UNIVERSITÉ DU QUÉBEC

MÉMOIRE

PRÉSENTÉ À

L'UNIVERSITÉ DU QUÉBEC À CHICOUTIMI

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN RESSOURCES RENOUVELABLES

PAR

ANNICK DROUIN

COMPARAISON DES COMMUNAUTÉS D'INVERTÉBRÉS ENTRE DES LACS AVEC ET SANS OMBLE DE FONTAINE (*SALVELINUS FONTINALIS*)

SEPTEMBRE 2006

Bibliothèque
Paul-Émile-Boulet

UQAC
Université du Québec
à Chicoutimi

Mise en garde/Advice

Afin de rendre accessible au plus grand nombre le résultat des travaux de recherche menés par ses étudiants gradués et dans l'esprit des règles qui régissent le dépôt et la diffusion des mémoires et thèses produits dans cette Institution, **l'Université du Québec à Chicoutimi (UQAC)** est fière de rendre accessible une version complète et gratuite de cette œuvre.

L'auteur conserve néanmoins la propriété du droit d'auteur qui protège ce mémoire ou cette thèse. Ni le mémoire ou la thèse ni des extraits substantiels de ceux-ci ne peuvent être imprimés ou autrement reproduits sans son autorisation.

Motivated by a desire to make the results of its graduate students' research accessible to all, and in accordance with the rules governing the acceptation and diffusion of dissertations and theses in this Institution, the **Université du Québec à Chicoutimi (UQAC)** is proud to make a complete version of this work available at no cost to the reader.

The author retains ownership of the copyright of this dissertation or thesis. Neither the dissertation or thesis, nor substantial extracts from it, may be printed or otherwise reproduced without the author's permission.

RÉSUMÉ

Suite à la dernière glaciation, certains lacs en tête de bassins versants de la région du Saguenay n'ont naturellement jamais été colonisés par les poissons. Les conditions physico-chimiques de ces lacs sont favorables à la survie des poissons et plusieurs d'entre eux ont déjà été ensemencés avec succès au profit de la pêche sportive. Toutefois, l'influence de cette activité sur l'intégrité biotique et la diversité biologique demeure inconnue. L'absence de poisson au sommet de la chaîne trophique peut influencer l'abondance des organismes, mais aussi la diversité et les assemblages d'espèces. De plus, l'importance des lacs sans poissons au sein de l'écosystème boréal est encore inconnue. Par exemple, les lacs sans poissons pourraient être un élément important impliqué dans la conservation de la population de l'est du Garrot d'Islande (*Bucephala islandica*) qui a reçu le statut d'espèce préoccupante. Il est possible qu'il y ait compétition entre cet oiseau et le poisson pour les ressources alimentaires.

Notre objectif était de comparer la structure des communautés d'invertébrés entre les lacs avec et sans poissons. Les organismes zooplanctoniques, nectoniques et benthiques ont été échantillonnés dans cinq lacs sans poissons et cinq lacs avec des populations monospécifiques d'omble de fontaine (*Salvelinus fontinalis*). Les données de la composition en espèces ont été échantillonnés à quatre reprises entre juin et septembre 2003 dans la région du Saguenay. Les données ont été analysées selon une approche univariée (abondance, richesse, indice de diversité de Shannon, équitabilité) et multivariée (PERMANOVA, nMDS). Les lacs sans poissons avaient une plus grande abondance d'organismes zooplanctoniques que les lacs avec poissons. Les assemblages d'espèces d'invertébrés chez les trois communautés étudiées étaient significativement différents entre les lacs avec poissons et les lacs sans poissons. Les résultats observés entre les deux groupes de lacs étaient généralement les mêmes à chacune des périodes d'échantillonnage. L'approche multivariée s'est avérée plus sensible que les indices de diversité communément utilisés pour illustrer la différence des communautés entre les deux types de lacs.

REMERCIEMENTS

Si derrière chaque grand homme, il y a une femme, derrière chaque grande (?!) femme, il y a deux hommes! J'aimerais donc remercier mes directeurs Pascal Sirois et Philippe Archambault. D'abord, pour m'avoir témoigné leur confiance en me proposant ce projet. Ensuite, pour m'avoir fait don de leurs connaissances et de leur amour du métier. Je n'aurais sincèrement pas pu rêver d'un meilleur encadrement. Mon ambition de continuer ma carrière en recherche ne leur est aucunement étrangère.

J'aimerais remercier Isabelle Poirier, à qui ce projet appartient autant qu'à moi. Elle a fait en sorte de rendre possible la tâche incommensurable de l'identification. La réalisation de cette maîtrise est directement reliée à son talent en taxonomie. Merci aussi à ceux qui m'ont aidée lors de l'échantillonnage et l'analyse des échantillons : Vicky Bouchard, François Villeneuve et David Cleary. Merci à Anne-Lise Fortin, pour m'avoir divulgué de précieux conseils, notamment sur l'art du sushi et la course à pied. Merci à tous les gens qui sont passés au laboratoire d'écologie aquatique envers lequel j'ai développé un fort sentiment d'appartenance. Parmi eux, j'aimerais spécialement remercier Véronique Leclerc, Marie-France Brisson et Isabelle Tremblay-Rivard qui sont devenues plus que des collègues pour moi.

Je tiens également à remercier Lysandre Landry, Guillaume De Lafontaine et Suzy Tremblay pour les innombrables discussions sur la Science, surtout celles qui se sont finies

tard le soir. Un merci tout particulier à Matthieu Huot, dont l'amour et le soutien m'ont servi plus d'une fois. Merci à Ginette, Marie-Claude, François et Isabelle Drouin, qui n'ont sans doute pas toujours compris ce qui me motive à demeurer une éternelle étudiante, mais qui n'ont jamais tenté de m'en dissuader et pour cela je leur suis reconnaissante. Finalement, c'est en tant que récipiendaire de la bourse Habitat Faunique 2004 que j'aimerais remercier la Fondation de la Faune du Québec pour son support financier.

TABLE DES MATIÈRES

LISTE DES TABLEAUX

LISTE DES FIGURES

LISTES DES ANNEXES

INTRODUCTION GÉNÉRALE

En plus d'avoir grandement façonné le relief de la région du Saguenay, la dernière glaciation a également influencé la distribution géographique des poissons dans les bassins versants. Ainsi, sur la rive nord du fleuve Saint-Laurent, au nord du fjord du Saguenay, se retrouvent des lacs situés en tête de bassin versant contenant uniquement des populations d'omble de fontaine (*Salvelinus fontinalis*) et d'autres sans poissons (Power *et al.* 1973). Ces lacs sans poissons n'ont naturellement jamais été colonisés en raison de la présence de seuils infranchissables marquant la limite du Plateau Laurentien (Power *et al.* 1973). L'absence de poissons est donc reliée à l'isolement géographique et non à des paramètres physico-chimiques, tel le pH ou l'anoxie hivernale, ne permettant pas le recrutement de populations de poissons. D'ailleurs, plusieurs de ces lacs sans poissons ont déjà été ensemencés avec succès pour le profit de la pêche sportive (e.g. Godbout et Peters 1988, Lachance et Magnan 1990, Kelso et Shaw 1995). L'ensemencement de lacs sans poissons a également été utilisé comme mesure compensatoire pour pallier à la perte d'habitat du poisson engendrée par la construction d'un barrage électrique (Hydro-Québec 2000, 2003). Afin de protéger la capacité de production des ressources halieutiques au Canada, la politique fédérale de gestion de l'habitat du poisson est dotée du principe directeur de ne pas enregistrer de bilan avec une perte nette d'habitat du poisson (Ministère des Pêches et des Océans 1986). Plusieurs options sont privilégiées pour protéger l'habitat du poisson des effets négatifs des interventions humaines et respecter le principe d'aucune perte et il est important de mentionner que l'ensemencement de compensation est considéré comme une mesure de dernier recours et n'est aucunement priorisée par la politique de gestion de l'habitat du poisson (Ministère des Pêches et des Océans 1986). Toutefois, que ce soit à des fins récréatives ou de compensation, l'ensemencement de lacs sans poissons se veut une introduction volontaire d'une espèce exotique dans un milieu. L'omble de fontaine est une espèce très convoitée pour la pêche sportive et son ensemencement est aussi une activité très répandue. Bien qu'il s'agisse d'une espèce de poisson indigène sur le territoire québécois, son introduction dans les lacs sans poissons peut avoir des répercussions sur la diversité biologique et l'intégrité biotique.

De plus, certaines évidences amènent à se questionner sur le rôle et l'importance de ces lacs au sein de l'écosystème. Dans la région à l'étude, les lacs sans poissons pourraient être impliqués dans la conservation du Garrot d'Islande (*Bucephala islandica*), un canard dont la population de l'est du Canada a reçu le statut de préoccupante en novembre 2000 (COSEWIC 2003). La sélection du lieu de reproduction par le Garrot serait grandement influencée par l'abondance d'insectes aquatiques, principale source de nourriture des adultes et des juvéniles lors de cette période (Eriksson 1978, 1983, Einarsson 1987). Une corrélation négative entre l'occupation des lacs par cette espèce et la présence de poissons indique qu'il pourrait y avoir compétition entre l'oiseau et le poisson qui utilisent les mêmes ressources alimentaires (Eriksson 1978, 1983, Einarsson 1987, Robert *et al.* 2000). Aussi, plusieurs organismes composant la faune dulcicole ont des cycles de vie complexes comprenant des stades larvaires aquatiques et des stades adultes terrestres. Une étude récente a démontré que l'effet de la prédation par le poisson sur les larves de libellules

(Odonata : Anisoptera) peut avoir une incidence positive sur la pollinisation des plantes riveraines (Knight *et al.* 2005). En s'alimentant des larves de libellules, le poisson réduit le nombre d'adultes émergeants qui sont des prédateurs d'insectes pollinisateurs (Knight *et al.* 2005). Ainsi, les effets de l'ensemencement de lacs sans poissons pourraient dépasser les limites aquatiques.

La prédation est reconnue comme un facteur pouvant structurer le fonctionnement des écosystèmes lentiques en agissant comme une force descendante (*top-down control*) sur les niveaux trophiques inférieurs (Carpenter *et al.* 1985). Dépendamment du prédateur au sommet de la chaîne trophique, les effets directs et indirects sur les populations de proie peuvent se répercuter jusqu'au niveau de la production primaire (Carpenter *et al.* 1985). Autant les prédateurs vertébrés qu'invertébrés ont la capacité d'influencer l'abondance et la composition spécifique de leur proie (e.g. Brooks et Dodson 1965, Pope et Carter 1975, MacKay *et al.* 1990, McPeek 1990). Toutefois, ces deux classes de prédateurs structurent les communautés de façon distincte car elles possèdent des caractéristiques d'alimentation qui sont qualitativement différentes (Wellborn *et al.* 1996). Par exemple, les poissons peuvent s'alimenter de proies de plus grande taille que les invertébrés pour qui la taille des proies est critique à leur capture et à leur ingestion (Zaret 1980, Pope *et al.* 1989, Wellborn *et al.* 1996). Plusieurs études ont d'ailleurs renforcé l'hypothèse initiée par les travaux de Hrbacek (1962) et de Brooks et Dodson (1965), voulant que la prédation sélective des poissons sur les individus de plus grande taille influence la composition spécifique et la taille des proies zooplanctoniques. D'après ce modèle de prédation sélective, la taille moyenne des organismes retrouvés dans les lacs avec poissons serait inférieure et les espèces de plus petite taille devraient dominer la communauté. À l'inverse, les espèces et les individus de plus grande taille caractériseraient la communauté zooplanctonique des lacs sans poissons. D'autres mécanismes tels la détection des proies, le mode de chasse et la vitesse de poursuite peuvent contribuer à la dissimilarité entre le mode d'action des prédateurs vertébrés et invertébrés (Wellborn *et al.* 1996) et subséquemment à la dissimilarité de leurs effets sur les communautés de proies. De plus, les attributs morphologiques et comportementaux ainsi que les cycles vitaux des proies les rendent plus vulnérables à un type de prédateur qu'à un autre (Wellborn *et al.* 1996). Les travaux de McPeek (1990, 1998) ont démontré que la composition spécifique de certaines espèces de demoiselles (Odonata : Zygoptera) dépend du principal prédateur présent dans la communauté dans laquelle elles évoluent. Certaines espèces sont plus adaptées à coexister avec la prédation du poisson et d'autres à celle des libellules qui deviennent leur principal prédateur dans les lacs sans poissons. Ainsi, la structure trophique des lacs sans poissons, au même titre que celle des lacs avec poissons, pourrait favoriser certaines espèces en leur fournissant un habitat plus favorable à leurs caractéristiques morphologiques ou comportementales.

L'omble de fontaine vivant en allopatrie est reconnue pour s'alimenter principalement en zone littorale, mais dépendamment des saisons, du cycle de vie et des populations, se nourrit également en zone pélagique des plus gros organismes zooplanctoniques (Magnan 1988; Tremblay & Magnan 1991; Lacasse et Magnan 1992, Bourke *et al.* 1999). Au sein d'une même population, certains individus peuvent se nourrir presque exclusivement de proies benthiques et d'autres de proies zooplanctoniques (Bourke *et al.* 1999). La proportion entre les deux types de spécialistes serait dépendante de la richesse spécifique retrouvée dans les communautés de poissons. Chez les populations monospécifiques d'omble de fontaine, le nombre de spécialistes benthivores étaient plus élevés que chez les populations vivants en sympatrie avec le meunier noir (*Castostomus commersoni*) et le mulet à cornes (*Semotilus atromaculatus*) (Bourke *et al.* 1999). En réponse à la plus forte compétition pour les organismes benthiques, les ombles utiliseraient davantage la niche pélagique et s'alimenterait donc principalement d'organismes zooplanctoniques (Bourke *et al.* 1999). Toutefois selon une étude récente, il a été démontré que les ombles provenant de populations monospécifiques sélectionnent activement certaines proies zooplanctoniques telles le cladocère *Leptodora kindtii* et les larves de diptère du genre *Chaoborus* (Tremblay-Rivard *et al.*, Laboratoire d'écologie aquatique UQAC, données non-plubliées). De plus, la composition des contenus stomacaux des poissons étudiés suggèrent une alimentation plus généralistes (Tremblay-Rivard *et al.*, Laboratoire d'écologie aquatique UQAC, données non-plubliées).

La présente étude a pour but de caractériser les communautés d'invertébrés des lacs avec et sans poissons situés en forêt boréale dans la région du Saguenay. Les objectifs visés étaient 1) de comparer l'abondance, les indices de diversité et les assemblages d'espèces composant le zooplancton en zone limnétique ainsi que le necton et le zoobenthos en zone littorale entre des lacs avec poissons et sans poissons, et 2) d'établir ces comparaisons à plusieurs moments de la période libre de glace. Les hypothèses sous-jacentes à ces objectifs étaient 1) que les lacs sans poissons auraient une plus grande abondance et diversité d'invertébrés et que les assemblages d'espèces devraient être différents entre les deux types de lac, et 2) que les deux types de lac ne présentent pas les mêmes patrons de variations sur une échelle temporelle.

Ce mémoire de maîtrise est présenté en deux chapitres rédigés en anglais sous forme d'article scientifique. Le premier chapitre relate des objectifs mentionnés précédemment en se rapportant aux communautés zooplanctoniques et le second chapitre aux communautés nectoniques et benthiques.

CHAPITRE I

DISCRIMINATING ZOOPLANKTON COMMUNITY STRUCTURE BETWEEN LAKES WITH A SINGLE FISH POPULATION (BROOK TROUT, *SALVELINUS FONTINALIS*) AND FISHLESS LAKES

1.1 Introduction

The absence of fish in lakes may be related to unsuitable physical conditions, such as winterkill in shallow lakes or acidity, but some topographic features may also be involved. For instance, the lack of fish in some headwater lakes of the Canadian Boreal Shield in the province of Quebec is the result of natural barriers and escarpments that inhibited the post-glacial colonisation by fish (Power *et al.* 1973). Since recruitment conditions are not related to the absence of fish, many of these naturally fishless lakes have been stocked for recreational purposes with brook trout *Salvelinus fontinalis* Mitchill, a dominant species in the area (e.g., Godbout and Peters 1988, Lachance and Magnan 1990, Kelso and Shaw 1995, Hydro-Québec 2000, 2003).

A growing body of evidence suggests that the introduction of nonnative trout in lakes and streams can have effects at many ecological levels, from the individual to the ecosystem (Simon and Townsend 2003, Dunham *et al.* 2004). Furthermore, the results of recent studies have supported a linkage between aquatic and terrestrial food webs (Murakami and Nakano 2002, Knight *et al.* 2005). These studies revealed that the consequences of nonnative trout on freshwater ecosystems may extend beyond the lake's boundaries. Currently, the relevance of fishless lakes for local biodiversity is of great interest since they can be an important element in the conservation of a duck, the Barrow’s Goldeneye (*Bucephala islandica* Gmelin). This waterfowl species has a status of special concern in eastern Canada (COSEWIC 2003), and its presence on lakes during its breeding period could depend on complex competitive interactions for food with fish (Eriksson 1978, 1983; Einarsson 1987; Robert *et al.* 2000). These observations support the hypothesis that fishless lakes could offer prime habitats for some aquatic and terrestrial species.

Predation by fish and invertebrates is a significant factor structuring species abundance and composition in zooplankton communities (e.g. Brooks and Dodson 1965; Hall *et al.* 1970; Hutchinson 1971; Pope and Carter 1975; Lynch 1979; Zaret 1980; Neill 1981). However, it may be suggested that the contrasting outcomes of predation by vertebrates and invertebrates lead to different community structures. Fish (gape-limited predators) have access to a larger range of prey than invertebrates, which are limited in their prey size (size-dependent predator) (Zaret 1980). Moreover, species having evolved in communities without a fish predator may have developed different anti-predator strategies and be more adapted to a specific predation pressure (McPeek 1990, 1998). Furthermore, competitive interactions among prey species could be affected by predation intensity and the type of predators present. All the biotic processes together, directly or indirectly generated by differences in top-down control, may cause differences in the community structure in lakes with and without fish, and this could be reflected in the zooplankton community structure.

