

UNIVERSITÉ DU QUÉBEC

MÉMOIRE

PRÉSENTÉ À

L'UNIVERSITÉ DU QUÉBEC À CHICOUTIMI

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN RESSOURCES RENOUVELABLES

PAR

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B.SC.

VARIABILITÉ À LONG TERME DES CLADOCÈRES DANS DES LACS DE LA
FORÊT BORÉALE SOUMIS À DES PERTURBATIONS NATURELLES ET
ANTHROPIQUES

MAI 2009



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RÉSUMÉ

Les perturbations naturelles ou anthropiques, telles les feux de forêts et les coupes forestières, entraînent des modifications significatives de la physico-chimie et de l'écologie des lacs associés aux bassins versants touchés. Cela résulte en une source additionnelle dans la variation interannuelle de la structure des communautés zooplanctoniques. Afin de connaître l'importance relative de ces perturbations à court terme, il est important d'acquérir de meilleures connaissances sur les variations naturelles à long terme des communautés zooplanctoniques de ces lacs. Ces études à long terme peuvent être réalisées à l'aide de méthodes paléolimnologiques, plus particulièrement par l'étude des cladocères fossiles.

Notre objectif était de caractériser la variabilité naturelle des cladocères dans des lacs en forêt boréale ainsi que les possibles effets des perturbations naturelles qui y sont associées. Ensuite, la visée était d'intégrer la variabilité à court terme entraînée par les opérations forestières à cette variabilité naturelle. Des carottes de sédiments ont été prélevées dans trois lacs dans la forêt boréale au nord du Lac Saint-Jean. Tous les lacs ont subis des feux ou des coupes forestières sur leur bassin versant au courant des dernières décennies. Les carottes ont été par la suite amenées en laboratoire pour être âgées et préparées avant analyses des cladocères. Nos résultats ont démontré une importante variabilité à long terme pour la plupart des 39 espèces répertoriées. Aucuns effets ne purent être attribués aux feux de forêts dans les lacs affectés. Un faible effet relié aux périodes d'activités forestières a pu être détecté sur les assemblages de cladocères; ce dernier s'insère cependant dans l'amplitude naturelle des variations observées au cours du dernier siècle dans les communautés de cladocères.

REMERCIEMENTS

L'étude de cladocères fossiles constitue un excellent exercice pour affûter la patience car, je puis vous dire qu'un projet comme celui-ci en requiert décidément une bonne quantité ! La réussite de ce projet repose sur plusieurs personnes qui m'ont fourni une aide tout au long des parties sur le terrain et en laboratoire de ce projet. Ainsi, je commencerais donc en remerciant mon directeur de maîtrise, Pascal Sirois. Je lui suis redevable tant pour la confiance qu'il a placé en moi pour la réalisation de ce projet, que pour son encadrement judicieux et instructif au cours de sa réalisation. À plusieurs reprises, il m'a fourni des pistes de réflexion me permettant de trouver par moi-même la solution aux problèmes rencontrés. C'est à mon sens le meilleur moyen pour apprendre la méthode scientifique... ou pour apprendre tout court !

À juste titre, une toute aussi grande partie du succès de cette maîtrise revient tout spécialement à une autre personne, Véronique Gravel. À mon arrivée sur le projet, elle avait déjà rassemblé une impressionnante banque de données sur les cladocères fossiles et maîtrisait très bien autant la méthode de tri des sédiments que l'identification des espèces. Elle a très bien su m'apprendre à identifier et à assembler mentalement la multitude de minuscules fragments de carapaces propres à chaque espèce, tâche colossale demandant patience, minutie et... une bonne dose de foi ! Sa curiosité mordante et sa passion pour le projet ont contribué à maintenir bien vivante ma propre motivation !

Je tiens également à remercier tous les gens qui sont passés au laboratoire d'écologie aquatique; leur constante bonne humeur et leur soutien furent très appréciés ! Parmi ces gens, un gros merci à Anne-Lise Fortin, Isabelle Poirier et Véronique Leclerc pour leurs nombreux conseils dans l'identification des cladocères, l'analyse des données et dans la rédaction de ce mémoire. Merci également à Isabelle Tremblay-Rivard, Sofia Dimitriadis, François Tremblay et Véronique Gravel, l'équipe de terrain qui a récolté les échantillons initiaux, de même qu'à Germain Savard, Jean-Guy Girard, Myriam Bergeron et Marie-Claude Duchesne, du laboratoire d'écologie végétale avec qui ce fut un réel plaisir d'aller récolter les rondelles qui leur ont permis de dater les feux de forêt.

Un merci tout particulier à mes amis pour les nombreux party que nous avons fait au courant du baccalauréat et de la maîtrise; on dira ce que l'on voudra mais faire la fête aidera toujours à conserver le moral et une motivation à toute épreuve ! De ce nombre, un merci à Charleen Salesse pour la correction de l'anglais. Merci également Claire, Laval, Sylvie, Guillaume et Samuel, ma famille, pour leur présence et leur support durant mes longues années d'étude ! Finalement, je suis très reconnaissant à l'Institut National de Recherche Scientifique (INRS) pour son support financier ainsi que pour les conseils de la professeure Isabelle Larocque.

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INTRODUCTION GÉNÉRALE

Les lacs parsemés sur le territoire de la forêt boréale québécoise constituent une richesse naturelle très importante. Les communautés de poissons qu'ils abritent supportent une activité de pêche sportive qui génère d'importants revenus à la province. La forêt boréale québécoise est affectée au fil du temps par une multitude de perturbations d'origine naturelle ou anthropique tels les feux et les coupes forestières. Ces événements entraînent des bouleversements majeurs sur les bassins versants, qui sont susceptibles de se répercuter à même les écosystèmes lacustres (Carignan *et al.* 2000).

En fait, les recherches visant à mesurer les effets à court terme de ces perturbations sur la qualité de l'eau des lacs ont relevé un accroissement de l'apport de certains nutriments tels le phosphore total (PT) et l'azote organique total (NOT) ainsi qu'une augmentation de la concentration en carbone organique dissous (COD) (Carignan *et al.* 2000; Rask *et al.* 1998; Winkler *et al.* 2009). Cet accroissement du COD est détecté uniquement lorsque plus de 30% du bassin versant est affecté par la coupe forestière (Carignan *et al.* 2000), ce qui suppose que la superficie affectée influence l'apport en nutriments dans le lac. La réponse biologique à cet apport est beaucoup plus difficile à évaluer compte tenu que la réponse des organismes peut différer d'une espèce à l'autre ainsi que dans le temps (Räsänen *et al.* 2007). La hausse de l'apport en nutriments dans un écosystème lacustre suivant un feu ou une coupe forestière est connu pour entraîner un

faible accroissement de la production primaire (Planas *et al.* 2000). Or, une étude réalisée après le passage d'un feu sur le bassin versant de lacs subarctiques en forêt boréale a relevé une diminution de la richesse du phytoplancton (Mceachern *et al.* 2002). Dans des lacs en Finlande, on a remarqué une très faible différence entre les assemblages de diatomées avant et après la coupe forestière (Räsänen *et al.* 2007). Bien que les travaux de Winkler *et al.* (2009) aient détecté une hausse du PT et du COD après coupe dans les lacs étudiés, aucune différence n'a été détectée dans la biomasse du phytoplancton, mesurée à l'aide de la Chl *a*. Ainsi, il est difficile d'affirmer si les changements observés à court terme sur les variables physico-chimiques se répercutent ou non sur les producteurs primaires car le degré de réponse de ces derniers vis-à-vis des perturbations est très variable d'une étude à l'autre.

Les impacts à court terme de ces perturbations sur les communautés zooplanctoniques ont également fait l'objet de plusieurs travaux de recherche. Une étude réalisée sur des lacs en Finlande a révélé une faible augmentation de la densité des cladocères et des copépodes en réponse aux opérations forestières (Rask *et al.* 1998). En forêt boréale québécoise, des chercheurs ont observé un accroissement de la biomasse des calanoïdes dans des lacs au bassin versant brûlé et une diminution de cette dernière dans des lacs au bassin versant coupé. Dans les deux cas, ces effets ont été détectés uniquement les deux premières années après perturbation (Patoine *et al.* 2000). Des travaux subséquents effectués dans les mêmes lacs ont observé une grande variabilité interannuelle de la richesse et des assemblages zooplanctoniques, tant dans les lacs témoins que dans les lacs affectés, qui semble dépendre davantage de facteurs environnementaux régionaux que de perturbations locales (Patoine *et*

al. 2002a). De même, l'étude de Winkler *et al.* (2009) a également détecté une importante variation spatiale et temporelle dans l'abondance et la biomasse des communautés zooplanctoniques à la fois dans des lacs témoins et dans des lacs affectés par les coupes forestières. Cette variation n'a pu être reliée à aucune perturbation connue. La synthèse des conclusions de ces études suggèrent que la grande résilience des communautés zooplanctoniques de la forêt boréale vis-à-vis des feux et des coupes forestières (Jalal *et al.* 2005) semblerait reposer sur une dynamique naturelle fortement variable et conséquemment davantage dépendante des facteurs environnementaux régionaux que des perturbations ponctuelles importantes touchant le bassin versant.

Afin d'approfondir cette dynamique, il est primordial de mettre en perspective les effets à court terme avec l'évolution naturelle des communautés zooplanctoniques sur une échelle de temps beaucoup plus grande. En effet, en dépit de toutes les informations utiles que l'on recueille par les échantillonnages ponctuels, on ne possède pas encore beaucoup de données à long terme sur les communautés zooplanctoniques. De ce fait, la comparaison avec l'état des écosystèmes aquatiques avant les perturbations est difficile à établir. La paléolimnologie s'avère donc essentielle afin de comprendre l'importance écologique des effets à court terme puisqu'elle permet d'établir des séries temporelles à long terme en étudiant les fossiles trouvés dans les sédiments.

