UNIVERSITÉ DU QUÉBEC À CHICOUTIMI

MÉMOIRE DE RECHERCHE

PRÉSENTÉ À

MME. MILLA RAUTIO

ET

MME. BERNADETTE PINEL-ALLOUL

PAR

DAVID-ALEXANDRE GAUTHIER

STRUCTURE DES COMMUNAUTÉS DE ROTIFÈRE DANS LES LACS BORÉAUX ET LEUR CONTRIBUTION POTENTIELLE AU TRANSFÈRE DU CARBONE ALLOCHTONE DANS LES RÉSEAUX TROPHIQUES AQUATIQUES

AOÛT 2017

RÉSUMÉ

Malgré la forte importation de carbone allochtone dans les lacs boréaux du Québec, peu d'information est disponible concernant les mécanismes qui permettraient à cette matière organique de cheminer dans les réseaux trophiques aquatiques. Les bactéries seraient le principal consommateur de carbone allochtone. Ces dernières pourraient faire partie de la diète de plusieurs groupes de zooplancton, permettant ainsi l'entrée du carbone allochtone dans les réseaux trophiques aquatiques. Parmi le zooplancton, les rotifères sont plus petits que les crustacés et ils pourraient être mieux adaptés à consommer des bactéries. Nonobstant la forte abondance des rotifères dans les lacs boréaux et leur position clé dans les réseaux trophiques, ce groupe de zooplancton a été beaucoup moins étudié que les cladocères et les copépodes et leur rôle dans les écosystèmes est encore mal compris. Cette étude visait donc à remplir deux objectifs spécifiques. En premier, l'étude visait à décrire et à expliquer la structure et la distribution des communautés de rotifères dans les lacs boréaux. Deuxièmement, l'étude visait à déterminer la contribution des rotifères dans le transfert du carbone allochtone vers les niveaux trophiques supérieurs. Plus spécifiquement, il était question de mesurer *in situ* les taux d'ingestion de phytoplancton et de bactérioplancton par les rotifères. Pour atteindre le premier objectif, 22 lacs situés dans la région du Saguenay-Lac-Saint-Jean dans la province de Québec ont été échantillonnés au cours de l'automne 2013. Les résultats ont permis de déterminer que la structure et la distribution des communautés de rotifères varient en fonction des caractéristiques environnementales des lacs et des bassins versants. Les résultats ont également permis de confirmer que la structure des communautés de rotifères dans les lacs exposés à de plus fortes concentrations de carbone allochtone est différente de celle des lacs où le carbone allochtone est plus dilué. Cependant, les résultats n'ont pas permis de confirmer que le niveau de connectivité entre les lacs influence la distribution et la structure des communautés de rotifères. Les résultats n'ont également pas permis de confirmer que l'absence de poissons prédateurs induit un effet cascade sur les réseaux trophiques observable au niveau des populations de rotifères. Pour atteindre le deuxième objectif, une expérimentation a été effectuée en marquant du phytoplancton et des bactéries à l'aide de marqueurs radioactifs, qui ont été ensuite présentés à une population de rotifères afin de mesurer leur ingestion respective. Les résultats ont permis de démontrer que les rotifères ingèrent des bactéries de façon passive en se nourrissant de phytoplancton. En ingérant ainsi des bactéries, les rotifères contribuent à transférer le carbone allochtone aux niveaux trophiques supérieurs.

REMERCIEMENTS

En premier lieu, mes remerciements les plus sincères vont à ma directrice de recherche à la maîtrise, Milla Rautio, qui m'a épaulé et guidé tout au long de ce projet. Je la remercie notamment pour la confiance et la patience témoignées à mon égard jusqu'à l'aboutissement de ce mémoire. Je tiens également à remercier ma co-directrice de recherche, Bernadette Pinel-Alloul. Son appui ainsi que son expertise m'ont été d'une aide inestimable. Par ailleurs, un merci particulier à tout le personnel du Laboratoire des Science Aquatiques de l'UQAC pour leur support et leur aide dans l'aboutissement de cette recherche, en commençant par Pierre Carrier-Corbeil. Ces connaissances sur la microbiologie aquatique, ces compétences techniques en laboratoire et nos nombreuses discussions m'ont apporté beaucoup d'aide et permis d'avancer mon projet. Merci à mes collègues Guillaume Grosbois, Tobias Schneirder et Maxime Wauthy pour leur appui et leur aide sur le terrain et en laboratoire. Merci à Patrick Plourde-Lavoie pour sa contribution dans les analyses géomatiques. Un merci particulier à Joannie Venne pour son implication et la finalisation de la partie expérimentale. Sans elle, cette partie du projet n'aurait jamais pu être complétée. Merci également à Mathieu Cusson pour son aide dans le traitement des données et l'analyse statistique. Finalement, merci à tout le monde qui a contribué de près ou de loin à la réalisation de ce projet de maîtrise.

AVANT-PROPOS

Ce mémoire à été réalisé dans le cadre de la maîtrise en ressources renouvelables de l'Université du Québec à Chicoutimi. La structure choisie est celle d'un mémoire sous forme d'article scientifique. Le cœur du mémoire se présente en un seul chapitre, rédigé en anglais et mis sous la forme d'un article scientifique. Une introduction générale, en français, met le sujet en perspective et une conclusion générale en français revient sur les hypothèses et termine ce mémoire.

L'étude porte sur les rotifères des lacs boréaux du Québec. En plus de répondre à des objectifs et des hypothèses spécifiques, le projet aborde plusieurs aspects généraux liés à l'écologie de ce groupe de zooplancton. Une description taxonomique de la structure des communautés de rotifères est effectuée. Les espèces les plus importantes dans les assemblages de rotifères ainsi que certaines espèces plus rares et moins récurrentes sont présentées. De plus, une analyse de l'influence de certains facteurs environnementaux sur la distribution géographique des rotifères en région boréale est également effectuée. Il était important pour nous de mettre en perspective le groupe des rotifères parmi les communautés de zooplancton. Ainsi, une comparaison de l'importance des rotifères par rapport aux groupes des copépodes et des cladocères est incluse dans l'étude. Finalement, une emphase a été mise sur l'implication des rotifères dans les réseaux trophiques et leur capacité à transférer le carbone dans la chaîne alimentaire aquatique.

TABLE DES MATIÈRES

RÉSUMÉ i
REMERCIEMENTS ii
AVANT-PROPOS iii
TABLE DES MATIÈRES iv
LISTE DES TABLEAUX vi
LISTE DES FIGURES viii
1 INTRODUCTION GÉNÉRALE 1
1.1 Le carbone autochtone et allochtone dans l'environnement aquatique 1
1.2 Le carbone dans les réseaux trophiques aquatiques 4
1.2.1 Le phytoplancton et le bactérioplancton 4
1.2.2 Le zooplancton métazoaire 6
1.2.3 Les rotifères 7
1.2.4 Les poissons et les invertébrés 11
1.3 La forêt boréale 12
1.4 Objectifs 15
2 ROTIFER DISTRIBUTION IN SMALL OLIGOTROPHIC BOREAL LAKES AND POTENTIAL CONTRIBUTION IN THE TRANSFER OF ALLOCHTHONOUS CARBON IN THE AQUATIC FOOD WEB 17
2.1 Introduction 17
2.2 Methods 21
2.2.1 Study area 21
2.2.2 Lake selection 23
2.2.3 Zooplankton sampling and limnological measurements 25
2.2.4 Rotifer distribution and structure data analysis 28
2.2.5 Rotifer grazing experiment 29
2.2.6 Grazing rate measurements 34
2.2.7 Estimating grazing rates on sampled lakes 36
2.3 Results 37

2.3.1 Physico-chemical characteristics of the sampled lakes 37
2.3.2 Zooplankton community structure 41
2.3.3 Rotifer distribution 46
2.3.4 Rotifer population structure according to shore 48
2.3.5 Most structuring species 52
2.3.6 Environmental variables structuring Rotifer populations 55
2.3.7 Grazing experiments results 57
2.4 Discussion 61
2.4.1 Rotifer population structure and distribution 61
2.4.2 Grazing experiment 65
2.4.3 Grazing rates estimation of natural lake population 67
3 CONCLUSION GÉNÉRALE 69
RÉFÉRENCES 72

LISTE DES TABLEAUX

Table 1. Location and catchment properties of the sampled lakes. Letters after lake names refer to the clusters Brébeuf (*B*), Chauvin (*C*) and Martin-Valin (*MV*). 27

Table 2. Bacteria and phytoplankton biomass ratios ($\mu g \cdot C \cdot L^{-1}$) used in the grazing experiment. The bold characters indicate the food source that was labelled with ^{3}H (bacteria) or ^{14}C (phytoplankton). The control was run with dead zooplankton to account for passive radioisotope uptake. 31

Table 3. Summary statistics of the physico-chemical characteristics of the sampled lakes. Letters after lakes names refers to fish (*F*) or no fish (*NF*) populations present in the lakes..... 38

Table 4. Distance-based test results for homogeneity of dispersions based on data from Figure 6 by comparing distance from centroid for environmental samples from the north shore and environmental samples from the south shore (n=22). 40

Table 5. Zooplankton taxa identified in the 22 lakes sampled during September and October of 2013 and mean lake abundance ($ind \cdot L^{-1}$) and biomass ($\mu g \cdot L^{-1}$). 43

Table 6. Mean zooplankton abundance and biomass for all the lakes sampled in September and October of 2013 (n=22). 44

Table 7. Results of nonparametric permutational multivariate analyses of variance (PERMANOVA) testing the effect of clusters (Valin, Chauvin, Brébeuf), shore (north or south of the Saguenay Fjord) and fish (presence/absence) on rotifer and crustacean assemblages using log transformed abundance and biomass data. Lakes are nested within each factor. 47

Table 8. Distance-based test results for homogeneity of dispersions (Fig. 5) by comparing distance from centroid for rotifer biomass samples from the north shore and rotifer biomass samples from the south shore (n=62). 50

Table 9. Similarity percentage (SIMPER) method results showing the contribution (%) of the most important species in creating similarity between samples for the north and the south shores based on the biomass data. 53

Table 10. Similarity percentage (SIMPER) method results showing the contribution (%) of the most important species in creating dissimilarity between shores based on Bray-Curtis distances and biomass. Mean biomass data for each shore is also included. 54

Table 11. Primer 6 BIO-ENV analysis: best results of environmental variables contribution (variables from Tables 1 and 3) in explaining rotifer biomass distribution across the 22 sampled lakes. 56

Table 12. Rotifer grazing rates estimated on five sampled lakes using known rotifer, phytoplankton and bacteria abundance and biomass (Vatcher, Perdrix, Hamel, Lisa - Autumn 2013 data; Simoncouche – Autumn 2011 data). Filtration rates (Fi) were calculated accord to the equations of the response curves obtained in the grazing experiment (Figs. 10 and 11) where 'x' was replaced with known phytoplankton abundance or biomass for each lake and population feeding rates (PFe) were calculated using equation 2. 60

LISTE DES FIGURES

Figure 1. Le « budget » de carbone dans les lacs et les réservoirs en fonction de différents types de milieux terrestres. La forêt boréale canadienne est associée à l'image (B). DIC est le carbone inorganique dissout; DOC est le carbone organique dissout; POC est le carbone particulaire dissout; TOC est le carbone totale dissout. À noter que la distinction entre le carbone autochtone et allochtone n'est pas effectuée. *Figure tiré intégralement de Tranvik et al. (2009).* 2

Figure 2. Schéma latéral d'un rotifère type. *Figure tiré intégralement de Wallace and Snell (2010).* 9

Figure 3. Localisation géographique de la forêt boréale au Canada. *Figure tiré intégralement de NRCAN (2016).* 13

Figure 4. Map of the study area and location of the 22 lakes sampled in 2013 showing the Martin-Valin, Chauvin and Brébeuf clusters as well as Lake Simoncouche (site 22 to the left). The numbers associated to each lake identify each one and can be visualized in Tables 1 and 3. 24

Figure 5. Absorbance reference curve for different *Nanochorophis* biomass provided by INRS-ETE. 32

Figure 6. Non-metric multidimensional scaling (nMDS) ordination based on the Euclidian dissimilarity matrix calculated on normalized watershed characteristics and environmental data from Tables 1 and 3 for lakes from the north shore (white) and south shore (black) of the Saguenay Fjord. Numbers represent lakes as identified in Table 1 and 3. 39

Figure 7. Mean rotifer, nauplii, copepod, and cladoceran abundance (a) and biomass (b) per lake (n=22). Abundance (ind·L^{-1}) and biomass (µg·L^{-1}) data is log transformed. 45

Figure 8. Non-metric multidimensional scaling (nMDS) ordination based on the Bray-Curtis dissimilarity matrix calculated on log transformed rotifer biomass data for samples from the north shore (white) and south shore (black) of the Saguenay Fjord. Numbers represent lakes as identified in Table 1 and 3. 49

Figure 9. Rotifer distribution according to biomass of each shore (north n= 12; south n=10) according to (a) mean biomass per lake (b) mean number of species per lake (c) mean Simpson diversity per lake and (d) mean species evenness per lake; vertical bars indicate standard error; different letters indicate significant difference. 51

Figure 10. Rotifer filtration rates on bacteria (Fi_{bact}) in relation to phytoplankton biomass. Rotifers concentration remained the same in all treatments (100 rotifers per beaker) and were exposed to an increasing gradient of phytoplankton concentration (0, 5, 17, 35 and 70 µgC·L^{-1};

x-axis) while bacteria concentration remained constant (44 µgC·L^{-1}). Trend line was added. Vertical lines represent standard error bars. 58

Figure 11. Rotifer filtration rates on phytoplankton (Fi_{phyto}) in relation to phytoplankton biomass. Rotifers concentration remained the same in all treatments (100 rotifers per beaker) and were exposed to an increasing gradient of phytoplankton concentration (0, 5, 17, 35 and 70 µgC·L^{-1}; x-axis) while bacteria concentration remained constant (44 µgC·L^{-1}). Trend line was added. Vertical lines represent standard error bars..... 59

1 INTRODUCTION GÉNÉRALE

1.1 Le carbone autochtone et allochtone dans l'environnement aquatique

Le carbone joue un rôle capital dans la biosphère car il influence les processus biogéochimiques, les processus physico-chimiques et les dynamiques énergétiques des réseaux trophiques (IPCC, 2001). Dans les milieux aquatiques le carbone peut se retrouver sous de nombreuses formes, provenir de diverses sources et influencer de plusieurs façons les écosystèmes (Fig. 1). Par exemple, le carbone inorganique dissous (CID), tel que le CO_2, provient de la respiration des organismes hétérotrophes et des échanges gazeux entre le milieux aquatique et l'atmosphère (Tranvik et al., 2009). Le CO_2 est utilisé par les organismes autotrophes pour effectuer la photosynthèse. Par ailleurs, le carbone aquatique sous formes organiques dissoute (COD) et particulaire (COP) forme les réserves de carbone organique total (COT). Le COD et le COP dans les milieux aquatiques sont produits par les processus biologiques de la communauté vivante de l'ensemble de la biosphère. Le carbone organique peut provenir soit des écosystèmes aquatiques (carbone autochtone) ou avoir été importé des écosystèmes terrestres (carbone allochtone) (Cole et al., 2007; Tranvik et al., 2009).

Le carbone autochtone est composé de matière issue des processus biologiques de la communauté aquatique. La production primaire du phytoplancton représente la source principale de carbone autochtone. Ces organismes unicellulaires photosynthétiques constituent une source de nourriture importante pour le zooplancton (Lindeman, 1942; Wetzel, 1984). Plusieurs groupes de zooplancton se nourrissent également de décomposeurs tels que des bactéries et des protozoaires (Kankaala, 1988; Jürgens and Jeppesen, 2000; Agasild and Nõges, 2005). Lorsqu'ils meurent, le phytoplancton et le zooplancton sont recyclés par les décomposeurs. De cette façon, une bonne partie du carbone autochtone est continuellement recyclé et réintégré dans les réseaux trophiques aquatiques (Ask et al., 2009b). Par contre, une certaine portion est également acheminée vers l'océan ou accumulé au fond des lacs dans les sédiments.

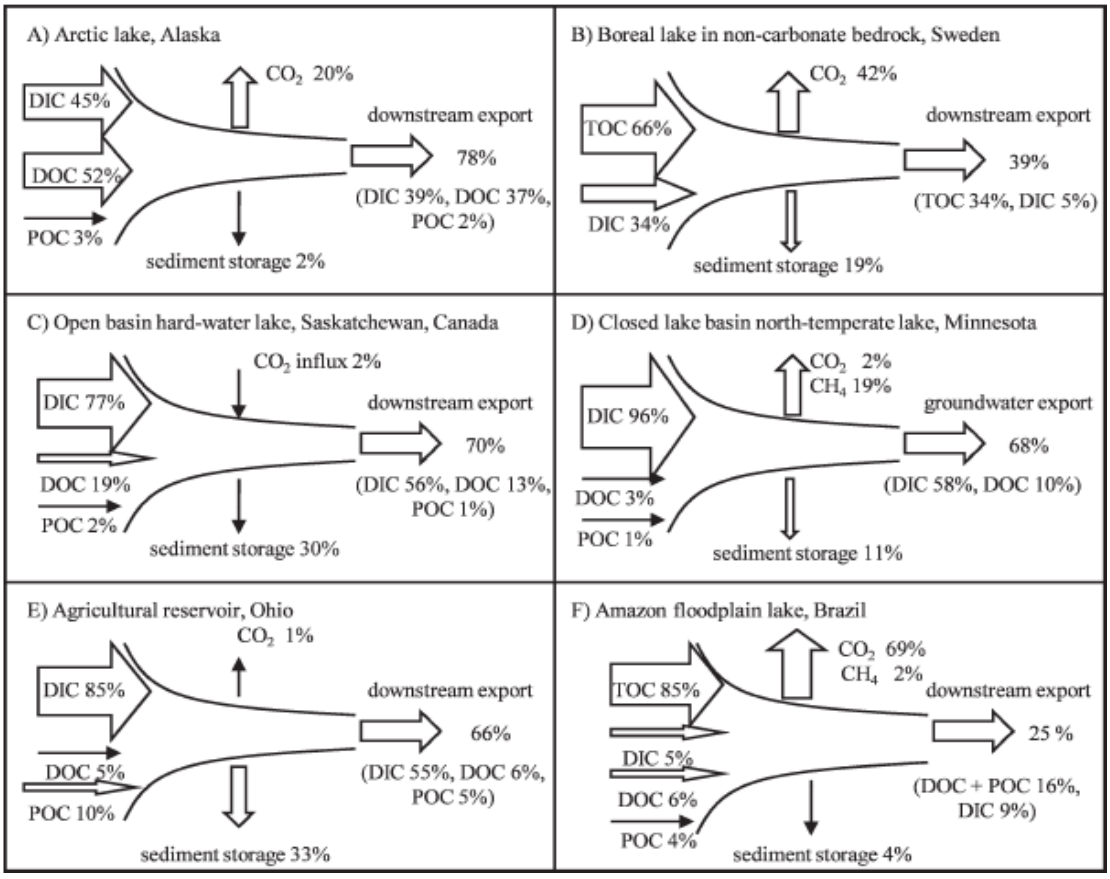

Figure 1. Le « budget » de carbone dans les lacs et les réservoirs en fonction de différents types de milieux terrestres. La forêt boréale canadienne est associée à l'image (B). DIC est le carbone inorganique dissout; DOC est le carbone organique dissout; POC est le carbone particulaire dissout; TOC est le carbone totale dissout. À noter que la distinction entre le carbone autochtone et allochtone n'est pas effectuée. *Figure tiré intégralement de Tranvik et al. (2009).*

Le carbone allochtone est produit par les écosystèmes terrestres et il pénètre dans les environnements aquatiques par le ruissellement d'eau de surface et souterraine dans les bassins versants. Cette eau transporte de la matière organique particulaire et dissoute et l'ajoute aux réserves de COT aquatique (Wetzel, 1984). Il est de plus en plus reconnu que le carbone allochtone pourrait constituer une source d'énergie alternative au carbone autochtone dans les

réseaux trophiques aquatiques. Le zooplancton ne peut pas se nourrir directement de carbone allochtone. Par contre, les décomposeurs tels que les bactéries et les protozoaires peuvent l'utiliser comme source d'énergie (Arvola and Tulonen, 1998; Kritzberg et al., 2004) et puisque plusieurs groupes de zooplancton se nourrissent de décomposeurs (Starkweather, 1980; Bogdan and Gilbert, 1982; Azam et al., 1983; Jürgens and Jeppesen, 2000; Agasild and Nõges, 2005) le carbone allochtone est de cette façon intégré aux réseaux trophiques aquatiques.

Le carbone allochtone influence les propriétés physico-chimiques des milieux aquatiques (Findlay and Sinsabaugh, 2004; Pace et al., 2004). Dans les lacs oligotrophes de la forêt boréale, il peut être présent en forte concentration et influencer l'activité phytoplanctonique et bactérienne (Berggren et al., 2007; Cole et al., 2007; Ask et al., 2012). Certains ont observé une diminution de la production primaire du phytoplancton et une augmentation de la production secondaire bactérienne le long d'un gradient croissant de COD allochtone (Ask et al., 2012; Roiha et al., 2016). Ceci est causé par la couleur foncée des composés humiques présents dans le COD allochtone. La couleur foncée diminue la profondeur de la zone euphotique et réduit la capacité photosynthétique du phytoplancton (Ask et al., 2009a). En outre, lorsque la respiration bactérienne excède la production primaire phytoplanctonique, certains milieux aquatiques peuvent être davantage hétérotrophes qu'autotrophes (del Giorgio and Peters, 1994; Zwart et al., 2015). Ces écosystèmes émettent du CO_2 atmosphérique au lieu d'en capturer. Il est également connu que le carbone allochtone peut influencer bien d'autres paramètres physico-chimiques tels que l'acidité des milieux, la floculation de la matière organique (Wachenfeldt, 2008) et l'adsorption de métaux, de polluants et de nutriments (Jones et al., 1993; Tipping, 1993).

C'est seulement récemment que l'importance du carbone allochtone dans les écosystèmes aquatiques a été reconnue. Autrefois, il était considéré que la majorité du carbone allochtone influençait peu les milieux d'eau douce et qu'il était simplement accumulé au fond dans les sédiments ou transporté jusqu'aux océans. Aujourd'hui, les effets du carbone allochtone sont de plus en plus documentés et intégrés aux modèles du cycle du carbone (Cole et al., 2007). Il a été démontré que la quantité de carbone allochtone dans les milieux

aquatiques a augmenté au cours des dernières décennies causant un phénomène de brunification de l'eau. Plusieurs facteurs expliquent cette augmentation, notamment : l'utilisation et l'exploitation anthropiques des bassins versants, l'augmentation des précipitations, le dérèglement saisonnier causé par les changements climatiques et par la réhabilitation de l'acidification anthropogénique des plans d'eau reliée à la nouvelle législation de purification de l'air mis en vigueur dans les années 1990 (Tranvik and Jansson, 2002; Evans et al., 2005; Monteith et al., 2007; Zhang et al., 2010; Larsen et al., 2011; Hansson et al., 2013). Les effets d'un changement des concentrations de carbone allochtone sur les écosystèmes d'eau douce dans les régions boréales sont encore mal compris et imprévisibles.

1.2 Le carbone dans les réseaux trophiques pélagique

1.2.1 Le phytoplancton et le bactérioplancton

Le phytoplancton et le bactérioplancton sont des organismes unicellulaires microscopiques. Une différence importante entre les deux groupes réside dans le fait que la plupart du phytoplancton est autotrophe alors que la plupart du bactérioplancton est hétérotrophe. A noter que la mixotrophie (à la fois autotrophe et hétérotrophe) existe également chez les deux groupes (Flynn et al., 2012). Ainsi, le phytoplancton est généralement un producteur primaire qui fixe du CO_2 en utilisant l'énergie du soleil (photosynthèse) alors que le bactérioplancton est généralement un décomposeur qui recycle la matière organique morte.

