
Braconidae	2	0	1	2	1	1	1
Pyralidae	5	0	1	5	5	1	1

Table 4. Contribution to inter-groups dissimilarity of macroinvertebrate taxa in comparison between lakes as classified according water characteristics variables. (G_{Oligo} = Oligotrophic lakes group; $G_{OligoMeso}$ = Oligo-mesotrophic lakes group G_{Meso} = Mesotrophic lakes group; $G_{MesoEutro}$ = Meso-eutrophic lakes group; G_{Eutro} = Eutrophic lakes group).

Trophic group and taxa	Contribution to dissimilarity (%)				
	Within-group	Pairwise			
		$G_{OligoMeso}$	G_{Meso}	$G_{MesoEutro}$	G_{Eutro}
G_{Oligo}					
Heptageniidae	26.5	22.7	22.7	24.3	22.8
Chironomidae (l)	16.3	10.0	9.6	7.9	12.4
Psephenidae	8.6	9.1	8.7	8.8	9.7
Oligochaeta	8.2	6.4	6.1	6.5	10.9
Amphipoda	1.9	9.7	14.2	21.5	6.5
$G_{OligoMeso}$					
Cladocera	11.7	-			10.1
Heptageniidae	10.4	-			7.3
Amphipoda	7.5	-			16.8
Elmidae (l)	7.4	-			5.5
Chironomidae (l)	6.8	-			7.5
Oligochaeta	6.0	-			8.55
G_{Meso}					
Amphipoda	16.5		-		21.4
Caenidae	10.6		-		7.4
Oligochaeta	8.4		-		14.9
Heptageniidae	7.9		-		5.6
Cladocera	7.1		-		7.3
Chironomidae (l)	7.9		-		6.3
$G_{MesoEutro}$				-	
Amphipoda	18.5			-	30.9
Oligochaeta	14.7			-	10.7
Chironomidae (l)	8.8			-	9.5

Table 5. Results of redundancy analysis (RDA) of macroinvertebrates data on all variables for a) each variable taken individually and b) forward-selection of variables. Only significant results (p<0.05) are shown.

Variable	**% Variance**	***F***	**p**
a) Marginal effect			
Lake scale			
Lake area	9.5	10.296	0.0010
Sinuosity	2.9	2.910	0.0030
Catchement scale			
Catchement area / lake area	2.2	2.181	0.0190
Buildings / Catchment area	3.9	3.958	0.0010
Road / Catchment area	3.8	3.898	0.0020
Forest in catchment surface	3.4	3.479	0.0010
Wetland in catchment surface	3.4	3.402	0.0340
Agriculture in catchment surface	4.4	4.486	0.0010
Mean slope in catchment surface	4.3	4.383	0.0010
Riparian zone scale			
Buildings / riparian zone	2.6	2.613	0.0040
Road / Riparian zone	5.3	5.536	0.0010
Forest in riparian zone	2.2	2.253	0.0220
Wetland in riparian zone	2.4	2.437	0.0090
Agriculture in riparian zone	2.1	2.118	0.0300
Mean slope in riparian zone	1.8	1.840	0.0430
Sampling site scale			
Substratum	3.9	3.982	0.0010
Macrophyte presence	3.9	3.962	0.0010
Human disturbance in shore	2.3	2.272	0.0250
Water characteristics at lake scale			
Secchi depth	3.9	3.985	0.0020
Dissolved organic carbon	5.9	6.143	0.0010
Chlorophyll *a*	2.8	2.810	0.0030
Total phosphorus	2.0	1.991	0.0270
Dissolved oxygen	4.8	4.969	0.0020
Water characteristics at sampling site scale			
Chlorophyll *a* at sampling site	2.2	2.153	0.019
b) Conditional effect	**% Variance**	***F***	**p**
Lake area	9.5	10.30	0.001
Dissolved organic carbon	4.1	4.62	0.001
Forest in catchment surface	3.8	4.38	0.001

Chlorophyll *a*	3.5	5.34	0.001
Agriculture in catchment surface	3.4	4.03	0.001
Agriculture in riparian zone	2.9	4.60	0.001
Forest in riparian zone	2.7	3.75	0.001
Sinuosity	2.4	2.95	0.001
Buildings / riparian zone	2.4	3.05	0.001
Substratum	2.2	2.85	0.002
Mean slope in riparian zone	2.2	2.95	0.001
Buildings / Catchment area	2.2	3.22	0.002
Mean slope in catchment surface	2.0	2.56	0.007
Road / Riparian zone	1.9	2.53	0.006
Total phosphorus	1.8	2.44	0.009
Temperature at sampling site	1.1	2.47	0.002
Secchi depht	1.1	1.83	0.039

Table 6. Summary of results of redundancy analysis (RDA) conducted to partition the variance in macroinvertebrates data explained by variables according to a) their type, b) their scale or c) each one individually. (Only significant results (p<0.05) are shown).