Les exosquelettes de chitine de certaines espèces d'organismes zooplanctoniques peuvent être préservés dans les sédiments et potentiellement être utilisés comme indicateurs de la structure présente ou passée des communautés zooplanctoniques (Frey 1986). Ces derniers étant un maillon essentiel de la chaîne trophique en milieu lacustre, ils constituent une source de nourriture importante pour les poissons et les invertébrés planctonivores en plus d'être d'importants brouteurs d'algues et de détritiques organiques. Ils jouent de par ce fait un rôle crucial dans le recyclage des éléments nutritifs des niveaux inférieurs de la chaîne trophique vers les niveaux supérieurs (Korhola and Rautio 2001; Sweetman and Smol 2006). Parmi les grands groupes zooplanctoniques, les cladocères sont les organismes les plus fréquemment utilisés en paléolimnologie. Ils sont d'excellents indicateurs biologiques, sensibles non seulement aux changements biologiques et aux cascades trophiques qui en découlent, mais également aux changements physico-chimiques survenant dans le milieu (Patoine *et al.* 2002a). De plus, leurs fossiles sont bien conservés dans les sédiments et ils sont parmi les organismes aquatiques les mieux représentés laissant régulièrement des fossiles dans les sédiments (Korhola 1999). Pour ces raisons, les cladocères sont donc un choix pertinent et judicieux dans le cadre d'une étude paléolimnologique visant à comprendre la variabilité naturelle du zooplancton.

L'évolution à long terme de la structure des communautés de cladocères sous l'influence de perturbations forestières, bien que moins examinée qu'à court terme, a néanmoins déjà fait l'objet de quelques travaux. Dans une étude réalisée dans la région des Adirondacks (États-unis), Paterson (1994) a décelé des changements intéressants dans le

taux d'accumulation et dans la richesse des cladocères au fil du temps, concluant cependant qu'il existait très peu d'évidences que les coupes forestières effectuées au début du 20^{ème} siècle en soient responsables. L'auteur a plutôt déterminé qu'il devait s'agir d'une perturbation régionale car les changements étaient beaucoup trop synchronisés entre les lacs pour suspecter l'influence du bassin versant. Une autre recherche, réalisée sur six lacs en Colombie-Britannique (Canada), avait pour but de déterminer si de faibles changements sur la composition des diatomées suivant une coupe forestière observés dans une étude précédente (Laird and Cumming 2001) étaient également décelables sur la composition des cladocères (Bredesen *et al.* 2002). Sur les six lacs analysés, quatre lacs ont affiché à basse résolution (décennie) des changements significatifs dans la composition des espèces de cladocères suite à l'activité forestière. À plus haute résolution (~2 ans), seulement deux lacs ont démontré des changements qui s'avéreraient significatifs. Les auteurs ont suggéré que ces changements pourraient être attribuables à un apport accru en nutriments associé à la coupe forestière (Bredesen *et al.* 2002).

Le premier objectif de ce projet était de décrire la variabilité à long terme des communautés zooplanctoniques observée dans des lacs en forêt boréale au Québec. Le second objectif visait à comparer la variabilité à court terme des communautés zooplanctoniques suite à une perturbation anthropique, la coupe forestière, ou à une perturbation naturelle, les feux de forêt, avec la variabilité naturelle à long terme de ces mêmes communautés.

LONG-TERM VARIABILITY OF CLADOCERANS IN BOREAL SHIELD LAKES UNDER NATURAL AND HUMAN DISTURBANCES

1. Introduction

In Quebec, the high number of lakes scattered over the boreal forest biotope constitutes an important natural resource. The fish communities they shelter sustain a popular recreational fishing activity that generates important income for the province. Over time, the boreal forest is affected by natural and human disturbances such as wildfires and forest harvesting. These events induce major disruptions on watersheds that are likely to have consequences on aquatic ecosystems (Carignan *et al.* 2000).

Zooplankton is a major component of lake ecosystems. They act as an important food source for fish and planktivore invertebrates as well as being effective algae and organic matter grazers. Therefore, the role they play in recycling nutrients from the bottom to the top of the food-chain is crucial within aquatic ecosystems (Korhola and Rautio 2001; Sweetman and Smol 2006). Many short-term studies have been conducted to determine the consequences of natural and human watershed disturbances on zooplanktonic communities inhabiting boreal forest lakes. A study of Finnish lakes revealed a slight increase in copepod and cladoceran densities in response to forestry operations (Rask *et al.* 1998). In Quebec (Canada), Patoine *et al.* (2000) observed an increase of calanoid biomass in lakes within a burned watershed and a decrease in lakes within harvested watersheds during the first two years following a disturbance. However, no significant differences were observed

in zooplankton richness and assemblages after perturbations, though variation among lakes and among sampling dates were important (Patoine *et al.* 2002a). A more recent study on Quebec Boreal Shield lakes also could not detect any effects on zooplanktonic community structure from forest harvesting (Winkler *et al.* 2009). The results of these studies indicate a great range in zooplankton response to watershed disturbance. Even lakes without forestry perturbation on their watershed seemed to show high variation in the structure of their zooplankton communities over the years. This suggests that various naturally occurring events might induce enough impact on zooplankton communities to contribute significantly to their short-term response to watershed disturbances. Therefore, to assess the importance of this natural contribution and to better understand the ecological significance of short-term effects, it is essential to look at the evolution of zooplankton communities over a longer time frame.

Paleolimnology allows the reconstruction of long-term time series of zooplankton communities' structure. Exoskeletons of some zooplankton species are preserved in benthic sediments and can be used as indicators of past and present-day communities' structure (Frey 1986). Cladocerans are the most frequently used biological indicators among the main zooplankton groups, as they are sensitive not only to biological changes and to their trophic implications but also to physicochemical alterations (Patoine *et al.* 2002a). Furthermore, among all the organisms frequently leaving fossils in sediments, cladocerans are the best preserved (Korhola 1999).

Long term structural evolution of cladoceran communities under watershed disturbances has been examined in many papers. Paterson (1994) observed changes in cladoceran accumulation rates and richness over time in lakes of the Adirondack Mountains (United States), though there was not enough evidence linking these variations to the harvesting operations that occurred at the beginning of 20th century. The impressive temporal synchronization of these variations between studied lakes led the author to suspect the predominance of a regional disturbance over watershed-only events. Another study aimed to verify if subtle changes observed in diatom composition following forest harvesting (Laird and Cumming 2001) were also detectable in cladoceran communities of the same lakes over time (Bredesen *et al.* 2002). Four of the six studied lakes showed significant changes at decadal resolution in cladoceran communities' structure following forestry operations. At higher resolution (~2 years), only two of these lakes showed significant changes. The increase of nutrients associated with harvesting activities on watersheds was pointed out as an explanation of these results.

The main goal of this project is to understand and describe the natural variability of zooplanktonic communities in Quebec boreal forest lakes. This study also aims to compare the short-term variability of zooplanktonic communities following a human or a natural disturbance, such as forest harvesting and wildfires respectively, along with the long-term natural variability of these communities.

2. Methods

2.1 Study site and lakes

The study region is located around latitude 50° in the boreal forest, north of Lac Saint-Jean in Québec, Canada (Fig. 1). The vegetation in the area, part of the Western black spruce feathermoss domain, mainly consists of black spruce (*Picea mariana* (Mills.)), balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). Three lakes (Chantale, Maurice and Aux Huards) were selected on the basis of their comparable geographical and morphological parameters, as well as their disturbance history (Table 1). All lakes had a 20-m buffer strip of forest kept standing around them and along their streams after forest harvesting. Though laminated sediments were not found in any lakes, cores' integrity was thoroughly checked using x-rays and later confirmed with ^{210}Pb dating.