Le phytoplancton est composé de protistes (eucaryotes) et de cyanobactéries (procaryotes) qui sont présents dans pratiquement tous les milieux d'eau salée et d'eau douce de la planète. Ces organismes constituent la source principale de carbone autochtone dans les milieux aquatiques. Leur taille varie entre 1 et 200 µm (Lund, 1965). En région boréale, on retrouve généralement de 10^3 à 10^4 cellules de phytoplancton par millilitre. L'importance de leur biomasse fluctue selon les conditions des milieux notamment : l'hydrographie, la physico-chimie de l'eau, la disponibilité des nutriments, les conditions climatiques et la prédation zooplanctonique (Nuccio et al., 2003; Naselli-Flores and Padisák, 2016). Lorsque les conditions

sont favorables, le phytoplancton peut être extrêmement abondant et peut même provoquer l'eutrophisation des milieux. Ceci peut nuire à l'écosystème et diminuer la biodiversité des milieux aquatiques. Le phytoplancton contribue de façon significative à l'activité photosynthétique mondiale, ce qui aide à fixer le CO_2 atmosphérique en plus de constituer une source de nourriture importante pour le zooplancton (Starkweather, 1980; Kankaala, 1988; Sanders et al., 1989; Kleppel, 1993). Le phytoplancton et le carbone autochtone ont longtemps été considérés comme étant la seule source d'énergie pour les réseaux trophiques aquatiques (Lindeman, 1942).

Depuis quelques décennies, la découverte de la boucle microbienne (Pomeroy, 1974) et l'importance de son interaction avec le carbone allochtone ont poussé beaucoup de chercheurs à considérer la production bactérienne comme une source d'énergie supplémentaire et alternative à celle du carbone autochtone dans les écosystèmes aquatiques. Par conséquent, les milieux aquatiques oligotrophes de la forêt boréale pourraient être supportés en partie par de l'énergie provenant des milieux terrestres. Le bactérioplancton hétérotrophe est très abondant dans la colonne d'eau des milieux boréaux. On y retrouve de 10^5 à 10^6 cellules bactériennes par millilitre et la taille de ces organisme varie entre 0,2 µm et 2,0 µm. (Letarte and Pinel-Alloul, 1991a; b). Les bactéries vivent généralement en condition aérobique, quoi que plusieurs groupes se retrouvent également en condition anaérobique. Elles décomposent la matière morte en suspension dans la colonne d'eau (Pace et al., 2004; Carpenter et al., 2005). Par conséquent, la densité du bactérioplancton aérobique varie en fonction de la quantité de matière organique présente dans le milieu, la disponibilité des nutriments et la concentration en oxygène dissous (Güde, 1988). Les bactéries sont en mesure d'utiliser le carbone allochtone comme source d'énergie (Arvola and Tulonen, 1998; Kritzberg et al., 2004; Berggren et al., 2007). De plus, il a été démontré qu'elles peuvent représenter une composante importante de l'alimentation des protozoaires et de plusieurs groupes de zooplancton, dont potentiellement les rotifères (Starkweather, 1980; Bogdan and Gilbert, 1982; Azam et al., 1983; Jürgens and Jeppesen, 2000; Agasild and Nõges, 2005).

1.2.2 Le zooplancton métazoaire

Le zooplancton métazoaire d'eau douce est constitué d'animaux multicellulaires de petite taille en suspension dans la colonne d'eau qui se nourrissent de phytoplancton, de bactérioplancton, de protozoaires et d'autres zooplanctons. Ces organismes représentent une source d'énergie importante pour les invertébrés et les poissons planctivores. Par conséquent, le zooplancton occupe une position clé dans les écosystèmes car il crée un lien entre le carbone autochtone et allochtone fixé par le phytoplancton et les bactéries et les niveaux trophiques supérieurs. Le zooplancton métazoaire d'eau douce est constitué de trois grands groupes: les copépodes, les cladocères et les rotifères. Les copépodes et les cladocères font partie du sous-phylum des crustacés. Ils sont d'importantes composantes du zooplancton d'eau douce et influencent significativement les réseaux trophiques aquatiques en raison de leur forte abondance et biomasse. En région boréale, on peut retrouver quelques centaines d'individus par litre lorsque les conditions sont favorables. Les études sur le zooplancton ont mis énormément d'emphase sur l'analyse des copépodes et des cladocères.

Les copépodes se retrouvent autant en milieu marin qu'en eau douce. Environ 2800 espèces ont à ce jour été décrites en eau douce (Balian et al., 2008). La taille de ces crustacés varie entre 500 µm et 2000 µm. Les nauplii et les copépodites, forme immature des copépodes, sont toutefois plus petits. Au cours de leur cycle de vie les copépodes traversent plusieurs métamorphoses aux stades naupliens et copépodites avant d'atteindre le stade adulte passant ainsi progressivement de filtreur à prédateur. Une fois adultes, la plupart des copépodes sont omnivores et prédateurs d'une grande variété de proies allant du phytoplancton à de petits cladocères. Les différentes espèces s'alimentent de façon sélective. Ils peuvent chercher et capturer activement leur nourriture et choisir d'ingérer ou de rejeter des particules alimentaires (Kleppel, 1993). Même si les copépodes peuvent parfois se nourrir de grosses bactéries, ces dernières ne constituent pas une source importante de nourriture car la plupart sont trop petites (Sommer and Sommer, 2006). Par contre, les copépodes se nourrissent de protozoaires et de rotifères qui eux ingèrent des bactéries (Wiliamson and Butler, 1986; Burns and Gilbert, 1993; Sommer and Sommer, 2006; Sommer et al., 2012). Néanmoins, les copépodes ne constituent

pas un lien important pour le cheminement du carbone allochtone vers les niveaux trophiques supérieurs. Notons que le groupe des copépodes d'eau douce se divise en deux ordres distincts, soit les calanoïdes et les cyclopoïdes.

Les cladocères vivent principalement en eau douce et ce groupe est composé d'environ 600 espèces. La taille des individus varie entre 200 µm et 5000 µm. Les cladocères sont des filtreurs très efficaces qui se nourrissent essentiellement de phytoplancton, mais ils sont également capables d'ingérer des protozoaires et des bactéries et certain sont prédateurs comme *Leptodora kindtii* (Kankaala, 1988; Agasild and Nõges, 2005; Chetelat and Amyot, 2009). Leur mode d'alimentation ne leur permet pas d'être sélectifs dans leur choix de nourriture. Ils sont tout de même capables de « trier » les particules alimentaires selon leur taille. En effet, leurs appendices filtreurs agissent comme un tamis qui retient les grosses particules pour les ingérer et laisse passer les plus petites. Pour cette raison, les cladocères ne sont pas reconnus pour être d'importants consommateurs de petites bactéries (Geller and Müller, 1981). Cependant, ils seraient en mesure d'ingérer des bactéries plus grosses et des protozoaires de façon passive et involontaire lorsqu'ils se nourrissent de phytoplancton (Kankaala, 1988; Jack and Gilbert, 1993; Bertilsson et al., 2003). Ainsi, les cladocères pourraient être impliqués dans le transfert du carbone allochtone aux niveaux trophiques supérieurs. Lorsque les conditions sont favorables et qu'ils se retrouvent en forte abondance, les cladocères peuvent exercer une forte pression sur les populations de phytoplancton et influencer négativement leur abondance (Lampert et al., 1986). Par ailleurs, due à leur forte biomasse, les cladocères constituent une source importante de nourriture pour plusieurs invertébrés et espèces de poissons planctivores (Jeppesen et al., 2004).

1.2.3 Les rotifères

L'écologie des rotifères représente le sujet principal de ce projet de maîtrise. Les rotifères font partie du phylum *Rotifera*. Ce groupe compte plus de 2000 espèces dont la plupart réside en eau douce (Balian et al., 2008). Le phylum est divisé en trois classes : les Seisonides (2 genres, 3 espèces), les Bdelloides (19 genres et plus de 460 espèces) et les Monogonontes

(100 genres, 1570 espèces). Plus spécifiquement, les rotifères sont des invertébrés métazoaires microscopiques dont la taille varie généralement entre 50 µm et 2000 µm. Les gros individus sont beaucoup plus rares et la moyenne de taille se situe entre 50 µm et 500 µm. La morphologie des différentes espèces est très variée. Leur corps peut être cylindrique, sphérique, cubique, conique, en forme de sac, ou même avoir l'allure d'un ver. Les rotifères sont abondants en région boréale et leur nombre varie entre 10^2 à 10^3 individus par litre (parfois plus) lorsque les conditions sont favorables. Leur importance en tant que zooplancton dans les réseaux trophiques aquatiques d'eau douce commence de plus en plus à être reconnue.

Les rotifères ont colonisé tous les types de milieu d'eau douce et quelques espèces exclusivement dans la classe des Seisonides ont également colonisé les milieux marins (Ricci et al., 1993). De plus, beaucoup d'espèces sont cosmopolites. Les rotifères vivent généralement en solitaires mais certains sont coloniaux. Quelques espèces sont des parasites d'algues, d'éponges, d'autres rotifères, d'oligochètes, d'œufs d'escargots, de crustacés et de poissons. Beaucoup d'espèces sont pélagiques et vivent en suspension dans la colonne d'eau alors que d'autres sont benthiques et s'accrochent à un substrat à l'aide de leur pied qui est typique chez la majorité des espèces. Ce pied peut être considérablement réduit chez les espèces pélagiques (Herzig, 1987). Un autre trait caractéristique des rotifères est leur structure buccale. Cette structure est constituée d'une couronne ciliée qui effectue des mouvements circulaires similaires aux mouvements d'une roue. La couronne ciliée sert à aspirer l'eau à l'intérieur d'un pharynx chitineux nommé « mastax » afin d'attraper la nourriture en suspension. Des mâchoires situées dans le mastax nommé « trophis » déchiquètent les particules alimentaires et les envoient dans le tube digestif (Herzig, 1987). Les trophis peuvent être disséquées et utilisées afin de différencier les espèces de rotifères avec précision (Thorp and Covich, 2009). En plus de l'alimentation, la couronne ciliée intervient dans la locomotion. Les espèces pélagiques l'utilisent pour se propulser et se déplacer dans la colonne d'eau afin d'attraper la nourriture en suspension.

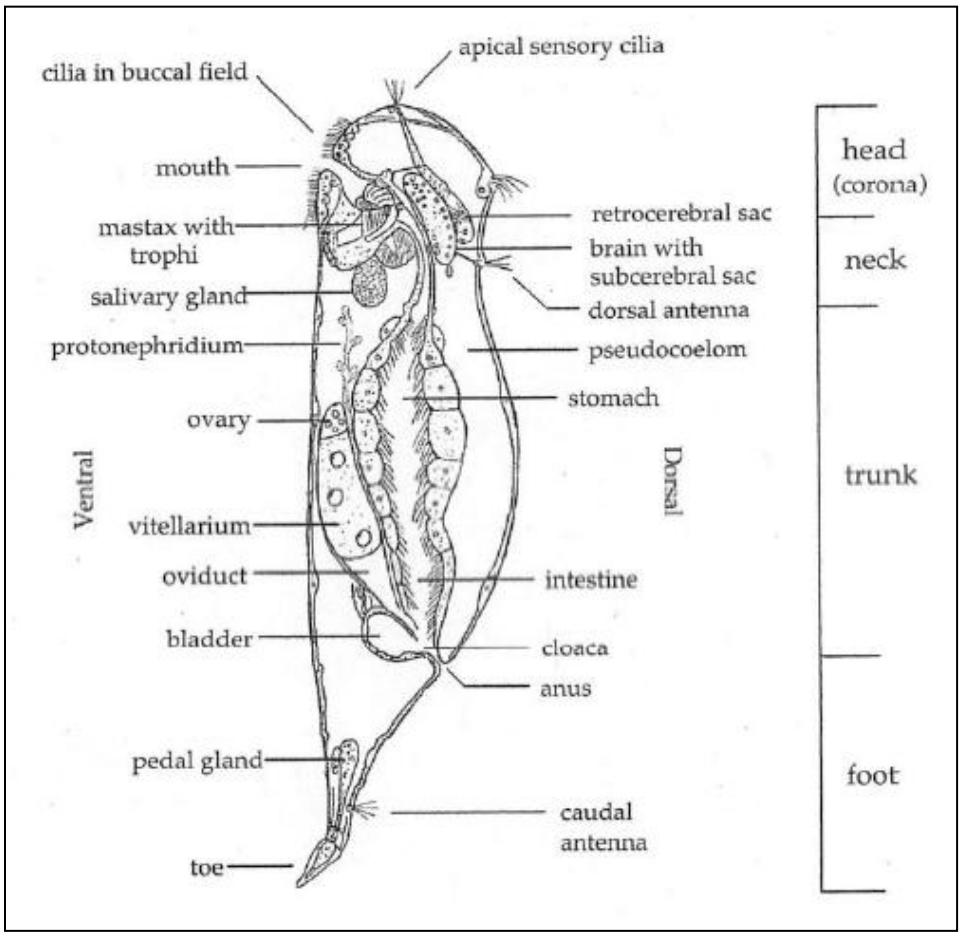

Figure 2. Schéma latéral d'un rotifère type. *Figure tiré intégralement de Wallace and Snell (2010).*

Les rotifères possèdent différents types de reproduction qui varie selon chaque classe. Les Seisonides se reproduisent de façon sexuée et on retrouve en même temps dans l'environnement des mâles et des femelles. À l'inverse, toutes les espèces de la classe des Bdelloides se reproduisent de façon asexuée par parthénogenèse. Par conséquent, on ne retrouve dans l'environnement qu'un seul sexe. Aucune trace d'organes sexuels mâles, d'hermaphrodites ou de méiose n'a encore été observée chez les Bdelloides. Ceci représente le plus haut rang taxonomique auquel le phénomène de parthénogenèse opère dans le règne animal (Flot et al., 2013). Encore aujourd'hui, ce groupe défie le principe voulant que la reproduction asexuée mène inévitablement une espèce vers l'extinction. Par ailleurs, les

Bdelloides sont très résistants au stress hydrique dû à de puissants mécanismes de réparation qui opèrent au niveau de l'ADN (Hespeels et al., 2014).

Finalement, dans le grand groupe des Monogonontes les deux types de reproduction opèrent et s'alternent selon les conditions du milieu. Lorsque les conditions sont favorables (température et photopériode adéquate, nourriture abondante), la reproduction s'effectue par parthénogenèse. On retrouve donc dans le milieu que des femelles diploïdes et amictiques. Ce cycle de clonage s'effectue jusqu'à ce que les conditions environnementales deviennent défavorables. À ce moment, les femelles présentes dans le milieu commencent à donner naissance à des femelles mictiques qui produisent des œufs haploïdes. Si l'œuf n'est pas fécondé il donnera naissance à un mâle tandis que s'il est fécondé il produira une femelle amictique. L'œuf fécondé s'enkystera et n'éclora pas avant un retour des conditions favorables. Ainsi, si les conditions sont favorables, le cycle de vie des rotifères peut s'avérer très court. Une femelle peut survivre une à trois semaines et produire environ vingt-quatre œufs (Kalff, 2002). Ils ont donc un taux de croissance et de renouvellement relativement rapide.

Les rotifères comme les autres groupes de zooplancton occupent une position clé dans les réseaux trophiques aquatiques puisqu'ils se nourrissent de phytoplancton (Agasild and Nõges, 2005). Pour certaines espèces le spectre d'alimentation est maximal à 8 μm (Rothhaupt, 1990) se qui correspond a la taille du phytoplancton. Le spectre d'alimentation des rotifères pourrait également s'étendre jusqu'à des particules de la grosseur des bactéries (Starkweather et al., 1979; Bogdan et al., 1980; Sanders et al., 1989; Arndt, 1993; Ooms-Wilms et al., 1995). Les rotifères sont eux-mêmes une source de nourriture pour plusieurs groupes de zooplancton, d'autres invertébrés et des poissons planctivores (Brandl, 2005; Sampson et al., 2009). Ainsi, les rotifères pourraient contribuer à transférer le carbone allochtone consommé par les bactéries aux niveaux trophiques supérieurs.

La présence des rotifères en tant que composante du zooplancton est étudiée depuis longtemps (Gosse, 1856; Jennings, 1900; Samuel, 1934). Les rotifères sont généralement beaucoup plus nombreux que les copépodes et les cladocères (Orcutt and Pace, 1984; Pace et

al., 1992; Drouin et al., 2009) et leur densité peut dans certain cas atteindre plusieurs milliers d'individus par litre (Pennak, 1955). Par conséquent, lorsque les conditions sont favorables ils peuvent occuper la plus grande portion de la biomasse zooplanctonique (Pace and Orcutt, 1981). De plus, la diversité d'espèces de rotifères présents dans un milieu est souvent plus grande que celles des copépodes et des cladocères combinées. Il ne fait donc aucun doute que les rotifères sont une composante importante du zooplancton en eau douce. Pourtant, les études sur le zooplancton ont souvent marginalisé ce groupe au détriment des copépodes et des cladocères (Carpenter et al., 1985; Jurgens et al., 1999; Jürgens and Jeppesen, 2000; Chick et al., 2010) et beaucoup moins d'études portent sur les rotifères comparativement aux deux groupes de crustacés. Cependant, davantage d'efforts ont été consacrés à l'étude des rotifères au cours des dernières années. Ce projet de maîtrise vise à contribuer à l'avancement des connaissances sur l'écologie des rotifères en milieu boréal et à analyser leur importance dans les réseaux trophiques aquatiques.

1.2.4 Les poissons et les invertébrés prédateurs

Les poissons et les invertébrés prédateurs présents dans les milieux aquatiques boréaux constituent les niveaux trophiques supérieurs. Les invertébrés sont généralement des larves d'insectes. Ils sont présents dans tous les milieux d'eau douce de la zone boréale et ils peuvent être d'importants prédateurs du zooplancton. L'abondance des invertébrés peut varier en fonction de la présence ou de l'absence de poissons. Dans la forêt boréale du Québec, des barrières géographiques naturelles ont empêché la colonisation postglaciaire des poissons dans plusieurs lacs de tête au sommet des bassins hydrographiques. Ces lacs constituent des systèmes fermés avec peu de connectivité à d'autres plans d'eau abritant des populations de poissons. On retrouve donc des lacs dans lesquels se sont développées des communautés en absence de prédation par les poissons. Ceci influence de façon considérable la structure et la distribution des communautés aquatiques (zooplancton et invertébrés). Drouin et al. (2009) ont observé dans des lacs sans poissons au nord de la Rivière Saguenay une diminution de l'abondance des cladocères et une augmentation de l'abondance des rotifères comparativement au lacs avec poissons. Cela est attribué à une plus forte présence d'invertébrés qui est causée

par l'absence de prédation par les poissons. La plus grande taille des crustacés les rendraient plus vulnérables à la prédation par les invertébrés que les rotifères qui sont plus petits. Par ailleurs, Brooks and Dodson (1965) ont observé une diminution importante de l'abondance des cladocères et des copépodes en présence de poissons planctivores dans plusieurs lacs de la Nouvelle Angleterre. En absence de poissons, la communauté de cladocères et de copépodes est plus abondante. Ainsi, les rotifères seraient moins vulnérables à la prédation exercée par les invertébrés prédateurs et les poissons planctivores due à leur petite taille. La connectivité entre les systèmes aquatiques influence donc la capacité colonisatrice de la faune ichthyenne et régule les populations de zooplancton.

1.3 La forêt boréale

La forêt boréale, également connue sous le nom taïga, représente le plus grand biome terrestre au monde. Elle forme un anneau situé entre la forêt tempérée au sud et la toundra au nord. Cet anneau fait toute la circonférence de la planète. Par ailleurs, la forêt boréale couvre près d'un tiers de la superficie forestière totale de la terre. Elle est principalement présente au Canada et en Russie mais on la retrouve également en Alaska, en Suède, en Finlande, en Norvège, dans les régions nordiques du Kazakhstan, de la Mongolie et du Japon. La composition de la végétation, de la diversité animale, de la nature des sols, de la longueur des saisons, des précipitations moyennes et des températures moyennes varient énormément géographiquement.

Figure 3. Localisation géographique de la forêt boréale au Canada. *Figure tiré intégralement de NRCAN (2016).*

Au niveau mondial, sur les 304 millions de lacs estimés globalement, 91 % auraient une superficie située entre 0,01 et 0,1 hectare (Downing et al., 2006). Ainsi, la grande majorité des lacs boréaux sont peu profonds et de petite taille. Par ailleurs, les lacs situés en région boréale sont généralement oligotrophes. Ils sont reconnus pour recevoir de fortes quantités de carbone allochtone. Des précipitations abondantes, des forêts productives, quatre saisons distinctes, l'accumulation et la fonte annuelle de neige et le lessivage important des sols au printemps sont tous des facteurs caractéristiques de la forêt boréale qui contribuent à expliquer la forte exportation de carbone allochtone vers les milieux aquatiques. Par ailleurs, plusieurs études ont démontré que la concentration moyenne de carbone allochtone dans les plans d'eau des régions boréales aurait augmenté au cours des dernières décennies (Tranvik and Jansson, 2002; Evans et al., 2005; Monteith et al., 2007; Hansson et al., 2013). Cela serait attribuable aux effets des changements climatiques tels que l'augmentation des précipitations et des hivers plus courts, ainsi que l'utilisation anthropique de la forêt et des bassins versants. Les impacts qu'une modification des concentrations de carbone allochtone pourrait avoir sur les écosystèmes aquatiques boréaux sont encore mal compris.

En outre, la forêt boréale au Canada couvre une superficie de plus de 3 millions de kilomètres carrés (Steedman et al., 2004). Elle renferme une quantité considérable

d'écosystèmes terrestres et aquatiques et fournit de nombreux services à l'homme qui l'exploite abondamment de façon industrielle, commerciale et récréative. La forêt boréale canadienne démontre un degré considérable d'hétérogénéité. Il existe un important gradient latitudinal lorsque l'on considère la composition de la communauté d'espèces arborescentes. Au sud, elle est fortement à composition mixte: sapinière à bouleau blanc incluant beaucoup d'autres espèces telles que de l'épinette blanche et noire, du pin gris, du mélèze, du peuplier faux tremble, du bouleau jaune et de l'érable rouge (MFFP, 2016). En direction nord, on constate une diminution importante de la diversité arborescente. La présence de feuillus diminue laissant place aux pessières à mousses. À la limite nordique de la forêt continue, la communauté est pratiquement monospecifique et composée uniquement d'épinette noire (MFFP, 2016). Finalement, une forêt éparse et discontinue d'épinette noire s'étend jusqu'à la toundra près du 58^{e} parallèle (MFFP, 2016). La composition des sols varie également en fonction du couvert végétal ainsi que du climat. Ceci affecte la quantité et la nature du carbone organique dans les sols, la stabilité et la profondeur verticale de l'horizon organique des sols et la façon dont le carbone est assimilé par les micro-organismes (Laganière et al., 2012; Laganière et al., 2013). L'hétérogénéité de la forêt boréale influence la quantité et le type de carbone allochtone qui est exporté vers les lacs. Il a déjà été démontré que différent systèmes terrestres provoquent des effets écologiques différents dans les milieux aquatiques (Berggren et al., 2007).

Par ailleurs, l'hétérogénéité de la forêt boréale peut également être observée à plus petite échelle, en particulier dans la région du Saguenay-Lac-Saint-Jean au Québec. En effet, la dernière glaciation a façonné la topographie de cette région. On y retrouve de hautes montagnes de granite et de roches Précambrienne de type igné métamorphique qui sont recouvertes d'un épais manteau de conifères. Ces montagnes sont connues sous le nom de « Plateau Laurentien » (MRNF, 2006). Elles entourent une ancienne mer maintenant asséchée, la Mer de Champlain (plus particulièrement le Golfe de Laflamme) qui révèle des sols riches composés de dépôts marins et de roches sédimentaires. Il s'agit des Basses terres du Saguenay-Lac-Saint-Jean qui sont recouvertes d'une dense forêt mixte (MRNF, 2006). Cette zone est d'avantage considérée comme étant une zone de type tempérée nordique (MFFP, 2016). La composition des sols et des forêts du Saguenay-Lac-Saint-Jean est donc très variable, ce qui pourrait engendrer des

différences dans les caractéristiques environnementales des lacs de cette région et ainsi influencer la distribution et la structure des communautés aquatiques. Par ailleurs, la connectivité des lacs et des bassins versants dans la région du Saguenay-Lac-Saint-Jean est entrecoupée par une immense barrière, soit le fjord du Saguenay. Les communautés aquatiques de cette région de part et d'autre du fjord sont susceptibles d'avoir évolué séparément ce qui pourrait entrainer des différences dans leur structure. De plus, la quantité de carbone terrestre exporté dans les lacs de cette région pourrait également varier géographiquement et influencer la distribution et la structure des communautés aquatiques. Finalement, la présence ou l'absence de poissons dans les lacs du Saguenay-Lac-Saint-Jean pourrait également influencer les communautés aquatiques.