Several studies have evaluated the effects of fish or invertebrate predators on communities using such things as biomass, species composition, or the density of particular species as responses to predation effect (e.g. Pope and Carter 1975; Lynch 1979; Chess *et* *al.* 1993; Wissel and Benndorf 1998), but few studies have measured the effect of predation on the species richness and diversity of zooplankton (but see Bradford *et al.* 1998 and Donald *et al.* 2001). However, Downes *et al.* (2002) highlighted that multivariate indicators are more sensitive than univariate indicators (e.g. species richness, diversity) to describe community structure. Also, many field experiments used fish exclusion or introduction to assess the impact of fish predation on the zooplankton community (e.g. Lynch, 1979; Chess *et al.* 1993) and one used a long-term biomanipulation experiment (Wissel and Benndorf 1998). When fish are introduced into a community that evolved without a fish predator, major changes in the community may occur, but this only reveals information over a short-term period. In contrast, the study of predation differences between lakes with and without fish species may provide useful information on the fundamental role of predation in community structuring (Wellborn *et al.* 1996). We still have poor knowledge of spatio-temporal patterns occurring in naturally evolved lake communities with fish-present and fishless lakes. That information is particularly valuable for understanding the effects of predation by fish through natural variability, but also to evaluate the integrity of the systems (Angermeier and Karr 1994). Much effort is being expended to restore naturally fishless lakes to their original state in cases where fish have been introduced (Drake and Naiman 2000; Parker *et al.* 2001). The assessment of diversity and community structure could be of great interest for management to recreate self-sustainable systems representative of the native biota (Angermeier and Karr 1994).

The principal objective of this study was to describe zooplankton communities in eastern Canadian Boreal Shield lakes with a single species of fish (brook trout) and lakes with no fish populations throughout the ice-free season. Univariate and multivariate statistical methods were used to compare zooplankton communities in terms of abundance, richness, evenness, diversity, and species assemblages. More specifically, the hypotheses were: 1) the community characteristics of zooplankton (abundance, richness, evenness and diversity) and the structure of zooplankton species assemblages between fish-present and fishless lakes should differ as a result of different top-down control from predation by fish and/or invertebrates, and 2) these differences in community characteristics and structure should occur over the complete duration of the ice-free season.

1.2 Methods

1.2.1 Description of study lakes

The study was conducted during the summer of 2003 in small natural oligotrophic lakes on Boreal Shield bedrock north of the Saguenay Fjord in Quebec, Canada (Table 1, Fig. 1). The current distribution of fish in this area has been modulated by postglacial colonisation, where natural barriers permitted the upriver dispersion by salmonids only (Power *et al.* 1973). Fewer species occur upstream, where monospecific fish populations of brook trout (*Salvelinus fontinalis*) dominate and some lakes remain fishless above the escarpment marking the edge of the Laurentian Plateau (Power *et al.* 1973).

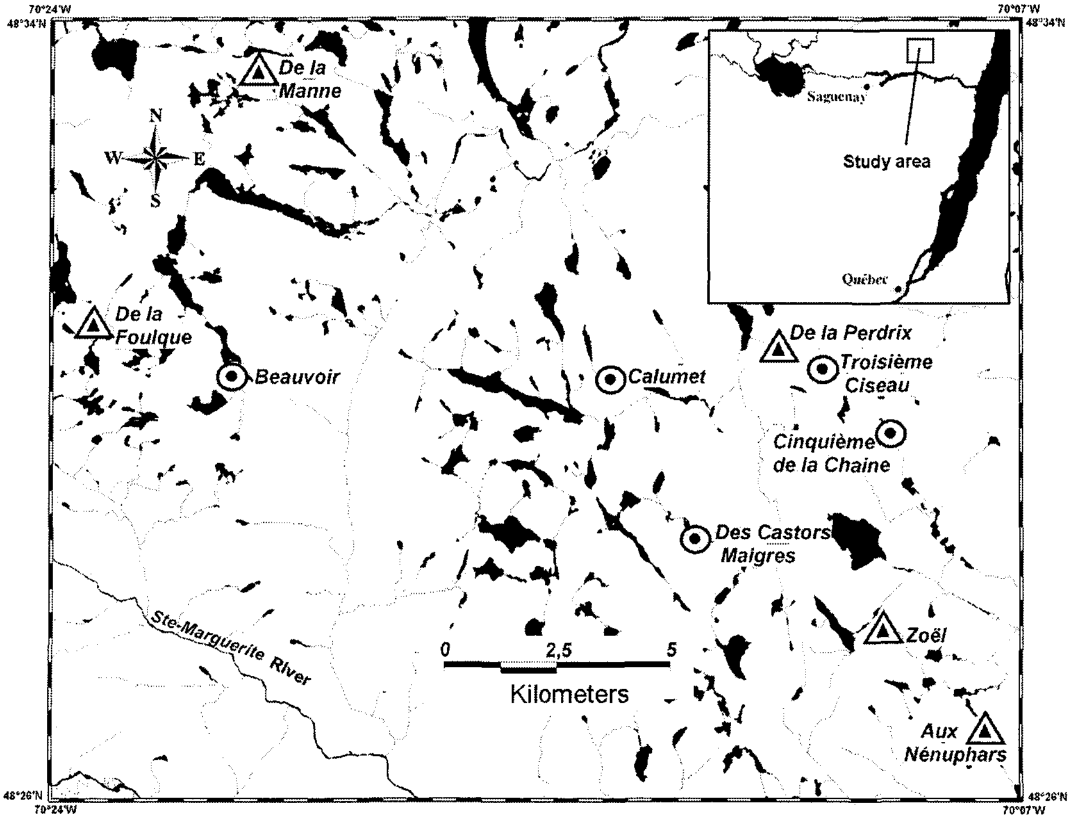

Figure 1. Location of the 10 study lakes within the study area. Circles indicate lakes with brook trout populations and triangles fishless lakes.

1.2.2 Experimental design

This study involved ten lakes, five that contained natural (non-stocked) monospecific fish populations of brook trout and five fishless lakes. All lakes were located in two controlled harvested zones (ZEC Martin-Valin and ZEC Chauvin). The presence and the absence of fish in the selected lakes were corroborated by the recreational fisheries statistics of brook trout between 1994 and 2003 (Table 1). The absence of fish was validated in June 2001 in four fishless lakes (de la Foulque, de la Manne, aux Nénuphars and de la Perdrix) using experimental gillnet (unpublished data, Ministère des Ressources Naturelles et de la Faune du Québec).

The lakes were sampled four times during the ice-free season, which lasts from June to October in this area. Sampling periods were done between the 23 - 29 June, 14 - 19 July, 11 - 16 August and 8 - 13 September, hereafter referred to as June, July, August and September. The lakes were chosen because their geographical and morphological parameters were comparable (Table 1). Lake depth and transparency were estimated using a graduated cable and Secchi disk. Water temperature, dissolved oxygen concentration, pH and conductivity were measured (Table 1) with an YSI model 556 MPS (Yellow Springs Instrument Co., Yellow Springs, Ohio).

Table 1. Position and morphological and physicochemical characteristics of the studied lakes. Parameters are expressed as the mean of the four sampling periods with the standard error of the mean in parentheses.

Parameter	Fish-present lakes					Fishless lakes				
	Beauvoir	Calumet	Des Castors Maigres	Cinquième lac de la Chaîne	Troisième lac Ciseau	De la Foulque	De la Manne	Aux Nénuphars	De la Perdrix	Zoël
Latitude	48°30′32″	48°30′28″	48°28′36″	48°29′48″	48°30′38″	48°31′00″	48°34′00″	48°26′15″	48°30′47″	48°27′26″
Longitude	-70°21′07″	-70°14′23″	-70°12′50″	-70°09′30″	-70°10′38″	-70°23′28″	-70°20′00″	-70°07′47″	-70°11′21″	-70°09′27″
Altitude (m)	754	712	655	688	713	775	804	621	726	729
Surface area (km^2)	0.067	0.039	0.086	0.020	0.051	0.049	0.054	0.063	0.033	0.039
Maximum depth (m)	15	10	16	9	9	5	23	8	15	10
Secchi depth (m)	5.4 (0.8)	3.4 (0.5)	3.0 (0.5)	3.0 (0.4)	4.5 (0.5)	2.3 (0.9)	3.6 (0.5)	3.1 (0.8)	3.3 (0.3)	3.9 (0.6)
pH*	7.31	6.02	6.88	7.08	7.33	7.48	6.18	6.22	7.31	6.05
Temperature (°C)	18.28 (4.70)	18.02 (4.23)	18.73 (2.67)	19.52 (2.61)	17.64 (4.23)	19.04 (4.76)	18.20 (3.92)	19.25 (3.50)	18.67 (2.84)	18.58 (3.78)
Conductivity (µS/cm)	13.2 (2.3)	10.5 (1.3)	10.7 (2.3)	12.7 (3.1)	9.4 (2.5)	15.0 (1.5)	6.9 (2.2)	8.4 (1.4)	9.1 (0.9)	6.7 (1.1)
Dissolved oxygen (mg/L)	10.20 (2.13)	9.91 (2.02)	9.23 (1.63)	9.34 (1.47)	9.66 (2.15)	10.31 (1.91)	9.71 (1.74)	8.8 (1.78)	9.83 (1.90)	9.51 (1.97)
Mean annual catch of trout 1994-2003	154	214	375	100	179					
Total allowable catch for trout 1994-2003	150	200-250	400-450	100	250					
Mean weight of trout caught 1994-2003 (g)	195	85	116	112	125					

* pH values for July only because of probe malfunction

1.2.3 Sample collection

In the stratified zone of each lake, near the deepest point, three vertical hauls were made from 1 m off-bottom to the surface using a cantilevering net with a circular mouth opening of 0.25 m and mesh size of 53 µm (Filion *et al.* 1993). All samples were collected during daytime (between 10:00 and 15:00). Organisms were anaesthetised with carbonated water and preserved in 4% buffered formaldehyde. In the laboratory, samples were split into two size fractions of 53-355 µm and >355 µm to facilitate the identification of the small-sized zooplankters. *Chaoborus* larvae (Chaoboridae, Diptera) were removed from the >355 µm fraction to be counted and analysed separately. Organisms were sub-sampled by aliquot using a pipette with a 4-mm opening and then identified to the lowest taxonomic level possible, usually to the species level (Edmondson 1959; Pennak 1978, see list in Annexe 1). Some juvenile daphnids were identified to be a part of the *Daphnia pulex* group, which can include the following species: *D. pulex* Leydig, *D. catawba* Coker, *D. pulicaria* Forbes and *D. minnehaha* Herrick (Schwartz *et al.* 1985; Hebert and Loaring 1986).

1.2.4 Data analyses

Data were analysed by univariate and multivariate approaches using the PRIMER v5 statistical package (Clarke and Warwick 1994; Clarke and Gorley 2001). Diversity indices (species richness, S; Shannon-Wiener diversity, *H'*; Pielou's evenness, *J'*) were calculated on species abundance data for each sample as univariate variables. Three-way partly nested analyses of variance (ANOVAs) were used to compare univariate variables (total abundance; abundances of cladocerans, copepods, rotifers, *Daphnia* spp., and three taxa of *Chaoborus*; and S, *H'*, *J'*). Sources of variation were 1) lake type (fish-present lakes and fishless lakes), 2) individual lakes (5 lakes nested in each treatment), 3) sampling time (June, July, August, September), and 4) interactions among these factors. The assumptions of homoscedasticity and normality were verified by the spread of residuals as suggested by Quinn and Keough (2002). A logarithmic transformation (x + 0.001) was used according to Legendre and Legendre (1998) to respect the statistical assumptions when necessary. *A posteriori* comparisons were made using the Tukey's test (Underwood 1997).

Multivariate procedures on species assemblages were based on the Bray-Curtis dissimilarity matrix (Bray and Curtis 1957; Clarke 1993). Species assemblages were calculated using fourth-root transformed data ($\sqrt[4]{x}$) to down-weigh the importance of very abundant taxa and take into account rare taxa while maintaining their order (Clarke 1993; Clarke and Warwick 1994; Thorne *et al.* 1999). Species assemblage analyses were also performed on transformed presence/absence data to assess the importance of species richness. As suggested by Clarke and Warwick (1994), taxa showing a single occurrence were removed from the dataset before computing the Bray-Curtis dissimilarities since the similarities between rare species have little meaning and they tend to confuse the similarity matrix. The ordination of dissimilarity measures were represented through non-metric multidimensional scaling (nMDS). The hypothesis related to zooplankton assemblage compositions was tested using non-parametric multivariate analysis of variance (PERMANOVA v1.6; Anderson 2001; McArdle and Anderson 2001; Anderson 2005), a statistical method based on permutations. The similarity percentage and the identification of discriminating species between species assemblages based on the fourth-root transformed (abundance) and the presence/absence (diversity) data were recognized using the SIMPER procedure (Clarke and Warwick 1994).

1.3 Results

1.3.1 Abundance, species composition and diversity

Totals of 23 taxa of rotifers, 10 taxa of cladocerans, and 14 taxa of copepods were identified among the lakes and considering all sampling times. The total abundance of zooplankton was significantly higher in fishless lakes at each sampling time (Table 2, Fig. 2). This higher abundance was mainly related to the abundance of rotifers, which was higher in fishless lakes at each sampling time (Table 2, Fig. 2). The abundance of cladocerans was higher in fish-present lakes, but marginally not significant ($P = 0.0866$; Table 2). The total number of copepods was similar between lake types (Table 2). The abundance of *Daphnia* was significantly higher in fish-present lakes throughout the season. *Chaoborus* larvae were found in 68% and 93% of the zooplankton samples from fish-present and fishless lakes, respectively. Their abundance was higher, but marginally not significant ($P = 0.0833$) in the fishless lakes at each sampling time (Table 2, Fig. 2).

Identification to the species level revealed that *C. americanus* Johannsen was more abundant in fishless lakes and that *C. flavicans* Meigen and *C. trivitattus* Loew had similar abundances in both types of lakes (Table 2, Fig. 2). No significant differences were observed between lake types for the diversity indices (species richness, S; Shannon-Wiener index, *H'*; Pielou's evenness, *J'*; Table 3, Fig. 3). We did not observe significant temporal variations or interactions in taxon abundances (Table 2) or diversity indices (Table 3). In general, the variations among the lakes were high for the abundance (Table 2) and diversity indices (Table 3), and the lakes also varied differently among the sampling times.

Table 2. Results of three-way partly nested ANOVAs testing the effect of lake types (fish present or fishless), lake nested within the type, sampling time (June, July, August and September) and their interactions on the abundance of total organisms, cladocerans, copepods, rotifers, *Daphnia*, *Chaoborus* larvae and three *Chaoborus* species. Data were all transformed as ln(x+0.001).

Source of variation	df	Total organisms			Cladoceran			Copepod		
		Mean square	*F*	*P*	Mean square	*F*	*P*	Mean square	*F*	*P*
Type	1	21.78	6.53	0.0339	253.62	3.81	0.0866	0.26	0.05	0.8286
Lake (Type)	8	3.34	3.95	<0.0001	66.51	11.21	<0.0001	5.12	8.24	<0.0001
Time	3	1.68	1.99	0.1428	4.79	0.81	0.5016	1.20	1.94	0.1507
Type x Time	3	1.13	1.34	0.2864	4.19	0.71	0.5574	0.88	1.42	0.2626
Lake (Type) x Time	24	0.84	15.21	<0.0001	5.93	6.52	<0.0001	0.62	3.44	<0.0001
Residual	80	0.06			0.91			0.18		

Source of variation	df	Rotifer			*Daphnia*			*Chaoborus* larvae		
		Mean square	*F*	*P*	Mean square	*F*	*P*	Mean square	*F*	*P*
Type	1	34.33	7.92	0.0227	571.17	9.31	0.0158	82.96	3.91	0.0833
Lake (Type)	8	4.33	3.49	<0.0001	61.29	21.69	<0.0001	21.21	6.46	<0.0001
Time	3	2.65	2.13	0.1226	10.80	3.82	0.0227	1.13	0.34	0.7938
Type x Time	3	2.23	1.79	0.1751	0.74	0.26	0.8514	0.16	0.05	0.9852
Lake (Type) x Time	24	1.24	15.43	<0.0001	2.83	16.70	<0.0001	3.28	6.51	<0.0001
Residual	80	0.08			0.17			0.50		

Source of variation	df	*C. americanus*			*C. flavicans*			*C. trivittatus*		
		Mean square	*F*	*P*	Mean square	*F*	*P*	Mean square	*F*	*P*
Type	1	123.15	5.61	0.0454	4.80	2.00	0.1945	11.48	0.90	0.3711
Lake (Type)	8	21.95	14.41	<0.0001	2.39	2.37	<0.0001	12.79	8.48	<0.0001
Time	3	3.78	2.48	0.0855	3.05	3.01	0.0498	1.50	0.99	0.4119
Type x Time	3	4.55	2.99	0.0511	1.61	1.59	0.2183	0.25	0.17	0.9177
Lake (Type) x Time	24	1.52	5.97	<0.0001	1.01	5.47	<0.0001	1.51	2.54	0.0010
Residual	80	0.26			0.18			0.59		

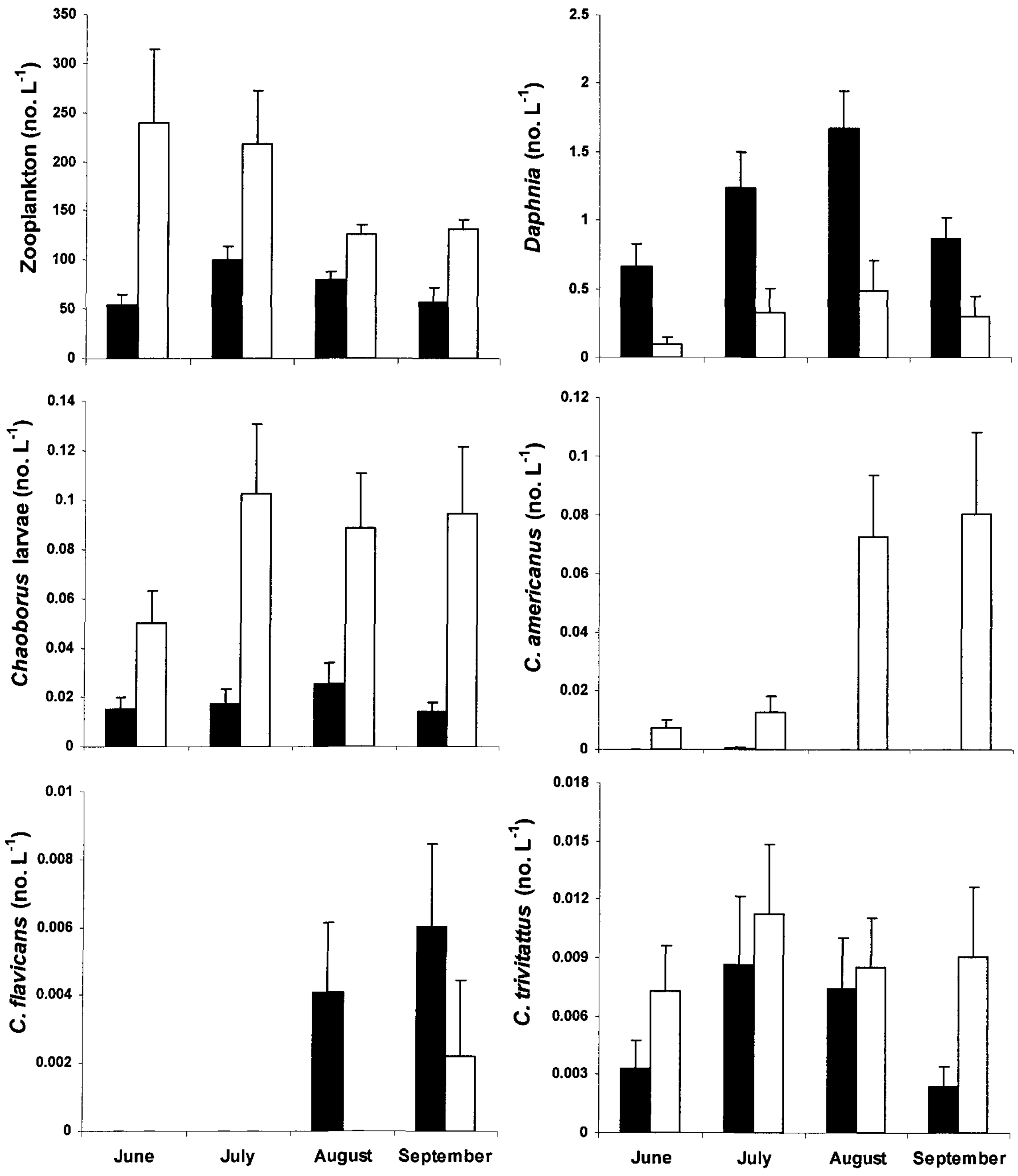

Figure 2. Mean abundance (+SE) of all zooplankton organisms, Daphnia., Chaoborus larvae, C. americanus, C. flavicans and C. trivitattus in fish-present (black) and fishless (white) lakes for the different sampling time.