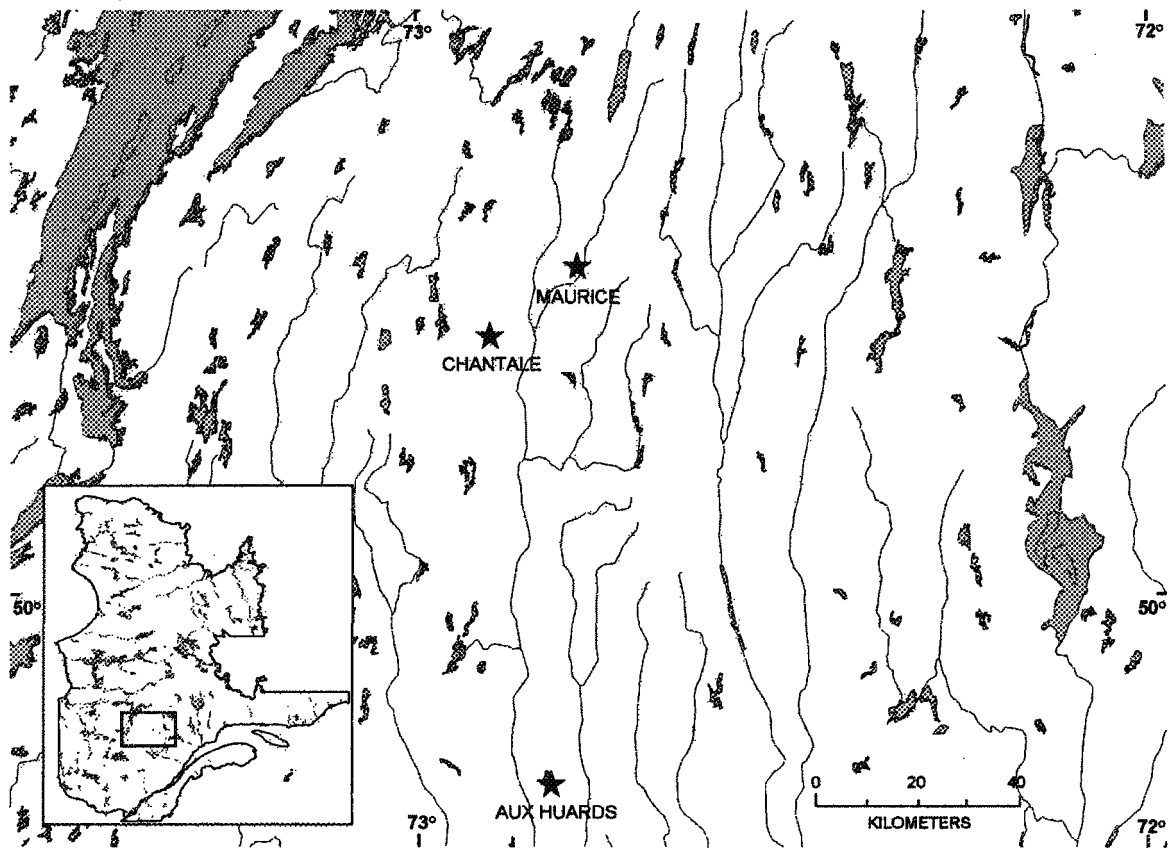


Figure 1. Location of the lakes within the study area.

Table 1. Geographical and morphological details of the studied lakes

Parameter	Lake		
	Chantale	Maurice	Aux Huards
Latitude (N)	50°26'21.6"	50°33'47.3"	49°40'13.3"
Longitude (W)	72°48'36.6"	72°33'20.4"	72°38'41.6"
Altitude (m)	478	492	383
Fetch (km)	1.57	2.12	2.83
Surface area (SA) (km ²)	0.42	0.71	2.56
Maximum depth (m)	14.70	9.70	20.00
Watershed surface area (WA) (km ²)	6.97	4.92	21.53
Drainage ratio (WA:SA)	16.59	6.89	8.41
Mean watershed slope (%)	11.70	6.59	8.26
Forest harvesting years on watershed	2000-2001	2002-2003	1990-1994, 2000
Watershed affected by cut (%)	20.90	57.90	42.60

2.2 Sampling

Sediment cores were recovered at the deepest point of each lake using a HTH gravity corer (Glew *et al.* 2001; Renberg and Hansson 2008) with a tube length of 50 cm and an internal diameter of 8 cm, operated from a twin-anchored inflatable Zodiac. A total of two 36-cm cores were obtained in Lac Chantale, two 28-cm cores in Lac Maurice and two 33-cm cores in Lac Aux Huards. The first core recovered from each lake was extruded using a close-interval extruder into 0.25 cm intervals (Glew 1988). Sediments were then quickly transferred to labelled clip-lock bags and immediately frozen (-20°C) until laboratory

processing. The second core was frozen intact, then examined using an x-ray machine for any varves that were not immediately visible and kept as reference material.

2.3 Sample preparation

Samples were freeze-dried prior to analysis. For each lake, one 0,25-cm interval was analysed in each 1-cm strata. A precise weight of dried sediment, varying from 0.0096 to 0.7590 grams, was subsampled for each 0.25 cm interval. The weight needed was determined by performing a quick scan of two random intervals to ensure that the quantity of fossil pieces was enough for analysis (Frey 1986). Weighted dry sediment subsamples were deflocculated in a 10% potassium hydroxide (KOH) solution, stirred and heated on a hotplate (80°C) until complete homogenization. Filtration was performed on the homogenized sediments through two different sieves: a 63 µm mesh size sieve for larger *chydoridae* headshells and cladoceran ephippia, and a 32 µm mesh size sieve to collect the leftovers and the smaller parts. Filtered sediments were placed onto slides, using a micropipette, and deposited on a hotplate until most of the water was evaporated. Slices were then mounted using slides and cover slips.

2.4 Cladoceran analysis

Cladoceran remains were observed under a Leica microscope at 400X magnification and identified at the lowest possible taxonomic level following Chengalath and Hall (1981), Edmonston (1959), Frey (1960), Frey (1962), Frey (1965), Korhola and Rautio (2001), Smirnov (1992) and Smirnov (1996). When identification to the species level was not possible, taxa were grouped either by genus (e.g. *Daphnia* spp.) or by identical morphological features within genus (e.g. *Alona rectangularis/guttata/circumfibrata*). For each species or genera, though all recognizable pieces were accounted, only the most frequently recovered piece of exoskeleton were used in later abundance counts to prevent multiple counts of the same organism (Annexe I). A minimum of approximately 100 exoskeleton pieces were counted for each sub-sample (Frey 1986).

2.5 Sediments and wildfires dating

The establishment of a chronology for each obtained core was realized through analysis of sediments for ^{210}Pb activity. It was estimated by ^{210}Pb distillation and alpha spectrometry methods (Eakins and Morrison 1978) on samples of the core at intervals ranging from 1 to 5 cm, including surface sediments. Dates and sedimentation rates were calculated according to the constant rate of supply (CRS) model, which uses ^{210}Pb activity and cumulative dry mass estimations. Complete chronologies were based on linear interpolations of the intervals between dated points (Appleby and Oldfield 1978). Wildfire

occurrences were dated using complete tree ring analysis. On each watershed, a total of 40 ground level disks were collected from trees cut in four sites (10 disks/site), each located in different stands. Disk were sanded and two paths counted on each using a binocular. Wildfire presence and approximate years were determined in each watershed using data from all of the collected disks. A linear interpretation between ^{210}Pb dated points and the base of each core was used to link dated sediment to established fire years. A check for presence and size of charcoals was performed in every subsample as to support tree ring analysis results.

2.6 Data analysis

Data from each lake is split *a posteriori* into two different groups according to ^{210}Pb estimation dates: sediments from before and after forest harvesting operations. Analysis of the assemblage was then made on fourth-root transformed data, using Bray-Curtis dissimilarity matrixes built in the statistical package PRIMER (version 5.2.2). Analysis of similarity (ANOSIM) was performed on these two groups in order to determine the differences in species assemblages. The closer the R-Statistic was to 0 value, the lower is the similarity between the two groups, as samples within groups are no more similar to each other than between groups. A SIMPER procedure was performed to compare the contribution of species to the average dissimilarity, between the years before and after forestry operations.

3. Results

3.1. Sediments and wildfires aging

A reliable time scale, reaching back approximately 150 years, was established in each lake using sediment ^{210}Pb dating (Fig. 2). The maximum depth at which dating was possible varied between lakes due to differences in sedimentation rates. Sediments were aged up to AD 1823 (25.0 cm) in Lac Chantale, AD 1839 (9.0 cm) in Lac Maurice and AD 1877 (13.0 cm) in Lac Aux Huards. Tree ring analyses performed on each watershed allowed the tracing back of the latest fires. Our results indicated even age stands in Lac Maurice and Lac Aux Huards; this allowed to date a fire event between AD 1805 and AD 1819 on Lac Maurice watershed and between AD 1815 and AD 1829 on Lac Aux Huards watershed. On the later, a more recent smaller fire event was dated between AD 1860 and AD 1870 though results indicated that it affected only partially the watershed. Since aged stands were of uneven age on Lac Chantale watershed, it was impossible to date a fire event more recent than AD 1736. Sediment ^{210}Pb dating and acquired information on studied watershed perturbations allowed the linking of both harvesting and wildfire perturbation years with collected sediment samples (Table 2). Charcoals of various sizes were found commonly in almost all analysed subsamples in all lakes, therefore it was impossible to determine if they originated from the watershed itself or from another watershed in the area.

