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PAR
MARTIN BÉLANGER

IMPACT DES COUPES FORESTIÈRES SUR L'ALIMENTATION ET LA CROISSANCE DE L'OMBLE DE FONTAINE (*Salvelinus fontinalis*) DANS DES LACS DU BOUCLIER BORÉAL CANADIEN

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RÉSUMÉ

La récolte forestière modifie les écosystèmes terrestres, mais a également un effet indirect sur les écosystèmes aquatiques. Jusqu'à maintenant, beaucoup d'études ont examiné l'impact des coupes forestières sur les écosystèmes lotiques. Toutefois, les effets sur les milieux lacustres et la faune ichtyenne ont été moins étudiés. De ce fait, il est très important de documenter davantage les impacts des coupes forestières afin de mieux comprendre leurs effets sur les espèces piscicoles en lac. Ces connaissances sont nécessaires pour permettre aux compagnies forestières et aux gouvernements d'améliorer la gestion de cette ressource renouvelable, tout en assurant aux pêcheurs sportifs de bénéficier d'une bonne qualité de pêche dans les zones d'exploitation forestière. L'objectif de cette étude était de déterminer les impacts à court terme des coupes forestières sur l'alimentation et la croissance de l'omble de fontaine (*Salvelinus fontinalis*) dans les lacs oligotrophes du Bouclier boréal canadien. Pour atteindre cet objectif, des ombles ont été capturés au cours de trois années (juillet 2008-2010), dans quatre lacs dont le bassin versant n'avait subi aucune perturbation et dans quatre lacs perturbés par les coupes forestières après la première année. Afin de vérifier l'effet d'une telle perturbation environnementale sur la diète du salmonidé, l'analyse des contenus stomacaux a été effectuée. Ces analyses n'ont pas permis de déceler des changements quant aux assemblages, aux indices de diversités et l'abondance des types de proies dans l'alimentation des individus âgées de 3 et 4 ans + capturés suite à la récolte forestière. La variabilité entre les lacs est plus importante que celle attribuable aux coupes forestières. Les otolithes ont été utilisés pour mesurer la croissance chez les ombles de fontaine âgés de trois et quatre ans. Les récoltes forestières n'ont provoqué aucune modification des taux de croissance. Finalement, les résultats suggèrent que malgré une augmentation en phosphore total et en carbone organique dissous dans les lacs perturbés par la coupe forestière, aucune différence n'a été détectée dans l'alimentation et la croissance des ombles de fontaine. Cette étude supporte l'hypothèse selon laquelle l'effet des coupes forestières est dilué chez les espèces situées au sommet du réseau trophique comme l'omble de fontaine adulte dans les lacs de la forêt boréale.

AVANT-PROPOS ET REMERCIEMENTS

Ce mémoire est présenté sous la forme d'un article scientifique en anglais et comprend également une introduction ainsi qu'une conclusion générale en français.

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TABLE DES MATIÈRES

RÉSUMÉ ii
AVANT-PROPOS ET REMERCIEMENTS iii
TABLE DES MATIÈRES v
LISTE DES TABLEAUX vi
LISTE DES FIGURES vii
INTRODUCTION GÉNÉRALE 1
1. INTRODUCTION 9
2. METHODS 12
  2.1 Study area and design 12
  2.2 Fish sampling 13
  2.3 Laboratory procedures 16
    2.3.1 Diet composition 16
    2.3.2 Otoliths analysis 17
  2.4 Data analysis 18
    2.4.1 Size and age structure 18
    2.4.2 Diet composition 18
    2.4.3 Growth 20
3. RESULTS 22
  3.1 Size and age structure 22
  3.2 Diet composition 23
    3.2.1 Prey abundance 23
    3.2.2 Dry weight of prey 25
    3.2.3 Diversity indices 26
    3.2.4 Prey assemblage 29
  3.3 Growth 31
4. DISCUSSION 35
  4.1 Diet composition 35
  4.2 Growth 37
CONCLUSION GÉNÉRALE 40
RÉFÉRENCES 43

LISTE DES TABLEAUX

Table 1. Lake characteristics of the eight studied Canadian Boreal Shield lakes (UP: unperturbed; P: perturbed). Temperature, conductivity dissolved oxygen (DO), pH, Chl *a*, dissolved organic carbon (DOC), total phosphorus (TP), dissolved inorganic phosphorus (DIP) and dissolved inorganic nitrogen (DIN) are reported as means (SD) of the sampling stations in the photic zone before the perturbation (2008). Lake UP3 was not deep enough for sampling secchi depth (Glaz et al. 2012). 15

Table 2. Result of three-way partly nested ANOVAs on log X+1 transformed abundance data testing the effect of treatment and sampling year interactions (YR x TR) on the abundance of prey by functional groups for age 3+ and age 4+ brook trout........................24

Table 3. Result of three-way partly nested ANOVAs on log X+1 transformed dry weight abundance data testing the effect of treatment and sampling year interactions (YR x TR) on the abundance of prey by functional groups for age 3+ and age 4+ brook trout. *Hirudinea* and vertebrates were excluded for dry weight analysis. 25

Table 4. Results of the nonparametric multivariate analyses of variance (PERMANOVA) testing the effect of lake treatment, lakes nested within treatment, sampling year, and their interactions on the assemblages of ingested prey taxa. The species assemblages were calculated on fourth-root transformed data. Taxonomic resolution as described in Appendix 1 and 2...31

LISTE DES FIGURES

Figure 1. Study area in the eastern Canadian Boreal Shield, showing the location of the eight lakes sampled in 2008, 2009 and 2010. UP, unperturbed; P, perturbed (harvested in 2008) (Glaz et al. 2012). 13

Figure 2. Relationship between total length (LT) and otolith rostral radius (RR) of brook trout for growth analysis in unperturbed (circle) and perturbed (triangle) lakes in 2008, 2009, and 2010. 21

Figure 3. Brook trout total length (mm) frequency distribution for all sampling dates (2008, 2009, and 2010) in unperturbed (black bars; n = 247) and perturbed lakes (white bars; n = 293). 22

Figure 4. Brook trout age frequency distribution for all sampling dates (2008, 2009, and 2010) in unperturbed (black bars; n = 211) and perturbed lakes (white bars; n = 274). 23

Figure 5. a) Log X+1 transformed abundances, b) richness (S), c) Pielou's evenness (*J'*) and d) Shannon's diversity index (*H'*) of prey in diet of age 3+ brook trout in unperturbed (black bars) and perturbed (white bars) lakes for the three sampling dates (2008 to 2010). Vertical and dashed lines represent standard errors of mean lake values and forest harvesting, respectively. 27

Figure 6. a) Log X+1 transformed abundances, b) richness (S), c) Pielou's evenness (*J'*) and d) Shannon's diversity index (*H'*) of prey in diet of age 4+ brook trout in unperturbed (black bars) and perturbed (white bars) lakes for the three sampling dates (2008 to 2010). Vertical and dashed lines represent standard errors of mean lake values and forest harvesting, respectively. 28

Figure 7. Nonmetric multidimensional scaling results, illustrating variations in prey assemblages (square root transformed data) ingested by a) age 3+ and b) age 4+ brook trout from unperturbed (black triangles) and perturbed (white triangles) lakes. Results of the corresponding permutational multivariate ANOVAs are given in Table 4. 30

Figure 8. Comparison between years and lake treatments (unperturbed (black bars), perturbed (white bars)) for the mean back-calculated last year growth rate of a) age 3+, and b) age 4+ brook trout caught for all sampling dates (2008, 2009 and 2010). Vertical and dashed lines represent standard errors of mean lake values and forest harvesting, respectively. 33

Figure 9. Comparison between years and lake treatments (unperturbed (black squares), perturbed (white circles)) for the mean back-calculated lengths-at-age growth rate of a) age 3+, and b) age 4+ brook trout caught in 2010. Vertical and dashed lines represent standard errors of mean lakes values and forest harvesting, respectively. 34

LISTE DES ANNEXES

Appendix 1 : Mean percentage by number and by dry weight of taxa found in age 3+ brook trout stomachs in four unperturbed and four perturbed lakes. Stomachs with Hirudinea and vertebrate were excluded for mean percentage by dry weight 51

Appendix 2: Mean percentage by number and by dry weight of taxa found in age 4+ brook trout stomachs in four unperturbed and four perturbed lakes. Stomachs with Hirudinea and vertebrate were excluded for mean percentage by dry weight 53

INTRODUCTION GÉNÉRALE

Au Canada, la forêt boréale s'étend sur plus de trois millions de kilomètres carrés, ce qui en fait la forêt la plus importante du territoire canadien, surpassant tout autre type de forêts canadiennes mises ensemble (Steedman et al. 2004). Celle-ci est séparée en trois écozones forestières : la Cordillère boréale, les Plaines boréales ainsi que le Bouclier boréal (EnvC 2000). À lui seul, le Bouclier boréal compte plus de 1,8 million de kilomètres carrés répartis sur cinq provinces du Canada (Steedman et al. 2004). Plus de 70% du territoire québécois fait partie du Bouclier boréal (EnvC 2000) et est dominé par les conifères , surtout l'épinette noire (*Picea mariana*), le sapin baumier (*Abies balsamea*) et le pin gris (*Pinus Banksiana*). On y retrouve aussi quelques essences décidues, telles que le bouleau jaune (*Betula alleghaniensis*) et le peuplier faux-tremble (*Populus tremuloides*) (Steedman et al. 2004). De par sa très grande superficie, cette écozone renferme un très grand nombre d'écosystèmes aquatiques et terrestres.

Depuis le début de la colonisation, la forêt boréale est assujettie à de grands changements, directement ou indirectement d'origine anthropique. Qu'on parle d'exploitation forestière ou de suppression des incendies forestiers, tous ont des impacts considérables sur la structure et le fonctionnement de ces écosystèmes. Au Québec, en 2008, l'industrie forestière embauchait environ 128 000 travailleurs et représentait 11 milliards de dollars pour l'économie de la province (MRNF 2008). La foresterie a subi quelques bouleversements au cours de la dernière décennie avec la Commission publique sur la gestion de la forêt publique du Québec. Dans le rapport qui a été remis au gouvernement en 2004, la Commission a proposé des voies permettant d'améliorer le régime forestier dans toutes ses dimensions (Coulombe 2004). Depuis quelques années, le Québec vit une crise qui vise l'ensemble du secteur forestier. Les causes de cette crise sont multiples et remontent loin dans le temps. Le ministère des Ressources naturelles et de la Faune entame présentement une réforme du régime forestier (MRNF 2008). Il est donc important d'identifier les impacts de l'exploitation sur les écosystèmes afin d'alimenter la réflexion sur la réforme du régime forestier.

La récolte forestière ne modifie pas seulement le paysage forestier. Elle peut aussi avoir un impact sur les écosystèmes aquatiques qui se comptent par milliers sur le territoire québécois. Les lacs et les cours d'eau sont eux aussi très important pour l'économie québécoise. Ceux-ci sont convoités par environ 700 000 adeptes provinciaux ainsi que plusieurs visiteurs pour leurs ressources halieutiques. Ces amants provinciaux de la pêche sportive dépensent au total près de 1,6 milliard de dollars dans la province (MPO 2010).

Au Québec, l'espèce la plus prisée des pêcheurs sportifs est sans contredit l'omble de fontaine (*Salvelinus fontinalis*). Ce poisson est fort recherché pour la qualité de sa chair et sa combativité (Bernatchez and Giroux 2000). Au Canada, on retrouve l'omble de fontaine dans les quatre provinces maritimes ainsi qu'au Labrador et au Québec. On le retrouve aussi dans l'ouest du pays dans le bassin des Grands Lacs en Ontario jusqu'au nord-est du Manitoba puis vers le nord jusqu'à la baie James et la baie d'Hudson. Ce poisson fait partie de la famille des salmonidés et préfère les eaux fraîches, claires et bien oxygénées. Il possède un corps plutôt allongé, légèrement comprimé latéralement. Sa longueur moyenne est de 254-305 millimètres. Lors de la période de fraie, le mâle arbore parfois un crochet à l'avant de la mâchoire inférieure. Celui-ci lui confèrerait un avantage pour séduire une femelle lors de la reproduction. La reproduction a lieu pendant le jour, tard en été ou en automne. L'acte se déroule la plupart du temps sur les fonds de gravier, en eau peu profonde et à la tête des cours d'eau (Scott and Crossman 1974).

L'omble de fontaine est facilement identifiable avec sa nageoire adipeuse et sa coloration allant du vert olive au brun foncé sur le dessus, les flancs plus pâles, puis changeant au blanc argenté en dessous et muni de tâches pâles souvent avec un halo bleu sur les flancs (Scott and Crossman 1974). On peut différencier cette espèce du touladi (*Salvelinus namaycush*) et de l'omble de chevalier (*Salvelinus alpinus*) par sa queue qui est très peu fourchue (Bernatchez and Giroux 2000). L'omble de fontaine est un poisson carnivore généraliste qui peut se nourrir d'une vaste variété d'animaux (Scott and Crossman 1974). Pour ce qui est des jeunes et des spécimens de taille moyenne, ils avalent de grandes quantités d'insectes terrestres et de larves d'insectes aquatiques. Les individus de plus grande taille ont un régime alimentaire semblable, bien qu'ils puissent à l'occasion ingérer de petits mammifères. Le cannibalisme a aussi été observé chez cette espèce qui se nourrit à l'occasion de ses œufs et de ses jeunes au printemps (Ricker 1932). Il a été démontré que les populations d'ombles de fontaine allopatriques se nourrissent principalement de zoobenthos (Glaz et al. 2012), tandis que ceux qui vivent en sympatrie avec le meunier noir (*Catostomus commersoni*) s'alimentent davantage de zooplancton (Tremblay and Magnan 1991). Des végétaux ont déjà été observés lors d'examens du contenu stomacal de ce poisson (Scott and Crossman 1974). Les connaissances actuelles ne permettent pas de bien comprendre l'impact des activités forestières sur la production en lac de l'omble de fontaine et des effets subséquents sur la pêche sportive.