Table 3. Results of three-way partly nested ANOVAs testing the effect of lake types (fish present or fishless), lake nested within the type, sampling time (June, July, August and September) and their interactions on the univariate diversity indices (species richness, evenness, diversity).

Source of variation	df	Species richness (S)			Evenness (*J'*)			Diversity (*H'*)		
		Mean square	*F*	*P*	Mean square	*F*	*P*	Mean square	*F*	*P*
Type	1	14.70	0.35	0.5690	0.07	0.94	0.3604	0.85	1.06	0.3327
Lake (Type)	8	41.69	18.53	<0.0001	0.07	30.27	<0.0001	0.80	34.42	<0.0001
Time	3	16.72	2.70	0.0684	0.03	1.11	0.3648	0.14	0.61	0.6167
Type x Time	3	13.08	2.11	0.1255	0.02	0.83	0.4929	0.25	1.13	0.3576
Lake (Type) x Time	24	6.20	2.75	0.0004	0.03	11.39	<0.0001	0.22	9.62	<0.0001
Residual	80	2.25			0.002			0.02		

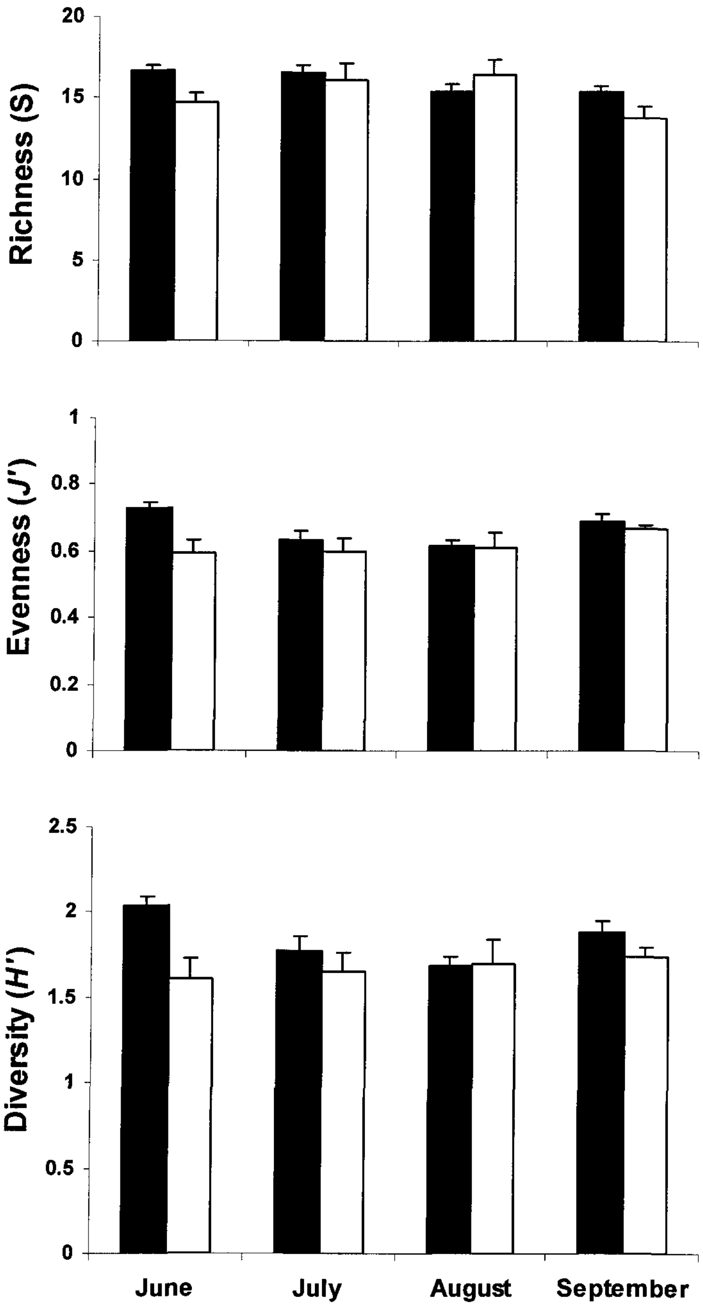

Figure 3. Mean (+SE) univariate diversity indices (S, *J'*, *H'*) in fish-present (black) and fishless lakes (white) for each sampling time.

1.3.2 Species assemblages

The permutational multivariate analysis of variance (Anderson 2001; McArdle and Anderson 2001) revealed that species assemblages based on Bray-Curtis dissimilarities, were significantly different between the two lake types (Table 4). This relationship is illustrated by a non-metric multidimensional scaling (nMDS) graphic, which clearly shows different clusters for fish-present and fishless lakes (Fig. 4). The stress of 0.21 indicates that this two-dimensional representation of the multivariate ordination, which represents a total of 120 samples, can be visually acceptable (Clarke and Warwick 1994). Significant variations in species assemblages among the sampling times were observed. For both lake types, assemblages in June were significantly different from those in August and September (PERMANOVA, pair-wise *a posteriori* comparisons). We also observed high variability among lakes of the same type.

Table 4. Results of the nonparametric multivariate analyses of variance (PERMANOVA) testing the effect of lake types (fish present or fishless), lake nested within the type, sampling time (June, July, August and September) and their interactions on species assemblages based on the Bray-Curtis dissimilarity matrix. The species assemblages were calculated on fourth-root transformed data ($\sqrt[4]{x}$) and presence/absence data.

Source of variation	df	Mean square	Pseudo-*F*	*P* (perm)
Fourth-root				
Type	1	27940.24	3.52	0.0087
Lake (Type)	8	7929.01	36.45	<0.0001
Time	3	4865.44	4.80	<0.0001
Type x Time	3	1284.17	1.27	0.1917
Lake (Type) x Time	24	1013.67	4.66	<0.0001
Residual	80	217.50		
Presence/absence				
Type	1	24851.72	4.53	0.0092
Lake (Type)	8	5484.42	29.84	<0.0001
Time	3	4524.75	8.52	<0.0001
Type x Time	3	538.75	1.01	0.4596
Lake (Type) x Time	24	531.15	2.89	<0.0001
Residual	80	183.76		

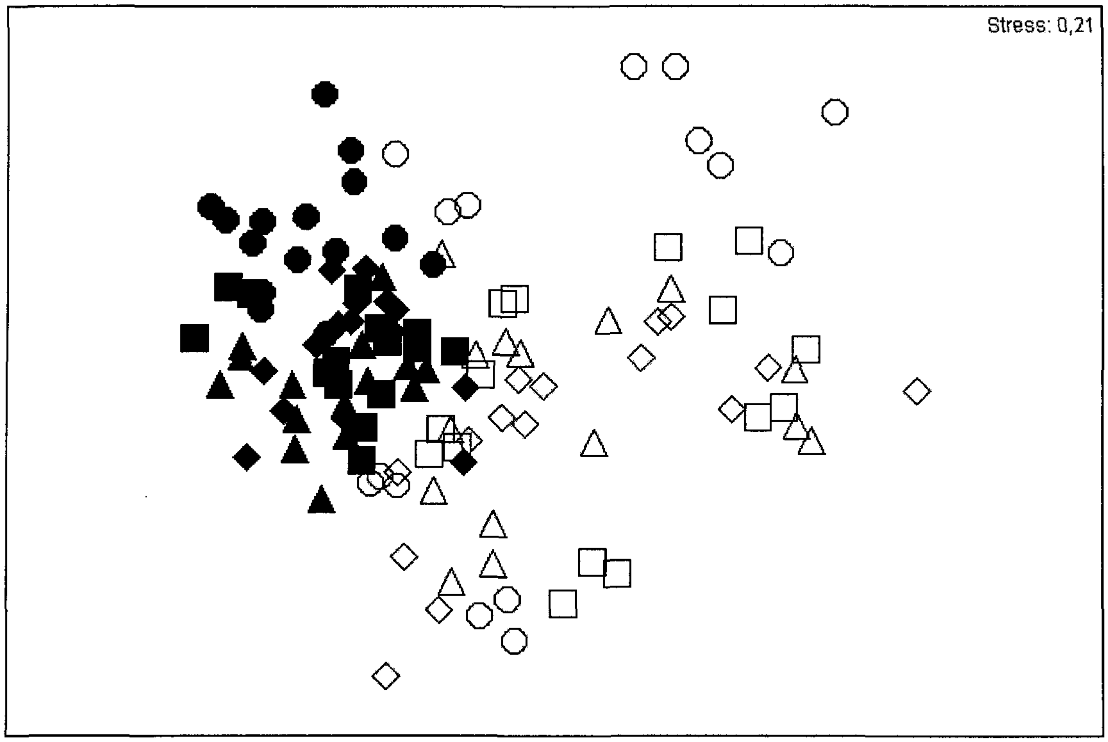

Figure 4. Non-metric multidimensional scaling (nMDS) ordination based on the Bray-Curtis dissimilarity matrix calculated on fourth-root transformed data ($\sqrt[4]{x}$) for zooplankton samples collected in fish-present (black) and fishless lakes (white) during the ice-free season (circles = June, squares = July, triangles = August, diamonds = September).

According to the Similarity Percentage analysis (SIMPER, Clarke and Warwick 1994), the zooplankton assemblage compositions were 53.45% dissimilar between the two lake types based on fourth-root transformed data and 46.00% dissimilar based on the transformed presence/absence data. From these results, it seems that the discrimination between lake types was predominantly due to the higher abundance of rotifer species (mainly *Conochilus unicornis* Rousselet, *Keratella cochlearis* Gosse, *Conochiloides dossuarius* Hudson and *Kellicottia longispina* Kellicott*)* and the very low abundance of daphnids in fishless lakes (Table 5).

Table 5. Dissimilarity percentages (%) of zooplankton assemblages between lake types based on fourth-root and presence/absence transformed data of the zooplankton taxa with the greatest contribution to the dissimilarity.

Species	Average dissimilarity of 53.45 %	
	Contribution %	Cumulative %
Fourth-root		
Conochilus unicornis	6.77	6.77
Keratella cochlearis	6.65	13.42
Conochiloides dossuarius	6.12	19.54
Kellicottia longispina	5.38	24.92
Keratella taurocephala Myers	5.19	30.11
Keratella quadrata Müller	4.59	34.70
Collotheca sp.	3.88	38.58
Polyarthra sp.	3.88	42.46
Species	Average dissimilarity of 46.00 %	
	Contribution %	Cumulative %
Presence/absence		
*Daphnia pulex**	5.12	5.12
Conochiloides dossuarius	4.78	9.89
Daphnia sp.**	4.44	14.33
Conochilus unicornis	4.24	18.57
Keratella taurocephala	4.23	22.80

**Daphnia pulex* group, including *D. pulex*, *D. catawba*, *D. pulicaria* and *D. minnehaha* (Schwartz *et al.*, 1985; Hebert & Loaring, 1986)
** Immature individuals

1.4 Discussion

Our study demonstrates that zooplankton community structure was different between lakes with brook trout as the only fish species and naturally fishless lakes throughout the ice-free period, indicating that brook trout influenced the zooplankton species assemblages and contributed to maintaining the community structure during this period. However, zooplankton species richness and diversity were not different between the two lake types. Hence, indicator choice affects whether or not patterns in community structure will be revealed: the multivariate indicator (Bray-Curtis dissimilarity) was more sensitive than the univariate diversity indices. Although there was high variability in the community characteristics and species assemblages among individual lakes, we observed a general pattern of community structure for each lake type.

1.4.1 Brook trout effect on zooplankton community structure

Many studies (Brooks and Dodson 1965; Hutchinson 1971; Carpenter *et al.* 1985; Vanni 1987) have shown that larger zooplankton forms are preferentially selected by fish and thus permit the dominance by smaller herbivores that can escape predation and are no longer competitively eliminated by the large herbivores. Contrary to these studies, we observed that communities dominated by small herbivorous species were associated with fishless lakes. The total abundance of organisms was lower in fish-present lakes at each sampling time, but the abundance of the large herbivorous zooplankton, such as *Daphnia*, a known prey of brook trout (Magnan 1988; Tremblay & Magnan 1991; Lacasse and Magnan 1992), was highest in the presence of fish. The rotifer group mainly added to the higher total abundance of organisms in fishless lakes, and numerous species from this group contributed to the average dissimilarity between the species assemblages. The scarcity of mature and immature daphnids in fishless lakes also contributed to the dissimilarity between the species assemblages. According to the size efficiency hypothesis of Brooks and Dodson (1965), the predation intensity by brook trout was low since the largest prey species were not removed in its presence. Thus, the larger zooplankters were more abundant in fish-present lakes. The presence in the systems of *Chaoborus* larvae, which are selective predators able to structure the zooplankton community (Dodson 1974; Fedorenko 1975a; Pope and Carter 1975; Neill 1981), could explain the observed patterns. Thus, brook trout was not the sole predator of zooplankton because *Chaoborus* larvae were important planktivores in fishless lakes. Moreover, predation by fish is known to influence the abundance and species distribution of *Chaoborus* larvae (Pope *et al.* 1973; von Ende 1979; Wissel *et al.* 2003). We observed that the total abundance of *Chaoborus* larvae was higher in fishless lakes at each sampling time, but this was not statistically significant at the 0.05 level of significance (P = 0.08). However, this trend seems susceptible to inter-annual variations: significant differences in *Chaoborus* larvae abundance between fish-present and fishless lakes were found in 2002 in the same area (Archambault and Sirois, unpublished data). Most of the larvae collected into the water column during the daytime were immature, but identification to the species level of the final instar larvae revealed differences in species composition between fish-present and fishless lakes. While *C.*

flavicans and *C. trivittatus* larvae co-occurred with fish, *C. americanus* larvae were strongly associated with fishless lakes. The first instar larvae can benefit from a size refuge and escape predation, but larger final instars adopt predator avoidance behaviours such as diel vertical migration (LaRow 1968, 1969). However, this behaviour is not observed in *C. americanus* larvae, and so it only occurs in fishless lakes (Pope *et al.* 1973; von Ende 1979; Wissel *et al.* 2003). The third and fourth instars of *Chaoborus* larvae are strong predators (Fedorenko 1975b; Swift and Fedorenko, 1975; MacKay *et al.* 1990; Yan *et al.* 1991), and the continuous presence of those *Chaoborus americanus* instars into the water column could result in a high intensity of predation on zooplankton communities. The exclusion of *Chaoborus* species by fish appears to depend directly on the intensity of predation in lakes. In general, *C. flavicans* and *C. trivitattus* are mostly found in small lakes with lower fish density (von Ende 1982) or fewer fish species (Wissel *et al.* 2003). As well, we observed a few (three specimens only) mature *C. americanus* larvae despite the presence of brook trout, and the presence of this species which is generally known to occur only in lakes without fish can be linked to predation intensity by the fish species (von Ende 1979).

Our observations suggest that invertebrate predation had a stronger effect than brook trout on large herbivore populations, particularly *Daphnia pulex*. This is in agreement with the results of Wissel and Benndorf (1998), who observed that predation by *C. obscuripes* (van der Wulp) larvae was very effective on small young daphnids. The removal of these small young daphnids by invertebrate predation has a stronger effect on the daphnid population than predation on larger specimens because the latter have already reproduced. Furthermore, studies by MacKay *et al.* (1990) demonstrated that predation by *Chaoborus americanus* affects young individuals and directly controls populations of *Daphnia pulex*. This phenomenon has important implications in the community structure of fishless lakes because large herbivores such as *Daphnia pulex* are known to be highly effective grazers and can be involved in trophic cascades influencing phytoplankton biomass (Carpenter 1988). Also, many studies have demonstrated the competitive dominance of daphnids over smaller herbivores such as *Keratella cochlearis* (Neill 1984; Gilbert and Stemberger 1985; Arvola and Salonen 2001), *Kellicottia* sp. (Neill 1984) and copepod nauplii (Vanni 1986), which is consistent with our results.

Biotic factors other than predation may drive *Daphnia pulex* populations in fishless lakes. Algal quality and quantity could also influence herbivore population performance and abundance: high algal levels have been found to favour *Daphnia* abundance whereas small taxa maintained higher population growth rates and dominated communities at low algal levels (Romanovsky and Feniova 1985). Lakes are oligotrophic within the study area, and this may influence the general performance of large herbivores. Nevertheless, the absence of *Daphnia pulex* has been observed to be positively correlated with significantly higher biomasses of phytoplankton in fishless lakes in July 2002 (Archambault and Sirois, unpublished data). Moreover, Pope and Carter (1975) observed the absence or low abundance of *Daphnia pulex* in fishless lakes of the eastern Canadian Boreal Shield near our study area. Conversely, this cladoceran species was abundant in lakes that contained brook trout as the only fish species. They interpreted this phenomenon as planktivory and not as a biogeographical anomaly since this *Daphnia* species was found in small ponds near their study lakes. In the present research, the low abundance of daphnids in fishless lakes was likely linked to predation.