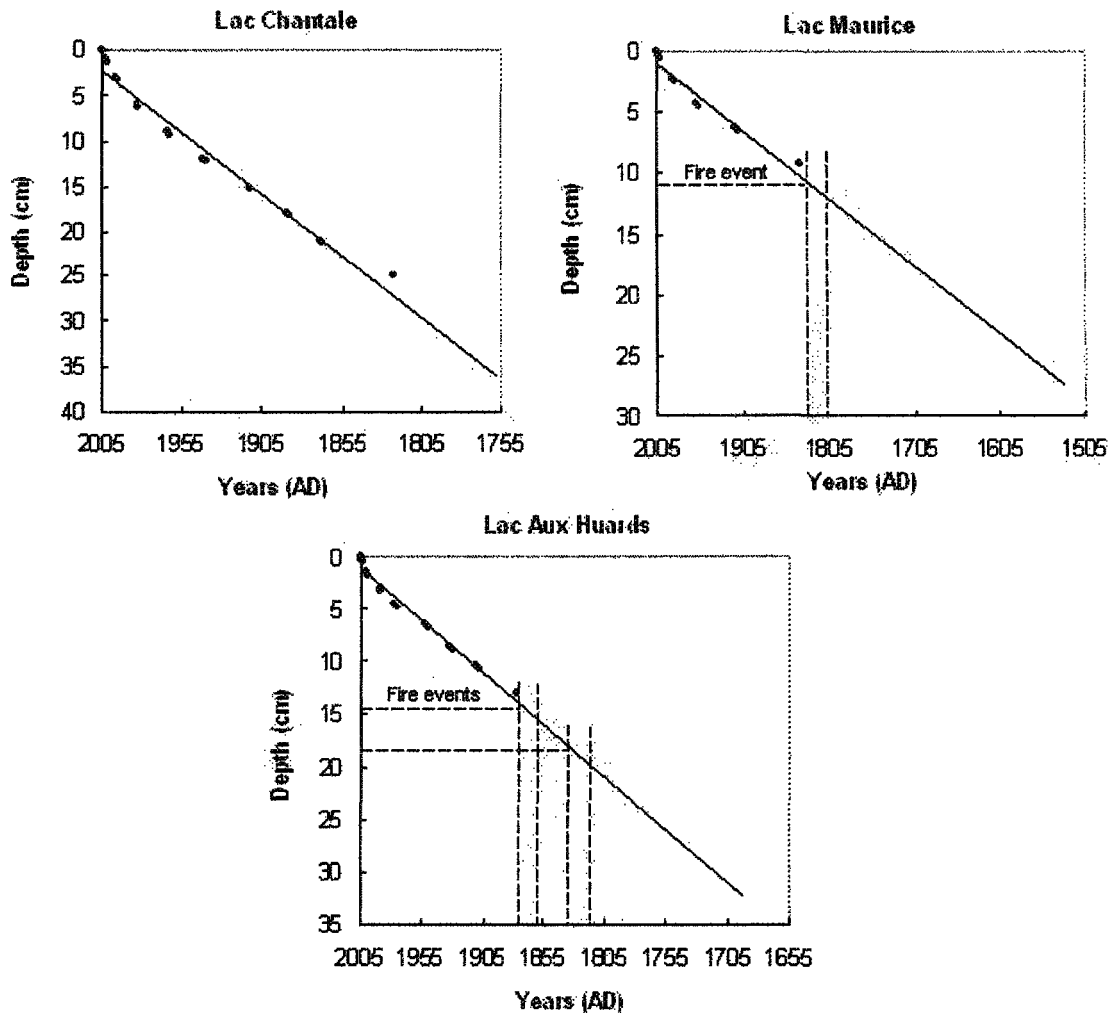


Figure 2. Age-depth profiles based on ^{210}Pb dating for each lake. The solid line represents a linear function going through ^{210}Pb dated points; it continues as an extrapolation between the dated points and the base of the core. The dashed line represents fire event depths calculated from the linear interpretation.

Table 2. Age-depth relations between wildfire, forestry operations and sediments.

	Lakes		
	Chantale	Maurice	Aux Huards
Core length (cm)	36.0	28.0	33.0
Mean sedimentation rate (g m ⁻² an ⁻¹)	162.0	126.0	100.0
Wildfire years	No recent	AD 1805-1819	AD 1815-1829
Corresponding core depth	-	12.1cm-11.4 cm	20.0 cm-18.5 cm AD 1860-1870 14.5-15.5 cm
Forestry years	AD 2002-2003	AD 2000-2001	AD 1990-1994,
Corresponding core depth	1.8 cm	1.0 cm	AD 2000 3.50 cm, 1.50 cm

3.2. Cladoceran analysis

3.2.1 Abundance

A total of 39 taxa of cladoceran were identified within the sediments of the three lakes. Among these, it was possible to identify 32 of them at species level. Other taxa were grouped as explained in the methodology. Our results indicated a higher overall number of taxa in Lac Aux Huards (37 taxa) in comparison with Lac Chantale (31 taxa) or Lac Maurice (34 taxa) (Annexe II). All taxa with relative abundance lower than 2% were removed from further analysis to prevent errors due to the difficulty in determining reliability of low counts (Bos and Cumming 2003). Each identified taxon was associated either with pelagic or littoral habitats using cladoceran habitat preferences established in Korhola and Rautio (2001). At any given depth, fossils of pelagic organisms were much

more numerous than littoral ones. Littoral organisms only accounted for 14% (78 577 org.·g⁻¹) of total organisms in Lac Chantale, 6% (19 761 org.·g⁻¹) in Lac Maurice and 11% (79 773 org.·g⁻¹) in Lac Aux Huards. *Bosmina* spp. showed up to be the most common pelagic genera in all lakes with a mean relative abundance per sample of 9% (7317 org.·g⁻¹), while *Alona quadrangularis* was the most common littoral species with a mean relative abundance of 5% (168 org.·g⁻¹).

Abundance data for species revealed an important variability over time in all studied lakes (Fig. 3; Fig. 4; Fig. 5). There is no evidence linking this variability to a particular habitat since only a few species in each habitat showed important signs of variation over the years. Over all, *Bosmina* spp. and *Daphnia* spp. displayed the highest variability in all lakes. For instance, *Bosmina* spp. reached up to 1939% of variability over time in Lac Chantale, 684% in Lac Maurice and 668% in Lac Aux Huards.

Variability is rarely synchronized between species in any of the lakes. Of these rare synchronisations, only few occurred in years following a disturbance. In Lac Chantale, a common increase of the *Daphnia pulex* complex, *Ophryoxus gracilis*, *Holopedium gibberum*, *Eurycerus* spp. and *Alona rectangula* in abundance was observed following forestry operations (Fig 3). In Lac Maurice, an increase in abundance of many species (*Acroperus harpae* / *Camptocercus* spp., *Alona quadrangularis*, *Alona excisa*, *Alonella nana*, *Chydorus bicornutus*, *Chydorus sphaericus* complex and *Disparalona* spp.) was observed about thirty years following the wildfire (Fig 4). Results for Lac Aux Huards

showed fewer of these events, though it is interesting to point out a generalized decrease of pelagic abundance (*Bosmina* spp., *Daphnia pulex*, *Holopedium gibberum*, *Sida crystallina*) happening in the same time period of a forest harvest, around 1.50 cm depth (Fig 5). Analysis of *Daphnia ephippium* revealed no major variations coinciding with any of the disturbances in lakes Chantale, Maurice or Aux Huards.

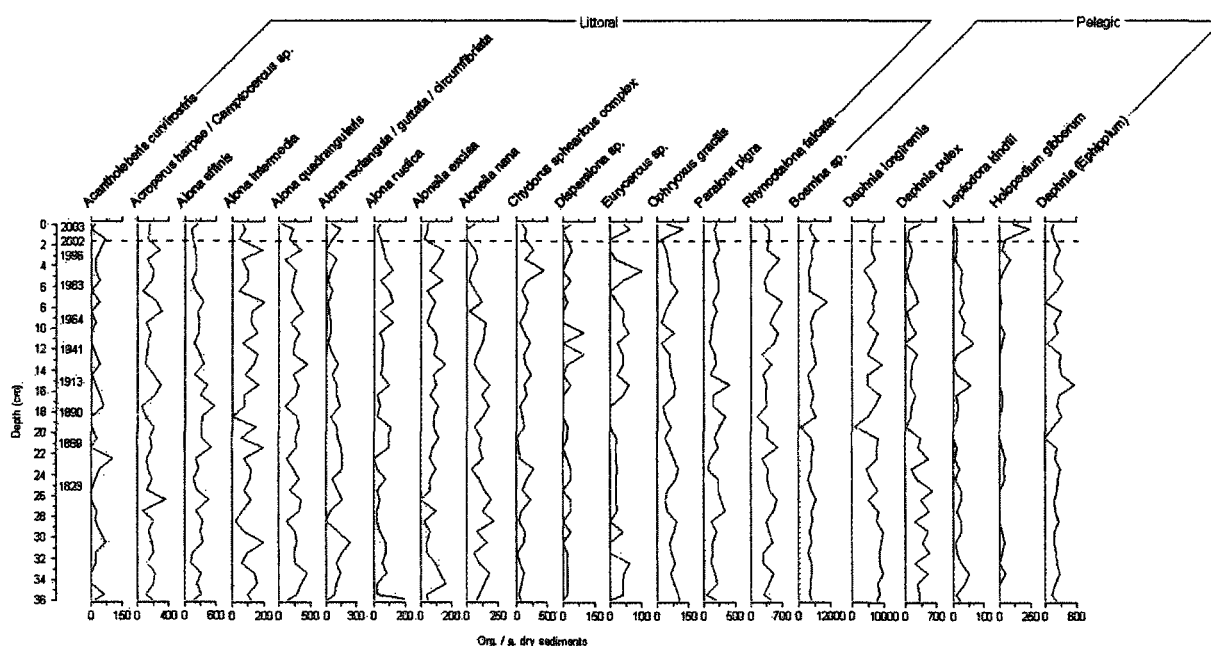


Figure 3. Abundance (org. \cdot g $^{-1}$ dry sediment) of cladoceran taxa found in Lac Chantale sediment core. Dashed line indicates forest harvesting.

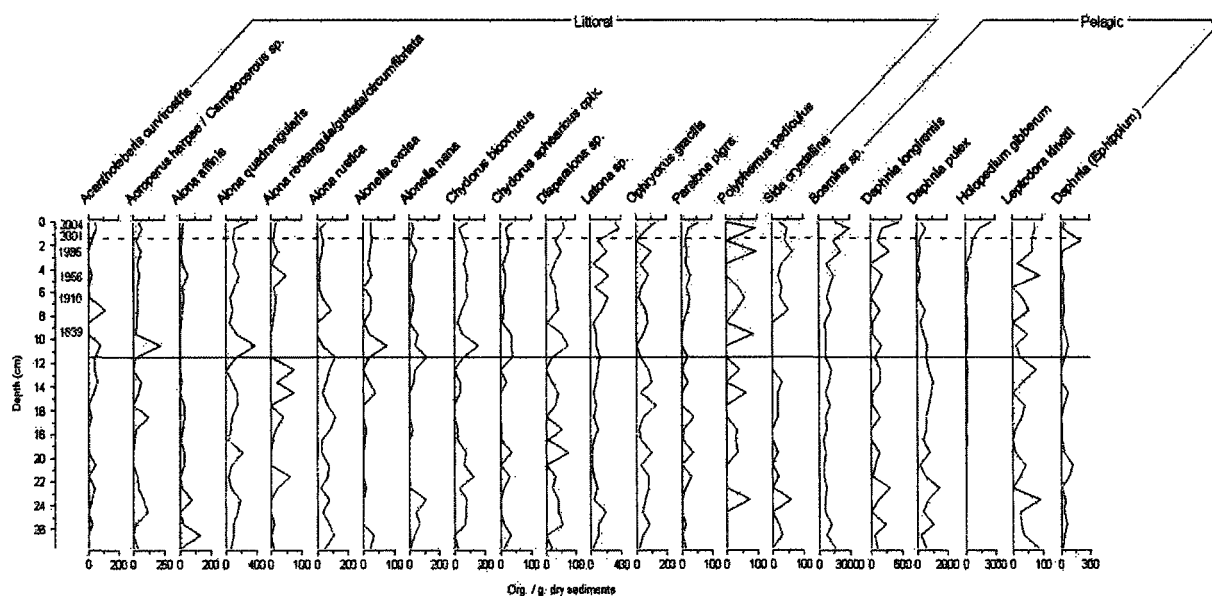


Figure 4. Abundance (org.·g⁻¹ dry sediment) of cladoceran taxa found in Lac Maurice sediment core. Dashed line indicates forest harvesting years while solid line indicates wildfires.

