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Impact des coupes forestières sur l'écologie des jeunes stades de vie chez la perchaude (*Perca flavescens*) : perspectives pour la survie et le recrutement des populations

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Qui cueille une fleur dérange une étoile

Francis Thomson

Résumé

Les hypothèses actuelles en science halieutique prédisent un fort recrutement des populations de poissons lorsque les conditions environnementales favorisent la croissance rapide durant les jeunes stades de vie. Les coupes forestières dans les bassins versants provoquent une augmentation de la concentration en éléments nutritifs de l'eau dans les lacs oligotrophes boréaux. Ces changements environnementaux sont susceptibles de modifier les conditions d'alimentation et de croissance des larves et des juvéniles et ultimement, ils risquent d'influencer la survie et le recrutement des populations de poissons. L'objectif de cette étude était de déterminer l'impact des coupes forestières sur l'écologie des jeunes stades de vie chez la perchaude (*Perca flavescens*) dans les lacs du bouclier boréal laurentien. Pour atteindre cet objectif, des perchaudes de l'année ont été capturées durant trois années consécutives (2003, 2004 et 2005), dans trois lacs dont le bassin versant a subi des coupes forestières après la première année d'échantillonnage et dans trois lacs non perturbés. Les caractéristiques de croissance individuelle ont été mesurées chez ces perchaudes à l'aide de l'analyse de la microstructure de l'otolithe. Les coupes forestières ont provoqué une augmentation des taux de croissance durant les stades larvaire et juvénile en 2005, qui était accompagnée d'une augmentation de la biomasse algale. Nous avons vérifié l'influence trophique des modifications environnementales en pratiquant l'analyse des contenus stomacaux des perchaudes en 2005. Ces analyses ont montré que les perchaudes à croissance rapide avaient une diète différente, basée sur les proies du genre *Daphnia*. Nous avons aussi mesuré une plus grande abondance de

Daphnia spp. et des concentrations de carbone organique dissous plus élevées dans les lacs perturbés en 2005. Les résultats suggèrent que les jeunes perchaudes ont bénéficié d'une plus grande abondance de proies qui, couplée à une meilleure détection, a mené à une croissance rapide. L'influence des conditions environnementales favorables sur la croissance rapide des perchaudes des lacs perturbés a été confirmée en écartant la possibilité que la croissance rapide ait été créée par une survie sélective à la croissance ou par un potentiel pour la croissance rapide déjà présent à l'éclosion. Les analyses de survie sélective à la croissance ont montré que la croissance rapide n'était pas toujours sélectionnée; elles ont plutôt montré que la direction de la sélection était variable d'une population à l'autre. Enfin, les implications des conditions environnementales et de la sélection pour la croissance rapide ou lente ont été discutées dans une perspective de prédiction du recrutement des populations de perchaudes. Nos résultats suggèrent que les conditions environnementales favorisant la croissance sont en grande partie responsables de la force du recrutement, mais que la direction et l'intensité de la survie sélective à la croissance peuvent en ajuster le niveau du recrutement.

Abstract

Current hypotheses in fisheries science predict a strong recruitment in fish populations, when environmental conditions favour rapid growth during early life stages. Forest harvesting in catchments cause an increase in nutrient concentrations in oligotrophic boreal lakes. These environmental changes are susceptible to modify larval and juvenile feeding conditions and growth and ultimately, they could influence survival and the recruitment in fish populations. The objective of this study was to determine the impact of forest harvesting on the ecology of early life stages of yellow perch (*Perca flavescens*) in Boreal Shield lakes. To reach this objective, young-of-the-year yellow perch were sampled throughout three years (2003, 2004 and 2005), in three lakes where forest harvesting occurred in the catchment after the first year, and in three unperturbed lakes. Individual growth characteristics were obtained using otolith microstructure analysis. Forest harvesting has caused an increase in early life growth rates in 2005, along with an increase in algal biomass. We verified the trophic influence of the environmental modifications, using stomach content analyses on 2005 yellow perch. These analyses have shown that fast-growing yellow perch had a different diet based on preys of the genus *Daphnia*. We measured a higher *Daphnia* spp. abundance and higher dissolved organic carbon concentrations in perturbed lakes in 2005. These results suggested that yellow perch larvae and juveniles have benefited from higher prey abundance that, coupled to higher prey visibility, have lead to higher growth. We have confirmed the influence of environmental conditions on fast growth of yellow perch in perturbed lakes, by rejecting the possibility that fast growth may have been caused by growth-selective survival, or by a potential for growth already present at hatching. Growth-selective survival analyses have shown that fast growth was not always selected; rather, the direction and intensity of growth-selective survival was variable between yellow perch populations. Finally, the implications of environmental conditions, selection for fast growth or selection for slow growth were discussed in the perspective of recruitment prediction. Our results suggested that environmental conditions favouring fast growth are largely responsible for the recruitment strength, but that the direction and the intensity of growth-selective survival may adjust recruitment levels.

Avant-propos

Cette thèse doctorale comporte cinq parties. Les chapitres 1 et 5 correspondent respectivement à l'introduction et la conclusion de la thèse. Les chapitres 2, 3 et 4 présentent les résultats de l'étude sous la forme d'articles scientifiques rédigés en anglais dont voici les références :

Chapitre 2 : **Leclerc, V**, Sirois, P, Bérubé P Impact of forestry activity in boreal lakes catchments on larval and juvenile growth of yellow perch (*Perca flavescens*);

Chapitre 3 : **Leclerc, V,** Sirois, P, Planas, D, Bérubé P Diet and feeding success of fast-growing yellow perch (*Perca flavescens*) larvae and juveniles in perturbed small oligotrophic boreal lakes;

Chapitre 4 : **Leclerc, V**, Sirois, P, Planas, D, Bérubé P. Discriminating the influence of environmental conditions, growth-selective survival and potential for growth at hatching on early growth in yellow perch (*Perca flavescens*) populations.

Chacun de ces chapitres sera soumis à un périodique en science aquatique. Les résultats décrits dans ces trois chapitres ont également fait l'objet de communications scientifiques lors de congrès nationaux et internationaux :

Leclerc, V, Sirois, P, Bérubé, P (2008) Impact of forest harvesting on growth of YOY yellow perch: An example of a bottom-up effect. 138th annual meeting of the American Fisheries Society, Ottawa, ON, 18-21 août, présentation orale;

Leclerc, V, Sirois, P, Bérubé, P (2008) Feeding success of YOY yellow perch in Canadian Boreal Shield lakes: abiotic and biotic impacts of forest removal in catchments. 32th Annual Larval Fish Conference, Kiel, Allemagne, 1-4 août, présentation orale;

Leclerc, V, Sirois, P, Bérubé, P (2007) Selection for growth during early life of yellow perch in small oligotrophic lakes subjected to forest harvesting in drainage basin. 31th Annual Larval Fish Conference, St.John's, TN, 9-12 juillet, présentation orale;

Leclerc, V, Sirois, P, Bérubé, P (2007) Is yellow perch larval and juvenile growth influenced by forest logging in small oligotrophic Boreal Shield lakes? 60^e Conférence canadienne sur les pêcheries, Montréal, QC, 4-6 janvier, présentation par affiche;

Leclerc, V, Sirois, P, Bérubé, P (2006) Is yellow perch larval and juvenile growth influenced by forest logging in small oligotrophic Boreal Shield lakes? 30th Annual Larval Fish Conference, Lake Placid, NY, 10-14 septembre, présentation orale;

Leclerc, V, Sirois, P, et Bérubé, P (2005) Impact of forest harvesting on young-of-the-year yellow perch (*Perca flavescens*) growth in Quebec Boreal Shield lakes. 58^e Conférence canadienne sur les pêcheries, Windsor, ON, 6-9 janvier, présentation orale.

L'étude présentée dans cette thèse s'inscrit dans un programme de recherche initié en 2002 par le Laboratoire des sciences aquatiques de l'Université du Québec à Chicoutimi (UQAC), en partenariat avec la Direction de la recherche sur la faune du ministère des Ressources naturelles et de la Faune du Québec (MRNF), aujourd'hui connue sous le nom de la Direction de l'expertise sur la faune et ses habitats. Ce programme a pour objectif de mesurer l'impact des coupes forestières sur les divers compartiments de l'écosystème lacustre en milieu boréal soit la qualité de l'eau, le phytoplancton, le zooplancton, les organismes benthiques et les poissons. L'étude qui sous-tend cette thèse de doctorat porte spécifiquement sur l'impact des coupes forestières sur l'écologie des jeunes stades de vie des poissons; elle a été amorcée dans le cadre d'une maîtrise en septembre 2002. Puisque l'étude permettait d'approfondir davantage le sujet, il m'a été possible de réaliser un passage direct de la maîtrise au doctorat en janvier 2004.

J'ai dirigé et pris part à toutes les campagnes d'échantillonnage sur le terrain, de 2003 à 2005. Les analyses de chlorophylle *a* ont été réalisées dans les laboratoires de Dolors Planas de l'Université du Québec à Montréal (UQAM). Les échantillons de zooplancton ont été traités au Laboratoire des sciences aquatiques de l'UQAC par Isabelle Poirier. J'ai procédé à toutes les analyses de la microstructure de l'otolithe, avec l'aide de Chantale Girard pour l'extraction. J'ai, avec l'aide de Julie Brassard, participé à l'identification du contenu stomacal. Enfin, j'ai réalisé l'ensemble des analyses statistiques. Mon directeur de thèse, Pascal Sirois, m'a orientée, conseillée et supervisée dans l'interprétation des résultats et la rédaction des manuscrits. Ma co-directrice, Dolors Planas, ainsi que Pierre Bérubé, partenaire scientifique au MRNF, ont aussi agit à titre de coauteurs des manuscrits. Finalement, mon directeur ainsi que Pierre Bérubé, ont mis à ma disposition les ressources financières et logistiques nécessaires à cette étude.

Ayant dirigé toutes les campagnes d'échantillonnage des projets liés à celui présenté dans cette thèse, j'ai aussi contribué à l'analyse des données en laboratoire, à l'interprétation, aux analyses statistiques et à la rédaction, à titre de coauteur, d'un article scientifique portant sur l'impact des coupes forestières sur la qualité de l'eau, le phytoplancton et le zooplancton dont voici la référence :

Winkler, G, **Leclerc, V**, Sirois, P, Archambault, P, Bérubé, 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: 323-333.

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Mes remerciements vont d'abord à mon directeur de thèse le professeur Pascal Sirois. Depuis le début, il m'a fait confiance, a su identifier mes points faibles et valoriser mes points forts grâce à toutes les opportunités de développement intellectuel qu'il m'a offertes. Ces années passées sous sa supervision ont été très enrichissantes, tant d'un point de vue professionnel que personnel. Je désire aussi remercier ma co-directrice Dolors Planas, femme de science et de cœur, pour ses conseils toujours judicieux. Je tiens à souligner l'aide de notre partenaire scientifique Pierre Bérubé, avec qui les discussions sont toujours tellement utiles. Je remercie aussi mon jury d'évaluation de thèse dont les commentaires constructifs auront fait évoluer ma pensée scientifique : Pascal Sirois et Dolors Planas à la direction, Marc Mingelbier, de la Direction de l'expertise sur la faune et ses habitats du ministère des Ressources naturelles et de la Faune (MRNF), et Jun Shoji, professeur associé à l'Université d'Hiroshima, en tant qu'examinateurs externes, et Pedro Perez-Neto, professeur-chercheur à l'UQAM, à titre de président.

J'adresse des remerciements spéciaux à toutes ces personnes qui avec moi ont vaincu la crainte des ours, les mouches, le mal des transports, les orages électriques, la pluie et les *cross-wind*. Merci à mes coéquipiers de terrain des étés 2002 à 2005 sans qui je n'aurais pu amasser toutes ces belles et précieuses données : Amélie Bérubé, Yan Bhérer, Mylène Bourque, Christian Brazeau, Marie-France Brisson, Tommy Castegan, David Cleary, Anne-Lise Fortin, Philippe Gagné, Sonya Lévesque, Annie Ménard, Audrey Sanfaçon, François Tremblay, Isabelle Tremblay Rivard, ainsi que Saint-Pierre, saint patron des pêcheurs, pour son intervention mystique en 2005. Je souligne également l'aide apportée par les travailleurs forestiers du camp Jean-Charles et le personnel d'Air Saguenay.

Toutes les données acquises sur le terrain auraient été bien inutiles sans la contribution compétente d'Isabelle Poirier pour son travail méticuleux d'identification, d'Anne-Lise Fortin pour sa logistique sans faille, de Julie Brassard pour l'identification des contenus stomacaux, de Chantale Girard pour l'extraction des otolithes, d'Annick Drouin pour l'aide en statistiques et de Dominique Robert pour ses conseils en analyse de croissance.

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Dix années d'études universitaires sous-tendent la réalisation de ce doctorat. De dures épreuves ont ponctué ce cheminement dont la perte de ma mère Rosanne, en juin 2001, et la perte de mon père Philippe, en novembre 2006. Ces épreuves m'ayant fait trébucher, mes études m'ont évitée de tomber et toutes les personnes mentionnées dans cette section m'ont aidée à me relever et à guérir mes blessures.

Je termine en remerciant ma famille : d'abord mes parents qui m'ont toujours poussée à aller plus loin, à persévérer et aujourd'hui encore, ils continuent à le faire. Enfin, je veux remercier mes sœurs Claudie et Sandra et mon frère Marc-André pour avoir séché mes pleurs, pour leur compréhension et leur support.

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CHAPITRE 1

INTRODUCTION

1.1 RECRUTEMENT DES POPULATIONS DE POISSONS

Les poissons s'ont d'une importance capitale pour l'Homme, procurant nourriture et emploi à des millions de personnes à travers le monde. L'utilisation durable et la gestion responsable des stocks de poissons doit reposer sur une connaissance détaillée et précise de leur biologie et de leur rôle au sein des écosystèmes aquatiques. Depuis la fin du 19^e siècle, les fluctuations interannuelles d'abondance des populations de poissons marins et d'eau douce sont au cœur des recherches en science halieutique. À cette époque, on attribuait ces variations d'abondance principalement à la surpêche et aux migrations des poissons vers d'autres aires de pêche (Houde 2008). Les travaux pionniers de Hjort (1914) au sein du Conseil international pour l'exploration de la mer (International council for the exploration of the sea, ICES) ont démontré que les fluctuations d'abondance n'étaient pas tant créées par les variations dans les patrons de migrations que par le succès reproductif des poissons, i.e. le renouvellement des populations par le recrutement. En science halieutique, le recrutement signifie l'ajout d'une nouvelle cohorte de jeunes individus dans une population, qui participeront éventuellement à leur tour à son renouvellement. Actuellement, beaucoup d'efforts sont déployés afin de déterminer les facteurs qui influencent le recrutement des populations de poissons dans le but ultime de prévoir la force des classes d'âge et la force du recrutement et ainsi, s'assurer d'une gestion saine et durable de la ressource (Sissenwine 1984, Cowan & Shaw 2002).

Malgré presqu'un siècle complet de recherche, les processus qui influencent le recrutement des poissons marins et d'eau douce ne sont pas encore complètement décrits (Heath 1992, Pitchford et al. 2005). On sait aujourd'hui que c'est durant les jeunes stades de vie (stades œuf, larve et juvénile) que sont déterminés les niveaux de recrutement pouvant varier considérablement d'une année à l'autre (Houde 1987, Sale 1990). Les jeunes stades de vie chez les poissons sont caractérisés par de très hauts taux de mortalité, pouvant atteindre des valeurs variables et aussi élevées que 99,99% (Sale 1990, Houde 1994). La prédation, incluant le cannibalisme, est considérée comme la principale cause de mortalité (Bailey & Houde 1989, Houde 2002).

1.2 HYPOTHÈSE CROISSANCE-MORTALITÉ

Les premières hypothèses émises pour expliquer le recrutement variable des populations de poissons proposent que les larves doivent rencontrer des conditions d'alimentation favorables pour atteindre une croissance rapide et participer au recrutement (e.g. l'hypothèse de la période critique de Hjort (1914), l'hypothèse *match-mismatch* de Cushing (1990)). Ces premières hypothèses sur le déterminisme du recrutement chez les poissons ont mené à l'émergence d'un véritable paradigme associant croissance rapide, survie et recrutement. Dans le but d'orienter les recherches sur le recrutement, Anderson (1988) a rassemblé ces concepts dans un schéma conceptuel aujourd'hui connu sous le nom d'hypothèse croissance-mortalité. Conformément à cette hypothèse, les individus à forte croissance auraient une meilleure probabilité de survie considérant que : (1) à un âge donné, ils sont moins vulnérables à la prédation que leurs conspécifiques (le concept *bigger-is-better*, Miller et al. 1988); (2) ils sont exposés moins longtemps à la pression de prédation intense qui sévit durant le stade larvaire (le concept *stage-duration*, Chambers & Leggett 1987, Houde 1987); (3) à une taille donnée, ils sont davantage doués pour les comportements anti-prédateurs que leurs conspécifiques montrant une faible croissance (le concept *growth-selective predation*, Takasuka et al. 2003). La survie durant les jeunes stades de vie chez les poissons ne serait donc pas aléatoire parmi les individus d'une cohorte donnée; elle serait plutôt sélective à la croissance, favorisant les individus affichant une croissance plus rapide.

1.3 FACTEURS ENVIRONNEMENTAUX INFLUENÇANT LA CROISSANCE DURANT LES JEUNES STADES DE VIE DES POISSONS

L'hypothèse croissance-mortalité (Anderson 1988) constitue aujourd'hui le schéma conceptuel utilisé par plusieurs études en science halieutique afin d'expliquer les variations des taux de mortalité et des niveaux de recrutement. La plupart de ces travaux se sont penchés sur les facteurs environnementaux pouvant influencer la croissance durant les stades larvaires et juvéniles. Compte tenu du vaste spectre de travaux sur ce sujet, l'introduction de cette thèse se concentre sur les facteurs environnementaux susceptibles d'agir au sein d'écosystèmes aquatiques d'eau douce, tels les lacs boréaux.

Les principaux facteurs environnementaux abiotiques et biotiques influençant la croissance durant les stades larvaires et juvéniles sont la température de l'eau et l'abondance des proies (Anderson 1988, Jones 2002, Takahashi & Watanabe 2005, Takasuka & Aoki 2006, Robert et al. 2009). La croissance tend à augmenter de façon linéaire avec la température (Dower et al. 2002, Baumann et al. 2006, Robert et al. 2009) sauf lorsque la température optimale est atteinte. Dans ce cas, on observe plutôt une relation en forme de dôme (Baumann et al. 2003, Takasuka et al. 2007b). L'abondance des proies et constitue sans contredit le principal facteur qui influence la croissance durant le stade larvaire et juvénile. De façon générale, il existe une relation positive entre l'abondance des proies, le succès d'alimentation et la croissance chez les larves et les juvéniles de poisson (Mills et al. 1989, Bunnel et al. 2003, Robert et al. 2009). Cette relation peut être linéaire ou prendre la forme d'une relation fonctionnelle de type II où la croissance augmente de façon exponentielle à un taux décroissant jusqu'à l'atteinte d'un plateau de saturation, en fonction de l'abondance des proies (Houde & Schekter 1980, Miller et al. 1992, Hoxmeier et al. 2004, Robert et al. 2009).

La plupart des études sur la croissance et la survie ont mis l'accent sur les processus actifs durant les stades de vie suivant l'éclosion, soit les stades larvaire et juvénile. Cependant, certains travaux ont démontré que les larves survivantes étaient déjà de plus grande taille à l'éclosion (Meekan & Fortier 1996, Chambers 1997, Grønkjaer & Schytte 1999, Bang et al. 2006), suggérant ainsi l'existence d'un potentiel pour la croissance rapide dès l'éclosion. Ceci signifie que la croissance rapide pourrait aussi être indépendante des facteurs environnementaux agissant durant les stades larvaires et juvéniles. La température d'incubation des œufs et la contribution maternelle comptent parmi les facteurs majeurs déterminant la taille de l'œuf et de la larve à l'éclosion (Chambers 1997, Grønkjaer & Schytte 1999).

1.4 SURVIE SÉLECTIVE À LA CROISSANCE

Selon l'hypothèse croissance-mortalité, les individus à croissance rapide durant les jeunes stades de vie auraient de meilleures probabilités de survie (Anderson 1988). Cependant, d'autres hypothèses, basées celles-là sur les prédateurs, contredisent les prédictions de l'hypothèse croissance-mortalité. En effet, l'hypothèse de l'alimentation optimale prédit plutôt que les jeunes poissons à croissance rapide seraient davantage vulnérables à la prédation puisque les prédateurs sélectionneraient les proies les plus grandes possibles, celles-ci leur apportant un meilleur bénéfice énergétique (Werner & Gilliam 1984, Gerking 1994).

Beaucoup d'études corroborent l'hypothèse voulant que les survivants soient les individus à croissance rapide au sein d'une cohorte (e.g. Post & Prankevicius 1987, Hovenkamp 1992, Meekan & Fortier 1996, Sirois & Dodson 2000b, Searcy & Sponaugle 2001, Takasuka et al. 2003, Meekan et al. 2006, Shoji & Tanaka 2006a, Tanaka et al. 2006, Robert et al. 2007). Cependant, d'autres travaux ont montré que les survivants étaient plutôt les individus à croissance lente d'une cohorte (e.g. Litvak & Leggett 1992, Pepin et al. 1992, Gleason & Bengtson 1996b, 1996a, Takasuka et al. 2004a, 2004b, Gagliano et al. 2007, Nishimura et al. 2007, Takasuka et al. 2007a, Holmes & McCormick 2009). Enfin, certaines études ont observé que la survie était indépendante de la croissance (e.g. Takasuka et al. 2004b, Urpanen et al. 2005, Takasuka et al. 2007a).

Ces résultats contradictoires soulignent la variabilité dans la croissance mesurée chez les survivants d'une cohorte. Celle-ci peut être le reflet des conditions environnementales durant les stades œuf, larve ou juvénile et/ou de la survie sélective à la croissance. Par exemple, la croissance rapide chez les survivants peut être causée par des conditions environnementales de croissance favorables et/ou par le retrait sélectif des individus à croissance lente par les prédateurs (Robert et al. 2007). Conséquemment, pour réussir à prédire la force d'une classe d'âge et la force du recrutement, il importe d'identifier les facteurs qui influencent la croissance, ainsi que les processus de sélection pour la croissance.

En définitive, le recrutement des populations de poissons est régi par la survie des jeunes stades de vie, laquelle est intimement liée aux facteurs environnementaux abiotiques et biotiques, de même qu'à la prédation qui peut se montrer sélective à la croissance. À partir de ces considérations, toute perturbation risquant de modifier les conditions environnementales de croissance durant les jeunes stades de vie des poissons est susceptible de modifier les probabilités de survie des larves et des juvéniles ainsi que le recrutement des populations.

1.5 IMPACT D'UNE PERTURBATION ENVIRONNEMENTALE SUR L'ÉCOLOGIE DES JEUNES STADES DE VIE CHEZ LES POISSONS : LES COUPES FORESTIÈRES

Depuis quelques années, les citoyens se montrent davantage préoccupés par les impacts environnementaux des activités forestières. Au Québec, cette préoccupation a favorisé la tenue en 2003-2004, d'une commission d'étude sur la gestion de la forêt publique québécoise. Dans son rapport remis au gouvernement en décembre 2004, la commission Coulombe a suggéré cinq grands virages pour améliorer la gestion des forêts dont celui de gérer la forêt comme un tout, de manière écosystémique, incluant non seulement les écosystèmes forestiers, mais aussi les écosystèmes aquatiques (Coulombe et al. 2004). Le domaine de la forêt boréale québécoise fait l'objet d'une importante exploitation industrielle des matières ligneuses. Le territoire touché ne se limite cependant pas aux arbres qui y poussent. En effet, la forêt boréale comprend des milliers plans d'eau susceptibles d'attirer les pêcheurs sportifs. Le Québec compte plus de 800 000 adeptes de la pêche sportive qui dépensent annuellement plus d'un milliard de dollars pour la pratique de cette activité sportive[1]. Par conséquent, il s'avère nécessaire de documenter les effets des coupes forestières sur les écosystèmes aquatiques dans une perspective de développement durable et de conservation des écosystèmes.

La coupe forestière constitue une perturbation majeure pour les écosystèmes terrestres et elle a des répercussions sur les écosystèmes aquatiques. La majorité des études mesurant l'impact des coupes forestières sur les écosystèmes aquatiques se sont concentrées sur les

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[1] Ministère des Ressources naturelles et de la Faune, www.faunenatureenchiffres.gouv.qc.ca, consulté le 10 août 2009

écosystèmes lotiques (St-Onge et al. 2001, Northcote & Hartman 2004). Relativement peu d'études ont porté sur l'effet des coupes forestières sur les écosystèmes lacustres et, parmi celles-ci, très peu ont étudié les poissons.

Les coupes forestières provoquent des changements environnementaux dans les écosystèmes aquatiques qui sont susceptibles de se répercuter sur les populations de poissons des lacs touchés. Le principal effet des coupes forestières sur les écosystèmes lacustres boréaux concerne l'augmentation de la concentration en éléments nutritifs dans l'eau comme l'azote total (NT), le phosphore total (PT) et l'augmentation de la concentration en carbone organique dissous (COD) (Rask et al. 1998, Carignan et al. 2000, Prepas et al. 2001, Winkler et al. 2009). Le principal facteur responsable de la hausse de l'exportation des éléments nutritifs du bassin versant vers le lac serait la diminution de l'évapotranspiration consécutive au déboisement (Lamontagne et al. 2000), causant une augmentation du niveau de la table d'eau dans le sol entraînant une augmentation du ruissellement, ce qui favorise la mise en solution des éléments nutritifs et leur lessivage vers les plans d'eau (Verry 1986, Hinton et al. 1997).