Brook trout could play an indirect role in the process of competitive exclusion of rotifers by large herbivores by limiting the abundance of pelagic *Chaoborus americanus* larvae during daytime, and so regulate the zooplankton community structure in fish-present lakes. A recent study has demonstrated that brook trout, in single fish population, can strongly selected *Chaoborus* larvae ((Tremblay-Rivard *et al.*, Laboratoire d'écologie aquatique UQAC, unpublished data). Lynch (1979) observed similar results with experimental studies of predation intensity by invertebrates and fish on the zooplankton community composition. *Chaoborus* larvae and *Daphnia pulex* were present when fish predation was low, but not with increasing fish predation. Likewise, *Daphnia pulex* was reduced only under intense predation by *Chaoborus* larvae: the increased food availability created by this predation allows an increase in the abundance of small rotifers. Competitive exclusion by larger herbivores did not seem to occur in fishless lakes, probably because of the higher depletion of the daphnids population by *Chaoborus* larvae.

The observed patterns in fish-present lakes were strongly related to the presence of brook trout as the only fish population. In lakes containing more than one species of fish, large zooplanktonic herbivores such as *Daphnia pulex* have been found in low abundance (Pope and Carter 1975). A competitive interaction between fish species could enhance the predation intensity on the zooplankton community. In addition, fish species is another important factor structuring zooplankton community. Many studies that assessed the effect of fish predation refer to efficient planktivorous species such as alewife (Brooks and Dodson 1965; Hutchinson 1971) or sunfish (Wissel and Benndorf 1998). The difference between our results and others studies may be related to the intensity and effectiveness of the fish population that feeds on the zooplankton.

1.4.2 Univariate diversity indices and multivariate measures

The differences in the zooplankton community characteristics of fish-present and fishless lakes could not be detected with diversity indices, showing the importance of choosing appropriate indicators for the assessment of community structure, such as in biomonitoring studies. Species richness and diversity are widely used in impact assessment studies because of their easy interpretation, but these indices are not always representative of the ecological importance of a community or a change in community structure (Downes *et al.* 2002). The distinction between the zooplankton communities from fish-present and fishless lakes was observed as differences in the abundances of particular taxa and therefore depended on a taxonomic approach. Despite their popularity, many measures of diversity such as the Shannon-Wiener index or Pielou's evenness are not explicitly associated with named species, which restricts their utility (Magurran 2004). The species-independent method of community analysis such as the univariate diversity index can be less sensitive for detecting changes in communities and in differentiating community structure (Keough and Quinn 1991; Warwick and Clarke 1991; Downes *et al.* 2002). Moreover, multivariate analyses can have greater sensitivity and can be more informative than univariate methods because they integrate the effects of the abundance of many species or other variables into a single entity (Keough and Quinn 1991; Warwick and Clarke 1991; Downes *et al.* 2002). Using such a method can be particularly advantageous when the specific aspect of the discrimination is unknown because it increases the chance of finding a change in community composition (Downes *et al.* 2002).

The choice of variables for assessment must be relevant to the objectives of the study and not chosen purely by convention, habit or social pressure (Downes *et al.* 2002). In terms of management, this means that species richness and diversity should not be the only tools used to assess a community. Diversity is a socially accepted variable that is easy to understand, but it is not necessarily the most relevant for studying ecological processes or functions (Downes *et al.* 2002). When the evaluation of the intrinsic biotic integrity of a system is one objective of a study, multivariate approaches may create better indicators of integrity than species richness and diversity since they can reflect the biotic elements and the processes that generate and maintain those elements, whereas diversity describes only elements (Angermeier and Karr 1994). In our study, multivariate indicators identified patterns that were not revealed with the usual univariate indices.

1.4.3 Conclusion

Our results showed that predation could be an important element structuring the zooplankton community in the fish-present and fishless lakes on the eastern Canadian Boreal Shield. Differences in top-down control between brook trout and *Chaoborus* larvae were observed for the abundance and the multivariate species assemblages, but not for the species richness (S), the evenness (*J'*) or the diversity (*H'*). Thus, predation could control the zooplankton community structure without increasing or decreasing the diversity of the prey community. The low intensity of selective predation by brook trout on large herbivores coupled with its control on the abundance of *Chaoborus* larvae (at least during the daytime) appear to be the key factors for structuring the zooplankton community. The effect of fish on the zooplankton communities was continuous throughout the ice-free season. Moreover, the difference in the complexity of the food web between lakes with and without fish may be important in the ecology of non-aquatic species, since cascading effects may occur within the aquatic and adjacent terrestrial ecosystems (Knight *et al.* 2005). This study showed that fishless lakes could be of great importance in maintaining complex ecological interactions in the eastern Canadian Boreal Shield ecosystem.

CHAPITRE II

EFFECT OF FISH ON INVERTEBRATE COMMUNITIES IN LITTORAL ZONE: A COMPARISON STUDY USING SINGLE FISH POPULATION (BROOK TROUT, *SALVELINUS FONTINALIS*) AND FISHLESS LAKES

2.1 Introduction

Many fishless lakes in headwater ecosystems have been successfully introduced with nonnative trout for the benefit of recreational fisheries (Godbout and Peters 1988, Kelso and Shaw 1995, Bahls 1992, Knapp *et al.* 2001). Assessing the consequences of these invaders are presently of great interest since a growing body of evidence suggests that the presence of non-native fish may alter the behaviour of native species, threaten prey populations, change community interactions and disrupt ecological processes (Simon and Townsend 2003, Dunham *et al.* 2004). Moreover, consequences may also be reflected beyond the lake boundaries and loss in aquatic ecosystems could impact species which also have complex life cycles with terrestrial life stages, such as amphibians (Pilliod and Peterson 2001, Knapp 2005) and non-aquatic species such as birds (Murakami and Nakano 2002) and insect pollinators (Knight *et al.* 2005). Actually, the relevance of fishless lakes for local biodiversity in eastern Canada is of great interest since they can be an important element involved in the conservation of Barrow's Goldeneye (*Bucephala islandica* Gmelin). This waterfowl population has a status of special concern (COSEWIC 2003) and its presence on lakes during its breeding period could depend on complex competitive interactions for food with fish (Eriksson 1978, 1983, Einarsson 1987, Robert *et al.* 2000). Our knowledge on the structure and function of the fishless lakes at the ecosystem level is still low on the Eastern Canada Boreal Shield. Moreover, improvements of our understanding about the littoral freshwater communities in fishless lakes are important since evidence of trophic cascades across ecosystems has been found (Knight *et al.* 2005) and they represent a transition zone between terrestrial and aquatic systems.

Predators are known to influence the community composition and maintain the diversity in communities (Paine 1966, Zaret 1980, Thorp 1986). Furthermore, some have shown that due to contrasting foraging characteristics, predation by fish may lead to different community structures than predation by invertebrates (Wellborn *et al.* 1996). As well, prey vulnerability depends on traits which permit coexistence with predators (Wellborn *et al.* 1996). Many species have evolved in communities without a fish predator and have developed different anti-predator strategies, being more adapted to a specific predation pressure (McPeek 1990, 1998). Other biotic interactions such as competition also contribute to structure the community and could be indirectly affected by selective predation. Therefore, the summation of all biotic processes directly or indirectly generated by difference in top-down control could cause differences in invertebrate communities' structure in fish-present and fishless lakes, and this could be reflected on community characteristics.

Many studies have observed the effects of fish predation on invertebrate community via manipulative experiments of the predator density, their exclusion or their introduction (e.g. Thorp and Bergey 1981, Gilinsky 1984, Leppä *et al.* 2003). When manipulated, fish can generate major changes in communities such as the reduction of prey density or diversity. However, experimental introduction of fish can only lead to conclusions on prey organisms that have never co-evolved with fish. The study of the predatory shift between permanent fishless lakes and fish-present lakes may reveal important information about the fundamental role of predation in organising the nektonic and benthic communities (Wellborn *et al.* 1996). In addition, the relative importance of predation in communities could differ among environmental characteristics such as spatial and temporal variability within the communities. The spatio-temporal variance could affect biotic interactions and thus be involved as a structuring factor in the communities. Consequently, the examination of the effect of predation with adequate replication can provide valuable information on community patterns. In nature, the «equilibrium state» in communities is only observable through an unpredictable spatio-temporal variability, which needs consideration before attempting to generalise about patterns and thereafter processes (Underwood *et al.* 2000). As the basis of many theoretical and quantitative models, observational studies are important to make progress in our understanding of ecosystems (Underwood *et al.* 2000).

The principal objective of this study was to compare littoral invertebrate communities in fish-present and fishless lakes along an ice-free season in the eastern Canadian Boreal Shield. Univariate and multivariate statistical methods were used to compare nekton and zoobenthos communities in term of abundance, richness, evenness, diversity, and species assemblages. More specifically, the hypotheses tested for the nekton and zoobenthos were that; 1) community characteristics (abundance, richness, evenness and diversity) and structure of species assemblages between fish-present and fishless lakes should differ, as the result of the different top-down control from predation by fish and/or invertebrates and; 2) these differences in community characteristics and structure should occur during the complete duration of the ice-free season between the two types of lake.

2.2 Methods

2.2.1 Description of study lakes

The study site was located on the Boreal Shield bedrock, north of the Saguenay Fjord, Québec, Canada (Fig. 1, Chapitre I). Ten small oligotrophic lakes were sampled: five containing single fish population of brook trout (*Salvelinus fontinalis* Mitchill) and five fishless lakes. The distribution of fish in this area has been modulated by the lack of postglacial colonization by fish in reason of escarpments, which left some high altitude lakes to be colonized only by brook trout or to be fishless (Power *et al.* 1973). The presence and the absence of fish in the selected lakes were corroborated by the recreational fisheries statistics of brook trout between 1994 and 2003 (Table 1). The absence of fish was validated in June 2001 in four fishless lakes (de la Foulque, de la Manne, aux Nénuphars and de la Perdrix) using experimental gillnet (unpublished data, Ministère des Ressources Naturelles et de la Faune du Québec). The lakes have been selected for their comparable geographical and morphological parameters (Table 1, Chapitre I). All lakes were sampled four times during the ice-free season, which lasts from June to October in this area. The sampling periods were done during the following dates: 23 - 29 June, 14 - 19 July, 11 - 16 August and 8 - 13 September, hereafter referred to as June, July, August and September.

Lake depth and transparency were estimated using a graduated cable and Secchi disk. Water temperature, dissolved oxygen concentration, pH and conductivity were measured (Table 1, Chapitre I) with an YSI model 556 MPS (Yellow Springs Instrument Co., Yellow Springs, Ohio).

2.2.2 Sample collection

Nektonic (large zooplankters and swimming invertebrates) and benthic invertebrates were sampled randomly in the littoral zone of the lakes, at 1 m depth and 5 m away from the shoreline. At each sampling time, in all the lakes, four nekton samples and three zoobenthos samples were collected with a dip net of 1 mm mesh size. Nektonic organisms were sampled by scanning the water column with the dip net and benthic organisms by dragging the bottom on 0.5 m. Organisms were anaesthetized with carbonated water and preserved in 4% buffered formaldehyde.

In laboratory, all nektonic organisms were identified, except for the samples with abundance over 200 organisms, which have been sub-sampled with a 500 ml Folsom's splitter. Benthic organisms were split into two size fractions of 1 mm – 6.3 mm and > 6.3 mm to optimize the identification of larger organisms that may have been scarcer. We sorted a minimum of 100 organisms in the 1 mm – 6.3 mm fraction by a quantitative fixed-count method used by the U.S. Geological Surveys (Moulton II *et al.* 2000). All the invertebrates were identified at the lowest taxonomic level, dependently of the phylum and the instars (see Annexes 2 and 3 from Drouin *et al.* 2006).

2.2.3 Data analyses

Data for nekton and zoobenthos were first analysed using a univariate approach. The abundance (total or group of organisms), species richness (S), Pielou's evenness index (*J'*) and Shannon diversity index (*H'*) were calculated for each sample. Variations among (1) treatments (fish-present lakes, fishless lakes), (2) individual lakes (5 lakes nested in each treatment), (3) sampling time (hereafter June, July, August, and September), (4) interactions between those factors, and (5) an error term were statistically verified using a three way partly nested analysis of variance test (ANOVA). The assumptions of homoscedasticity and normality were verified by the distribution of the residuals on the predicted values as suggested by Quinn and Keough (2002). A logarithmic transformation [ln (x + 0,01) or ln (x+ 1)] was used according to the statistical assumptions when necessary, and has been notified when necessary. *A posteriori* comparisons were made using the Tukey's test (Underwood 1997).

Data were then analysed using multivariate species assemblages, based on Bray-Curtis dissimilarity distances (Bray and Curtis 1957, Clarke 1993). From fourth-root transformed data ($\sqrt[4]{x}$), Bray-Curtis dissimilarity matrix were calculated using the statistical package PRIMER v.5 (Clarke and Warwick 1994, Clarke and Gorley 2001). This transformation has the propriety to assign more importance to less common species by down-weighting the importance of very abundant ones and to keep the abundance order (Clarke 1993, Clarke and Warwick 1994, Thorne *et al.* 1999). As suggested by Clarke and Warwick (1994), the taxa with a single occurrence were removed from the data set before computing the Bray-Curtis dissimilarity to reduce the noise in the matrix caused by very rare species. Test of significance were then sought using a permutational multivariate analysis of variance, to test variations of species assemblages among the studied factors and pairwise comparisons (PERMANOVA v.1.6; Anderson 2005, Anderson 2001, McArdle and Anderson 2001). Non-metric multidimensional scaling (nMDS) were used to produce two-dimensional ordinations of the dissimilarities between samples (Clarke 1993, Clarke and Warwick 1994, Clarke and Gorley 2001). The discriminating species between the species assemblages from Bray-Curtis dissimilarity matrix based on the fourth-root transformed data were identified by the SIMPER procedure (Clarke 1993, Clarke and Warwick 1994, Clarke and Gorley 2001).

2.3 Results

2.3.1 Nektonic communities

From all the taxa identified among the lakes and along sampling periods, cladocerans dominated the abundance of samples in fish-present and fishless lakes, with 76% and 77% respectively. Chironomids were the most abundant insect taxa in fish-present lakes, with a mean of 17% of the sample abundances and *Chaoborus* larvae accounted for least than 1%. In fishless lakes, chironomids accounted for 5% and *Chaoborus* larvae for 15% of the sample abundances. Insects other than dipterans composed on average 3% and 2% of the fish-present and fishless lakes samples, respectively. The mean total abundance of nektonic organisms showed no significant difference between the two types of lakes (Fig. 5, Table 6). Temporally, the abundance of organisms in both types of lake varied significantly among the sampling period (Table 6) and the Tukey's test showed that the total abundance was significantly lower in June, and reached a significant higher maximum in August. The abundance of *Chaoborus* larvae was significantly more abundant in fishless lakes, with no significant temporal change among the sampling time (Fig. 5, Table 6). The species richness (S), the diversity (*H'*) and the evenness (*J'*) were similar between the fish-present and the fishless lakes (Fig. 6, Table 7). The species richness of the two types of lakes varied among the sampling time (Table 7). From the Tukey's test, a higher number of species were found in August than for all the other sampling periods (Fig. 6). The differences among the nested lakes, as for the interactions among them and the sampling period, were high for each of these univariate characteristics (Table 7).

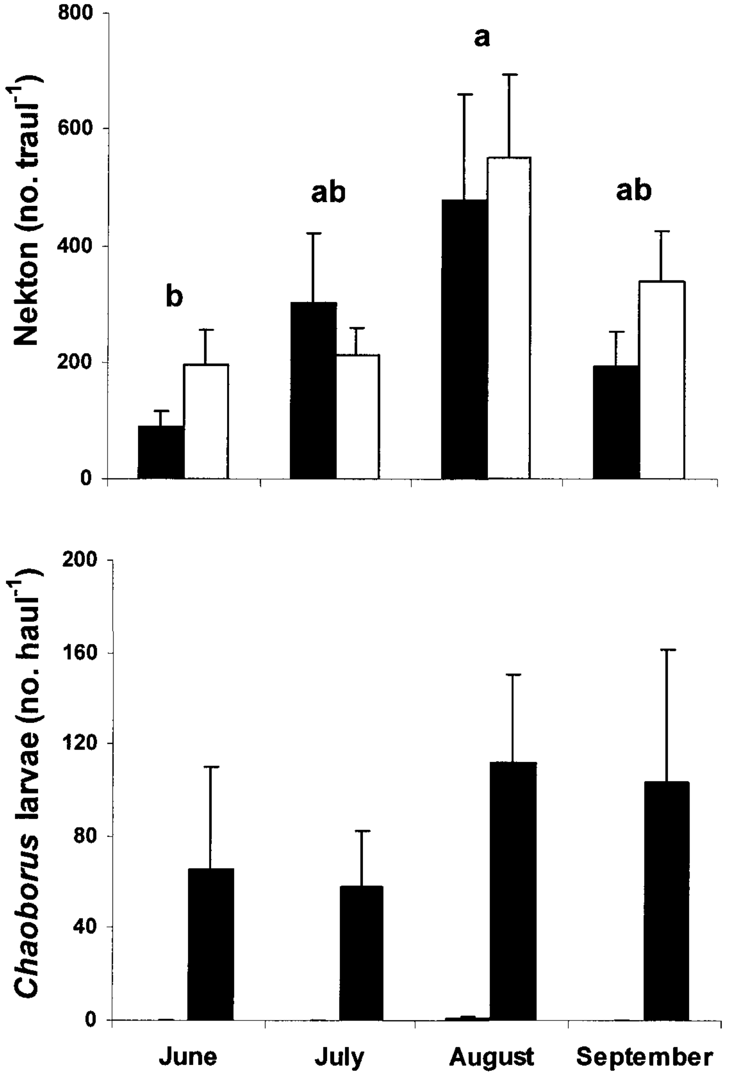

Figure 5. Average (+SE) abundance of nekton and *Chaoborus* larvae associated with lake types (fish-present (black), fishless lakes (white)) for each sampling time. The letters represent the result of the Tukey's test for the significant variation among the sampling time for both lake types. Bars not connected by same letter are significantly different.