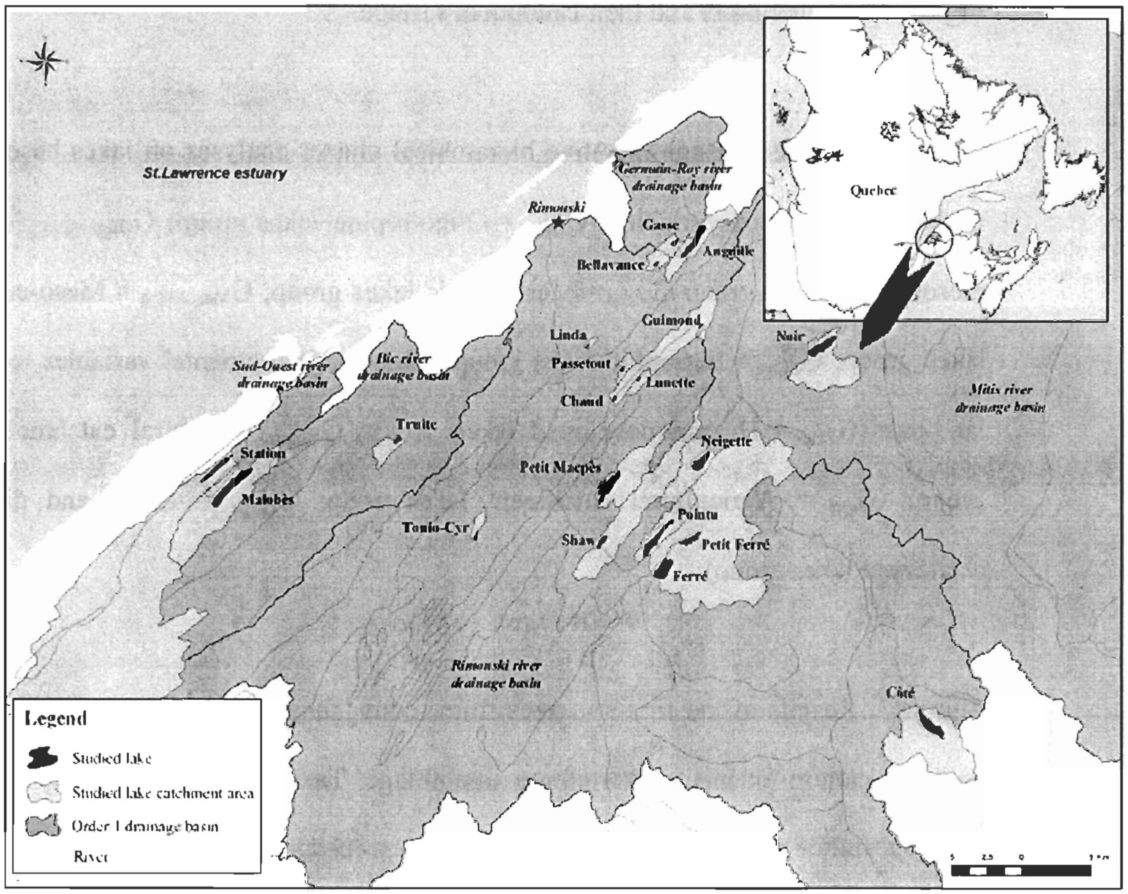
Series of RDA	Variables	Covariables	% Variance explained	*F*	p
A	All	No	49.6	4.756	0.001
	Environmental.	Water characteristics	34.1	4.631	0.001
	Water characteristics	Environmental	13.5	4.397	0.001
B	Water characteristics (lake scale)	All others	12.3	4.994	0.001
	Catchment	All others	12.2	4.953	0.001
	Riparian zone	All others	10.5	4.284	0.001
	Lake	All others	5.2	4.27	0.001
	Sample site	All others	2.7	4.363	0.001
	Water characteristics (sampling site scale)	All others	1.2	2.021	0.028
C	Chlorophyll *a*	All others	4.9	7.996	0.001
	Buildings / Catchment area	All others	4.9	7.982	0.001
	Mean slope in catchment surface	All others	4.9	7.969	0.001
	Total phosphorus	All others	4.2	6.812	0.001
	Mean slope in riparian zone	All others	3.1	5.128	0.001
	Dissolved organic carbon	All others	3.0	4.892	0.001
	Forest in catchment surface	All others	3.0	4.88	0.001
	Sinuosity	All others	2.9	4.782	0.001
	Substratum at sampling site	All others	2.7	4.363	0.001
	Agriculture in riparian zone	All others	2.4	3.964	0.001
	Lake area	All others	2.3	3.757	0.001
	Agriculture in catchment surface	All others	2.2	3.662	0.001
	Forest in riparian zone	All others	2.0	3.242	0.001
	Buildings / riparian zone	All others	1.7	2.83	0.005
	Road in riparian zone	All others	1.5	2.364	0.015
	Temperature at sampling site	All others	1.2	2.021	0.028
	Secchi depth	All others	1.1	1.826	0.028