L'augmentation de la concentration des éléments nutritifs peut engendrer des changements trophiques, en accord avec la théorie écologique des forces ascendantes ou *bottom-up* (McQueen et al. 1986), qui se traduisent en l'augmentation de la biomasse des différents niveaux trophiques. Plusieurs travaux confirment l'effet trophique de l'apport en nutriments consécutif aux coupes forestières, mesurant une biomasse algale plus importante dans les lacs perturbés (Planas et al. 2000, Steedman 2000, Nicholls et al. 2003, Ghadouani et al. 2006). Cependant, l'impact sur les producteurs primaires pourrait être moins important que prédit à partir de l'apport des nutriments, notamment en raison de l'atténuation lumineuse causée par le COD. En effet, le COD est une substance humique intimement lié à la couleur de l'eau; son augmentation résulte en une eau plus foncée (Molot & Dillon 1997, Carignan et al. 2000).

Les études mesurant l'impact des coupes forestières sur le compartiment trophique comprenant le zooplancton montrent des résultats contradictoires ou divergents: certains ne rapportent aucun impact sur l'abondance, la diversité, le spectre de taille et les assemblages d'espèces (Patoine et al. 2002a, 2002b, Winkler et al. 2009); tandis que d'autres observent une diminution de la biomasse des copépodes calanoïdes (Patoine et al. 2000), une augmentation de l'abondance des crustacés (Rask et al. 1998, Rask et al. 2000) ou de la biomasse des organismes zooplanctoniques <500 µm (Bertolo & Magnan 2007). La divergence dans ces observations peut être le fruit des forces trophiques descendantes (*top-down*) des organismes planctonivores sur leurs proies ou de la complexité accrue des relations dans les niveaux trophiques supérieurs.

Les études portant sur l'impact des coupes forestières sur les poissons obtiennent des résultats tout aussi variables. Étant donné que les forces trophiques ascendantes s'atténuent avec les niveaux trophiques supérieurs (McQueen et al. 1986, DeMelo et al. 1992), les jeunes stades de vie chez les poissons sont davantage susceptibles d'être affectés par des changements dans leur environnement que les adultes (Post 1990). Malgré cela, la plupart des études ont porté sur les poissons adultes. Par exemple, Bérubé et Lévesque (1998) ont mesuré une diminution d'abondance et de biomasse dans les statistiques de pêche de l'omble de fontaine (*Salvelinus fontinalis*) des lacs touchés par les coupes forestières dans la réserve faunique Mastigouche. L'approche utilisée dans cette étude ne permet pas d'expliquer les mécanismes biologiques sous-jacents à ces résultats. Cependant, d'autres travaux indiquent que l'omble de fontaine pourrait avoir subi des impacts sur les sites de reproduction ou dans leurs conditions d'alimentation. En effet, la coloration accrue de l'eau due à un apport en COD peut modifier le comportement d'alimentation de l'omble de fontaine en lac. L'omble de fontaine dans les lacs perturbés par la coupe forestière est davantage planctonivore relativement aux ombles des lacs contrôles qui eux sont davantage benthivores (Tremblay Rivard 2007). La diminution de la biomasse observée par Bérubé et Lévesque (1998) pourrait alors être associée au changement de diète puisqu'une diète composée de zoobenthos produit de meilleurs rendements de pêche (Magnan 1988).

À notre connaissance, seulement deux études ont mesuré l'impact des coupes forestières sur les jeunes stades de vie des poissons au Québec. St-Onge et Magnan (St-Onge & Magnan 2000) ont observé une plus faible abondance des petites classes de taille chez le meunier noir (*Catostomus commersonii*) et la perchaude (*Perca flavescens*) dans les lacs dont le bassin versant a subi des coupes forestières comparativement aux lacs contrôles. Cependant, les méthodes d'échantillonnage utilisées n'étaient pas destinées à capturer les jeunes stades de vie chez ces poissons et ont pu biaiser dans les résultats. Avec une méthode d'échantillonnage appropriée, Bertolo et Magnan (2007) ont plutôt observé que l'abondance des jeunes perchaudes de l'année était supérieure après les coupes forestières. Ces auteurs posent l'hypothèse voulant que le COD soit à l'origine de cette augmentation, soit par une stimulation du réseau trophique via la boucle microbienne, soit par une plus grande survie larvaire due à une protection des rayons UV dans une eau davantage colorée. La causalité dans l'observation d'une plus grande abondance des jeunes perchaudes post-coupes est cependant abordée de façon spéculative dans cette étude. On y traite de l'effet des coupes sur l'abondance des jeunes, sans cependant y investiguer les processus pouvant influencer la survie des jeunes et le recrutement.

1.6 LA PERCHAUDE

La perchaude fait partie de la famille des Percidés, de l'ordre des Perciformes. Elle est biologiquement et écologiquement équivalente à la perche européenne, *Perca fluviatilis* (Thorpe 1977, Craig 2000). Ensemble, la perchaude et la perche ont une répartition presque circumpolaire dans les eaux douces de l'hémisphère nord (Scott & Crossman 1973). En Amérique du Nord, la perchaude est répandue du sud au nord, de la Floride et l'Alabama jusqu'à la Baie James et, d'ouest en est, de l'Alberta à la Nouvelle-Écosse.

Cette espèce fraie au printemps en milieu littoral où des rubans d'œufs semi-pélagiques sont généralement fixés sur la végétation. Les larves éclosent à une taille variant entre 4 et 8 mm (Mansueti 1964, Auer 1982, Craig 2000). Dès l'éclosion, elles migrent vers le milieu pélagique et reviennent en milieu littoral lorsqu'elles atteignent une taille d'environ 25 mm (Kelso & Ward 1977, Whiteside et al. 1985, Post & McQueen 1988). Durant leur phase pélagique, les larves se retrouvent en surface où elles s'alimentent (Cucin & Faber 1985, Post & McQueen 1988). Les larves et les juvéniles de perchaudes sont planctonivores et adoptent une alimentation composée d'une proportion de zoobenthos croissant avec l'âge (Siefert 1972, Mills & Forney 1981, Whiteside et al. 1985, Post & McQueen 1988, Graeb et al. 2006). Cette espèce démontre une exceptionnelle plasticité dans la croissance, ces variations s'expliquant par des facteurs abiotiques et biotiques tels la température et l'abondance des proies (Carlander 1997, Craig 2000). Dans sa distribution la plus septentrionale, la mortalité hivernale peut influencer les populations de perchaude, les jeunes de l'année avec la meilleure croissance étant plus aptes à survivre à cette période de faible alimentation (Post & Evans 1989).

En raison de son importance pour la pêche sportive et commerciale, la perchaude fait l'objet d'une abondante littérature. Par exemple, le déclin de la population de perchaude au lac Michigan au début des années 1990 a forcé les agences ministérielles et les institutions universitaires à faire des efforts conjoints afin de comprendre les causes de ce déclin (Clapp & Dettmers 2004). Dès lors, des recherches sur les facteurs qui influencent le recrutement ont vu le jour, notamment sur l'abondance des proies disponibles (Dettmers et al. 2003), le succès d'alimentation, la croissance et la survie (Graeb et al. 2004, Fulford et al. 2006) ainsi que sur le transport des larves (Dettmers et al. 2005).

La perchaude constitue un excellent modèle biologique pour comprendre l'effet d'une perturbation telle la coupe forestière sur la croissance et la survie des jeunes stades de vie. Tout d'abord, la perchaude est une espèce de poisson fourrage très commune dans les lacs du bouclier boréal et les jeunes stades de vie sont faciles à capturer en phases littorale et pélagique (Cucin & Faber 1985, Whiteside et al. 1985). L'espèce complète son cycle de vie essentiellement en lac et fraie en eau libre en milieu littoral, éliminant les effets des coupes forestières en milieu lotique, comme par exemple la sédimentation sur les frayères à ombles de fontaine (Argent & Flebbe 1999, Hartman & McMahon 2004, Lachance et al. 2008). La microstructure des otolithes chez la perchaude est nette, permettant des analyses de croissance. De plus, la périodicité du dépôt des accroissements et la proportionnalité entre la largeur des accroissements et la taille du poisson ont déjà été validés en laboratoire (Powles & Warlen 1988, Dale 2000, Fitzgerald et al. 2001), rendant possible l'application de méthodes de rétro-calcul pour mesurer la croissance à un âge antérieur et ce, à l'échelle de l'individu. Enfin, les larves et les juvéniles de perchaudes sont planctonivores (Mills & Forney 1981, Whiteside et al. 1985, Post & McQueen 1988) et peuvent être influencées par un changement dans la communauté zooplanctonique (Dettmers et al. 2003).

1.7 HYPOTHÈSE ET OBJECTIFS

Considérant la vulnérabilité des jeunes stades de vie des poissons aux conditions environnementales abiotiques et biotiques, l'hypothèse de recherche de cette thèse est la suivante : les coupes forestières peuvent modifier les conditions environnementales et ainsi la croissance des larves et des juvéniles de perchaude via un effet trophique ascendant sur l'alimentation et influencer la survie et le recrutement des populations.

L'objectif général de cette thèse est donc de déterminer l'impact des coupes forestières sur l'écologie des jeunes stades de vie chez la perchaude dans les lacs du bouclier boréal laurentien. Pour atteindre cet objectif, des jeunes perchaudes de l'année ont été capturées durant trois années consécutives (2003, 2004 et 2005), dans trois lacs dont le bassin versant a subi des coupes forestières après la première année d'échantillonnage (lacs perturbés) et dans trois lacs non perturbés (lacs contrôles). Alors que le chapitre premier de cette thèse place l'étude dans une problématique de recherche, les chapitres 2, 3 et 4 présentent les résultats de la thèse en répondant chacun à un objectif spécifique de celle-ci.

Le chapitre 2 vise à mesurer l'impact de la coupe forestière sur la croissance larvaire et juvénile de la perchaude. L'impact des coupes forestières sur la dynamique trophique est également examiné afin de vérifier comment une perturbation dans le bassin versant peut influencer les différents niveaux trophiques lacustres jusqu'aux jeunes poissons. La croissance de la jeune perchaude et la biomasse phyto- et zooplanctonique ont été mesurées simultanément dans les six lacs, l'année précédant les coupes forestières (2003), ainsi que les deux années suivant celles-ci (2004-2005). Les résultats démontrent que la coupe forestière favorise la croissance larvaire et juvénile chez la perchaude deux ans après la coupe forestière, probablement via un effet trophique ascendant. Ces résultats ont donné naissance aux deux autres chapitres.

Le chapitre 3 a pour objectif de vérifier l'hypothèse voulant que la croissance rapide durant les stades larvaire et juvénile des perchaudes dans les lacs perturbés en 2005 ait été causée par des conditions d'alimentation favorables. Cet objectif est d'abord étudié en décrivant et en comparant la diète des larves et des juvéniles des lacs perturbés et contrôles. Ensuite, la disponibilité des principaux taxons de proies est mesurée et comparée dans les deux types de lacs. Enfin, la relation entre les conditions environnementales, le succès d'alimentation et la croissance récente y est vérifiée.

Le chapitre 4 vise à mesurer la contribution des conditions environnementales de température et d'alimentation, de la survie sélective à la croissance et du potentiel de croissance dans la divergence des taux de croissance larvaire et juvénile mesurée chez les différentes populations de perchaudes en 2005.

1.8 PORTÉE DE L'ÉTUDE

En lien avec la problématique, cette étude offre l'opportunité de mesurer l'impact d'une activité anthropique sur les jeunes stades de vie de la perchaude dans des lacs situés dans la partie la plus septentrionale de son aire de distribution. Bien que les jeunes stades de vie de cette espèce soient bien connus, cette étude est la première à analyser, à l'aide d'un plan d'expérience approprié, l'influence d'une perturbation sur la croissance, l'alimentation et la survie durant les stades larvaire et juvénile d'un poisson d'eau douce. De plus, la réplication spatiale nécessaire dans le cadre du plan d'expérience permet la réplication des populations étudiées, ce qui constitue une approche peu commune dans l'étude de l'écologie des jeunes stades de vie des poissons tant marins que d'eau douce. Les changements environnementaux appréhendés à la suite de coupes forestières instaurent aussi un contexte favorisant l'étude de l'influence de l'environnement sur l'alimentation et la croissance des larves et des juvéniles.

À notre connaissance, cette étude est la première à documenter l'effet des coupes forestières sur la dynamique des jeunes stades de vie chez la perchaude. Compte tenu de la volonté des instances politiques d'assurer une saine gestion des ressources naturelles forestières et fauniques, cette étude des jeunes stades de vie chez la perchaude pourrait apporter des informations utiles à l'élaboration de lignes directrices pour un développement durable des ressources forestières et ichthyennes.

CHAPITRE 2

IMPACT OF FOREST HARVESTING ON LARVAL AND JUVENILE GROWTH OF YELLOW PERCH (*PERCA FLAVESCENS*) IN BOREAL LAKES

2.1 ABSTRACT

Any factor modifying early growth in fish could lead to large recruitment variations. We investigated the impact of forest harvesting on growth rate and length-at-age of larval and juvenile yellow perch (*Perca flavescens*) and on the trophodynamics in small oligotrophic Canadian Boreal Shield lakes. Yellow perch, phytoplankton, and zooplankton were sampled in August or early September in three consecutive years (2003, 2004 and 2005) in three undisturbed lakes and in three lakes that had had logging in their watersheds catchment zones after the first year of sampling. Two years after the perturbation, forest harvesting was found to cause significant increases in yellow perch growth rate and length-at-age from hatching to age 40 days; an increase in algal biomass was also recorded. Taken together, the increases in algal biomass and early yellow perch growth rates suggest a bottom-up effect on lake trophodynamics. We hypothesized that post-harvest enhancements in nutrients and dissolved organic carbon concentrations likely generated bottom-up changes in larval and juvenile yellow perch feeding conditions such as increased prey abundance and visibility, thus stimulating growth rate.

2.2 RÉSUMÉ

Tout facteur modifiant la croissance chez les jeunes stades de vie des poissons peut mener à de grandes variations des niveaux de recrutement. Nous avons examiné l'impact des coupes forestières sur le taux de croissance et la longueur-à-l'âge chez les larves et les juvéniles de perchaude (*Perca flavescens*), ainsi que sur la dynamique trophique dans des lacs oligotrophes du Bouclier boréal canadien. Les perchaudes, le phytoplancton et le zooplancton ont été échantillonnés en août ou au début septembre durant trois années consécutives (2003, 2004 et 2005) dans trois lacs non-perturbés et dans trois lacs dont le bassin versant a subi des coupes forestières après la première année d'échantillonnage. Les coupes forestières ont causé des augmentations significatives du taux de croissance et de la longueur-à-l'âge des perchaudes, de l'éclosion à 40 jours et ce, deux ans après la perturbation. Une augmentation significative de la biomasse algale a aussi été mesurée après les coupes forestières. Ensemble, ces augmentations suggèrent un effet ascendant dans la dynamique trophique des lacs. Nous soumettons l'hypothèse que l'augmentation des nutriments et du carbone organique dissous à la suite des coupes forestières a probablement généré des changements trophiques ascendants dans les conditions d'alimentation des larves et des juvéniles de perchaudes, comme l'abondance des proies et leur visibilité, stimulant le taux de croissance.

2.3 INTRODUCTION

A considerable body of evidence suggests that high mortality experienced by fishes during their early life stages is not random (Houde 2002). The leading hypotheses concerning recruitment rather propose that mortality is size- or growth-selective. According to the "growth-mortality" hypothesis (Anderson 1988), fast-growing individuals have a higher probability of survival considering that (1) they are less vulnerable to predation than smaller conspecifics at a given age (the "bigger-is-better" concept; Miller et al. 1988), (2) they spend less time in the highly vulnerable larval stage (the "stage-duration" concept; Chambers & Leggett 1987, Houde 1987), and (3) they are more likely to escape from predators at a given size (the "growth-selective predation" concept; Takasuka et al. 2003). Given the critical importance of growth during the early life stages, factors influencing growth rate could lead to significant fluctuations in survival and recruitment.

The environmental conditions experienced by fishes may vary from one freshwater system to another, and these variations could have a strong influence on larval growth (Claramunt & Wahl 2000). Environmental conditions may also change following a perturbation and could generate variations in fish feeding, growth, and survival. Forest harvesting in catchments is a major perturbation for northern Canadian Boreal Shield lakes. Several studies have documented the impact of forest harvesting on water quality and trophodynamics in Boreal Shield lakes (see Pinel-Alloul et al. 2002b). In general, forest harvesting in lake watersheds increases the concentration of nutrients such as total nitrogen (TN) and total phosphorus (TP), as well as dissolved organic carbon (DOC) in the water (Rask et al. 1998, Carignan et al. 2000, France et al. 2000, Steedman 2000, O'Driscoll et al.

2006, Winkler et al. 2009). Bottom-up forces may act at the primary producer level, as revealed by the slight enhancement of pelagic and periphytic algal biomass noted in several studies (Planas et al. 2000, Steedman 2000, Nicholls et al. 2003, Ghadouani et al. 2006). However, effects on primary producers could be smaller than expected considering the increased nutrient input because of light attenuation caused by higher DOC concentrations (Pinel-Alloul et al. 2002a). Impact studies of forest harvesting on zooplankton had shown conflicting results: some reported no impact on abundance, diversity, size spectra, or species assemblages (Patoine et al. 2002a, 2002b, Winkler et al. 2009), while others revealed a decrease in calanoid copepod biomass (Patoine et al. 2000), an increase in crustacean abundance (Rask et al. 1998), or an increase in the biomass of zooplankton <500 μm in size (Bertolo & Magnan 2007). These inconsistencies in the reported effects of forest harvesting on zooplankton could be due to top-down forces driven by zooplanktivorous organisms or an enhanced complexity of interactions with higher levels of the trophic web.

Results concerning the impact of forest harvesting on fish are also variable. Almost all studies have focused on adult fishes. However, early life stages are more likely than adults to be affected by trophic perturbations given the attenuation of bottom-up forces with higher trophic levels (McQueen et al. 1986, DeMelo et al. 1992). Only two field studies have documented the impact of forest harvesting on early life stages of fish. St-Onge and Magnan (2000) have reported a decrease in the abundance of small size classes of yellow perch (*Perca flavescens*) and white sucker (*Catostomus commersonii*) in eastern Canadian Boreal Shield lakes. However, their methods were not intended to catch young-of-the-year

(YOY) fish, possibly inducing bias in the results (Bertolo & Magnan 2007). Using gear appropriate for sampling young fish, Bertolo and Magnan (2007) showed an increase in YOY yellow perch abundance after forest harvesting in lake catchments.

Yellow perch is a common forage fish in Boreal Shield lakes, and early life stages are easy to capture in their pelagic and littoral phases (Cucin & Faber 1985, Whiteside et al. 1985). Yellow perch is an open-substrate spawner and completes its entire life cycle within the lake, so it is not affected by spawning ground siltation that typically results from forest harvesting (Hartman & McMahon 2004). Yellow perch larvae and early juveniles are zooplanktivorous (Mills & Forney 1981, Whiteside et al. 1985, Post & McQueen 1988, Graeb et al. 2004) and could be affected by a change in their prey field due to bottom-up effects related to logging in the watershed.

The principal objective of this study was to measure the impact of forest harvesting on the growth rate and length-at-age of larval and juvenile yellow perch in small oligotrophic Boreal Shield lakes. We also tried to determine if variations in growth rate and length-at-age were related to algal and zooplankton biomass. We hypothesized that early life stages of yellow perch in perturbed lakes may take advantage of a slight increase in productivity due to forest harvesting, resulting in higher growth rates than fish in unperturbed lakes.

2.4 MATERIAL AND METHODS

2.4.1 Study sites and sampling design

The lakes examined in this study were located in the Canadian Boreal Shield ecoregion in the province of Quebec, near Lake Mistassini (50°17′ to 50°41′N and 73°15′ to 72°49′W) (Fig. 2.1, Table 2.1). Lakes in this area are typically oligotrophic and shelter fish communities mainly composed of northern pike (*Esox lucius*), walleye (*Sander vitreus*), white sucker, and yellow perch (Table 2.1). This region is characterized by spruce-moss landscapes exploited by the forest industry.

Six lakes were selected and assigned to one of two different lake treatments: perturbed or unperturbed, hereafter referred to as "cut" or "control" lakes (Table 2.1). A multivariate procedure was used to evaluate the similarity of the variables most closely related to productivity between lake treatments. No significant difference was found between the two treatments for 11 variables measured at the onset of the study: shoreline development, catchment area, turnover rate, secchi depth, euphotic zone temperature and dissolved oxygen (DO), surface pH and conductivity, total nitrogen (TN), dissolved organic carbon (DOC), and chlorophyll *a* (Chl *a*) (Table 2.1, ANOSIM procedure on euclidian distances matrix: $R = 0.48$, $P = 0.10$, Clarke & Warwick 2001).

The sampling design included one survey before the perturbation (2003) and two surveys after forest harvesting (2004 and 2005). Forest harvesting occurred in autumn 2003 and/or winter 2004 (Table 2.1). Access to cut lakes in 2003 and control lakes was only possible by seaplane due to their pristine watersheds. An impact of forest harvesting on Boreal Shield lake water quality is more likely to occur when the drainage ratio of the lake

Table 2.1. Limnological parameters of the six studied lakes in 2003, before the perturbations.

	Cut lakes			Control lakes		
Lake parameters	Cut-1	Cut-3	Cut-5	Control-1	Control-3	Control-4
Morphological parameters						
Altitude (m)	492	478	497	504	513	482
Latitude N	50° 33' 48"	50° 20' 56"	50° 34' 07"	50° 41' 19"	50° 32' 19"	50° 17' 50"
Longitude W	72° 33' 30"	73° 18' 30"	72° 35' 50"	72° 33' 45"	72° 49' 44"	73° 15' 10"
Maximum depth (m)	9.8	12.6	13.4	10.9	24.0	14.5
Lake area (km^2)	0.7	0.4	1.5	1.1	0.6	0.5
Lake perimeter (km)	7.7	5.1	8.6	5.6	6.2	4.4
Fetch (km)	2.1	1.6	2.9	2.2	1.5	1.7
Shoreline development (km)	2.6	2.0	2.0	1.5	2.3	1.7
Catchment area (km^2)	4.2	3.0	7.6	3.8	2.5	1.2
Catchment perimeter (km)	12.4	9.4	17.4	11.0	8.2	6.8
Catchment mean slope (%)	6.6	8.2	11.5	5.4	5.7	6.6
Drainage ratio	5.9	7.1	5.0	3.5	4.3	2.3
Order	1	2	2	1	1	1
Lake volume (10^3 m^3)	1 835.2	1 931.6	8315.7	4 299.1	3 990.3	2 957.8
Turnover rate (N per year)	1.2	1.0	1.1	0.5	0.4	0.3
Harvested area (% of catchment area)	57.1	50.6	33.5	-	-	5.1
Time of harvest	Autumn 03	Winter 04	Autumn 03	-	-	-
Physicochemical parameters						
Secchi depth (m)[a]	1.5	1.5	2.1	2.0	3.0	3.8
Euphotic zone temperature (°C)[a]	12.8	12.2	13.4	12.9	11.9	12.7
Euphotic zone DO (mg·L^{-1})[a]	11.0	7.5	10.6	11.1	7.7	7.8
Surface pH [a]	6.9	7.4	6.7	6.7	7.7	7.4
Surface conductivity (µS·cm^{-1}) [a]	14.6	15.0	12.0	9.2	13.0	17.0
Mean TN (SD) (mg·L^{-1})[a]	242.2 (30.5)	225.9 (12.8)	207.4 (25.9)	198.2 (33.8)	182.3 (74.6)	149.3 (6.1)
Mean DOC (SD) (mg·L^{-1})[a]	9.2 (0.3)	9.4 (0.1)	7.0 (0.3)	7.2 (0.1)	5.0 (0.1)	4.4 (0.1)
Mean Chl *a* (SD) (mg·L^{-1})[a]	2.1 (0.1)	2.2 (0.2)	1.7 (0.1)	3.6 (0.3)	2.1 (0.1)	1.7 (0.1)
Biological parameters						
Yellow perch (*Perca flavescens*)	x	x	x	x	x	x
Lake chub (*Couesius plumbeus*)				x	x	
Mottled sculpin (*Cottus bairdi*)	x		x	x		
Burbot (*Lota lota*)				x	x	x
White sucker (*Catostomus commersonii*)	x	x	x	x	x	
Lake whitefish (*Coregonus clupeaformis*)		x	x			
Walleye (*Sander vitreus*)		x	x		x	
Northern pike (*Esox lucius*)	x	x	x	x	x	x

[a] Value measured in September 2003, before the perturbation (data from Winkler et al. 2009).

x Presence of the fish species.

(catchment area/lake area) exceeds 4 and when more than 30% of the catchment area is deforested (Carignan et al. 2000). Since all cut lakes had a drainage ratio >5 and at least 33% of the catchment area was deforested (Table 2.1), we anticipated an impact on water quality.