Table 6. Results of three-way partly nested ANOVAs testing the effect of lake types (fish present, fishless), lake nested within the type, sampling time (June, July, August and September) and their interactions on the total abundance of nektonic organisms and *Chaoborus* larvae. Total nekton abundance data were transformed as ln(x+1) and *Chaoborus* larvae as ln(x+0.01).

		Nekton			*Chaoborus* larvae		
Source of variation	df	Mean square	*F*	*P*	Mean square	*F*	*P*
Type	1	7.39	0.58	0.4673	879.73	7.52	0.0254
Lake(Type)	8	12.69	9.11	<0.0001	117.04	37.41	<0.0001
Time	3	7.74	3.49	0.0311	4.94	0.77	0.5217
Type x Time	3	0.97	0.43	0.7285	1.52	0.24	0.8698
Lake(Type) x Time	24	2.22	1.59	0.0541	6.41	2.05	0.0061
Residual	120	1.39			3.13		

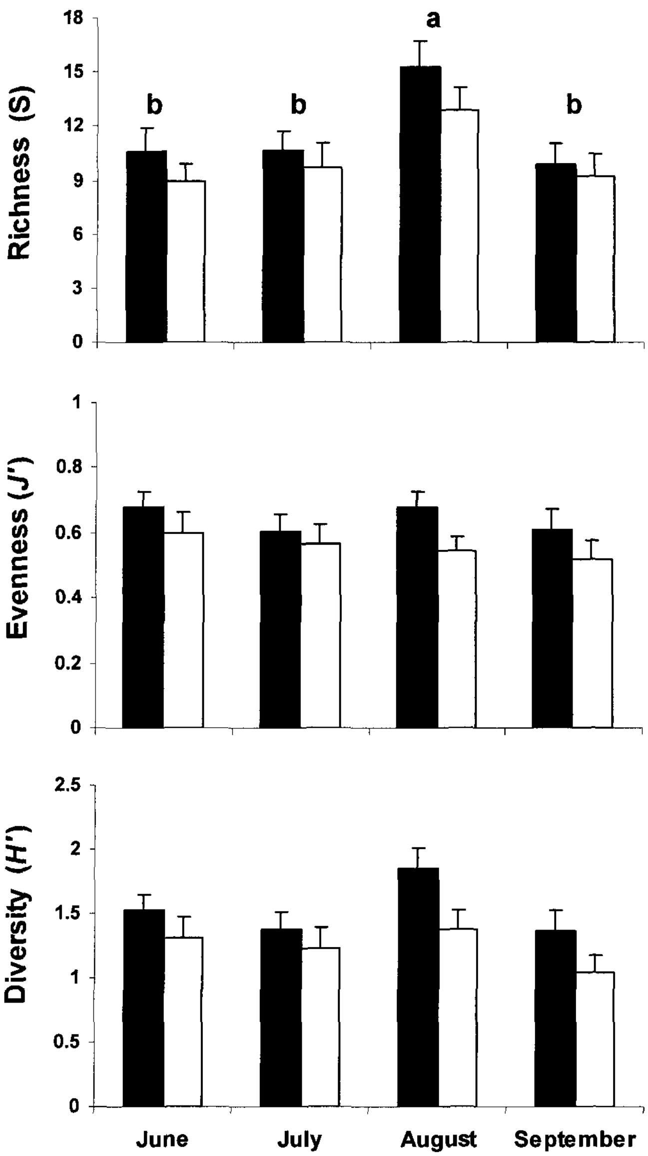

Figure 6. Average (+SE) univariate characteristics of nekton communities (S, *J'*, *H'*) in fish-present (black) and fishless lakes (white) for each sampling time. The letters represent the result of the Tukey's test for the significant variation among the sampling time for both lake types. Bars not connected by same letter are significantly different.

Table 7. Results of three-way partly nested ANOVAs testing the effect of lake type (fish present, fishless), lake nested within the type, sampling time (June, July, August and September) and their interactions on the nektonic organisms' univariate diversity indices (species richness, evenness, diversity).

Source of variation		Species richness (S)			Evenness (*J'*)			Diversity (*H'*)		
		Mean square	*F*	*P*	Mean square	*F*	*P*	Mean square	*F*	*P*
Type	1	87,02	2,40	0,1602	0,20	0,73	0,4172	2,52	1,82	0,2141
Lake(Type)	8	36,31	0,94	0,4842	0,27	6,67	<0,0001	1,39	3,43	0,0014
Time	3	207,78	16,67	<0,0001	0,04	0,44	0,7242	1,03	2,37	0,0959
Type x Time	3	7,68	0,61	0,6113	0,01	0,11	0,9527	0,19	0,43	0,7301
Lake(Type) x Time	24	12,46	0,32	0,9989	0,08	2,07	0,0054	0,43	1,07	0,3829
Residual	120	38,51			0,04			0,40		

The permutational multivariate analysis of variance revealed that the nektonic species assemblages in fish-present lakes were significantly different from those in fishless lakes (Table 8). This result was clearly visible on the non-metric multidimensional scaling (nMDS) ordination, which showed a distinct cluster for each type of lake (Fig. 7). The stress value of 0.23 is acceptable for the illustration of 160 samples, and indicates how faithfully the 2-dimensional ordination is representative of the multivariate ordination, (Clarke and Warwick 1994). The interaction between the type of lake and the sampling periods was significant (Table 8). *A posteriori* pairwise comparisons revealed that nekton assemblages in fishless lakes were similar among sampling periods, contrary to the species assemblages of fish-present lakes (Table 9). The nekton assemblages of lakes with fish in August and in September were significantly different between each other as well as to those found in June and in July (Table 9) Assemblages in June and July were not different. However, the species assemblages between fish-present and fishless lakes were significantly different at each sampling period. From SIMPER analysis, the average dissimilarity between the nekton assemblages of the two types of lakes was of 86.12 % (Table 10). The more discriminating taxa were *Daphnia pulex* Leydig, which was more abundant in fish-present lake assemblages and *Holopedium gibberum* Zadach, *Chaoborus* larvae, *Sida crystallina* Müller and *Latona setifera* Müller, which were more abundant in fishless lake assemblages (Table 10).

Table 8. Results of the nonparametric multivariate analyses of variance (PERMANOVA) testing the effect of lake types(fish present, fishless), lake nested within the type, sampling time (June, July, August and September) and their interactions on nektonic species assemblages based on the Bray-Curtis dissimilarity matrix. The species assemblages were calculated on fourth-root transformed data ($\sqrt[4]{x}$).

	Nekton assemblages			
Source of variation	df	Mean square	Pseudo-*F*	*P* (perm)
Type	1	47051.40	3.68	0.0383
Lake(Type)	8	12776.86	5.09	<0.0001
Time	3	11625.40	3.63	<0.0001
Type x Time	3	4628.03	1.45	0.0244
Lake(Type) x Time	24	3199.31	1.27	0.0002
Residual	120	2508.02		

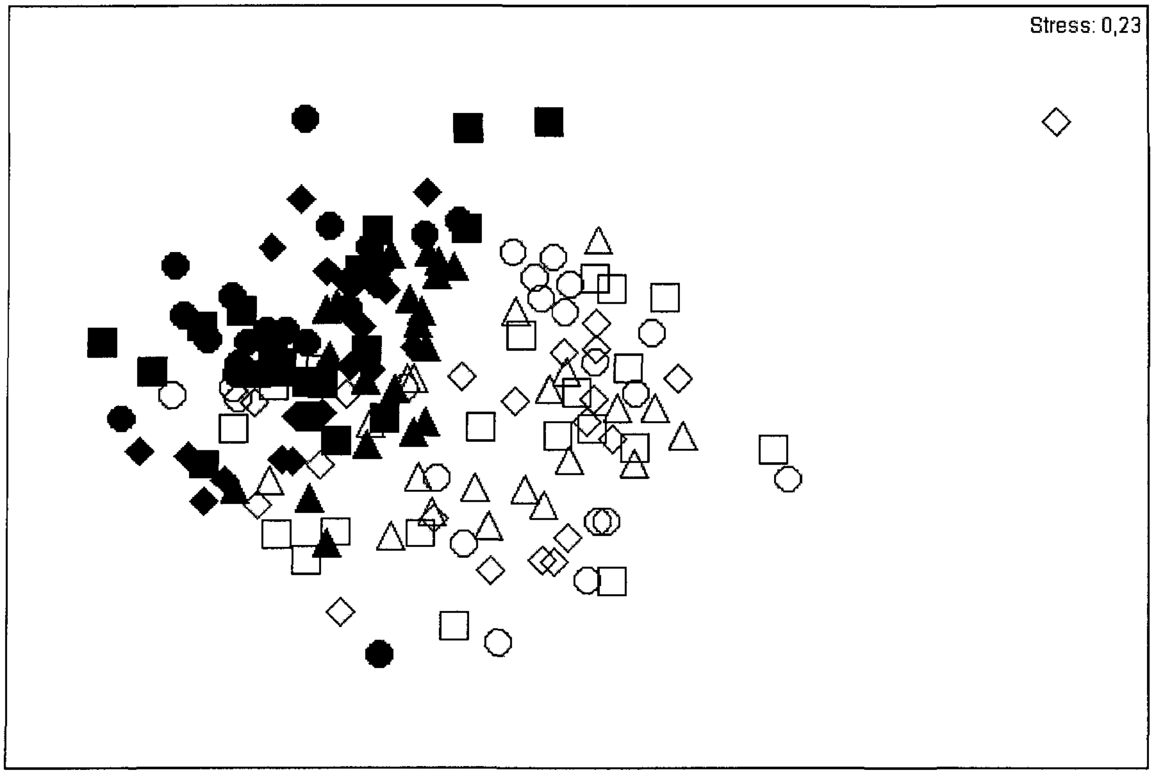

Figure 7. Non-metric multidimensional scaling (nMDS) ordination based on the Bray-Curtis dissimilarity matrix calculated on fourth-root transformed data ($\sqrt[4]{x}$) for nekton samples collected in fish-present (black) and fishless lakes (white) during the ice-free season (circles = June, squares = July, triangles = August, diamonds = September).

Table 9. Results of *a posteriori* pairwise comparisons testing the interaction between lake types and sampling time for nekton species assemblages. Comparisons were done between sampling time for each lake types (fish-present, fishless) and among fish-present and fishless lakes at each sampling time (June, July, August and September).

Comparisons	Fish-present		Fishless	
	t	*P* (perm)	*t*	*P* (perm)
June - July	1.07	0.3201	0.92	0.5427
June - August	1.67	0.0087	1.21	0.1680
June - September	1.81	0.0087	0.93	0.5776
July - August	1.33	0.0403	1.05	0.3920
July - September	1.64	0.0241	0.91	0.5837
August - September	1.54	0.0238	0.81	0.7617

	Fish-present - Fishless	
	t	*P* (perm)
June	1.60	0.0380
July	1.63	0.0324
August	1.61	0.0093
September	1.75	0.0387

Table 10. Dissimilarity percentages (%) of nekton assemblages between lake types based on fourth-root transformed data ($\sqrt[4]{x}$) and taxa with the greatest contribution to the dissimilarity.

Species	Average dissimilarity of 86.12 %	
	Contribution %	Cumulative %
Daphnia pulex[†]	8.01	8.01
Chaoborus sp.*	6.31	14.32
Holopedium gibberum *	4.73	19.05
Sida crystallina *	4.18	23.23
Latona setifera *	3.24	26.48

[†] More abundant in fish-present lakes

* More abundant in fishless lakes

2.3.2 Zoobenthic communities

Chironomids were the most abundant taxa identified in zoobenthos samples from fish-present and fishless lakes and represented respectively 54% and 51% of the mean abundance. Molluscs composed on average 21% of the fish-present and 9% of the fishless lake samples. Amphipods composed on average 9% of the fishless lake samples and 3% of the fish-present lake samples. Non-dipterans insects accounted for at least 10% of the zoobenthic organisms in the samples in fish-present and fishless lakes samples. The abundance of each non-dipteran insect group was analysed separately and no differences were observed between the types of lakes for the mayflies (*Ephemeroptera*), the caddisflies (*Trichoptera*), the dragonflies (*Odonata*) and the alderflies (*Megaloptera*) (Table 11). The water boatmen (*Corixidae*, *Hemiptera*) and the diving beetles (*Dytiscidae*, *Coleoptera*) were significantly more abundant in fishless lakes (Table 11). The total abundance and mean diversity indices (S, *J'*, *H'*) were not significantly different between lake types and there were no interactions among this factor and sampling period (Table 12, Fig. 8). Significant temporal variations of mean total abundance, mean species richness and mean Shannon-Wiener diversity index were observed for both types of lake (Table 12). According to the Tukey's test, the mean total abundance of benthic organisms was significantly lower in June than in other periods (Fig. 8). The mean number of species present was significantly lower in June than in July and in September. The mean diversity index value found in June was significantly lower than in July. As for the nektonic organisms, the variation among the nested lakes was high for the abundance and diversity indices (Table 12).

Table 11. Results of three-way partly nested ANOVAs testing the effect of the lake types (fish present or fishless), lake nested within the type, sampling time (June, July, August and September) and their interactions on the abundance of different groups of benthic organisms. Abundance data were all transformed as ln(x=0.01) except for *Chironomidae* which were transformed as ln(x+1).

		Chironomidae			*Mollusca*			*Amphipoda*		
Source of variation	df	Mean square	*F*	*P*	Mean square	*F*	*P*	Mean square	*F*	*P*
Type	1	3.66	1.45	0.2627	257.21	7.11	0.0285	1.45	0.02	0.8807
Lake(Type)	8	2.53	3.26	0.0029	36.16	6.11	<0.0001	60.21	28.07	<0.0001
Time	3	1.87	2.60	0.0756	5.83	1.02	0.3999	26.27	5.39	0.0056
Type x Time	3	0.46	0.63	0.6002	3.80	0.67	0.5806	6.55	1.34	0.2833
Lake(Type) x Time	24	0.72	0.93	0.5634	5.70	0.96	0.5218	4.87	2.27	0.0035
Residual	80	0.77	0.77		5.92			2.14		

		Coleoptera			*Ephemeroptera*			*Hemiptera*		
Source of variation	df	Mean square	*F*	*P*	Mean square	*F*	*P*	Mean square	*F*	*P*
Type	1	113.87	15.29	0.0045	13.14	1.55	0.2488	484.20	56.55	<0.0001
Lake(Type)	8	7.45	0.89	0.5286	8.49	0.54	0.8231	8.56	1.65	0.1230
Time	3	34.69	3.38	0.0348	124.47	9.93	0.0002	57.06	13.15	<0.0001
Type x Time	3	27.85	2.71	0.0675	15.79	1.26	0.3104	57.06	13.15	<0.0001
Lake(Type) x Time	24	10.27	1.23	0.2445	12.54	0.80	0.7298	4.34	0.84	0.6794
Residual	80	8.36			15.73			5.18		

		Megaloptera			*Odonata*			*Trichoptera*		
Source of variation	df	Mean square	*F*	*P*	Mean square	*F*	*P*	Mean square	*F*	*P*
Type	1	21.52	0.54	0.4827	36.34	0.82	0.3929	65.00	5.18	0.0524
Lake(Type)	8	39.73	3.03	0.0050	44.56	4.48	0.0002	12.55	1.50	0.1713
Time	3	20.33	1.63	0.2092	45.57	5.39	0.0056	59.73	5.03	0.0076
Type x Time	3	3.98	0.32	0.8117	7.90	0.93	0.4392	12.52	1.05	0.3867
Lake(Type) x Time	24	12.49	0.95	0.5344	8.45	0.85	0.6656	11.87	1.42	0.1264
Residual	80	13.11			9.95			8.38		

Table 12. Results of three-way partly nested ANOVAs testing the effect of lake types (fish present or fishless), lake nested within the type, sampling time (June, July, August and September) and their interactions on the zoobenthos' univariate characteristics (abundance, species richness, evenness and diversity).

Source of variation		Abundance			Species richness (S)		
		Mean square	F	P	Mean square	F	P
Type	1	2.02	1.35	0.2791	44.41	0.69	0.4286
Lake(Type)	8	1.50	3.69	0.0046	63.88	1.49	0.1093
Time	3	3.71	9.13	0.0003	281.19	6.56	0.0021
Type x Time	3	0.78	1.91	0.1550	35.61	0.83	0.4901
Lake(Type) x Time	24	0.41	0.83	0.6873	42.87	1.15	0.3171
Residual	80	0.49			37.41		

Source of variation		Diversity (H')			Evenness (J')		
		Mean square	F	P	Mean square	F	P
Type	1	0.24	0.31	0.5913	0.004	0.08	0.7838
Lake(Type)	8	0.75	8.72	<0.0001	0.05	8.60	<0.0001
Time	3	0.39	4.47	0.0125	0.002	0.40	0.7581
Type x Time	3	0.10	1.13	0.3583	0.004	0.73	0.5425
Lake(Type) x Time	24	0.09	0.74	0.8006	0.006	0.74	0.7975
Residual	80	0.12			0.008		

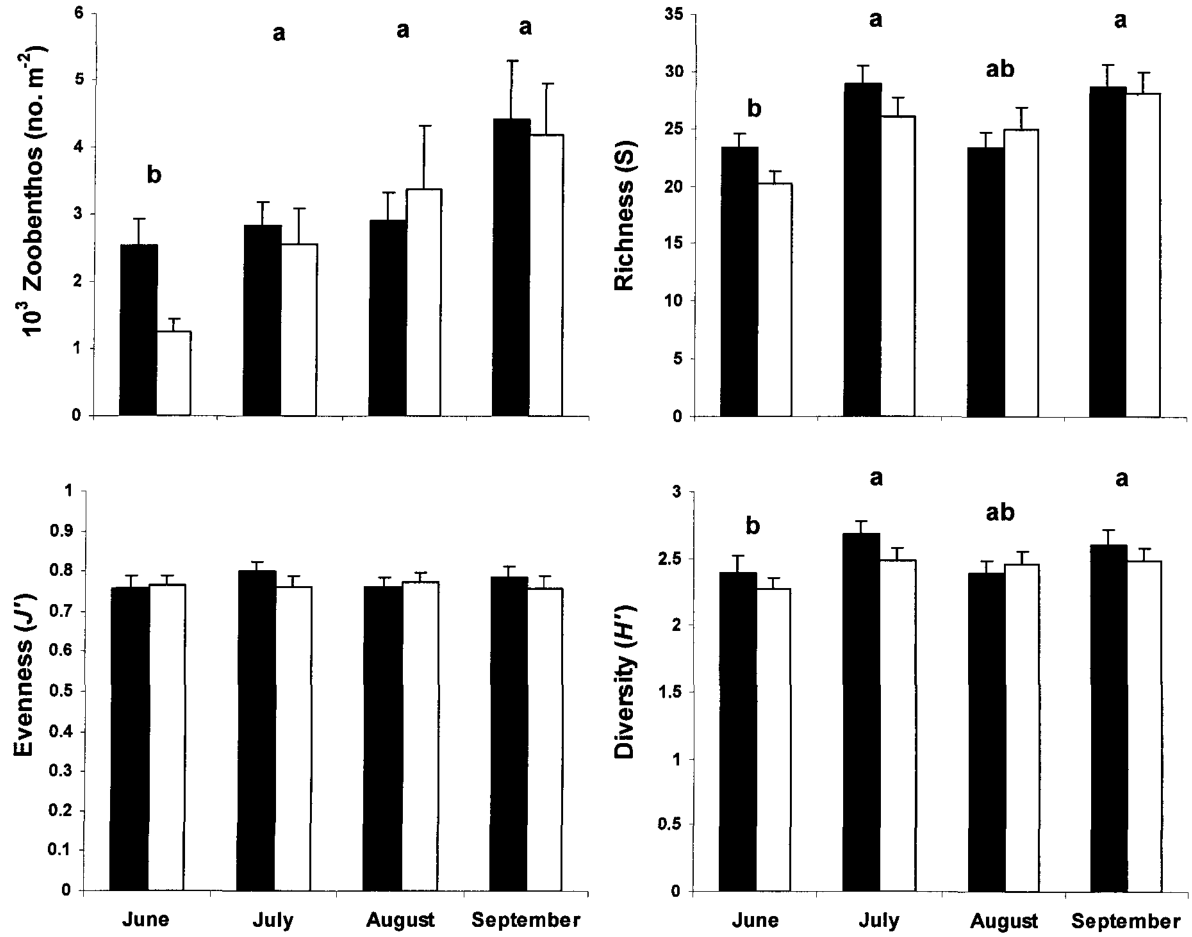

Figure 8. Average (+SE) univariate characteristics of zoobenthos communities (abundance, S, *J'*, *H'*) in fish-present (black) and fishless lakes (white) for each sampling time. The letters represent the result of the Tukey's test for the significant variation among the sampling time for both lake types.