L'impact des coupes forestières sur les écosystèmes aquatiques en forêt boréale a été étudié par plusieurs équipes de recherche au cours des dernières années. En lac, les études ont principalement été réalisées sur la qualité de l'eau (Rask et al. 1998, Carignan and Steedman 2000, Martin and Hornbeck 2000, Steedman 2000, Prepas et al. 2001, Steedman et al. 2001, Winkler et al. 2009), les organismes planctoniques ou benthiques (Wallace and Gurtz 1986, Pinel-Alloul et al. 1998, Rask et al. 1998, Patoine et al. 2000, Scrimgeour et al. 2000, Patoine et al. 2002a, Nicholls et al. 2003, Jalal et al. 2005) et sur les communautés ichtyologiques (Bérubé and Lévesque 1998, Rask et al. 1998, Gunn and Sein 2000, St-Onge and Magnan 2000, Steedman and Kushneriuk 2000, St-Onge et al. 2001, Tonn et al. 2003, Bertolo and Magnan 2007, Tremblay-Rivard 2007, Leclerc et al. 2011a, Leclerc et al. 2011b). Les impacts des coupes forestières sur les poissons sont beaucoup plus connus en milieu lotique qu'en lac.

L'étude de Rask *et al.* (1998) réalisée en Finlande a démontré que les coupes forestières pouvaient occasionner une légère augmentation du phosphore total (PT), de la coloration de l'eau ainsi que de l'apport en matières organiques, bien que celle-ci soit modeste en raison de la zone de protection riveraine de 50 m. Cependant, lors de cette étude, seulement 15-37% du bassin versant des lacs ont été perturbés. De son côté, Steedman (2000) a lui aussi observé un changement modeste dans les concentrations de carbone organique dissous (COD), de nutriments ainsi que dans la concentration des ions majeurs suivant une coupe forestière autour de lacs profonds dans le Nord-Ouest de l'Ontario. Une étude conduite au Québec par Carignan et *al.* (2000) a donné lieu à des résultats similaires. L'étude réalisée sur plusieurs lacs pendant les trois années suivant la perturbation a dévoilé une augmentation du COD, du coefficient d'atténuation lumineuse, du PT, et de l'azote total (NT) par rapport aux lacs témoins (Carignan *et al.* 2000). Les différents résultats observés sont dus au fait que les écosystèmes aquatiques réagissent différemment selon la morphométrie des lacs, le ratio de drainage ainsi que le temps de renouvellement de l'eau (Carignan and Steedman 2000).

Selon le principe de cascade trophique, les changements observés sur la qualité de l'eau influenceront la base des réseaux trophiques lacustres et devraient donc avoir un impact sur les maillons trophiques supérieurs comme le zooplancton, le zoobenthos et les poissons. Les organismes zooplanctoniques sont influencés par les apports organiques ainsi que par la luminosité (Rask *et al.* 1998). Les résultats des études réalisées sur la biomasse de zooplancton suivant une coupe forestière sont très partagés. En effet, certaines études observent une augmentation de la biomasse de zooplancton (Rask et al. 1998, Leclerc et al. 2011a) tandis que d'autres n'observent aucun changement (Pinel-Alloul et al. 1998, Patoine et al. 2000, Winkler et al. 2009) ou bien une diminution de la biomasse chez les copépodes calanoïdes seulement (Patoine *et al.* 2000). Les effets ressentis sur le zooplancton sont de courte durée, dépassant rarement deux ans (Patoine *et al.* 2000). Comme l'explique Jalal et *al.* (2005), les lacs de la forêt boréale ont une bonne résilience face aux perturbations naturelles ou anthropiques. Selon Roberge (1996), la réponse des communautés d'invertébrés dépendrait surtout de l'importance de la production primaire et du transport sédimentaire, mais aussi de la quantité et la qualité des apports organiques. Encore une fois, les résultats sont très partagés suite à la suppression du couvert forestier. Une étude réalisée par Scrimgeour *et al.* (2000) n'a pas permis de déceler de différences au niveau de la densité et de la diversité des espèces benthiques dans les lacs perturbés comparativement aux témoins. Les travaux de Rask *et al.* (1998) ont, quant à eux permis d'observer une augmentation de la densité des invertébrés benthiques.

À ce jour, les réponses des écosystèmes aquatiques aux coupes forestières ont été très variables. Pour cela, il est important de vérifier les impacts directs ou indirects sur les populations de poissons. Bérubé et Lévesque (1998) ont réalisé une étude sur l'impact de l'activité forestière sur le nombre et le poids moyen de l'omble de fontaine dans vingt lacs de la réserve faunique Mastigouche (Québec). Leurs travaux se sont penchés sur la collecte de statistiques de pêche. Ils n'ont noté aucun changement en ce qui concerne la masse moyenne entre les trois périodes de l'étude, c'est-à-dire avant, pendant et après les coupes. Toutefois, les captures par unité d'effort (CPUE) ainsi que la biomasse par unité d'effort (BPUE) ont diminué de 18% et 22% respectivement après les coupes. D'autres auteurs n'obtiennent aucune perte d'habitat chez le touladi (Gunn and Sein 2000, Steedman and Kushneriuk 2000). Leclerc *et al.* (2011a) ont observé une augmentation de la croissance des larves et juvéniles perchaudes (*Perca flavescens*). Celle-ci serait due à une augmentation des nutriments et de la concentration en COD suite à la perturbation, ce qui augmenterait le nombre de proies disponibles et faciliterait leur détection par les jeunes perchaudes. Une étude réalisée par Tremblay-Rivard (2007) sur l'alimentation de l'omble de fontaine suite à une opération forestière, a révélé qu'il s'alimentait davantage d'organismes zooplanctoniques.

Ce qui distingue notre projet de recherche des autres est l'approche expérimentale. Jusqu'à présent les travaux réalisés ont, pour la majorité, ignoré l'état naturel des lacs puisqu'ils ont comparé des lacs différents en excluant les données précédant la coupe forestière (St-Onge and Magnan 2000, Tremblay-Rivard 2007). Rask *et al.* (1998) ont comparé des plans d'eaux dont le bassin versant a subi une perturbation avec seulement un lac témoin. Plusieurs travaux ont quant à eux porté sur des espèces ayant un cycle de vie différent de celle de l'omble de fontaine, qui lui se reproduit et débute ses premiers stades de vies principalement en rivière (Rask et al. 1998, Gunn and Sein 2000, St-Onge et al. 2001, Bertolo and Magnan 2007, Leclerc et al. 2011a, Leclerc et al. 2011b). Finalement, les résultats de l'étude de Bérubé et Lévesque (1998) qui porte sur l'omble de fontaine sont basés sur des statistiques de pêche et non sur des variables biologiques. Notre étude utilise l'approche la plus valide pour ce type de recherche, c'est-à-dire avant/après la coupe forestière ainsi que la réplication de témoins. Ce type d'approche permet de bien cerner la variation naturelle entre les lacs.

L'objectif de cette présente étude est de déterminer l'impact des coupes forestières sur l'alimentation et la croissance de l'omble de fontaine dans des lacs de la forêt boréale. Pour ce faire, le régime alimentaires et la croissance de l'omble de fontaine seront comparés dans huit lacs avant et après la récolte forestière sur les bassins versants. Sur la base des résultats de l'étude de Tremblay Rivard (2007), les deux hypothèses de travail sont :

Le régime alimentaire de l'omble de fontaine qui est normalement dominé par le zoobenthos, changera pour une alimentation majoritairement zooplanctonique suite à la perturbation.

Ce changement attendu dans le régime alimentaire provoquera une diminution de la croissance des individus dans les lacs perturbés, suite à la récolte forestière.

1. INTRODUCTION

Forests are subject to many human-induced pressures such as intensive logging activities. Forestry activities can have impacts on aquatic ecosystems and associated fisheries resources. Current knowledge on the impact of logging on lake ecosystems and subsequent effects on fish is still unclear. It is therefore essential to further examine these potential impacts (Northcote and Hartman 2004).

Many studies have examined the impact of logging on aquatic ecosystems in the boreal forest. In lakes, studies have mainly been conducted on water quality (Rask et al. 1998, Carignan and Steedman 2000, Martin and Hornbeck 2000, Steedman 2000, Prepas et al. 2001, Steedman et al. 2001, Winkler et al. 2009), plankton or benthic organisms (Wallace and Gurtz 1986, Pinel-Alloul et al. 1998, Rask et al. 1998, Patoine et al. 2000, Scrimgeour et al. 2000, Patoine et al. 2002a, Nicholls et al. 2003, Jalal et al. 2005) and fish communities (Bérubé and Lévesque 1998, Rask et al. 1998, Gunn and Sein 2000, St-Onge et al. 2001, Tonn et al. 2003, Bertolo and Magnan 2007, Tremblay-Rivard 2007, Leclerc et al. 2011a, Leclerc et al. 2011b). However the impact of forestry on fish have been better documented in lotic ecosystems than in lakes.

The study of Rask et al. (1998) conducted in Finland showed that logging could lead to a slight increase in total phosphorus (TP), water color and supply of organic matter, although effects are modest due to the 50-m forested strip kept on the shores of lakes.

Steedman (2000) also observed a weak change in dissolved organic carbon (DOC) concentration, nutrients and major ions in perturbed deep lakes in northwest Ontario. A study conducted in Quebec by Carignan *et al.* (2000) three years after disturbance led to similar results. In fact, their results revealed an increase in the DOC concentration, light penetration, TP, and total nitrogen (TN) compared to control lakes (Carignan *et al.* 2000). The different results observed are due to the fact that aquatic ecosystems react differently depending on lake morphometry, the drainage ratio and water renewal times.

Brook trout (*Salvelinus fontinalis*) is a common game fishing species in North American waters. It is a generalist carnivore fish, feeding on a wide variety of prey. Adults feed predominantly on terrestrial insects or aquatic insect larvae and occasionally on fish and small mammals (Scott and Crossman 1974). Their growth rate is related to temperature, prey availability, intra and interspecific competition (Magnan 1988) and environmental factors that affect the visual environment and feeding success (De Robertis et al. 2003).

In this study, we anticipate a decrease in the growth of brook trout in perturbed lakes following forest harvesting. This decrease might be caused by a change in diet. After logging, increase in COD may improve contrast of zooplankton prey and make them easier to catch than zoobenthos. Zooplankton prey are less effective at the energy level so we would expect a decrease in growth of brook trout.

The aim of the study was to determine the impact of forest harvesting on feeding and growth rate of brook trout in boreal forest lakes. To achieve this objective, diet and growth of fish was assessed before and after logging on watersheds of eight lakes (four lakes sampled before and after the perturbation plus four unperturbed reference lakes sampled at the same time).

2. METHODS

2.1 Study area and design

The lakes examined in this study are located in the province of Quebec, in the Canadian Boreal Shield ecoregion, on the Mistassibi drainage basin (50° 7'30" N, 71° 35'59" W) (Figure 1). The forest in this area is dominated by black spruce (*Picea mariana*), an important species for the forest industry. Lakes are oligotrophic and mainly contain brook trout in allopatry or in sympatry with white sucker (*Catostomus commersonii*).

Eight lakes with similar morphometric characteristics were selected according to the logging plan in the study area (Table 1). Each lake contains an allopatric brook trout population, except lake P4, which also contains a small number of white sucker. These lakes were assigned to one of two treatments: perturbed (P) or unperturbed (UP). The sampling design included one survey before the perturbation (2008) and two surveys after forest harvesting (2009-2010). Forest harvesting took place in autumn 2008. Trees were felled following the Careful Logging Around Advanced Growth (CLAAG) strategy and 20-m strips of standing forest were left along lakes and streams after harvesting. All perturbed lakes correspond to the criteria of a drainage ratio higher than 4 (Carignan *et al.* 2000) and a deforestation of more than 40% of the catchment area (Pinel-Alloul *et al.* 2002).

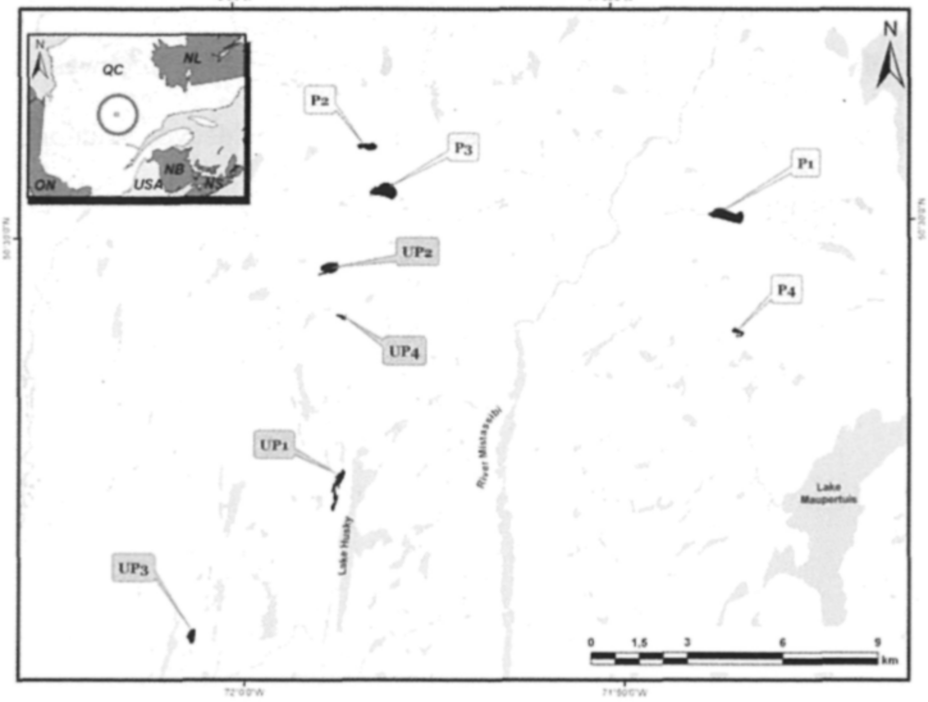

Figure 1. Study area in the eastern Canadian Boreal Shield, showing the location of the eight lakes sampled in 2008, 2009 and 2010. UP, unperturbed; P, perturbed (harvested in 2008) (Glaz et al. 2012).