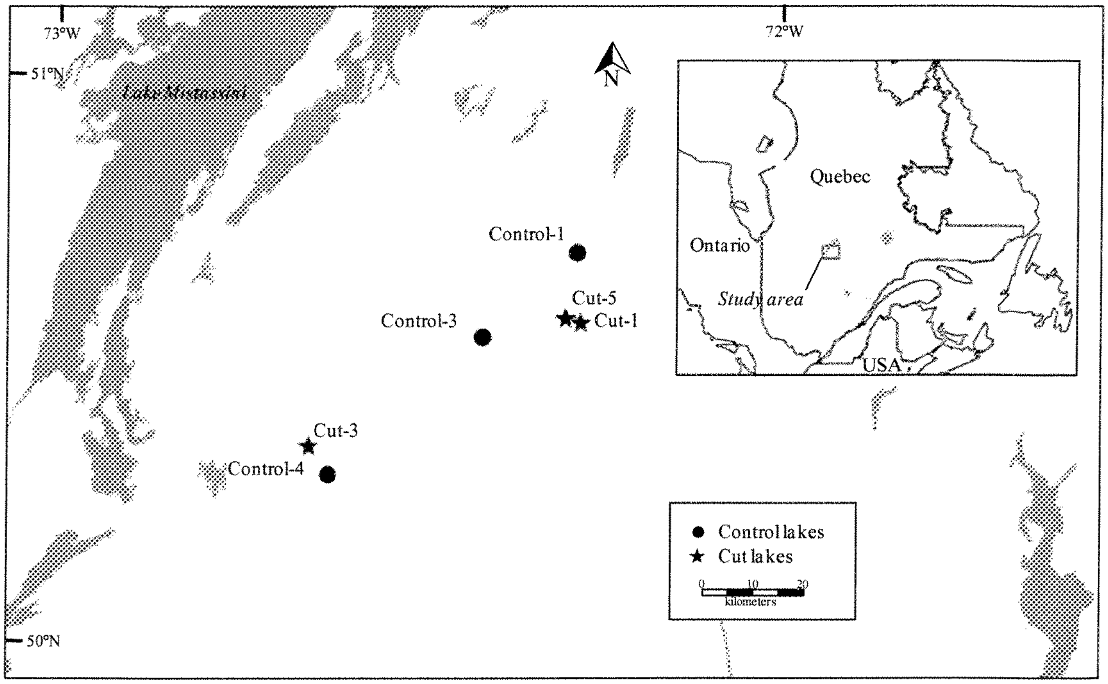

Figure 2.1. Map of the study area showing the locations of cut and control lakes.

2.4.2 Field sampling

2.4.2.1 Fish

YOY yellow perch were sampled from 12 to 28 August in 2003, 17 August to 1 September in 2004, and 1 to 4 August in 2005. YOY fish were captured with experimental monofilament gillnets 22.86 m long x 2 m deep that had three randomly placed panels with mesh sized of 9.5, 12.7, and 19.1 mm. Ten gillnets were randomly set perpendicular to the shore in each lake for one night on each sampling date. Due to the early sampling in 2005, we used an additional sampling method to target all size classes as suggested by Scharf et al. (2009): YOY fish were also caught with a beach seine (4 m long x 1 m deep, 500 μm mesh) at six sampling stations in each lake. All fish samples were preserved in 95% ethanol. Ethanol was replaced within 24 h to avoid alcohol dilution and otolith damage (Butler 1992).

2.4.2.2 Plankton

Pelagic phytoplankton was sampled on 2–9 September 2003, 8–9 September 2004, and 8 August 2005. Three independent, integrated water samples were taken at the deepest point of each lake in the euphotic zone, estimated as 1.25 times the Secchi depth for eastern Boreal Shield lakes (R. Carignan, Université de Montréal, pers. comm.).

Pelagic zooplankton was sampled during the same surveys as the phytoplankton except in 2005, when zooplankton was sampled during the fish survey (1–4 August 2005). Three vertical hauls were taken from 1 m off-bottom to the surface at the deepest point of each lake using a cantilevering zooplankton net (53 μm mesh) with a circular mouth opening of 0.25 m (Winkler et al. 2009). Zooplankton was anaesthetized with carbonated water and preserved in 4% buffered formaldehyde.

2.4.3 Laboratory procedure

2.4.3.1 Fish

All sampled fish were identified and standard length was measured. Fish captured during the 2005 gillnet and seine samplings did not differ in length range, so samples were pooled. For growth analyses, 15 young YOY perch were randomly selected from each lake and for each year in such a way that the length frequency groups were sampled in proportion to their numbers.

Individual growth characteristics were obtained from otolith microstructure analysis. We used the lapillar otoliths because accessory primordia and sub-daily increments are often observed in sagittal otoliths (Fig. 2.2). The left and right lapillar otoliths were removed under a dissecting microscope and mounted on a microscope slide with thermoplastic glue. Otoliths were polished with a 3 or 5 μm lapping film. Left otoliths were measured using an image-analysis system (SigmaScanPro 5.0) connected to a light microscope at 400 to 1000x magnification. Three measurements were taken along the longest axis: hatch mark radius (μm), otolith radius (μm), and individual increment widths (μm) (Fig. 2.2). All otoliths were analyzed twice by the same reader at an interval of >1 month and each count estimate was ranked according to the confidence of the reading. The single best increment estimate count for all otoliths was used as the age estimation since the coefficient of variation in the number of increments counted between the first and the second reading never exceed 10% (Campana & Jones 1992). We examined 366 otoliths: 99, 63, and 204 from the 2003, 2004, and 2005 samplings, respectively (Table 2.2).

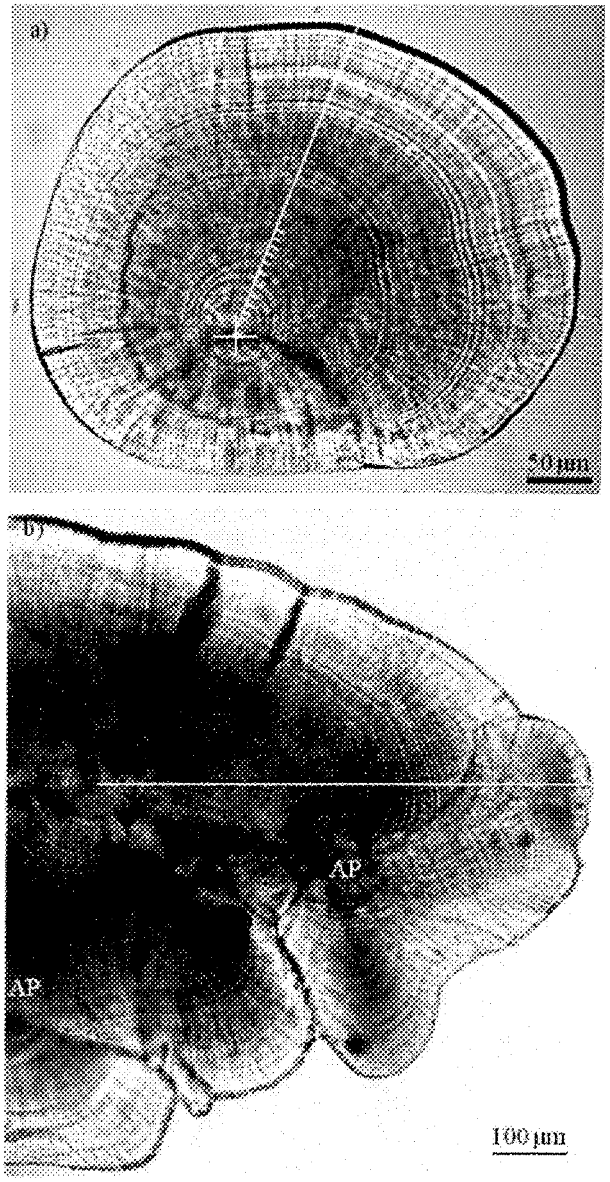

Figure 2.2. Yellow perch otoliths at 400x magnification. a) Lapilli of a 33.15 mm juvenile: the size of central cross indicates the hatch mark diameter, and the first 10 daily increments are highlighted with marks on the measurement axis (solid line). b) Sagitta of a 44.45 mm juvenile showing accessory primordia (AP) that complicate increment measurement on the axis (solid line).

Table 2.2. Sample size (n) of YOY yellow perch used for otolith analysis.

	Cut lakes			Control lakes			
Year	Cut-1	Cut-3	Cut-5	Cont-1	Cont-3	Cont-4	Total
2003	12	20	19	17	14	17	99
2004	19	15	-	-	16	13	63
2005	57	43	55	11	-	38	204
Total	88	78	74	28	30	68	366

2.4.3.2 Plankton

Phytoplankton samples were air-transported to the laboratory for algal biomass (Chl *a*) determination. A known volume of water (usually 1000 mL) was filtered through Whatman GF/C filters within 12 h of sampling. Filters were immediately frozen and kept at -80°C until extraction according to Planas et al. (2000).

Zooplankton samples were treated in order to measure biomass as ash-free dry weight (AFDW m^{-3}). Samples were first sorted to remove *Chaoborus* larvae (Chaoboridae, Diptera) and divided into four equal fractions using a Folsom splitter. One quarter was used for biomass measurements on decreasing size fractions according to Patoine et al. (2000). Subsamples were passed through 212 µm and 53 µm sieves and then filtered onto precombusted GF/A glass fibre filters, dried for 18 h, weighed, ashed at 500°C for 18 h, and weighed again. The organic mass was calculated as the difference between dry weight and combusted weight. Organisms from a subsample of both size fractions were identified. The 212 µm size fraction was mostly composed of copepodites, adult copepods, and cladocerans. Rotifers and copepod nauplii were dominant in the 53 µm size fraction.

2.4.4 Data analysis

2.4.4.1 Fish

YOY yellow perch growth rate over the first 40 days ($G_{0\text{-}40d}$) was computed using the equation

$$(1)\ G_{0-40d} = L_{40} - L_0/40$$

where L_{40} is the back-calculated standard length at 40 d and L_0 is the standard length at hatching as determined by the biological intercept (see next paragraph). Variations in growth rate were analyzed using a two-way ANOVA with lake treatment and year as factors. The principal source of variations of interest for impact assessment was the interaction between lake treatment and year. When interaction factors were statistically significant ($P < 0.05$), Tukey's HSD tests were performed to identify the differences.

Fish length back-calculation methods based on otolith microstructure have to meet two criteria: (1) increments must be deposited on a daily basis and (2) otolith growth must be proportional to fish growth (Campana 1990). It has already been demonstrated that YOY yellow perch otoliths have daily increments (Powles & Warlen 1988, Dale 2000). In addition, to support the proportionality between otolith and somatic growth, a significant positive relationship between fish length and otolith radius was observed for YOY yellow perch caught in the three years of the study in both cut and control lakes (Fig. 2.3, $F_{1,364} = 1690.40$, $P < 0.0001$). The biological intercept procedure (Campana 1990) was then used to back-calculate length-at-age (L_t) using the equation

$$(2)\ L_t = L_c + (O_t - O_c)(L_c - L_0)(O_c - O_0)^{-1}$$

where L = standard fish length at the biological intercept (L_0) and at capture (L_c), and O = otolith radius at the biological intercept (O_0) and at capture (O_c). L_0 was determined in the laboratory by measuring yolk-sac larvae newly hatched from incubated eggs collected in Lake Saint-Pierre, Quebec, Canada. A mean hatching standard length of 7.53 mm (SD = 1.53, n = 94) and the observed individual core radius were used as the biological intercept. Growth trajectories of all fish were reconstructed using back-calculated lengths at 5 d age intervals. One-factor ANOVAs were performed to identify differences in back-calculated lengths-at-age between treatments. All analyses on length-at-age were performed on $\log_{10}$ transformed data since variance increased with age. Since lakes are the experimental units, statistical analyses on growth rates and lengths-at-age were conducted on the mean lake values.

2.4.4.2 Plankton

Variations in algal and zooplankton biomass were analyzed using two-way ANOVAs with lake treatment and year as factors. When required, data were $\log_{10}$ transformed. In all analyses, Tukey's HSD tests were performed to identify the differences when sources of variations were significant ($P < 0.05$). All statistical analyses were done using lakes as experimental units.

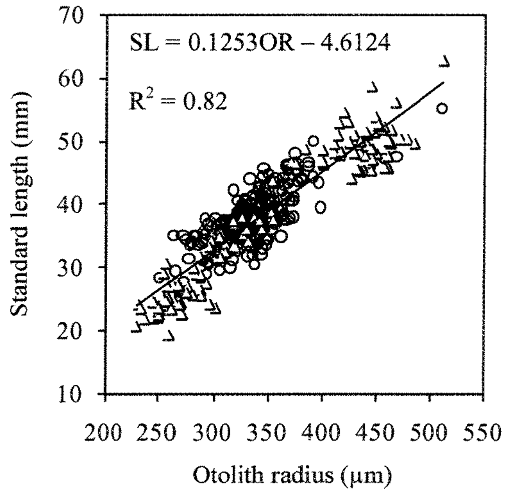

Figure 2.3. Relationship between standard length (SL) and otolith radius (OR) of yellow perch subsampled for growth analyses in cut lakes (circles) and control lakes (triangles) in 2003, 2004, and 2005.

2.5 RESULTS

2.5.1 Growth rate

The growth rate of yellow perch from hatching to age 40 d showed a significant interaction between lake treatment and year (Fig. 2.4, lake treatment x year: $F_{2,9} = 8.90$, $P = 0.0074$). In natural conditions, i.e., in control lakes, the growth rate decreased significantly from 2003 to 2005. In cut lakes, growth rates were similar to those of control lakes before forest harvesting but were significantly higher after the perturbation in 2005 (0.63 mm·d^{-1} in cut lakes vs. 0.44 mm·d^{-1} in control lakes).

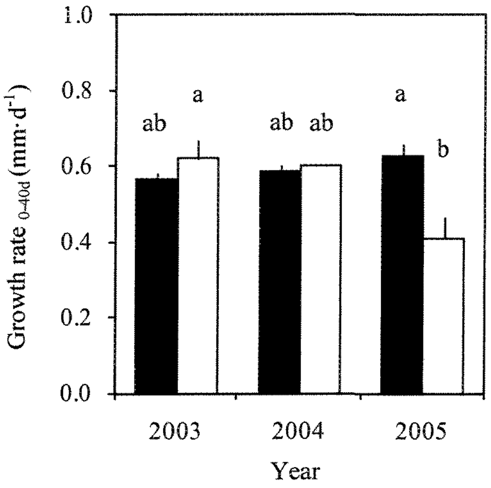

Figure 2.4. Comparison between years (2003, 2004, and 2005) and treatments (cut lakes: solid bars; control lakes: open bars) for the mean back-calculated growth rate of yellow perch from hatching until age 40 d. Vertical lines represent standard errors of mean lake values. Bars with different letters indicate groups with significantly different mean growth rates (Tukey's HSD, $P < 0.05$).

2.5.2 Length-at-age

Before the perturbation in 2003 as well as during the first year after the perturbation in 2004, the back-calculated lengths-at-age from ages 5 to 40 d were not statistically different between fish from both treatments (Fig. 2.5a,b). In 2005, the back-calculated lengths-at-age were higher for fish in cut lakes from ages 10 to 40 d (Fig. 2.5c, one-factor ANOVA: $F_{1,4}$, $P < 0.05$), emphasizing the differences in growth rates between the treatments in 2005. Fish in cut lakes had reached a mean back-calculated length of 32.58 mm at 40 d compared to 25.22 mm for YOY yellow perch in control lakes.

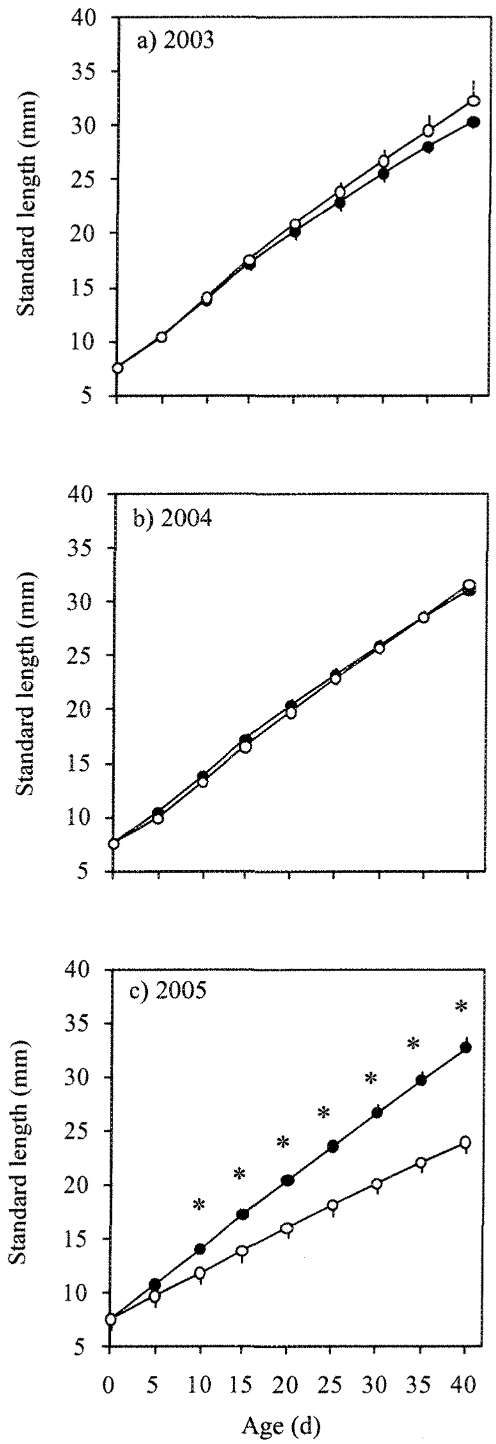

Figure 2.5. Mean back-calculated growth trajectories of yellow perch sampled in cut lakes (black circles) and control lakes (open circles) in a) 2003, b) 2004, and c) 2005. Vertical lines represent standard errors of mean lake values. Asterisks indicate significant between-treatment differences in the back-calculated length-at-age (one-way ANOVA, $P < 0.05$).

2.5.3 Plankton biomass

A significant increase in algal biomass was recorded in cut lakes in 2005, two years after forest harvesting, whereas the Chl *a* levels remained the same among years in the three control lakes (Table 2.3, Fig. 2.6a,). The mean Chl *a* concentration in cut lakes was nearly two-fold higher than in control lakes in 2005 (3.90 $\mu g \cdot L^{-1}$ vs 1.81 $\mu g \cdot L^{-1}$).

No statistical interaction between treatment and year was detected for zooplankton biomass either for the rotifer–nauplii size fraction or for the copepod–cladoceran size fraction (Fig. 2.6b, c, Table 2.3). Cut lakes had significantly higher zooplankton biomass of both size classes even before the perturbation (Table 2.3, Fig. 2.6b, c).

Table 2.3. Results of the analyses of variance testing the effects of treatment (tr), year (yr), and their interaction on plankton biomass. Data were transformed as indicated.

Variable	Source	df	MS	*F*	$p > F$
$\log_{10}$ algal biomass	tr	1	0.13	3.02	0.1078
	yr	2	0.01	2.33	0.1394
	tr x yr	2	0.38	9.01	**0.0041**
	Residual	12	0.04		
	Total	17			
Rotifer-nauplii size fraction biomass	tr	1	144.84	30.68	**0.0001**
	yr	2	15.52	3.29	0.0727
	tr x yr	2	8.59	1.82	0.2040
	Residual	12	4.72		
	Total	17			
Copepod-cladoceran size fraction biomass	tr	1	883.82	22.45	**0.0005**
	yr	2	18.28	0.46	0.6394
	tr x yr	2	7.89	0.20	0.8211
	Residual	12	39.37		
	Total	17			

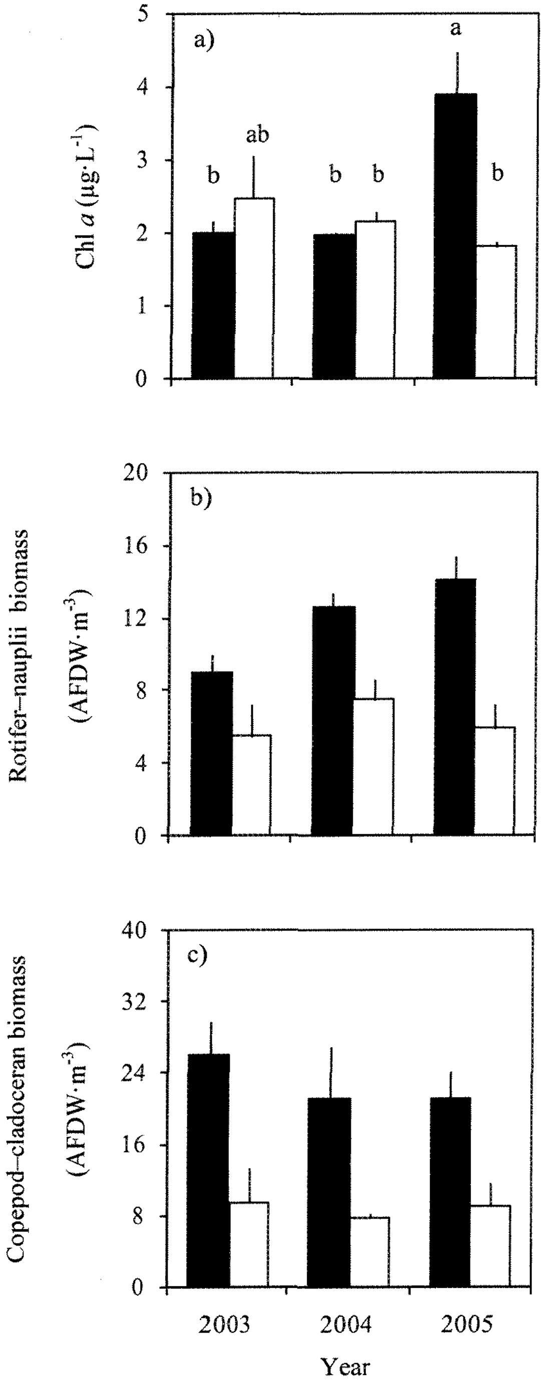

Figure 2.6. Comparison between years (2003, 2004, and 2005) and treatments (cut lakes: solid bars; control lakes: open bars) of a) mean algal biomass, b) mean rotifer–nauplii size fraction biomass, and c) mean copepod–cladoceran size fraction biomass. Vertical lines represent standard errors of mean lake values. The corresponding statistical results are presented in Table 2.3. Bars with different letters indicate groups with significantly different mean growth rates (Tukey's HSD, $P < 0.05$).

2.6 DISCUSSION

2.6.1 Forest harvesting effects on YOY yellow perch growth

Growth of YOY yellow perch was significantly higher in cut lakes two years after forest harvesting. The higher growth rate of fish in cut lakes was observed from ages 10 d to 40 d, which encompasses the complete larval stage of yellow perch in Boreal Shield lakes.

Before forest harvesting, growth rates were similar in all lakes, despite some differences in productivity indices such as in turnover rate, secchi depth, DOC concentration, and zooplankton biomass. In control lakes, we observed natural interannual variations including a decrease in growth rate in 2005. Given that all lakes were subjected to the same interannual variations in environmental conditions except for forest harvesting in catchments, the higher growth rates and greater lengths-at-age of fish in cut lakes in 2005 are likely to have been caused by the perturbation.

Our results suggest that fish in cut lakes encountered better environmental growth conditions than fish in control lakes in 2005. Early growth in fish mainly depends on temperature and feeding conditions (Anderson 1988, Jones 2002, Takahashi & Watanabe 2005, Takasuka & Aoki 2006, Robert et al. 2009). In YOY yellow perch, it has been reported that growth is mostly related to zooplankton biomass (Abbey & Mackay 1991, Bremigan et al. 2003, Clapp & Dettmers 2004, Graeb et al. 2004). The lake surface temperature of the study lakes remained unchanged after forest harvesting (Winkler, Leclerc, Sirois, Archambault & Bérubé, unpublished data). Hence, the observed enhanced growth in cut lakes was likely due to modifications in feeding conditions.

2.6.2 Effects of forest harvesting on lake trophodynamics

Our results on the impact of forest harvesting on algal and zooplankton biomass corroborated the hypothesis of a bottom-up effect on lake trophodynamics, up to the fish level. We measured a significant difference in pelagic algal biomass between cut and control lakes two years after the perturbation. We propose that an increase in nutrients due to forest harvesting, which was observed in our study lakes (Winkler et al. 2009) as well as in lakes examined during other studies (Rask et al. 1998, Carignan et al. 2000, Steedman 2000), may have generated a bottom-up effect on algal biomass, as has been reported in other studies (Planas et al. 2000, Nicholls et al. 2003, Ghadouani et al. 2006).

There was also an increasing trend in the biomass of the rotifer–nauplii size fraction after the perturbation, even though this result was not statistically significant. This trend of a post-harvest increase in small zooplankton biomass was also observed by Bertolo and Magnan (2007). The rotifer–nauplii size fraction biomass may have been stimulated by the bottom-up effect observed in algal biomass and/or via the microbial loop (Arndt 1993). The most widely reported impact of forest harvesting on boreal lakes concerns the increase in DOC (Rask et al. 1998, Carignan et al. 2000, France et al. 2000, O'Driscoll et al. 2006, Winkler et al. 2009). For example, in our study lakes, DOC increased from 8.7 $mg \cdot L^{-1}$ (SD 0.3) before to 10.3 $mg \cdot L^{-1}$ (SD 0.3) after forest harvesting (Winkler et al. 2009). In aquatic systems, DOC serves as carbon and nutrient sources for bacterioplankton and protistan zooplankton (Arvola et al. 1996, De Lange et al. 2003, Carpenter et al. 2005), which are grazed by rotifers and *Daphnia* spp. (Arndt 1993, Sanders et al. 1996). DOC enhancement could then have transferred energy to the zooplankton level and generated a bottom-up effect.