1.4 Objectifs

Ce projet de maîtrise a été réalisé au cœur de la forêt boréale canadienne dans la région du Saguenay-Lac-Saint-Jean, située dans la province de Québec. Dix pour cent du territoire du Québec est recouvert d'eau douce. La province abrite des centaines de milliers de rivières, plus de 3 millions de lacs et possède 3 % des réserves en eau douce renouvelables de la planète (MDDELCC, 2016). Malgré la forte importation de carbone allochtone dans les lacs boréaux du Québec, peu d'information est disponible concernant les mécanismes qui permettraient à cette matière organique de cheminer dans les réseaux trophiques aquatiques, notamment via la boucle microbienne et l'alimentation des rotifères. De plus, le Saguenay-Lac-Saint-Jean montre beaucoup de variabilité physiographique (Plateau Laurentien, Basse Terres du Saguenay-Lac-Saint-Jean, Fjord du Saguenay). Cette variabilité pourrait avoir un impact sur la distribution et la structure des communautés de zooplancton. L'écologie des rotifères dans les lacs boréaux n'a à peu près pas été étudiée. Par conséquent, la distribution spatiale et la structure de leurs communautés sont peu connues. Par ailleurs, comparé aux copépodes et aux cladocères, peu d'études portent sur l'écologie des rotifères. Ce projet de maîtrise vise donc à répondre à deux objectifs spécifiques.

Pour le premier objectif, le projet vise à décrire et à expliquer la structure et la distribution des communautés de rotifères dans les lacs boréaux du Saguenay-Lac-Saint-Jean. Quatre hypothèses ont été élaborées pour cet objectif. Premièrement, nous posons l'hypothèse que la structure et la distribution des communautés de rotifères vont varier en fonction des caractéristiques environnementales des lacs et des bassins versants (topographique, biologique, climatique, etc.). Deuxièmement, nous posons l'hypothèse que l'importance de la connectivité entre les lacs influencera la distribution et la structure des communautés de rotifères. Ainsi les lacs plus proches géographiquement auront des populations de rotifères plus similaires que celles des lacs plus distancés. Troisièmement, nous posons l'hypothèse que la distribution et la structure des communautés de rotifères dans les lacs exposés à de plus fortes concentrations de carbone allochtone seront différentes de celles des lacs ou l'effet du carbone allochtone est plus dilué. Quatrièmement, nous posons l'hypothèse que l'absence de poissons prédateurs imposera un effet cascade sur les réseaux trophiques qui sera observable au niveau des populations de rotifères.

Pour le deuxième objectif, le projet vise à déterminer la contribution des rotifères dans le transfert du carbone allochtone vers les niveaux trophiques supérieurs. Plus spécifiquement, le projet vise à mesurer *in situ* les taux d'ingestion de phytoplancton et de bactérioplancton par les rotifères. Nous posons l'hypothèse que les rotifères seront en mesure de se nourrir efficacement de bactéries lorsque ces dernières seront présentes en plus forte concentration que le phytoplancton. Ainsi, les rotifères contribueront à transférer le carbone allochtone aux niveaux trophiques supérieurs.

2 ROTIFER DISTRIBUTION IN SMALL OLIGOTROPHIC BOREAL LAKES AND POTENTIAL CONTRIBUTION IN THE TRANSFER OF ALLOCHTHONOUS CARBON IN THE AQUATIC FOOD WEB

2.1 Introduction

Lakes situated in boreal regions are generally oligotrophic and are known to receive high quantities of allochthonous humic matter (Tranvik et al., 2009). Strong precipitations, productive forests, carbon rich soils, four distinctive seasons and the yearly accumulation and melting of the snow cover with high water runoffs in spring are all reasons that contribute in explaining high leaching of organic matter from terrestrial environments to aquatic boreal systems. The vast majority of lakes in the boreal forest are small and shallow. In fact, it is estimated that 91 % of lakes worldwide have surface areas ranging between 0.01 and 0.1 hectares (Downing et al., 2006). These small systems are more fragile to perturbation in the watershed than larger stable lakes since they have smaller watershed-lake ratio. Smaller watershed-lake ratio implicates that these lakes have small watershed compared to lake surface area. Therefore perturbation in the watershed are a lot less “diluted” then in larger systems with larger watershed-lake ratio. Certain studies have observed that allochthonous dissolved organic carbon (DOC) in boreal lakes have increased over the last few decades, a phenomenon known as browning. This is mainly due to indirect impacts of climate change (higher precipitation, shorter winters), anthropogenic land use and acidification of lakes (Tranvik and Jansson, 2002; Evans et al., 2005; Monteith et al., 2007; Zhang et al., 2010; Larsen et al., 2011; Hansson et al., 2013). Impacts of such DOC increases on aquatic ecosystem dynamics are uncertain. However, evidence shows that allochthonous carbon is assimilated in the aquatic food web and not simply flushed through lakes and rivers to the oceans or stored in the sediments, as it was originally thought (Cole et al., 2007; Karlsson et al., 2012).

The Canadian boreal forest shows a high degree of environmental heterogeneity. A large latitudinal gradient exists in terms of climate and tree species composition, from southern mixed forest to monospecific coniferous forest at the northern tree line limit (MFFP, 2016).

Tree cover and climate affects soil biological dynamics and composition. This may in turn create geographical variability in the quantity of carbon to lakes because a large portion of the allochthonous carbon exported to lakes is dissolved and originates from the soils. It has been shown that landscape and watershed characteristics do impact ecological processes in fresh water boreal systems. Heterogeneous forest-derived carbon can contain young, potentially bioavailable carbon compounds as well as slow degrading and more recalcitrant carbon compounds (Berggren et al., 2007; 2009). This geographical variability and hence differences in carbon quality can even be observed at smaller geographical scale, as it is the case in the Saguenay-Lac-Saint Jean region situated in the province of Québec. The last ice age has carved the landscape of this region, creating high mountains of granite and Precambrian igneous metamorphic rock covered by a thick coniferous forest. This area is known as the Laurentian Plateau (MRNF, 2006). These mountains surrounds dried up ancient sea, the Champlain Sea (more precisely the Laflamme Golfe), revealing rich soils composed of marine deposits of sedimentary limestone covered by a dense mixed forest. This area is known as the Saguenay-Lac-Saint-Jean lowlands (MRNF, 2006). These two areas show major differences in forest cover which could further translate in important differences in soil composition (Laganière et al., 2012; Laganière et al., 2013). This could create variability in environmental characteristics of lakes and allochthonous carbon inputs of the region. The post-glacial colonisation of lakes in the Saguenay-Lac-Saint-Jean has been impacted by the presence of natural barriers largely affecting lakes connectivity and modulating the distribution of fish and other aquatic species. Hence, many headwater lakes remain totally fishless with aquatic communities evolving without this predatory pressure (Drouin et al., 2009). This has influenced the distribution of zooplankton and the structure of aquatic communities (Drouin et al., 2009). The structuring effect that the absence of fish has on zooplankton communities has been observed in other studies as well (Brooks and Dodson, 1965; Drouin et al., 2009). Furthermore, a 900 million years old graben has also carved a large crevasse in the landscape of the Saguenay-Lac-Saint-Jean region known as the Saguenay Fjord. This fjord is more than one hundred kilometers long with rocky cliffs hundreds of meters high that split the region in two.

Despite the strong importation of allochthonous carbon to boreal lakes, not much information is available concerning mechanisms permitting this matter to flow up the aquatic food web. Information is especially lacking concerning the role of small size zooplankton in consuming and transferring terrestrial carbon in the food chain. Among zooplankton, rotifers are smaller animals than crustaceans and they are better adapted to feed on bacteria (Starkweather et al., 1979; Arndt, 1993). Bacteria are the primary decomposers and users of terrestrial carbon in aquatic environments. Rotifer numbers are generally higher than other zooplankton (Orcutt and Pace, 1984; Pace et al., 1992; Drouin et al., 2009) and their density can sometimes reach thousands of individual per liter which is rarely the case for crustacean zooplankton (Pennak, 1955). When conditions are favorable, rotifers can occupy the largest portion of the zooplankton biomass (Pace and Orcutt, 1981). Their diversity in freshwater systems is almost always higher than crustaceans (Herzig, 1987). Rotifers are a potential food source for higher components of the food web such as other zooplankton, insect larvae and fish (Brandl, 2005; Sampson et al., 2009). By feeding on bacteria, rotifers might be highly involved in aquatic food web dynamics by transferring allochthonous carbon to higher trophic levels.

The high abundance of rotifers and their adaptation to feeding on bacteria has not been taken into account in calculations of terrestrial carbon transfer rates in the planktonic food web. Zooplankton studies in the past have often focused mainly on crustaceous zooplankton such as copepods and cladocerans, minimizing the implication of rotifers in aquatic food web dynamics (Carpenter et al., 1985; Jurgens et al., 1999; Jürgens and Jeppesen, 2000; Chick et al., 2010). This could partly be explained by the fact that rotifers are a lot smaller than most crustaceous zooplankton and are hence harder to observe and manipulate. Rotifers' smaller size may also have led to the use of inadequate sampling techniques such as large zooplankton nets resulting in underestimation of their abundance and diversity (Chick et al., 2010) , which is nevertheless usually very high. Therefore, less is known about their population structure, distribution and feeding preference in freshwater boreal ecosystems.

Terrestrial carbon adds a non-phytoplankton (non-autochthonous) energy source to the aquatic food web and this carbon source eventually connects autochthonous and allochthonous

resources together in fueling ecosystems. A recent study by Guillemette et al. (2015) estimated that 76% of the aquatic bacteria biomass is based on consuming terrestrial carbon. Furthermore, although bacterioplankton can be supported by allochthonous organic matter, phytoplankton primary production cannot. In fact, allochthonous organic matter can even be a nuisance to phytoplankton and is negatively related to primary production (Ask et al., 2012). This is mainly due to the dark humic compounds present in terrestrial matter and their effects on the browning of the water color which limits light penetration and decreases photosynthesis (Karlsson et al., 2009). Therefore, terrestrial imports of organic humic matter in aquatic systems can impact food webs dynamics with potential influence on zooplankton community composition via changes in the relative abundance between their algal and bacterial food source and hence the overall energy flow through the aquatic food chain.

This project aims to answer two specific objectives. The first objective is to describe rotifer distribution and community structure in 22 boreal lakes of the Saguenay-Lac-Saint-Jean region situated in the province of Québec. Four hypotheses were elaborated for this objective. For the first hypothesis, we predict that rotifer distribution and community structure will vary according to the environmental characteristics of the lakes and their watersheds. For the second hypothesis, we predict that the importance of lake connectivity will influence the distribution and community structure of rotifers. Therefore, lakes which are geographically closer together will have more similar species assemblages than lakes that are distant from each other. For the third hypothesis, we predict that rotifer populations located in lakes exposed to higher concentration of allochthonous carbon will differ from that of lakes where terrestrial carbon inputs are more diluted. For the forth hypothesis, we predict that the absence of predatory fish will impose a cascading effect on the food web observable to the rotifer trophic level.

The second objective is to evaluate rotifer's importance in the transfer of allochthonous carbon to higher trophic levels. More specifically, we aim at measuring *in situ* ingestion rates of rotifers on phytoplankton and bacterioplankton. We hypothesise that rotifers will be able to feed efficiently on bacteria when they are found in greater concentration than phytoplankton

and that they can efficiently transfer allochthonous carbon to higher trophic levels of the food chain.

2.2 Methods

2.2.1 Study area

This study took place in the heart of the Canadian boreal forest of the Saguenay-Lac-Saint-Jean region, in the province of Quebec. Ten percent of the Quebec territory is covered by fresh water. Moreover, this province contains tens of thousands of rivers and more than three million lakes, representing 3 % of the worldwide renewable freshwater resource (MDDELCC, 2016) therefore providing an excellent ecosystem for testing carbon cycling and the coupling between terrestrial and aquatic habitats. Most of the Saguenay-Lac-Saint-Jean region is part of the Laurentian Plateau which is geologically composed of a thick coat of granite and Precambrian igneous and metamorphic rock such as gneiss and anorthosite (MRNF, 2006). In the heart of the region, the Saguenay-Lac-Saint-Jean lowlands cut through the Laurentian Plateau and extends along the Lake Saint-Jean and Saguenay River perimeter. To the east of the lowlands, the Saguenay Fjord, long of its 100 kilometers, further divides the Laurentian Plateau extending west to east from the Saguenay-Lac-Saint-Jean lowlands to the St. Lawrence River. The plateau on both northern and southern areas of the plain and the Fjord is characterised by mountains ranging between 200 and 1100 meters. This landscape design is the post glacial heritage of the eroding effect of the retrieving glaciers shaping the terrain.

A continental climate dominated by cold temperatures and moderate humidity characterizes the region. Temperature fluctuations are important according to altitude and latitude, influencing the initiation and duration of the growth season of plants. Likewise, differences in temperatures between summer and winter can reach more than 60 °C. The mean annual temperature for the year 2013 was 3.4 °C with a maximum of 33.4 °C recorded in July, and a minimum -32.7 °C recorded in February (Environnement Canada, 2015). Total annual precipitations for the year 2013 were 960.7 millimeters, and fell as snow for 7 months of the

year from October to April (Environnement Canada, 2015). Although annual precipitations of the region are among the lowest in the province of Quebec, snow accumulation in winter is considerable, especially in the high hills of the Laurentian Plateau north and south of the Saguenay River, where several meters of snow cover the ground 6 months per year (MRNF, 2006). A total of 199.3 cm of snow was recorded for the year of 2013 at the Bagotville airport weather station, which is actually situated in the Saguenay lowlands (Environnement Canada, 2015). In the hills of the Laurentian Plateau where the lakes of this study were situated, much more snow is known to accumulate. Therefore, high inputs of terrestrial material occur in lakes of the boreal region during spring when all this snow melts. Additionally, a thick sheet of ice (maximum of about 70 cm) covers most lakes and rivers for five months per year.

The region is part of the Saguenay River watershed which is the fourth largest hydrographic basin in Québec (MRNF, 2006) It is characterised by thousands of lakes and rivers of all sizes spreading across the entire territory and draining large amounts of water from the terrestrial landscapes. Lakes of the region are therefore generally dark in color from the high inputs of terrestrial material. Almost 90 % of the Saguenay-Lac-Saint-Jean region is covered by boreal forest, one third of it being composed of mature trees that are more than 90 years old (MFFP, 2013). White spruce, black spruce, jack pine, cedar, balsam fir, white birch, and yellow birch compose the boreal forest of the region, with 60 % of the entire territory being mainly covered by black spruce between the 50th and 52nd latitude (MFFP, 2013). However, the study site for this project was located beneath the 50^{th} latitude where the boreal forest is generally composed of white spruce, fir, and white birch but also includes all of the other species mentioned, only in lesser proportions. The south shore of the Saguenay Fjord is mainly covered by populations of white birch coupled with fir but also includes other groups such as spruce, larch, poplar, and sometimes maple (MFFP, 2016). While part of the north shore also includes this composition of trees, the forest is less diverse and the diminution of the abundance of deciduous trees is evident. Spruce and other coniferous dominates the landscape with total absence of any deciduous trees in many areas. Therefore, there is high variability on the forest composition across the whole Saguenay-Lac-Saint-Jean region and especially between the south and north shores of the Saguenay fjord.

The past ice ages have contributed in shaping the landscape of the Saguenay-Lac-Saint-Jean as well as shaping the distribution of fish species across the territory by creating natural geographic barriers, such as waterfalls, impassable for many species (Power et al., 1973). Lakes in the study area mainly contain fish populations of brook trout (*Salvelinus fontinalis)*, and also often include white sucker (*Catastomus commersoni*), and cyprinids (MFFP, unpublished data). It is important to note that Brook trout have colonised the territory naturally while white sucker and cyprinids have been accidently introduced by men over the last decades. In the higher hills of the Laurentian Plateau, geographic barriers created many lakes that remain naturally fishless, having never been colonized by any fish population.

2.2.2 Lake selection

A total of twenty-two (22) small natural boreal lakes were selected for zooplankton sampling and analysis in this project (see Table 1 for geographical coordinates and general characteristics of the lakes selected). All the lakes were entirely situated between the 48th and 49th latitude. In order to address each hypothesis, lakes were selected according to their geographical locations and watershed characteristics. Ten lakes were located in the deciduous/coniferous mixed forests of the south shore of the Saguenay Fjord and twelve were located in the coniferous forest on the north shore (Fig. 4). They were further divided in three clusters according to their location in the Martin-Valin (north-east), Chauvin (north-west) and Brébeuf (south) sectors, with the exception of Lake Simoncouche that was distant from the clusters. This lake was included since it is part of the Forêt d'Enseignement et de Recherche Simoncouche (FERS) which has been largely studied by the Laboratoire des sciences aquatiques (LASA) of UQAC. The 22 lakes therefore covered a wide geographical area of more than 3000 km^2, assuring no connectivity between clusters, while lakes within clusters organized in tight groups. Lakes from the south shore were mainly located within the white birch and fir dominated forests while lakes on the north shore were mainly located within the spruce and fir dominated forests. Seven of the lakes were fishless, containing no fish population at all. All the 22 lakes were relatively shallow and small in size (min: 1.2 ha; max 81 ha; mean:

9.1 ha). They were selected as to represent as much as possible the natural variability of the boreal forest flora, landscape and watershed topography, zooplankton distribution and physico-chemical characteristics of the small and shallow boreal lakes of the Saguenay-Lac-saint-Jean region.

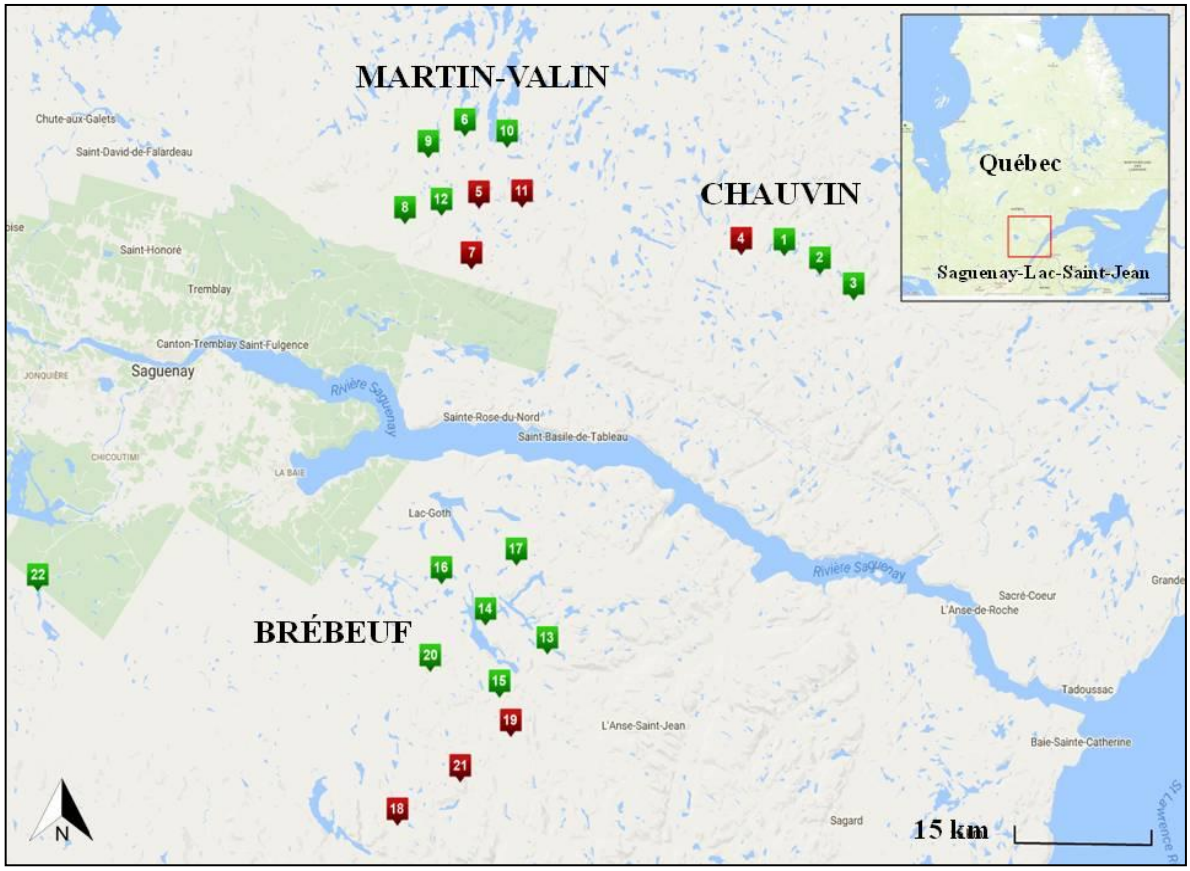

Figure 4. Map of the study area and location of the 22 lakes sampled in 2013 showing the Martin-Valin, Chauvin and Brébeuf clusters as well as Lake Simoncouche (site 22 to the left). Green represent lakes with fish and red represents lake without fish. The numbers associated to each lake identify each one and can be visualized in Tables 1 and 3.

2.2.3 Zooplankton sampling and limnological measurements

Sampling was achieved between September 30 and October 9, 2013. The 22 lakes selected were sampled at their deepest possible point using a two litres Limnos water sampler (Limnos Ltd, Turku, Finland). A total of ten litres of water was collected for zooplankton analysis. The Limnos sampler was dropped five times at depths chosen in such a way as to cover the entire water column, starting at the surface to a maximum of 10 meters, and integrated into a bucket. For lakes less than ten meters, the Limnos samples were collected up to a maximum of one meter from the bottom. The intergraded water sample was then filtered through a 20 µm sieve and the zooplankton was stored into plastic containers with formaldehyde (4% final concentration). Three replicate samples were collected at each lake. Zooplankton was counted and identified using an Utermohl sedimentation chamber with a Zeiss Axiovert inverted microscope at 100X to 400X magnification. Rotifers were identified and counted according to species. Cladocerans and copepods were counted and identified according to major groups (nauplii, Calanoida and Cyclopoida for copepods; genus level for cladocerans).

Zooplankton mean biomass ($\mu g \cdot L^{-1}$) was calculated for each species from length and width measurements using microphotographs taken from the Zeiss Axiovert inverted microscope camera. Rotifer biovolumes were calculated according to (McCauley, 1984). The wet biomass to biovolume ratio was considered to be 1:1, and these values were converted to dry biomass according to a coefficient of 0.1 (McCauley, 1984). Body length and width of copepods and cladocerans were measured to estimate their biomass according to the regression curves in Dumont et al. (1975), Bottrell et al. (1976), Rosen (1981), and McCauley (1984).

The twenty two lakes were examined for limnological properties to determine the environmental characteristics of each lake during the sampling campaign. Mean temperature, conductivity, dissolved oxygen and pH of the water column was measured at one meter interval using an YSI multiparameter probe 6820 V2-2 (Yellowsprings Instruments, USA) to a maximum depth of ten meters in deeper lakes. Lake surface area and watershed surface area

were calculated using ArcGIS. Mean chlorophyll *a* concentration of each lake was determined by filtering 250 ml of lake water on GF/F glass fiber filters stored at -80°C. Chl *a* extraction was achieved in 95% ethanol using the combined spectrofluorometric method according to Nusch (1980). Mean bacterial abundance of each lake was determined by fixing lake water with a filtered (0.02 µm) solution of formaldehyde (4% final concentration) which was stored frozen at -80 °C. Cells were stained using SYBR Green I (Invitrogen) and enumerated based on their fluorescence (FL1) and side-scatter characteristics (SSC) in a FACScalibur flow cytometer (BDBiosciences) as described in (del Giorgio et al., 1996). Total phosphorus (TP) was analysed from unfiltered water preserved with H_2SO_4 (final concentration of 0.15%). The samples were stored in acid-washed glass bottles in dark and cold (4°C) until further analysis at INRS as in Breton et al. (2009). An aliquot of water was filtered through a pre-rinsed cellulose acetate filter (0.2 µm pore size; Advantec MFS Inc.) for the analyses of dissolved organic carbon concentration (DOC) and for optical analyses of DOM to characterize the dissolved carbon pools in the lakes. Samples were stored in amber glass bottles in dark and cold (4°C) until the analyses. DOC was quantified using a carbon analyzer (Shimadzu TOC-5000A) calibrated with potassium biphthalate. The CDOM absorbance was measured from 200 to 800 nm with a spectrophotometer (Agilent), using 1-cm quartz cuvettes on dual-beam mode at 1 nm. Null-point adjustment was performed using the mean value from 750-800 nm, and the absorption coefficients ($a\lambda$) were calculated from absorbance measurements ($A\lambda$) at 254 and 320 nm using $a\lambda = 2.303\ A\lambda/L$, where L is the length of the cuvette in meters (Mitchell et al., 2002). The absorption coefficient at 320 nm (a320) was used as an index of DOM concentration. Specific UV absorbance–index (SUVA254) was determined from DOC normalized absorbance at 254 nm (A254) and used as an index of aromaticity. SUVA provides insights into the chemical composition of carbon and is used as a guide to the relative importance of autochthonous versus allochthonous carbon inputs to a lake, the higher the value the higher the proportion of allochthonous carbon (Jaffé et al., 2008). The DOC (absorption at 440 nm) to chlorophyll *a* ratio (DOC/Chl*a*) acts as an allochthony indicator because DOC concentrations serve as indicators of allochthonous inputs while chlorophyll *a* serves as an indicator of autochthonous production (Carpenter et al., 2005; Bade et al., 2007).