The permutational multivariate analysis of variance revealed that the benthic species assemblages in fishless lakes were significantly different from those in fish-present lakes (Table 13). This relation has not been graphically represented since the stress value of 0.28 indicates that the nMDS was not a good two-dimensional representation of the multidimensional ordination and for this reason was not showed (Clarke and Warwick 1994). The assemblages varied significantly among the sampling time (Table 13). From the pairwise *a posteriori* comparisons (PERMANOVA), the zoobenthos assemblages were significantly different among all the sampling time, excepted for the assemblages found in August and September which were similar (Table 14). According to the SIMPER procedure, the average dissimilarity in zoobenthos species assemblages between fish-present and fishless lakes was of 62.52 % (Table 15). The most discriminating taxa of this average dissimilarity were Pelecypoda, *Psectrocladius* sp. and *Cladotanytarsus* sp., which were more abundant in fish-present assemblages, and *Hyalella azteca* Saussure, which was more abundant in fishless lakes (Table 15).

Table 13. Results of the nonparametric multivariate analyses of variance (PERMANOVA) testing the effect of lake types (fish present or fishless), lake nested within the type, sampling time (June, July, August and September) and their interactions on zoobenthos species assemblages based on the Bray-Curtis dissimilarity matrix. The species assemblages were calculated on fourth-root transformed data ($\sqrt[4]{x}$).

	Zoobenthos assemblages			
Source of variation	df	Mean square	Pseudo-*F*	*P* (perm)
Type	1	8753,01	1,79	0,0231
Lake(Type)	8	4892,14	1,80	0,0002
Time	3	7837,28	2,99	<0,0001
Type x Time	3	2701,66	1,03	0,3908
Lake(Type) x Time	24	2618,13	0,96	0,6563
Residual	80	2717,32		

Table 14. Results of the pairwise *a posteriori* comparisons among the level of the significant factor «time» on zoobenthos species assemblages.

Comparisons	*t*	*P* (perm)
June - July	1.31	0.0227
June - August	1.50	0.0028
June - September	1.83	0.0001
July - August	1.55	0.0008
July - September	1.77	0.0001
August - September	1.19	0.1141

Table 15. Dissimilarity percentages (%) of zoobenthos assemblages between lake types based on fourth-root transformed data ($\sqrt[4]{x}$) and taxa with the greatest contribution to the dissimilarity.

Species	Average dissimilarity of 62,52 %	
	Contribution %	Cumulative %
Pelecypoda[†]	2,67	2,67
Hyallela azteca *	2,51	5,18
Psectrocladius sp.[†]	2,19	7,37
Cladotanytarsus sp.[†]	2,17	9,54

[†] More abundant in fish-present lakes

* More abundant in fishless lakes

2.4 Discussion

Upper littoral zones of fish-present and fishless lakes in the study area had a similar number of organisms, species richness, evenness and diversity, despite marked differences in multivariate species assemblages. Evidence of top-down effect of brook trout predation on littoral invertebrates was linked with the indicators used. The distinctions between the nektonic and benthic assemblages from fish-present and fishless lakes were mainly related to differences in abundance of specific taxa. Moreover, a high variability in the community characteristics and species assemblages among individual lakes was observed. Variability within space (individual lakes) most certainly affects the demonstration of a general pattern for a type of lake; nevertheless this reflects the natural fluctuations that can take place in communities. The same seasonal variations were generally observed in the two types of lakes for the considered variables.

2.4.1 Nekton community structure

The nekton community characteristics and structure were similar to those observed in zooplankton of the limnetic area, with the exception of the abundance (Drouin *et al.* submitted). As in the limnetic area, in this study it was observed that *Daphnia pulex* was more abundant in presence of fish rather than in absence and this could be correlated with the high density of *Chaoborus* larvae present into the water column during daytime. Fish are known to influence *Chaoborus* larvae composition and distribution (Pope *et al.* 1973, von Ende 1979, Wissel *et al.* 2003) and some *Chaoborus* species make diurnal migration to avoid fish predation (LaRow 1968, 1969). Their absence from the nekton samples of fish-present lakes may result from direct predation by brook trout or from behavioural change as a response to fish predation. Additionally, studies have demonstrated the capacity of *Chaoborus* larvae to regulate *Daphnia pulex* populations (Wissel and Benndorf 1998, MacKay *et al.* 1990). Thus, the brook trout could indirectly regulate *Daphnia* population through its influence on a predacious invertebrate density, *Chaoborus* larvae. Other large cladocerans contributed to the dissimilarity between nekton assemblages by being more abundant in fishless lakes. The abundance of *Holopedium gibberum*, *Sida crystallina* and *Latona setifera* seemed more affected by biotic interactions that occurred in fish-present lakes communities.

2.4.2 Zoobenthos community structure

It is evident from previous studies that single brook trout populations preferentially feed in the littoral zone of lakes, mainly on macroinvertebrates (Tremblay and Magnan 1991, Lacasse and Magnan 1992). Our results obtained through the study of the zoobenthic community show that the effect of predation by brook trout could modify the species assemblages, as for the nektonic community. The taxa that most contributed to the dissimilarity between the species assemblages were *Hyalella azteca* (amphipod), which was more abundant in the fishless lakes assemblages, and Pelecypoda (mollusc), *Psectrocladius* sp. and *Cladotanytarsus* sp. (chironomids), which were more abundant in the fish-present lakes' assemblages. The low abundance of *Hyalella azteca* in the fish-present assemblages could be associated to direct predation by fish, based on other studies that have noted their consumption by salmonids (Luecke 1990, Lacasse and Magnan 1992). As for the nekton communities, the patterns observed in the benthic assemblages are probably not all related to the direct effect of fish predation. This implies that other biotic factors such as competition with other taxa or invertebrate predation must be involved in the structuring of species assemblages. A number of studies have observed that fish can have a negative impact on predacious chironomids (Gilinsky 1984, Goyke and Hershey 1992). Generally, predators are more mobile and can be detected more effectively by fish, which are visual predators (Zaret 1980, Blois-Heulin *et al.* 1990, Wellborn *et al.* 1996). The depletion of predacious chironomids could be advantageous to collectors such as *Psectrocladius* sp. and *Cladotanytarsus* sp., which could benefit from the reduction of predation pressure exerted on them. Also, the abundance and the species composition of prey are not the only characteristics of populations where predation can have an effect. For example, Wellborn (1995) has observed that different predator composition can influence individual-size and life history in populations of *Hyalella* sp. When associated to invertebrate predators (fishless habitat), the amphipod populations had a large morphotype, while when associated to fish predators (high density of centrarchid fish), populations had a small morphotype (Wellborn 1995). However, the adaptation of body size to predator composition also seems to depend on the intensity of predation pressure as the large morphotype of *Hyalella* has been observed in presence of salmonid fish which weakly feed on amphipod (Strong 1972).

Predation by fish can have negative effects on the abundance of the larger invertebrates (mainly insect taxa) (Evans 1989, Blois-Heulin *et al.* 1990, Bendell and McNicol 1995, Tate and Hershey 2003) and change their species composition (McPeek 1990). In our study, because they represented a small proportion of the samples and were not present in all of them, their overall weight in the dissimilarity between the species assemblages over the entire community was not important (see Clarke and Warwick 1994). The total abundance of non-dipteran insects from the zoobenthos samples was similar between lake types, but when analysed separately, we observed a significantly higher abundance of hemipterans and coleopterans in fishless lakes, similarly as in other studies (Evans 1989, Bendell and McNicol 1995, Tate and Hershey 2003). Several large insect taxa are predators and the effect of fish on them could be important in a top-down view. By preying on other predators, fish can indirectly control untargeted prey populations and thus affect the community structure. Many studies have reported this type of population control by showing increased proportions of predacious invertebrates in fishless lakes (Gilinsky 1984, Goyke and Hershey 1992, Evans 1989, Blois-Heulin *et al.* 1990, Tate and Hershey 2003, Rennie and Jackson 2005). Well structured patterns of the top-down control on benthic communities are harder to develop than for the nekton or the zooplankton communities since they have not been studied as much, because of the complexity of the littoral habitat and the life cycles of the organisms that are present.

2.4.3 Predation, diversity and complexity in littoral area

The brook trout affected the abundance of few invertebrate species and the multivariate species' assemblages; however, this was not reflected on the diversity patterns of the littoral communities. Predation interactions in freshwater habitat could be the cause at the origin of the diversity or a factor maintaining it in a community (Thorp 1986). Thus, the post-glacial colonization by fish may have affected diversity through selective feeding or coevolution between predator-prey interactions, but predation is not necessarily a factor that regulates diversity in the current communities. According to Thorp (1986), to be the agent controlling diversity, a predator has to exclude some species (or at least reduce the rate of demographic expansion) and competitive exclusion has to occur. By suppressing dominant competitive relationships, the predator could lead the community to experience an increase in diversity (Paine 1966, Thorp 1986). In this study, no difference of diversity in littoral communities between fish-present and fishless lakes was observed. It can be expected that predation had no effect on a dominant competitive relationship or that the top-down control in fish-present or fishless lakes had similar effect on biotic interactions. However, Drouin *et al.* (submitted) observed from the zooplankton in the limnetic area of our fishless lakes that *Chaoborus americanus* contributed to alter a well known competitive relationship among *Daphnia* and small herbivores, but this had no effect on the species richness, evenness or diversity when compared to fish-present lake communities. Thus, it seems that predation could regulate the community structure without influencing the diversity or by being detectable over this variable.

Other studies have also mentioned the complexity in space as a factor which can limit the effect of predation on littoral community in freshwater habitat (Mittelbach 1981, Thorp and Bergey 1981, Luecke 1990, Rennie and Jackson 2005). The spatial complexity in the littoral habitat leads to an increase in the amount of refuges for prey and thus restrains the effect of predation by brook trout on prey populations (Mittelbach 1981, Thorp and Bergey 1981, Gilinsky 1984, Luecke 1990, Rennie and Jackson 2005). Prey species with efficient hiding strategies that can find refuges and live in a complex spatial habitat could maintain population density in presence of fish as high as in fishless lakes. Luecke (1990) has observed that the *H. azteca* residing in areas with little space-refuges were strongly depleted by cutthroat trout (*Oncorhynchus clarki* Richardson). Moreover, the utilisation of space-refuges could be more appropriate against fish predation than invertebrate predation (Rennie and Jackson 2005) and thus the spatial complexity can be an important element maintaining the prey population densities in fish-present lakes.

According to Thorp and Bergey (1981), the food web complexity in the littoral zone of freshwater habitat can also be a factor which can buffer the effect of fish predation on invertebrate communities. There are many invertebrate predator taxa in the benthic communities with different feeding strategies which, coupled with the spatial complexity of the environment, could limit the monopolistic control of resources by a single predator species.

2.4.4 Conclusion

The results of our study showed the sensitivity and the effectiveness of multivariate analyses over the univariate diversity indices in the study of biological interactions at the community level. Species richness and diversity are widely used in impact assessment studies because of their ease of interpretation, but these indices are not always representative of the ecological importance of a community or a change in community structure (Downes *et al.* 2002). Similar results were observed for the limnetic zooplanktonic community by Drouin *et al.* (submitted) in the same lake as in this study. The distinction between the nekton and zoobenthic communities from fish-present and fishless lakes was observed as differences in the species assemblages throughout the ice-free period. Understanding the processes controlling the diversity in freshwater habitat requires more investigations.

CONCLUSION GÉNÉRALE

Les résultats obtenus dans le cadre de ce mémoire ont démontré qu'il existe des différences entre la structure des communautés zooplanctoniques, nectoniques et benthiques des lacs avec et sans poissons de la région du Saguenay. Toutefois, cette conclusion n'aurait pu être avancée sans l'application d'une approche multivariée pour caractériser les assemblages d'espèces. Chez les trois communautés d'invertébrés étudiées, l'abondance (sauf pour le zooplancton) et les mesures de diversité univariées (richesse spécifique S, équitabilité de Pielou J', diversité de Shannon-Wiener H') étaient similaires entre les deux types de lacs. Les assemblages d'espèces étaient, quant à eux, significativement différents entre les lacs avec et sans poissons. L'approche multivariée s'est avérée plus sensible pour distinguer les différences entre les communautés d'invertébrés des lacs étudiés. La mesure d'assemblage d'espèces qui a été utilisée, soit la dissimilarité de Bray-Curtis, se rapporte à la présence et à l'absence des taxons répertoriés dans l'ensemble des échantillons ainsi qu'à leur abondance respective. Par comparaison un à un des assemblages, la similarité ou dissimilarité était par la suite établit entre chacun des échantillons et pour l'ensemble de ceux-ci. Contrairement aux assemblages d'espèces, les indices de diversité utilisés sont avant tout des mesures comparatives se rapportant au nombre total d'espèces et à leur proportion respective, sans liens qualitatif avec les taxons répertoriés. Pour ces raisons, les indices de diversité, bien que largement utilisé, ne sont souvent pas démonstratif de toute la complexité et l'authenticité d'un milieu (voir Downes *et al.* 2002). Cette étude démontre bien l'importance du choix des variables dépendantes lors de l'évaluation de l'intégrité biotique d'un milieu. L'utilisation d'assemblage d'espèces comporte cependant aussi certaine limite. Par exemple, il est difficile de quantifier la variation temporelle entre les assemblages sur une échelle linéaire. Il pourrait être pertinents, à l'aide d'un logiciel d'analyse adéquat, de réussir à obtenir cette mesure afin d'être en mesure de mieux identifier les mécanismes derrières ces changements.

L'arrangement de l'échantillonnage (design expérimental) a permis de distinguer les différences entre les deux types de lacs, mais aussi d'observer la variabilité des communautés dans le temps et l'espace. Selon les patrons biologiques observés, il existe des différences significatives entre les assemblages d'espèces provenant de lacs avec et sans poissons, mais aussi entre les lacs d'un même groupe. Ainsi, même si les lacs sans poissons étudiés étaient pour la plupart très significativement différents entre eux, ils étaient aussi significativement différents de ceux retrouvés dans les lacs avec poissons. Temporellement, des variations significatives ont été observées entre les différents moments d'échantillonnage, mais la distinction entre les assemblages d'espèces des deux types de lac demeurait généralement robuste à ces changements. L'observation de ces patrons biologiques permet d'avoir une idée de l'échelle spatiale et temporelle à laquelle la distinction entre les deux types de lac est applicable. Aussi, les tests d'hypothèses relatives aux patrons biologiques sont à la base de la démarche scientifique. Sans d'abord faire l'observation de phénomène, il est difficile (voir douteux) de développer des modèles expliquant les mécanismes biologiques qui régissent les populations, communautés et écosystèmes (Underwood *et al.* 2000). Ces tests sont d'autant plus pertinent lorsqu'ils tiennent compte de la variabilité spatio-temporelle qui découle en nature (Underwood *et al.* 2000). La variabilité naturelle qui existe entre deux espaces et/ou intervalles de temps est souvent perçue comme une entrave à la distinction de différences significatives, mais est toutefois réelle et imprédictible (Underwood *et al.* 2000). Bien au contraire, la variabilité pourrait être considérée comme une valeur intrinsèque pouvant servir à qualifier une population ou encore une communauté.

D'après les comparaisons faites dans cette étude, il est peu probable que les ensemencements de lacs sans poissons effectués jusqu'à maintenant aient causé l'extinction d'espèces à l'échelle régionale. Toutefois, il est primordial de rester vigilant face à cette activité. Les lacs avec omble de fontaine sont indigènes dans la région du Saguenay et de ce point de vue, l'ensemencement de cette espèce dans les lacs sans poissons ne crée pas un milieu exotique à l'échelle régionale. Cependant, cette activité peut contribuer à la diminution de la diversité des habitats aquatiques à cette échelle. Une étude réalisée par le laboratoire d'écologie aquatique de l'UQAC a décelé que les assemblages d'espèces zooplanctoniques présents dans les lacs sans poissons, suite à leur ensemencement, n'étaient pas dissociables de ceux retrouvés dans les lacs avec des populations naturelles d'omble de fontaine (Archambault et Sirois, données non publiées). Il est donc possible de croire que l'introduction de poissons dans des lacs qui en étaient dépourvus affecte également les communautés nectoniques et benthiques. De plus, selon les travaux de Shurin et Allen (2001) la relation de la diversité entre l'échelle locale et régionale n'est pas nécessairement linéaire. Ainsi, bien que les valeurs moyennes des indices de diversité chez les communautés d'invertébrés étudiées étaient généralement similaires entre les deux types de lacs, il est possible que ce patron soit différent à plus grande échelle. La présence de lacs avec et sans poissons soutiendrait l'hétérogénéité des habitats disponibles et donc favoriseraient la création de refuges spatiaux. Par ce fait, certaines espèces qui ne peuvent coexister localement en présence d'un prédateur ou d'un compétiteur pourraient être présentes régionalement et ainsi augmenter la diversité biologique à l'échelle régionale (Shurin et Allen 2001).