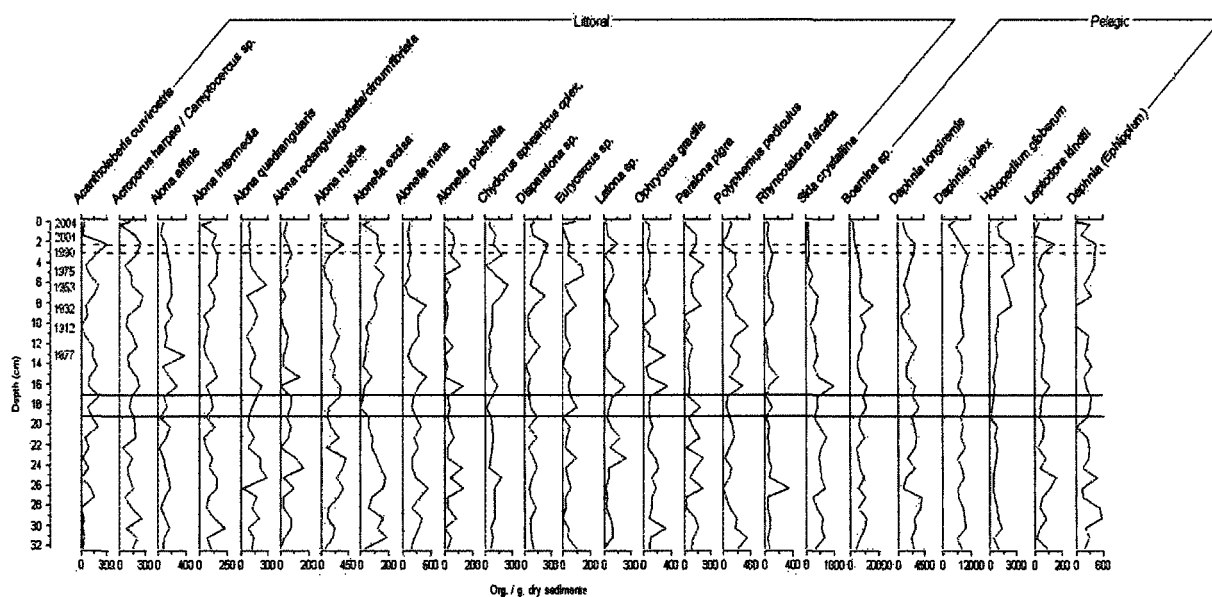


Figure 5. Abundance (org.·g⁻¹ dry sediment) of cladoceran taxa found in Lac Aux Huards sediment core. Dashed lines indicate forest harvesting years while solid lines indicate wildfires.

Cumulative abundance examined in relation with both habitats (Fig. 6) also highlights temporal variability as an important factor, as observed in previous graphs showing abundance per taxa (Fig. 3; Fig. 4; Fig. 5). Independent of habitat, no clear trend in abundance was observed after a forest harvest surrounding Lac Chantale. While littoral dwellers only showed subtle changes in Lac Maurice, pelagic taxa tended to increase substantially after harvesting, though this increase seems to have been initiated around the middle of the 20th century. An opposite trend characterized abundance response to watershed tree harvesting for both habitats-dwelling taxa in Lac Aux Huards. Wildfire events did not seem to coincide with any specific changes in pelagic communities in Lac Maurice and Lac Aux Huards. However, they seem to be followed, in littoral communities of those lakes, by an important increase in abundance leading to the highest values of each core. Estimated time delays between fires and these peaks are approximately ten years (1 cm) in Lac Maurice and thirty years (3 cm) in Lac Aux Huards. Cladoceran richness was also examined and did not change significantly over time in any of the lakes.

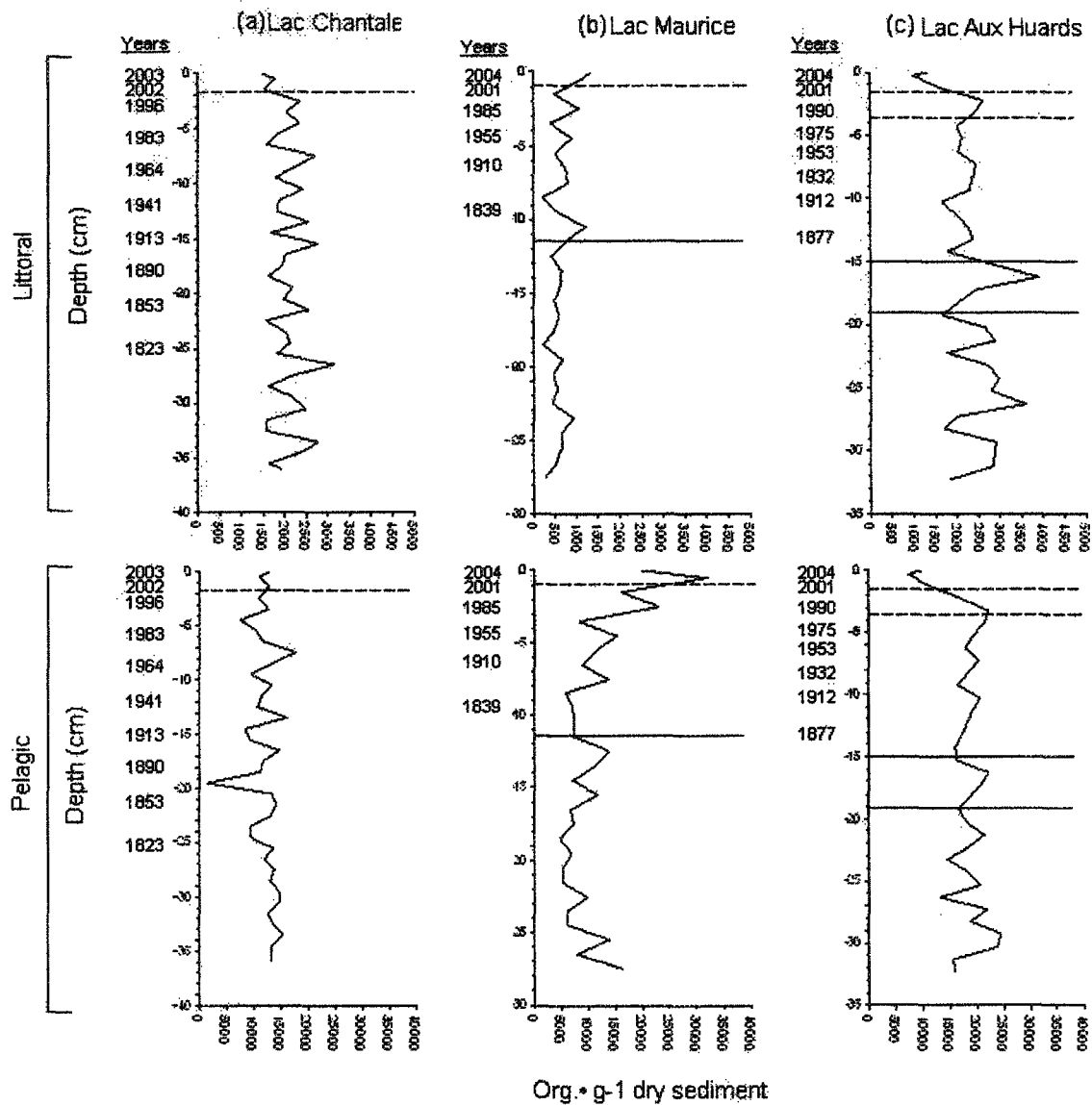


Figure 6. Cumulative abundance (org. • g⁻¹ dry sediment) calculated for littoral and pelagic cladocerans for each lake. Dashed lines indicate forest harvesting years while solid lines indicate wildfires.

3.2.2 Assemblages

A multivariate analysis of similarities (ANOSIM) allowed the comparison of cladoceran assemblages found in the sediments deposited after forest harvesting with those deposited before disturbance. Similarities between the assemblages are illustrated in non-metric multidimensional scaling (nMDS) ordinations (Fig. 7; Fig. 8; Fig. 9). The more the circles are clustered together, the more the species assemblages are similar. The reliability of the visual representation of the nMDS ordinations was given by the stress level values ranging from 0.22 to 0.25, which were acceptable according to previously determined threshold values (Clarke and Warwick 1994). In two lakes, the nMDS ordinations showed a series of points surrounding all others in marginal positions. In Lac Chantale, species assemblages following forest harvesting differed significantly from non-disturbed years ($p=0.0039$) (Fig. 7). In Lac Maurice, although no statistical effects were found by ANOSIM procedures ($p=0.4950$), post-disturbance assemblages were grouped together in a marginal position with three other non-disturbed assemblages (Fig. 8). Analysis of similarity performed between harvested and non-disturbed years in Lac Aux Huards gave the strongest signal of dissimilarity of all three lakes ($p=0.0004$) (Fig. 9). Assemblages following wildfire disturbances both in lakes Maurice and Aux Huards did not appear to be marginal, thus not showing any significance level.