Table 1. Location and catchment properties of the sampled lakes. Letters after lake names refer to the clusters Brébeuf (*B*), Chauvin (*C*) and Martin-Valin (*MV*).

Lake ID number	Lake names	Sampling date	Area (ha)	Watershed (ha)	Watershed to lake ratio	Altitude (m)	Deepest measured depth (m)	Latitude (N°)	Longitude (W°)
	North								
1	CLC *(C)*	3/10/2013	2.2	46.4	21.0	687	10.2	48.498	-70.159
2	QLC *(C)*	3/10/2013	6.4	154.7	24.3	616	8.2	48.487	-70.152
3	TLC *(C)*	3/10/2013	6.5	261.8	40.2	462	11.5	48.483	-70.148
4*	Perdrix *(C)*	3/10/2013	3.2	35.8	11.3	726	16.7	48.514	-70.190
5*	Aimé *(MV)*	1/10/2013	10.6	114.1	10.8	747	14.0	48.546	-70.610
6	Drapeau *(MV)*	30/9/2013	4.4	90.3	20.7	726	13.5	48.586	-70.663
7*	Écureuil *(MV)*	1/10/2013	9.9	400.8	40.4	698	11.3	48.532	-70.632
8	En Pointe *(MV)*	1/10/2013	2.0	187.2	95.5	711	6.0	48.543	-70.631
9	Huard *(MV)*	30/9/2013	9.6	84.0	8.7	676	8.2	48.592	-70.646
10	Lac 1 *(MV)*	30/9/2013	2.2	46.4	21.0	687	10.2	48.616	-70.624
11*	Vatcher *(MV)*	1/10/2013	10.5	117.4	11.2	790	18.0	48.597	-70.563
12	Voyer *(MV)*	30/9/2013	9.0	209.5	23.2	682	5.8	48.594	-70.654
	South								
13	Allen *(B)*	2/10/2013	11.0	157.0	14.3	255	8.2	48.173	-70.548
14	Aux Herbes *(B)*	2/10/2013	2.1	68.4	32.0	265	1.9	48.203	-70.554
15	Buise *(B)*	2/10/2013	1.2	27.4	23.4	239	4	48.166	-70.571
16	ELB *(B)*	2/10/2013	1.8	451.4	256.5	233	5.0	48.228	-70.640
17	Hamel *(B)*	2/10/2013	6.3	328.1	52.2	259	7.2	48.230	-70.586
18*	Jacques *(B)*	4/10/2013	4.4	65.8	14.8	603	11.7	48.023	-70.724
19*	Lisa *(B)*	4/10/2013	2.0	140.0	71.0	510	9.1	48.102	-70.558
20	Pierre *(B)*	2/10/2013	7.3	134.9	18.4	260	11.3	48.174	-70.615
21*	Stolan *(B)*	4/10/2013	6.9	61.1	8.9	473	14.2	48.113	-70.566
22	Simoncouche	10/10/2013	81.0	883.2	10.9	348	9.0	48.231	-71.251

* fishless lakes

2.2.4 Rotifer distribution and structure data analysis

All the data were analyzed using the Primer 6 v6.1.11 & Permanova+ v1.0.1 software from Primer-E Ltd (Clarke and Warwick, 1994). A combination of univariate and multivariate procedures were performed. In order to answer the hypotheses and investigate possible patterns of rotifer distribution related to environmental structuring, lake connectivity and presence/absence of fish, the data were treated according to three factors (shore, cluster, presence/absence of fish) and visualized by non-metric multidimensional scaling (nMDS) ordination based on the Bray-Curtis dissimilarity matrix (Bray and Curtis, 1957) calculated on log transformed rotifer biomass data and Euclidean dissimilarity matrix calculated on normalized environmental data. Note that Lake Simoncouche was included within the Brébeuf cluster. A nonparametric permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity was performed to test for differences between subgroups within each factor, with lakes nested within each factor to also analyse the structure between lakes and not just factors (Anderson, 2001). Finally, a distance-based test for homogeneity of dispersions (PERMDISP) by comparing distance from centroid was performed to test for variance within each factor (Anderson, 2006).

To further analyse distribution patterns, univariate analysis of rotifer populations was done by calculating diversity indices (species richness, S; Simpson diversity, 1-λ; Pielou's eveness, *J'*) on rotifer biomass data for each sample. A nonparametric permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity was performed to test for differences between subgroups within each factor for each diversity variable analysed (Bray and Curtis, 1957; Anderson, 2001). Species contribution in creating similarity (or dissimilarity) between samples from factors showing community structure differences was analysed using the similarity percentage (SIMPER) method based on Bray-Curtis similarity and biomass data (Clarke and Warwick, 1994). This analysis breaks down the contribution of each species to the observed similarity (or dissimilarity) and allows identifying the species that are most important in creating the patterns observed between samples.

PERMANOVA was additionally performed to test for differences in mean biomass of each significant species according to shore.

To test the hypothesis that rotifer community structure in lakes exposed to higher concentration of allochthonous DOC will be different from that of lakes where terrestrial carbon inputs are more diluted, Primer's "BIOENV" function was used to determine which combination of environmental variables, including carbon related variables, best explained rotifer distribution structure across the study area. Variables selected by the BIOENV function were further tested by PERMANOVA to identify mean differences between shores.

2.2.5 Rotifer grazing experiment

To understand and estimate how the rotifer abundance in the 22 boreal lakes studied translates to the transfer of autochthonous and allochthonous carbon to higher trophic levels, a grazing experiment was conducted in September of 2015. Rotifer grazing on bacterioplankton and phytoplankton were measured in different relative concentrations of bacteria and algae in order to determine which food source is preferred by Rotifers. Although the experience took place two years later than the original 22 lakes sampling, climatic and environmental conditions were similar during both events. Both took place in fall and the lake was still stratified.

The experiment was conducted using Lake Simoncouche which is located in the boreal forest of the Saguenay-Lac-Saint-Jean region, Québec. A research station is located by the lake and animals and material could be immediately collected from the lake and brought freshly to the lab where the experiment was conducted. An estimation of the principal rotifer species present in the samples used for the experiment was visually assessed by microscope although no actual counting of rotifer abundance was achieved. Species observed included *Keratella cochlearis*, *Keratella hiemalis*, *Keratella serrulata*, *Asplanchna* spp., *Kellicottia* spp., *Polyarthra* spp., and *Conochilus* spp.. Data from previous research done by the LASA has demonstrated fluctuating phytoplankton to bacteria biomass ratios in Lake Simoncouche during the year. Phytoplankton biomass in the lake is known to be very low in winter under the ice

cover; it blooms and peaks in spring, decreases but still remains high in summer and peaks again in autumn during the lake turnover. On the other hand, bacteria biomass remains relatively constant throughout the year. Therefore, within each treatment, bacteria biomass was constant at 44 $\mu gC \cdot L^{-1}$ while phytoplankton biomass increased according to 0, 5, 17, 35, and 70 $\mu gC \cdot L^{-1}$ in order to represent Lake Simoncouche natural variability in biomass ratios (Table 2).

Table 2. Bacteria and phytoplankton biomass ratios ($\mu g \cdot C \cdot L^{-1}$) used in the grazing experiment. The bold characters indicate the food source that was labelled with ^{3}H (bacteria) or ^{14}C (phytoplankton). The control was run with dead zooplankton to account for passive radioisotope uptake.

Sample	**Bacteria (^{3}H)** : Phytoplankton	Sample	Bacteria **: Phytoplankton (^{14}C)**
1-2-3	**44** : 0	28-29-30	44 : **0**
4-5-6	**44** : 5	16-17-18	44 : **5**
7-8-9	**44** : 17	19-20-21	44 : **17**
10-11-12	**44** : 35	22-23-24	44: **35**
13-14-15	**44** : 70	25-26-27	44 : **70**
31-32(control)	**44** : 0	33-34 (control)	0 : **70**

The algae for the feeding experiment were obtained from a pure *Nannochloropsis sp.* culture which was grown two weeks before the experiment. This alga has a stretched shape and varies in size between 5 and 13 μm. Initially, it was planned to grow and use algae from Lake Simoncouche in the experiment but bacterial contamination was inevitable and a pure culture was never obtained. Therefore, a sterile strain was grown instead. Phytoplankton concentration in the culture was regularly measured using the spectrophotometer method which consists in measuring the absorption (λ = 665 nm) at different phytoplankton concentration and comparing the results to a reference curve with known cell abundance for a given absorbance. The reference curve was provided by INRS-ETE where the culture originated (Fig. 5).

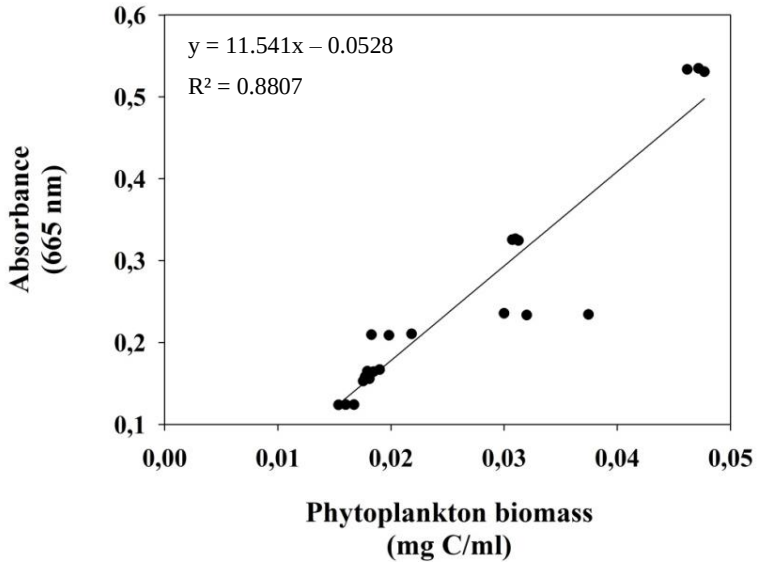

Figure 5. Absorbance reference curve for different *Nanochorophis* biomass provided by INRS-ETE.

Once a dense pure culture was obtained about 20 ml was labeled using a radioactive isotope, ^{14}C in bicarbonate form, which is naturally taken up by the algae during photosynthesis. In order to prepare the labelled algae, 50 μL of the ^{14}C solution (working solution concentration of 80 μCi/ml) was added to 20 ml of *Nanochloropsis* sp. culture and incubated in a diffuse sunlight for two hours. The solution was then centrifuged twice at 6000 rpm for 5 minutes to separate the labelled algae from the solution containing unbound ^{14}C. The

algae were reintroduced in clean 20 ml of sterilized lake water and the labeled phytoplankton concentration was measured using the spectrophotometer method. The same process was also done on a second sample, but without ^{14}C-labelling, which was to be used during the labeled bacteria feeding experiments

Bacteria for the feeding experiment come from Lake Simoncouche. Two weeks prior to the experiment, bacteria were collected by filtering lake water through a 50 μm sieve and then through 1.2 μm GFC filters to remove zooplankton and phytoplankton. The bacteria present in the filtrate was grown and concentrated in the dark using nutrients and an oxygenator. Bacteria concentration in the culture was measured using the slide fixation method as in Rautio et al. (2011). This technique consists in staining bacteria with DAPI which were extracted from a known quantity of culture and mounted on a slide to be counted under an inverse epifluorescence microscope (1000X, UV light at 365 nm). Abundance was converted to biovolumes assuming average cell size at 0.1 μm^3 (Bertilsson et al., 2003) and then converted to biomass assuming a conversion coefficient of 0.308 $pgC \cdot \mu m^{-3}$ (Fry, 1988). Once the bacterial culture was dense, an aliquant of 20 ml was removed and labeled using a radioactive isotope, ^{13}H-leucine (working solution concentration of 59 μCi/ml). The amino acid leucine is naturally used in bacterial protein synthesis and was therefore a proper choice for the experiment (Kirchman, 1985). In order to prepare the labelled bacteria, 230 μL of the ^{13}H-leucine solution was added to 20 ml of bacterial culture and incubated for 2 hours. The solution was then centrifuged twice at 10 000 rpm for 10 minutes to separate the labelled bacteria from the solution. Immediately before the grazing experiment, the bacteria were reintroduced in clean 20 ml of sterilized lake water and the labeled bacteria concentration was measured using the slide fixation method. The same process was also done on a second sample, minus the radioactive ^{13}H-leucine, which were to be used during the labeled phytoplankton feeding experiments.

The grazing experiment was run in five different biomass ratios of bacteria and phytoplankton (Table 2) with three replicates. Each experimental unit needed at least 300 rotifer individuals, which were collected from the lake the day of the experiment. Rotifers were

collected by filtering six liters of lake water through a 50 µm zooplankton net. Its content was carefully manipulated and incorporated to 250 ml GFF filtered lake water contained in 500 ml clean plastic bottles ready for the experiment. It was not recommended to mix both labels within each treatment (Kankaala, 1988). and the experiment was therefore duplicated in order to measure labeled phytoplankton and labeled bacteria grazing rates separately. In total, 34 experimental units were therefore set up. Known amounts of labeled and unlabeled phytoplankton and bacteria cultures were injected to each sample to obtain the desired food concentrations (Table 2), which covered the natural lake concentrations of algae and bacteria. Rotifers from each unit were exposed to both labeled food sources for 5 minutes which was considered a shorter time than required for the food to pass through the gut. Experiments were terminated by adding alkaline soda to each samples and then adding formaldehyde (4% concentration). Control experiments were also conducted using euthanized rotifers in order to measure passive absorption of radioactivity from each animal without direct ingestion. This information was later used to correct radioactivity absorption results from live rotifers by subtracting passive absorption. Moreover, during the feeding experiment, subsamples of the labelled bacteria (1 ml) and of the labeled phytoplankton (4 ml) were collected in order to determine bacteria and phytoplankton radioactivity within in each treatment. This was needed to later calculate feeding rates (DPM_e in equation 1).

2.2.6 Grazing rate measurements

Each sample was gently filtered through a 20 µm sieve and rinsed with milliQ water. Rotifers in the sieve were transferred to counting dishes. Using a binocular microscope (X100) and fine pincers, 300 rotifers were carefully extracted per sample. They were then transferred to separate scintillation vials (34 in total) and two milliliters of scintillation cocktail as well as solvent were added to dissolve rotifers. The samples were vortexed for 5 seconds and incubated for 24 hours, after which radioactivity was measured using a scintillation counter. Results obtained were in disintegration per minutes (DPM) per sample. The higher the DPM, the higher the radioactivity and therefore the higher feeding rate of the rotifers measured. Note that the DPM for both ^{14}C and ^{3}H had to be corrected for certain samples which had not received the

exact 5 minutes feeding time. Therefore, they were adjusted at 4 minutes when calculating filtration rates. Moreover, mean DPM values obtained from control experiments of each label, which contained dead rotifers, was subtracted from all samples in order to correct for passive radioisotope labelling. Finally, DPM was also measured from the labelled bacteria and phytoplankton samples collected from each label solution during the feeding experiment which is needed in later calculations. DPM values from each treatment was converted to individual filtration rates per rotifer using these formulas as in Kankaala (1988) :

Equation 1: Fi: individual filtration rate ($ml \cdot ind^{-1} \cdot h^{-1}$)

$$Fi = \frac{DPMa/Ne}{DPMe/ml} \times \frac{60}{t}$$

Where DPMa is the rotifer radioactivity (in disintegration per minutes), DPMe is the phytoplankton or bacteria radioactivity (in disintegration per minutes), Ne is the total number of individual per sample, t is the length of the experience (in minutes) and *ml* is the volume of the samples in millilitres. Obtained response curves of filtration rates for different phytoplankton biomass were applied to the lake data to estimate how rotifers feeding on algal versus bacteria vary in the lakes sampled. This was done by calculating community feeding rates for phytoplankton and bacteria.

Equation 2: PFe: community feeding rate ($\mu gC \cdot L^{-1} \cdot h^{-1}$)

$$PFe = Fi \times BB \times RA \quad \text{or} \quad PFe = Fi \times PB \times RA$$

Where BB and PB are the bacteria and phytoplankton biomass respectively ($\mu gC \cdot ml^{-1}$) and RA is the rotifer abundance ($ind \cdot L^{-1}$) in a given lake.

2.2.7 Estimating grazing rates on sampled lakes

In order to apply experimental results to sampled lakes and estimate carbon ingestion rates, the reference curves for both phytoplankton and bacterioplankton experimental grazing were calculated and used to obtain estimated filtration rates (*Fi)* on five lakes (Vatcher, Perdrix, Hamel, Lisa and Simoncouche). Calculations were based on known phytoplankton biomass for each lake, calculated from phytoplankton and bacteria samples that were collected at the same time as other lake data (see below) which was used as the independent variable within each equation. Population feeding rates (*PFe)* was then calculated using equation 2 and known phytoplankton, bacterioplankton and rotifer biomass in a given lake.

To calculated phytoplankton biomass, integrated water samples of each lake had been collected during the sampling campaign of October 2013 and conserved in Lugol. A known amount of the conserved samples was diluted in an Uthermöl sedimentation chamber for more than twelve hours. Portions of each sample were than observed at 100X magnification using an inverse microscope (Zeiss Observer .A1). A minimum of ten visual fields were additionally analysed at 430X magnification. In all cases, phytoplankton cells from each genus were identified, photographed and measured using Axiovision. Biovolumes were calculated according to Hillebrand et al. (1999). Biovolume results for each genus were than transformed to carbon contents according to Menden-Deuer and Lessard (2000) and related to abundance data to obtain lake total biomass. Bacteria biomass was calculated according to method described in section 2.2.5. Rotifer abundance data from the October 2013 sampling campaign was used for lakes Vatcher, Perdrix, Hamel and Lisa. Problems occurred with Lake Simoncouche phytoplankton samples and data for rotifers, phytoplankton and bacterioplankton from autumn 2011 was therefore used for this lake since the LASA had the data available due to prior sampling.

2.3 Results

2.3.1 Physico-chemical characteristics of the sampled lakes

Table 3 summarizes the physico-chemical characteristics of the sampled lakes. The results represent the mean values of the water column of each lake obtained by measuring variables at the same depths from which water was collected for zooplankton sampling (5 sampled depths to a maximum of 10 meters). Figure 6 shows the non-metric multidimensional scaling (nMDS) ordination based on the Euclidian dissimilarity matrix calculated on normalized physico-chemical data. The data used in the nMDS analysis can be found in Tables 1 and 3. Lakes sampled revealed important environmental heterogeneity across the whole study area. Furthermore, lakes situated in different forest composition showed different structure in terms of physico-chemical composition. Lakes situated in coniferous forest watersheds composed mainly of spruce and fir, as is the case on the north shore of the Saguenay Fjord, appear more clustered together on the nMDS analysis (Fig. 6) which indicates more similarity in terms of environmental structure. On the other hand, lakes situated in the mixed forest watershed composed of deciduous and coniferous trees, as is the case on the south shore, were not clustered together but rather spread out on the nMDS analysis indicating less similarity in terms of environmental structure. To test for similarity within each group, a distance-based test for homogeneity of dispersion was done on samples from each shore which revealed a significant difference in dispersion between samples from the north compared to samples from the south ($P = 0.013$) (Table 4). Mean distance from centroid for samples from the north shore was 2.87, while it was 4.09 for samples from the south shore.

Table 3. Summary statistics of the physico-chemical characteristics of the sampled lakes. Letters after lakes names refers to fish (*F*) or no fish (*NF*) populations present in the lakes.

Lake ID number	Lake	Temp (°C)	Cond (µs/cm)	pH	O_2 (%)	TP (µg P/L)	Bacteria (cells/ml)	Chl-a (ug/L)	DOC (mg C/L)	CDOM (color a320)	DOC/Chla	SUVA (A254/DOC·L)
	NORTH											
1	CLC *(F)*	8.8	24.4	6.21	60.6	11.4	$2.0*10^6$	3.0	12.3	19.6	4.10	1.6
2	QLC *(F)*	10.9	19.2	6.23	70.3	9.56	$2.2*10^6$	1.4	3.48	14.1	2.48	4.24
3	TLC *(F)*	11.1	18.6	5.90	63.6	7.84	$1.3*10^6$	6.8	4.73	19.3	0.69	4.23
4	Perdrix *(NF)*	9.6	12.8	6.16	72.9	11.0	$1.9*10^6$	1.2	3.94	14.7	3.28	3.94
5	Aimé *(NF)*	10.6	11.2	5.59	86.1	6.69	$1.4*10^6$	2.8	3.84	16.1	1.37	4.41
6	Drapeau *(F)*	13.4	89.5	7.24	79.6	9.82	$1.1*10^5$	1.4	5.85	25.4	4.18	4.41
7	Écureuil *(NF)*	9.4	85.4	6.46	72.5	8.33	$2.3*10^6$	3.2	7.03	36.7	2.20	5.09
8	En Pointe *(F)*	13.4	42.5	6.92	65.9	7.55	$4.4*10^5$	1.1	7.85	36.6	7.14	4.68
9	Huard *(F)*	11.2	16.0	6.11	79.9	7.12	$1.1*10^6$	1.2	8.71	31.6	7.26	3.63
10	Lac 1 *(F)*	9.8	15.4	6.16	82.6	7.24	$4.6*10^5$	9.0	4.32	22.4	0.48	5.25
11	Vatcher *(NF)*	9.7	8.4	4.56	79.7	7.52	$4.2*10^5$	1.1	5.17	21.4	4.70	4.36
12	Voyer *(F)*	10.2	14.8	6.28	81.7	7.38	$5.7*10^5$	0.7	8.15	40.2	5.70	4.84
	Mean	10.68	29.85	6.15	74.6	8.45	$1.2*10^6$	1.6	6.28	24.85	3.92	4.22
	SOUTH											
13	Allen *(F)*	13.7	63.4	7.13	97.6	15	$1.6*10^5$	1.8	6.71	12.3	3.72	2.16
14	Aux Herbes (*F)*	11.7	60.4	6.92	85.2	23.2	$2.8*10^5$	2.4	8.6	24.2	3.58	3.04
15	Buise *(F)*	14.1	74	7.19	84.6	23.4	$1.7*10^5$	1.6	4.03	26.9	2.52	7.79
16	ELB *(F)*	10.3	10.0	5.14	80.3	12.7	$1.2*10^6$	1.6	10.8	46.0	6.75	4.39
17	Hamel *F)*	9.5	12.2	5.15	79.3	13.2	$1.5*10^6$	1.2	7.1	54.5	5.91	7.67
18	Jacques *(NF)*	8.9	33.0	6.35	51.5	15.8	$7.6*10^5$	2.4	4.98	36.1	2.08	7.45
19	Lisa *(NF)*	8.1	31.4	5.89	45.2	19.8	$1.2*10^6$	2.8	12.9	71.6	4.61	5.3
20	Rivière Pierre *(F)*	11.5	49.6	7.11	76.3	15.9	$4.8*10^5$	1.6	8.52	39.5	5.32	4.66
21	Stolan *(NF)*	10.5	151.0	6.40	55.0	11.3	$5.3*10^5$	3.9	7.02	15.6	1.80	2.5
22	Simoncouche (F)	12.1	133.0	7.06	92.2	15.8	$2.2*10^5$	2.3	6.21	14.0	2.7	2.91
	Mean	11.1	61.8	6.43	74.7	16.6	$6.5*10^5$	2.2	7.68	34.1	3.49	4.69

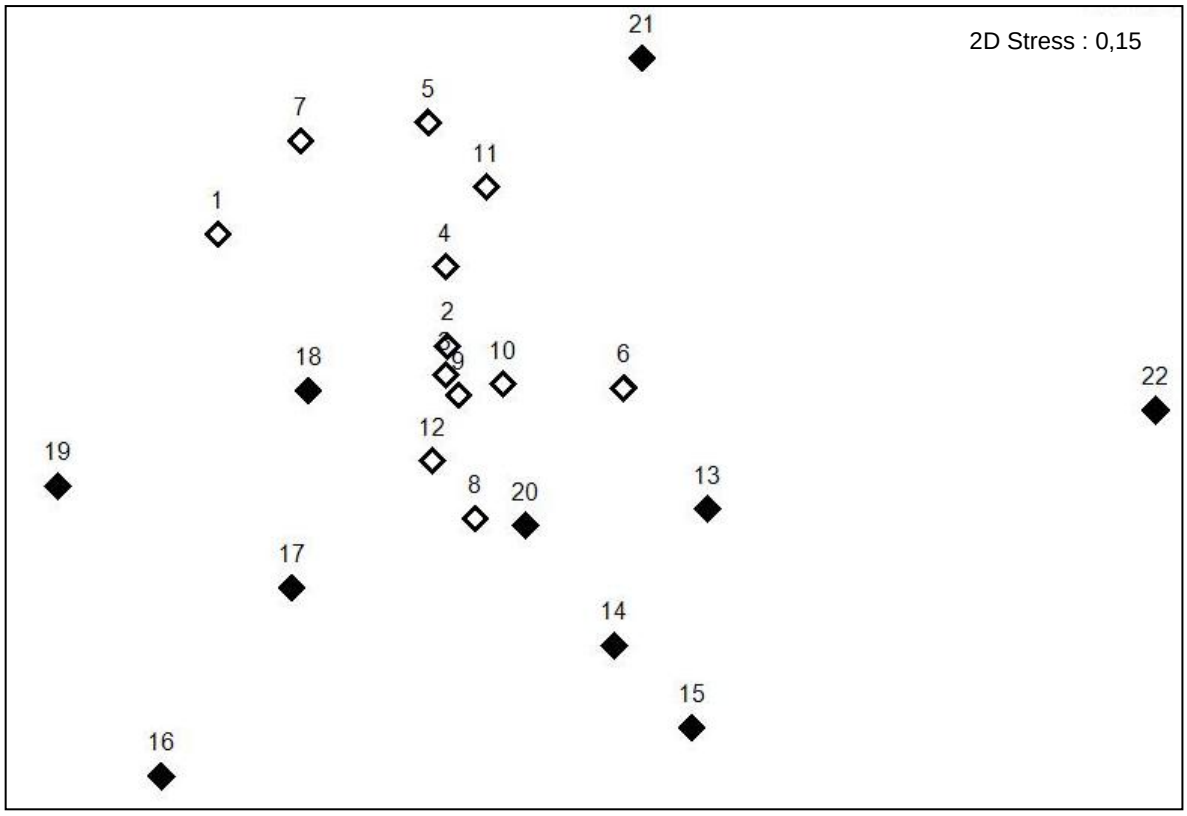

Figure 6. Non-metric multidimensional scaling (nMDS) ordination based on the Euclidian dissimilarity matrix calculated on normalized watershed characteristics and environmental data from Tables 1 and 3 for lakes from the north shore (white) and south shore (black) of the Saguenay Fjord. Numbers represent lakes as identified in Table 1 and 3.