Figure 1. Studied lakes and their catchment surface.

Figure 2. Results of agglomerative hierarchical cluster analyses on lakes based on a) water characteristics variables (G_{Oligo} = Oligotrophic lakes group; $G_{OligoMeso}$ = Oligo-mesotrophic lakes group G_{Meso} = Mesotrophic lakes group; $G_{MesoEutro}$ = Meso-eutrophic lakes group; G_{Eutro} = Eutrophic lakes group) and b) environmental variables related to land-use (G_{Hdev}= Human developed lakes group; $G_{Natural}$ = Natural catchment lakes group; G_{Agri} = Agricultural catchment lakes group; G_{Large} = Large and disturbed catchment lakes group).

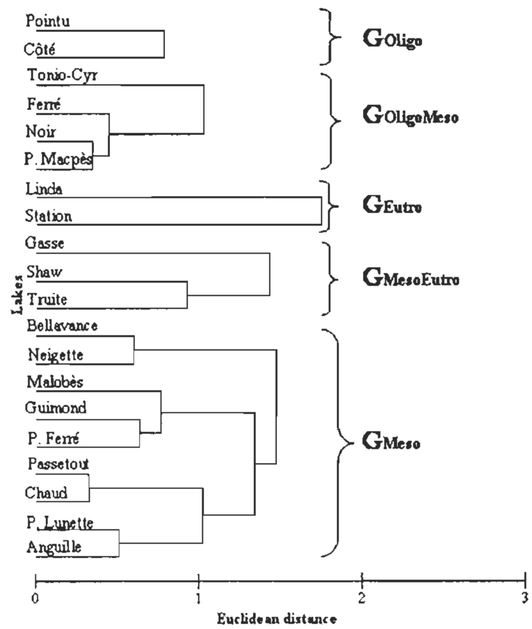
Figure 3. Results of the first two axes from redundancy analysis (RDA) of catchment land-use pattern on macroinvertebrate assemblage. Taxa are those sorted by SIMPER analysis and/or by cumulative fit per species procedure (underscore=taxa sorted by both; in brackets= % explained by the taxa) (G_{Hdev}= Human developed lakes group; $G_{Natural}$ = Natural catchment lakes group; G_{Agri} = Agricultural catchment lakes group; G_{Large} = Large and disturbed catchment lakes group).

Figure 4. First two axes resulting from redundancy analysis (RDA) of the five variables best correlated with macroinvertebrate assemblage as chosen by forward selection procedure. Taxa are those sorted by simper analysis and/or by cumulative fit per species procedure (underscore=taxa sorted by both; in brackets= % explained by the taxa).