2.2 Fish sampling

Brook trout were sampled on three occasions, from 9 to 18 July 2008, from 15 to 22 July 2009, and from 8 to 15 July 2010. In each lake, fish were caught using six experimental gill nets (each gill net has six panels 3.8 meters (m) in length and 1.8 m in height, mesh sizes of 1", 1½", 2", 2½" 3", 3½") according to the Ministère des Ressources naturelles et de la Faune du Québec standard protocol. Gill nets were set simultaneously around the lake, perpendicular to the shore with the finest mesh toward the shore. Gill nets were left for 12 hours overnight. The total length of each brook trout was measured and the stomach removed and preserved in a 4% buffered formaldehyde solution. All individuals were then identified and frozen at -20°C.

Table 1. Lake characteristics of the eight studied Canadian Boreal Shield lakes (UP: unperturbed; P: perturbed). Temperature, conductivity dissolved oxygen (DO), pH, Chl *a*, dissolved organic carbon (DOC), total phosphorus (TP), dissolved inorganic phosphorus (DIP) and dissolved inorganic nitrogen (DIN) are reported as means (SD) of the sampling stations in the photic zone before the perturbation (2008). Lake UP3 was not deep enough for sampling secchi depth (Glaz et al. 2012).

	UP1	UP2	UP3	UP4	P1	P2	P3	P4
Latitude N	50° 25' 44"	50° 29' 22"	50° 23' 13"	50° 28' 34"	50° 30' 9"	50° 31' 25"	50° 30' 40"	50° 28' 11"
Longitude W	71° 57' 28"	71° 57' 32"	72° 1' 24"	71° 57' 15"	71° 47' 1"	71° 56' 26"	71° 56' 5"	71° 46' 51"
Lake area (km^2)	0.170	0.169	0.063	0.031	0.288	0.090	0.277	0.043
Catchment area (km^2)	0.916	2.799	0.586	0.202	2.895	1.761	2.416	0.339
Drainage area (km^2)	0.746	2.630	0.523	0.171	2.606	1.671	2.138	0.296
Drainage ratio	4.388	15.562	8.301	5.516	9.024	18.567	7.706	6.883
Secchi depth (m)	1.25	1.50	n/a	1.75	1.50	1.65	1.40	1.40
Temperature (°C)	17.86 (0.80)	17.09 (0.65)	16.71 (0.74)	16.99 (0.24)	17.13 (0.36)	16.71 (0.06)	17.45 (0.24)	15.65 (0.50)
Conductivity (μS cm^{-1})	11.93 (0.64)	12.50 (0.05)	19.00 (0.54)	9.40 (0.15)	13.40 (0.00)	11.92 (0.12)	12.65 (0.14)	14.67 (0.45)
DO (mg l^{-1})	8.61 (0.13)	9.52 (0.68)	7.51 (0.38)	7.22 (0.15)	8.47 (0.20)	8.24 (0.08)	8.21 (0.23)	8.46 (0.57)
pH	5.92 (0.10)	5.75 (0.02)	5.94 (0.05)	5.87 (0.07)	5.92 (0.06)	5.02 (0.05)	5.62 (0.15)	5.38 (0.28)
Harvested area (% of catchment area)	-	-	-	-	72.9	69.1	71.6	77.0
Chl *a* (μg l^{-1})	0.427 (0.065)	0.390 (0.061)	0.617 (0.200)	0.363 (0.050)	0.982 (0.212)	0.546 (0.060)	0.681 (0.161)	0.486 (0.072)
DOC (mg l^{-1})	5.05 (0.26)	4.95 (0.52)	5.77 (0.50)	5.13 (1.01)	5.09 (0.70)	4.69 (0.47)	5.26 (0.70)	4.65 (0.55)
TP (μg l^{-1})	10.78 (0.57)	12.06 (0.58)	12.56 (1.01)	12.33 (0.48)	11.91 (0.73)	9.82 (0.40)	8.98 (0.43)	13.73 (1.04)
DIP (μg l^{-1})	1.81 (0.31)	2.10 (0.58)	1.29 (0.56)	1.49 (0.41)	1.88 (0.74)	1.54 (0.41)	1.20 (0.14)	2.04 (0.91)
DIN (μg l^{-1})	0.24 (0.12)	0.75 (0.51)	0.31 (0.18)	n/a	0.60 (0.12)	n/a	0.73 (0.10)	0.320.27)

2.3 Laboratory procedures

2.3.1 Diet composition

In the laboratory, the stomach content of each brook trout was examined under a stereoscopic microscope Leica MZ 12.5. Each prey found was identified to the family level whenever possible. If the number of prey was too high (≥ 1000), a folsom splitter was used. The development stage was determined for insects (larvae, pupae or adult). The following identification keys were used: Edmondson (1959) and Pennak (1978) for copepods and other zooplankton species, McCafferty (1981), Merritt and Cummins (1995), Peckarsky et al. (1990), and Wiggins (1977) for immature insects, and Borror et al. (1981) for adult insects. Dry mass of each prey taxa found in the stomach was estimated with length/dry weight relationships. A maximum of 10 specimens for each taxa were randomly selected, measured (body length or head width) and dry weights were estimated for all the individuals in the stomach. The following publications were used for dry weight estimation: Lawrence et al. (1987) and Malley et al. (1989) for copepods and other zooplankton species, Baumgartner and Rothhaupt (2003), Benke et al. (1999), Culver et al. (1985), Johnston and Cunjak (1999), Meyer (1989), Sage (1982), and Sample et al. (1993) for immature and adult insects. When no length/dry weight relationship for a taxa level was available, the relationship was selected from the nearest taxa level was selected (e.g., same order).

2.3.2 Otoliths analysis

Individual growth characteristics were obtained from otolith analysis. The left and right sagittal otoliths were removed and mounted on a microscope slide with thermoplastic glue. Otoliths were polished with a lapping film (200 to 1000 μm). Calcified structures were analyzed under stereoscopic microscope with transmitted light. Three measurements were registered: rostral radius (μm), reading radius on the postero-dorsal axis (μm) and annual increment widths (μm). All otoliths were measured twice by two different readers and each count estimate was ranked according to the confidence of the reading (i.e., 1- very good; 2- good and 3- poor condition). In the case of discrepancy between the two readings, otoliths were re-analysed by the two readers together in order to obtain a common measure. A total of 485 otoliths were analysed: 157, 164, and 164 from the 2008, 2009, and 2010 samplings, respectively. A total of 149 otoliths were re-analysed by the two readers to obtain a common measure and 55 otoliths in poor condition were excluded from the analysis.

2.4 Data analysis

2.4.1 Size and age structure

A Kolmogorov-Smirnov analysis was used to identify significant differences in brook trout total length frequency and age distributions in the two types of lakes. This analysis was performed using SAS 9.1.3 statistical software.

2.4.2 Diet composition

Prey abundance and ingested dry weight (DW) were estimated in unperturbed (UP) and perturbed (P) lakes by functional groups: aquatic predators and aquatic primary consumers (zoobenthos), zooplankton, terrestrial insects, and vertebrate. The diversity was examined using four diversity indices calculated using PRIMER v6 statistical software (Clarke and Gorley 2001, Clarke and Warwick 2001, Anderson et al. 2008): total abundance, species richness (S), Pielou's evenness (*J'*) and Shannon's diversity (*H'*). All stomach contents with vertebrate and *Hirudinea* prey species were excluded for dry weight analysis to avoid bias in the results. Three way partly nested analyses of variance (ANOVAs) were used to compare abundance and diversity indices: lake treatments (TR, perturbed/unperturbed, fixed factor), sampling year [YR, before (2008)/after (2009-2010), fixed factor], lakes [LA(TR), four lakes nested in treatment, random factor] and their interactions [YR x TR and YR x LA(TR)]. Data were log X+1 transformed to achieve normality and homogeneity of variance when necessary. The principal source of variation of interest for impact assessment was the interaction between treatment (perturbed/unperturbed) and sampling year (before/after) (YR x TR). Analyses were conducted on 275 and 122 fish aged three and four years, respectively and with at least one prey item in the stomach.

Multivariate analysis of variance was used to evaluate differences in ingested prey assemblages. First, the non-metric multi-dimensional scaling (nMDS) ordination on fourth-root transformed data (abundance data) was performed using the Bray-Curtis similarity measure was performed (Clarke and Warwick 2001). Second, permutational multivariate analysis of variance (PERMANOVA) (Anderson et al. 2008) with lake treatment (TR, perturbed/unperturbed, fixed factor), sampling year [YR, before (2008)/after (2009-2010), fixed factor], lake [LA(TR), four lakes nested in treatment, random factor] and their interactions [YR x TR and YR x LA(TR)] as factor were used to test for differences in ingested prey assemblages. Data were fourth-root transformed and the Bray-Curtis dissimilarity of abundance data was used. Number of permutations used was 9999. Fish with at least one prey item in the stomach were used in multivariate analyses.

2.4.3 Growth

Back-calculation methods of fish length based on otolith rely on two assumptions: 1) increments must be deposited on an annual basis, and 2) otolith growth must be proportional to fish growth (Panfili et al. 2002). To support the proportionality between otolith and somatic growth, a relationship between fish total length (TL) and otolith rostral radius (RR) was performed for all brook trout caught in the study in both perturbed and unperturbed lakes. The body proportional hypothesis (BPH) was used to back-calculate length-at-age (L_i) using the equation of Francis (1990):

$$L_i = [(c + dS_i) / (c + dS_c)]L_c$$

where c is the intercept and d the slope of the TL on RR regression (Figure 2), L_c is fish total length at capture, S_c is otolith radius at capture, S_i and L_i correspond to the measurement of otolith and fish length-at-age at the time of formation, respectively. Two types of growth were analysed: 1) back-calculated length increase since the formation of the last annulus on the otolith (transversal approach), and 2) growth trajectory of fish caught in 2010 (longitudinal approach). The same ANOVA model as for abundances and diversity indices was performed for growth analysis.

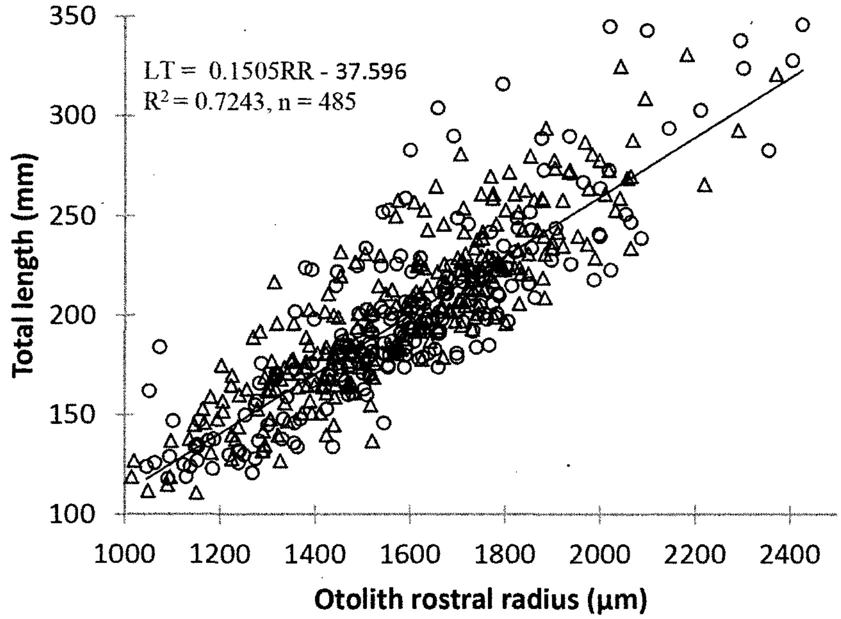

Figure 2. Relationship between total length (LT) and otolith rostral radius (RR) of brook trout for growth analysis in unperturbed (circle) and perturbed (triangle) lakes in 2008, 2009, and 2010.

3. RESULTS

3.1 Size and age structure

Brook trout total lengths from all sampling dates ranged between 111 mm and 415 mm. There was no significant difference between total length frequency distribution in unperturbed and perturbed lakes (Figure 3; p = 0.572).

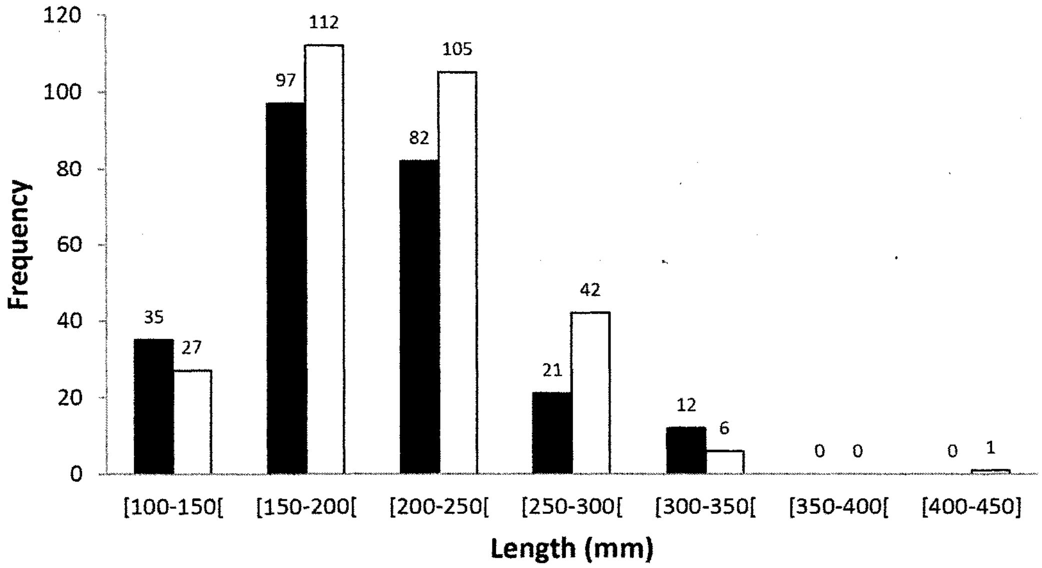

Figure 3. Brook trout total length (mm) frequency distribution for all sampling dates (2008, 2009, and 2010) in unperturbed (black bars; n = 247) and perturbed lakes (white bars; n = 293).