Table 4. Distance-based test results for homogeneity of dispersions based on data from Figure 6 by comparing distance from centroid for environmental samples from the north shore and environmental samples from the south shore (n=22).

Shore	**Number of samples**	**Average deviation from centroid**	**Standard error**	***P***
North	12	2.87	0.22	0.013
South	10	4.09	0.39	

2.3.2 Zooplankton community structure

A total of 35 rotifer taxa were identified in the 22 lakes sampled. The mean number of species per lake was 9, with a maximum of 12 species identified in Lake Aux Herbes, and a minimum of 5 species in both lakes Hamel and Lake Cinquième lac de la Chaîne (CLC). The five most frequent species encountered throughout the lakes sampled in terms of occurrence included *Polyarthra* sp. (22 lakes), *Keratella cochlearis* (22 lakes), *Kellicottia bostoniensis* (20 lakes), *Kellicottia longispina* (20 lakes), and *Conochilus unicornis* (19 lakes) (Table 5).

When comparing zooplankton average densities per lake in terms of abundance, rotifers showed higher numbers of individuals than copepodites and adult copepods, nauplii copepods and cladocerans in 20 of the 22 lakes sampled (Table 6). Only lakes Hamel and Stolon showed lower numbers of rotifers than crustaceans. On the other hand, rotifers mean biomass per lake was generally lower than cladocerans and copepods, but similar to that of nauplii. Only one lake, Simoncouche, showed higher rotifer biomass than other crustacean groups. Nauplii were almost always more abundant than copepods and cladocerans. Cladocerans were generally the least abundant group, but had the highest biomass of all zooplankton.

Mean rotifer abundance per lake (n=22) was 127.6 ind·L^{-1} with a maximum of 1603.8 ind·L^{-1} in Lake Jacques and a minimum of 1.3 ind·L^{-1} in Lake Hamel. Mean biomass per lake was 2.8 µg·L^{-1}, with a maximum of 16.4 µg·L^{-1} and a minimum of 0.04 µg·L^{-1}, again for lakes Jacques and Hamel respectively (Table 6). The five most abundant species encountered (mean ind·L^{-1} per lake) included *Keratella cochlearis* (86.6), *Polyarthra* sp. (18.0), *Kellicottia bostoniensis* (5.6), *Kellicottia longispina* (4.5) and *Conochilus unicornis* (3.7) (Table 5). In terms of mean biomass (µg·L^{-1} per lake) the species with the highest values included, *Keratella cochlearis* (0.94), *Asplanchna* sp. (0.71), *Polyarthra* sp. (0.62), *Kellicottia longispina* (0.10), and *Conochilus unicornis* (0.10). All rotifer species, and especially *Asplanchna* sp., contributed differently in shaping rotifer populations depending on weather considering abundance or biomass.

Major groups of crustacean zooplankton encountered in the 22 lakes totalised seven taxa divided amongst copepods (Calanoida, Cyclopoida) and cladocerans (*Bosmina sp., Daphnia sp., Holopedium sp*., Chydoridae, and Sididae) (Table 5). Both copepods and cladocerans were present in all the lakes sampled, and copepods were more abundant than cladocerans. Juvenile copepods (nauplii) had the highest numbers with a mean of 11.0 ind·L^{-1} per lake, followed by adult cyclopoid copepods at 4.1 ind·L^{-1} and adult calanoid copepods at 2.5 ind·L^{-1}. The two most abundant cladoceran taxa were *Holopedium sp.* with 1.1 ind·L^{-1} and *Daphnia sp.* with 0.9 ind·L^{-1}. However, cladocerans had higher mean biomass per lake than copepods. This is mainly due to the large size of *Holopedium sp*. which had the highest mean biomass per lake with 30.2 µg·L^{-1}, followed by *Daphnia sp.* with 7.9 µg·L^{-1} and calanoida copepods with 7.4 µg·L^{-1}.

Excluding nauplii, Lake Jacques had the highest concentration of copepods both in abundance and biomass with 26.8 ind·L^{-1} and 39.6 µg·L^{-1} respectively. Lake Écureuil had the lowest abundance with 0.8 ind·L^{-1} and Lake Aimé had the lowest biomass with 2.3 µg·L^{-1}. Cladocerans had the highest abundance and biomass in Lake Lac 1 with 18.6 ind·L^{-1} and 283.1 µg·L^{-1} respectively. Lake Buise had the lowest mean abundance of cladocerans per lake at 0.1 ind·L^{-1} and Lake Simoncouche had the lowest biomass per lake at 0.4 µg·L^{-1}. Nauplii were present in all the lakes. Lake QLC had the highest abundance and biomass of nauplii with mean values of 28.8 ind·L^{-1} and 5.5 µg·L^{-1} respectively, while Lake Buise had the lowest values with a mean abundance of 0.3 ind·L^{-1} and a mean biomass of 0.05 µg·L^{-1}.

When considering all the lakes, rotifers had the highest mean abundance per lake, followed by nauplii, copepods and cladocerans (Fig 7). In terms of biomass, rotifers showed the third highest values surpassing nauplii, but being exceeded by cladocerans followed by copepods.

Table 5. Zooplankton taxa identified in the 22 lakes sampled during September and October of 2013 and mean lake abundance (ind·L^{-1}) and biomass (µg·L^{-1}).

Taxa	Number of lakes included	Mean abundance (ind·L^{-1})	Mean l biomass (µg·L^{-1})
Rotifera			
Kellicottia longispina	20	4.45	0.0996
Kellicottia bostoniensis	20	5.55	0.0826
Keratella hiemalis	9	0.52	0.0134
Keratella cochlearis	22	86.61	0.9409
Keratella taurocephala	4	0.38	0.0092
Keratella serrulata	3	0.005	0.0003
Keratella tecta	3	0.07	0.0011
Conochiloides dossuarius	15	1.36	0.0487
Conochilus unicornis	19	3.73	0.0985
Anuraeopsis fissa	10	0.03	0.0006
Ascomorpha sp.	15	0.48	0.0051
Euchlanis calpidia	1	0.002	0.0003
Euchlanis alata	1	0.002	0.0001
Lecane inermis	2	0.003	0.00003
Lecane mira	5	0.02	0.0003
Lecane flexilis	2	0.01	0.00004
Trichocerca cylindrica	6	0.46	0.0574
Trichocerca capucina	2	0.01	0.0008
Trichocerca rousseleti	15	0.58	0.0029
Trichocerca pusilla	1	0.002	0.0001
Asplanchna sp.	9	0.59	0.7068
Synchaeta lackowitziana	10	0.46	0.0232
Gastropus sp.	7	0.13	0.0022
Tylotrocha monopus	1	3.08	0.0339
Filinia longiseta	7	0.34	0.0089
Notholca foliacea	1	0.005	0.00002
Lepadella patella	1	0.002	0.00002
Monostyla sp.	6	0.03	0.0001
Collotheca mutabilis	4	0.44	0.0105
Wierzejskiella velox	1	0.01	0.0001
Cephalodella intuta	1	0.002	0.00002
Polyarthra sp.	22	17.95	0.6229
Lophocharis sp.	2	0.02	0.0003
Pompholyx sulcata	2	0.09	0.0008
Testudinella sp.	5	0.15	0.0012
Cladocera			
Daphnia sp.	17	0.90	7.88
Bosmina sp.	19	0.42	0.64
Holopedium sp.	15	1.14	30.23
Chydoridae	4	0.01	0.01
Sididae	14	0.20	1.29
Copepoda			
Cyclopoida	16	4.10	4.26
Calanoida	22	2.50	7.38
Nauplii	22	10.97	1.97

Table 6. Mean zooplankton abundance and biomass for all the lakes sampled in September and October of 2013 (n=22).

Lake	Abundance(ind·L^{-1})				Biomass (µg·L^{-1})			
	Rotifer	Nauplii copepods	Copepodites and adult Copepods	Cladocera	Rotifera	Nauplii copepods	Copepodites and adult Copepods	Cladocera
Aimé	23.6	3.5	1.6	3.0	0.67	0.67	2.30	31.87
Allen	24.0	19.5	1.1	7.9	0.70	3.70	2.90	122.58
Aux Herbes	71.1	4.2	4.0	2.9	6.57	0.80	10.99	41.08
Buise	199.2	0.3	4.5	0.1	8.63	0.05	12.47	2.20
Drapeau	55.5	1.1	5.7	2.8	1.82	0.20	15.79	22.45
Ecureuil	40.6	18.1	0.8	0.5	1.05	2.35	5.45	6.36
ELB	46.2	14.5	5.1	1.1	1.58	2.76	7.71	18.35
En pointe	43.2	21.0	2.6	2.0	0.96	3.98	7.11	44.21
Hamel	1.3	15.8	12.9	1.4	0.04	3.00	14.78	2.36
Huard	49.2	6.3	14.6	1.2	1.33	1.20	35.43	13.56
Jacques	1603.8	28.4	26.8	0.8	16.42	3.88	39.57	126.77
Lac1	31.5	7.6	15.2	18.6	0.71	1.45	29.97	283.08
CLC	42.5	10.9	9.7	0.4	0.86	2.07	13.54	1.72
QLC	15.6	28.8	4.7	3.5	0.37	5.48	6.47	21.08
TLC	31.6	5.9	1.7	3.1	0.92	1.12	2.54	29.26
Lisa	20.5	5.7	8.3	1.7	0.63	1.08	10.89	17.32
Perdrix	45.9	11.5	5.0	5.1	1.18	2.19	5.80	84.55
Pierre	234.5	13.7	3.9	1.5	4.03	2.61	7.48	2.06
Simoncouche	156.4	1.4	2.2	0.3	10.59	0.27	6.00	0.40
Stolon	5.3	8.2	3.2	0.5	0.11	1.55	4.65	4.08
Vatcher	43.0	8.7	6.4	0.2	1.27	1.65	8.06	0.67
Voyer	22.0	6.3	5.5	0.3	0.57	1.20	6.07	5.20
Total mean	127.6	11.0	6.6	2.7	2.8	2.0	11.6	40.1

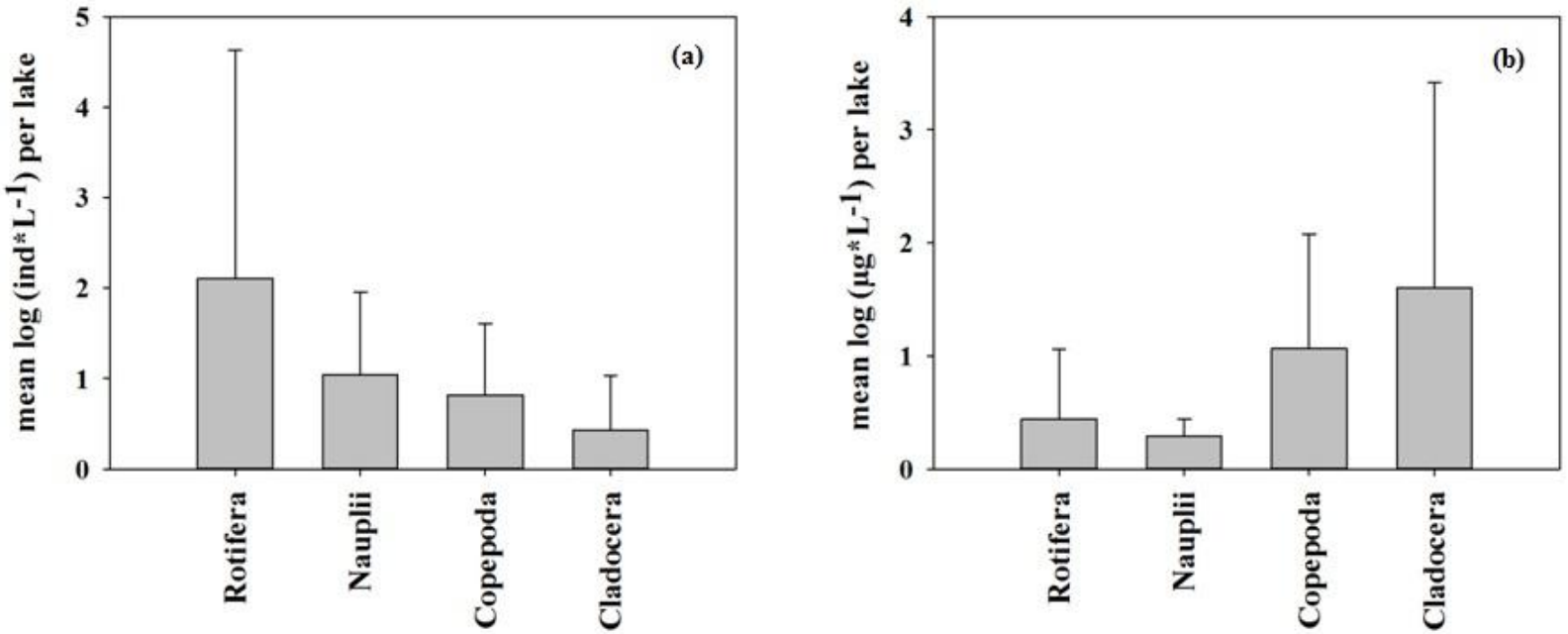

Figure 7. Mean rotifer, nauplii copepods, copepodites and adult copepods, and cladoceran abundance (a) and biomass (b) per lake (n=22). Abundance (ind·L^{-1}) and biomass (µg·L^{-1}) data is log transformed.

2.3.3 Rotifer distribution

Since zooplankton species contribution in shaping lake communities differed when comparing abundance to biomass, both variables were considered in the analysis. Permanova analysis using lakes nested within each factor showed that all the zooplankton groups showed significant differences in community structure among lakes when considering either abundance or biomass.

Rotifer biomass was significantly different in lakes between the north and the south shore of the Saguenay Fjord (Table 7). All other results obtained revealed no significant difference in rotifer or crustacean zooplankton structure for both abundance and biomass. Indeed, rotifer species assemblages showed no significant differences when considering biomass data among the three clusters or the occurance of fish in the lakes. Furthermore, rotifer species assemblages showed no significant differences based on abundance for none of the three factors tested. Likewise, crustacean zooplankton species assemblages based both on abundance and biomass showed no significant difference for any of the three factors tested.

.

Table 7. Results of nonparametric permutational multivariate analyses of variance (PERMANOVA) testing the effect of clusters (Valin, Chauvin, Brébeuf), shore (north or south of the Saguenay Fjord) and fish (presence/absence) on rotifer and crustacean assemblages using log transformed abundance and biomass data. Lakes are nested within each factor.

Source of variation	**df**	**Rotifer abundance**			**Rotifer biomass**		
		Mean square	***F***	***P***	**Mean square**	***F***	***P***
Fish	1	4215.8	1.212	0.267	6509.4	1.157	0.305
Lake(Fish)	20	3636.1	11.543	0.001	5874.8	9.937	0.001
Cluster	3	3700.4	1.019	0.441	7991.1	1.416	0.140
Lake(Cluster)	18	3699.8	11.745	0.001	5750.6	9.726	0.001
Shore	1	5485	1.551	0.108	14367	2.644	0.009
Lake(Shore)	20	3615.4	11.477	0.001	5551.1	9.389	0.001
Source of variation	**df**	**Crustacean abundance**			**Crustacean biomass**		
		Mean square	***F***	***P***	**Mean square**	***F***	***P***
Fish	1	3668.8	1.448	0.250	3293.6	1.007	0.374
Lake(Fish)	20	2651.2	15.558	0.001	3417.6	11.048	0.001
Cluster	3	3329.7	1.270	0.247	2420.4	0.701	0.663
Lake(Cluster)	18	2600.9	15.263	0.001	3520.8	11.382	0.001
Shore	1	2633.5	0.987	0.388	3778.7	1.131	0.349
Lake(Shore)	20	2729.4	16.017	0.001	3416.3	11.044	0.001

2.3.4 Rotifer population structure according to shore

The results obtained earlier oriented further testing in considering rotifer biomass according to the factor shore and exploring deeper the structure of species assemblages both to the north and to the south of the Saguenay Fjord.

Therefore, rotifer species assemblage in samples from each shore based on biomass data was visualized by non-metric multidimensional scaling (nMDS) (Fig. 8). This revealed an apparent difference in similarity between samples within each group. Samples from the north (n=34) appear to be clustered tightly together in the center of the figure. This suggests species assemblages in each lake are similar. Furthermore, samples from the south (n= 28) appear to be less clustered and more spread out along the horizontal axis which suggests species assemblages from each samples are less similar.

To test for similarity within each group, a distance-based test for homogeneity of dispersions was done on samples from each shore which revealed a significant difference in dispersion between samples from the north compared to samples from the south ($P = 0.001$) (Table 8). Mean distance from centroid for samples from the north shore was 38.8, while it was 52.6 for samples from the south shore. Therefore, in terms of species assemblages according to biomass, samples from the north shore are more similar to each other than are samples from the south shore.

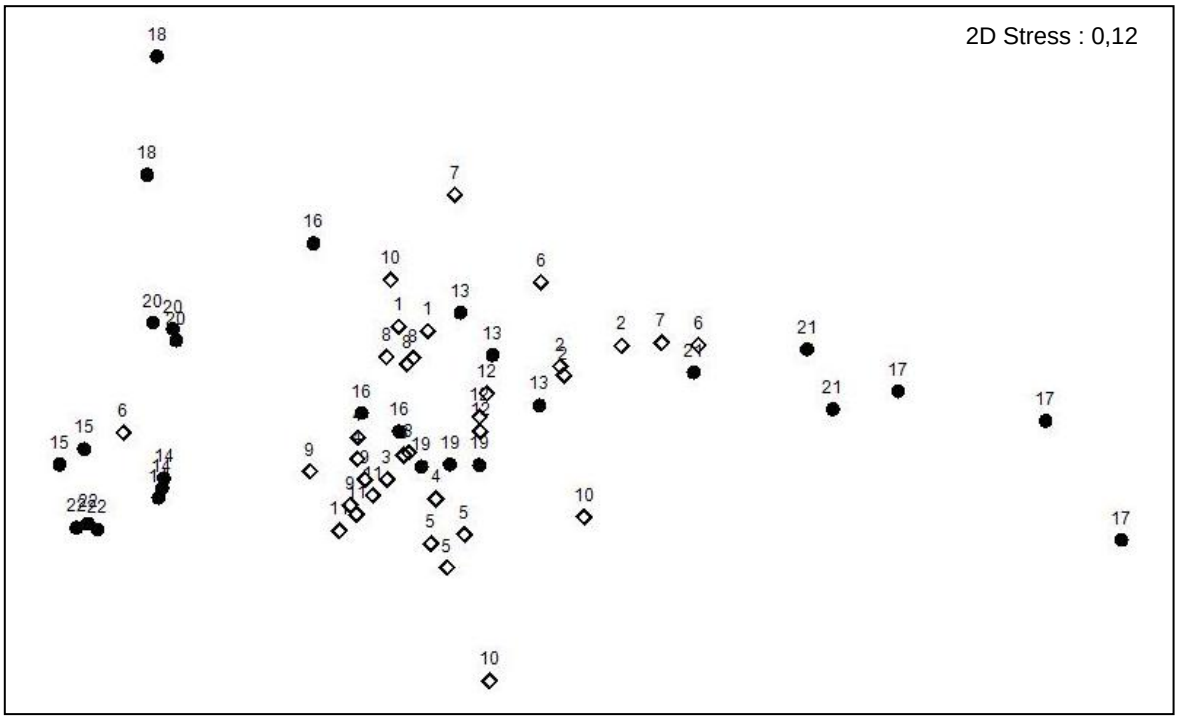

Figure 8. Non-metric multidimensional scaling (nMDS) ordination based on the Bray-Curtis dissimilarity matrix calculated on log transformed rotifer biomass data for samples from the north shore (white) and south shore (black) of the Saguenay Fjord. Numbers represent lakes as identified in Table 1 and 3.

Table 8. Distance-based test results for homogeneity of dispersions (Fig. 5) by comparing distance from centroid for rotifer biomass samples from the north shore and rotifer biomass samples from the south shore (n=62).

Shore	**Number of samples**	**Average deviation from centroid**	**Standard error**	***P***
North	34	38.795	1.7072	0.001
South	28	52.637	1.8726	

Rotifer distribution according to biomass data for mean rotifer biomass (µg·L^{-1}) per lake, mean number of species per lake, mean Simpson diversity index per lake, and mean species evenness per lake for the north and the south shore were compared and tested by PERMANOVA. This revealed significant differences for mean rotifer biomass per lake between the north and the south shores. Mean rotifer biomass in lakes on the south shore was more than six times higher than in lakes on the north shore, with values of 5.71 µg·L^{-1}and 0.94 µg·L^{-1} respectively. The analysis revealed no significant differences between shores for the other three variables tested.