La présente étude se veut essentiellement descriptive et amène une bonne comparaison des communautés d'invertébrés entre les lacs avec et sans poissons. Toutefois, aucunes mesures directes n'ont été prises quant au taux de prédation ou à la sélection des proies. La suite logique de cette étude serait de tester les modèles de prédation suggérés par les patrons biologiques, dont ceux pour l'omble de fontaine et les larves de *Chaoborus americanus*. L'introduction expérimentale de poissons dans des lacs sans poissons et le retrait de poissons des lacs avec poissons pourraient permettre de tester *in situ* ces modèles.

RÉFÉRENCES

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32-46.

Anderson, M. J. 2005. PERMANOVA: a FORTAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, New Zealand.

Angermeier, P. L. et Karr, J. R. 1994. Biological integrity versus biological diversity as policy directives. BioScience 44: 690-697.

Arvola, L. et Salonen, K. 2001. Plankton community of a polyhumic lake with and without *Daphnia longispina*. Hydrobiologia 445: 141-150.

Bahls, P.F. 1992. The status of fish populations and management of high mountain lakes in western United States. Northwest Science 66: 183-193.

Bendell, B. E. et McNicol, D. K. 1995. Lake acidity, fish predation, and the distribution and abundance of some littoral insects. Hydrobiologia 302: 133-145.

Blois-Heulin, C., Crowley, P. H., Arrington, M. et Johnson, D. M. 1990. Direct and indirect effects of predators on the dominant invertebrates of two freshwater littoral communities. Oecologia 84: 295-306.

Bourke, P., Magnan, P. et Rodriguez, M. 1999. Phenotypic responses of lacustrine brook charr in relation to the intensity of interspecific competition. Evolutionary ecology 13: 19-31.

Bradford, D. F., Cooper, S. D., Jenkins, T. M., Kratz, J. K., Sarnelle, O. et Brown, A. D. 1998. Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes. Canadian Journal of Fisheries and Aquatic Sciences 55: 2478-2491.

Bray, J. R. et Curtis, J. T. 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs 27: 325-349.

Brooks, J. L. et Dodson, S. I. 1965. Predation, body size, and composition of plankton. Science 150: 28-35.

Carpenter, S. R. 1988. Complex interactions in lake communities. Springer-Verlag, New York.

Carpenter, S. R., Kitchell, J. F. et Hodgson, J. R. 1985. Cascading trophic interactions and lake productivity: fish predation and herbivory can regulate lake ecosystems. Bioscience 35: 634-638.

Chess, D. W., Gibson, F., Scholz, A. T. et White, R. J. 1993. The introduction of lahontan cutthroat trout into a previously fishless lake: feeding habits and effects upon the zooplankton and benthic community. Journal of Freshwater Ecology 8: 215-225.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Clarke, K. R. et Gorley, R. N. 2001. Primer *v*5: User manual/tutorial. Primer-E Ltd., Plymouth.

Clarke, K. R. et Warwick, R. M. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth.

COSEWIC 2003. Canadian Species at Risk, November 2003. Committee on the Status of Endangered Wildlife in Canada.

Dodson, S. I. 1974. Zooplankton competition and predation: An experimental test of the size-effiency hypothesis. Ecology 55: 605-613.

Donald, D. B., Vinebrooke, R. D., Anderson, R. S., Syrgiannis, J. et Graham, M. D. 2001. Recovery of zooplankton assemblages in mountain lakes from the effects of introduced sport fish. Canadian Journal of Fisheries and Aquatic Sciences 58: 1822-1830.

Downes, B. J., Barmuta, L. A., Fairweather, P. G., Faith, D. P., Keough, M. J., Lake, P. S., Mapstone, B. D. et Quinn, G. P. 2002. Monitoring ecological impacts: concepts and practice in flowing waters. Cambridge University Press, Cambridge.

Drake, D. C. et Naiman, R. J. 2000. An evaluation of restoration efforts in fishless lakes stocked with exotic trout. Conservation Biology 14: 1807-1820.

Drouin, A., Sirois, P. et Archambault, P. 2006. Structure des communautés d'invertébrés et des espèces d'amphibiens dans des lacs avec et sans omble de fontaine (*Salvelinus fontinalis*) en forêt boréale. Canadian Technical Report of Fisheries and Aquatic Sciences, 2628.

Dunham, J. B., Pilliod, D. S. et Young, M. K. 2004. Assessing the consequences of nonnative trout in headwater ecosystems in Western North America. Fisheries 29: 18-25.

Edmondson, W. T. 1959. Fresh-water biology. John Wiley & Sons Inc., New York.

Einarsson, A. 1987. Distribution and movements of Barrow's Goldeneye *Bucephala islandica* young in relation to food. IBIS 130: 153-163.

Eriksson, M. O. G. 1978. Lake selection by Goldeneye ducklings in relation to the abundance of food. Wildfowl 29: 81-85.

Eriksson, M. O. G. 1983. The role of fish in the selection of lakes by nonpiscivorous ducks: Mallard, Teal and Goldeneye. Wildfowl 34: 27-32.

Evans, R. A. 1989. Response of limnetic insect populations of two acidic, fishless lakes to liming and brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 46: 342-351.

Fedorenko, A. Y. 1975a. Feeding characteristics and predation impact of *Chaoborus* (Diptera, Chaoboridae) larvae in a small lake. Limnology and Oceanography 20: 250-258.

Fedorenko, A. Y. 1975b. Instar and species-specific diets in two species of *Chaoborus*. Limnology and. Oceanography 20: 238-249.

Filion, J.-M., Chain, P. et Futter, M. 1993. Cantilevering vertical tow nets to reduce tow-line-induced zooplankton avoidance. Journal of Plankton Research 15: 581-587.

Gilbert, J. J. et Stemberger, R. S. 1985. Control of *Keratella* populations by interference competition from *Daphnia*. Limnology and Oceanography 30: 180-188.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology 65: 455-468.

Godbout, L. et Peters, R. H. 1988. Potential determinants of stable catch in the brook trout (*Salvelinus fontinalis*) sport fishery in Québec. Canadian Journal of Fisheries and Aquatic Sciences 45: 1771-1778.

Goyke, A. P. et Hershey, A. E. 1992. Effects of fish predation on larval chironomid (*Diptera*: *Chironomidae*) communities in an arctic ecosystem. Hydrobiologia. 240: 203-211.

Hall, D. J., Cooper, W. E. et Werner, E. E. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnology and Oceanography 15: 839-928.

Hebert, P. D. N. et Loaring, J. M. 1986. Systematics of the *Daphnia pulex* group: variation in an Agamic complex and description of a species new to North America. Biochemical Systematics and Ecology 14: 333-340.

Hutchinson, B. P. 1971. The effect of fish predation on zooplankton of ten Adirondack lakes, with particular reference to the alewife, *Alosa pseudoharengus*. Transactions of the American Fisheries Society 100: 325-335.

Hrbacek, J. 1962. Species composition and the amount of zooplankton in relation to the fish stock. Rozpravy Československé Akademie Věd. 72: 1-14.

Hydro-Québec 2000. Environmental performance report 2000. Hydro-Québec, Québec.

Hydro-Québec 2003. Construction of the Sainte-Marguerite-3 hydroelectric development 1994-2002 environmental highlights. Hydro-Québec, Québec.

Kelso, J. R. M. et Shaw, M. A. 1995. Annual biomass and production of brook charr (*Salvelinus fontinalis*) introduced into a historically fishless lake. Ecology of Freshwater Fish 4: 47-52.

Keough, M. J. et Quinn, G. P. 1991. Causality and the choice of measurements for detecting human impacts in marine environments. Australian Journal of Marine and Freshwater Research 42: 539-554.

Knapp, R. A. 2005. Effects of nonnative fish and habitat charateristics on lentic herpetofauna in Yosemite National Park, USA. Biological Conservation 121: 265-279.

Knapp, R. A., Corn, P. S. et Schindler, D. E. 2001. The introduction of nonnative fish into wilderness lakes: good intentions, conflicting mandates, and unintended consequences. Ecosystems 4: 275-278.

Knight, T. M., McCoy, M. W., Chase, J. M., McCoy, K. et Holt, R. D. 2005. Trophic cascades across ecosystems. Nature 437: 880-883.

Lacasse, S. et Magnan, P. 1992. Biotic and abiotic determinants of the diet of brook trout, *Salvelinus fontinalis*, in lakes of the Laurentian Shield. Canadian Journal of Fisheries and Aquatic Sciences 49: 1001-1009.

Lachance, S. et Magnan, P. 1990. Comparative ecology and reproductive potential of wild, domestic and hybrid strains of brook trout, *Salvelinus fontinalis*, after stocking. Canadian Journal of Fisheries and Aquatic Sciences 47: 2285-2292.

LaRow, E. J. 1968. A persistent diurnal rhythm in *Chaoborus* larvae. I. The nature of the rhythmicity. Limnology and Oceanography 13: 250-256.

LaRow, E. J. 1969. A persistent diurnal rhythm in *Chaoborus* larvae. II. Ecological significance. Limnology and Oceanography 14: 213-218.

Legendre, P. et Legendre, L. 1998. Numerical ecology, 2nd English edition. The Netherlands, Amsterdam.

Leppä, M., Hämäläinen, H. et Karjalainen, J. 2003. The response of benthic macroinvertebrates to whole-lake biomanipulation. Hydrobiologia 498: 97-105.

Luecke, C. 1990. Changes in abundance and distribution of benthic macroinvertebrates after introduction of Cutthroat trout into previously fishless lake. Transaction of the American Fisheries Society 119: 1010-1021.

Lynch, M. 1979. Predation, competition, and zooplankton community structure: An experimental study. Limnology and Oceanograghy 24: 253-272.

MacKay, N. A., Carpenter, S. R., Soranno, P. A. et Vanni, M. J. 1990. The impact of two *Chaoborus* species on a zooplankton community. Canadian Journal of Zoology 68: 981-985.

Magnan, P. 1988. Interactions between brook charr, *Salvelinus fontinalis*, and nonsalmonid species: ecological shift, morphological shift, and their impact on zooplankton communities. Canadian Journal of Fisheries and Aquatic Sciences 45: 999-1009.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Science, Oxford.

McArdle, B. H. et Anderson, M. J. 2001. Fitting multivariate models to community data: A comment on distance-based redundancy analysis. Ecology 82: 290-297.

McPeek, M. A. 1990. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. Ecology 71: 83-98.

McPeek, M. A. 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. Ecological Monographs 68: 1-23.

Ministère des Pêches et des Océans. 1986. Politique de gestion de l'habitat du poisson du Ministère des Pêches et des Océans. Ottawa.

Mittelbach, G. G. 1981. Patterns of invertebrate size and abundance in aquatic habitats. Canadian Journal of Fisheries and Aquatic Sciences 38: 896-904.

Moulton II, S. R., Carter, J. L., Grotheer, S. A., Cuffney, T. F. et Short, T. M. 2000. Methods of analysis by the U.S. Geological Survey National Water Quality Laboratory — Processing, taxonomy, and quality control of benthic macroinvertebrate samples, Open-file report 00-212,U.S. Geological Survey (USGS), Denver, Colorado.

Murakami, M. et S. Nakano, 2002. Indirect effect of aquatic insect emergence on a terrestrial insect population through by birds predation. Ecology Letters 5: 333-337.

Neill, W. E. 1981. Impact of *Chaoborus* predation upon the structure and dynamics of a crustacean zooplankton community. Oecologia 48: 164-177.

Neill, W. E. 1984. Regulation of rotifer densities by crustacean zooplankton in an oligotrophic mountain lake in British Columbia. Oecologia 61: 175-181.

Paine, R. T. 1966. Food web complexity and species diversity. The American Naturalist 100: 65-75.

Parker, B. R., Schindler, D. W., Donald, D. B. et Anderson, R. S. 2001. The effects of stocking and removal of a nonnative salmonid on the plankton of an alpine lake. Ecosystems 4: 334-345.

Pennak, R. W. 1978. Freshwater invertebrates of the United States 2nd Ed. John Wiley & Sons Inc., New York.

Pilliod, D. S. et Peterson, C. R. 2001. Local and landscape effects of introduced trout on amphibians in historically fishless watersheds. Ecosystems 4: 322-333.

Pope, G. et Carter, J. C. H. 1975. Crustacean plankton communities of the Matamek River system and their variation with predation. Journal of the Fisheries Research Board of Canada 32: 2530-2535.

Pope, G., Carter, J. C. H. et Power, G. 1973. The influence of fish on the distribution of *Chaoborus* spp. (Diptera) and density of larvae in the Matamek River system, Québec. Transactions of the American Fisheries Society 4: 707-714.

Pope, G., Tarissants, M.-C., Frenette, J.-J., Verreault, G. et Desgranges, J.-L. 1989. Effets des facteurs biotiques et abiotiques sur la structure et les relations trophiques de communautés planctoniques et benthiques : revue des hypothèses. Rapport technique canadien des sciences halieutiques et aquatiques No 1687. Mont-Joli, Ministère des Pêches et des Océans: vii+ 62p.

Power, G., Pope, G. F. et Coad, B.W. 1973. Postglacial colonization of the Matamek River, Quebec, by fishes. Journal of the Fisheries Research Board of Canada 30: 1586-1589.

Quinn, G. P. et Keough, M. J. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

Rennie, M. D. et Jackson, L. J. 2005. The influence of habitat complexity on littoral invertebrate distributions: patterns differ in shallow prairie lakes with and without fish. Canadian Journal of Fisheries and Aquatic Sciences 62: 2088-2099.

Robert, M., Benoît, R. et Savard, J.-P. L. 2000. COSEWIC status report on the eastern population of the Barrow's Goldeneye (*Bucephala islandica*) in Canada. Canadian Wildlife Service, Sainte-Foy, Québec.

Romanovsky, Y. E. et Feniova, I. Y. 1985. Competition among *Cladocera*: effect of different levels of food supply. Oikos 44: 243-252.

Schwartz, S. S., Innes, D. J. et Hebert, P. D. N. 1985. Morphological separation of *Daphnia pulex* and *Daphnia obtusa* in North America. Limnology and Oceanography 30: 189-197.

Shurin, J. B. et Allen, E. G. 2001. Effects of competition, predation, and dipsersal on species richness at local and regional scales. American Naturalist 158:624-637.

Simon, K. S. et Townsend, C. R. 2003. Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. Freshwater Biology 48: 982-994.

Strong, D. R., Jr. 1972. Life history variation among populations of an amphipod (*Hyalella azteca*). Ecology 53: 1103-1111

Swift, M. C. et Fedorenko, A. Y. 1975. Some aspects of prey capture by *Chaoborus* larvae. Limnology and Oceanography 20: 418-425.

Tate, A. W. et Hershey, A. E. 2003. Selective feeding by larval dytiscids (*Coleoptera*: *Dytiscidae*) and effects of fish predation on upper littoral zone macroinvertebrate communities of arctic lakes. Hydrobiologia 497: 13-23.

Tremblay, S. et Magnan, P. 1991. Interactions between two distantly related species brook trout (*Salvelinus fontinalis*) and white sucker (*Catostomus commersoni*). Canadian Journal of Fisheries and Aquatic Sciences 48: 857-867.

Thorne, R. S. J., Williams, P. et Cao, Y. 1999. The influence of the data transformations on biological monitoring studies using macroinvertebrates.Water Research 33: 343-350.

Thorp, J. H. 1986. Two distinct roles for predators in freshwater assemblages. Oikos 47: 75-82.

Thorp, J. H. et Bergey, E. A. 1981. Field experiments on responses of a freshwater, benthic macroinvertebrate community to vertebrate predators. Ecology 62: 365-375.

Underwood, A. J. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge.

Underwood, A. J., Chapman, M. G. et Connell, S. D. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. Journal of experimental Marine Biology and Ecology 250: 97-115.

Vanni, M. J. 1986. Competition in zooplankton communities: Suppression of small species by *Daphnia pulex*. Limnology and Oceanography 31: 1039-1056.

Vanni, M. J. 1987. Effects of food availability and fish predation on a zooplankton community. Ecological Monographs 57: 61-88.

von Ende, C. N. 1979. Fish predation, interspecific predation, and the distribution of two *Chaoborus* species. Ecology 60: 119-128.

von Ende, C. N. 1982. Phenology of four *Chaoborus* species. Environmental Entomology 11: 9-16.

Warwick, R. M. et Clarke, K. R. 1991. A comparison of some methods for analysing changes in benthic community structure. Journal of the Marine Biological Association of the United Kingdom 71: 225-244.

Wellborn G. A. 1995. Predator community composition and patterns of variation in life history and morphology among *Hyalella* (Amphipoda) populations in southeast Michigan. American Midland Naturalist 133: 322-332.

Wellborn, G. A., Skelly, D. K. et Werner, E. E. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27: 337-363.

Wissel, B. et Benndorf, J. 1998. Contrasting effects of the invertebrate predator *Chaoborus obscuripes* and planktivorous fish on plankton communities of a long term biomanipulation experiment. Archiv fur hydrobiologie 143: 129-146.

Wissel, B., Yan, N. D et Ramcharan, C. W. 2003. Predation and refugia: implications for *Chaoborus* abundance and species composition. Freshwater Biology 48: 1421-1431.

Yan, N. D., Keller, W., MacIsaac, H. J. et McEachern, L. J. 1991. Regulation of zooplankton community structure of an acidified lake by *Chaoborus*. Ecological Applications 1: 52-65.

Zaret, T. M. 1980. Predation and freshwater communities. Yale University Press, New Haven, Connecticut.

ANNEXES

LISTES DES TAXONS D'INVERTÉBRÉS RÉPERTORIÉS

Annexe 1 : Liste des taxons d'organismes zooplanctoniques répertoriés et nombre d'échantillons de lacs avec poissons (LAP, n=60) et sans poissons (LSP, n=60) contenant ces taxons.