No post-harvest increase in zooplankton biomass was measured in the copepod–cladoceran size fraction. A combination of bottom-up and top-down effects may explain these results. Given that algal biomass and small zooplankton biomass as well as YOY yellow perch growth was enhanced two years after forest harvesting, we assume that the bottom-up effects on the copepod–cladoceran size fraction were present but not measurable due to top-down control. Winkler et al. (2009) observed a marginally significant increase in *Daphnia* spp. abundance in cut lakes following forest harvesting. We propose that YOY yellow perch predation on large copepods and cladocerans (Noble 1975, Mills et al. 1989, Schael et al. 1991, Wahl et al. 1993, Wallus 2006) may have masked the increase in the copepod–cladoceran biomass and the zooplankton biomass measured in cut lakes. It is widely known that planktivorous fish exert a negative effect on zooplankton (Carpenter et al. 1987, Post & McQueen 1987, Romare et al. 1999, Finlay et al. 2007). For example, it has been demonstrated that YOY yellow perch can strongly deplete *Daphnia pulex* populations (Mills & Forney 1983), and this could have been the case in our study.

2.6.3 Other considerations for fish feeding success and growth

Successful feeding results from a combination of many factors in a fish's early life, with prey abundance being one of the most important variables that determines feeding success as well as the growth and survival of young fish (Hjort 1914, Anderson 1988, Cushing 1990, Welker et al. 1994, Jones 2002, Houde 2008). The plankton biomass measured in this study suggests that feeding conditions were modified in cut lakes. However, our results also showed that cut lakes had naturally higher zooplankton biomass than control lakes (i.e., higher biomasses were measured before the perturbation). Despite naturally higher prey abundance, fish in cut lakes did not grow at higher rates before forest harvesting, suggesting that a factor other than prey biomass alone enhanced feeding success and growth after the perturbation. We propose that prey visibility may also have been improved after forest harvesting, principally due to DOC photoproducts.

In addition to its nutritional benefits, DOC affects water colour and influences light transmission (Molot & Dillon 1997, France et al. 2000), which in turn influences the way fish detect and perceive prey items. It has been observed that fish feeding success and/or growth may increase with turbidity (Miner & Stein 1993, Sirois & Dodson 2000a, Utne-Palm 2002, De Robertis et al. 2003). In addition to its positive impact on prey abundance via the microbial loop or protistan zooplankton, increased DOC in cut lakes could also have improved prey visibility via an enhanced contrast with the background and, consequently, led to higher growth rates for YOY yellow perch.

In conclusion, our results showed that forest harvesting enhanced YOY yellow perch growth probably via a bottom-up effect on lake trophodynamics. YOY yellow perch may benefit from the higher prey abundance, but higher prey visibility due to the increased DOC after forest harvesting may also be a factor. Robert et al. (2007) demonstrated that fast growth in a larval fish population can either reflect optimal environmental growth conditions or the removal of slow growing larvae by predators (or both). Our results suggest that good feeding conditions lead to fast growth for fish in cut lakes. According to the "growth-mortality" hypothesis, higher growth rates in early life stages after forest harvesting could favour short-term survival and recruitment in yellow perch populations.

2.7 ACKNOWLEDGMENTS

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CHAPITRE 3

DIET AND FEEDING SUCCESS OF FAST-GROWING YELLOW PERCH (*PERCA FLAVESCENS*) LARVAE AND JUVENILES IN PERTURBED SMALL OLIGOTROPHIC BOREAL LAKES

3.1 ABSTRACT

A recent study has demonstrated that young-of-the-year (YOY) yellow perch (*Perca flavescens*) grow at higher rates in forest harvesting impacted lakes. The present study tested the hypothesis that enhanced early life growth of yellow perch in those lakes was due to favourable feeding conditions after the perturbation. Yellow perch larvae and juveniles and their zooplanktonic preys were sampled three times in three lakes where forest harvesting occurred in the catchment two years before (cut lakes) and in three control lakes. Analyses of the diet of YOY yellow perch in both treatments showed that fish in cut lakes preyed principally on *Daphnia* spp. and *Polyphemus pediculus* while fish in control lakes preyed on more diverse food items. Cut lakes showed higher dissolved organic carbon concentrations, algal biomass and *Daphnia* spp. abundance than control lakes. YOY yellow perch feeding success on *Daphnia* spp. and recent growth rates showed a significant type-II functional relationship with abundance of *Daphnia* spp.. At a given *Daphnia* spp. abundance, yellow perch in cut lakes always exhibited higher feeding success and growth rate. We hypothesized that higher prey abundance in a more coloured environment may have favoured prey detection and growth for larval and juvenile yellow perch, and that these conditions may have an impact on population recruitment.

3.2 RÉSUMÉ

Une étude récente a montré une augmentation du taux de croissance larvaire et juvénile chez la perchaude (*Perca flavescens)* dans des lacs perturbés par des coupes forestières. La présente étude a testé l'hypothèse que l'augmentation dans la croissance durant les jeunes stades de vie de la perchaude de ces lacs a été causée par des conditions d'alimentation favorables après la perturbation. Les larves et les juvéniles de perchaude, ainsi que leur proies zooplanctoniques, ont été échantillonnées à trois reprises dans trois lacs contrôles et dans trois lacs dont le bassin versant a subi des coupes forestières deux ans auparavant (lacs perturbés). L'analyse de la diète des jeunes perchaudes de l'année dans les deux traitements ont montré que les poissons des lacs perturbés se sont nourris principalement de *Daphnia* spp. et de *Polyphemus pediculus* tandis que les poissons des lacs contrôles se sont nourris de proies plus diversifiées. Les lacs perturbés présentaient des concentrations de carbone organique dissous, une biomasse algale et une abondance de *Daphnia* spp. supérieures à celles des lacs contrôles. Une relation fonctionnelle de tyupe II explique la variation du succès d'alimentation sur *Daphnia* spp. et de la croissance récente des jeunes perchaudes en fonction de l'abondance de *Daphnia* spp. dans le milieu. De plus, pour une abondance donnée de *Daphnia* spp dans l'environnnement, les perchaudes des lacs perturbés montraient toujours un plus grand succès d'alimentaiton et un taux de croissance plus élevé. Nous émettons l'hypothèse qu'une plus grande abondance de proies dans un environnement plus coloré ait favorisé la détection des proies et la croissance chez les larves et les juvéniles de perchaude, et que ces conditions peuvent avoir un impact sur le recrutement des populations.

3.3 INTRODUCTION

Central hypotheses in fishery science assume that availability of adequate prey during the larval stage can explain a large proportion of the recruitment variability in marine and freshwater fish populations (Hjort 1914, Lasker 1975, Anderson 1988, Cushing 1990, Dettmers et al. 2003, Houde 2008). Low prey abundance could lead to high mortality rates directly through starvation (critical period hypothesis, Hjort 1914), or indirectly through integrated processes on growth (growth-mortality hypothesis, Anderson 1988, Leggett & Deblois 1994). In fact, according to the growth-mortality hypothesis, slow growth lowers survival rates of larval fish by increasing their vulnerability to predators due to their smaller size at a given age (Anderson 1988, Miller et al. 1988, Takasuka et al. 2004a) or to their lower age at a given size (Takasuka et al. 2003, 2004a).

Factors susceptible to influence prey availability in freshwater lakes could therefore affect larval fish feeding success and growth and generate large variations in recruitment. Several studies reported that forest harvesting in lake catchments could modify water quality and limnoplankton community structure (Rask et al. 1998, Carignan et al. 2000, Patoine et al. 2000, Planas et al. 2000, Rask et al. 2000, Winkler et al. 2009). In a recent work (Chapter 2)(Leclerc et al. submitted)(Leclerc et al. submitted)(Leclerc et al. submitted)(Leclerc et al. submitted)(Leclerc et al. submitted)(Leclerc et al. submitted) we have shown that young-of-the-year (YOY) yellow perch (*Perca flavescens*) exhibited higher growth rate and length-at-age after forest harvesting in eastern Canadian Boreal Shield lakes. These results suggested that modifications in water quality and plankton community structure due to forestry activities may have influenced feeding success of

YOY yellow perch, causing such changes in growth. The impact of forest harvesting on fish populations are not well described, and very few studies have focused on early life stages of fish (Northcote & Hartman 2004). Moreover, the processes by which forest harvesting may enhance yellow perch growth during early life are still unknown.

Yellow perch is a well studied and common forage fish in North American waters whose early life stages are zooplanktivorous, feeding on copepods and cladocerans (Hansen & Wahl 1981, Mills et al. 1984, Whiteside et al. 1985, Post & McQueen 1988, Mills et al. 1989, Confer et al. 1990, Craig 2000). Yellow perch growth and recruitment have been shown to be closely related to prey availability (Evans 1986, Crowder et al. 1987, Abbey & Mackay 1991, Bremigan et al. 2003, Dettmers et al. 2003, Clapp & Dettmers 2004). Therefore, forest harvesting in lake catchments may impact recruitment success via changes in prey communities.

The general objective of the study was to test the hypothesis that enhanced growth rate of YOY yellow perch in forest harvesting impacted boreal lakes was due to favourable feeding conditions after the perturbation. To reach this objective, we first described and compared the diet of larval and juvenile yellow perch from perturbed and control lakes. Second, we compared the availability of the principal prey taxa in both lake types. Finally, we investigated the influence of environmental conditions such as prey abundance and water quality on the feeding success and the recent growth rate of YOY yellow perch.

3.4 MATERIALS AND METHODS

3.4.1 Study sites and field sampling

The study area was located in the Canadian Boreal Shield ecoregion, north of the 50th parallel, approximately 60 km south-east of Lake Mistassini in the province of Quebec, Canada (Fig. 3.1). Lakes in this area are typically oligotrophic and shelter fish communities mainly composed of northern pike (*Esox lucius*), walleye (*Sander vitreus*), white sucker (*Catostomus commersonii*), burbot (*Lota lota*) and yellow perch. This region is also characterised by spruce-moss landscapes exploited by forest industry.

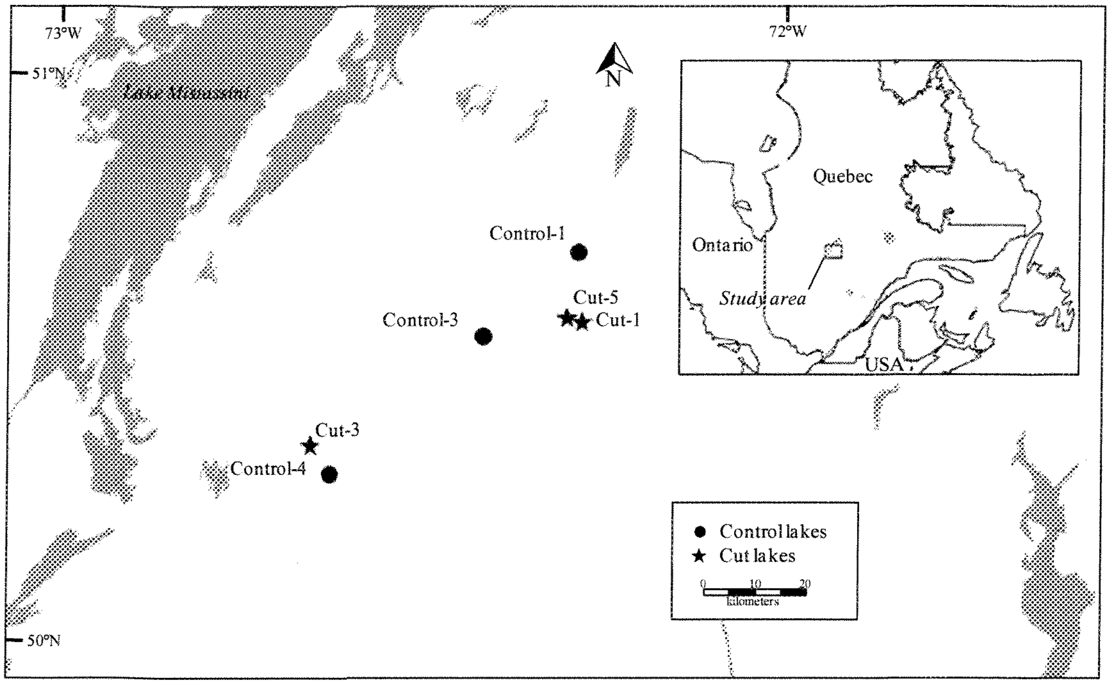

Figure 3.1. Map of the study area showing the location of cut and control lakes.

A total of six headwater lakes were selected for this study (Fig. 3.1, see Table 2.1 for a detailed description of lakes). All lakes were sampled in summer 2005. At the time of sampling, three lakes were control sites, without any perturbation in the drainage area. The three other lakes, hereafter referred as cut lakes, were perturbed by forest harvesting occurring two years before, in a proportion of 57%, 51% and 34% of the drainage area of lakes Cut-1, Cut-3 and Cut-5 respectively. Cut and control lakes had similar geographical, morphological and physicochemical parameters measured before the perturbation (Chapter 2).

Larval and juvenile yellow perch and their zooplanktonic preys were collected in three surveys in each lake: early July (4-8 July 2005), mid-July (19-22 July 2005) and early August (1-4 August 2005). YOY yellow perch undertake ontogenic changes of habitat; early in the season, yellow perch hatch in the littoral zone and undergo a migration to the pelagic zone until it reaches approximately 25 mm long, and then return to the littoral zone (Whiteside et al. 1985, Post & McQueen 1988). Given these size-specific migrations, we used a sampling design in order to have a complete collection of all size-classes as suggested by Scharf et al. (2009). During the early July survey, fish were sampled at six pelagic and six littoral stations to catch larvae and/or early juveniles. The pelagic sampling gear consisted of two push-nets (mesh of 500 μm and 50 cm diameter mouth aperture), deployed on each side of the boat. Push-nets were opened out at the lake surface for 10 minutes at a constant speed of 2 km h^{-1}, between 21:00 and 02:00 h. The littoral sampling gear consisted of a 500 μm mesh beach seine 4 m long and 1 m deep, opened out on a 30 m transect, between 14:00 and 19:00 h. During the mid-July and the early August surveys, fish were sampled in the littoral zone only. Once captured, sampled fish were immediately immersed in a tricaine methane sulfonate (MS-222) solution (100 $mg{\cdot}L^{-1}$) for 2-4 minutes to avoid stomach content evacuation before to be preserved in 95% ethanol.

Ethanol was replaced within 24 h to avoid alcohol dilution and otolith damages (Butler 1992).

Zooplankton community was collected at each survey, in the pelagic and the littoral zone. Three vertical hauls made from 1 m off-bottom to the surface using a 53 µm mesh net of 25 cm diameter mouth aperture were done in the pelagic zone of each lake. Three other replicates were done in the littoral zone with the same sampling device but pushed out on a 30 m transect at the water surface on the 1 m isobath. The volume of water filtered was measured by a General Oceanic flowmeter. Zooplankton was anesthetised in carbonated water and preserved in 4% buffered formaldehyde.

Water quality and algal biomass were measured in all lakes on the 8 August 2005. Temperature, Secchi depth, dissolved organic carbon (DOC) and Chlorophyll *a* (Chl *a*) concentrations were measured in the euphotic zone at the deepest point of each lakes (see Winkler et al. 2009 for complete methods).

3.4.2 Diet composition analyses

Yellow perch were sorted and measured from all samples. In each lake, stomach content analysis was performed on a random sub-sample of YOY yellow perch proportionally selected from fish length frequencies distributions observed at each survey (Table 3.1). The entire stomach content of a total of 287 fish was examined under a stereoscopic microscope at 50X magnification (Table 3.1). All preys contained in the stomach were identified to the lowest taxonomic level (species in most cases). The developmental stage was noted for copepods (nauplii or copepodite stages CI-CVI) and immature insects (larvae, pupae or adult). The following keys were used for identification: Edmondson (1959) for general identification, Smith & Fernando (1978) and Czaika (1982) for copepods, Hebert & Finston (1996, 1997) for *Daphnia* spp., and Merritt & Cummins (1996) for immature insects. Developmental stages of copepods were determined using the criterions of Czaika (1982). Incomplete or digested organisms and immature copepods that did not allow a proper identification to the species level were assigned to species that were present in the stomach in proportion to their relative abundance (Robert et al. 2008). This procedure was applied to less than 2% of all preys.

Table 3.1. Number of fish used for feeding and growth analyses in each lake, at each sampling survey.

Sampling survey	Cut lakes			Control lakes			
	Cut-1	Cut-3	Cut-5	Cont-1	Cont-3	Cont-4	Total
Early July	35	21	18	18	3	13	108
Mid-July	26	19	15	23	0	23	106
Early August	19	9	15	10	0	20	73
Total	80	49	48	51	3	56	287

Sub-sampled fish were grouped in six classes of 5 mm of standard length (Table 3.2). The smallest length class was underrepresented in cut lakes, and the largest one was not represented in control lakes. Fish in the three length class common to the two lake treatments (15-20, 20-25, and 25-30 mm) have been used for most of the analyses.

Yellow perch diet was firstly characterised in terms of total number of ingested preys. Three-way partly nested analyses of variance (ANOVAs) were used to compare total number of ingested preys. Sources of variations were lake treatment (cut/control, fixed

Table 3.2. Diet composition by lake treatments and length classes expressed as the mean percent contribution in numbers of the different prey taxa for fish containing food, followed by feeding statistics. Non-available data indicated by *n/a*.

Prey taxon[a]		Cut lakes						Control lakes					
		10-15 mm	15-20 mm	20-25 mm	25-30 mm	30-35 mm	35-40 mm	10-15 mm	15-20 mm	20-25 mm	25-30 mm	30-35 mm	35-40 mm
Rotifera		*n/a*	-	0.09	-	0.02	0.02	2.08	3.67	2.67	-	-	*n/a*
Copepoda													
Nauplii		*n/a*	10.12	0.43	0.26	-	-	-	0.32	4.63	5.96	-	*n/a*
Calanoida													
Leptodiaptomus minutus	CI-CV	*n/a*	10.25	11.70	3.31	1.00	3.08	-	3.33	0.93	0.05	-	*n/a*
	CVI	*n/a*	10.46	14.65	2.94	0.85	1.04	31.19	5.23	2.64	3.08	1.32	*n/a*
Skistodiaptomus oregonensis	CVI	*n/a*	-	-	-	-	0.12	-	-	-	-	-	*n/a*
Epischura lacustris	CI-CV	*n/a*	0.61	0.34	0.17	0.12	-	-	-	1.00	0.47	-	*n/a*
	CVI	*n/a*	12.97	0.83	4.04	5.07	0.01	12.47	5.54	1.67	3.22	-	*n/a*
Cyclopoida													
Cyclops scutifer	CVI	*n/a*	-	-	-	-	-	2.92	1.90	-	0.03	-	*n/a*
Mesocyclops edax	CI-CV	*n/a*	-	-	0.24	0.11	-	-	-	-	-	-	*n/a*
	CVI	*n/a*	-	0.12	0.09	1.51	0.01	4.46	-	-	0.05	-	*n/a*
Microcyclops v. rubellus	CVI	*n/a*	-	-	-	-	-	-	-	-	0.37	-	*n/a*
Acanthocyclops capillatus	CI-CV	*n/a*	-	-	-	-	-	-	-	-	0.14	-	*n/a*
	CVI	*n/a*	-	-	-	-	0.01	-	-	0.02	0.45	-	*n/a*
Acanthocyclops vernalis	CI-CV	*n/a*	-	0.05	-	0.09	0.37	-	0.33	0.09	0.41	-	*n/a*
	CVI	*n/a*	-	0.11	-	0.32	1.40	2.23	0.29	1.28	2.48	-	*n/a*
Eucyclops agilis	CI-CV	*n/a*	-	-	-	0.25	0.02	-	0.08	1.17	2.24	-	*n/a*
	CVI	*n/a*	-	-	-	0.27	0.17	-	0.32	1.74	8.46	-	*n/a*
Macrocyclops albidus	CI-CV	*n/a*	-	-	0.95	0.26	0.50	-	-	-	-	-	*n/a*
	CVI	*n/a*	-	-	0.01	0.56	1.42	-	-	0.47	0.03	-	*n/a*
Tropocyclops p. mexicanus	CI-CV	*n/a*	1.97	0.49	-	-	0.35	-	-	0.47	1.33	-	*n/a*
	CVI	*n/a*	0.57	3.12	-	0.19	0.73	-	-	5.38	7.58	-	*n/a*
Cladocera													
Leptodoridae													
Leptodora kindtii		*n/a*	1.57	0.13	-	0.12	-	-	-	-	-	-	*n/a*
Sididae													
Latona setifera		*n/a*	-	-	-	0.03	0.06	-	9.29	13.27	4.14	-	*n/a*
Sida crystallina		*n/a*	0.75	0.48	0.21	0.48	-	-	14.34	7.95	1.59	-	*n/a*
Diaphanosoma spp.		*n/a*	-	-	3.44	2.40	1.28	-	-	-	-	-	*n/a*
Holopedidae													
Holopedium gibberum		*n/a*	1.00	0.96	0.01	-	-	-	11.96	7.94	10.01	0.36	*n/a*
Daphnidae													
Daphnia longiremis complex[b]		*n/a*	-	18.06	13.08	12.24	14.08	7.37	6.79	0.06	-	-	*n/a*
Daphnia pulex complex[c]		*n/a*	0.29	22.42	12.27	24.49	28.76	-	-	-	-	-	*n/a*
Ceriodaphnia reticulata		*n/a*	-	-	-	2.00	0.23	-	-	0.04	-	-	*n/a*
Bosminidae													
Bosmina spp.		*n/a*	1.36	2.74	7.50	6.93	1.44	37.28	14.19	12.32	5.92	22.37	*n/a*
Macrothricidae													
Acantholeberis curvirostris		*n/a*	-	-	-	0.54	2.28	-	0.08	0.05	0.02	-	*n/a*
Ophryoxus gracilis		*n/a*	-	-	-	10.69	11.60	-	-	1.94	3.30	-	*n/a*
Parophryoxus tubulatus		*n/a*	-	-	-	0.12	0.11	-	-	-	-	-	*n/a*
Chydoridae													
Acroperus harpae		*n/a*	-	0.21	0.48	0.59	2.52	-	1.17	7.30	2.19	1.09	*n/a*
Alona affinis		*n/a*	-	-	-	0.42	0.51	-	-	0.71	0.07	-	*n/a*
Alona costata		*n/a*	-	-	-	0.18	0.11	-	-	-	-	1.82	*n/a*
Alona quadrangularis		*n/a*	-	-	0.07	-	-	-	0.63	0.05	0.78	-	*n/a*
Alona rustica		*n/a*	-	-	0.07	0.03	0.08	-	1.45	1.24	0.09	-	*n/a*
Chydorus sphaericus		*n/a*	-	0.02	-	0.07	0.16	-	0.44	2.23	0.76	-	*n/a*
Eurycercus spp.		*n/a*	-	-	-	1.34	1.22	-	-	0.05	0.03	-	*n/a*
Rhynchotalona falcata		*n/a*	-	-	0.03	0.10	0.03	-	-	8.69	22.47	72.22	*n/a*
Other Chydoridae[d]		*n/a*	-	0.09	0.24	0.38	-	-	-	0.58	0.62	-	*n/a*
Polyphemidae													
Polyphemus pediculus		*n/a*	47.64	22.45	47.84	22.05	5.84	-	17.93	9.51	2.53	0.36	*n/a*
Insecta													
Hemiptera													
Corixidae Corixinae	larvae	*n/a*	-	-	-	0.45	1.46	-	-	0.10	0.63	-	*n/a*
Diptera	larvae	*n/a*	-	-	2.07	2.13	10.95	-	0.40	1.21	3.94	0.36	*n/a*
Diptera	pupae	*n/a*	-	0.42	0.42	1.16	2.17	-	-	0.28	1.38	-	*n/a*
Others	larvae	*n/a*	0.22	-	-	0.11	0.69	-	-	0.12	0.14	-	*n/a*
Amphipoda													
Hyalella azteca		*n/a*	-	-	-	0.22	1.25	-	-	0.03	1.23	-	*n/a*
Others[e]		*n/a*	0.22	0.09	0.26	0.11	3.92	-	0.32	0.17	1.81	0.10	*n/a*
Pelagic zooplankton		*n/a*	98.81	98.69	92.71	78.48	59.58	100	71.88	54.04	54.81	24.41	*n/a*
Vegetation-associated zooplankton		*n/a*	0.75	0.80	4.54	17.35	19.96	-	27.40	44.05	36.06	75.23	*n/a*
Benthic macroinvertebrates		*n/a*	0.44	0.51	2.75	4.17	20.46	-	0.72	1.91	9.13	0.36	*n/a*
Number of fish analysed		1	20	43	29	46	38	18	20	48	22	2	*n/a*
Number of fish with≥ 1 prey		0	19	42	28	45	31	8	15	46	22	2	*n/a*
Feeding incidence (%)		0	95	98	97	98	82	44	75	96	100	100	*n/a*
Mean number of preys		0	33.8	47.1	132.3	98.9	101.4	19.6	19.0	61.6	49.0	87.5	*n/a*

[a] Taxon followed by developmental stage for copepods (CI-CVI) and immature insects (larvae, pupae).

[b] *Daphnia longiremis* complex includes : *D. longiremis, D. dubia, D. galeata mendotae, D. Rosea.*

[c] *Daphnia pulex* complex includes : *D. pulex, D. middendorffiana, D. catawba, D. pulicaria, D. Minnehaha.*

[d] Other Chydoridae includes: *Alonella excisa, Camptocercus rectirostris, Chydorus bicornutus, Chydorus piger, Graptoleberis testudinaria, Pleuroxus procurvus.*

[e] Others includes: Acariformes, Collembola, Harpacticoida, adult Insecta, Oligochaeta, Ostracoda.

factor), individual lakes (lakes nested within treatment, random factor), length class (15-20/20-25/25-30 mm, fixed factor) and their interactions. Data were $\log_{10}$ transformed to achieve normality and homoscedasticity. Total number of ingested preys was tested over all yellow perch ($n = 182$).