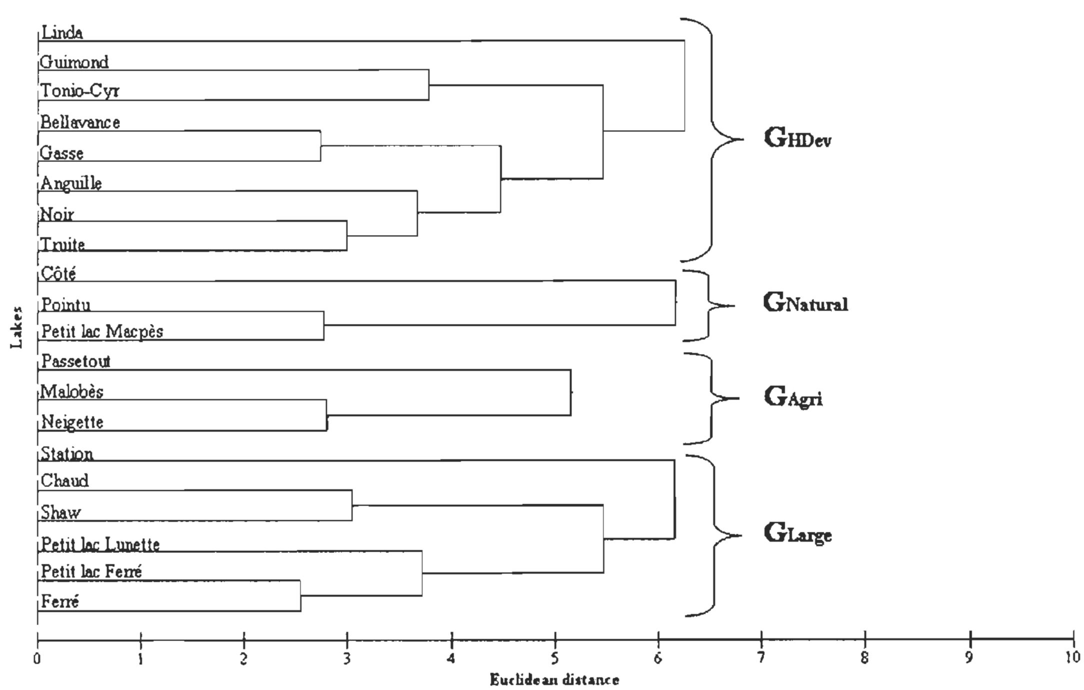


Normand *et al.*, **Fig.1**

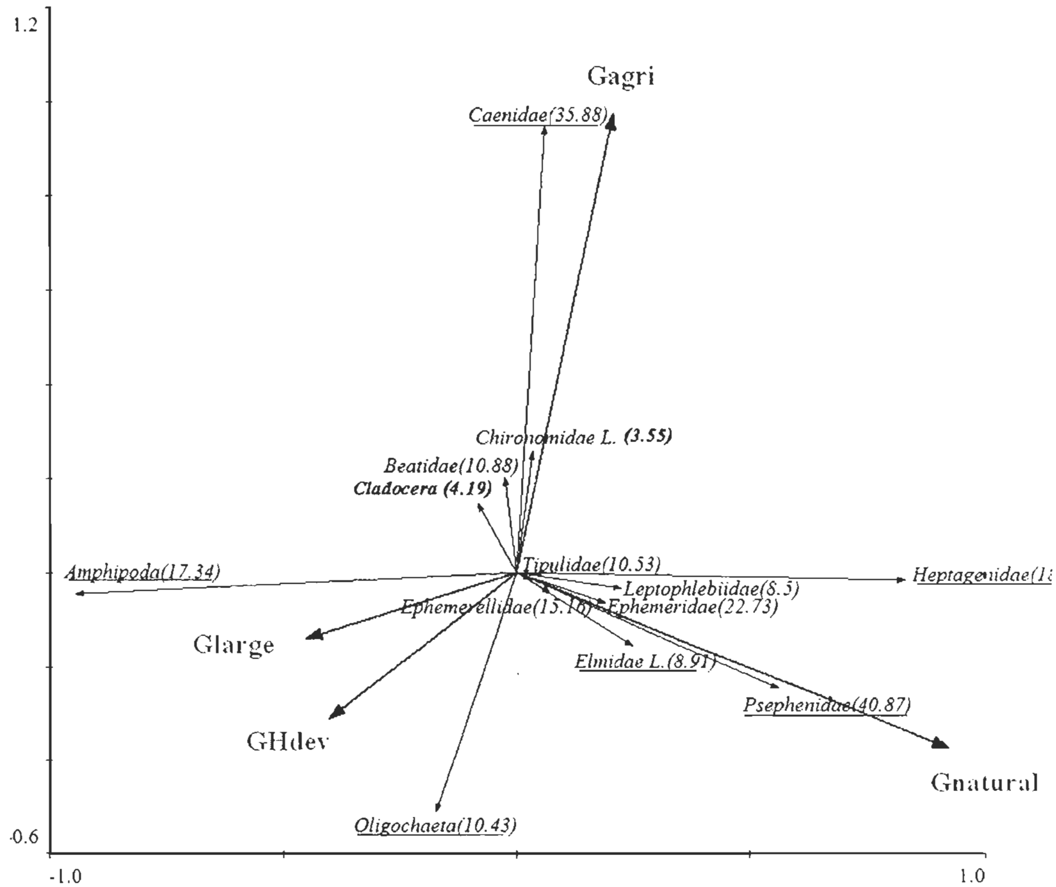
a)