Organismes			LAP	LSP
Cladocera			2	3
		Bosminidae	17	8
		Alona karua	0	1
		Daphnia sp.	55	23
		Daphnia galeata mendotae	1	0
		Daphnia longiremis	29	0
		*Daphnia pulex**	57	17
		*Diaphanosoma brachyurum *	0	8
		Holopedium gibberum	55	37
		Leptodora kindtii	1	0
		Polyphemus pediculus	1	4
Copepoda				
		Nauplius	60	56
	Calanoida		14	13
		Diaptomidae	33	50
		Aglaodiaptomus sp.	3	20
		Aglaodiaptomus leptopus	0	9
		Aglaodiaptomus spatulocrenatus	16	30
		Leptodiaptomus minutus	47	57
		Epischura lacustris	23	0
	Cyclopoida		48	37
		Acanthocyclops vernalis	1	3
		Cyclops sp.	7	4
		Cyclops scutifer	49	26
		Eucyclops speratus	1	0
		Macrocyclops fuscus	1	0
		Mesocyclops edax \\ leuckarti	18	17
		Orthocyclops modestus	0	2
Rotifera			15	21
		Ascomorpha sp.	13	8
		Asplanchna priodonta	0	17
		Cephalodella sp.	1	1
		Collotheca sp.	37	23
		Conochiloides dossuarius	5	42
		Conochilus unicornis	49	22
		Gastropus stylifer	24	29
		Kellicottia bostoniensis	20	30
		Kellicottia longispina	60	38
		Keratella cochlearis	50	53
		Keratella quadrata	42	36
		Keratella taurocephala	7	37
		Lecane sp.	3	2
		Lepadella sp.	1	2
		Monommata sp.	1	0
		Monostyla sp.	2	1
		Notholca sp.	0	1

Annexe 1 : suite et fin

Organismes		LAP	LSP
Rotifera	*Ploesoma* sp.	1	10
	Polyarthra sp.	51	56
	Synchaeta sp.	7	22
	Testudinella sp.	1	0
	Trichocerca sp.	6	25
	Trichotria sp.	1	1

*Comprend : *D. pulex*, *D. catawba*, *D. pulicaria* et *D. minnehaha*

Annexe 2. Liste des taxons d'organismes nectoniques répertoriés et nombre d'échantillons de lacs avec poissons (LAP, n=80) et sans poissons (LSP, n=80) contenant ces taxons.

Phylum / Sous-Phylum	**Classe**	**Ordre / Sous-Ordre**	**Famille / Sous-Famille / Tribu**	**Espèce**	**LAP**	**LSP**
Annelida					1	0
	Hirudinea				1	4
		Pharyngobdellida	*Erpobdellidae*		0	2
		Rhynchobdellida	*Glossiphoniidae*		1	0
				Glossiphonia sp.	1	0
				Helobdella sp.	1	1
				Theromyzon sp.	0	1
	Oligochaeta				3	2
			Enchytraeidae		5	4
			Lumbriculidae	*Lumbriculus variegatus*	5	2
			Naididae		9	6
				Amphichaeta sp.	1	0
				Bratislavia sp.	1	0
				Chaetogaster sp.	3	2
				Nais sp.	29	16
				Pristinella sp.	4	3
				Slavina appendiculata	7	3
				Vejdovskyella comata	17	11
Arthropoda /Chelicerata		*Acariformes*			7	5
			Arrenuridae	*Arrenurus* sp.	1	3
			Eylaidae	*Eylais* sp.	0	5
			Hydrachnidae	*Hydrachna* sp.	1	2
			Hydrodromidae	*Hydrodroma despiciens*	4	9
			Lebertidae	*Lebertia* sp.	1	0
			Oxidae	*Frontipoda americana*	0	1
			Pionidae		0	2
				Hydrochoreutes sp.	1	0
				Piona sp.	34	10
			Unionicolidae	*Unionicola* sp.	41	5
/Crustacea		*Amphipoda*		*Hyallela azteca*	10	15
		Cladocera	*Bosminidae*		11	2
			Chydoridae	*Alona affinis*	0	1
				Alonopsis elongata	1	0
				Acroperus harpae	0	2
				Eurycercus lamellatus	17	19
			Daphnidae	*Daphnia* sp.	32	12
				Daphnia dentifera\galeata mendotae	1	0
				Daphnia pulex	68	29
				Scapholeberis sp.	3	0
				Simocephalus serrulatus	0	6
			Macrothricidae	*Acantholeberis curvirostris*	4	13
				Ilyocryptus spinifer	0	1

Annexe 2 : (suite)

Phylum / Sous-Phylum	**Classe**	**Ordre / Sous-Ordre**	**Famille / Sous-Famille / Tribu**	**Espèce**	**LAP**	**LSP**
Arthropoda						
/Crustacea		*Cladocera*	*Macrothricidae*	*Ophryoxus gracilis*	40	12
			Polyphemidae	*Polyphemus pediculus*	24	13
			Holopedidae	*Holopedium gibberum*	45	18
			Sididae		0	1
				Latona parviremis	10	11
				Latona setifera	4	40
				Sida crystallina	25	42
			Leptodoridae	*Leptodora kindtii*	7	0
		Copepoda			2	3
		/Calanoida			4	4
			Diaptomidae		8	7
				Aglaodiaptomus sp.	0	1
				Aglaodiaptomus leptopus	1	9
				Aglaodiaptomus spatulocrenatus	3	9
				Leptodiaptomus minutus	3	8
			Temoridae	*Epischura lacustris*	3	0
		/Cyclopoida			1	1
				Cyclops sp.	1	0
				Eucyclops agilis	1	0
				Macrocyclops albidus	1	1
				Macrocyclops fuscus	2	2
				Mesocyclops edax\leuckarti	2	1
		/Harpacticoida			0	3
				Attheyella obatogamensis	0	4
				Bryocamptus cuspidatus	0	1
/Uniramia	*Insecta*	*Coleoptera*	*Chrysomelidae*		0	1
			/Galerucinae		0	3
			Dytiscidae		0	2
				Agabus sp.	1	2
			/Ditiscinae	*Dytiscus* sp.	0	3
				Graphoderus sp.	0	2
			/Hydroporinae		0	1
				Oreodytes sp./Hydroporus sp.	1	1
			/Laccophilinae	*Laccophilus* sp.	0	3
			Gyrinidae	*Gyrinus* sp.	0	2
			Staphylinidae		1	1
		Diptera			7	1
			Ceratopogonidae			
				Bezzia sp./Palpomyia sp.	2	3
				Culicoides sp.	2	0
			Chaoboridae		0	4
				Chaoborus sp.	5	52

Annexe 2 : (suite)

Phylum / Sous-Phylum	Classe	Ordre / Sous-Ordre	Famille / Sous-Famille / Tribu	Espèce	LAP	LSP
Arthropoda /Uniramia	*Insecta*	*Diptera*	*Chironomidae*		6	4
			/Chironominae		3	0
			/Chironomini		7	5
				Cryptochironomus sp.	1	0
				Cryptotendipes sp.	1	0
				Dicrotendipes sp.	16	21
				Chironomus sp..	1	4
				Endochironomus sp.	6	8
				Lauterborniella sp.	0	2
				Limnophyes sp.	0	1
				Microtendipes sp.	10	8
				Nilothauma sp.	0	1
				Pagastiella sp.	5	2
				Parachironomus sp.	4	2
				Polypedilum sp.	4	6
				Stenochironomus sp.	1	0
				Tribelos sp.	1	0
			/Tanytarsini		3	1
				Cladotanytarsus sp.	12	9
				Constempellina sp.	1	0
				Paratanytarsus sp.	12	7
				Stempellinella sp.	0	1
				Tanytarsus sp.	33	31
			/Orthocladiinae		7	17
				Brillia sp.	1	0
				Corynoneura sp.	1	3
				Cricotopus sp.	11	4
				Orthocladius sp.	3	1
				Heterotanytarsus sp.	1	5
				Heterotrissocladius sp.	7	4
				Parakiefferiella sp.	1	0
				Psectrocladius sp.	38	21
			/Tanypodinae		5	7
			/Coelotanypodini			
				Clinotanypus sp.	1	0
			/Pentaneurini		1	1
				Ablabesmyia sp.	20	15
				Guttipelopia sp.	1	0
			/Procladiini	*Procladius* sp.	15	8
		Ephemeroptera			3	5
			Caenidae	*Caenis* sp.	3	0
			Ephemeridae	*Eurylophella* sp.	10	1
			Leptophlebiidae		4	10
			Siphlonuridae		0	1
			Baetidae		0	3

Annexe 2 : (suite et fin)

Phylum / Sous-Phylum	**Classe**	**Ordre / Sous-Ordre**	**Famille / Sous-Famille / Tribu**	**Espèce**	**LAP**	**LSP**
Arthropoda						
/Uniramia	*Insecta*	*Ephemeroptera*	*Baetidae*	*Siphlonurus* sp.	0	1
		Hemiptera	*Corixidae*	*Graptocorixa* sp.	0	1
			/Corixinae		0	4
			/Corixini		0	3
			Mesoveliidae ou Hebridae		1	0
			Notonectidae		0	2
		Hymenoptera	*Formicidae*		0	1
			Megaspilidae		0	1
		Neuroptera	*Sisyridae*	*Sisyra vicaria*	2	0
		Odonata				
		/Anisoptera	*Corduliidae*	.	7	9
			Libellulidae	*Leucorrhinia* sp.	0	1
		/Zygoptera	*Coenagrionidae*		11	13
		Trichoptera			3	2
			Hydroptilidae		1	0
				Hydroptila sp.	6	2
				Oxyethira sp.	23	9
			Leptoceridae	*Mystacides* sp.	3	0
				Oecetis sp.	9	7
			Limnephilidae		2	4
				Limnephilus sp./ *Asynarchus* sp.	2	1
				Platycentropus sp.	1	1
			Phryganeidae / Limnephilidae		1	0
			Phryganeidae		1	3
				Agrypnia sp./ *Fabria* sp	9	12
				Phryganea sp.	0	2
			Polycentropodidae	*Polycentropus* sp.	14	7
Mollusca	*Gasteropoda*		*Planorbidae*		1	0
			Ancylidae	*Ferrissia* sp.	3	1
Nematoda					25	18
Rotifera				*Trichotria* sp.	1	0
			Conochilidae	*Conochilus unicornis*	9	2
			Flosculariidae		0	1
			Notommatidae		1	0
Tardigrada		*Eutardigrada*			1	1

*Comprend : *D. pulex*, *D. catawba*, *D. pulicaria* et *D. minnehaha*

Annexe 3 : Liste des taxons d'organismes benthiques répertoriés et nombre d'échantillons de lacs avec poissons (LAP, n=60) et sans poissons (LSP, n=60) contenant ces taxons.

Phylum / Sous-Phylum	**Classe**	**Ordre / Sous-Ordre**	**Famille / Sous-Famille/ Tribu**	**Espèce**	**LAP**	**LSP**
Annelida	*Hirudinea*				1	3
		Pharyngobdellida			1	0
			Erpobdellidae		14	7
				Nephelopsis obscura/ Dina parva	4	2
		Rhynchobdellida	*Glossiphoniidae*		1	0
				Glossiphonia sp.	6	1
				Helobdella sp.	15	19
				Placobdella sp.	1	2
	Oligochaeta				12	0
			Enchytraeidae		20	15
			Lumbriculidae		15	8
				Lumbriculus variegatus	32	16
			Naididae		10	7
				Amphichaeta sp.	13	8
				Arcteonais lomondi	1	0
				Bratislavia sp.	0	1
				Nais sp.	12	6
				Pristinella sp.	11	12
				Slavina appendiculata	3	0
				Vejdovskyella comata	7	2
Arthropoda /Chelicerata		*Acariformes*	*Arrenuridae*	*Arrenurus* sp.	6	5
			Hydrachnidae	*Hydrachna* sp.	0	2
			Hydrodromidae	*Hydrodroma* sp.	7	14
			Limnocharidae	*Limnochares* sp.	1	4
			Oxidae	*Frontipoda* sp.	1	0
			Pionidae		1	0
				Piona sp.	2	1
			Unionicolidae	*Unionicola* sp.	12	1
				Neumania sp.	0	2
/Crustacea		*Amphipoda*		*Hyallela azteca*	23	30
		Cladocera	*Chydoridae*	*Alona affinis*	0	1
				Rhynchotalona falcata	0	1
				Eurycercus lamellatus	20	12
			Daphinidae	*Daphnia* sp.	2	1
				*Daphnia pulex**	19	12
				Simocephalus serrulatus	0	3
			Macrothricidae	*Acantholeberis curvirostris*	11	22
				Ophryoxus gracilis	24	12
			Holopedidae	*Holopedium gibberum*	2	3
			Sididae		0	1
				Latona parviremis	15	17
				Latona setifera	4	34

Annexe 3 : (suite)

Phylum / Sous-Phylum	**Classe**	**Ordre / Sous-Ordre**	**Famille / Sous-Famille/ Tribu**	**Espèce**	**LAP**	**LSP**
Arthropoda						
/Crustacea		*Cladocera*	*Sididae*	*Sida crystallina*	3	28
		Copepoda				
		/Calanoida			1	0
			Diaptomidae		1	0
				Aglaodiaptomus leptopus	0	4
			Temoridae	*Epischura lacustris*	1	0
		/Cyclopoida		*Cyclops* sp.	4	0
				Macrocyclops albidus	3	3
				Macrocyclops ater	1	0
				Macrocyclops fuscus	0	1
				Paracyclops fimbriatus poppei	0	1
				Bryocamptus sp.	1	1
/Uniramia	*Insecta*	*Coleoptera*	*Chrysomelidae*		0	2
				Donacia sp.	0	1
			/Galerucinae		0	1
			Dytiscidae		0	2
				Agabus sp.	3	3
				Dytiscus sp.	0	1
				Hydroporus sp.	0	1
				Laccophilus sp.	0	2
				Oreodytes sp.	4	10
			Gyrinidae	*Gyrinus* sp.	0	5
		Diptera	*Ceratopogonidae*		3	0
				Bezzia sp./*Palpomyia* sp.	55	51
				Culicoides sp.	9	4
				Leptoconops sp.	2	1
				Serromyia sp.	0	3
			Chaoboridae	*Chaoborus* sp.	1	21
			Chironomidae		7	5
			/Chironominae		2	4
			/Chironomini		21	16
				Chironomus sp..	11	3
				Cryptochironomus sp.	13	21
				Cryptotendipes sp.	29	21
				Demicryptochironomus sp.	0	3
				Dicrotendipes sp.	49	49
				Endochironomus sp.	7	18
				Epoicocladius sp.	1	0
				Lauterborniella sp.	2	5
				Microtendipes sp.	33	22
				Nilothauma sp.	11	8
				Pagastiella sp.	28	20
				Polypedilum sp.	45	30
				Pseudochironomus sp.	0	2

Annexe 3 : (suite)

Phylum / Sous-Phylum	**Classe**	**Ordre / Sous-Ordre**	**Famille / Sous-Famille/ Tribu**	**Espèce**	**LAP**	**LSP**
Arthropoda						
/Uniramia	*Insecta*	*Diptera*	*Chironomidae*			
			/Chironominae			
			/Chironomini	*Stenochironomus* sp.	0	2
				Stictochironomus sp.	0	1
				Tribelos sp.	12	11
				Xenochironomus sp.	2	2
			/Tanytarsini		29	23
				Cladotanytarsus sp.	48	37
				Paratanytarsus sp.	15	11
				Stempellina sp.	6	5
				Stempellinella sp.	0	5
				Tanytarsus sp.	66	67
			/Diamesinae	*Corynoneura* sp.	1	0
				Cricotopus sp.	10	17
				Pagastia sp.	1	0
				Potthastia sp.	1	0
				Protanypus sp.	0	1
			/Orthocladiinae		9	7
				Heterotanytarsus sp.	14	25
				Heterotrissocladius sp.	24	26
				Paracricotopus sp.	0	1
				Parakiefferiella sp.	2	1
				Psectrocladius sp.	50	44
			/Tanypodinae		4	4
			/Coelotanypodini			
				Clinotanypus sp.	28	23
			/Pentaneurini		2	2
				Ablabesmyia sp.	39	41
				Guttipelopia sp.	4	1
				Larsia sp.	1	0
				Thienemannimyia sp.	7	2
			/Procladiini	*Procladius* sp.	57	54
			Tabanidae		2	7
				Chrysops sp.	1	1
			Tipulidae		1	0
		Ephemeroptera			9	17
			Baetidae		2	1
				Callibaetis sp.	1	3
			Caenidae	*Caenis* sp.	11	1
			Ephemerellidae	*Eurylophella* sp.	10	7
			Ephemeridae	*Litobrancha* sp.	4	6
			Leptophlebiidae		13	23
			Siphlonuridae	*Siphlonurus* sp.	14	14
		Hemiptera			0	1

Annexe 3 : (suite et fin)

Phylum / Sous-Phylum	**Classe**	**Ordre / Sous-Ordre**	**Famille / Sous-Famille/ Tribu**	**Espèce**	**LAP**	**LSP**
Arthropoda						
/Uniramia	*Insecta*	*Hemiptera*	*Corixidae*			
			/Corixini		0	28
				Corisella sp.	0	1
				Hesperocorixa sp.	0	2
			Notonectidae	*Notonecta* sp.	0	1
		Megaloptera	*Sialidae*	*Sialis* sp.	17	24
		Neuroptera		*Sisyra* sp.	5	0
		Odonata				
		Anisoptera			5	0
			Aeshnidae		3	9
			Corduliidae		48	34
			Libellulidae		0	4
				Leucorrhinia sp.	7	8
		Zygoptera			1	1
			Coenagrionidae		14	18
		Trichoptera			3	1
			Hydroptilidae		1	0
				Hydroptila sp.	18	8
				Oxyethira sp.	29	9
			Leptoceridae		4	3
				Ceraclea sp.	4	3
				Mystacides sp.	3	1
				Oecetis sp.	35	15
			Limnephilidae		1	1
				Glyphopsyche sp.	3	0
				Limnephilus sp.	4	0
				Platycentropus sp.	3	0
			Molannidae	*Molanna* sp.	1	4
			Phryganeidae		1	9
				Agrypnia sp./ *Fabria* sp.	9	16
				Banksiola sp.	1	0
			Dipseudopsidae	*Phylocentropus* sp.	7	6
			Polycentropodidae		0	1
				Polycentropus sp.	20	27
Mollusca	*Gastropoda*				5	0
				Ferrissia sp.	3	6
				Planorbella trivolvis	2	0
	Pelecypoda		*Unionidae*		60	49
Nematoda					45	30
Nematomorpha					0	1
Porifera	*Desmospongiae*		*Spongillidae*	*Spongilla* sp.	36	34

*Comprend : *D. pulex*, *D. catawba*, *D. pulicaria* et *D. minnehaha*