Species assemblages in the yellow perch diet were compared using three different multivariate procedures. Firstly, the same ANOVA model (see the preceding paragraph) was used to test for differences in ingested preys assemblages. This analysis was done using a permutational multivariate analysis of variance (PERMANOVA, Anderson 2001). The model had the same sources of variation as the one described above but used 4999 permutations to determine the test-statistics. PERMANOVA was performed on the Bray-Curtis similarity matrix of standardised abundance data (Bray & Curtis 1957). Secondly, species assemblages were illustrated by a non-metric multi-dimensional scaling (nMDS) ordination on standardised abundance data, using the Bray-Curtis similarity measure. Thirdly, similarity/dissimilarity analyses (SIMPER procedure, Clarke & Warwick 2001) were done on the Bray-Curtis similarity matrix of standardised abundance data to determine the species involved in the dissimilarity and to identify the principal prey taxa of fish in both treatments. Fish with empty stomach were not considered in multivariate analyses, only fish with ≥ 1 prey in the stomach ($n = 72$).

3.4.3 Prey field analyses

Zooplanktonic organisms from pelagic and littoral samples ($n = 100$) were sub-sampled by aliquot using a pipette with a 4 mm opening. Organisms were enumerated, identified and staged to the lowest taxonomic level, usually species, using the keys mentioned above.

The abundance of yellow perch prey taxa in cut and control lakes were compared with three-way partly nested ANOVAs, using zooplankton samples from both littoral and pelagic habitats as replicates. Sources of variation were lake treatment (cut/control, fixed factor), individual lakes (lakes nested within treatment, random factor), survey (early July/mid-July/early August, fixed factor), and their interactions. Data were transformed ($\log_{10}(x+1)$) to achieve normality and homoscedasticity. In addition to univariate analyses, the complete assemblages of zooplankton were compared between lake treatments with a three-way partly nested PERMANOVA on transformed data ($\log_{10}(x+1)$) with the same sources of variation as mentioned for univariate analyses on zooplankton.

3.4.4 Feeding success and recent growth analyses

A length-independent feeding success index of YOY yellow perch was measured as the number of preys ingested on the fish standard length (in N ingested preys·mm^{-1}). Recent growth rate was measured using otolith microstructure analysis as described in Chapter 2. Briefly, lapillar otoliths were removed, mounted on a microscope slide using thermoplastic glue and polished with a 3- or 5 µm lapping film. Daily increments were counted and measured using an image analysis system at 400 to 1000X magnification. Standard length-at-age was back-calculated using the biological-intercept method (Campana 1990). Recent growth rate was calculated as the average growth rate (in mm·d^{-1}) over the last three days prior to capture.

The functional relationships between prey abundance and the yellow perch feeding success and recent growth rate were assessed using the Ivlev (1961) equation :

$$(1)\quad y = a(1 - exp^{-bx})$$

where y is the predator response (feeding success or recent growth rate), x is the prey abundance, a is the maximum predator response, and b is the coefficient relating the change in prey abundance to the predator response. The regression model was fitted using SigmaPlot 10.0.

Other environmental variables such as water temperature, Secchi depth, DOC and Chl a concentrations were compared using two-way partly nested ANOVAs with lake treatment and individual lakes (nested in the treatment factor) as sources of variations.

3.5 RESULTS

3.5.1 Diet composition

The diet of YOY yellow perch in all length classes (10-40 mm) was mainly composed of zooplankton (Table 3.2). For the three length classes between 15 and 30 mm, YOY yellow perch in cut lakes preyed predominantly on *Polyphemus pediculus, Daphnia* spp. and *Leptodiaptomus minutus* CI-CVI, but *Bosmina* spp., *Rhynchotalona falcata, Latona setifera, Holopedium gibberum, Polyphemus pediculus*, and *Sida crystallina* were the most abundant food items consumed by larvae and juveniles in control lakes (Table 3.2). Cladoceran species represented more than 50% of the ingested preys by yellow perch between 15 and 30 mm in cut and control lakes (Table 3.2). However, pelagic species such as *Daphnia* spp. and *Polyphemus pediculus* were preferred in cut lakes, whereas a significant percentage (>25%) of cladoceran species consumed in control lakes were associated with the aquatic vegetation such as members of the Sididae and Chydoridae families (Table 3.2). In both types of lakes, as YOY yellow perch grew, they ingested less pelagic zooplankton and higher proportions of vegetation-associated zooplankton and benthic macroinvertebrates.

The feeding incidence of YOY yellow perch 15-30 mm long ranged from 95% to 98% in cut lakes and from 75% to 100% in control lakes and did not differed significantly between both treatments (Table 3.2, $\chi^2 = 1.79$, $P = 0.1812$). The mean number of preys ingested by YOY yellow perch 15-30 mm tended to increase with length class but the increase was only marginally significant (Table 3.2, length class: $F_{2,12.9} = 3.24$, $P = 0.0725$). Even if the mean number of preys appeared to be higher for fish in cut lakes, the difference was not statistically significant between treatments principally due to large variations within treatments (Table 3.2, lake treatment: $F_{1,3} = 2.63$, $P = 0.2032$).

The nMDS showed a clear distinction of species assemblages of the diet of 15-30 mm YOY yellow perch between cut and control lakes (Fig. 3.2). A PERMANOVA analysis indicated that species assemblages of ingested preys were statistically different between lake treatments (Table 3.3). SIMPER analysis showed that the ingested prey assemblages were more homogeneous among fish in cut lakes with an average similarity of 25.3% than in control lakes in which the similarity was only 12.3%. The species assemblages of the preys ingested were 92.8% dissimilar between fish in both treatments. Together, *Polyphemus pediculus*, *Daphnia* spp., *Bosmina* spp. and *Leptodiaptomus minutus* CVI accounted for 48.6% of the dissimilarity in the species assemblages of the diet between lake treatments (Table 3.4). These prey taxa were representative of the diet of YOY yellow perch in cut lakes, except *Bosmina* spp. that was more consumed by fish in control lakes (Table 3.2, Table 3.4).

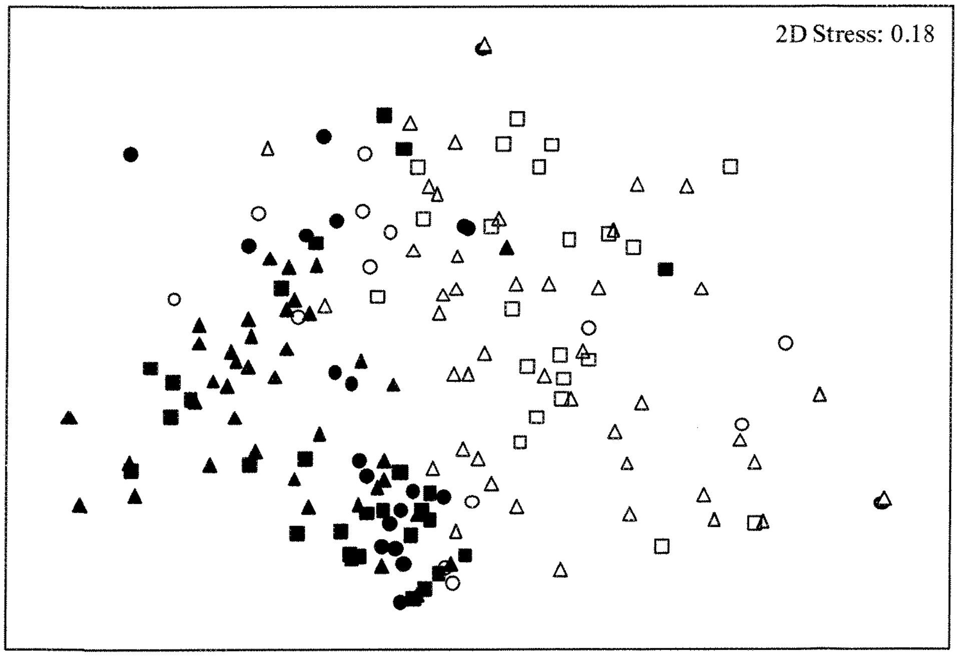

Figure 3.2. Non-metric multidimensional scaling (nMDS) illustrating variations in ingested prey assemblages (standardised data) by yellow perch 15-20 mm (circles), 20-25 mm (triangles), and 25-30 mm (squares) from cut lakes (black symbols) and control lakes (white symbols). Results of the corresponding PERMANOVA are given in Table 3.3.

Table 3.3. Results of three-way partly nested PERMANOVA on standardised data testing the effect of lake treatment (TR), lake nested in the treatment factor (LA(TR)) and yellow perch length class (LC) on the assemblages of ingested preys taxa. Taxonomic resolution as described in Table 3.2.

Source of variation	df	MS	Pseudo-*F*	$P_{\text{(Monte Carlo)}}$
TR	1	20 699.0	2.2563	**0.0394**
LA(TR)	3	9225.7	3.1056	**0.0002**
LC	2	4675.4	0.7778	0.7304
TR x LC	2	5824.8	0.9690	0.4856
LA(TR) x LC	6	7121.5	2.3973	**0.0002**
Residuals	157	2970.7		
Total	171			

Table 3.4. Results of SIMPER analysis on standardised data showing the major discriminating prey taxa in the diet of yellow perch, their average abundance, average dissimilarity and cumulative contribution to the dissimilarity between the assemblages of ingested preys by fish in cut and control lakes across fish length classes 15-30 mm.

Taxa	Av. abundance (%)		Av. dissim.	Cum. contrib. (%)
	Cut	Control		
Polyphemus pediculus	35.6	9.2	18.5	20.0
Daphnia pulex complex	14.4	0.0	7.2	27.7
Daphnia longiremis complex	13.1	1.3	6.8	35.1
Bosmina spp.	3.9	11.0	6.6	42.2
Leptodiaptomus minutus CVI	9.9	3.2	5.9	48.6
Rhynchotalona falcata	0.0	10.8	5.4	54.4
Latona setifera	0.0	10.1	5.1	59.8
Holopedium gibberum	0.9	9.2	4.7	64.9
Leptodiaptomus minutus CI-CV	8.6	1.1	4.7	69.9
Sida crystallina	0.5	7.4	3.8	74.1

3.5.2 Prey field

A total of 39 and 31 zooplankton taxa were identified in cut and control lakes respectively. By numbers, copepod species dominated the zooplankton community representing in average 85% and 90% of the samples in cut and control lakes respectively. Among all the prey taxa listed in Table 4 that were responsible for the difference in the diet of YOY yellow perch between lake treatments, only *Daphnia* spp. showed a statistical difference: they were more abundant in cut lakes throughout the sampling surveys (Fig. 3.3, lake treatment: $F_{1,4} = 8.63$, $P = 0.0420$). There was no statistical difference in the species assemblages of the prey field between cut and control lakes (lake treatment: pseudo-$F_{1,4} = 1.26$, $P_{(\text{MonteCarlo})} = 0.2912$).

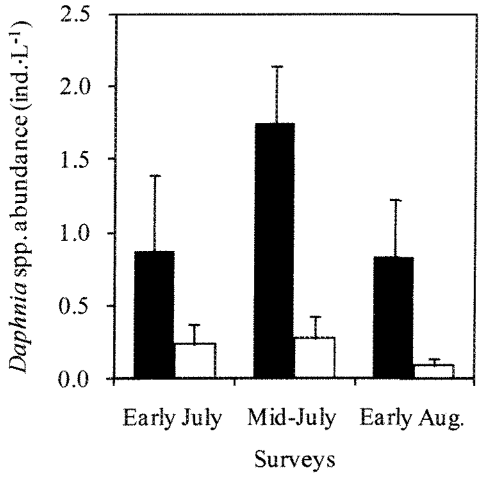

Figure 3.3. *Daphnia* spp. abundance (mean ± SE) in cut lakes (black bars) and control lakes (white bars). Each bar represents the averaged abundance over the littoral and pelagic plankton of the three lakes in the corresponding treatment.

3.5.3 Feeding success and growth of YOY yellow perch in relation to biotic and abiotic environmental factors

No significant relationships were found between the feeding success or the recent growth rate of YOY yellow perch and the abundance of prey taxa listed in Table 3.4, except for *Daphnia* spp. (Fig. 3.4). An Ivlev function using *Daphnia* spp. abundance as independent variable explained 29% and 47% of the variability in the feeding success on *Daphnia* spp. and in the recent growth rate respectively (Fig. 3.4a, $F_{1,14} = 5.73$, $P = 0.0312$; Fig 3.4b, $F_{2,13} = 5.84$, $P = 0.0155$). The maximum recent growth rate was reached at an abundance of approximately 0.23 *Daphnia* spp.$\cdot$L^{-1} (Fig. 3.4b), while the maximum feeding success was not reached yet at the maximum observed of 0.62 *Daphnia* spp.$\cdot$L^{-1} (Fig 3.4a). On average, fish in cut lakes exhibited a higher mean feeding success on *Daphnia* spp. than fish in control lakes (Fig. 3.4a, lake treatment: $F_{1,4} = 12.10$, $P = 0.0254$). In addition, fish in cut lakes had a higher mean recent growth rate than fish in control lakes (Fig. 3.4b, lake treatment: $F_{1,4} = 21.64$, $P = 0.0096$). For a given abundance of *Daphnia* spp., YOY yellow perch in cut lakes always exhibited a higher feeding success and a faster growth than in control lakes.

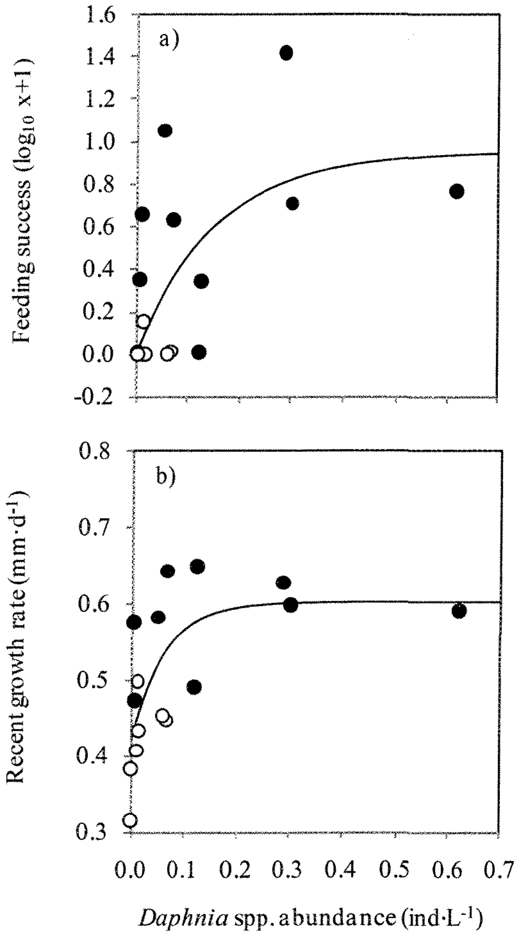

Figure 3.4. Larval and juvenile yellow perch a) feeding success on *Daphnia* spp. and b) recent growth rate, related to the abundance of *Daphnia* spp.. Individual feeding success and recent growth rate were averaged within lake and survey and associated with the mean abundance of *Daphnia* spp. in the habitat of fish sampling. Black dots correspond to fish in cut lakes and white dots, fish from control lakes. Curves fitted with an Ivlev function: a) $y = 0.952\ (1 - \exp^{-6.564x})$, $R^2 = 0.29$, b) $y = 0.421 + 0.182\ (1 - \exp^{-15.787x})$, $R^2 = 0.47$.

DOC and Chl *a* concentrations were significantly higher in cut lakes than in control lakes (Table 3.5). Water transparency, as indicated by the Secchi depth, tended to be lower in cut lakes, suggesting higher turbidity than in control lakes (Table 3.5). Water temperature did not differ significantly between lake treatments.

Table 3.5. Physico-chemical variables and algal biomass in cut and control lakes. ANOVA results testing the effect of lake treatment are shown.

	Mean value (SD)			
Variable	Cut lakes	Control lakes	$F_{1,4}$	$P > F$
Temperature (°C)	18.11 (0.21)	17.93 (0.17)	0.42	0.5507
Secchi depth (m)	2.05 (0.28)	3.35 (0.40)	7.24	0.0546
DOC (mg·L^{-1})	8.50 (0.52)	4.93 (0.67)	17.60	**0.0138**
Chl *a* (µg·L^{-1})	3.90 (0.57)	1.81 (0.07)	13.35	**0.0217**

3.6 DISCUSSION

3.6.1 Diet composition of fast- and slow-growing larval and juvenile yellow perch

In a recent work, we have demonstrated that growth rate of YOY yellow perch from hatching to 40 days of age was 1.43 times higher in fish from perturbed lakes compared to fish from control lakes two years after forest harvesting in lake catchments (Chapter 2). Results of the present study support the hypothesis that enhanced growth rate of YOY yellow perch in perturbed lakes was related to favourable feeding conditions after the perturbation.

Several studies have described the YOY yellow perch diet composition, but few of them used a species taxonomic resolution and none employed a multivariate approach (Hansen & Wahl 1981, Mills & Forney 1981, Mills et al. 1984, Whiteside et al. 1985, Post

& McQueen 1988, Confer et al. 1990, Wahl et al. 1993, Graeb et al. 2004, Fulford et al. 2006). As showed by these studies conducted on southern populations, YOY yellow perch (10-40 mm) of north-eastern Boreal Shield lakes fed on pelagic and vegetation-associated zooplanktonic preys, mostly cladocerans. The smaller fish (<15 mm) were caught in the pelagic zone of control lakes, and all of them had ingested prey taxa that were characteristic of the pelagic zone, as observed by studies on ontogenic migration and feeding of yellow perch (Whiteside et al. 1985, Post & McQueen 1988, Dettmers et al. 2005). The observed combination of pelagic and vegetation-associated zooplankton ingested by larger fish (>15 mm) suggest that they have probably fed in different habitats. These results are consistent with the observations of Post & McQueen (1988) that have demonstrated that YOY yellow perch (16-34 mm) migrate from offshore to nearshore at dawn returning at dusk, standing in the nearshore zone all day long.

The high taxonomical resolution presented in this study have demonstrated that despite similar proportions of copepods, cladocerans and macroinvertebrates in their diet, fast-growing yellow perch from perturbed lakes fed primarily on pelagic cladoceran species such as *Daphnia* spp. and *Polyphemus pediculus*. On the other hand, slow-growing yellow perch in control lakes preyed on diverse food items, including a substantial proportion of vegetation-associated cladocerans. Many other studies have showed that YOY yellow perch that feed on *Daphnia* tended to reach the higher growth rates (Noble 1975, Hansen & Wahl 1981, Mills & Forney 1981, Mills et al. 1989, Schael et al. 1991). Multivariate analyses on species assemblages have corroborated the differences in the diet between fish in the two lake treatments. *Daphnia* spp. and *Polyphemus pediculus* explained a substantial part of the dissimilarity (~30%) between the diets of fish from both lake treatments and were preferred preys of fast-growing fish from cut lakes. We have therefore hypothesised that feeding on these two cladocerans has resulted in higher growth rates for YOY yellow perch in forest harvesting impacted lakes compared to fish in control lakes feeding on a greater variety of prey types. The enhanced growth rate of YOY yellow perch in cut lakes was related to the availability of *Daphnia* spp., but also likely related to changes in the visual feeding conditions due to forest harvesting.

3.6.2 Forest harvesting impacts on prey availability

The abundance of preys available for young fish may limit growth, lead to poor nutritional condition, and increase susceptibility to predation (Anderson 1988, Houde 2008). Therefore, zooplankton availability was considered as a limiting factor for yellow perch recruitment (Evans 1986, Crowder et al. 1987, Bremigan et al. 2003, Dettmers et al. 2003, Clapp & Dettmers 2004). As feeding incidence was high for fish in both lake treatments, prey abundance may be not limiting for yellow perch. Assemblages of zooplankton taxa were not different between cut and control lakes, suggesting that yellow perch larvae and juveniles in both lakes treatments have made different food choices. However, the abundance of *Daphnia* spp. was higher in cut lakes over the sampling surveys.

Several interacting factors may have caused the higher abundance of *Daphnia* spp. in cut lakes. First of all, forest harvesting is known to increase total phosphorus (TP) and DOC (Carignan et al. 2000, France et al. 2000, Winkler et al. 2009, this study) that are likely to be responsible for the enhancement of *Daphnia* spp. abundance in forest harvesting impacted lakes. Forest harvesting creating a slight increase in phytoplankton biomass (Planas et al. 2000, Nicholls et al. 2003, this study), the P-input could have created a bottom-up effect on *Daphnia* spp. abundance, directly through phytoplankton enhancement. Moreover, *Daphnia* species are recognized to be more sensitive to P-input than other crustacean zooplankton since these cladocerans have a higher P-demand compared to copepods that have a higher nitrogen demand (Hessen 1997). DOC may also create bottom-up effects on *Daphnia* abundance through its influence on bacterioplankton and protists (Wetzel 1995, Arvola et al. 1996, De Lange et al. 2003) on which *Daphnia* efficiently graze (Sanders et al. 1996), or an indirect effect by reducing the detrimental ultra-violet radiation (Cooke et al. 2006). As a result, the TP- and DOC-input following forest harvesting could together have caused a multitrophic bottom-up effect on *Daphnia* abundance or a reduction in harmful radiation. In the same lakes of the present study, Winkler et al. (2009) have observed a marginally significant increase of *Daphnia* spp. abundance the year after forest harvesting. The top-down effects of fish on *Daphnia* spp. in response to the bottom-up effect of nutrient increase could have lessened the expected increase in *Daphnia* spp. abundance in this study (Chapter 2).

3.6.3 Feeding success and growth of YOY yellow perch in relation to biotic and abiotic environmental factors

Feeding success and growth rate could be influenced by a variety of environmental factors, prey availability being one of the most important. We found no functional response between the feeding success or the recent growth rate, and the total zooplankton abundance or other taxonomical grouping such as crustacean zooplankton, copepods or cladocerans. However, we found a significant relationship between *Daphnia* spp. abundance and the feeding success and the recent growth rate. This functional response with *Daphnia* spp. abundance justified the taxonomical resolution achieved in this study. Several field studies showed a strong link between prey abundance and growth (Mills et al. 1989, Bunnel et al. 2003, Robert et al. 2009), some others did not (Baumann et al. 2003, Takahashi & Watanabe 2005) or observed only a weak relationship (Takasuka & Aoki 2006, Robert et al. 2009). As suggested by our results, the lack of prey preference determination coupled to low taxonomical resolution could explain the discrepancy in these results.

This study has demonstrated that both feeding success on *Daphnia* spp. and recent growth rate of YOY yellow perch followed a type-II functional response with *Daphnia* spp. abundance. Interestingly, for a same *Daphnia* spp. abundance, fish in cut lakes had generally a higher feeding success on it, and also a higher recent growth rate. The stomach content analyses indicated that for the same *Daphnia* spp. abundance in the environment, fish in control lakes rather ingest other smaller cladoceran taxa such as the vegetation-associated Sididae and Chydoridae. The higher *Daphnia* spp. consumption and the higher recent growth rates reached by fish in cut lakes at a given *Daphnia* spp. abundance, suggest that cut lakes may have provided a visual environment favouring a *Daphnia* spp. feeding regime for YOY yellow perch.

It has already been demonstrated that larval fish reach higher growth rates when feeding in a turbid environment (Boehlert & Morgan 1985, Miner & Stein 1993, Sirois &

Dodson 2000a, Utne-Palm 2002). We propose that cut lakes may have provided better feeding conditions for larval and juvenile yellow perch and thereby, have favoured the feeding success and consequently the recent growth rate. The humic compounds of DOC being the major factor controlling water color in Boreal Canadian Shield lakes (Molot & Dillon 1997, Pace & Cole 2002), the observed higher DOC concentrations in cut lakes may have provided a more coloured environment where *Daphnia* spp. could have been more conspicuous for visual predators such as yellow perch larvae and juveniles (Hinshaw 1985, Wahl et al. 1993). Rearing experiments have shown that the ability of yellow perch larvae to acquire food is largely influenced by the visibility of the prey, resulting from the contrast with the background environment (Hale & Carlson 1972, Hinshaw 1985, Sandström 1999, Strand et al. 2007). We proposed that, such as higher turbidity, the higher DOC concentrations in cut lakes may have promoted the visibility of the nearly transparent *Daphnia* spp. and may explain that at a given *Daphnia* spp. abundance, fish in cut lakes had a higher feeding success on it than fish in control lakes. From an energetic perspective, turbidity could increase the energy allowed to growth by favouring prey detection and decreasing expenses due to food searching activity (Sirois & Dodson 2000a, Utne-Palm 2002, Shoji et al. 2005). The increase of DOC in cut lakes may have lead to higher growth rate by favouring prey detection and lowering energy costs allocated to prey searching when feeding on *Daphnia* spp. The enhancement of feeding with increasing turbidity may be explained by the higher detection of preys as well as an increase in feeding activity caused by a lowered risk of predation (Gregory & Northcote 1993, Utne-Palm 2002, Shoji & Tanaka 2006b).

3.6.4 Conclusion

Our results have showed that growth of YOY yellow perch in forest harvesting impacted lakes was largely influenced by feeding conditions. Perturbed lakes had higher *Daphnia* spp. abundance, coupled to higher DOC concentrations. We suggested that these changes in biotic and abiotic environmental feeding conditions have promoted growth by offering a higher abundance of suitable preys that were more conspicuous, thereby lowering costs in energy allocated to food searching. Given the importance of growth for survival and recruitment of fish populations, we therefore hypothesized that the perturbations in boreal lakes catchments may impact survival and recruitment of yellow perch populations through changes in biotic and abiotic environmental conditions.