A total of 485 fish were aged. Brook trout aged from one to six years were caught. There was no significant difference between age frequency distributions from unperturbed and perturbed lakes (Figure 4; p = 0.0541). However 275 and 122 fish aged three and four years, respectively were analysed for last year growth.

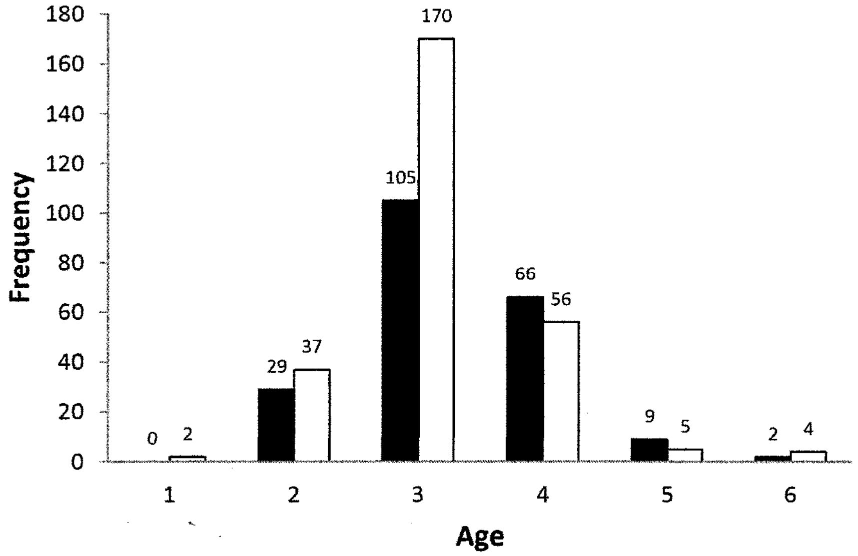

Figure 4. Brook trout age frequency distribution for all sampling dates (2008, 2009, and 2010) in unperturbed (black bars; n = 211) and perturbed lakes (white bars; n = 274).

3.2 Diet composition

3.2.1 Prey abundance

A total of 71 and 57 prey taxa have been identified in the stomach contents of age 3+ and age 4+ fish, respectively. The most abundant functional group found in the diet of age 3+ and age 4+ brook trout, before and after forest harvesting was the aquatic primary consumers. In both age classes, for each treatment sampling year, aquatic predators, terrestrial insects, zooplankton and vertebrate were also ingested, but in smaller numbers than aquatic primary consumers (Appendix 1, 2). Aquatic predators were the second largest group in abundance of prey. No significant differences were observed for each functional group abundance in the diet between the sampling years and lake treatments interactions (YR x TR) for age 3+ and age 4+ brook trout (Table 2). Dominant taxa were *Chaoboridae*, *Chironomidae* and *Diptera* (Appendix 1, 2).

Table 2. Result of three-way partly nested ANOVAs on log X+1 transformed abundance data testing the effect of treatment and sampling year interactions (YR x TR) on the abundance of prey by functional groups for age 3+ and age 4+ brook trout.

Age class	Variable	df	MS	F	p = level
3	Aquatic predators	2	0.5229	1.6521	0.2188
	Aquatic primary consumers	2	0.2345	0.3241	0.7286
	Terrestrial insects	2	0.0353	0.2427	0.9654
	Zooplankton	2	0.0692	0.0463	0.9549
	Vertebrate	2	0.0011	0.6511	0.5345
4	Aquatic predators	2	0.1614	0.2924	0.7508
	Aquatic primary consumers	2	0.0563	0.1913	0.8278
	Terrestrial insects	2	0.0365	0.4150	0.6657
	Zooplankton	2	0.0230	0.0535	0.9480
	Vertebrate	2	0.0019	0.2158	0.8084

3.2.2 Dry weight of prey

For the dry weight, the importance of terrestrial insects is similar to aquatic predators. Aquatic primary consumers were also the dominant prey in terms of dry weight in the brook trout diet. For the YR x TR interactions in dry weight abundance of all functional groups, no statistical difference was observed in age 3+ and age 4+ fish (Table 3).

Table 3. Result of three-way partly nested ANOVAs on log X+1 transformed dry weight abundance data testing the effect of treatment and sampling year interactions (YR x TR) on the abundance of prey by functional groups for age 3+ and age 4+ brook trout. *Hirudinea* and vertebrates were excluded for dry weight analysis.

Age class	Variable	df	MS	F	p = level
3	Aquatic predators	2	0.1986	0.6045	0.5578
	Aquatic primary consumers	2	0.3704	0.3721	0.6954
	Terrestrial insects	2	0.1806	0.0531	0.9485
	Zooplankton	2	0.0628	0.4377	0.6541
4	Aquatic predators	2	0.0103	0.0251	0.9753
	Aquatic primary consumers	2	0.0513	0.1240	0.8841
	Terrestrial insects	2	0.6054	1.0274	0.3764
	Zooplankton	2	0.0072	0.2161	0.8081

3.2.3 Diversity indices

Diversity indices of prey in brook trout diet did not vary significantly between sampling years in perturbed and unperturbed lakes. There was no significant difference in the YR x TR interactions for total abundance (N), richness (S), evenness (J'), and diversity index (H') of age 3+ and age 4+ brook trout (Figure 5 and 6).

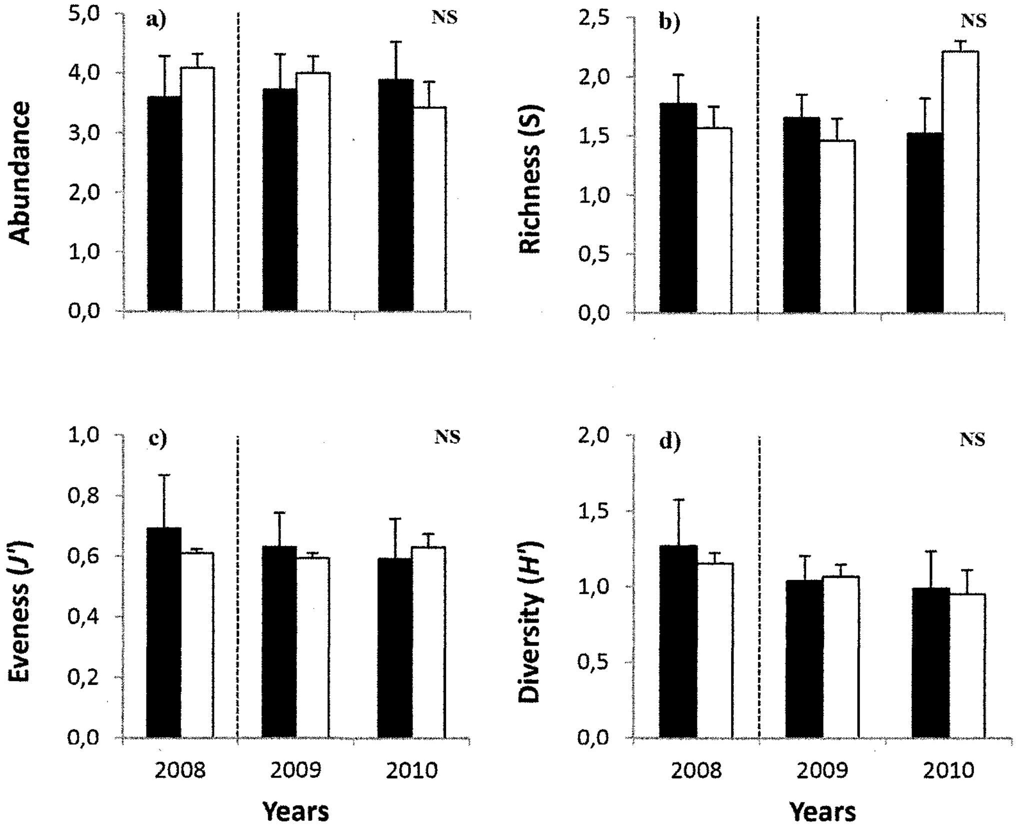

Figure 5. a) Log X+1 transformed abundances, b) richness (S), c) Pielou's evenness (*J'*) and d) Shannon's diversity index (*H'*) of prey in diet of age 3+ brook trout in unperturbed (black bars) and perturbed (white bars) lakes for the three sampling dates (2008 to 2010). Vertical and dashed lines represent standard errors of mean lake values and forest harvesting, respectively.

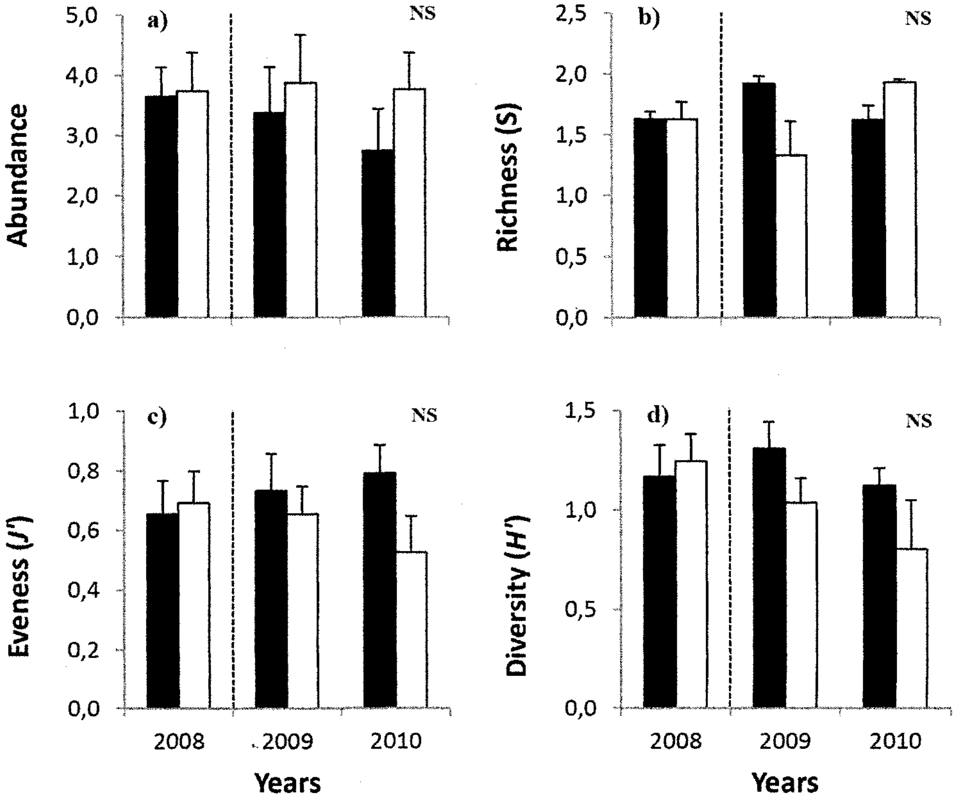

Figure 6. a) Log X+1 transformed abundances, b) richness (S), c) Pielou's evenness (*J'*) and d) Shannon's diversity index (*H'*) of prey in diet of age 4+ brook trout in unperturbed (black bars) and perturbed (white bars) lakes for the three sampling dates (2008 to 2010). Vertical and dashed lines represent standard errors of mean lake values and forest harvesting, respectively.

3.2.4 Prey assemblage

For each lake, ingested species assemblages were relatively similar between each sampling year for both age classes (Figure 7). The PERMANOVA indicated that species assemblages of ingested prey did not vary significantly (YR x TR) for both 3+ and 4+ brook trout (Table 4).