Results of the SIMPER procedures indicated a different pattern of species contribution to dissimilarity within each lake (Table 3). In Lac Chantale, *Alonella nana* average

abundance decreased with harvesting while *Holopedium gibberum* increased. In Lac Maurice, the major contributions came from *Holopedium gibberum*, *Diaphanosoma* and *Bosmina* spp, which average abundances all increased after harvesting. Contributions in Lac Aux Huards were well balanced between species; only *Bosmina* spp. stood out as its average abundance was also decreased. Dissimilarity percentage related to changes in littoral cladocerans in comparison to pelagic cladocerans was higher in Lac Chantale (79%), Lac Maurice (73%) and Lac Aux Huards (79%).

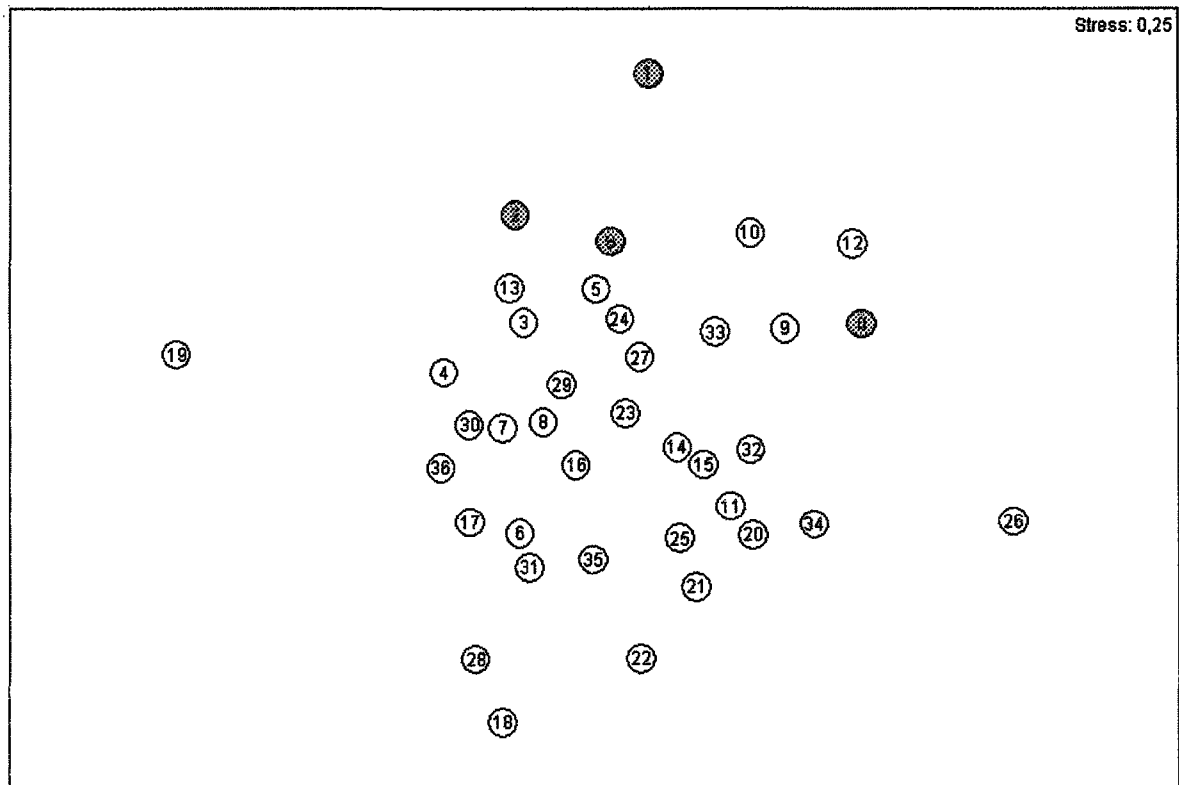


Figure 7. Non-metric multidimensional scaling (nMDS) ordination based on the Bray-Curtis dissimilarity matrix calculated on fourth-root transformed data ($\sqrt[4]{x}$) for cladoceran samples collected in Lac Chantale. Grey circles indicate harvesting years while white circles represents years without known perturbations. Numbers indicates the depth at which samples were taken; 1 indicates a sample taken in sediments between 1 and 2 cm depth; S stands for surface sediments.

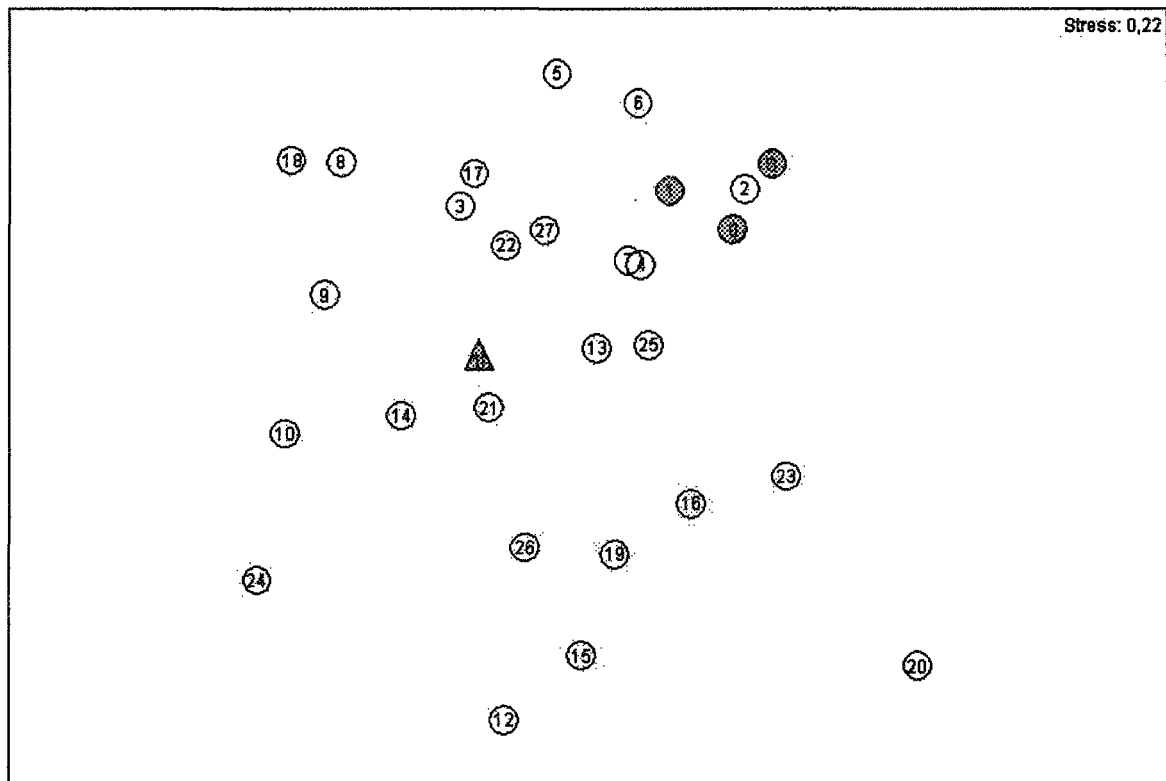


Figure 8. Non-metric multidimensional scaling (nMDS) ordination based on the Bray-Curtis dissimilarity matrix calculated on fourth-root transformed data ($\sqrt[4]{x}$) for cladoceran samples collected in Lac Maurice. Grey circles represent harvesting years, upward black triangle represents wildfire years and white circles represents years without known perturbation. Numbers indicates the depth at which samples were taken; 1 indicates a sample taken in sediments between 1 and 2 cm depth; S stands for surface sediments.