3.7 ACKNOWLEDGEMENTS

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CHAPITRE 4

DISCRIMINATING THE INFLUENCE OF ENVIRONMENTAL CONDITIONS, GROWTH-SELECTIVE SURVIVAL AND POTENTIAL FOR GROWTH AT HATCHING ON EARLY GROWTH IN YELLOW PERCH (*PERCA FLAVESCENS*) POPULATIONS

4.1 ABSTRACT

Recent works have shown that growth during early life may vary substantially among yellow perch (*Perca flavescens*) populations in small oligotrophic Boreal Shield lakes in relation to perturbations in catchments. In this paper, we discriminate the influence of environmental conditions, growth-selective survival and potential for growth at hatching on early life growth discrepancy observed among these yellow perch populations. Environmental conditions such as temperature, dissolved organic carbon (DOC), algal biomass and *Daphnia* spp. abundance were estimated in each lake. Growth-selective survival and size at hatching were measured and compared between survivors (>40 days) and reference populations of younger fish between and within lakes. Perturbed lakes showed higher DOC concentration, algal biomass and *Daphnia* spp. abundance. Both selection for fast growth and selection for slow growth were observed among fast-growing cohorts and did not explain the variability in early life growth among lakes. Moreover, there was no indication of potential for growth at hatching, emphasizing that fast growth was likely due to favourable environmental feeding conditions during the larval and the juvenile stages of yellow perch. Differences in the direction of growth-selective survival were hypothesized to be caused by various species and size structure of potential predators in each lake. Finally, environmental conditions, growth and growth-selective survival were discussed in the perspective of recruitment prediction.

4.2 RÉSUMÉ

Des travaux récents ont montré que la croissance durant les jeunes stades de vie peut varier substantiellement entre les populations de perchaude (*Perca flavescens*) des lacs du bouclier boréal, en relation avec les perturbations dans le bassin versant. Dans cette étude, nous distinguons l'influence des conditions environnementales, de la survie sélective à la croissance, et du potentiel pour la croissance à l'éclosion, sur la divergence dans la croissance observée entre ces populations. Les conditions environnementales telles la température, le carbone organique dissous (COD), la biomasse algale, et l'abondance de *Daphnia* spp. ont été estimées dans chaque lac. La survie sélective à la croissance et la taille à l'éclosion ont été mesurées chez les survivants (>40 jours) et chez des perchaudes à un plus jeune âge. Ces variables ont été comparées entre les lacs, de même qu'à l'intérieur de chaque lac. Les lacs perturbés ont montré des valeurs plus élevées de DOC, de biomasse algale et d'abondance de *Daphnia* spp. La sélection pour la croissance rapide de même que la sélection pour la croissance lente ont été observées dans les populations de perchaude à croissance rapide et ne contribuaient pas à expliquer la variabilité dans la croissance entre les lacs. De plus, aucune indication de potentiel pour la croissance à l'éclosion n'a été décelée, accentuant l'hypothèse que la croissance rapide a été causée par des conditions d'alimentation favorables durant les stades larvaire et juvénile chez la perchaude dans les lacs perturbés. Les différences dans la direction de la sélection pour la croissance ont probablement été causées par des différences inter-lacs dans la composition en espèces et la structure de taille des prédateurs potentiels. Enfin, les conditions environnementales, la croissance et la sélection pour la croissance ont été discutées dans une perspective de prédiction du recrutement.

4.3 INTRODUCTION

Recruitment in fishes is determined during the early life stages that are subjected to high mortality rates, principally caused by predation (Bailey & Houde 1989, Sogard 1997, Houde 2002, 2008). A considerable body of literature showed that fish surviving to the larval stage are not randomly selected (see review in Leggett & Deblois 1994, Hare & Cowen 1997, Takasuka et al. 2003, Houde 2008). The Anderson's growth-mortality hypothesis rather propose that survival would be growth-selective, according to fast-growing individuals higher probabilities of survival (Anderson 1988). In this conceptual framework, fast-growing individuals are most likely to survive considering that: (1) they are less vulnerable to predation than smaller conspecifics at a given age (the "bigger-is-better" concept, Miller et al. 1988), (2) they spend less time in the highly vulnerable larval stage (the "stage-duration" concept, Chambers & Leggett 1987, Houde 1987), and (3) they are more likely to escape to predators at a given size (the "growth-selective predation" concept, Takasuka et al. 2003). On the other hand, all the above hypotheses are in contradiction with the optimal foraging theory that predicts predators will select the largest fish larvae as possible (Werner & Gilliam 1984, Gerking 1994).

Numerous studies observed that the survivors at the end of the larval stage were the fast-growing members of a cohort (e.g. Post & Prankevicius 1987, Hovenkamp 1992, Meekan & Fortier 1996, Sirois & Dodson 2000b, Searcy & Sponaugle 2001, Takasuka et al. 2003, Meekan et al. 2006, Shoji & Tanaka 2006a, Tanaka et al. 2006, Robert et al. 2007). However, many studies shown that the survivors were rather the slow-growing members of a cohort (e.g. Litvak & Leggett 1992, Pepin et al. 1992, Gleason & Bengtson

1996a, 1996b, Takasuka et al. 2004a, 2004b, Gagliano et al. 2007, Nishimura et al. 2007, Takasuka et al. 2007a, Holmes & McCormick 2009). Furthermore, other studies indicated that the survivors could also be randomly selected, without preference between fast- or slow-growing individuals at the end of the larval stage (e.g. Takasuka et al. 2004b, Urpanen et al. 2005, Takasuka et al. 2007a). These conflicting results highlight the importance to determine the factors generating the variability in the growth of the survivors, in order to understand the link between growth, survival and ultimately recruitment of fish populations.

Growth achieved by a fish cohort at the end of the larval stage is determined by a combination of factors. First, growth is largely influenced by environmental conditions experienced by fish, especially temperature and food, (Anderson 1988, Jones 2002, Takahashi & Watanabe 2005, Takasuka & Aoki 2006, Robert et al. 2009). Second, growth-selective survival may also contribute to the growth observed on the survivors of a fish cohort. Finally, some studies have observed that fast growth of survivors was associated with larger size at hatching (Meekan & Fortier 1996, Grønkjaer & Schytte 1999, Good et al. 2001, Vigliola & Meekan 2002), suggesting that survivors could already have a potential for growth at hatching, independently of the environmental conditions and the growth-selective mortality experienced during the larval stage. Consequently, the growth observed on fish at the end of the larval stage is a synergic result of environmental conditions, growth-selective survival and traits present at hatching. These factors have to be disentangled in order to better understand their respective influence on early life growth, survival and recruitment.

In a recent work, Leclerc et al. (Chapter 2)(submitted) have shown that young-of-the-year (YOY) yellow perch (*Perca flavescens*) grew faster in Canadian Boreal Shield lakes after forest harvesting occurring in catchments . Furthermore, Leclerc et al. (Chapter 3) have demonstrated that these fast-growing YOY yellow perch have predominantly preyed on *Daphnia* spp. and higher abundances of this cladoceran were observed in perturbed lakes when compared to control lakes. Together, these results suggest that modifications in environmental feeding conditions have favoured early life growth after the perturbation. In this paper, we aim to discriminate the influence of environmental conditions, growth-selective survival, and potential for growth at hatching to explain the growth rates discrepancy observed in several yellow perch cohorts in perturbed and non-perturbed Boreal Shield lakes. To reach this objective, we compared the environmental conditions, the direction and intensity of growth-selective survival and the size at hatching of five populations of larval and juvenile yellow perch in Boreal Shield lakes. Finally, we discussed the influence of environmental conditions, growth and selection for growth for the recruitment of these populations.

4.4 MATERIAL AND METHODS

4.4.1 Study sites and field sampling

The study area was located in the Canadian Boreal Shield ecoregion, north of the 50th parallel, approximately 60 km south-east of Lake Mistassini in the province of Quebec, Canada (Fig. 4.1). Lakes in this area are typically oligotrophic and shelter fish communities mainly composed of northern pike (*Esox lucius*), walleye (*Sander vitreus*), white sucker

(*Catostomus commersonii*), burbot (*Lota lota*) and yellow perch. This region is also characterised by spruce-moss landscapes exploited by forest industry.

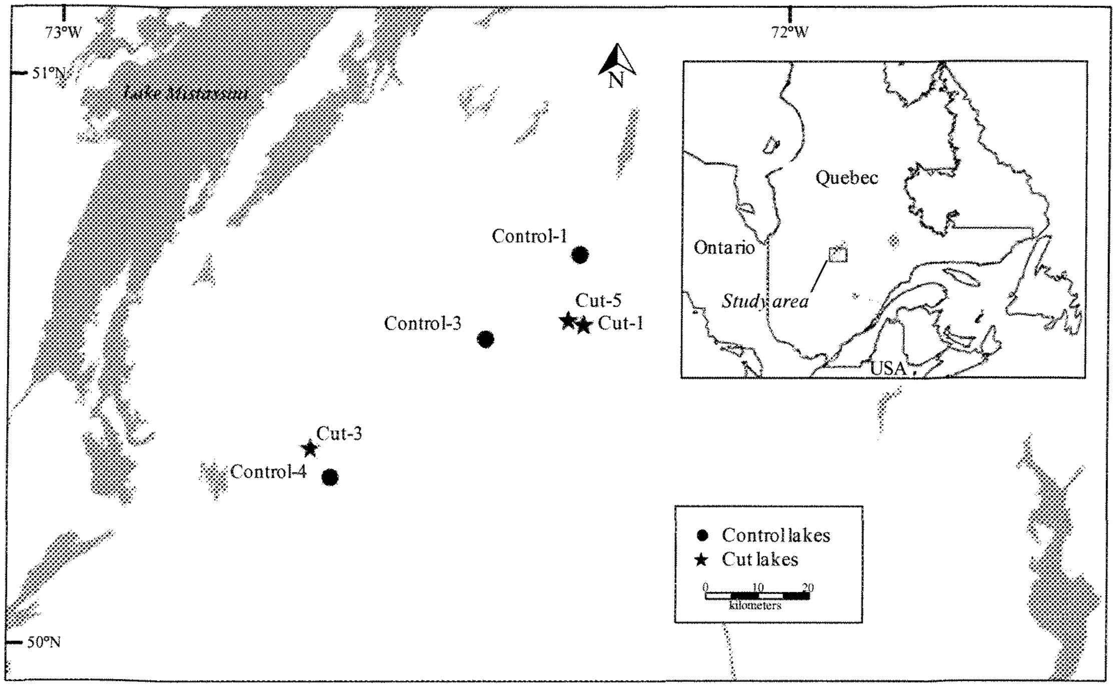

Figure 4.1. Map of the study area showing the location of cut and control lakes.

A total of six headwater lakes were selected for this study (Fig. 4.1). All lakes were sampled in summer 2005. At the time of sampling, three lakes, hereafter referred as "cut" lakes, were perturbed by forest harvesting occurring two years before, in a proportion of 57%, 51% and 34% of the drainage area of lakes Cut-1, Cut-3 and Cut-5 respectively. The three other lakes were control sites (Control-1, Control-3 and Control-4), without any perturbation in the drainage area. Cut and control lakes had similar geographical, morphological and physicochemical parameters measured before the perturbation (Chapter 2). Potential predators of YOY yellow perch were adult yellow perch and northern pike in all lakes, in association with walleye in lakes Cut-3 and Cut-5, and burbot in control lakes.

Larval and juvenile yellow perch were collected in three surveys in each lake: in early July (4-8 July 2005), mid-July (19-22 July 2005) and early August (1-4 August 2005). YOY yellow perch undertake ontogenic changes of habitat; early in the season, yellow perch hatch in the littoral zone and undergo a migration to the pelagic zone until it reaches approximately 25 mm long, and then return to the littoral zone (Kelso & Ward 1977, Whiteside et al. 1985, Post & McQueen 1988). Given these size-specific migrations, we used a sampling design to have a complete collection of all size-classes as suggested by Scharf et al. (2009). Sampling sites were randomly located within each survey. During the early July survey, fish were sampled at six pelagic and six littoral stations to catch larvae and/or early juveniles. The pelagic sampling gear consisted of two push-nets (mesh of 500 µm and 50 cm diameter mouth aperture) deployed on each side of the boat. Push-nets were opened out at the lake surface for 10 minutes at a constant speed of 2 $km \cdot h^{-1}$, between 21:00 and 02:00 h. The littoral sampling gear consisted of a 500 µm mesh beach seine, 4 m long and 1 m deep, opened out on a 30 m transect, between 14:00 and 19:00 h. During the mid-July survey, fish were sampled in six littoral stations only, with the beach seine described above. In the early August survey, in addition to six stations sampled with the beach seine, 10 experimental gill nets, with three randomised panels of 10, 13 and 19 mm meshes, 22.86 m long x 2 m deep, were randomly set perpendicular to the shore for one night in each lake. Abundance of surviving YOY yellow perch in each lake was estimated as the catch per unit of effort (CPUE), i.e. the number of fish per gill net per night. At capture, sampled fish were immediately preserved in 95% ethanol. Ethanol was replaced within 24 h to avoid alcohol dilution and otolith damages (Butler 1992).

4.4.2 Otolith analysis

Standard length was measured on all yellow perch. Stratified sub-sample of larvae and juveniles was done by randomly selecting fish from the length frequencies distribution within each lake and survey. For the early August survey, all sampled fish were grouped together and a sub-sample was randomly selected from the pooled length frequency distribution because gillnet and seine captured fish of the same range of length in each lake. A total of 611 fish were selected for otolith microstructure analyses as described in Leclerc et al. (Chapter 2). Briefly, lapillar otoliths were removed, mounted on a microscope slide using Crystalbound thermoplastic glue and polished with a 3- or 5 μm lapping film. Hatch mark radius and daily increments were measured using an image analysis system at 400 to 1000X magnification. The assumption of proportionality between otolith and somatic growth was verified by the significant linear relationship between otolith maximum radius (OR) and standard length (SL) measured at capture for all the YOY selected ($SL = 0.11OR + 0.55$, $R^2 = 0.87$, $P < 0.0001$, $n = 611$). On each selected individual, length-at-age was back-calculated using the biological-intercept method (Campana 1990), enabling the reconstruction of growth trajectory and the computation of growth rate over different age intervals (Chapter 2).

4.4.3 Data analysis

All fish captured were divided into four age classes (Table 4.1). Given the low sample size, the lake Control-3 was excluded from analyses (Table 4.1). Growth trajectories of fish have been reconstructed using back-calculated standard length at 2 d intervals. Two-way ANOVAs were executed to identify differences in back-calculated length-at-age, with lake treatment and lakes nested in the treatment factor (random factor) as source of variations. All analyses on length-at-age were done on $\log_{10}$-transformed data since variance in length increased with age.

Table 4.1. Number and range of age at capture of yellow perch used to compare growth during different growth intervals. Survivors were represented by fish >40 days at capture.

Growth interval (d)	Range of age (d) at capture	Sample size					
		Cut-1	Cut-3	Cut-5	Cont-1	Cont-3	Cont-4
1-10	11-25	39	34	21	41	3	40
11-20	21-30	53	41	19	30	0	27
21-30	31-40	24	27	23	15	1	56
31-40	>40	58	59	55	10	18	32

Growth-selective survival was estimated within each lake by comparing growth of the survivors (>40 d at capture) with growth of a reference population of fish captured at younger age (Hovenkamp 1992, Meekan & Fortier 1996, Takasuka et al. 2004a). The age interval of the survivors did not extended beyond 57 d. Ideally, the back-calculated growth of the survivors over a given growth interval should be compared to the growth of fish captured immediately after this growth interval (Meekan & Fortier 1996). For example, growth trajectories of surviving fish from hatching to 10 d of age should be compared to that of fish captured at 11 d to avoid the cumulative selection for growth after 10 d. However, it is realistically impossible to meet this condition in field studies because of the limited number of fish sampled at a precise age. In the present analysis, we therefore used fish aged 1 to 15 d older than the upper limit of the growth interval studied (Table 4.1). When comparing the survivors with a reference population of fish captured at younger ages testing the growth-selective survival, both of them must originated from the same population or cohort (Hovenkamp 1992, Meekan & Fortier 1996, Takasuka et al. 2004a). This assumption was met considering that hatch date frequencies distributions within each lake were unimodal, and that hatch dates ranged from 3 June to 1 July 2005 in each lake and for the three surveys.

Growth-selective survival was measured using two procedures. First, growth trajectories of the survivors and the reference population over the growth intervals 0-10, 0-20 and 0-30 d were compared using RM-MANOVAs and post-hoc one factor ANOVAs on $\log_{10}$-transformed data. Second, growth-selective survival was measured by comparing the growth rate frequencies distributions of the survivors with that of the reference population over three different growth intervals, 1-10, 11-20 and 21-30 d, using Kolmogorov-Smirnov two-sample tests. Growth rate over a given growth interval was calculated as the difference between back-calculated standard length at the limits of the interval over the elapsed time.

Potential for growth was estimated using hatch mark radius as a proxy of size at hatching since the otolith growth was found proportional to fish length. The mean hatch mark radius was compared between fish from cut and control lakes using two-way ANOVAs with lake treatment and lake nested in the treatment factor (random factor) as sources of variations. The mean hatch mark radius was also compared between the four age classes within lakes, using one-way ANOVAs with age classes as source of variation.

4.5 RESULTS

4.5.1 Environmental conditions and growth

Water temperature was similar between lakes (Table 4.2). On the other hand, dissolved organic carbon (DOC) concentration, algal biomass and *Daphnia* spp. abundance were higher in cut lakes than in control lakes (Table 4.2). Moreover, surviving fish in cut lakes reached higher growth rates and were also more abundant than fish in control lakes (Table 4.2). Fast growth was then associated with favourable environmental conditions as revealed by higher values of productivity indices of nutrients, primary and secondary production.

Table 4.2. Environmental conditions (temperature, dissolved organic carbon, algal biomass and food abundance) within each lake with corresponding growth rates of the survivors from hatching to 40 d and abundance of fish in the last survey measured as catch per unit of effort (CPUE). Values represent mean followed by standard deviation in parentheses.

	Cut lakes			Control lakes	
Variables	Cut-1	Cut-3	Cut-5	Cont-1	Cont-4
Temperature (°C)^{ab}	18.51	18.06	17.75	18.14	18.07
Dissolved organic carbon (mg·L^{-1})^{ab}	9.27 (0.15)	8.73 (0.06)	7.50 (0.30)	6.23 (0.06)	4.00 (0.35)
Chlorophyll *a* (μg·L^{-1})^{ab}	3.28 (0.25)	3.39 (0.09)	5.04 (0.18)	1.82 (0.15)	1.69 (0.10)
Daphnia spp. abundance (ind.·L^{-1})^{ac}	0.76 (0.77)	0.80 (0.58)	1.90 (0.57)	0.17 (0.10)	0.41 (0.19)
Growth rate$_{0\text{-}40d}$ (mm·d^{-1})	0.57 (0.07)	0.66 (0.07)	0.65 (0.07)	0.35 (0.04)	0.47 (0.10)
CPUE (fish·gill net^{-1})	3.8	11.3	9.4	0.1	0.9

[a] Data from Leclerc et al.(Chapter 2).
[b] Value measured the 8 August 2005.
[c] Averaged over the 3 sampling surveys.

4.5.2 Growth-selective survival

Yellow perch were similar in back-calculated length for fish <20 d at capture (Fig 4.2a, b, lake treatment: $P > 0.05$). On the other hand, yellow perch in cut lakes were larger-at-age from 6-30 d when comparing fish aged 31-40 d at capture (Fig. 4.2c, lake treatment: $P < 0.05$), and from 2-40 d when comparing fish aged >40 d at capture (Fig. 4.2d, lake treatment: $P < 0.05$). The most important difference in length between fish in both lake treatments was achieved by the survivors (>40 d); at 40 d, fish in cut lakes had reached a mean length of 32.6 mm while fish in control lakes had reached in average 25.1 mm, a difference of 7.5 mm (Fig. 4.2d).

The comparison of the survivors with the reference populations within lakes showed variable directions of growth-selective survival among lakes: selection for slow growth, selection for fast growth and no selection. Significant selection for slow growth was observed in lakes Cut-1, Cut-3 and Control-1, when comparing the mean growth trajectory of the survivors to that of the reference population over the growth intervals 0-10, 0-20 and 0-30 d (Fig. 4.3, Table 4.3). In these three lakes, the survivors were systematically smaller-at-age from 2 d after hatching, in each growth interval (post-hoc ANOVAs $P < 0.007$). Selection for slow growth was also supported by the comparison of the growth rate frequencies distributions of the survivors and the reference population over the growth intervals 1-10, 11-20 and 21-30 d (Fig. 4.4). In lakes Cut-1 and Control-1, the growth rate frequencies distribution of the survivors shifted to lower values than that of the reference population in all the growth intervals measured. Along with growth trajectories analysis, growth rate frequencies distributions analysis indicated that the selection for slow growth was sustained until at least 30 d of age. In the lake Cut-3 however, the survivors had a lower growth rate in the first 10 d only (Fig. 4.4). Together, these results indicated a strong selection for slow growth in lakes Cut-1 and Control-1, and a mild selection for slow growth in lake Cut-3.

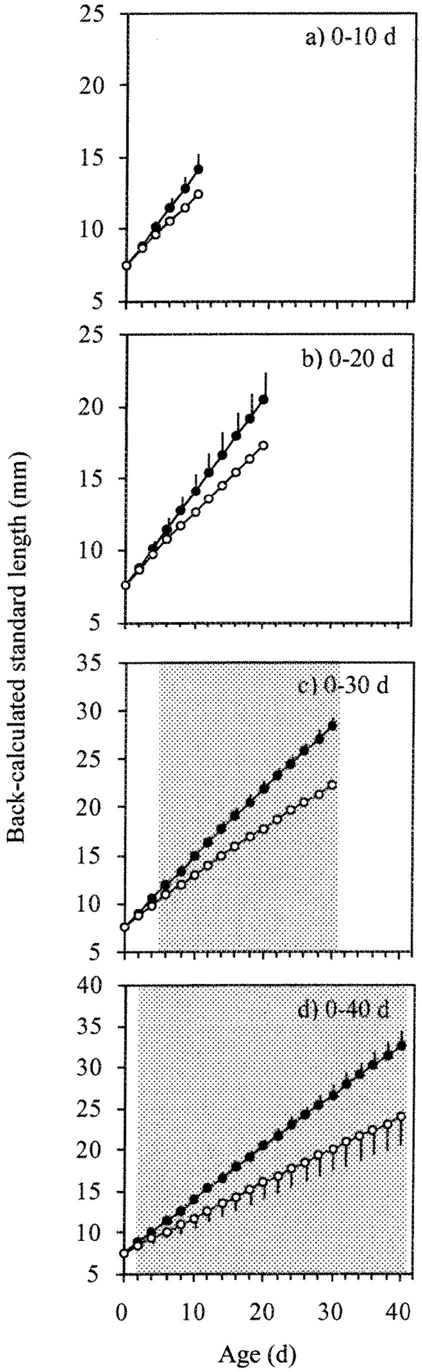

Figure 4.2. Mean growth trajectories of yellow perch from cut lakes (black dots) and control lakes (white dots) over the growth intervals a) 0-10, b) 0-20, c) 0-30 and d) 0-40 d. Vertical bars represent standard deviation and shaded areas correspond to statistically significant difference in length-at-age between fish in both treatment (lake treatment $P < 0.05$).

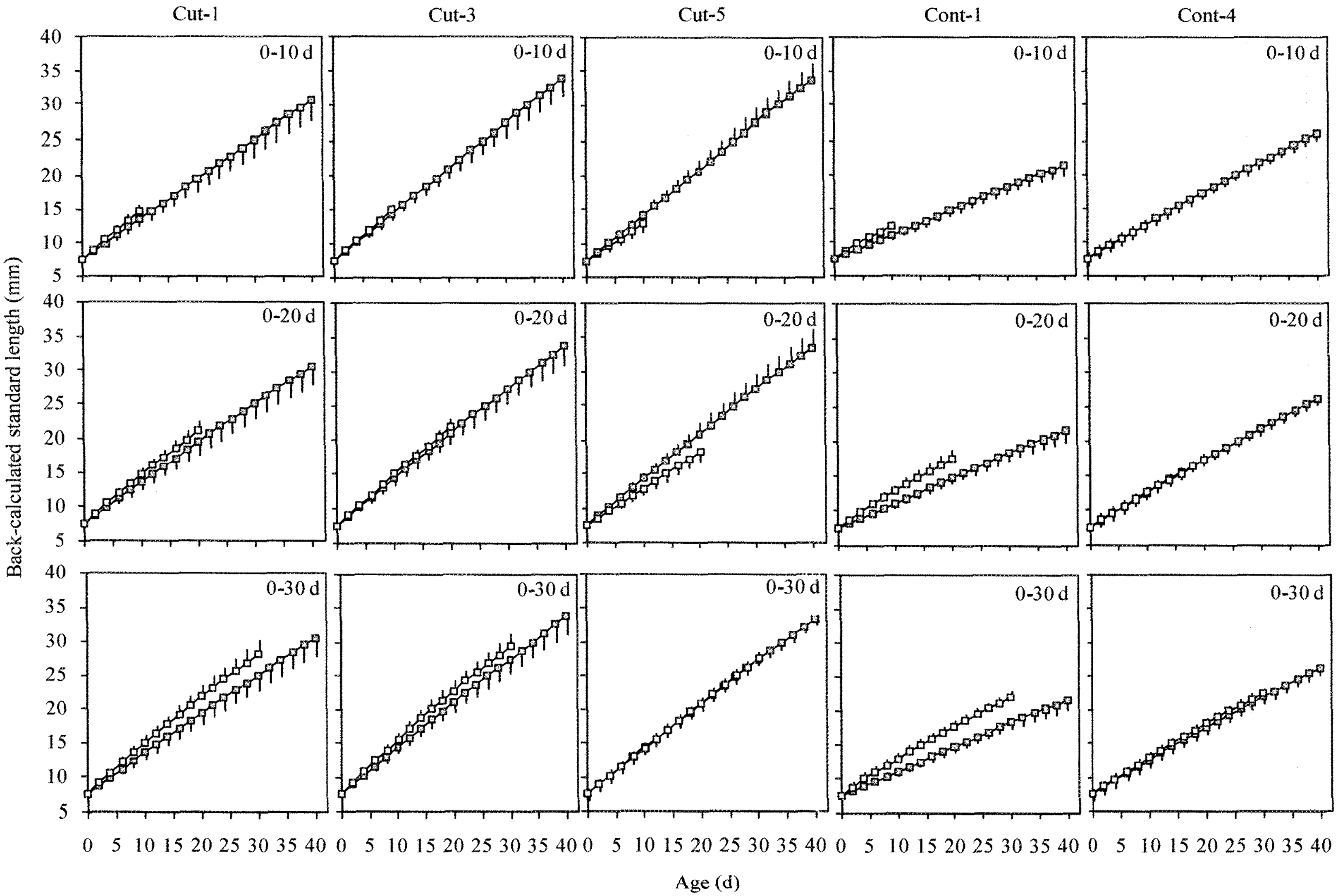

Figure 4.3. Yellow perch mean growth trajectories for the reference population (open squares) and the survivors (filled squares) over the growth intervals 0-10, 0-20 and 0-30 d, in cut and control lakes. Vertical bars represent standard deviation and corresponding statistical results are presented in Table 4.3.