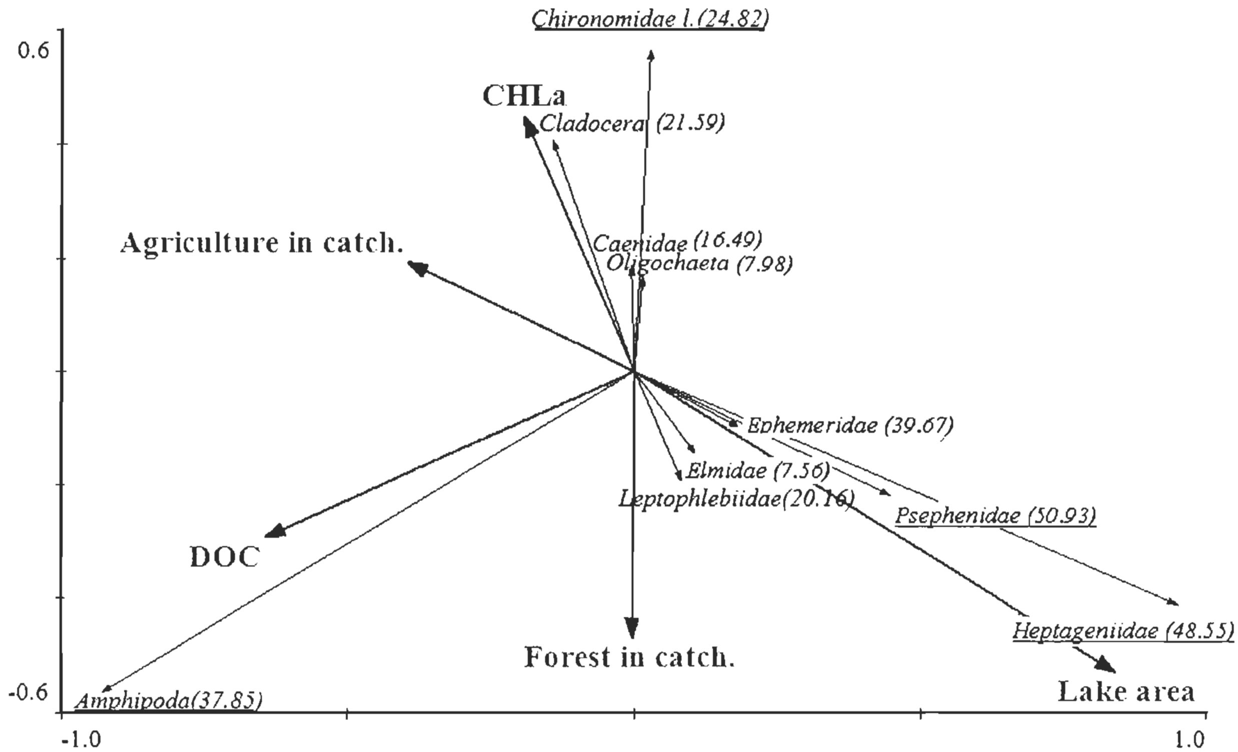
b)



Normand *et al.*, **Figure 2**



Normand *et al.*, **Figure 3**.



Normand *et al.*, **Figure 4.**

CHAPITRE 3

CONCLUSION DU MÉMOIRE

Il est généralement reconnu qu'une importante relation existe entre les perturbations anthropiques du paysage et l'intégrité biotique des écosystèmes aquatiques (e.g. Burt *et al.*, 1991; Casper, 1994; Allan et Johnson, 1997; Cooke et Prepas, 1998; Johnson, 1998; Johnson *et al.*, 2004; Cuffney *et al.*, 2005). Cette relation peut s'expliquer par un phénomène dit d'entonnoir caractéristique d'un lac par rapport à son bassin versant. En effet, un lac reçoit et concentre toutes les sources d'eaux telles que le ruissellement des terres, des routes, des fossés de drainage ou en provenance des cours d'eau. Une meilleure compréhension des liens écologiques entre les plans d'eau et leur bassin versant est donc importante dans la compréhension de l'influence des activités anthropiques terrestres sur les écosystèmes aquatiques.