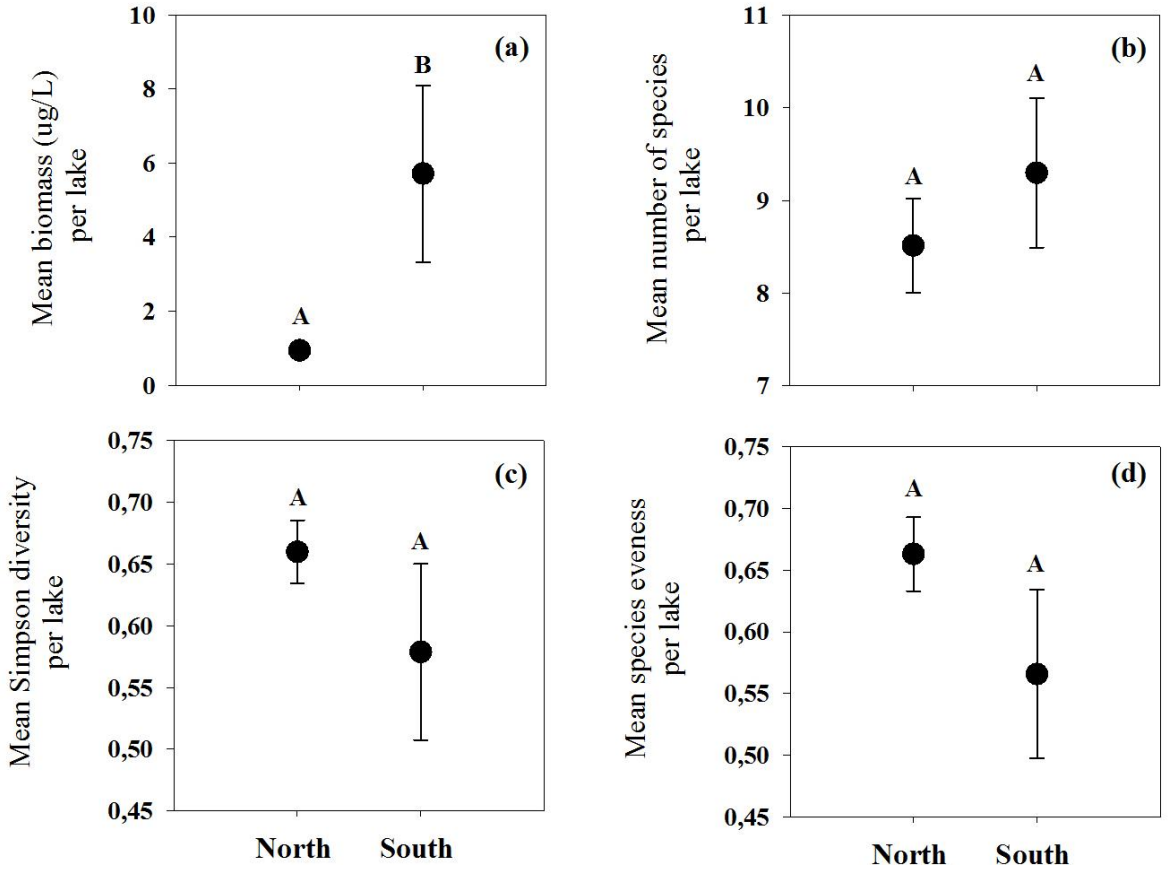

Figure 9. Rotifer distribution according to biomass of each shore (north n= 12; south n=10) according to (a) mean biomass per lake (b) mean number of species per lake (c) mean Simpson diversity per lake and (d) mean species evenness per lake; vertical bars indicate standard error; different letters indicate significant difference.

2.3.5 Most structuring species

Species contribution in creating similarity (or dissimilarity) between samples from each shore was analysed using the similarity percentage (SIMPER) method based on Bray-Curtis similarity and biomass data (Tables 9 and 10). This analysis breaks down the contribution of each species to the observed similarity (or dissimilarity) and allows identifying the species that are most important in creating the patterns observed between samples.

The test revealed that average similarity between samples from the north shore was 42.9, and 21.6 for the south shore (Table 9). Furthermore, the species contributing the most in creating similarity between samples of the north shore were *Polyarthra sp.* (49.3%), *Kellicottia longispina* (20.8%), *Keratella cochlearis* (12.6%), and *Conochilus unicornis* (8.6%). Species contributing the most in creating similarity in the south shore included *Polyarthra sp.* (43.4%), *Asplanchna sp.* (20.3%), *Keratella cochlearis* (14.5%), and *Kellicottia longispina* (9.6%). Furthermore, *Polyarthra sp.* populations in the north had an average similarity between samples that was more than twice that of the south shore. Likewise, *Kellicottia longispina* had an average similarity in the north that was more than four times the south. *Keratella cochlearis* similarity between samples was also higher in the north shore, but to a lesser extent. Interestingly, *Asplanchna sp.* had an important role in structuring rotifer populations in the south shore, but not in the north shore.

Species contributing the most in creating similarity within samples of each shore were also the same species responsible for creating the most dissimilarity between shores. Indeed, *Polyarthra sp., Asplanchna sp*., *Kellicottia longispina, Keratella cochlearis* and *Conochilus unicornis* were responsible for creating 80 % of the dissimilarity in rotifer population structure between the north and the south shores (Table 10). All species show higher mean biomass in the south than in the north, with the exception of *Kellicottia longispina.*

Table 9. Similarity percentage (SIMPER) method results showing the contribution (%) of the most important species in creating similarity between samples for the north and the south shores based on the biomass data.

Species	Average similarity between samples	Contribution (%) in creating similarity	Cumulative (%)
North shore (similarity between samples = 42.94)			
Polyarthra sp.	21.16	49.27	49.27
Kellicottia longispina	8.91	20.76	70.03
Keratella cochlearis	5.42	12.61	82.64
Conochilus unicornis	3.70	8.62	91.27
South shore (similarity between samples = 21.55)			
Polyarthra sp.	9.36	43.41	43.41
Asplanchna sp.	4.39	20.35	63.76
Keratella cochlearis	3.13	14.50	78.27
Kellicottia longispina	2.06	9.58	87.84

Table 10. Similarity percentage (SIMPER) method results showing the contribution (%) of the most important species in creating dissimilarity between shores based on Bray-Curtis distances and biomass. Mean biomass data for each shore is also included.

Species	Mean lake biomass (µg/L) North	Mean lake biomass (µg/L) South	Mean North-South dissimilarity (%)	Contribution North-South dissimilarity (%)	Cumulative (%)
Polyarthra sp.	0.43	0.83	19.01	25.2	25.2
Asplanchna sp.	0.05	1.47	17.62	23.34	48.54
Keratella cochlearis	0.11	2.01	14.24	18.87	67.41
Kellicottia longispina	0.11	0.08	5.67	7.51	74.92
Conochilus unicornis	0.09	0.1	4.55	6.03	80.95
Kellicottia bostoniensis	0.05	0.12	3.87	5.13	86.08
Trichocerca cylindrica	0.02	0.07	2.44	3.23	89.31
Conochiloides dossuarius	0.03	0.07	2.1	2.78	92.09
Average North-South lake dissimilarity (%)	75.46				

2.3.6 Environmental variables structuring rotifer populations

All the variables from tables 1 and 3 were used in the BIOENV analysis. SUVA, conductivity, total phosphorus (TP) and watershed surface area explained together 50 % of the observed pattern (Table 11). SUVA alone explained 43 % of the observed pattern, followed by conductivity (27%), total phosphorus (21%) and watershed surface area (15%). When coupling SUVA with conductivity, almost 52 % of the rotifer community structure distribution was explained by the pair.

Mean lake values in each shore for SUVA, conductivity, watershed surface area and total phosphorus were calculated and analysed with PERMANOVA to test for differences between the north and the south shores. This revealed that only TP had mean values per lake significantly different between shores ($p < 0.05$) with values of 8.4 µg $P \cdot L^{-1}$ for the north shore and 16.6 µg $P \cdot L^{-1}$ for the south shore.

Table 11. Primer 6 BIO-ENV analysis: best results of environmental variables contribution (variables from Tables 1 and 3) in explaining rotifer biomass distribution across the 22 sampled lakes.

Best correlation when using variables alone	**SUVA**	**Conductivity**	**TP**	**Watershed area**
	43%	27%	21%	15%
Best correlation when combining two variables	**SUVA + Conductivity**			
	51,7%			
Best correlation when combining three variables	**SUVA + Conductivity + Watershed area**			
	50,5%			
Best correlation when combining four variables	**SUVA + Conductivity + Total phosphorus + Watershed area**			
	50 %			

2.3.7 Grazing experiments results

The results of the grazing experiments revealed that rotifer grazing rates on bacteria increased linearly when phytoplankton concentrations increased from 0 to 35 $\mu gC \cdot L^{-1}$ (Fig. 10). Mean filtration rates on bacteria varied between 0 and 0.0041 $ml \cdot ind^{-1} \cdot h^{-1}$. The functional response curve (quadratic equation: $y = -0.00009x^2 + 0{,}0081x - 0.0095$; $r^2 = 0.96$) indicates a plateau around phytoplankton concentration of 40 $\mu gC \cdot L^{-1}$ followed by decreasing ingestion rates at 70 $\mu gC \cdot L^{-1}$. Error bars on the last treatments makes it difficult to predict the exact situation of the curve on the last treatment but might indicate feeding saturation beyond 40 $\mu gC \cdot L^{-1}$. The functional response curve of grazing rates on phytoplankton (linear equation: $y = 0.0023x - 0{,}0096$; $r^2 = 0.97$) increased linearly when phytoplankton concentrations increased from 0 to 70 $\mu gC \cdot L^{-1}$ (Fig. 11). Mean filtration rates on phytoplankton varied between 0 and 0.0023 $ml \cdot ind^{-1} \cdot h^{-1}$. Every treatment is associated with large error bars, especially in the 70 $\mu gC \cdot L^{-1}$ treatments which make it hard to predict the curve at that moment, but it could suggest feeding saturation at higher phytoplankton biomass.

Rotifer grazing rates estimated on five sampled lakes (Vatcher, Perdrix, Hamel, Lisa, Simoncouche) showed that they were the highest on both phytoplankton and bacteria in Lake Perdrix (16.54 $\mu gC \cdot L^{-1} \cdot h^{-1}$ and 7.83 $\mu gC \cdot L^{-1} \cdot h^{-1}$ respectively) (Table 12). Lake Simoncouche showed almost equally high grazing on bacteria (6.19 $\mu gC \cdot L^{-1} \cdot h^{-1}$) but very low grazing rates on phytoplankton (0.35 $\mu gC \cdot L^{-1} \cdot h^{-1}$). Lake Hamel had the lowest rotifer grazing rates on both phytoplankton and bacteria (0.21 $\mu gC \cdot L^{-1} \cdot h^{-1}$ and 0.17 $\mu gC \cdot L^{-1} \cdot h^{-1}$ respectively).

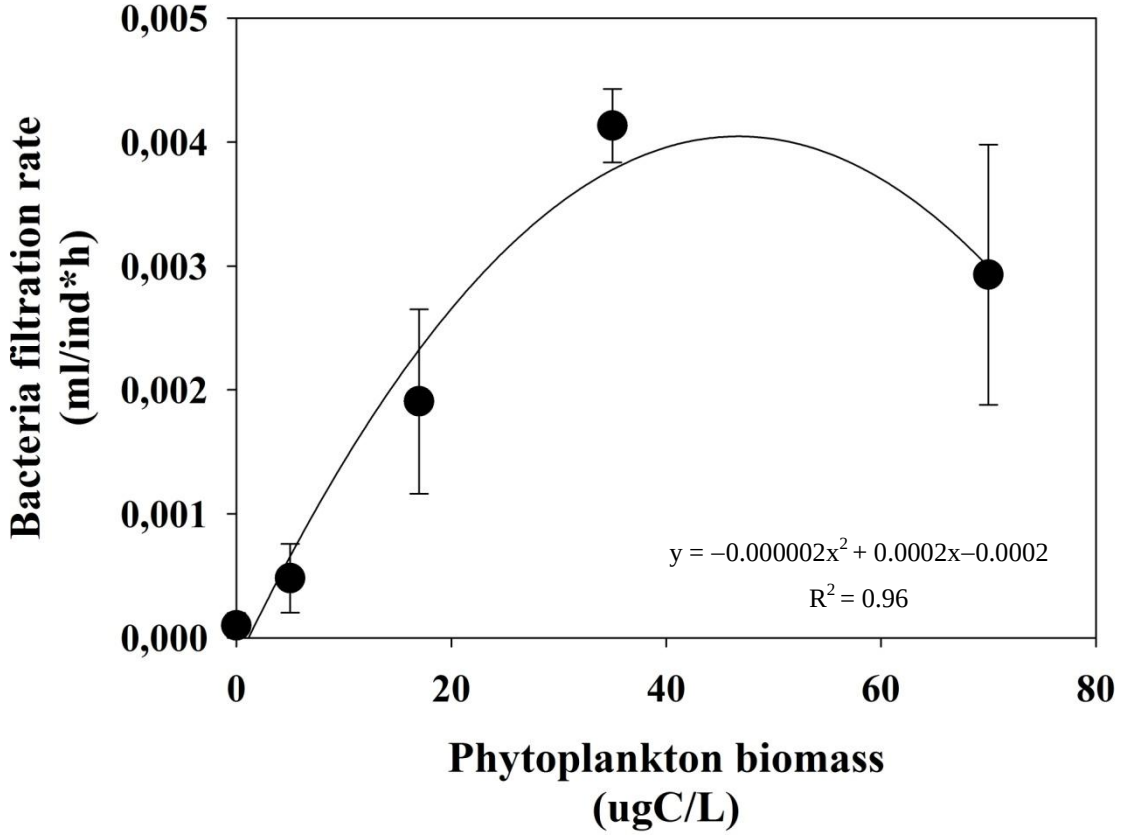

Figure 10. Rotifer filtration rates on bacteria (Fi_{bact}) in relation to phytoplankton biomass. Rotifers concentration remained the same in all treatments (100 rotifers per beaker) and were exposed to an increasing gradient of phytoplankton concentration (0, 5, 17, 35 and 70 $\mu gC \cdot L^{-1}$; x-axis) while bacteria concentration remained constant (44 $\mu gC \cdot L^{-1}$). Trend line was added. Vertical lines represent standard error bars.

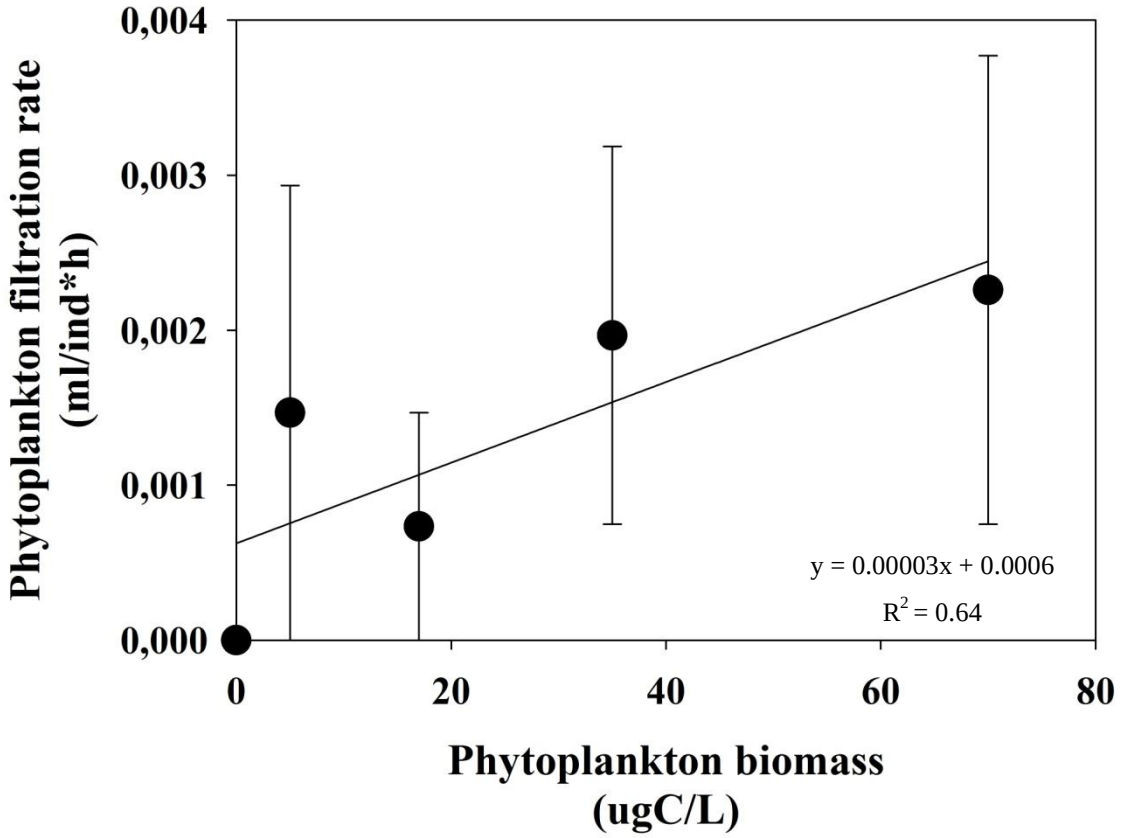

Figure 11. Rotifer filtration rates on phytoplankton (Fi_{phyto}) in relation to phytoplankton biomass. Rotifers concentration remained the same in all treatments (100 rotifers per beaker) and were exposed to an increasing gradient of phytoplankton concentration (0, 5, 17, 35 and 70 $\mu gC \cdot L^{-1}$; x-axis) while bacteria concentration remained constant (44 $\mu gC \cdot L^{-1}$). Trend line was added. Vertical lines represent standard error bars.

Table 12. Rotifer grazing rates estimated on five sampled lakes using known rotifer, phytoplankton and bacteria abundance and biomass (Vatcher, Perdrix, Hamel, Lisa - Autumn 2013 data; Simoncouche – Autumn 2011 data). Filtration rates (Fi) were calculated accord to the equations of the response curves obtained in the grazing experiment (Figs. 10 and 11) where 'x' was replaced with known phytoplankton abundance or biomass for each lake and population feeding rates (PFe) were calculated using equation 2.

Lake	**Rotifer abundance ($ind \cdot L^{-1}$)**	**Phyto biomass ($\mu gC \cdot L^{-1}$)**	**Phyto Fi ($ml \cdot ind^{-1} \cdot L^{-1}$)**	**Phyto PFe ($\mu gC \cdot L^{-1} \cdot h^{-1}$)**
Vatcher	43.0	37.34	0.0017	2.73
Perdrix	45.9	100.13	0.0036	16.54
Hamel	1.3	61.84	0.0026	0.21
Lisa	20.5	81.87	0.0030	5.03
Simoncouche	33.9	11.37	0.0009	0.35
Lake	**Rotifer abundance ($ind \cdot L^{-1}$)**	**Bact biomass ($\mu gC \cdot L^{-1}$)**	**Bact Fi ($ml \cdot ind^{-1} \cdot L^{-1}$)**	**Bact PFe ($\mu gC \cdot L^{-1} \cdot h^{-1}$)**
Vatcher	43.0	13.0	0.0045	2.51
Perdrix	45.9	58.8	0.0029*	7.83
Hamel	1.3	46.2	0.0029*	0.17
Lisa	20.5	6.9	0.0029*	0.41
Simoncouche	33.9	101.4	0.0018	6.19

* Feeding saturation is thought to occur at phytoplankton biomass > 40 $\mu gC \cdot L^{-1}$

2.4 Discussion

2.4.1 Rotifer population structure and distribution

The first objective of this study was to describe rotifer community structure and distribution in the boreal lakes of the Saguenay-Lac-Saint-Jean region. For the first hypothesis, we had predicted that rotifer distribution and community structure would vary according to the environmental characteristics of the lakes and their watersheds. Our results confirm this hypothesis. Results suggest that different watersheds and different lake environmental structures between the North and South shores modulated rotifer population assemblages. Lakes from the north shore shared more similar rotifer community structures than lakes from the south shore. Furthermore, certain rotifer species were exclusively found on the north shore (*Euchlanis sp., Lecane inermis, Notholca foliacea, Lepadella patella*) while others were exclusively found on the south shore (*Trichocerca pusilla, Tylotrocha monopus, Wierzejskiella velox, Cephalodella intuta*). We believe that differences in the types of watersheds characterizing each shore explain this result. Lakes on the north shore all share similar coniferous covered watershed mainly composed of white spruce and balsam fir, while lakes on the south shore have mixed watersheds composed of many deciduous and coniferous species. However, these results do not clearly indicate if the differences observed between shores are caused by the Saguenay Fjord acting as natural barrier to species colonisation. The difference in forest types between shores is likely due to lakes from the north shore being almost all situated over 600 meters of altitude while lakes from the south vary between 200 and 600 meters of altitude. Altitude has a strong impact on forest type and diversity and it has been shown that forest cover influence soil characteristics (Laganière et al., 2012; Laganière et al., 2013). Therefore, different watershed characteristics will have various impacts on aquatic systems such as the importance of water discharge (Wissmar et al., 2004), dissolved organic matter concentrations (Frost et al., 2006), nutrients imports (Prepas et al., 2001), allochthonous carbon inputs, bacterial respiration and production (Berggren et al., 2007), zooplankton distribution and aquatic biodiversity (Dodson et al., 2005; Dodson et al., 2007; Dodson, 2008).

For the second hypothesis, we had predicted that the importance of lake connectivity would influence the distribution and community structure of rotifers and lakes which are geographically closer together would have more similar species assemblages than lakes that are distant from each other. This hypothesis was not confirmed by the results. Lakes from the north shore were farther apart from each other than lakes from the south shore. Also, most lakes from the north shore shared no direct water connections. Lakes from the south shore were almost all part of large Lake Brébeuf watershed and shared water connections. However, lakes from the north shore had more similar rotifer species structures than lakes from the south shore. We believe the 22 lakes in this study were not geographically distant enough from each other to implicate connectivity as a significant structuring power for rotifer populations. Rotifers means of geographical dispersion does not rely solely on water connections and can also include animals, aquatic birds and even the wind for transportation (Herzig, 1987). Watershed characteristics and lakes environmental profiles seem to have bigger impacts on rotifer population's structure than connectivity at smaller scale. However, a variety of evidence supports the idea that connectivity as well as internal lake environmental conditions will structure zooplankton communities (Jenkins and Buikema, 1998; Shurin and Havel, 2002; Cottenie et al., 2003; Beisner et al., 2006). Nevertheless, it is uncertain if the presence of the Saguenay Fjord as a natural barrier has limited the dispersal of certain rotifer species. Watershed characteristics and lakes environmental profiles seems more likely to explain why a few species such as *Euchlanis sp., Lecane inermis, Notholca foliacea, Lepadella patella* were only found in the north while *Trichocerca pusilla, Tylotrocha monopus, Wierzejskiella velox, Cephalodella intuta* were only found in the south.

For our third hypothesis, we had predicted that rotifer communities in lakes exposed to higher concentration of allochthonous carbon would differ from that of lakes where terrestrial carbon inputs are more diluted. This hypothesis has been confirmed by our results. Primer's BIOENV analysis revealed that SUVA, an indicator of terrestrial carbon presence (Jaffé et al., 2008), was the most structuring of all the variables tested when considering rotifer assemblages, explaining alone 43 % of the observed rotifer population pattern across study area. This indicates that the variation in allochthonous carbon concentration in the lakes creates

variation in rotifer species assemblages. Our results do not, however, indicate if higher concentrations of allochthonous carbon benefits or not rotifers. It appears more likely that species will respond differently according to their own unique preferences. Allochthonous carbon has a significant impact on water chemistry and fluctuations in its concentration and quality will generate different environmental conditions within the system. The recalcitrant allochthonous carbon can be harder to assimilate by bacteria (Pace et al., 2004) therefore creating variability in secondary production and bacteria abundance based on carbon quality. This will impact the direct or indirect ingestion of bacteria by rotifers and therefore influence energy inputs to the population. Certain rotifer species may be benefited by this while others may not. Moreover, allochthonous carbon can have a major impact on water color, phytoplankton primary production and therefore phytoplankton availability as a food source for rotifers. It can also affect temperature and oxygen stratification throughout the water column. Since different rotifer species demonstrates different life strategies and different environmental conditions in which they prefer to flourish (Herzig, 1987; Walz, 1987; Duggan et al., 2002; Zhou et al., 2009), all the impacts that allochthonous carbon has on water chemistry will structure rotifer populations by benefiting some species but disadvantaging others. Therefore, we believe that different types of watersheds will provide different quantities and qualities of allochthonous carbon to lakes imposing variable effects on rotifers. Hence, watershed modification due to climate change and anthropogenic land use will have impacts on rotifer populations and potentially on aquatic food web dynamics.