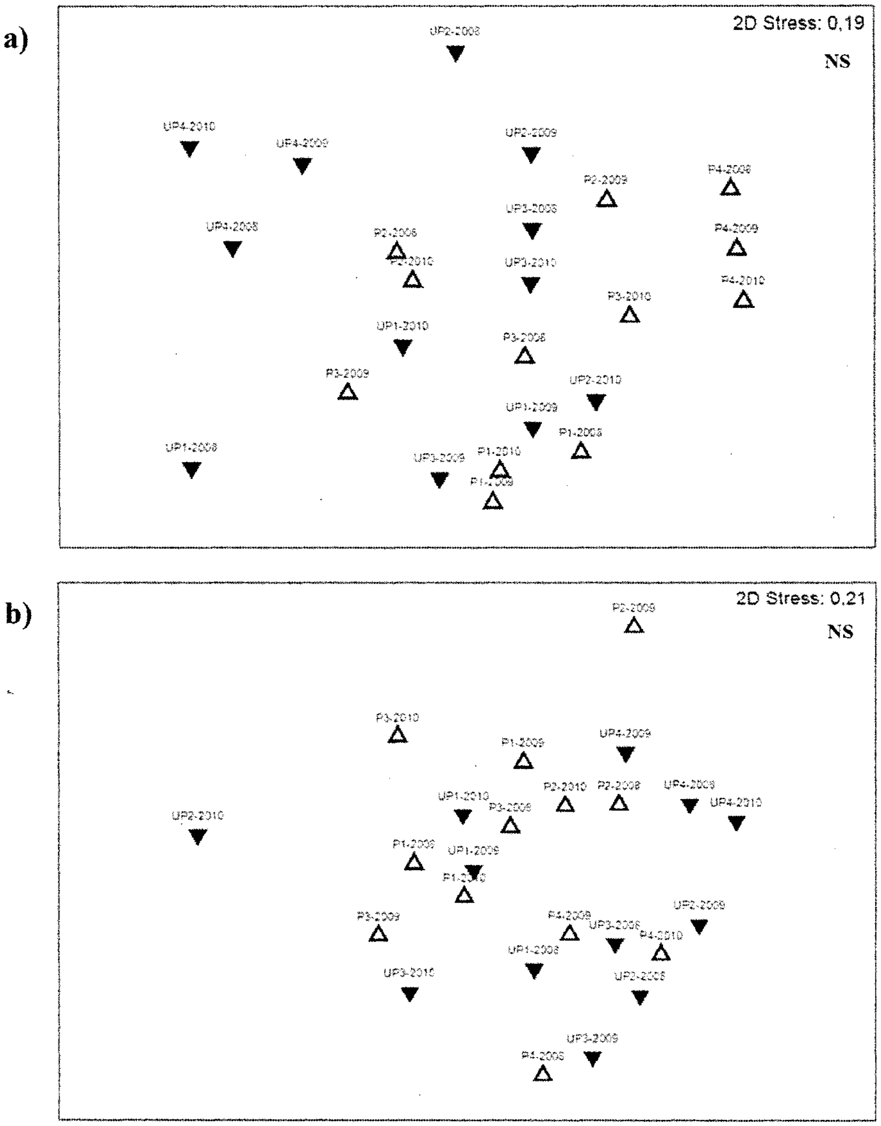

Figure 7. Nonmetric multidimensional scaling results, illustrating variations in prey assemblages (square root transformed data) ingested by a) age 3+ and b) age 4+ brook trout from unperturbed (black triangles) and perturbed (white triangles) lakes. Results of the corresponding permutational multivariate ANOVAs are given in Table 4.

Table 4. Results of the nonparametric multivariate analyses of variance (PERMANOVA) testing the effect of lake treatment, lakes nested within treatment, sampling year, and their interactions on the assemblages of ingested prey taxa. The species assemblages were calculated on fourth-root transformed data. Taxonomic resolution as described in Appendix 1 and 2.

Age class	Source of variation	df	MS	Pseudo-F	$P_{(\text{monte Carlo})}$
3+	YR	2	6070.3	1.1474	0.1650
	TR	1	31797	1.1388	0.1982
	LA(TR)	6	27922	11.099	***0.0002***
	YR x TR	2	4663.9	0.8815	0.5012
	YR x LA(TR)	12	5290.6	2.103	***0.0002***
	Residuals	239	2515.7		
	Total	262			
4+	YR	2	3169.6	0.7634	0.6986
	TR	1	9273.5	0.7697	0.5988
	LA(TR)	6	12048	5.085	***0.0002***
	YR x TR	2	2482.8	0.5980	0.8882
	YR x LA(TR)	12	4152	1.7524	***0.0002***
	Residuals	86	2369.4		
	Total	109			

3.3 Growth

The growth rate of brook trout aged 3+ was not significantly different between lake treatments and years (Figure 8a; YR x TR: $F_{2,18} = 1.07$, $p = 0.3679$). In 2008 and 2009 the growth rate seems to be higher but not significant in perturbed lakes (14.24 mm and 11.47 mm in unperturbed lakes *vs* 15.46 mm and 13.41 mm in perturbed lakes, respectively). However, in 2010 fish from unperturbed lakes have grown faster than in perturbed lakes, but this difference was not significant (YR x TR: $F_{2,18} = 3.9418$, $p = 0.0669$). Similarly, there was no significant difference in growth rate for age 4+ brook trout (Figure 8b; YR x TR: $F_{2,18} = 0.50$, $p = 0.6146$). Last year growth correspond to the marginal otolith increment information.

In 2010, brook trout aged 3+ and 4+ have the same growth trajectory in perturbed and unperturbed lakes (Figure 9a; YR x TR: $F_{2,18} = 0.04$, $p = 0.9595$ and Figure 9b; YR x TR: $F_{3,24} = 0.08$, $p = 0.9718$, respectively). The mean length at capture for fish in unperturbed lakes was 191.85 mm and 182.47 mm in perturbed lakes at age 3+ for mean length at the capture (Figure 9a). The mean length at capture for age 4+ adult trout, in unperturbed lakes was 223.13 mm and 233.26 for fish in perturbed lakes (Figure 9b).

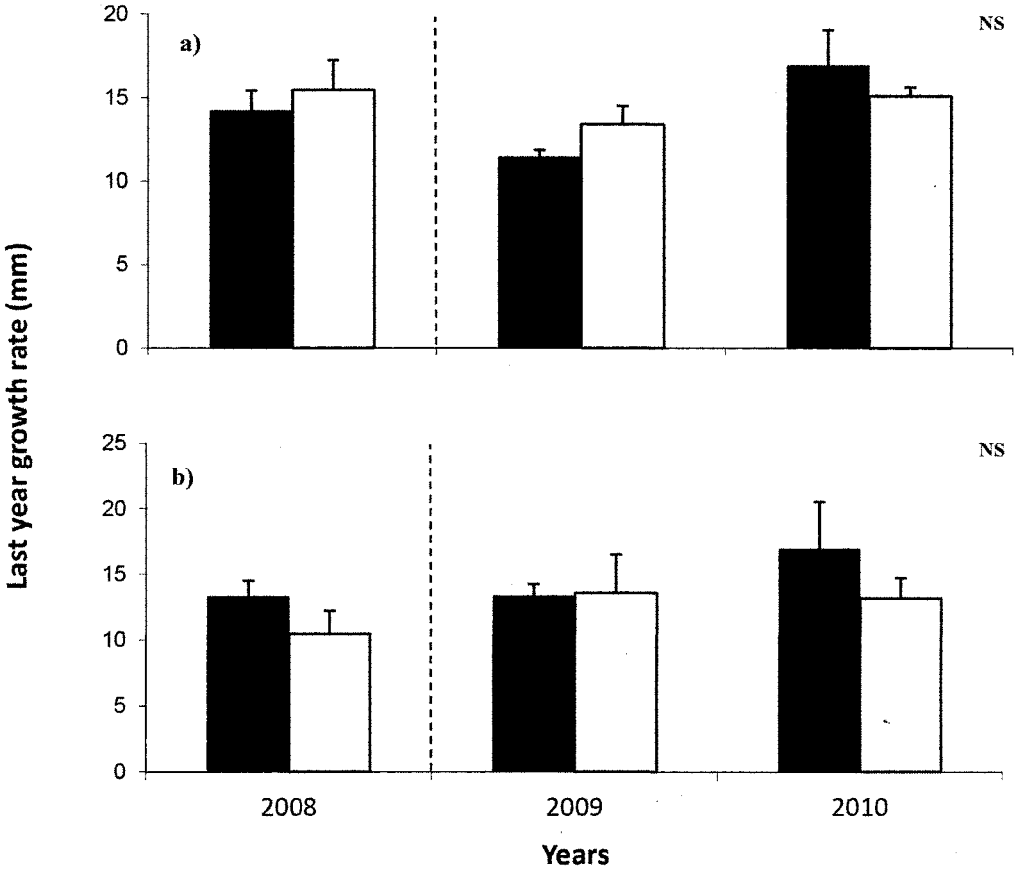

Figure 8. Comparison between years and lake treatments (unperturbed (black bars), perturbed (white bars)) for the mean back-calculated last year growth rate of a) age 3+, and b) age 4+ brook trout caught for all sampling dates (2008, 2009 and 2010). Vertical and dashed lines represent standard errors of mean lake values and forest harvesting, respectively.

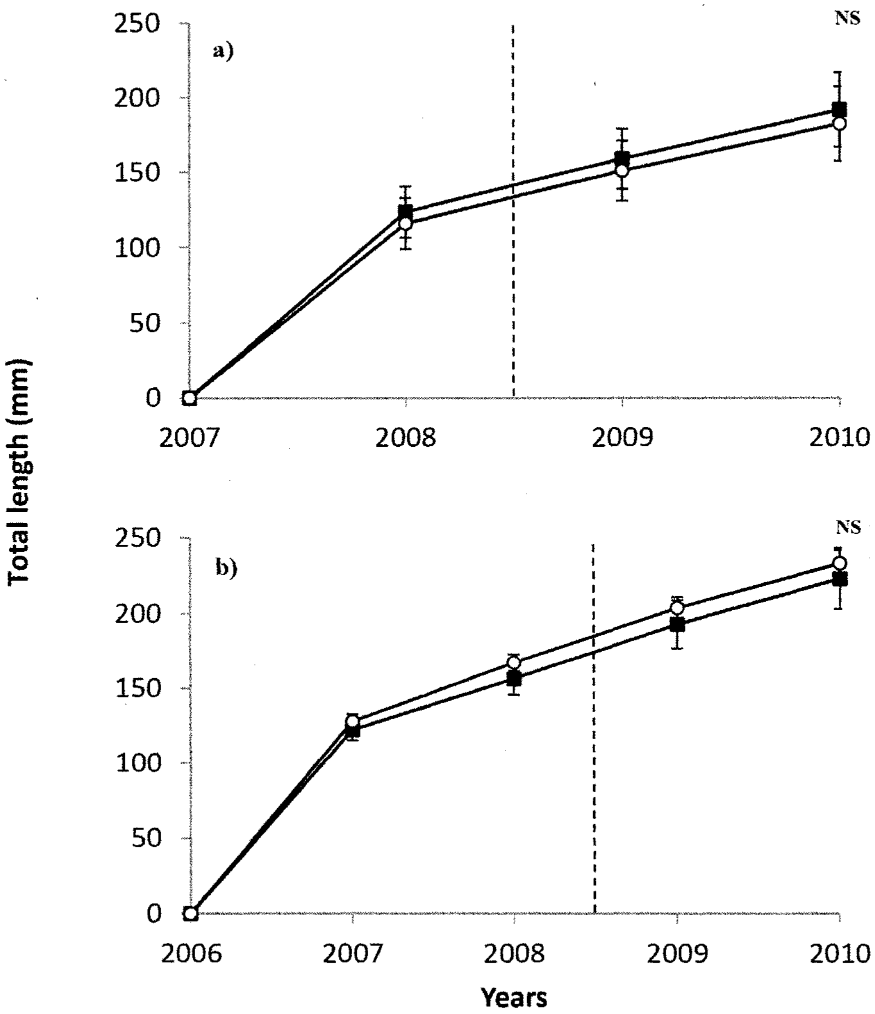

Figure 9. Comparison between years and lake treatments (unperturbed (black squares), perturbed (white circles)) for the mean back-calculated lengths-at-age growth rate of a) age 3+, and b) age 4+ brook trout caught in 2010. Vertical and dashed lines represent standard errors of mean lakes values and forest harvesting, respectively.

4. DISCUSSION

The principal objective of this study was to determine the short-term impact of logging on the feeding and growth of brook trout in oligotrophic lakes of the Canadian Boreal Shield. Brook trout diet composition was not affected by forest harvesting in this study. They were feeding mainly on zoobenthic species in perturbed and unperturbed lakes for each sampling date, despite an increase in P and DOC, year after logging (Glaz et al. 2014). No bottom-up or top-down effects were detected. Our results did not support those of Tremblay-Rivard (2007) and with the hypothesis of improved visibility of zooplankton prey in turbid water (De Robertis et al. 2003, Leclerc et al. 2011b). Our study also showed no significant difference in growth of brook trout in perturbed lakes, one and two years after forest harvesting.

4.1 Diet composition

Our results showed no significant differences in the diet between perturbed and unperturbed lakes. In fact, fish aged 3+ and 4+ were feeding mainly on aquatic primary consumers in both perturbed and unperturbed lakes for each sampling date. These results differ from Tremblay-Rivard (2007) who revealed a difference in the feeding of brook trout between perturbed and unperturbed lakes. In perturbed lakes, brook trout feed more on zooplankton prey than in unperturbed lakes (Tremblay-Rivard 2007). They interpreted this result to the enhanced contrast of zooplanktonic prey with their background environment in perturbed lakes since no effects of logging were detected on zooplankton and zoobenthos communities (Tremblay-Rivard 2007). Unlike our study, Tremblay-Rivard (2007) did not consider the initial state of the perturbed lakes before logging. In addition, it is difficult to compare our results with the literature since few studies have described the diet composition of brook trout in lakes and no one has used a multivariate approach to determine prey assemblages. In general, the principal factor affecting fish diet is the predator/prey interaction (Drenner et al. 1978). These interactions can be subdivided in four independent events: 1) detection, 2) attack, 3) capture and 4) ingestion. These events could be affected by biotic and abiotic factors such as physicochemical parameters or prey/predator relationships (Lacasse and Magnan 1992, Miller et al. 1992). Because of the absence of significant difference in the feeding of brook trout between perturbed and unperturbed lakes, we cannot reach a conclusion on the impact of forest harvesting on brook trout diet.

Several studies have observed an increase of COD in perturbed lakes leading to higher turbidity (Rask et al. 1998, Carignan et al. 2000, Winkler et al. 2009). Light absorption by suspended material in turbid lakes limits visibility by decreasing light penetration. This factor reduces detection of large prey, such as fish and zoobenthos, but improves the detection of smaller prey, such as zooplankton, by increasing contrast between the animal and its background. Therefore, in turbid lakes, planktivorous fish are favored by a decreased predation and increased zooplankton prey capture due to enhanced contrast (De Robertis et al. 2003). With an experimental approach similar to ours, Leclerc et al. (2011b) also showed a change in diet for larval and juvenile yellow perch in perturbed lakes. Their result was related to the availability of *Daphnia* spp. but was also probably linked to changes in the visual feeding condition following logging (Leclerc et al. 2011b).