Après plusieurs années d'études reliant les activités humaines avec la physico-chimie de l'eau et les processus d'eutrophisation des lacs, les recherchent tendent maintenant à démontrer que les changements d'états trophiques entraînent également des changements dans la structure des écosystèmes (e.g. Jeppesen *et al.*, 2000; Brauns *et al.*, 2007). Ces recherches utilisent fréquemment les communautés de macro-invertébrés benthiques comme indicateurs biologiques de ces changements. Dans cette optique, la présente étude avait pour objectif général de caractériser les liens entre les communautés de macro-invertébrés benthiques et les variables environnementales à l'échelle géographique du paysage.

Principaux résultats de l'étude

Des différences claires entre les communautés de macro-invertébrés des lacs oligotrophes et eutrophes ont d'abord été montrées. Si l'on considère que les paramètres physico-chimiques des lacs sont influencés par le milieu terrestre, ce résultat a permis de pousser plus loin les analyses et de confirmer aussi une relation significative avec plusieurs attributs du paysage. De plus, il a été montré que les paramètres environnementaux seuls, après le retrait de l'influence des paramètres de qualité d'eau, expliquaient plus du tiers de la variabilité totale entre les communautés.

En approfondissant l'importance de chaque échelle spatiale individuellement (bassin versant, bande riveraine, lac, station d'échantillonnage), les communautés de macro-invertébrés ont montré une relation plus forte avec les variables environnementales à l'échelle du bassin versant comparativement aux autres échelles géographiques. Les variables associées à la bande riveraine et au lac lui-même révélaient ainsi une importance inférieure, tandis que celles mesurées à l'échelle de la station d'échantillonnage, i.e. l'habitat lui-même, s'avéraient de peu d'importance dans l'explication des différences interlacs entre les communautés. La présente étude suggère que les variables associées au milieu terrestre ont des effets autant sur des traits d'habitat que sur les macro-invertébrés eux-mêmes. De plus, l'importance d'une bande riveraine naturelle pour l'intégrité des lacs pourrait dépendre en grande partie de la pression provenant des activités à l'échelle du bassin versant. En fait, en supposant que différents types d'utilisation du sol entraînent différents types et intensités d'influences, l'importance d'une bande riveraine naturelle comme dernier bouclier devraient alors varier, selon le type et le volume d'activités humaines sur le territoire en amont.

En assumant que l'influence de l'utilisation du sol sur l'intégrité de lacs varient de différentes façons selon le type d'activités et leurs interactions avec les paramètres naturels, de simples patrons généraux d'utilisation du sol pouvaient expliquer une certaine portion de la variabilité inter lacs entre les communautés. Ainsi, la présence de taxons peu tolérants tels que certains éphéméroptères (heptageniida, leptophlebiidae, ephemeridae and ephemerellidae), coléoptères (elmidae) et plécoptères (psephenidae) s'est avérée être fortement associée aux lacs montrant un bassin versant naturel; lacs préalablement catégorisés comme oligotrophes. De plus, les lacs ayant de grandes superficies de bassin versant présentaient une association semblable avec les communautés de macro-invertébrés que les lacs caractérisés par un bassin versant plus petit, mais un développement humain plus intense. Ce phénomène peut s'expliquer par le fait que l'urbanisation et les grands bassins versants pourraient avoir sensiblement la même influence sur l'écoulement des eaux vers le lac. Ainsi, alors que l'urbanisation créer une multitude de surfaces imperméables (Paul et Meyer, 2001) et accélère le drainage de l'eau, les grands bassins versants et les systèmes hydrologiques qui leurs sont associés drainent un territoire plus grand, apportant donc une plus grande quantité d'eau.

Cependant, sachant que les lacs sont des systèmes écologiques complexes dans lesquels les paramètres biotiques et abiotiques sont en étroite relation, il est finalement pertinent de se demander quels paramètres environnementaux expliquent davantage les variations entre communautés et, donc, les différences en termes d'intégrité biotique. Ainsi, le modèle expliquant le mieux cette variance s'est avéré être celui comportant la superficie du lac, les concentrations en carbone organique dissous (COD) et en chlorophylle *a* ainsi que les proportions forestière et agricole du bassin versant. La forte relation avec l'aire du lac peut s'expliquer par l'hétérogénéité d'habitats associée à de plus grands lacs (Johnson & Goedkoop, 2002; Brauns *et al.*, 2007; Heino, 2000, 2008), à l'action des vagues (Weatherhead *et al.*, 1998; Johnson & Goedkoop, 2002; Johnson *et al.*, 2004; Brauns *et al.*, 2007) ainsi qu'à la prédation (Bendell & McNicol, 1987; Jackson, 1993; Heino, 2000; Leppä *et al.*, 2003).