The other variables identified as best explaining rotifer assemblages included conductivity, TP and watershed surface area which, when considered together, explained 50 % of the rotifer structure. We believe a link exists between these four variables which contribute in explaining environmental heterogeneity between lakes, carbon inputs to lakes and rotifer distribution and population structure. Watershed surface area will impact the proportion of terrestrial environment that will inevitably be drained to the lake; this will affect the quantity and quality of organic and inorganic material imported to the lake; this will in turn modulate the intensity of allochthonous carbon inputs (SUVA), nutrients loading (TP) and dissolved salts and inorganic material (conductivity). Therefore, based on our results, it appears clear that

watershed characteristics and terrestrial environments have an important impact on lake chemistry, allochthonous inputs and rotifer populations. Much of the variation observed in rotifer assemblages between shores resides in rotifer biomass distribution which was six times higher on the south shore than on the north shore. We believe that biomass differences can be explained by the significantly higher mean TP concentration per lake on the south shore. Lakes trophic state, often measured by the concentration of nutrients and total phosphorus, is known to favor rotifers (Duggan et al., 2001; Yoshida et al., 2003). Important watershed differences between shores, mainly in type of forest cover and soil biological activity, probably best explain the higher loading of nutrients to lakes in the south.

For our forth hypothesis, we had predicted that the absence of predatory fish would further impose a cascading effect on the food web observable to the rotifer trophic level and therefore influence their distribution and structure. This was not the case in this study and the hypothesis was not confirmed. No patterns emerged from any of the statistical analysis conducted. Our results contradict those of other studies. Drouin et al. (2009) had shown that the total abundance of rotifers was significantly higher in fishless lakes. They argue that rotifer's small size reduces their exposure to predatory invertebrates where-as large crustacean are easier prey. Invertebrates such as *Chaoborus americanus* larvae are important zooplankton predators but they are also an important food source for planctivores fish (Pinel-Alloul, 1995). In absence of fish, invertebrate numbers should be higher, imposing stronger predatory pressure on crustaceous zooplankton. Therefore rotifer numbers should be higher in fishless lakes. Wissel and Benndorf (1998) had come to the same conclusion in a previous study. It is possible that our results are different than other studies because this study took place in a colder autumn weather just before lake turnover and conditions were not favorable for invertebrates to flourish. Studies have shown that *Chaoborus* numbers can be strongly related to temperature (Lamontagne et al., 1994). *Chaoborus* abundance was very low in our study (data not shown). We argue that this reduced considerably their predatory pressure on crustaceans who's numbers were similar in fish and fishless lakes. Rotifers could not take advantage of an absence of crustaceans in the fishless lakes and therefore zooplankton communities in both types of lakes were very similar.

2.4.2 *Grazing experiment*

The second objective of this study was to determine rotifer's contribution in transferring allochthonous carbon to higher trophic levels of the food chain. For this objective, we had hypothesised that rotifers would be able to feed efficiently on bacteria when they are found in greater concentration than phytoplankton and that they could therefore efficiently contribute in transferring allochthonous carbon to higher trophic level of the food chain. Firstly, it is important to mention that results of grazing rates by rotifers on both phytoplankton and bacteria was consistent with literature values which usually range between 0.0001 to 0.009 $ml \cdot ind^{-1} \cdot h^{-1}$ for phytoplankton size particles (Haney, 1973; Bogdan et al., 1980; Bogdan and Gilbert, 1982; Agasild and Nõges, 2005) and from less than 0.0001 to 0,0062 $ml \cdot ind^{-1} \cdot h^{-1}$ for bacteria size particles (Bogdan et al., 1980; OomsWilms, 1997; Agasild and Nõges, 2005). Our results partly confirmed our hypothesis. Results suggest that rotifers tend to adjust their feeding rates according to phytoplankton biomass and may be ingesting bacteria passively in the process. It has been shown that rotifers can be stimulated by an increase in food availability (Starkweather and Gilbert, 1977). It is also possible that bacteria aggregates with phytoplankton causing unintentional bacteria ingestion (OomsWilms, 1997). Previous work on ingestion rates has often identified phytoplankton as being a more important food source for rotifers than bacteria (Bogdan et al., 1980; Bogdan and Gilbert, 1982; OomsWilms, 1997; Agasild and Nõges, 2005). Other studies such as Hwang and Heath (1999) report results of rotifers as excellent bacteria grazers but do not include any data on phytoplankton filtration rates and therefore did not consider passive ingestion of bacteria. Eating larger size particles such as phytoplankton rather than bacteria might be more energetically advantageous for rotifers. Hotos (2003) demonstrated that rotifers need to ingest up to 3 times their dry weight when eating smaller particles (< 5 μm) while they need to ingest only 1.5 times their dry weight when eating larger particles (> 16 μm). Being deficient in certain fatty acids essential for reproduction (Porter and McDonough, 1984), bacteria may be a secondary food source for zooplankton (Ooms-Wilms et al., 1995). These essential fatty acids are however present in phytoplankton. We suggest that they may be

energetically difficult to obtain from phytoplankton and passive ingestion of bacteria may provide the necessary energy to digest and metabolise phytoplankton fatty acids. In that case, bacteria would represent an essential food source for rotifers. The existence of gut bacteria in zooplankton has long been recognized (Harris, 1993; Tang, 2005). Moreover, gut bacteria are known to provide important nutrients, such as essential amino acids and vitamins (Fong and Mann, 1980). Note that according to our results, saturation in rotifer filtration rates seems to occur somewhere passed the 35 $\mu gC \cdot L^{-1}$ phytoplankton treatment. High concentration of seston particles is known to negatively affect the food collection process of zooplankton (Tóth, 1992). Correspondingly, phytoplankton filtration curve shows very high error bars in the 70 $\mu gC \cdot L^{-1}$ treatment which could indicate a change in filtration efficiency by rotifers at that point.

Although maybe passive and dependant on phytoplankton ingestion, our results nevertheless clearly suggests that an important bacteria uptake did occur during the experiment even surpassing phytoplankton carbon uptake. This may mean that in oligotrophic ecosystems where both phytoplankton and bacteria are present in relatively high numbers, rotifers will have in important allochthonous carbon uptake which could contribute more to their feeding diet than autochthonous carbon. However, our results should be interpreted with caution. Many studies on rotifers state that high food selectivity exists within a population and feeding preferences will vary according to species assemblages (Bogdan et al., 1980; Starkweather, 1980; Bogdan and Gilbert, 1982; Herzig, 1987; Agasild and Nõges, 2005). It is possible to classify rotifer species according to ecological niche depending on food preference (Starkweather, 1980). A rich spectrum of edible particles of various sizes may favour the co-existence of numerous species and reduce competition (Herzig, 1987). We included only *Keratella cochlearis*, *Keratella hiemalis*, *Keratella serrulata*, *Asplanchna spp.*, *Kellicottia spp.*, *Polyarthra spp.*, and *Conochilus spp*. as grazers in our experiment. Other groups, such as *Pompholyx sulcata* and *Anuraeopsis fissa*, are thought to be excellent bacteria grazers in boreal lakes (Hwang and Heath, 1999) but they were not included in our grazing experiment. The relative proportions of the different rotifer species were not considered when estimating grazing rates. Also, the phytoplankton food source included only a monospecific culture of *Nannochloropsis sp.* ranging between 5 and 13 μm in length. The natural phytoplankton community includes a lot more species with a much wider size spectrum. Also note that the

effect of temperature was not considered in this experiment while it is likely that it has an impact on grazing rates in natural systems (Montagnes et al., 2001). Another thing to consider when analyzing these results is the phytoplankton grazing curve which has only a 0.65 correlation with the data and shows very large error bars. Moreover, the amount of animals included in treatments was highly concentrated (400 ind/litres), which could have underestimated rotifers grazing rates as well as influenced the feeding saturation limit (Børsheim and Olsen, 1984). Bacteria concentration was also fixed while their biomass, as well as phytoplankton biomass, would fluctuate considerably in different natural systems.

2.4.3 *Grazing rates estimation of natural lake population*

Rotifers ingestion rates estimations on the five sampled lakes suggest that they feed unequally on both phytoplankton and bacteria depending on lake food concentration and rotifer abundance. Although Lake Perdrix had the highest estimated phytoplankton and bacteria ingestion rates, this result must be analysed cautiously because phytoplankton biomass in this lake was estimated at 100.13 $\mu gC \cdot L^{-1}$ which might result in feeding impairment due to food saturation. Bacteria filtration rates were readjusted to plateau at around 0.0029 $ml \cdot ind^{-1} \cdot L^{-1}$. On the other hand, rotifer concentrations in the experimental treatments were concentrated 8-fold that of Lake Perdrix's natural animal densities recorded during the autumn sampling. It is therefore possible that although high phytoplankton biomass was registered in Lake Perdrix, lower rotifer numbers may permit better filtration (Børsheim and Olsen, 1984). Note that the animal densities recorded during autumn in all the sampled lakes were many times smaller than that of the experimental treatments. Therefore the 40 $\mu gC \cdot L^{-1}$ limit before feeding saturation occurs will probably vary according to rotifer densities and food concentration. Bacteria ingestion rates for lakes Hamel and Lisa also had to be adjusted at 0,0029 $ml \cdot ind^{-1} \cdot L^{-1}$ due to high phytoplankton biomass. Low rotifer numbers and bacteria biomass respectively resulted in low bacterial carbon uptake estimations for these lakes. Lake Simoncouche had low phytoplankton biomass. Nevertheless, it was high enough to engage grazing and high bacteria biomass coupled with high rotifer abundance resulted in very high bacterial carbon uptake in that lake precisely. This demonstrates that although bacteria are mostly ingested passively, once

phytoplankton filtration by rotifers is underway large amounts of bacteria are also ingested. Finally, note that bacteria filtration in Lake Vatcher may be less than calculated since bacteria biomass in the lake was only 13 $\mu gC \cdot L^{-1}$ while it was 44 $\mu gC \cdot L^{-1}$ in the experiment.

Although these estimated ingestion rates from the sampled lakes have been calculated with the experimental data and should be used with caution for many reasons (fixed and high rotifer densities in treatments; fixed bacterial biomass in treatments but variable in sampled lakes; monospecific population of phytoplankton used for experiment; correlation of 0.65 for the phytoplankton curve), they do give insight on the probable variability of phytoplankton and bacterial carbon uptake by rotifers within lakes, showing it will most certainly vary according to both food source concentration as well as rotifer biomass. As shown by our environmental lake data and rotifer distribution and community structure, high variability may exist within the Québec boreal forest at both large and small scale. This will in turn affect rotifers distribution and community structure which will react differently to terrestrial carbon inputs. Hence, we believe that rotifers have a significant but variable implication in aquatic food webs which are largely dependent to watershed characteristics. Phytoplankton concentrations have to be high enough to engage grazing by rotifers. Hereafter, when rotifers are present in high enough numbers they are capable of ingesting important quantities of bacterial carbon (probably passively) and sometimes dominate phytoplankton grazing. In lakes where bacterial secondary production is highly dependent on terrestrial organic inputs and conditions permits high rotifer numbers, they may provide an important link between allochthonous carbon and higher trophic levels of the food web.

3 CONCLUSION GÉNÉRALE

Les résultats de cette étude ont permis de confirmer l'hypothèse stipulant que la structure et la distribution des communautés de rotifères varient en fonction des caractéristiques environnementales des lacs et des bassins versants. En effet, les profils environnementaux des 22 lacs échantillonnés s'organisent en fonction des caractéristiques des bassins versants, notamment le couvert forestier et l'altitude. Les analyses statistiques ont démontré que la structure des communautés de rotifères suit la même organisation géographique que l'organisation environnementale des lacs. En termes de caractéristiques environnementales, les lacs étaient plus similaires au nord qu'au sud du Fjord du Saguenay. La structure des populations de rotifères était également plus similaire au nord qu'au sud du Fjord du Saguenay. Par ailleurs, certaines espèces étaient uniquement présentes au nord alors que d'autres étaient uniquement présentes au sud. Les résultats ont également permis de rejeter l'hypothèse stipulant que l'importance de la connectivité entre les lacs influence la distribution et la structure des communautés de rotifères. Les lacs plus proches géographiquement n'avaient pas des populations de rotifères plus similaires que ceux plus distancés. En effet, les lacs au nord du Fjord du Saguenay étaient plus éloignés les uns des autres que les lacs au sud. De plus, les lacs au nord ne partageaient aucune liaison hydrique alors que les lacs au sud faisaient tous partie du bassin versant du Lac Brébeuf et partageaient un lien hydrique via ce dernier.

D'autre part, les résultats ont également permis de confirmer l'hypothèse stipulant que la structure des communautés de rotifères dans les lacs exposés à de plus fortes concentrations de carbone allochtone est différente de celle des lacs où l'effet est plus dilué. En effet, l'indice SUVA, qui est un indicateur de la teneur en carbone allochtone, expliquait 43 % de la structure des populations de rotifères. Cette étude n'a cependant pas permis de déterminer de quelle façon le carbone allochtone affecte les populations de rotifères. Le carbone allochtone a des effets variables dans les milieux aquatiques et les différentes espèces de rotifères démontrent différentes stratégies de survie. Nous supposons donc que les différentes espèces réagiront différemment au carbone allochtone. Certaines espèces seront avantagées alors que d'autres

seront désavantagées. Par ailleurs, nous supposons que l'hétérogénéité des bassins versants influence l'importance des importations de carbone allochtone aux lacs, ce qui explique les tendances observables dans la structure et la distribution des populations de rotifères.

En revanche, les résultats n'ont pas permis de confirmer l'hypothèse voulant que l'absence de poissons prédateurs impose un effet cascade sur les réseaux trophiques qui sera observable au niveau des populations de rotifères. Aucune analyse statistique n'a permis d'identifier une tendance liée à la présence ou l'absence de poissons. Notre étude contredit d'autres études ayant démontré que le petit zooplancton est souvent avantagé en absence de poissons (Drouin et al., 2009). Nos résultats s'expliquent probablement par le fait que l'échantillonnage a été réalisé à l'automne et que, conséquemment, les populations d'invertébrés étaient très faibles.

Par ailleurs, les résultats ont permis de confirmer partiellement l'hypothèse que les rotifères sont en mesure de se nourrir efficacement de bactéries lorsque ces dernières sont présentes en plus forte concentration que le phytoplancton et qu'ainsi, ils contribuent à transférer le carbone allochtone aux niveaux trophiques supérieurs. Les résultats ont davantage permis de suggérer que les rotifères ingèrent des bactéries de façon passive en se nourrissant de phytoplancton. Ainsi, même si les bactéries sont présentes en forte concentration, aucune filtration n'est effectuée en absence de phytoplancton. À l'inverse, la présence du phytoplancton semble activer l'ingestion et à ce moment des bactéries sont également ingérées. Nous proposons l'idée que les bactéries sont importantes dans l'alimentation de certaines espèces de rotifères puisqu'elles fournissent de l'énergie complémentaire à la digestion de phytoplancton et aident ainsi à obtenir certains acides gras essentiels uniquement présents chez le phytoplancton. En ingérant ainsi des bactéries, les rotifères contribuent donc à transférer le carbone allochtone aux niveaux trophiques supérieurs. Cependant, l'importance du transfert de carbone allochtone varie en fonction de la quantité de bactéries ingérées qui elle varie en fonction de la densité de phytoplancton et de rotifères présents dans le milieu.

Somme toute, cette étude a été réalisée dans le but de contribuer à l'avancement des connaissances sur l'écologie des rotifères en milieu boréal et à analyser leur importance dans les réseaux trophiques aquatiques. Deux objectifs étaient visés: le premier était de décrire et d'expliquer la structure et la distribution des communautés de rotifères dans les lacs boréaux du Saguenay-Lac-Saint-Jean ; le second visait à déterminer la contribution des rotifères dans le transfert du carbone allochtone vers les niveaux trophiques supérieurs. L'étude permet d'affirmer que les caractéristiques environnementales des lacs, essentiellement régies par les caractéristiques des bassins versants, jouent un rôle important dans la structure des populations de rotifères. Plus important encore, l'étude permet d'affirmer que les apports de carbone allochtone influencent la distribution et la structure des populations de rotifères. Des modifications aux bassins versants des lacs boréaux causés par les changements climatiques ou l'utilisation anthrophiques de ces derniers auront des impacts sur les populations de rotifères et les réseaux trophiques aquatiques. Également, il a été démontré que les rotifères sont en mesure d'ingérer passivement des bactéries et ainsi de transférer du carbone allochtone aux niveaux trophiques supérieurs. Cette étude aide donc à comprendre davantage le lien qui existe entre les milieux terrestres et aquatiques. Dans notre époque où l'exploitation des milieux naturels et l'utilisation des ressources naturelles est en croissance, il importe de poursuivre des études portant sur les liens qui existent entre les milieux terrestre et aquatiques.

RÉFÉRENCES

Agasild, H., Nõges, T., 2005. Cladoceran and rotifer grazing on bacteria and phytoplankton in two shallow eutrophic lakes: in situ measurement with fluorescent microspheres. Journal of Plankton Research 27, 1155-1174.

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

Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62, 245-253.

Arndt, H., 1993. Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) — a review. Hydrobiologia 255-256, 231-246.

Arvola, L., Tulonen, T., 1998. Effects of allochthonous dissolved organic matter and inorganic nutrients on the growth of bacteria and algae from a highly humic lake. Environment International 24, 509-520.

Ask, J., Karlsson, J., Jansson, M., 2012. Net ecosystem production in clear-water and brown-water lakes. Global Biogeochemical Cycles 26.

Ask, J., Karlsson, J., Persson, L., Ask, P., Bystrom, P., Jansson, M., 2009a. Terrestrial organic matter and light penetration: Effects on bacterial and primary production in lakes. Limnology and Oceanography, 54, 2034-2040.

Ask, J., Karlsson, J., Persson, L., Ask, P., Byström, P., Jansson, M., 2009b. Whole-lake estimates of carbon flux through algae and bacteria in benthic and pelagic habitats of clear-water lakes. Ecology 90, 1923-1932.

Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., Thingstad, F., 1983. The ecological role of the water-column microbes in the sea. Marine Ecology Series 10, 257-263.

Bade, D.L., Carpenter, S.R., Cole, J.J., Pace, M.L., Kritzberg, E., Van de Bogert, M.C., Cory, R.M., McKnight, D.M., 2007. Sources and fates of dissolved organic carbon in lakes as determined by whole-lake carbon isotope additions. Biogeochemistry 84, 115-129.

Balian, E., Segers, H., Martens, K., Lévéque, C., 2008. The freshwater animal diversity assessment: an overview of the results, Freshwater Animal Diversity Assessment, Springer, 627-637.

Beisner, B.E., Peres-Neto, P.R., Lindström, E.S., Barnett, A., Longhi, M.L., 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. Ecology 87, 2985-2991.

Berggren, M., Laudon, H., Jansson, M., 2007. Landscape regulation of bacterial growth efficiency in boreal freshwaters. Global Biogeochemical Cycles 21.

Berggren, M., Laudon, H., Jansson, M., 2009. Hydrological control of organic carbon support for bacterial growth in boreal headwater streams. Microbial Ecology 57, 170-178.

Bertilsson, S., Hansson, L.-A., Graneli, W., Philibert, A., 2003. Size-selective predation on pelagic microorganisms in Arctic freshwaters. Journal of Plankton Research 25, 621-632.

Bogdan, K., Gilbert, J., Starkweather, P., 1980. In Situ Clearance Rates of Planktonic Rotifers, Hydrobiologia 73, 73-77.

Bogdan, K.G., Gilbert, J.J., 1982. Seasonal patterns of feeding by natural populations of *Keratella, Polyarthra,* and *Bosmina*: Clearance rates, selectivities, and contributions to community grazing. Limnology and Oceanography 27, 918-934.

Børsheim, K., Olsen, Y., 1984. Grazing activities by *Daphnia pulex* on natural populations of bacteria and algae. Verhandlungen des Internationalen Verein Limnologie 22, 644-648.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., E., G., Herzig, A., Hillbricht-Ilkowska, A., H., K., Larsson, P., Weglenska, T., 1976. A review of some problems in zooplankton production studies. Norwegian Journal of Zoology 24, 419-456.

Brandl, Z., 2005. Freshwater copepods and rotifers: predators and their prey. Hydrobioliga 546, 475-489.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological monographs 27, 325-349.

Breton, J., Vallières, C., Laurion, I., 2009. Limnological properties of permafrost thaw ponds in northeastern Canada. Canadian Journal of Fisheries and Aquatic Sciences 66, 1635–1648.

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

Burns, C.W., Gilbert, J.J., 1993. Predation on ciliates by freshwater calanoid copepods: rates of predation and relative vulnerabilities of prey. Freshwater Biology 30, 377-393.

Carpenter, S.R., Cole, J.J., Pace, M.L., Van de Bogert, M., Bade, D.L., Bastviken, D., Gille, C.M., Hodgson, J.R., Kitchell, J.F., Kritzberg, E.S., 2005. Ecosystem subsidies: terrestrial support of aquatic food webs from 13C addition to contrasting lakes. Ecology 86, 2737-2750.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. BioScience 35, 634-639.

Chetelat, J., Amyot, M., 2009. Elevated methylmercury in High Arctic Daphnia and the role of productivity in controlling their distribution. Global Change Biology 15, 706-718.

Chick, J.H., Levchuk, A.P., Medley, K.A., Havel, J.H., 2010. Underestimation of rotifer abundance a much greater problem than previously appreciated. Limnology and Oceanography-Methods 8, 79-87.

Clarke, K., Warwick, R., 1994. An approach to statistical analysis and interpretation. Change in Marine Communities 2. Primer-E, Plymouth.

Cole, J.J., Prairie, Y.T., Caraco, N.F., McDowell, W.H., Tranvik, L.J., Striegl, R.G., Duarte, C.M., Kortelainen, P., Downing, J.A., Middelburg, J.J., Melack, J., 2007. Plumbing the Global Carbon Cycle: Integrating Inland Waters into the Terrestrial Carbon Budget. Ecosystems 10, 172-185.

Cottenie, K., Michels, E., Nuytten, N., De Meester, L., 2003. Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. Ecology 84, 991-1000.

del Giorgio, P.A., Bird, D.F., Prairie, Y.T., Planas, D., 1996. Flow cytometric determination of bacterial abundance in lake plankton with the green nucleic acid stain SYTO 13. Limnology and Oceanography 41, 783-789.

del Giorgio, P.A., Peters, R.H., 1994. Patterns in planktonic P: R ratios in lakes: Influence of lake trophy and dissolved organic carbon. Limnology and Oceanography 39, 772-787.

Dodson, S.I., 2008. Biodiversity in southern Wisconsin storm-water retention ponds: correlations with watershed cover and productivity. Lake and Reservoir Management 24, 370-380.

Dodson, S.I., Everhart, W.R., Jandl, A.K., Krauskopf, S.J., 2007. Effect of watershed land use and lake age on zooplankton species richness. Hydrobiologia 579, 393-399.

Dodson, S.I., Lillie, R.A., Will-Wolf, S., 2005. Land use, water chemistry, aquatic vegetation, and zooplankton community structure of shallow lakes. Ecological Applications 15, 1191-1198.

Downing, J., Prairie, Y., Cole, J., Duarte, C., Tranvik, L., Striegl, R., McDowell, W., Kortelainen, P., Caraco, N., Melack, J., 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnology and Oceanography 51, 2388-2397.

Drouin, A., Archambault, P., Sirois, P., 2011. Distinction of nektonic and benthic communities between fish-present *(Salvelinus fontinalis*) and natural fishless lakes. Boreal environment research 16, 101-114.

Drouin, A., Sirois, P., Archambault, P., 2009. Discriminating zooplankton communities in lakes with brook trout (*Salvelinus fontinalis*) and in fishless lakes. Écoscience 16, 271-281.

Duggan, I., Green, J., Shiel, R., 2001. Distribution of rotifers in North Island, New Zealand, and their potential use as bioindicators of lake trophic state, Hydrobioligia 153, 155-164.

Duggan, I.C., Green, J.D., Shiel, R.J., 2002. Distribution of rotifer assemblages in North Island, New Zealand, lakes: relationships to environmental and historical factors. Freshwater Biology 47, 195-206.

Dumont, H., Velde, I., Dumont, S., 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19, 75-97.