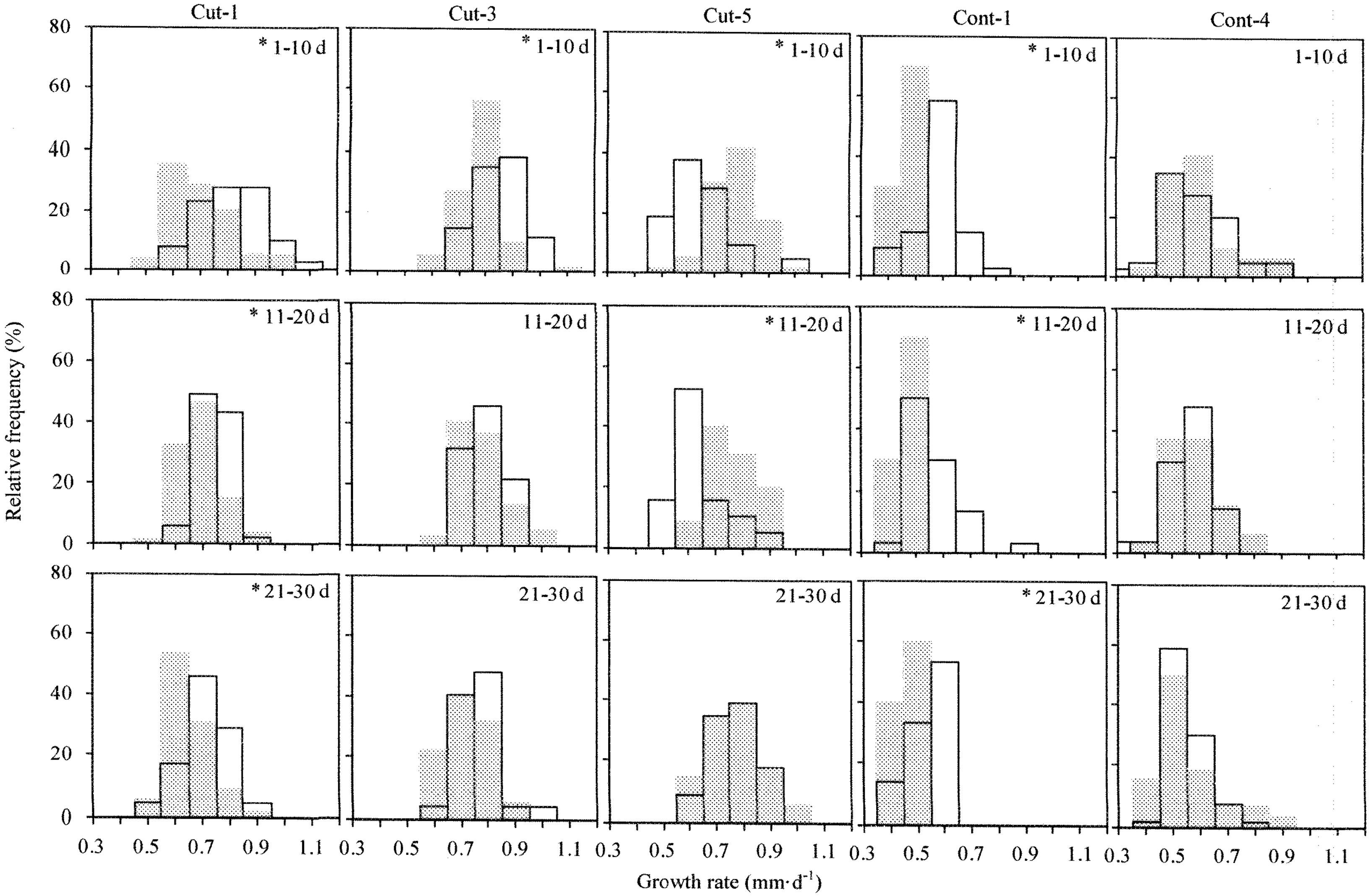

Figure 4.4 Yellow perch growth rate frequency distributions for the population (open bars) and the survivors (filled bars) over the growth intervals 1-10, 11-20 and 21-30 d, in cut and control lakes. Significant differences between population and survivors distributions are marked of an asterisk beside the growth interval (Kolmogorov-Smirnov two-sample test $P < 0.05$).

Table 4.3. Results of the RM-MANOVAs comparing in each lake, the mean growth trajectory of the survivors to that of the reference population, over the growth intervals 0-10, 0-20 and 0-30 d.

Lake	Growth interval (d)	d.f.	*F*	*P* > *F*
Cut-1	0-10	5, 91	5.61	**0.0002**
	0-20	10, 10	3.65	**0.0004**
	0-30	15, 66	3.32	**0.0004**
Cut-3	0-10	5, 97	3.89	**0.0031**
	0-20	10, 89	2.54	**0.0098**
	0-30	15, 70	2.70	**0.0027**
Cut-5	0-10	5, 70	5.22	**0.0004**
	0-20	10, 63	5.01	**<0.0001**
	0-30	15, 62	0.76	0.7194
Cont-1	0-10	5, 45	6.16	**0.0002**
	0-20	10, 29	5.37	**0.0002**
	0-30	15, 9	3.76	**0.0252**
Cont-4	0-10	5, 66	1.14	0.3462
	0-20	10, 48	1.39	0.2101
	0-30	15, 72	1.11	0.3624

In the lake Cut-5, significant selection for fast-growing individuals was observed in the first 20 d of age, after which, selection for growth was no longer observed. The survivors had a higher mean growth trajectory when compared to the reference population in the growth intervals 0-10 and 0-20 d (Fig. 4.3, Table 4.3). Survivors in these growth intervals were longer-at-age than fish of the reference populations from 2 d after hatching (post-hoc ANOVAs, P <0.0005). The growth rate frequencies distributions of surviving yellow perch in the growth intervals between 1-10 and 11-20 d shifted towards higher values than that of the reference populations (Fig. 4.4). Together, results indicated a mild selection for fast growth in lake Cut-5.

Finally, fish in lake Control-4 showed no evidence of selection for growth. Growth trajectory of surviving yellow perch >40 d, as well as their growth rate frequency distribution were similar to that of reference populations composed of fish of younger age at capture (Fig. 4.3, Table 4.3, Fig. 4.4).

4.5.3 Potential for growth at hatching

There was no indication that fish in cut lakes had a higher growth potential at hatching than fish in control lakes. Mean hatch mark radius of fish from both lake treatments were similar, pooling fish independently of their age (cut lakes, 14.4 µm (SD 2.1), control lakes, 14.3 µm (SD 2.1)) and did not differed statistically (lake treatment: $F_{1,3} = 0.08$, $P = 0.8003$).

Yellow perch mean hatch mark radius was also compared between the four age classes within each lake. In all lakes, there was no indication that fish surviving at older age were different in size at hatching (Fig. 4.5). In lakes where selection for slow growth was detected, fish surviving >40 d were not smaller at hatching than younger individuals (Fig. 4.5, Cut-1: $F_{3,170} = 0.90$, $P = 0.4447$, Cut-3: $F_{3,157} = 1.27$, $P = 0.2877$, Control-1: $F_{3,92} = 0.23$, $P = 0.8742$), indicating no predisposition for growth-selective survival present at hatching. In lake Cut-5 where selection for fast growth was observed, surviving fish were similar in size at hatching to fish from reference populations (Fig. 4.5, $F_{3,114} = 1.97$, $P = 0.1223$). Finally, in lake Control-4 where no selection for growth has been observed, fish were also similar in size at hatching independently of their age at capture (Fig. 4.5, $F_{3,151} = 1.38$, $P = 0.2498$).

4.6 DISCUSSION

4.6.1 Factors influencing early life growth of survivors in yellow perch

Growth is the central tenet of major hypotheses on recruitment determination (Chambers & Leggett 1987, Houde 1987, Anderson 1988, Miller et al. 1988, Takasuka et al. 2003, Houde 2008). In a previous study measuring the impact of forest harvesting in Boreal lakes catchments on early life history of yellow perch, we linked the increase in growth to favourable environmental conditions measured after the perturbation (Chapter 2). In the present study, we have demonstrated that early growth was higher for YOY yellow perch in cut lakes, not only for fish having survived to the summer as reported in Chapter 2, but also for fish captured earlier in the season.

4.6.1.1 Environmental conditions

Most studies on growth and survival during early life stages of fish attributed the variability in growth to environmental conditions of temperature and food (Houde 1987, Anderson 1988, Takasuka & Aoki 2006, Houde 2008, Robert et al. 2009). As observed by Claramunt and Wahl (2000) in several freshwater systems, larval growth variability is largely influenced by zooplankton abundance. The fast-growing yellow perch populations in this study were associated with higher dissolved organic carbon concentration, algal biomass and *Daphnia* spp. abundance relative to slow-growing populations. Since temperature did not varied between lakes, we assumed that favourable environmental feeding conditions have largely contributed to the fast growth of YOY yellow perch in cut lakes. A recent work (Chapter 3) has shown that fast growth of YOY yellow perch in these lakes was linked with the abundance of *Daphnia* spp. in the environment, that were probably more conspicuous for yellow perch larvae and juveniles due to the higher DOC concentrations in cut lakes. Together, *Daphnia* spp. abundance and DOC concentration are likely to have induced the rapid growth of yellow perch in cut lakes.

4.6.1.2 Growth-selective survival

If fast growth measured on fish sampled in cut lakes could actually resulted of favourable environmental conditions, it could also resulted of the non-random survival of fast-growing individuals. However, the lake-by-lake analyses of selection have demonstrated that selection for growth was not unidirectional within each lake treatment (Table 4.4). The overall fast growth of fish in cut lakes could not have been due to selection for fast growth alone. Selection for fast growth was in fact observed in only one lake (Cut-5), while selection for slow growth was observed in the two other cut lakes, Cut-1 and Cut-3 (Table 4.4). Considering that in lakes Cut-1 and Cut-3, the surviving fish were the slowing members of the population, the effect of favourable feeding conditions on growth observed in cut lakes may have been more important than initially suspected. On the other hand, the selection for slow growth measured in lake Control-1, coupled to the absence of selection measured in lake Control-4, may have reinforced the slow growth that characterised YOY yellow perch in control lakes (Table 4.4). These results did not match those of Post and Prankevicious (1987) who observed that selection for fast growth was stronger in the slow-growing yellow perch population of lake Dickie than in the fast-growing population of lake St. George U.S.A. Both the spatial replication of our study (five lakes), and the replication of fast- and slow-growing populations (three and two populations respectively), allowed the observation of contrasted combination of growth-selective survival directions that are, selection for fast growth, selection for slow growth and absence of selection (Table 4.4).

Table 4.4. Summary of the factors influencing early growth and relative abundance measured in the last sampling survey in five YOY yellow perch populations followed by relative expected recruitment strength.

	Cut lakes			Control lakes	
Factor	Cut-1	Cut-3	Cut-5	Cont-1	Cont-4
Growth	fast	fast	fast	slow	slow
Environmental conditions	favourable	favourable	favourable	less	less
Selection for growth					
Direction	slow	slow	fast	slow	no sel.
Strength	strong	mild	mild	strong	-
Potential for growth at hatching	no	no	no	no	no
Relative abundance	+	++	++	--	-
Relative expected recruitment	+	++	+++	--	-

4.6.1.3 Potential for growth at hatching

Most studies about growth-selective survival have focused on the influence of environmental conditions on growth (mostly temperature and food) during the larval and the juvenile stages (e.g. Takasuka & Aoki 2006, Robert et al. 2007, 2009). Recent studies now pay attention on the carry-over effects of a potential for growth already present at hatching, on the size achieved by fish during the larval and juvenile period of life and on the growth-selective survival (Buckley et al. 1991, Letcher et al. 1996, Meekan et al. 1998, Grønkjaer & Schytte 1999, Good et al. 2001, Vigliola & Meekan 2002, Macpherson & Raventos 2005, Bang et al. 2006). According to these studies, both the maternal influence (e.g. egg size) and the bioenergetic factors (e.g. incubation temperature) during the egg stage are involved in determining the size at hatching and result in a potential for growth already present at hatching. For example, Grønkjaer and Schytte (1999) have observed that Baltic cod (*Gadus morhua*) larvae that were larger at hatching were most likely to survive. The same pattern was observed for Atlantic cod (*Gadus morhua*), linking strong selection for fast growth to larger size at hatching (Meekan & Fortier 1996).

In this study, there was no indication that potential for growth at hatching may have caused the growth rate discrepancy among lakes. Moreover, potential for growth at hatching did not have determined, neither the growth achieved by fish throughout the season, nor the growth-selective survival observed in the different populations. These observations strengthened the idea that the fast growth of yellow perch larvae and juveniles in cut lakes was actually the result of favourable feeding conditions.

As summarized in Table 4.4, the favourable environmental conditions measured in cut lakes have promoted early growth of yellow perch and have contributed to most of the growth rates discrepancy between cohorts. Growth-selective survival within each lake explained the growth measured on the survivors, but it could not have explained the discrepancy in growth between populations because (1) the discrepancy in growth was already present early in the season (when growth-selective survival just started) and (2), the direction of the selection differed between lake treatments (Table 4.4). Finally, potential for growth at hatching did not contribute in the growth discrepancy between these yellow perch cohorts.

4.6.2 Selection for fast growth vs. selection for slow growth

The widespread expectation that fast-growing fish are most likely to survive have shaped thinking in fisheries science (Leggett & Frank 2008). The prediction of the growth-mortality hypothesis is that as larvae get older and grow, their vulnerability to predation decrease with the decreasing number of predators (the size spectrum theory, Sheldon et al. 1972), and with the improvement of their anti-predator behaviours (the "growth-selective predation" hypothesis Takasuka et al. 2003). Numerous studies have observed such results (e.g. Post & Prankevicius 1987, Hovenkamp 1992, Meekan & Fortier 1996, Sirois & Dodson 2000b, Searcy & Sponaugle 2001, Takasuka et al. 2003, Meekan et al. 2006, Shoji & Tanaka 2006a, Tanaka et al. 2006, Robert et al. 2007). In our study however, only in one yellow perch population (lake Cut-5) were the fast-growing individuals surviving.

As other studies (e.g. Litvak & Leggett 1992, Pepin et al. 1992, Gleason & Bengtson 1996a, 1996b, Takasuka et al. 2004a, 2004b, Gagliano et al. 2007, Nishimura et al. 2007, Takasuka et al. 2007a, Holmes & McCormick 2009), we also observed the unequivocal existence of selection for slow growth in the yellow perch populations of lakes Cut-1, Cut-3 and Control-1. Our results are counter to the current thinking that fast-growing fish are most likely to survive the vulnerable early life stages. Several reasons may justify the selection for slow growth during the early life stages of fish. First of all, according to the optimal foraging theory (Werner & Gilliam 1984, Gerking 1994), the predators actively select the prey conferring the better net energy gain (benefits/costs). Predators could therefore select for the larger prey item possible from a prey field. Other reasons are linked to the higher probability of detection and capture with increasing swimming speed, encounter rate and conspicuousness of fast-growing individuals (Folkvord & Hunter 1986, Bailey & Houde 1989, Fuiman 1989).

In the approach based on the characteristics of survivors, it is quite impossible to directly identify the sources of mortality (Takasuka et al. 2004a). Without considering dispersion because yellow perch completes its entire life cycle in lakes (Scott & Crossman 1973, Whiteside et al. 1985, Post & McQueen 1988), we assumed that the principal source of mortality was predation. The different direction and strength of growth-selective survival between populations could have been caused by the potential predators that characterised each system. Growth-selective survival can differ substantially, and the direction of this difference can be reversed by changes in predator species and size structure (Litvak & Leggett 1992, Rice et al. 1993, Takasuka et al. 2003, McCormick & Hoey 2004, Takasuka et al. 2004b, Takasuka et al. 2007a). The principal species suspected to prey on yellow perch larvae and juveniles were adult yellow perch and northern pike in all lakes, in association with walleye in lakes Cut-3 and Cut-5 and burbot in control lakes. The exact identity and size-structure of the predators actually removing yellow perch larvae and juveniles in each population was not investigated and therefore, we could not have identified the exact causes of the direction of the growth-selective survival observed in each lake.

4.6.3 Implications for recruitment

As discussed by Leggett and Frank (2008), fisheries research focusing on the importance of size ("bigger-is-better" concept), development rate ("stage-duration" concept) and growth rate ("growth-predation" concept) has promoted advances in the knowledge of larval ecology, but it does not have contributed so much to the understanding of recruitment processes in fishes. Our study, as several others, has demonstrated that survival was not always selecting fast-growing individuals. Therefore, is fast growth a prerequisite for strong recruitment?

Fast growth during early life stages of fish turns out to be a necessary, but not a sufficient condition for strong recruitment. As observed in haddock, *Melanogrammus aeglefinus* (Fortier & Quiñonez-Velazquez 1998), and Atlantic mackerel, *Scomber scombrus* (Robert et al. 2007), slow growth invariably resulted in weak recruitment but fast growth resulted in both weak and strong recruitment. Strong recruitment may occur when fish encounter optimal environmental conditions for growth and suffer low predation pressure (Robert et al. 2007). The fact that sometimes slow-growing members of a cohort are most likely to survive may indicate that predators remove fast-growing member of a cohort. However, it does not indicate that selection for slow growth will systematically lead to weak recruitment. The intensity of the selection for growth, i.e. the predation pressure, could be relatively more important than its direction. Indeed, the number of survivors and the recruitment strength will be lower if predation pressure is strong, independently of the direction of selection for growth.

Summarized in the Table 4.4 are the conditions that could help to interpret the recruitment strength in the six lakes. As discussed by Robert et al. (2007), favourable environmental conditions and mild selection for growth are necessary conditions for fast-growing survivors to be recruited in the population in sufficient number. We therefore considered that favourable environmental conditions and fast growth are necessary for strong recruitment and thus, that yellow perch in cut lakes must have had a stronger recruitment relative to fish in control lakes (Table 4.4). We also considered that selection for fast growth must lead to stronger recruitment than selection for slow growth, as do mild selection relative to strong one. At the end, considering all these conditions, the yellow perch population we expected to have had the stronger recruitment was in lake Cut-5 because of the combination of favourable environmental conditions, fast growth and mild selection for fast growth. Using the same reasoning, we suggested that the yellow perch cohort from lake Control-1 have had the weaker recruitment. The abundance measured in August corroborated these predictions and match the results of Bertolo and Magnan (2007) who have observed an increase in YOY yellow perch abundance at the end of the first growing season following forest harvesting in boreal lake catchments.

4.6.4 Conclusion

In small oligotrophic Boreal Shield lakes, the growth rates discrepancy among YOY yellow perch populations appears to be largely regulated by variability in environmental feeding conditions. Growth-selective survival and potential for growth at hatching have not explained the discrepancy in growth among cohorts. Growth-selective survival was not unidirectional among lakes and detailed predation should help explaining such differences. We hypothesised that favourable environmental conditions inducing fast growth during early life have to be coupled to mild selective predation to lead to strong recruitment in yellow perch populations.

4.7 ACKNOWLEDGMENTS

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CHAPITRE 5

DISCUSSION ET CONCLUSION

5.1 LES COUPES FORESTIÈRES... DU BASSIN VERSANT AUX POISSONS

L'étude décrite dans cette thèse constitue une contribution significative à notre connaissance des mécanismes par lesquels une perturbation anthropique dans le bassin versant des lacs boréaux peut, à court terme, influencer l'écologie des jeunes stades de vie chez les poissons d'eau douce. Elle identifie des facteurs environnementaux abiotiques et biotiques modifiés par la coupe forestière ayant une incidence directe ou indirecte sur l'alimentation et la croissance de la perchaude durant les stades larvaire et juvénile. Elle détermine aussi comment la croissance influence la survie dans ces lacs, et si les modifications environnementales post-coupes sont susceptibles d'influencer le recrutement des populations.

5.1.1 Impact des coupes sur les conditions environnementales abiotiques et biotiques de croissance et d'alimentation des jeunes stades de vie

Le principal effet des coupes forestières sur l'écosystème lacustre boréal est sans contredit l'apport en PT et en COD (Rask et al. 1998, Carignan et al. 2000, Prepas et al.

2001, Winkler et al. 2009). Ces apports constituaient le fondement de la formulation de l'hypothèse de base de cette thèse à savoir : les coupes forestières peuvent modifier, à court terme, les conditions environnementales de croissance des larves et des juvéniles de perchaude via un effet trophique ascendant sur l'alimentation. L'apport en PT et en COD peut avoir influencé l'écologie des jeunes stades de vie chez la perchaude de deux façons : (1) par la stimulation de la productivité des réseaux trophiques et (2) par des changements physiques dans les conditions d'alimentation. Les résultats observés dans cette étude corroborent cette hypothèse.

Le P est un élément nutritif considéré limitant pour la productivité des écosystèmes aquatiques d'eau douce. Dans les mêmes lacs que ceux étudiés ici, Winkler et al. (2009) ont mesuré une augmentation significative de la concentration en PT et en COD l'année suivant les coupes. L'augmentation en PT peut vraisemblablement expliquer les augmentations de la biomasse algale mesurée dans cette étude (Chapitres 2 et 3), et dans des études comparables (Planas et al. 2000, Nicholls et al. 2003, Ghadouani et al. 2006). Le COD est, quant à lui, utilisé par le bactérioplancton et les protistes (Arvola et al. 1996, De Lange et al. 2003, Carpenter et al. 2005), ceux-ci servant à leur tour de nourriture aux organismes zooplanctoniques comme les daphnies (Sanders et al. 1996). Selon la théorie des forces ascendantes (McQueen et al. 1986), il est plausible que les effets du PT et du COD sur le phytoplancton, le bactérioplancton et les protistes se soient répercutés positivement sur le zooplancton, expliquant l'abondance accrue de *Daphnia* spp. mesurée dans les lacs perturbés deux ans après la perturbation (Chapitre 3). Cela supporte l'augmentation de la biomasse ou de l'abondance chez les organismes zooplanctoniques de grande taille comme les cladocères obtenus par des études comparables (Rask et al. 1998, Rask et al. 2000, Bertolo & Magnan 2007, Winkler et al. 2009).

Dans cette étude, les lacs perturbés montraient, deux ans après les coupes, une concentration de COD plus élevée que celle des lacs contrôles (Chapitres 2 et 3). Ce résultat concorde avec l'augmentation de COD mesurée à l'aide d'une comparaison avant-après coupes dans les mêmes lacs par Winkler et al. (2009). Le COD, en plus de sa fonction nutritive dans les écosystèmes, comporte des propriétés particulières pouvant modifier l'environnement physique des lacs boréaux. Le COD confère une couleur jaune-brun à l'eau et y influence la transmission lumineuse (Molot & Dillon 1997, France et al. 2000). Ces caractéristiques peuvent avoir modifié le comportement d'alimentation des jeunes perchaudes (Chapitre 3) et par conséquent leur croissance (Chapitre 2). Les chapitres 2 et 3 de l'étude ont montré que les variations post-coupes dans la dynamique trophique et l'environnement physique des lacs sont probablement tous deux responsables des changements observés dans l'écologie des larves de perchaude à la suite des coupes forestières dans le bassin versant des lacs boréaux.

5.1.2 Coupe forestière et croissance larvaire et juvénile chez la perchaude

La croissance durant les jeunes stades de vie chez les poissons est à la base de plusieurs hypothèses en science halieutique. Selon celles-ci, tout facteur provoquant un changement dans la croissance peut engendrer de grandes variations dans le taux de mortalité et la force du recrutement des populations (Houde 1987, Anderson 1988, Houde 2008). Le premier objectif de cette thèse était de vérifier l'hypothèse selon laquelle les coupes forestières dans le bassin versant des lacs boréaux peuvent provoquer des changements environnementaux et modifier la croissance durant les jeunes stades de vie chez la perchaude.