L'importance de la proportion de la forêt dans le bassin versant peut aussi s'expliquer par l'hétérogénéité des habitats offerts. En effet, les zones forestières fournissent, de par leur canopée, leurs débris et leurs racines, un ombrage ainsi qu'une bonne diversité d'habitats et de sources alimentaires (Heino, 2000; Brauns *et al.*, 2007; Kreutzweiser *et al.*, 2008). Enfin, il est connu que les zones forestières entraînent des effets positifs sur l'eau et la qualité des écosystèmes aquatiques en limitant le drainage et en filtrant les nutriments (Schauman, 2000). L'importance, dans notre modèle, de l'utilisation des terres du bassin versant par les activités agricoles peut aussi s'expliquer par des effets opposés à ceux des zones forestières. En effet, le déboisement associé à l'agriculture implique une augmentation de la quantité et la vitesse du ruissellement ainsi que la sédimentation et la migration des nutriments entraînant, entre autres, une augmentation de la concentration en chlorophylle *a*.

Ce rapport entre l'agriculture, le déboisement et l'apport de nutriment est un bon exemple des interrelations entre variables indépendantes, caractéristiques des modèles empiriques associés aux lacs. Cet effet confondant, préalablement observé par Johnson & Goedkoop (2002), implique donc qu'une proportion non négligeable de la variance expliquée par certaines variables se trouve masquée par ces interrelations entre facteurs locaux et régionaux. Dans cette perspective, une autre méthode a donc été utilisée afin de déterminer la contribution propre de chaque paramètre environnemental, indépendamment des interactions avec les autres. Cette approche différente a donc permis de mettre de l'avant l'effet d'autres paramètres, auparavant confondus. Ainsi, de nouvelles et fortes corrélations sont apparues entre les communautés de macro-invertébrés benthiques et la concentration en phosphore, l'urbanisation du bassin versant (tel qu'exprimé par la densité de bâtiments) ainsi que les pentes moyennes du bassin versant et de la bande riveraine. Ceci, en plus des fortes relations préalablement observées avec les concentrations en chrolophylle *a* et en COD.

L'émergence de ces variables s'explique d'abord par le fait que le phosphore est généralement considéré comme le nutriment le plus limitant en eau douce (Edwards *et al.*, 2000) et faisant partie des variables environnementales les plus importantes dans la structure fonctionnelle des communautés (Brodersen *et al.*, 1998; Jeppesen *et al.*, 2000; Knoll *et al.*, 2003; Brauns *et al.* 2007; Heino, 2000, 2008). Cependant, les sources d'enrichissement en phosphore sont multiples, expliquant les différences de résultats dans nos analyses précédentes. Les liens entre l'utilisation du sol et les apports de phosphore ont, entre autres, précédemment été établis avec les activités agricoles (D'Arcy & Carignan, 1997; Carpenter *et al.*, 1998; Cooke & Prepas, 1998), particulièrement avec l'agriculture intensive (Edwards *et al.*, 2000), ainsi qu'avec les eaux usées industrielles et urbaines (Carpenter *et al.*, 1998; Edwards *et al.*, 2000; Brauns *et al.*, 2007). Aussi, et tel que spécifié précédemment, en plus d'être une source importante de nutriments, l'urbanisation entraîne l'imperméabilisation des surfaces et l'accélération du drainage.

L'ajout des pentes du bassin versant et de la bande riveraine comme variables à considérer dans la présente étude suppose que ces paramètres tirent leur importance en amplifiant l'influence d'autres paramètres tels que l'agriculture, de la même façon que les surfaces imperméables et la densité de routes apportées par l'urbanisation. La quantité et la vitesse d'écoulement de l'eau de drainage s'avèrent donc être des paramètres critiques pour l'intégrité des plans d'eau, bien que leur influence soit confondue dans les modèles standards, focalisant sur les interactions entre variables.