Environnement Canada, 2015. Rapport de données mensuelles pour 2013. (Page consulté le 5 septembre 2015) Gouvernement du Canada, http://climat.meteo.gc.ca/climateData/monthlydata_f.html?timeframe=3&Prov=QC&StationID=5889&mlyRange=1942-5801-5801|2014-5812-5801&Year=2013&Month=5801&Day=5801.

Evans, C.D., Monteith, D.T., Cooper, D.M., 2005. Long-term increases in surface water dissolved organic carbon: Observations, possible causes and environmental impacts. Environmental Pollution 137, 55-71.

Findlay, S.E.G., Sinsabaugh, R.L., 2004. Aquatic ecosystems: interactivity of dissolved organic matter. Journal of North American Benthological Society 23, 662-663.

Flot, J.-F., Hespeels, B., Li, X., Noel, B., Arkhipova, I., Danchin, E.G., Hejnol, A., Henrissat, B., Koszul, R., Aury, J.-M., 2013. Genomic evidence for ameiotic evolution in the bdelloid rotifer *Adineta vaga*. Nature 500, 453-457.

Flynn, K.J., Stoecker, D.K., Mitra, A., Raven, J.A., Glibert, P.M., Hansen, P.J., Granéli, E., Burkholder, J.M., 2012. Misuse of the phytoplankton–zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. Journal of Plankton Research 35, 3-11.

Fong, W., Mann, K., 1980. Role of gut flora in the transfer of amino acids through a marine food chain. Canadian Journal of Fisheries and Aquatic Sciences 37, 88-96.

Frost, P.C., Larson, J.H., Johnston, C.A., Young, K.C., Maurice, P.A., Lamberti, G.A., Bridgham, S.D., 2006. Landscape predictors of stream dissolved organic matter concentration and physicochemistry in a Lake Superior river watershed. Aquatic Science 68, 40-51.

Fry, J., 1988. Determination of biomass. Methods in aquatic bacteriology. Wiley, 27-72.

Geller, W., Müller, H., 1981. The filtration apparatus of Cladocera: Filter mesh-sizes and their implications on food selectivity. Oecologia 49, 316-321.

Gosse, P.H., 1856. On the structure, functions, and homologies of the manducatory organs in the class Rotifera. Philosophical Transactions of the Royal Society of London 146, 419-452.

Güde, H., 1988. Direct and indirect influences of crustacean zooplankton on bacterioplankton of Lake Constance. Hydrobiologia 159, 63-73.

Guillemette, F., McCallister, S.L., del Giorgio, P.A., 2015. Selective consumption and metabolic allocation of terrestrial and algal carbon determine allochthony in lake bacteria. The ISME Journal 10, 1373-1382.

Haney, J., 1973. An in situ examination of the grazing activities of natural zooplankton communities. Archiv fur Hydrobiologie Journal 72.

Hansson, L.-A., Nicolle, A., Granéli, W., Hallgren, P., Kritzberg, E., Persson, A., Björk, J., Nilsson, P.A., Brönmark, C., 2013. Food-chain length alters community responses to global change in aquatic systems. Nature Climate Change 3, 228-233.

Harris, J.M., 1993. The presence, nature, and role of gut microflora in aquatic invertebrates: a synthesis. Microb Ecol 25, 195-231.

Herzig, A., 1987. The analysis of planktonic rotifer populations: A plea for long-term investigations, Hydrobiologia 147, 163-180.

Hespeels, B., Flot, J.-F., Derzelle, A., Van Doninck, K., 2014. Evidence for ancient horizontal gene acquisitions in bdelloid rotifers of the genus *Adineta*. Evolutionary Biology: Genome Evolution, Speciation, Coevolution and Origin of Life, 207-225.

Hillebrand, H., Dürselen, C.D., Kirschtel, D., Pollingher, U., Zohary, T., 1999. Biovolume calculation for pelagic and benthic microalgae. Journal of phycology 35, 403-424.

Hotos, G.N., 2003. Growth, filtration and ingestion rate of the rotifer *Brachionus plicatilis* fed with large (*Asteromonas gracilis*) and small (*Chlorella sp.*) celled algal species. Aquaculture Research 34, 793-802.

Hwang, S.-J., Heath, R.T., 1999. Zooplankton bacterivory at coastal and offshore sites of Lake Erie. Journal of Plankton Research 21, 699-719.

IPCC, 2001. The carbon cycle and atmospheric carbon dioxide. In: IPCC, Climate Change 2001. Cambridge University Press, Cambridge, 183–37.

Jack, J.D., Gilbert, J.J., 1993. Susceptibilities of different-sized ciliates to direct suppression by small and large cladocerans. Freshwater Biology 29, 19-29.

Jaffé, R., McKnight, D., Maie, N., Cory, R., McDowell, W., Campbell, J., 2008. Spatial and temporal variations in DOM composition in ecosystems: The importance of long-term monitoring of optical properties. Journal of Geophysical Research: Biogeosciences 113.

Jenkins, D.G., Buikema, A.L., 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. Ecological Monographs 68, 421-443.

Jennings, H.S., 1900. Rotatoria of the United States: With special reference to those of the Great Lakes. US Government Printing Office.

Jeppesen, E., Jensen, J.P., Søndergaard, M., Fenger-Grøn, M., Bramm, M.E., Sandby, K., Møller, P.H., Rasmussen, H.U., 2004. Impact of fish predation on cladoceran body weight distribution and zooplankton grazing in lakes during winter. Freshwater Biology 49, 432-447.

Jones, R.I., Shaw, P.J., De Haan, H., 1993. Effects of dissolved humic substances on the speciation of iron and phosphate at different pH and ionic strength. Environmental science & technology 27, 1052-1059.

Jürgens, K., Jeppesen, E., 2000. The impact of metazooplankton on the structure of the microbial food web in a shallow, hypertrophic lake. Journal of Plankton Research 22, 1047-1070.

Jurgens, K., Skibbe, O., Jeppesen, E., 1999. Impact of metazooplankton on the composition and population dynamics of planktonic ciliates in a shallow, hypertrophic lake. Aquatic Microbial Ecology 17, 61-75.

Kalff, J., 2002. Limnology: inland water ecosystems. Prentice Hall, New Jersey, 592 pages.

Kankaala, P., 1988. The relative importance of algae and bacteria as food for Daphnia longispina (Cladocera) in a polyhumic lake. Freshwater Biology 19, 285-296.

Karlsson, J., Berggren, M., Ask, J., Byström, P., Jonsson, A., Laudon, H., Jansson, M., 2012. Terrestrial organic matter support of lake food webs: evidence from lake metabolism and stable hydrogen isotopes of consumers. Limnology and Oceanography 57, 1042.

Karlsson, J., Bystrom, P., Ask, J., Ask, P., Persson, L., Jansson, M., 2009. Light limitation of nutrient-poor lake ecosystems. Nature 460, 506-509.

Kirchman, D.E.A., 1985. Leucine incorporation and its potential as a measure of protein synthesis by bacteria in natural aquatic system. Applied and Environmental Microbiology 49, 599-607.

Kleppel, G.S., 1993. On the diets of calanoid copepods. Marine ecology progress series 99, 183-195.

Kritzberg, E.S., Cole, J.J., Pace, M.L., Grane´li, W., Bade, D.L., 2004. Autochthonous versus allochthonous carbon sources of bacteria: Results from whole-lake 13C addition experiments. Limnology and Oceanography 49, 588-596.

Laganière, J., Paré, D., Bergeron, Y., Chen, H.Y., 2012. The effect of boreal forest composition on soil respiration is mediated through variations in soil temperature and C quality. Soil Biology and Biochemistry 53, 18-27.

Laganiere, J.M., Paré, D., Bergeron, Y., Chen, H.Y., Brassard, B.W., Cavard, X., 2013. Stability of soil carbon stocks varies with forest composition in the Canadian boreal biome. Ecosystems 16, 852-865.

Lamontagne, S., Donald, D.B., Schindler, D.W., 1994. The distribution of four Chaoborus species (Diptera: Chaoboridae) along an elevation gradient in Canadian Rocky Mountain lakes. Canadian Journal of Zoology 72, 1531-1537.

Lampert, W., Fleckner, W., Rai, H., Taylor, B.E., 1986. Phytoplankton control by grazing zooplankton: A study on the spring clear-water phase. Limnology and Oceanography 31, 478-490.

Larsen, S., Andersen, T.O.M., Hessen, D.O., 2011. Climate change predicted to cause severe increase of organic carbon in lakes. Global Change Biology 17, 1186-1192.

Letarte, Y., Pinel-Alloul, B., 1991a. Rôle du bactérioplancton en milieu lacustre pélagique: prépondérance des plus grosses bactéries. Canadian journal of microbiology 37, 465-473.

Letarte, Y., Pinel-Alloul, B., 1991b. Variations spatio-temporelles de l'abondance et de la production du bactérioplancton dans un lac humique du Bouclier canadien. Canadian Journal of Microbiology 37, 64-73.

Lindeman, R.L., 1942. The Trophic-Dynamic Aspect of Ecology. Ecology 23, 399-417.

Lund, J., 1965. The ecology of the freshwater phytoplankton. Biological Reviews 40, 231-290.

McCauley, E., 1984. The estimation of the abundance and biomass of zooplankton in samples. A manual on methods for the assessment of secondary productivity in fresh waters, 228-265.

MDDELCC, 2016. Ministère du Dévèloppement durable, de l'Environnement et Lutte contre les changements climatiques. Gourvenement du Québec.

Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnology and Oceanography 45, 569-579.

MFFP, 2013. (Page consulté le 4 septembre 2015), Gros plan sur le Saguenay-Lac-Saint-Jean. Ministère des Forêt, de la Faune et des Parcs Gouvernement du Québec, https://www.mffp.gouv.qc.ca/saguenay-lac-saint-jean/questions/boreale.jsp.

MFFP, 2016. (Page consulté le 4 octobre 2016), Zone de végétation et domaine bioclimatique du Québec. Ministère des Forêts, de la Faune et des Parcs Gouvernement du Québec, https://www.mffp.gouv.qc.ca/forets/inventaire/inventaire-zones carte.jsp#pessiereMousses.

Mitchell, B.G., Kahru, M., Wieland, J., Stramska, M., 2002. Determination of spectral absorption coefficients of particles, dissolved material and phytoplankton for discrete water samples. Ocean optics protocols for satellite ocean color sensor validation Revision, 231–257.

Montagnes, D., Kimmance, S., Tsounis, G. and Gumbs, J., 2001. Combined effect of temperature and food concentration on the grazing rate of the rotifer Brachionus plicatilis. Marine Biology, 139, pp.975-979.

Monteith, D.T., Stoddard, J.L., Evans, C.D., de Wit, H.A., Forsius, M., Hogasen, T., Wilander, A., Skjelkvale, B.L., Jeffries, D.S., Vuorenmaa, J., Keller, B., Kopacek, J., Vesely, J., 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature 450, 537-540.

MRNF, 2006. Portrait territoriale du Saguenay-Lac-Saint-Jean. Ministère des Ressource naturelles et de la Faune Gouvernement du Québec.

Naselli-Flores, L., Padisák, J., 2016. Blowing in the wind: how many roads can a phytoplankton walk down? A synthesis on phytoplankton biogeography and spatial processes. Hydrobiologia 764, 303-313.

NRCAN, 2016. (Page consulté le 27 octobre 2016), Boreal Forest. Natural Ressources Canada Gouvernment of Canada, https://www.nrcan.gc.ca/forests/boreal/13071.

Nuccio, C., Melillo, C., Massi, L., Innamorati, M., 2003. Phytoplankton abundance, community structure and diversity in the eutrophicated Orbetello lagoon (Tuscany) from 1995 to 2001. Oceanologica Acta 26, 15-25.

Nusch, E., 1980. Comparison of different methods for chlorophyll and phaeopigment determination. Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie 14, 14-36.

Ooms-Wilms, A., Postema, G., Gulati, R., 1995. Evaluation of bacterivory of Rotifera based on measurements of in situ ingestion of fluorescent particles, including some comparisons with Cladocera. Journal of plankton research 17, 1057-1077.

OomsWilms, A.L., 1997. Are bacteria an important food source for rotifers in eutrophic lakes? Journal of Plankton Research 19, 1125-1141.

Orcutt, J., Jr., Pace, M., 1984. Seasonal dynamics of rotifer and crustacean zooplankton populations in a eutrophic, monomictic lake with a note on rotifer sampling techniques. Hydrobiologia 119, 73-80.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Van de Bogert, M.C., Bade, D.L., Kritzberg, E.S., Bastviken, D., 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. Nature 427, 240-243.

Pace, M.L., Findlay, S.E., Lints, D., 1992. Zooplankton in advective environments: the Hudson River community and a comparative analysis. Canadian Journal of Fisheries and Aquatic Sciences 49, 1060-1069.

Pace, M.L., Orcutt, J.D., Jr., 1981. The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. Limnology and Oceanography 26, 822-830.

Pennak, R.W., 1955. Fresh-water invertebrates of the United States. Hydrobiologia 7, 126-126.

Pinel-Alloul, B., 1995. Impacts des prédateurs invertébrés sur les communautés aquatiques. Limnologie Générale. Masson, Paris, 628-686.

Pomeroy, R., 1974. The ocean's foodweb, a changing paradigm. BioScience 24, 499-504.

Porter, K.G., McDonough, R., 1984. The energetic cost of response to blue-green algal filaments by cladocerans. Limnology and Oceanography 29, 365-369.

Power, G., Pope, G., Coad, B., 1973. Postglacial colonization of the Matamek River, Quebec, by fishes. Journal of the Fisheries Board of Canada 30, 1586-1591.

Prepas, E.E., Planas, D., Gibson, J.J., Vitt, D.H., Prowse, T.D., Dinsmore, W.P., Halsey, L.A., McEachern, P.M., Paquet, S., Scrimgeour, G.J., Tonn, W.M., Paszkowski, C.A., Wolfstein, K., 2001. Landscape variables influencing nutrients and phytoplankton communities in Boreal Plain lakes of northern Alberta: a comparison of wetland- and upland-dominated catchments. Canadian Journal of Fisheries and Aquatic Sciences 58, 1286-1299.

Rautio, M., Mariash, H., Forsstrom, L., 2011. Seasonal shifts between autochthonous and allochthonous carbon contributions to zooplankton diets in a subarctic lake. Limnology and Oceanography 56, 1513-1524.

Ricci, C., Melone, G., Sotgia, C., 1993. Old and new data on Seisonidea (Rotifera). Hydrobiologia 255, 495-511.

Roiha, T., Peura, S., Cusson, M., Rautio, M., 2016. Allochthonous carbon is a major regulator to bacterial growth and community composition in subarctic freshwaters. Scientific Reports 6.

Rosen, R.A., 1981. Length-Dry Weight Relationships of Some Freshwater Zooplanktona. Journal of Freshwater Ecology 1, 225-229.

Rothhaupt, K., 1990. Differences in particle size-dependent feeding efficiencies of closely related rotifer species. Limnology and Oceanography 35, 16-23.

Sampson, S., Chick, J., Pegg, M., 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. Biological Invasions 11, 483-496.

Samuel, E., 1934. A study of fresh-water plankton communities. Illinois biological monographs; 12.

Sanders, R.W., Porter, K.G., Bennett, S.J., DeBiase, A.E., 1989. Seasonal Patterns of bacterivory by flagellates, ciliates, rotifers, and cladocerans in a freshwater planktonic community. Limnology and Oceanography 34, 673-687.

Shurin, J.B., Havel, J.E., 2002. Hydrologic connections and overland dispersal in an exotic freshwater crustacean. Biological Invasions 4, 431-439.

Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J.L., Gaedke, U., Ibelings, B., Jeppesen, E., Lürling, M., Molinero, J.C., Mooij, W.M., van Donk, E., Winder, M., 2012. Beyond the Plankton Ecology Group (PEG) model: Mechanisms driving plankton succession. Annual Review of Ecology, Evolution and Systematics. 43, 429-448.

Sommer, U., Sommer, F., 2006. Cladocerans versus copepods: the cause of contrasting top–down controls on freshwater and marine phytoplankton. Oecologia 147, 183-194.

Starkweather, P., 1980. Aspects of the Feeding Behavior and Trophic Ecology of Suspension-Feeding Rotifers, in: Dumont, H.J., Green, J. (Eds.), Rotatoria, Springer Netherlands, pp. 63-72.

Starkweather, P., Gilbert, J., 1977. Feeding in the rotifer Brachionus calyciflorus. Oecologia 28, 133-139.

Starkweather, P., Gilbert, J., Frost, T., 1979. Bacterial feeding by the rotifer *Brachionus calyciflorus*: Clearance and ingestion rates, behavior and population dynamics. Oecologia 44, 26-30.

Steedman, R., Tonn, W., Paszkowski, C., Scrimgeour, G., Northcote, T., Hartman, G., 2004. Forestry and fish in the boreal region of Canada. Fishes and Forestry: Worldwide Watershed Interactions and Management, 413-438.

Tang, K.W., 2005. Copepods as microbial hotspots in the ocean: effects of host feeding activities on attached bacteria. Aquatic Microbial Ecology 38, 31-40.

Thorp, J.H., Covich, A.P., 2009. Ecology and classification of North American freshwater invertebrates. Academic press, 1021 pages.

Tipping, E., 1993. Modeling the competition between alkaline earth cations and trace metal species for binding by humic substances. Environmental science & technology 27, 520-529.

Tóth, L., 1992. Limiting effect of abioseston on food ingestion, postembryonic development time and fecundity of daphnids in Lake Balaton (Hungary). Journal of Plankton Research 14, 435-446.

Tranvik, L., Jansson, M., 2002. Climate change (Communication arising): Terrestrial export of organic carbon. Nature 415, 861-862.

Tranvik, L.J., Downing, J.A., Cotner, J.B., Loiselle, S.A., Striegl, R.G., Ballatore, T.J., Dillon, P., Finlay, K., Fortino, K., Knoll, L.B., 2009. Lakes and reservoirs as regulators of carbon cycling and climate. Limnology and Oceanography 54, 2298-2314.

Wachenfeldt, E.V., 2008. Flocculation of allochthonous dissolved organic matter – a significant pathway of sedimentation and carbon burial in lakes. Uppsala University, Disciplinary Domain of Science and Technology, Biology, Department of Ecology and Evolution, Limnolog. Doctoral thesis.

Wallace, R.L., Snell, T.W., 2010. Rotifera. In: Ecology and Classification of North American Freshwater Invertebrates. Eds J. Thorp Academic Press, 173-235.

Walz, N., 1987. Comparative population dynamics of the rotifers *Brachionus angularis* and *Keratella cochlearis*, Rotifer Symposium IV, Springer, 209-213.

Wetzel, R.G., 1984. Detrital dissolved and particulate organic carbon functions in aquatic ecosystems. Bulletin of Marine Science 35, 503-509.

Wiliamson, C.E., Butler, N.M., 1986. Predation on rotifers by the suspension-feeding Calaoid copepod Diaptomus pallidus. Limnol. Oceanogr. 31, 393-402.

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

Wissmar, R.C., Timm, R.K., Logsdon, M.G., 2004. Effects of changing forest and impervious land covers on discharge characteristics of watersheds. Environmental Management 34, 91-98.

Yoshida, T., Urabe, J., Elser, J.J., 2003. Assessment of ‘top-down’and ‘bottom-up’forces as determinants of rotifer distribution among lakes in Ontario, Canada. Ecological Research 18, 639-650.

Zhang, J., Hudson, J., Neal, R., Sereda, J., Clair, T., Turner, M., Jeffries, D., Dillon, P., Molot, L., Somers, K., 2010. Long-term patterns of dissolved organic carbon in lakes across eastern Canada: Evidence of a pronounced climate effect. Limnology and Oceanography 55, 30-42.

Zhou, S., Huang, X., Cai, Q., 2009. Temporal and spatial distributions of rotifers in Xiangxi Bay of the Three Gorges Reservoir, China. International Review of Hydrobiology 94, 542-559.

Zwart, J.A., Craig, N., Kelly, P.T., Sebestyen, S.D., Solomon, C.T., Weidel, B.C., Jones, S.E., 2015. Metabolic and physiochemical responses to a whole-lake experimental increase in dissolved organic carbon in a north-temperate lake. Limnology and Oceanography 61. 723-734.

Annexe 1

Tableau des équations utilisées pour chacuns des taxons

Taxons	Forumules	Type de longueur mesuré	Références
Rotifers			
Anuraeopsis fissa	$w = 0{,}03 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Ascomorpha sp.	$w = 0{,}12 \times l3 \times 0{,}1$	Totale	Mc Cauley 1984
Asplanchna sp.	$w = 0{,}23 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Cephalodella intuta	$w = 0{,}1 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Collotheca mutabilis	$w = 1{,}8 \times (l/7)^3 \times 0{,}1$	Totale	Mc Cauley 1984
Conochiloides dossuarius	$w = 0{,}26 \times l \times h^2 \times 0{,}1$	Totale	Mc Cauley 1984
Conochilus unicornis	$w = 0{,}26 \times l \times h^2 \times 0{,}1$	Totale	Mc Cauley 1984
Euchlanis alata	$w = 0{,}1 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Euchlanis calpidia	$w = 0{,}1 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Filinia sp.	$w = 0{,}13 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Gastropus sp.	$w = 0{,}20 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Kellicottia bostoniensis	$w = 0{,}03 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Kellicottia longispina	$w = 0{,}03 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Keratella cochlearis cochlearis	$w = 0{,}02 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Keratella hiemalis	$w = 0{,}22 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Keratella taurocephala	$w = 0{,}02 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Keratella tecta	$w = 0{,}02 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Keratella testudo	$w = 0{,}22 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Lecane flexilis	$w = 0{,}12 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Lecane inermis	$w = 0{,}12 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Lecane mira	$w = 0{,}12 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Lepadella patella	$w = 0{,}12 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Lophocaris sp.	$w = 0{,}1 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Monostyla sp.	$w = 0{,}12 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Monostyla closterocerca	$w = 0{,}12 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Monostyla copeis	$w = 0{,}12 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Monostyla lunaris	$w = 0{,}12 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Notholca foliacea	$w = 0{,}035 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Ploesoma sp.	$w = 0{,}1 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Polyarthra sp.	$w = 0{,}28 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Pompholyx sp.	$w = 0.15 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Synchaeta lackowitziana	$w = 0{,}1 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Testidunella sp.	$w = 0{,}08 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Trichocerca capucina	$w = 0{,}52 \times l \times h^2 \times 0{,}1$	Totale	Mc Cauley 1984
Trichocerca cylindrica	$w = 0{,}52 \times l \times h^2 \times 0{,}1$	Totale	Mc Cauley 1984
Trichocerca pusilla	$w = 0{,}52 \times l \times h^2 \times 0{,}1$	Totale	Mc Cauley 1984
Trichocerca rousseleti	$w = 0{,}52 \times l \times h^2 \times 0{,}1$	Totale	Mc Cauley 1984
Trichocerca similis	$w = 0{,}52 \times l \times h^2 \times 0{,}1$	Totale	Mc Cauley 1984
Tylotrocha monopus	$w = 0{,}12 \times l^3 \times 0{,}1$	Totale	Mc Cauley 1984
Wierzejskiella velox	$w = 0{,}26 \times l \times h^2 \times 0{,}1$	Totale	Mc Cauley 1984
Cladocerans			
Bosmina sp.	$w = 10^{(4{,}849 \log l - 3{,}857)} \times 1000000$	Totale	Rosen 1981
Chydoridae	$w = e^{(1{,}7512 + 2{,}6530 \mathrm{Ln} l)}$	Totale	Bottrell et al 1976
Daphnia sp.	$w = (1{,}5 * 10^{-8}) * l^{2{,}84}$	Totale	Dumont et al. 1975
Holopodium sp.	$w = e^{(2{,}4285 + (2{,}5195 \times \mathrm{Ln} l))}$	Totale	Malley et al. 1989
Polyphemus sp.	$w = (2{,}46 * 10^{-6}) * (l^{2{,}15})$	Totale	Dumont et al. 1975
Sididae	$w = 10^{(2{,}189 \log l - 5{,}108)} \times 1000000$	Totale	Rosen 1981
Copepods			
Calanoida	$w = e^{(1{,}0282 + 2{,}7523 \mathrm{Ln} l)}$	Totale	Malley et al. 1989
Cyclopoida	$w = 2{,}2 \times 10^{-8} \times l^{2{,}82}$	Totale	Dumont et al. 1975
Copépode Nauplii	$w = 10^{(4{,}849 \mathrm{Log} l - 3{,}857)} \times 1000000$	Totale	Rosen 1981