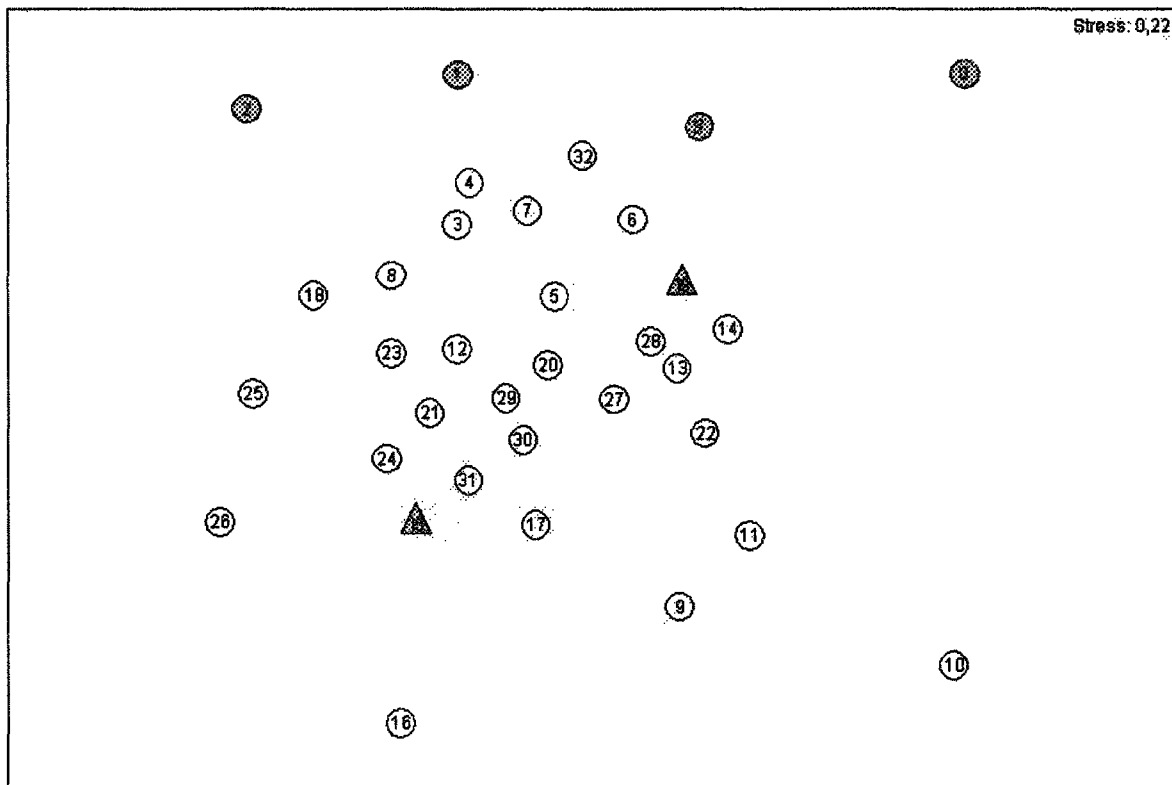


Figure 9. Non-metric multidimensional scaling (nMDS) ordination based on the Bray-Curtis dissimilarity matrix calculated on fourth-root transformed data ($\sqrt[4]{x}$) for cladoceran samples collected in Lac Aux Huards. Grey circles represent harvesting years, upward black triangle represents wildfire years and white circles represents years without known perturbation. Numbers indicates the depth at which samples were taken; 1 indicates a sample taken in sediments between 1 and 2 cm depth; S stands for surface sediments.

Table 3. Results of SIMPER procedures assessing for each lake the five most contributing taxa to the average dissimilarity between years before and after harvesting (species with (*) are pelagic).

Lac Chantale		Lac Maurice		Lac Aux Huards	
Average dissimilarity : 17,44 %		Average dissimilarity : 27,84 %		Average dissimilarity : 16,15 %	
Taxon	(%)	Taxon	(%)	Taxon	(%)
<i>Alonella nana</i>	8.87	<i>Holopedium gibberum</i> *	10,08	<i>Bosmina</i> spp. *	6,75
<i>Holopedium gibberum</i> *	8.73	<i>Diaphanosoma</i> spp.	6,84	<i>Alonella pulchella</i>	5,06
<i>A. curvirostris</i>	4.88	<i>Bosmina</i> spp. *	6,51	<i>Disparalona leei</i>	4,74
<i>Disparalona leei</i>	4.88	<i>Daphnia longiremis</i> *	4,39	<i>Sida crystallina</i>	4,68
<i>Eurycercus</i> spp.	4.85	<i>Ilyocryptus</i> spp.	4,14	<i>Acroperus harpae</i> / <i>Camptocercus</i> spp.	4,08

4. Discussion

Cladoceran remains collected in each lake allowed the reconstruction of cladoceran communities that thrived in ecosystems more than one hundred fifty years ago. Our study depicted cladoceran population abundances in boreal forest lakes as highly variable temporally, almost all species showing important variations in their abundance throughout the entire cores. Results also indicated assemblage differences in every lake between years without any human perturbation and years following forest harvesting, though they are within range of natural long-term assemblage variability. No changes were detected on abundance or assemblage in any lake following fire events.

4.1. Natural variability: wildfires

Natural variability is characterized in each lake by average values and by greater peaks we could qualify as extraordinary values. Results showed that these values never coincide with fire events, though higher peak in littoral cladocerans abundance could be detected within both affected lakes some 10 and 30 years afterward (Fig. 6b, c). Wildfires have been known to alter the mineral and nutrient inputs into aquatic ecosystems due to increased catchment erosion and runoff (Rhodes and Davis 1995). Such increased runoff might have happened, thus inducing in the littoral zone of both lakes an increase of algal food availability and therefore abundance of littoral cladocerans. This has already been supported by previous works, which also detected small consequences on diatoms

(Paterson *et al.* 2002) and on zooplankton biomass (100-200 μ m) (Patoine *et al.* 2000) following wildfire. On the other hand, many studies have shown that kind of response to be generally short-lived, happening in a period less than ten years from the disturbance (Paterson *et al.* 2002). To detect such short-lived disturbances in our lakes, a sharpened resolution (~2 years) might have been more relevant. Consequently, the link between wildfires and the increase of littoral cladocerans 10-30 years later was probably not causal, as supported by the multivariate analysis.

The fact that the strongest variations in abundance values could not be related to fire events in this study rather suggests that such values are population responses to years in which environmental conditions for cladoceran reproduction or survival were extraordinary. These conditions are known, according to literature, to affect more likely cladocerans and limnology than watershed disturbances such as fire or logging (Blais *et al.* 1998; Paterson *et al.* 1998). A recent study by Paterson *et al.* (2002) also pointed out that lakes with small drainage ratios (1.1 to 9.1) may be more sensitive to atmospheric pollution and climate change than to watershed disturbance (Blais *et al.* 1998; Paterson *et al.* 1998). Our results goes in accordance since both lakes that showed no effects from the fire events on their watershed (Lac Maurice, Lac Aux Huards) have drainage ratios under 9.1 (Table 1). Though the exact nature of such extraordinary environmental conditions is unknown, they might create excellent survival conditions, which effects might be accentuated in low drainage lakes, for certain cladocerans every couple of years and mask the less important effects of any possible watershed disturbances like wildfires.

4.2 Human impact: forest harvesting

Multivariate analysis of similarities showed significant differences between assemblages from before and after wood removal in the watersheds of lakes Chantale and Aux Huards. Lac Maurice post-disturbance assemblages were also marginal in the nMDS ordination but were not statistically different. Such changes are in accordance with previous results, which detected impacts from forestry operations on cladoceran communities' structure of four British Columbia (Canada) lakes at decadal resolution (Bredesen *et al.* 2002). In addition, our results showed littoral cladocerans as being the most contributing species to the assemblage dissimilarities observed in lakes Chantale and Aux Huards. This suggests that forestry-induced changes may affect more directly littoral cladoceran communities than pelagic ones since the littoral zones are being exposed directly to nutrient runoffs from the cut watershed (Rask *et al.* 1998; Winkler *et al.* 2009). It is very likely that part of these changes on littoral cladocerans could be due to bottom-up influences, since recent studies conducted on primary producers revealed quicker and greater short-term responses of littoral algae to watershed perturbations than pelagic algae (Desrosiers *et al.* 2006; Planas *et al.* 2000).

Variability occurring naturally among cladoceran assemblages, as characterized in this paper, was defined as a suite of uneven peaks in abundance rarely synchronized between species. Taking this variability into account, slight shifts in community structure such as the one described above are likely to have happened at some points in the past, thus not being

related at all to human activities. In fact, it was discovered that post-disturbance assemblages are not the only groups significantly standing out from the others, as seen visually on nMDS ordinations. Lac Aux Huards ordination illustrates particularly well that statement as assemblages of consecutive years corresponding to depths 9.25 cm, 10.25 cm, 11.25 cm are grouped; same can be seen from 15.25 cm, 16.25 cm, 17.25 cm and 24.25 cm, 25.25 cm, 26.25 cm depths. Distance of marginal values from the main set of points being comparable between all groups, it demonstrates that even though forest removal has subtle effects on cladoceran assemblages, they are of the same order of magnitude than the ones occurring naturally under exceptional environmental conditions.

The differential levels of response between the two significant lakes and the lack of response to harvesting in Lac Maurice both rise some interrogations as to why, even though responses are subtle, some lakes are not reacting as much as others to similar degree of modifications of their watershed. The low drainage ratio (6.89) in Lac Maurice watershed could partially explain the lack of response, since it is known that lake with high drainage ratio often show a greater response to disturbance (Paterson *et al.* 1998). Also, a recent work highlighted the ecological position of cladocerans as a factor explaining the different responses between lakes to forestry activities (Bredesen *et al.* 2002). Cladocerans are subject to both bottom and top-down trophic pressures from food availability and fish predation; different trophic structures are likely to have different influences on cladoceran populations (Bredesen *et al.* 2002). Also, previous studies pointed out the strong resilience of zooplanktonic organisms to environmental perturbations (Patoine *et al.* 2002a; Patoine *et*

al. 2002b; Rask *et al.* 1998; Winkler *et al.* 2009). This was supported by a study conducted on boreal forest lakes, in which the results indicated no short-term change in bottom-up and top-down effects of zooplankton groups due to forest harvesting activities (Winkler *et al.* 2009). Furthermore, any other closely related anthropogenic watershed disturbance may be accounted for. As an example, it is not improbable that human settlements on Lac Aux Huards played a role in the response seen in this lake MDS. Human occupation of the catchments has been linked in previous studies to eutrophication according to Tsugeki *et al.* (2003). In that case, the building of human settlements on the watershed in 1995 did not create any noticeable shifts in neither abundance nor in assemblages. The occupied area (23% of the lake's perimeter) is probably not important enough to induce changes but such human implantation and its indirect effects may have an impact, in addition to forestry operations and road building that occurred in the area (Bredesen *et al.* 2002).