Limitation de l'étude

La majorité des études portant sur les liens entre les milieux terrestres et aquatiques portent sur des paramètres environnementaux particuliers, comme l'exploitation forestière ou les activités de loisirs et/ou s'attardent principalement à une échelle et rarement à plusieurs plans d'eau présentant un ensemble de gradients d'état trophique. Les résultats varient donc considérablement entre les projets de recherche, rendant les comparaisons difficiles. En regard des objectifs fixés pour cette étude, le choix de traiter un plus grand nombre de lacs, présentant des gradients de patron d'utilisation du sol et de stades trophiques, a fait en sorte de limiter le temps et les ressources alloués au raffinement des paramètres de l'étude. Comme dans toute étude tentant d'expliquer des phénomènes écologiques, les variables possibles n'ont pour limites que celles des questions posées et des approches statistiques choisies. Ainsi, par exemple, la division des types d'utilisation du sol aurait pu être plus fine, en considérant les types de couvert forestier, les types d'agriculture ou encore les types de route (principales, secondaires, etc.). Les paramètres de caractéristiques de l'eau auraient pu être approfondis, en ce qui a trait au nombre de paramètres et d'échantillons analysés. D'autres facteurs naturels tels que la composition des sols ainsi que le régime des eaux souterraines auraient pu, si ils avaient été disponibles, nous apporter d'autres sources d'éclaircissement. Enfin, une attention aurait pu être apportée à d'autres indices d'activité humaine tels que la pression reliée à l'utilisation d'embarcations motorisées ou les systèmes d'évacuation des eaux usées. La proportion de variations expliquée par les paramètres choisies a, par contre, été suffisante pour obtenir un portrait de l'influence de l'utilisation du sol sur l'intégrité des plans d'eau de la région étudiée, telle que démontrée par l'étude des communautés de macro-invertébrés benthiques.

De plus, bien qu'une identification taxonomique des organismes à l'espèce ou au genre soit toujours souhaitable, l'identification à la famille a ici été convenable pour bien discerner les liens entre les paramètres d'utilisation du sol et les communautés de macro-invertébrés benthiques. Ce niveau taxonomique est en effet suffisamment fin pour discriminer les types d'organismes et de communautés sensibles aux changements de stade trophique des lacs et, plus spécifiquement, aux paramètres environnementaux liés à ces changements. L'identification à la famille peut donc s'avérer utile pour des études comparatives sur une courte échelle de temps, afin de détecter une dégradation ou une amélioration des conditions biologiques. Une éventuelle identification plus fine pourrait permettre l'élaboration d'un indice d'intégrité biotique adapté aux lacs de la région.

Contribution principale

Dans une optique de gestion du territoire, les résultats de cette étude suggèrent, d'abord, que le développement et l'artificialisation du pourtour des lacs devraient se faire en harmonie avec celui des bassins versants en entier. En effet, les conclusions associées à la zone étudiée montrent que l'attention des gestionnaires devrait particulièrement être portée sur les types d'utilisation du sol entraînant le déboisement et l'imperméabilisation de grandes surfaces ainsi qu'un enrichissement en nutriments. Une grande proportion de ces types d'usage dans un bassin versant devrait donc se voir systématiquement associée à un renforcement de l'importance d'une bande riveraine naturelle autour des lacs, comme dernier bouclier assurant la rétention des sédiments et la filtration des nutriments. Une attention précise devrait aussi être portée sur les facteurs naturels agissant à titre d'amplificateurs, tels que la taille du bassin versant et la pente du sol. À la lumière des résultats obtenus, il est permis de penser que, par exemple, un lac donc le bassin versant est de petite taille et présentant une faible pente pourrait être en mesure de supporter un développement urbain sur son pourtour plus intense qu'un lac de même taille dont le bassin versant présenterait un certain déboisement et une forte pente.

Cette étude révèle donc l'importance que peuvent avoir les paramètres naturels du milieu comme source d'interactions et d'amplification de l'influence des différents usages du territoire. À ce niveau, notre compréhension des effets de ces facteurs confondants devraient donc être approfondies. De plus, les connaissances acquises à partir des observations sur le terrain et des discussions avec les riverains suggèrent que la prise en considération de l'historique des lacs pourrait apporter une meilleure compréhension encore de ces milieux aquatiques et de leur façon de réagir aux différentes activités humaines. En effet, les lacs, de part le grand temps de résidence de l'eau, accumulent sur une longue période de temps les influences des activités passées. Ce paramètre est cependant très difficile à considérer dans le cadre du type d'étude effectuée ici. Il serait donc pertinent de développer une façon de faire et d'analyser les données qui permettraient d'inclure, dans l'étude des lacs, les divers éléments ayant marqué leur histoire.

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