In our study, despite an increase in TP and DOC the year after forest harvesting (Glaz et al. 2014), no change in the diet of brook trout has been detected in perturbed lakes. Our results did not allow us to support the conclusion of Tremblay-Rivard (2007) that an increased in DOC is positive for zooplankton prey detectability. However, in this study we did not test whether zooplankton and zoobenthos communities changed in perturbed lakes following logging. The variability of the diet between lakes appeared to be more important than the variability due the effect of forest harvesting.

Despite the abundance of aquatic primary consumers in the stomacs, stable isotopes indicated that the aquatic predators contributed the most to the diet of brook trout (Glaz et al. 2012). However, terrestrial insects were not considered in the study of Glaz et al. (2012).

4.2 Growth

This is the first study to test the effect of logging on growth of brook trout in lakes. No significant difference in growth was observed in perturbed lakes, one and two years after forest harvesting. The results supported the lack of effects observed in the diet of fish.

In fact, growth in fish mainly depends on temperature and feeding conditions (Jones 2002, Takahashi and Watanabe 2005).

Leclerc et al. (2011a) showed that young-of-the-year (YOY) yellow perch grew faster in perturbed lakes after forest harvesting. The change observed on growth in perturbed lakes was associated with higher feeding success. However, another study on YOY European perch did not detect any difference in growth following disturbance (Rask et al. 1998). These studies were performed on species with a different life cycle from brook trout. Yellow perch pass all life stages in lakes, while larval and juvenile brook trout are found mainly in creeks and rivers. Our study differs from Leclerc et al. (2011a) and Rask et al. (1998) because we tested the effect of logging on adult brook trout in lakes.

In conclusion, forest harvesting did not seem to have an impact on diet in mid-july and annual growth of adult brook trout in Canadian boreal shield lakes. Other studies have been performed in lakes, but on fish species with different life cycle from brook trout (e.g., yellow perch) (Rask et al. 1998, Leclerc et al. 2011a). In our study, variation between lakes seems to be more important than forestry effect on diet and growth of brook trout in lakes. The bottom-up theory still hold true, but this study showed that the higher up the trophic level, the more the effects of forest harvesting on adult brook trout in boreal forest lakes are diluted or even absent. We hypothesise that the forest harvesting strategies such as CLAAG in combination with 20 m buffer strips along streams and lakes might be an efficient protection against short-term effects on diet and growth of brook trout population and subsequently on sport fishing. In addition, few studies have reported a short-term impact on aquatic communities after logging (Patoine et al. 2000, Planas et al. 2000, Patoine et al. 2002b, a, Tremblay-Rivard 2007, Winkler et al. 2009, Leclerc et al. 2011a, Leclerc et al. 2011b). However our results do not apply to YOY brook trout in streams, where the effects have already been observed (Ringler and Hall 1975, Murphy and Milner 1997).

CONCLUSION GÉNÉRALE

Cette étude a été réalisée dans le but de déterminer les impacts à court terme des coupes forestières sur l'alimentation et la croissance de l'omble de fontaine dans les lacs oligotrophes du Bouclier boréal canadien.

Les résultats obtenus n'ont pas permis de déceler de différences significative dans l'alimentation et la croissance des ombles de fontaine entre les lacs perturbés et non perturbés, qui pourraient être associées à la coupe forestière. Suite à l'analyse des contenus stomacaux, les résultats ont montré que l'alimentation des ombles de fontaine était majoritairement constituée de consommateurs primaires (zoobenthos) peu importe le type de lac, et ce, pour chacune des années d'échantillonnages. En ce qui a trait à la diète en terme de poids/sec, encore une fois, les consommateurs primaires étaient dominants. Par ailleurs, aucune différence significative n'a été obtenue pour l'abondance des proies ingérées ou leur biomasse, et ce, pour les individus âgés de trois et quatre ans. De plus, aucun changement significatif n'a été observé sur les indices de diversités [abondance, richesse (*S*), équitabilité de Piélou (*J'*) et diversité de Shannon (*H'*)] du régime alimentaire des ombles âgés de trois et quatre ans. Des analyses multidimensionnelles ont également été réalisées sur l'assemblage des espèces de proies retrouvées dans l'estomac des ombles de fontaine et aucune différence n'a été décelée entre les lacs perturbés et non perturbés chez les poissons âgés de trois et quatre ans.

Par ailleurs, aucune différence significative n'a été observée sur la croissance durant la dernière année de tous les spécimens âgés de trois et quatre ans, capturés lors de chaque année d'échantillonnage. Les trajectoires de croissance des poissons capturés en 2010 ont aussi été mesurées et aucune différence n'a été détectée chez les poissons âgés de trois et quatre ans, capturés dans les lacs perturbés ou non perturbés, suite aux récoltes forestières. Ces résultats supportent ceux obtenus par les analyses de l'alimentation.

Les hypothèses de départ sont donc rejetées. Dans cette étude, une augmentation du COD a été observée dans les lacs perturbés, un an après la coupe forestière. Néanmoins, celle-ci s'estompe après la première année (Glaz et al. 2014). Les invertébrés benthiques sont associés au substrat et le zooplancton à la surface de l'eau. Étant donné que l'omble de fontaine est davantage retrouvé en surface où il devrait avoir une meilleure acuité visuelle dans les eaux turbides, on aurait pu s'attendre à une alimentation dirigée principalement vers le zooplancton, suivant les coupes forestières (Sweka and Hartman 2001, Tremblay-Rivard 2007, Leclerc et al. 2011b). Les organismes zooplanctoniques étant beaucoup moins efficaces sur le plan bioénergétique en comparaison aux proies zoobenthiques, on aurait dû observer une diminution de la croissance chez les ombles de fontaine suite à la récolte forestière.

Cette étude est basée sur une approche expérimentale qui tient compte de l'état initial des lacs, c'est-à-dire avant la coupe forestière et également après celle-ci (2 ans). Comparativement aux autres études largement citées dans ce travail, notre étude permet de bien comprendre les effets de la coupe forestière sur l'alimentation et la croissance de l'omble de fontaine dans les lacs du Bouclier Boréal Canadien. Elle permet également de déceler la variation entre les lacs.

Finalement, bien que les lacs perturbés de cette étude aient connu une augmentation du COD et du PT, l'année suivant la coupe forestière (Glaz et al. 2014), aucun effet de celle-ci n'a été détecté sur la diète pendant la mi-juillet ainsi que sur la croissance de l'omble de fontaine adulte. La variabilité entre chacun des lacs semble plus importante que l'effet des coupes elle-même. En lien avec la théorie des forces ascendantes, cette étude supporte l'hypothèse selon laquelle plus on monte dans le réseau trophique, plus l'effet semble être dilué. Dans le cadre de ce projet, Glaz et al., (2014) a remarqué à court terme un changement en production primaire dans les lacs après la coupe forestière. Cependant, il est clair que l'augmentation de la turbidité n'a eu aucun effet sur l'alimentation de l'omble de fontaine. Par conséquent, l'amélioration d'acuité visuelle permettant aux poissons de sélectionner davantage les proies zooplanctoniques ne s'applique pas aux ombles de fontaine adulte en lac. Les stratégies de coupes avec protection de la régénération et des sols (CPRS) ainsi que les mesures de protection actuelles comprenant la bande riveraine de 20 m semblent être adéquates afin d'éviter l'effet à court terme de la coupe forestière sur l'alimentation et la croissance de l'omble de fontaine adultes dans les lacs de la forêt boréale.

RÉFÉRENCES

Anderson, M.J., Gorley, R.N., and Clarke, K.R. 2008. Permanova+ for Primer: Guide to Software and Statistical Methods. Primer-E Ltd., Plymouth: 214 p.

Baumgartner, D., and Rothhaupt, K.O. 2003. Predictive length-dry mass regressions for freshwater invertebrates in a pre-alpine lake littoral. Int. Rev. Hydrobiol. **88**(5): 453-463.

Benke, A.C., Huryn, A.D., Smock, L.A., and Wallace, J.B. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. J. N. Am. Benthol. Soc. **18**(3): 308-343.

Bernatchez, L., and Giroux, M. 2000. Les poissons d'eau douce du Québec et leur répartition dans l'est du Canada. Éditions Broquet, Ottawa: 350 p.

Bertolo, A., and Magnan, P. 2007. Logging-induced variations in dissolved organic carbon affect yellow perch (Perca flavescens) recruitment in Canadian Shield lakes. Canadian Journal of Fisheries and Aquatic Sciences **64**(2): 181-186.

Bérubé, P., and Lévesque, F. 1998. Effects of forestry clear-cutting on numbers and sizes of brook trout, *Salvelinus fontinalis* (Mitchill), in lakes Mastigouche Wildlife Reserve, Québec, Canada. Fisheries Manag. Ecol. **5**(2): 123-137.

Borror, D.J., Triplehorn, C.A., and Johnson, N.F. 1981. Introduction to the Study of Insects. Fifth Edition, Saunders College Pub: 827 p.

Carignan, R., D'Arcy, P., and Lamontagne, S. 2000. Comparative impacts of fire and forest harvesting on water quality in Boreal Shield lakes. Canadian Journal of Fisheries and Aquatic Sciences **57**: 105-117.

Carignan, R., and Steedman, R.J. 2000. Impacts of major watershed perturbations on aquatic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences **57**: 1-4.

Clarke, C.W., and Gorley, R.N. 2001. Primer v5: User manual/tutorial. Primer-E Ltd., Plymouth: 190 p.

Clarke, K.R., and Warwick, R.M. 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. 2nd Edition. PRIMER-E, Plymouth.

Coulombe, G. 2004. Commission d'étude sur la gestion de la forêt publique québecoise. 314 p.

Culver, D.A., Boucherle, M.M., Bean, D.J., and Fletcher, J.W. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. Canadian Journal of Fisheries and Aquatic Sciences **42**(8): 1380-1390.

De Robertis, A., Ryer, C.H., Veloza, A., and Brodeur, R.D. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Canadian Journal of Fisheries and Aquatic Sciences **60**(12): 1517-1526.

Drenner, R.W., Strickler, J.R., and Obrien, W.J. 1978. Capture probability: the role of zooplankter escape in the selective feeding of planktivorous fish. J. Fish. Res. Board Can. **35**(10): 1370-1373.

Edmondson, W.T. 1959. Freshwater Biology. John Wiley & Sons, New York: 1248 p.

EnvC. 2000. Ecological assessment of the boreal shield ecozone. Indicators and Assessment Office. Cat. no. En40-600/2000F. Minister of Public Works and Government Services Canada: 71.

Francis, R. 1990. Back-calculation of fish length - A critical review. J. Fish Biol. **36**(6): 883-902.

Glaz, P., Sirois, P., Archambault, P., and Nozais, C. 2014. Impact of forest harvesting on trophic structure of eastern Canadian Boreal Shield lakes: Insights from stable isotope analyses. PLoS ONE **9**(4): e96143. doi:96110.91371/journal.pone.0096143.

Glaz, P., Sirois, P., and Nozais, C. 2012. Determination of food sources for benthic invertebrates and brook trout Salvelinus fontinalis in Canadian Boreal Shield lakes using stable isotope analysis. Aquat. Biol. **17**(2): 107-117.

Gunn, J.M., and Sein, R. 2000. Effects of forestry roads on reproductive habitat and exploitation of lake trout (Salvelinus namaycush) in three experimental lakes. Canadian Journal of Fisheries and Aquatic Sciences **57**: 97-104.

Jalal, W., Pinel-Alloul, B., and Méthot, G. 2005. Mid-term study of the ecological impacts of forest fires and timber harvesting on zooplankton communities in lakes of the boreal ecozone. Rev. Sci. Eau **18**(Spec. iss): 221-248.

Johnston, T.A., and Cunjak, R.A. 1999. Dry mass-length relationships for benthic insects: a review with new data from Catamaran Brook, New Brunswick, Canada. Freshw. Biol. **41**(4): 653-674.

Jones, C.M. 2002. Age and growth. In: Fuiman L.A. & Werner R.G. (eds). *Fishery science: The Unique Contributions of Early Life Stages*, Blackwell Science, Syracuse, New York: pp. 33-63.

Lacasse, S., and Magnan, P. 1992. Biotic and abiotic determinants of the diet of brook trout, *Salvelinus fontinalis*, in lakes of the Laurentian Shield. Canadian Journal of Fisheries and Aquatic Sciences **49**(5): 1001-1009

Lawrence, S.G., Malley, D.F., Findlay, W.J., Maclver, M.A., and Delbaere, I.L. 1987. Method for estimating dry weight of freshwater planktonic crustaceans from measures of length and shape. Can. J. Fish. Aquat. Sci. **44**(Suppl. 1): 264-274.

Leclerc, V., Sirois, P., and Berube, P. 2011a. Impact of forest harvesting on larval and juvenile growth of yellow perch (Perca flavescens) in boreal lakes. Boreal Environ. Res. **16**(5): 417-429.

Leclerc, V., Sirois, P., Planas, D., and Berube, P. 2011b. Diet and feeding success of fast-growing yellow perch larvae and juveniles in perturbed boreal lakes. Trans. Am. Fish. Soc. **140**(5): 1193-1205.

Magnan, P. 1988. Interactions between brook charr, Salvelinus-fontinalis, and nonsalmonid species - ecological shift, morphological shift, and their impact on zooplankton communities. Canadian Journal of Fisheries and Aquatic Sciences **45**(6): 999-1009.

Malley, D.F., Lawrence, S.G., Maclver, M.A., and Findlay, W.J. 1989. Range of variation in estimates of dry weight for planktonic crustacea and rotifera from temperate North American lakes. Can. Tech. Rep. Fish. Aquat. Sci. 1666: iv + 49 p.