Therefore, despite all these variables, our study revealed that watershed disturbances such as wildfires or wood removal in the boreal forest are not predominantly strong influences on cladoceran communities. We suspect the natural variability of cladocerans to be a strong force, supported by complex trophic interactions and strong species resilience. It can be influenced by watershed forest harvesting but not to a degree more than changes caused by exceptional environmental conditions. This goes in accordance with recent studies, which obtained similar conclusions on limnoplankton communities of Canadian Shield Boreal lakes (Patoine *et al.* 2002a; Patoine *et al.* 2002b; Patoine *et al.* 2000; Pinel-Alloul *et al.* 1998; Planas *et al.* 2000; Winkler *et al.* 2009).

5. Conclusion

The use of sedimentary cladoceran remains allowed the establishment of complete time series dating back to AD 1850 and before. Hence, it provided enough backward steps to characterize the natural evolution of cladoceran communities in boreal lake ecosystems. In every lake, natural variability proved to be important. Even though forest removal has shown subtle impacts on cladocerans assemblages, they were of the same order of magnitude than the ones occurring naturally under what could be qualified as exceptional environmental conditions. No impacts were detected on the natural variability by wildfire events on any lakes.

CONCLUSION GÉNÉRALE

Ce mémoire a permis d'acquérir de nouvelles connaissances quant à l'évolution des populations zooplanctoniques de lacs en forêt boréale depuis plus d'un siècle. En effet, l'analyse paléolimnologique de fossiles de cladocères enfouis dans les sédiments benthiques dans trois lacs ainsi que la datation de ces sédiments, ont permis d'établir une échelle temporelle fiable remontant à plus de cent cinquante ans dans chacun des plans d'eau. Cette échelle a fourni un recul temporel suffisamment grand pour permettre une caractérisation efficace de la variabilité naturelle des différentes communautés de cladocères que ces lacs abritent.

Dans un premier temps, cette étude a permis de constater que la variabilité naturelle des communautés de cladocères s'est de manière générale toujours avérée importante au fil du temps, et ce dans l'ensemble des lacs étudiés. Au sein de cette variabilité naturelle, les effets des feux de forêts sur la structure des communautés de cladocères ont été examinés. La correspondance établie entre les années de feux connues dans les deux lacs touchés et les données d'abondance et d'assemblage des cladocères de ces mêmes lacs n'a permis de déceler aucun impact significatif attribuable à ces perturbations. Ainsi, les feux de forêt ne semblent pas entraîner d'années d'abondance ou d'assemblages extraordinaire par rapport à la variabilité naturelle.

Dans un second temps, le projet a permis de relativiser les impacts à court terme des coupes forestières détectés sur les organismes zooplanctoniques par des travaux antérieurs, en les intégrant dans un plus vaste portrait tel que donné par la variabilité naturelle. Les résultats de l'approche multivariée démontrent que même si les coupes forestières entraînent des effets significatifs à court terme sur les assemblages de cladocères, ces dernières restent toujours très faibles. En comparatif, l'ordre de grandeur de ces effets est plus ou moins le même que certaines des variations naturelles les plus importantes. Comme ces variations naturelles ne peuvent pour le moment être reliés à aucune autre perturbation connue, il est possible que ces valeurs soient tout simplement dues à conditions environnementales exceptionnelles et dès lors, que le coupe forestière ne ferait qu'égaliser en terme de magnitude les effets de ces conditions sur la structure des communautés zooplanctoniques.

Ce projet suggère que les coupes forestières entraînent des impacts sur le zooplancton des lacs en forêt boréale, mais que ces effets ne sont pas plus importants que ceux entraînés par des années de conditions environnementales propices à l'abondance planctonique. Les résultats de ce projet contribuent donc à dépeindre un portrait beaucoup plus précis de la dynamique de réponse du plancton des lacs en forêt boréale face aux perturbations anthropiques. En effet, nos résultats sur les cladocères sont en parfait accord avec les conclusions précédentes, tirées dans d'autres lacs en forêt boréale canadienne, indiquant l'importance de la variabilité naturelle dans l'analyse des impacts détectés de perturbations du bassin versant sur le limnoplankton. De plus, la grande résilience des communautés

zooplanctoniques, combinée aux nouvelles méthodes de coupes, à la protection fournie par la bande de protection de 20 mètres ainsi qu'à la régénération rapide de la végétation du bassin versant peuvent contribuer à diminuer tant l'impact des opérations forestières sur les écosystèmes aquatiques, que le temps de rétablissement post-perturbation des communautés zooplanctoniques.

En conclusion, la méthode paléolimnologique a été un outil efficace afin de répondre aux interrogations et aux objectifs de ce projet. Il serait intéressant d'examiner les fossiles de cladocères dans les sédiments à plus grande résolution (~2 ans) puisque ces perturbations sont reconnues pour entraîner des impacts à court terme. Cela permettrait une meilleure caractérisation de la variabilité naturelle ainsi que le comportement des différentes espèces suivant les années correspondant aux feux ou aux coupes forestières. De même, il serait pertinent d'examiner davantage les paramètres d'abondance et d'assemblage des cladocères littoraux puisque notre projet a révélé chez eux davantage de changement aux perturbations du bassin versant. Les données météorologiques propres aux zones étudiées pourraient également être utiles afin d'identifier la nature des événements importants ponctuant la variabilité naturelle des cladocères. Finalement, il serait tout aussi pertinent d'étudier les cladocères dans les sédiments de lacs similaires n'ayant subis aucune opération forestière afin d'isoler la variable dite régionale, c'est-à-dire vérifier l'existence de phénomènes régionaux pouvant potentiellement influencer la variabilité naturelle dans la même période de temps que s'effectuent les coupes forestières.

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ANNEXES

Annexe 1. Liste des considérations relatives aux pièces d'exosquelette retrouvées.

Partie	Famille	Genre ou espèce	Considération		
			1 individu	½ individu	0 individu
Tête	Bosminidae	Tous	- Intacte avec 1 ou 2 antennules - Partie avec jonction des antennules	-1 antennule et une partie de tête	- Antennule seule ou tête seule
	Chydoridae	Tous, sauf : <i>Paralona pigra</i> , <i>Chydorus sphaericus</i> , <i>Alonella pulchella</i> et <i>Disparalona</i> spp.	- Intacte ou au moins ¾ avec pore - Portion postérieure avec pore		Fragment autre
	Chydoridae	<i>Paralona pigra</i> , <i>Chydorus sphaericus</i> , <i>Alonella pulchella</i> et <i>Disparalona</i> spp.	- Intacte ou au moins ¾ avec rostre - Portion antérieure avec rostre		Fragment autre
Épine caudale	Leptodoridae	Tous	Noter le nombre de fragments et les pièces complètes.		
	Polyphemidae	Tous			
Segment d'antenne	Sididae	Tous	Ils sont tous comptés puisque ces structures sont petites et rarement fragmentées.		
Griffe	Sididae	Tous			
	Daphnidae	Tous			
	Macrothricidae	Tous			
	Holopodidae	Tous			
Post-abdomen	Macrothricidae	Tous	- Marge dorsale complète ou portion distale avec denticules		Fragment autre
	Chydoridae	<i>Eurycercus</i> spp.			
Carapace	Macrothricidae	<i>Ilyocryptus</i> spp.	Habituellement très fragmentée; noter seulement le nombre de morceaux retrouvés (présence/absence).		
Ephippia	Daphnidae	Tous	Ephippia compose de 2 valves	- Une valve presque intacte - Plus que ½ d'une valve	Fragment autre

Annexe 2. Liste des taxons de cladocères répertoriés et leur présence en lac.

Cladocères	Présence		
	Chantale	Maurice	Aux Huards
<i>Acantholeberis curvirostris</i>	+	+	+
<i>Acroperus harpae</i> / <i>Camptocercus</i> spp.	+	+	+
<i>Alona affinis</i>	+	+	+
<i>Alona borealis</i>	+		
<i>Alona costata</i>		+	+
<i>Alona intermedia</i>	+	+	+
<i>Alona quadrangularis</i>	+	+	+
<i>Alona rectangula</i> / <i>guttata</i> / <i>circumfibrata</i>	+	+	+
<i>Alona rustica</i>	+	+	+
<i>Alonella excisa</i>	+	+	+
<i>Alonella exigua</i>	+	+	+
<i>Alonella nana</i>	+	+	+
<i>Alonella pulchella</i>	+	+	+
<i>Anchistropus minor</i>			+
<i>Bosmina</i> spp.	+	+	+
<i>Chydorus bicornutus</i>	+	+	+
<i>Chydorus faviformis</i>	+	+	
<i>Chydorus sphaericus</i> complex	+	+	+
<i>Daphnia longiremis</i>	+	+	+
<i>Daphnia pulex</i>	+	+	+
<i>Diaphanosoma</i> spp.		+	+
<i>Disparalona</i> spp.	+	+	+
<i>Eurycercus</i> spp.	+	+	+
<i>Graptoleberis testudinaria</i>	+	+	+
<i>Holopedium gibberum</i>	+	+	+
<i>Ilyocryptus</i> spp.	+	+	+
<i>Kurzia latissima</i>	+	+	+
<i>Latona parviremis</i>		+	+
<i>Latona setifera</i>	+	+	+
<i>Leptodora kindtii</i>	+	+	+
<i>Monospilus dispar</i>		+	+
<i>Ophryoxus gracilis</i>	+	+	+
<i>Paralona pigra</i>	+	+	+
<i>Pleuroxus chiangi</i>			+
<i>Pleuroxus straminus</i>			+
<i>Pleuroxus striatus</i>			+
<i>Polyphemus pediculus</i>	+	+	+
<i>Rhyncotalona falcata</i>	+	+	+
<i>Sida crystallina</i>	+	+	+