Basé sur un plan d'expérience avant-après perturbation, le chapitre 2 a démontré une augmentation marquée dans la croissance des jeunes perchaudes de l'année en 2005, deux ans après les coupes forestières dans le bassin versant des lacs. La comparaison des caractéristiques individuelles de croissance durant les 40 premiers jours des poissons capturés dans les lacs perturbés et dans les lacs contrôles a révélé qu'avant la coupe forestière, ainsi que l'année suivant celle-ci, la croissance des poissons des deux groupes de lacs était similaire. Par contre, une grande différence dans le taux de croissance et la longueur-à-l'âge a été mesurée en 2005. La diminution interannuelle du taux de croissance des lacs contrôles correspondant aux les fluctuations naturelles, la stabilité interannuelle des taux de croissance des poissons des lacs perturbés reflètent une meilleure croissance dans ces lacs. L'augmentation de la croissance, couplée à l'augmentation de la biomasse algale pélagique, suggère un effet trophique ascendant (*bottom-up*) des coupes forestières dans les réseaux trophiques des lacs perturbés. L'absence de réponse dans la biomasse zooplanctonique pourrait avoir été provoquée par les forces trophiques descendantes (*top-down*) des perchaudes sur leurs proies zooplanctoniques (Carpenter et al. 1985). L'impact trophique des modifications environnementales post-coupes semble responsable des résultats obtenus dans cette première série de résultats.

5.1.3 Alimentation et croissance chez la jeune perchaude en relation avec les changements abiotiques et biotiques post-coupes

L'hypothèse de l'impact trophique des coupes forestières sur l'alimentation et la croissance des jeunes perchaudes de l'année a été vérifiée dans le Chapitre 3. La description exhaustive et la comparaison de la diète des perchaudes capturées en 2005 a permis de confirmer que les poissons des lacs perturbés se nourrissaient principalement de deux espèces de proies, *Daphnia* spp. et *Polyphemus pediculus* alors que les poissons des lacs contrôles avaient une diète plus diversifiée. Par la comparaison de variables environnementales abiotiques et biotiques, on constate que les lacs perturbés ont offert des conditions environnementales d'alimentation différentes aux jeunes perchaudes. En effet, l'abondance de *Daphnia* spp. y était significativement supérieure, ainsi que les concentrations de Chl *a* et de COD suggérant, comme les résultats présentés dans le Chapitre 2, un effet trophique ascendant (*bottom-up*) des coupes, partant des éléments nutritifs jusqu'aux larves et juvéniles de perchaude. Il a aussi été observé que, de façon générale pour les jeunes perchaudes, le succès d'alimentation sur *Daphnia* spp, ainsi que la croissance récente augmentaient de façon exponentielle avec l'abondance de *Daphnia* spp. dans l'environnement jusqu'à l'atteinte d'un plateau de saturation. Ce type de relation fonctionnelle entre le prédateur et ses proies correspond à une relation fonctionnelle de type II (Houde & Schekter 1980, Mills et al. 1989, Miller et al. 1992). La haute résolution taxonomique du zooplancton contenu dans l'estomac a permis de raffiner cette relation fonctionnelle. Une relation qui n'a d'ailleurs pas été observée avec des groupes fonctionnels plus généraux, les cladocères par exemple.

On notera avec intérêt qu'à abondance égale de *Daphnia* spp. dans l'environnement, les jeunes perchaudes des lacs perturbés manifestaient un meilleur succès d'alimentation et une croissance récente plus rapide que les perchaudes des lacs contrôles. Cette observation suggère une influence positive d'une plus grande concentration de COD dans les lacs perturbés. En effet, le COD, en grande partie responsable de la couleur de l'eau, contribue à la transparence de l'eau et accentue le contraste. Or, les études sur l'écologie de l'alimentation des larves de poissons montrent une amélioration de la disponibilité des proies avec un léger accroissement de la turbidité (Sirois & Dodson 2000a, Utne-Palm 2002, Shoji et al. 2005). Les explications les plus communes étant (1) l'hypothèse de l'effet physique et (2) l'hypothèse de la motivation (Utne-Palm 2002). Selon la première hypothèse, une légère hausse de turbidité, favoriserait la visibilité et la capture des proies planctoniques par les poissons en raison d'une augmentation du contraste entre la proie et son milieu environnant (Hale & Carlson 1972, Hinshaw 1985, Sandström 1999, Strand et al. 2007). L'hypothèse de la motivation est basée sur la théorie voulant que la vision des poissons piscivores diminue avec la turbidité (De Robertis et al. 2003). Ainsi, une légère augmentation de turbidité diminuerait le risque de prédation des larves de poissons, leur procurant un refuge contre la prédation, tout en favorisant leur propre alimentation (Gregory & Northcote 1993). On peut enfin penser que les jeunes perchaudes de l'année des lacs perturbés ont bénéficié d'une plus grande abondance de proies, couplée à une détection plus facile de celles-ci, ce qui a pu diminuer le coût énergétique associé à la recherche de la nourriture, favorisant ainsi la croissance (Sirois & Dodson 2000a, Utne-Palm 2002, Rennie et al. 2005).

Le Chapitre 3 regroupe les résultats les plus informatifs en ce qui a trait à la compréhension du rapport de causalité entre la coupe forestière, la croissance rapide et l'augmentation de l'abondance chez les perchaudes des lacs boréaux observée par Bertolo et Magnan (2007). Nous y suggérons que le COD participe à la fois à l'augmentation de l'abondance de *Daphnia* spp., et à l'augmentation de sa détection par les larves et juvéniles de perchaudes, favorisant de la sorte leur croissance. Ainsi, comme cela avait été suggéré par Bertolo et Magnan (2007), les résultats de cette thèse font ressortir l'importance du COD dans les écosystèmes lacustres boréaux et suggèrent qu'une perturbation du bassin versant par les coupes forestières peut engendrer des modifications de l'habitat pouvant influencer l'alimentation, la croissance et donc, la survie des jeunes perchaudes.

5.1.4 Déterminants de la croissance rapide post-coupes chez la perchaude

Le dernier volet de la thèse avait pour objectif de vérifier la contribution (1) des conditions environnementales, (2) de la survie sélective à la croissance et (3) du potentiel de croissance sur la divergence dans la croissance larvaire et juvénile des perchaudes des différents lacs en 2005. La croissance rapide des jeunes perchaudes des lacs perturbés peut avoir été causée par des conditions environnementales de température et/ou d'alimentation favorables, tel que suggéré dans les chapitres 2 et 3. La croissance rapide peut aussi avoir été influencée par des facteurs indépendants de la coupe forestière comme le retrait sélectif d'individus à croissance lente par la prédation. Finalement, la croissance rapide peut aussi avoir été causée par un potentiel de croissance déjà présent à l'éclosion et donc indépendant de l'influence trophique des coupes forestières sur l'alimentation des larves et des juvéniles. La contribution de chacun de ces processus dans la croissance des survivants a dû être évaluée afin de comprendre plus exactement la participation de la perturbation dans les résultats.

D'abord, la température ne permettait pas d'expliquer la variation dans la croissance larvaire et juvénile des différentes populations de perchaudes en 2005. Par contre, les lacs perturbés présentaient des valeurs de COD, de biomasse algale et d'abondance de *Daphnia* spp. supérieures à celles des lacs contrôles. Nous suggérons donc que les conditions environnementales d'alimentation favorables dans les lacs perturbés expliquent en partie la croissance rapide des perchaudes dans ces lacs. Par ailleurs, la croissance rapide des perchaudes des lacs perturbés n'a pas été causée par une sélection pour la croissance rapide dans ces lacs. En effet, les survivants de deux des trois lacs perturbés se sont avérés être les individus à croissance lente; la sélection pour la croissance rapide n'a donc été observée que dans une seule population de perchaudes provenant des lacs perturbés. Cependant, la croissance lente des perchaudes des lacs contrôles a pu être accentuée par la sélection pour la croissance lente mesurée dans une des deux populations. La sélection pour la croissance ne peut donc expliquer la divergence dans la croissance des jeunes perchaudes des lacs perturbés et des lacs contrôles. Enfin, le potentiel pour la croissance dès l'éclosion n'a été observé dans aucune population. Ensemble, ces résultats suggèrent que la croissance plus rapide des jeunes perchaudes des lacs perturbés a bel et bien été provoquée par des conditions environnementales d'alimentation favorables la suite des coupes forestières.

5.2 SÉLECTION POUR LA CROISSANCE RAPIDE VS. SÉLECTION POUR LA CROISSANCE LENTE

Les résultats obtenus au Chapitre 4 ne correspondent pas aux prédictions découlant de l'hypothèse croissance-mortalité ayant orienté la plupart des recherches sur la survie larvaire. La réplication spatiale des populations de perchaudes qui caractérise cette étude a clairement démontré que ce ne sont pas toujours les individus à croissance rapide qui survivent. Parmi les cinq populations, la sélection pour la croissance rapide a été observée dans une seule population, tandis que la sélection pour la croissance lente a été identifiée dans trois autres populations, la dernière population ne démontrant aucune sélection pour la croissance. À l'évidence, la sélection pour la croissance existe parmi les populations de perchaudes des lacs boréaux mais les survivants ne sont pas nécessairement les individus à croissance rapide.

Souvent ignorées, nombre d'études ont, elles aussi, observé des évidences de sélection pour la croissance lente (e.g. Litvak & Leggett 1992, Pepin et al. 1992, Gleason & Bengtson 1996b, 1996a, Takasuka et al. 2004a, 2004b, Gagliano et al. 2007, Nishimura et al. 2007, Takasuka et al. 2007a, Holmes & McCormick 2009). La sélection pour la croissance lente dispose aussi de plusieurs arguments valables. Selon la théorie de l'alimentation optimale, les prédateurs tendent à sélectionner les proies offrant le meilleur rapport bénéfices/coûts (Werner & Gilliam 1984, Gerking 1994). Il ne serait donc pas étonnant que les prédateurs sélectionnent les plus grandes proies ingérables. En raison de leurs capacités natatoires supérieures et de leur plus grande détectabilité, les larves à croissance rapide présentent une probabilité de rencontre accrue avec les prédateurs, de même qu'une plus grande visibilité, ce qui augmente leur probabilité de se faire capturer par ceux-ci (Folkvord & Hunter 1986, Bailey & Houde 1989, Fuiman 1989).

Les caractéristiques des prédateurs sont probablement à l'origine de la variabilité dans la direction de la sélection pour la croissance observée entre les différentes populations de perchaudes en 2005. Comme certaines études l'ont observé, la composition en espèces et la structure de taille des prédateurs peuvent modifier la direction de la sélection pour la croissance (Rice et al. 1993, Takasuka et al. 2004a, 2004b, 2007a).

5.3 CROISSANCE ET RECRUTEMENT

Les recherches effectuées dans le contexte de l'hypothèse croissance-mortalité ont certes favorisé l'acquisition de nouvelles connaissances sur l'écologie larvaire; elles n'ont cependant pas contribué substantiellement à la compréhension des processus de recrutement (Leggett & Frank 2008). Cette étude, comme beaucoup d'autres, a démontré que la survie n'est pas toujours orientée vers les individus à croissance rapide. Par conséquent, la croissance rapide s'avère-t-elle un prérequis à un fort recrutement ? En ce sens, Fortier et Quiñonez-Velazquez (1998) ainsi que Robert et al. (2007) ont observé, chez l'aiglefin (*Melanogrammus aeglefinus*) et le maquereau (*Scomber scombrus*) respectivement, que la croissance lente mène invariablement à une année de faible recrutement, alors que la croissance rapide peut mener à une année de fort recrutement, mais aussi à une année de faible recrutement. La croissance rapide semble donc être une condition nécessaire mais non suffisante pour entraîner un fort recrutement. Robert et al.

(2007) ont d'ailleurs observé qu'un fort recrutement est associé non seulement à la croissance rapide mais aussi à une pression de prédation modérée.

La pression de prédation, comme les conditions environnementales, a un rôle important à jouer dans la détermination de la force du recrutement. La pression de prédation influence le nombre de survivants et la force du recrutement. Le *match* ou le *mismatch* entre les prédateurs et les larves de poissons pourrait donc influencer l'abondance des survivants et la force du recrutement et ce, indépendamment de la direction de la sélection.

La sélection pour la croissance lente indique que les prédateurs éliminent les individus à croissance rapide dans une population, mais elle peut tout de même mener à un fort recrutement si la pression de prédation est faible ou modérée. Dans le cas d'une faible pression de prédation, le nombre d'individus qui survivent sera nécessairement plus élevé que si la sélection pour la croissance est forte.

Certains critères permettent d'appuyer les indices d'abondance des survivants et de déterminer la force relative du recrutement parmi les différentes populations en 2005. Les critères favorables à un fort recrutement sont (1) des conditions environnementales optimales pour la croissance, (2) une croissance rapide, et (3) une pression pour la croissance modérée, sans direction ou favorisant la croissance rapide. Ces conditions ont été rencontrées pour la population de perchaudes du lac Cut-5. Par ailleurs, les populations des lacs perturbés présentant une croissance plus rapide que celles des lacs contrôles, nous estimons que le recrutement des cohortes des lacs perturbés a été supérieur à celui des lacs contrôles.

5.4 SIGNIFICATION DES RÉSULTATS POUR LA FORESTERIE

Les résultats obtenus dans le cadre de ce projet de doctorat démontrent comment la modification du bassin versant d'un lac peut influencer sa dynamique trophique, des éléments nutritifs, jusqu'aux larves et aux juvéniles de perchaude. Pour diverses raisons, les résultats obtenus ne justifient pas la modification des normes d'intervention en milieu forestier visant la protection de la faune aquatique. Les résultats de cette thèse peuvent semblent même suggérer un effet bénéfique des coupes forestières sur les poissons en général, du moins après deux ans. Tel n'est pas l'objet, ni la conclusion de cette étude. D'emblée, l'étude porte sur les larves et les juvéniles de perchaude. Il serait inadéquat d'extrapoler ces résultats aux perchaudes adultes et aux autres espèces de poisson.

D'autre part, cette étude porte sur le milieu lacustre et l'impact des coupes forestières sur les poissons en rivière peut s'avérer tout à fait différent. De plus, l'étude s'étendait sur une durée de deux ans post-coupes; il serait imprudent d'estimer des impacts à plus long terme sur la seule base de ces résultats. On peut même supposer que les impacts observés ne soient observables qu'à court terme puisque les effets des coupes sur les éléments nutritifs et le COD ne sont observés qu'à court terme (Pinel-Alloul et al. 2005b) et que les écosystèmes semblent résilients aux perturbations comme les coupes forestières (Jalal et al. 2005). Compte tenu de ces arguments, il serait inapproprié de conclure à un effet bénéfique des coupes forestières à la lumière des résultats de cette étude. Si les instances publiques décident de pratiquer un aménagement forestier écosystémique, elles devront considérer les impacts de façon elle aussi écosystémique, incluant les écosystèmes forestiers autant que les écosystèmes aquatiques, en rivière comme en lac.

5.5 CONTRIBUTION ET ORIGINALITÉ DE L'ÉTUDE

Cette thèse représente une contribution originale au domaine de l'écologie des jeunes stades de poisson. Les fondements de l'écologie larvaire ont d'abord été étudiés en milieu marin et, proportionnellement, très peu d'études ont traité de l'écologie des jeunes stades de vie chez les poissons en eau douce. Parmi les poissons d'eau douce, la perchaude est une espèce très bien décrite, étant commune dans les communautés de poissons des lacs en Amérique du Nord et faisant l'objet d'une pêche sportive ou commerciale importante. Malgré cela, il existe peu de littérature sur l'écologie des jeunes stades de vie de la perchaude dans les lacs oligotrophes de la partie la plus septentrionale de son aire de distribution.

Les études portant sur la survie sélective à la croissance chez les jeunes stades de vie des poissons a aussi été majoritairement réalisée en mer. L'étude de la perchaude en milieu aquatique boréal a permis de répliquer spatialement les variables mesurées et les phénomènes étudiés. Cette thèse est donc la première à décrire des cas de sélection pour la croissance de différentes directions, dans des populations de perchaudes distinctes et ce, en milieu naturel.

Le plan d'expérience avant-après privilégié dans la réalisation de cette thèse lui confère une partie de son originalité, en plus de s'avérer une façon rigoureuse et adaptée à détecter un impact anthropique. La plupart des études mesurant l'impact des coupes forestières en lac sont des études comparatives. En effet, celles-ci ont décrit et comparé des variables dans des lacs perturbés et dans des lacs non perturbés, déduisant que les différences mesurées dans ces variables étaient attribuables aux coupes forestières.

Cependant, ce type de plan d'expérience risque d'imputer aux coupes l'effet de la variabilité naturelle qui existe entre les écosystèmes lacustres (Keough & Mapstone 1995, Winkler et al. 2009).

La présente thèse tire aussi son originalité dans la spécificité l'écosystème dans lequel elle a été réalisée, ainsi que des stades du cycle de vie des poissons qui sont y étudiés. Les études de l'impact des coupes forestières sur les écosystèmes aquatiques ont surtout porté sur les écosystèmes lotiques et sur les espèces de poissons qui y sont associées, particulièrement les salmonidés (St-Onge et al. 2001, Northcote & Hartman 2004). Peu d'études ont porté sur les écosystèmes lentiques, et un plus petit nombre encore se sont concentrées sur les jeunes stades de vie, même si ceux-ci représentent une étape clé dans le cycle de vie des poissons en raison de leur grande vulnérabilité aux changements environnementaux.

L'originalité de cette thèse tient aussi au fait qu'elle constitue la seule étude traitant de l'impact des coupes forestières sur les poissons en s'intéressant aux jeunes stades de vie et en utilisant les caractéristiques individuelles des poissons. L'utilisation de données individuelles longitudinales permet d'évaluer certaines caractéristiques qui ne sont ainsi pas «gommées» par la moyenne de la population, considérant que la majorité des individus meurent en bas âge. Ainsi, dans cette étude, l'utilisation de la microstructure de l'otolithe s'est avéré un outil efficace pour extraire des données individuelles longitudinales de croissance, ainsi que l'âge des poissons et leur date d'éclosion. Tandis que certaines études ont utilisé les otolithes de type sagitta comme outil (Post & Prankevicius 1987, Powles & Warlen 1988), les lapilli ont été préférés dans d'autres dont celle-ci (Dale 2000, Fitzgerald et al. 2001, Fitzgerald et al. 2004). En effet, l'utilisation des lapilli permet une lecture plus nette : c'est pourquoi nous en avons fait mention au Chapitre 2.

5.6 PERSPECTIVES DE RECHERCHE

Cette thèse doctorale aborde l'écologie des jeunes stades de vie selon une approche appliquée à une problématique particulière, soit la perturbation par la coupe forestière des conditions environnementales abiotiques et biotiques des lacs boréaux. Elle permet d'approfondir les connaissances sur l'écologie de la perchaude durant les stades pré-recrue en utilisant un plan d'expérience précis et adapté au milieu naturel. Les résultats obtenus ouvrent la voie sur plusieurs nouvelles questions et perspectives de recherche.

5.6.1 Effets de la hausse de COD sur l'écologie de l'alimentation des larves et des juvéniles de perchaude

Nos résultats suggèrent que la hausse de COD post-coupes serait à l'origine de l'augmentation de l'abondance de *Daphnia* spp., de sa visibilité et de sa détection par les larves et les juvéniles de perchaudes des lacs perturbés, ces sujets affichant un meilleur succès d'alimentation et une meilleure croissance (Chapitres 2 et 3). Ce raisonnement s'appuie sur plusieurs études ayant observé qu'un environnement turbide favorise le succès d'alimentation des larves et des juvéniles de poissons (Boehlert & Morgan 1985, Miner & Stein 1993, Sandström 1999, Sirois & Dodson 2000a, Utne-Palm 2002). Pour la plupart, ces études considèrent la turbidité comme un indice de la quantité de matières en suspension et la mesurent en unités de turbidité néphélométriques (NTU). La teneur en

COD contribue à la transparence de l'eau, mais peu d'études se sont attardées à décrire l'influence de la couleur de l'eau sur l'alimentation et la croissance des jeunes stades de vie des poissons. La majorité des larves et des juvéniles de poissons comme la perchaude sont des prédateurs planctonivores visuels (Blaxter 1986, Wahl et al. 1993, Sandström 1999). La visibilité d'une proie pour un prédateur visuel requiert la détection d'une différence de contraste entre la proie et son environnement (arrière-plan), cette différence dépendant des propriétés optiques de l'objet (la proie), de l'arrière-plan et du médium (Hinshaw 1985, Utne-Palm 2002).

Une expérimentation en laboratoire permettrait de vérifier l'effet d'un gradient de COD sur la détection et le taux de capture des proies chez des perchaudes aux stades larvaire et juvénile, ainsi que son effet sur la croissance. En contrôlant la concentration de COD, il serait possible de mesurer l'influence des propriétés optiques de l'arrière-plan et du médium. De plus, en offrant aux jeunes poissons des proies de couleur et de taille variées, il serait possible de vérifier l'influence de la couleur de l'eau sur la sélection des proies en fonction de leur type ou de leur taille. De telles données amélioreraient nos connaissances sur l'écologie de l'alimentation des jeunes stades de vie des poissons des lacs boréaux reconnus pour avoir des concentrations de COD parmi les plus élevées.

5.6.2 Variations spatiales et ontogéniques de la survie sélective à la croissance

Nos résultats ont démontré que la croissance, l'alimentation, la direction et l'intensité de la sélectivité pour la croissance chez la perchaude peuvent différer d'un lac à l'autre.

Nous ignorons toutefois si ces facteurs varient de façon spatio-temporelle à l'intérieur de chaque lac.

La perchaude est un poisson qui effectue des migrations ontogéniques du milieu pélagique vers le milieu littoral (Whiteside et al. 1985, Post & McQueen 1988). Les zones pélagiques et littorales des lacs sont caractérisées par des communautés zooplanctoniques et ichthyennes variables. Par exemple, les communautés de prédateurs des lacs boréaux étudiées dans cette thèse étaient caractérisées par le doré jaune, un prédateur pélagique, et par le grand brochet, un prédateur davantage littoral. Les champs de proies et de prédateurs pouvant varier d'une zone à l'autre, les migrations ontogéniques de la perchaude peuvent exposer celles-ci à des conditions d'alimentation et de prédation différentes pouvant influencer leur croissance et leur survie (Whiteside et al. 1985, Post and McQueen 1988, Dettmers et al. 2005), comme cela a été décrit pour certaines espèces de poissons des récifs coralliens (Vigliola & Meekan 2002, Gagliano & McCormick 2007, Gagliano et al. 2007).

Il serait pertinent de vérifier l'hypothèse selon laquelle l'alimentation, la croissance et les patrons de sélectivité pour la croissance peuvent varier en fonction de l'habitat et de l'ontogénie. Pour tester cette hypothèse, il serait nécessaire de réaliser au moins quatre campagnes d'échantillonnage des jeunes poissons et de leurs proies zooplanctoniques, deux durant la phase larvaire pélagique, et les deux autres durant la phase juvénile littorale.

5.6.3 Influence des prédateurs sur la survie sélective à la croissance

À la lumière des résultats décrits au Chapitre 4, nous avons émis l'hypothèse que la composition spécifique des prédateurs propres à chaque lac pouvait expliquer la variabilité inter-lac dans la direction et l'intensité de la survie sélective à la croissance durant les jeunes stades de vie chez la perchaude. Bien que la composition en espèces des prédateurs potentiels soit précisée pour l'ensemble des lacs, l'identité réelle des prédateurs de jeunes stades de perchaudes demeure toutefois inconnue. Cette information permettrait de vérifier si la prédation peut effectivement expliquer les patrons de survie sélective à la croissance. D'abord, une analyse isotopique des atomes d'azote et de carbone ($\delta15N$ et $\delta13C$) des prédateurs potentiels et des larves et juvéniles de perchaude permettrait de vérifier la position trophique des prédateurs et leur source de nourriture. Conjointement, une analyse des contenus stomacaux des prédateurs potentiels pourrait fournir de l'information sur les caractéristiques individuelles des perchaudes ingérées et, comparée à celles des larves dans le milieu, permettrait d'identifier les mécanismes précis de prédation sélective à la croissance (Takasuka et al. 2003).

5.6.4 Recrutement des populations de perchaudes

Les résultats décrits aux Chapitres 2 et 3 ont indiqué que les coupes forestières favorisaient à court terme la croissance larvaire et juvénile chez la perchaude des lacs boréaux. Le Chapitre 4 a pour sa part montré que durant le premier été de vie, la croissance rapide n'était pas une condition essentielle à la survie jusqu'à la fin de l'été pour une population donnée. En effet, à l'encontre de l'hypothèse croissance-mortalité, les perchaudes à croissance lente peuvent être celles qui survivent à l'été dans certains lacs.

Le recrutement a été estimé à partir de l'indice d'abondance des survivants à la fin de l'été. Par contre, un échantillonnage mesurant l'abondance de cette même cohorte au printemps 2006 aurait été encore plus précis dans l'évaluation de la force du recrutement dans chacune des populations étudiées, considérant que la mortalité hivernale constitue le dernier facteur ajustant le niveau de recrutement des populations de perchaudes (Post & Evans 1989). Il serait tout à fait pertinent de vérifier l'importance relative des différentes conditions requises à un fort recrutement des populations dans la détermination de la force du recrutement soit, la croissance rapide, l'absence de sélection pour la croissance ou une sélection pour la croissance rapide et d'intensité modérée.

Pour atteindre cet objectif, il serait nécessaire d'élaborer un plan d'échantillonnage mesurant autant l'abondance des perchaudes à la fin de l'été et le printemps suivant, que la direction et l'intensité de la sélection pour la croissance. L'échantillonnage répété d'une autre cohorte appartenant aux mêmes populations permettrait de vérifier si la direction et l'intensité de la survie sélective à la croissance varient au sein d'une même population et si les mêmes différences sont observées entre populations. De tels résultats amélioreraient la compréhension des processus déterminant la force du recrutement des populations de perchaudes des lacs boréaux oligotrophes.

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