Martin, C.W., and Hornbeck, J.W. 2000. Impacts of intensive harvesting on hydrology and nutrient dynamics of northern hardwood forests. Canadian Journal of Fisheries and Aquatic Sciences **57**: 19-29.

McCafferty, W.P. 1981. Aquatic Entomology: The Fishermen's and Ecologist's Illustrated Guide to Insects and their Relatives. First Edition, Science Books International: 448 p.

Merritt, R.W., and Cummins, K.W. 1995. An Introduction to the Aquatic Insects of north America. Third Edition, Kendall Hunt Publishing company, Dubuque, Iowa: 862 p.

Meyer, E. 1989. The relationship between body length parameters and dry mass in running water invertebrates. Arch. Hydrobiol. **117**(2): 191-203.

Miller, T.J., Crowder, L.B., Rice, J.A., and Binkowski, F.P. 1992. Body size and the ontogeny of the functionnal response in fishes. Canadian Journal of Fisheries and Aquatic Sciences **49**(4): 805-812.

MPO. 2010. Enquête sur la pêche récréative au Canada, Pêche et Océans Canada.

MRNF. 2008. La forêt, pour construire le Québec de demain. Document synthèse. Ressources Naturelles et Faune, Québec: 16 p.

Murphy, M.L., and Milner, A.M. 1997. Alaska timber harvest and fish habitat. In: *Freshwater of Alaska*, (eds) A.M. Milner, M.W. Oswood, Ecological Studies **119**: 229-263.

Nicholls, K.H., Steedman, R.J., and Carney, E.C. 2003. Changes in phytoplankton communities following logging in the drainage basins of three boreal forest lakes in northwestern Ontario (Canada), 1991-2000. Canadian Journal of Fisheries and Aquatic Sciences **60**(1): 43-54.

Northcote, T.G., and Hartman, G.F. 2004. Fishes and Forestry. Worldwide Watershed Interactions and Management. Blackwell Science Ltd: 789 p.

Panfili, J., De Pontual, H., Troadec, H., and Wright, P.J. 2002. Manuel de Sclérochronologie des Poissons. Coédition Ifremer-IRD: 464 p.

Patoine, A., Pinel-Alloul, B., and Prepas, E.E. 2002a. Effects of catchment perturbations by logging and wildfires on zooplankton species richness and composition in Boreal Shield lakes. Freshw. Biol. **47**(10): 1996-2014.

Patoine, A., Pinel-Alloul, B., and Prepas, E.E. 2002b. Influence of catchment deforestation by logging and natural forest fires on crustacean community size structure in lakes of the Eastern Boreal Canadian forest. J. Plankton Res. **24**(6): 601-616.

Patoine, A., Pinel-Alloul, B., Prepas, E.E., and Carignan, R. 2000. Do logging and forest fires influence zooplankton biomass in Canadian Boreal Shield lakes? Canadian Journal of Fisheries and Aquatic Sciences **57**: 155-164.

Pennak, R.W. 1978. Freshwater Invertebrates of the United States. Second Edition, John Wiley and Sons Inc. New York: 656 p.

Perkarsky, B.L., Fraissinet, P.R., Penton, M.A., and Conklin Jr., D.J. 1990. Freshwater Macroinvertebrates of Northeastern North America. Constock Publishing Associates, Ithaca: 442 p.

Pinel-Alloul, B., Patoine, A., Carignan, R., and Prepas, E. 1998. Responses of lake zooplankton to natural fire and forest harvesting in the boreal ecozone in Quebec: preliminary study. Ann. Limnol.-Int. J. Limnol. **34**(4): 401-412.

Pinel-Alloul, B., Planas, D., Carignan, R., and Magnan, P. 2002. Synthèse des impacts écologiques des feux et des coupes forestières sur les lacs de l'écozone boréale au Québec. Rev. Sci. Eau **15**: 371-395.

Planas, D., Desrosiers, M., Groulx, S.R., Paquet, S., and Carignan, R. 2000. Pelagic and benthic algal responses in eastern Canadian Boreal Shield lakes following harvesting and wildfires. Canadian Journal of Fisheries and Aquatic Sciences **57**: 136-145.

Prepas, E.E., Pinel-Alloul, B., Planas, D., Mtthot, G., Paquet, S., and Reedyk, S. 2001. Forest harvest impacts on water quality and aquatic biota on the Boreal Plain: introduction to the TROLS lake program. Canadian Journal of Fisheries and Aquatic Sciences **58**(2): 421-436.

Rask, M., Kari, N., Markkanen, S.-L., and Ojala, A. 1998. Forestry in catchments: Effects on water quality, plankton, zoobenthos and fish in small lakes. Boreal Environ. Res. **3**: 75-86.

Ricker, K.E. 1932. Studies of speckled trout (*Salvelinus fontinalis*) in Ontario. Univ. Toronto Stud. Biol. Ser. 36, Publ. Ont. Fish. Res. Lab.(44): 67-110.

Ringler, N.H., and Hall, J.D. 1975. Effects of logging on water temperature and dissolved oxygen in spawning beds. Trans. Am. Fish. Soc. **104**: 111-121.

Roberge, J. 1996. Impacts de l'exploitation forestière sur le milieu hydrique. Ministère de l'Environnement et de la Faune du Québec. Direction des écosystèmes aquatiques: 68 p. et annexes.

Sage, R.D. 1982. Wet and dry-weight estimates of insects and spiders based on length. Am. Midl. Nat. **108**(2): 407-411.

Sample, B.E., Cooper, R.J., Greer, R.D., and Whitmore, R.C. 1993. Estimation of insect biomass by length and width. Am. Midl. Nat. **129**(2): 234-240.

Scott, W.B., and Crossman, E.J. 1974. Poisson d'eau douce du Canada. Bulletin n°184. Office des recherches sur les pêcheries du Canada. Environnement Canada. Service des pêches et des sciences de la mer. Ottawa, Ontario. Canada: 966 p.

Scrimgeour, G.L., Tonn, W.M., Paszkowski, C.A., and Aku, P.K.M. 2000. Evaluating the effects of forest harvesting on littoral benthic communities within a natural disturbance-based management model. Forest Ecology and Management **126**: 77-86.

St-Onge, I., Bérubé, P., and Magnan, P. 2001. Effets des perturbations naturelles et anthropiques sur les milieux aquatiques et les communautés de poissons de la forêt boréale. Le Naturaliste Canadien **125**: 81-95.

St-Onge, I., and Magnan, P. 2000. Impact of logging and natural fires on fish communities of Laurentian Shield lakes. Canadian Journal of Fisheries and Aquatic Sciences **57**: 165-174.

Steedman, R.J. 2000. Effects of experimental clearcut logging on water quality in three small boreal forest lake trout (Salvelinus namaycush) lakes. Canadian Journal of Fisheries and Aquatic Sciences **57**: 92-96.

Steedman, R.J., and Kushneriuk, R.S. 2000. Effects of experimental clearcut logging on thermal stratification, dissolved oxygen, and lake trout (Salvelinus namaycush) habitat volume in three small boreal forest lakes. Canadian Journal of Fisheries and Aquatic Sciences **57**: 82-91.

Steedman, R.J., Kushneriuk, R.S., and France, R.L. 2001. Initial effects of catchment deforestation around small boreal forest lakes in northwestern Ontario, Canada(1). *In* In International Association of Theoretical and Applied Limnology, Vol 27, Pt 2, Proceedings. *Edited by* W.D.e. Williams. E Schweizerbart'sche Verlagsbuchhandlung, Stuttgart. pp. 1101-1107.

Steedman, R.J., Tonn, W.M., Paszkowski, C.A., and Scrimgeour, C.M. 2004. Forestry and fish in the boreal region of Canada. In: Northcote, T.G. and Hartman, G.F. (eds), *Fishes and Forestry - Worldwide Watershed Interactions and Management*, Blackwell Science, Oxford: p. 413-438.

Sweka, J.A., and Hartman, K.J. 2001. Influence of turbidity on brook trout reactive distance and foraging success. Trans. Am. Fish. Soc. **130**(1): 138-146.

Takahashi, M., and Watanabe, Y. 2005. Effects of temperature and food availability on growth rate during late larval stage of Japanese anchovy (Engraulis japonicus) in the Kuroshio-Oyashio transition region. Fish Oceanogr. **14**(3): 223-235.

Tonn, W.M., Paszkowski, C.A., Scrimgeour, G.J., Aku, P.K.M., Lange, M., Prepas, E.E., and Westcott, K. 2003. Effects of forest harvesting and fire on fish assemblages in Boreal Plains lakes: A reference condition approach. Trans. Am. Fish. Soc. **132**(3): 514-523.

Tremblay-Rivard, I. 2007. Impacts des coupes forestières sur l'alimentation de l'omble de fontaine (*Salvelinus fontinalis*) et de la structure trophique de lacs en forêts boréale. Université du Québec à Chicoutimi: 53 p.

Tremblay, S., ând Magnan, P. 1991. Interactions between two distantly related species, brook trout (Salvelinus-fontinalis) and white sucker (Catostomus-commersoni). Canadian Journal of Fisheries and Aquatic Sciences **48**(5): 857-867.

Wallace, J.B., and Gurtz, M.E. 1986. Response of baetis mayflies (Ephemeroptera) to catchment logging. Am. Midl. Nat. **115**(1): 25-41.

Wiggins, G.B. 1977. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto press, Toronto: 401 p.

Winkler, G., Leclerc, V., Sirois, P., Archambault, P., and Berube, P. 2009. Short-term impact of forest harvesting on water quality and zooplankton communities in oligotrophic headwater lakes of the eastern Canadian Boreal Shield. Boreal Environ. Res. **14**(2): 323-337.

Appendix 1: Mean percentage by number and by dry weight of taxa found in age 3+ brook trout stomachs in four unperturbed and four perturbed lakes. Stomachs with *Hirudinea* and vertebrate were excluded for mean percentage by dry weight.

				2008				2009				2010			
				Perturbed		Unperturbed		Perturbed		Unperturbed		Perturbed		Unperturbed	
Phylum /Sub-Phylum	Class	Order /Sub-Order	Family /Sub-Family	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight
AQUATIC PREDATORS															
Annelida															
	Hirudinea[1]			0.185		1.174								0.107	
Arthropoda															
	Arachnida														
		Acariforme		1.669	1.474	0.266	0.044	2.728	1.163	1.388	0.217	2.026	0.433	1.876	0.439
	Insecta														
		Coleoptera													
			Gyrinidae	0.046	0.012	0.091	0.007					0.014	0.003		
			Dytiscidae	0.099	0.001	0.188	0.037	0.073	0.004	1.228	0.317			5.295	1.008
			Hydrophilidae									0.116	0.019		
			Other coleoptera									0.054	0.006		
		Diptera													
			Ceratopogonidae	0.110	0.031	0.068	0.009	0.194	0.017	0.122	0.045	0.014	0.003	0.190	0.005
			Chaoboridae	17.946	14.461	11.256	5.970	17.430	9.390	10.299	1.273	16.311	13.488	5.492	0.808
			Chironomidae	13.885	7.403	6.397	0.981	6.962	2.435	6.739	3.980	10.587	7.051	8.369	6.871
			Other diptera	13.512	5.859	9.785	1.655	15.919	9.997	9.750	3.459	5.901	2.728	4.623	2.488
		Megaloptera	Sialidae	0.073	0.073			0.242	0.126	0.163	0.246	0.069	0.058	0.009	0.161
		Odonata													
		/Anisoptera													
			Libellulidae/Corduliidae	1.287	3.839	2.402	3.213	1.228	1.568	5.866	6.975	2.595	3.726	2.136	2.304
			Aeshnidae	0.064	0.100	0.328	0.211	0.217	0.452	0.262	0.639	0.659	0.297	0.393	0.752
			Other anisoptera	0.090	0.384	0.087	0.000	0.076	0.075	1.226	1.348			0.300	0.389
		/Zygoptera													
			Coenagrionidae	0.341	1.403	0.090	0.481	0.212	0.178	0.364	0.853	0.329	0.566	0.496	1.611
			Lestidae			0.068	0.211	0.030	0.058						
			Other zygoptera											0.064	0.014
		/Other Odonata						0.148	0.080	0.208	0.136				
AQUATIC PRIMARY CONSUMERS															
Mollusca															
	Pelecypoda			1.580	0.171	0.078	0.000	1.705	0.089	0.342	0.014	0.382	0.013		
Arthropoda	Entomobryomorpha	Collembola		0.046	0.000			0.086	0.093						
	Insecta														
		Ephemeroptera													
			Siphlonuridae	1.436	1.737	0.370	0.460	1.065	3.491	0.188	0.245	1.276	1.850	0.222	0.450
			Ephemeridae	1.146	1.906	4.955	16.221	7.643	14.816	7.493	18.024	6.110	10.339	5.480	16.043
			Ephemerellidae	0.706	1.192			0.097	0.151			1.081	1.089		
			Other ephemeroptera	14.878	25.392	6.899	20.318	16.790	28.879	6.975	13.609	21.973	31.444	5.272	9.058
		Trichoptera													
			Limnephilidae					0.073	0.273			0.670	1.593	0.163	1.554
			Molannidae							0.003	0.017	0.182	0.042		
			Phryganeidae			3.969	3.984	0.643	1.112	0.868	1.447	0.003	0.079	0.044	1.602
			Polycentropodidae	0.397	0.192	0.347	0.175	0.249	0.216	1.633	0.47	0.370	0.147	1.236	0.965
			Leptoceridae			0.833	0.544			0.298	0.042				
			Hydropsychidae					0.021	0.009						
			Other trichoptera	0.481	0.903	1.167	1.129	0.216	0.125	0.806	0.962	0.80	0.515	3.635	2.566
		Hemiptera													
			Corixidae (larval)	0.275	0.168	9.796	4.493	0.298	0.032	10.4	6.091	0.071	0.016	18.604	12.361
			Corixidae (adult)	0.054	0.071	2.240	6.035	0.130	0.320	3.581	12.392			1.829	7.997
		Lepidoptera													
			Crambidae							0.034	0.266				
			Other lepidoptera			0.057	0.206					0.324	0.824		
TERRESTRIAL INSECTS															
	Insecta														
		Coleoptera													
			Scolytidae	0.378	0.705	0.946	1.295	0.054	0.040	0.191	0.666	0.084	0.110		
			Dytiscidae	0.027	0.015			0.021	0.028					0.421	1.123
			Tenebrionidae											0.053	0.107

Phylum /Sub-Phylum	Class	Order /Sub-Order	Family /Sub-Family	2008				2009				2010			
				Perturbed		Unperturbed		Perturbed		Unperturbed		Perturbed		Unperturbed	
				Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight
			Staphylinidae							0.255	0.043				
			Other coleoptera	5.456	9.517	5.199	6.331	3.476	5.016	5.380	8.848	7.293	6.580	1.103	3.684
		Ephemeroptera		0.146	2.948	0.056	0.265			0.255	1.327			0.037	0.887
		Hemiptera													
			Aradidae											0.123	0.095
			Pentatomidae	0.014	0.061	0.029	0.012								
			Other hemiptera	0.273	0.233			0.269	0.524	0.110	0.255	0.280	0.383	2.011	2.964
		Homoptera													
			Cicadellidae	0.382	0.546			0.046	0.017	0.342	0.153	0.287	0.120	0.202	0.233
			Cixiidae					0.018	0.005						
			Other homoptera	0.203	0.059	0.028	0.020	0.696	1.210	0.025	0.230	0.468	0.233	0.288	0.092
		Trichoptera													
			Phryganeidae			0.056	0.008								
			Other trichoptera	1.552	1.364	1.251	3.220	0.400	0.776	0.781	1.596	1.781	1.068	5.396	7.312
		Hymenoptera													
			Tenthredinidae	0.045	0.003										
			Formicidae					0.043	0.136			0.362	0.562		
			Other hymenoptera	0.845	1.328	1.261	1.753	1.493	2.635	1.199	1.886	1.667	1.188	0.497	0.386
		Odonata /Anisoptera													
			Libellulidae	0.099	2.145			0.008	0.202			2.083	2.083		
			Other Anisoptera					0.037	0.412						
		/Zygoptera		0.283	4.440	0.086	6.925	0.14	5.147			0.852	4.582	0.109	7.040
		/Other Odonata		0.238	4.601	0.157	6.449	0.105	2.278			0.672	4.367	0.148	1.979
		Diptera		2.283	1.725	0.885	0.611	5.015	4.053	1.056	0.923	1.324	0.621	0.397	0.268
		Orthoptera		0.017	0.000										
		Psocoptera						0.078	0.109						
		Lepidoptera												0.175	1.236
		Thysanoptera		0.096	0.028										
		Araneae		0.875	2.004	0.146	0.282	0.316	1.802	1.095	2.745	0.308	0.629		
		Other Insecta		0.307	0.366			0.042	0.019	0.137	0.311	0.098	0.141	0.123	0.053
ZOOPLANKTON															
Arthropoda															
	Branchiopoda	Cladocera													
			Daphniidae	3.409	0.252	1.076	0.004	4.139	0.076	3.904	1.837	4.855	0.415	10.412	1.695
			Sididae	0.048	0.000							1.982	0.511		
			Leptodoridae	1.723	0.150			0.751	0.002	1.951	0.493			2.166	0.176
			Chydoridae	8.955	0.705	19.788	6.395	6.254	0.299	16.411	5.453	3.608	0.071	7.153	0.987
			Holopedidae	1.812	0.032			1.475	0.056	4.060	0.168			3.312	0.235
			Bosminidae	0.026	0.001					0.000	0.000	0.003	0.000	0.002	0.001
			Macrothricidae	0.088	0.001	6.125	0.045	0.199	0.000					0.037	0.000
	Maxillopoda	Copepoda						0.450	0.009			0.036	0.007	0.002	0.002
VERTEBRATE															
Chordata	Actinopterygii[1]			0.100								0.039			
Total aquatic predators				**49.307**	**35.040**	**32.201**	**12.819**	**45.458**	**25.542**	**37.616**	**19.488**	**38.676**	**28.377**	**29.349**	**16.851**
Total aquatic primary consummers				**20.998**	**31.563**	**30.633**	**53.565**	**29.016**	**49.606**	**32.623**	**53.579**	**33.242**	**47.950**	**36.485**	**52.596**
Total terrestrial insects				**13.518**	**32.086**	**10.100**	**27.171**	**12.256**	**24.409**	**10.827**	**18.982**	**17.559**	**22.668**	**11.082**	**27.458**
Total zooplankton				**16.077**	**1.140**	**26.988**	**6.444**	**13.270**	**0.443**	**26.332**	**7.951**	**10.484**	**1.004**	**23.084**	**3.095**
Total vertebrate[1]				**0.100**								**0.039**			
Mean Richness (S)				**1.018**		**1.102**		**0.951**		**1.036**		**1.156**		**1.222**	
Mean Pielou's Eveness (J')				**0.901**		**0.891**		**0.892**		**0.908**		**0.870**		**0.875**	
Mean Shannon's diversity index (H')				**0.941**		**0.910**		**0.895**		**0.890**		**0.791**		**0.897**	
Number of stomachs with one prey or more				**61**	**57**	**29**	**26**	**59**	**59**	**33**	**33**	**45**	**44**	**37**	**36**
Total number of prey				**6667**		**2319**		**6288**		**4266**		**5816**		**4804**	
Mean prey number				**109.30**		**79.97**		**106.58**		**129.27**		**129.24**		**129.84**	

[1] **Stomach with this taxa exclude for Mean % by dry weight**

Appendix 2: Mean percentage by number and by dry weight of taxa found in age 4+ brook trout stomachs in four unperturbed and four perturbed lakes. Stomachs with *Hirudinea* and vertebrate were excluded for mean percentage by dry weight.

Phylum /Sub-Phylum	Class	Order /Sub-Order	Family /Sub-Family	2008				2009				2010			
				Perturbed		Unperturbed		Perturbed		Unperturbed		Perturbed		Unperturbed	
				Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight
AQUATIC PREDATORS															
Annelida															
	Hirudinea[1]			1.389						1.246		0.025			
Arthropoda															
	Arachnida														
		Acariforme		1.359	0.692	1.488	0.099	0.325	0.179	1.624	0.071	0.308	0.152	4.167	0.300
	Insecta														
		Coleoptera													
			Gyrinidae			0.086	0.006			0.747	0.410			0.202	0.055
			Dytiscidae			0.264	0.045			0.139	0.077			4.688	0.239
		Diptera													
			Ceratopogonidae	0.087	0.032	0.049	0.006	0.016	0.006	0.122	0.000	0.062	0.002	0.065	0.021
			Chaoboridae	18.967	15.611	20.585	6.823	32.448	19.613	10.299	15.924	37.679	25.048	6.312	2.943
			Chironomidae	7.401	4.962	4.512	2.265	13.917	10.462	2.633	0.399	9.929	3.134	9.557	9.033
			Other diptera	11.574	3.470	6.670	1.195	12.674	4.840	4.307	1.004	7.159	0.872	10.482	3.394
		Megaloptera	Sialidae			0.183	0.040	0.073	0.031	0.455	0.000	0.025	0.040		
		Odonata													
		/Anisoptera													
			Libellulidae/Corduliidae	6.316	3.217	1.858	2.291	3.437	3.066	8.735	4.475	0.240	0.542	1.755	1.190
			Aeshnidae	0.636	1.130	0.136	0.371	1.161	1.875	0.313	0.046	0.154	0.024	0.101	0.534
			Other anisoptera					0.208	0.217						
		/Zygoptera													
			Coenagrionidae	0.231	0.176	1.008	3.248	0.556	0.544	0.087	1.182	0.025	0.087	0.592	0.994
			Other zygoptera									0.004	0.037		
		/Other Odonata								1.250	1.975	0.012	0.130		
AQUATIC PRIMARY CONSUMERS															
Mollusca															
	Pelecypoda			1.781	0.167	0.737	0.053			0.929	0.023				
	Malacostraca	Amphipoda	Gammaridae			0.132	0.007							0.065	0.042
	Insecta														
		Ephemeroptera													
			Siphlonuridae	0.906	1.096	0.490	0.110	4.186	24.580	0.385	0.287	0.068	0.071	0.665	0.683
			Ephemeridae	2.862	8.072	3.710	11.975	3.091	14.163	7.940	20.841	14.389	20.837	6.616	20.13
			Ephemerellidae	0.376	0.100			0.417	0.372					0.174	0.087
			Leptophlebiidae							0.139	0.303				
			Other ephemeroptera	16.942	30.027	6.283	16.899	3.371	2.782	3.034	3.315	6.649	21.067	14.261	27.448
		Trichoptera													
			Limnephilidae									0.490	1.712		
			Phryganeidae			3.333	4.657	0.368	0.481	2.727	0.366				
			Polycentropodidae			0.825	0.247	1.109	0.287	5.834	0.095	0.210	0.047	0.521	0.019
			Leptoceridae			1.583	2.042			4.432	2.832				
			Other trichoptera	0.877	0.627	1.218	0.688	0.833	0.000	2.448	2.139	0.025	0.000	4.241	5.407
		Hemiptera													
			Corixidae (larval)	0.175	0.200	9.982	5.012			1.583	1.842	0.037	0.006	15.334	6.270
			Corixidae (adult)			2.964	5.893			0.503	1.697			1.369	4.842
		Lepidoptera													
			Other lepidoptera									0.130	0.547		
TERRESTRIAL INSECTS															
	Insecta														
		Coleoptera													
			Scolytidae			0.291	0.662								
			Dytiscidae							0.026	0.175			1.786	2.017
			Other coleoptera	1.864	3.133	3.171	4.31	8.301	8.659	6.032	3.195	2.622	9.113	3.153	1.615
		Ephemeroptera		0.110	3.392							0.125	0.000		
		Hemiptera													

Phylum /Sub-Phylum	Class	Order /Sub-Order	Family /Sub-Family	2008				2009				2010			
				Perturbed		Unperturbed		Perturbed		Unperturbed		Perturbed		Unperturbed	
				Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight	Mean % by number	Mean % by weight
			Gerridae/Veliidae			0.119	0.049								
			Other hemiptera	2.083	3.479	0.390	0.675	0.175	0.732	0.556	0.042	0.920	0.083		
		Homoptera													
			Cicadellidae									0.488	0.023		
			Other homoptera	0.135	0.006	0.120	0.103								
		Trichoptera													
			Polycentropodidae							0.174	1.304	0.298	0.768		
			Other trichoptera	4.627	5.087	6.214	6.561	0.243	1.022	5.216	6.865	0.636	0.174	0.322	0.774
		Hymenoptera													
			Sphecidae					0.208	0.123						
			Formicidae	0.417	0.455							0.819	5.790		
			Other hymenoptera	0.694	0.000	0.168	0.154	0.117	0.319	1.270	0.054	0.402	0.198	0.893	0.387
		Odonata													
		/Zygoptera		0.366	9.774	0.325	14.726			2.151	23.733				
		/Other Odonata				0.156	6.584					0.309	6.033	0.120	11.139
		Diptera		0.965	0.497	1.689	0.550	1.449	2.229	1.250	0.607	0.941	0.342		
		Araneae		3.392	2.610	0.119	0.071	0.948	2.669	1.641	3.412	0.614	1.770		
		Other Insecta		1.250	1.547	0.446	0.644	0.368	0.255	0.391	0.352	0.050	0.000		
ZOOPLANKTON															
Arthropoda															
	Branchiopoda	Cladocera													
			Daphniidae	4.078	0.002	0.293	0.001							0.893	0.001
			Sididae			0.057	0.000								
			Leptodoridae	0.183	0.000	0.292	0.017			0.714	0.002	12.138	1.309	2.852	0.070
			Chydoridae	6.480	0.437	8.950	0.774	8.333	0.493	7.966	0.953	1.327	0.045	8.751	0.366
			Holopedidae			1.308	0.054								
			Bosminidae			0.018	0.000							0.065	0.000
			Macrothricidae	0.087	0.001	7.778	0.096			0.174	0.002	0.391	0.001		
VERTEBRATE															
Animalia	Mammalia	Rodentia[1]		1.389				0.833							
Chordata	Actinopterygii[1]							1.667							
Total aquatic predators				47.960	29.290	36.839	16.388	64.816	40.883	31.956	25.562	55.621	30.067	37.920	18.704
Total aquatic primary consummers				23.919	40.289	31.257	47.583	13.374	42.666	29.954	33.741	21.998	44.287	43.245	64.928
Total terrestrial insects				15.904	29.980	13.209	35.087	11.810	16.007	18.705	39.740	8.222	24.292	6.274	15.931
Total zooplankton				10.828	0.440	18.696	0.942	8.333	0.493	8.854	0.957	13.856	1.354	12.561	0.437
Total vertebrate[1]				1.389				2.500							
Mean Richness (S)				1.257		1.051		1.032		1.280		0.951		1.305	
Mean Pielou's Eveness (J')				0.906		0.903		0.885		0.929		0.873		0.955	
Mean Shannon's diversity index (H')				1.026		0.903		0.842		0.964		0.782		0.897	
Number of stomachs with one prey or more				13	12	33	33	13	12	16	14	24	22	13	13
Total number of prey				1010		1854		1204		896		3465		385	
Mean prey number by stomach				77.69		56.18		92.62		56,00		144.38		29.62	

[1] **Stomach with this taxa exclude for Mean % by dry weight**