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Échantillonnage et modélisation de l'habitat des communautés de poissons de rivière des basses Laurentides

par

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Échantillonnage et modélisation de l'habitat des communautés de poissons de rivière des basses Laurentides

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Résumé

Plusieurs études à grande échelle ont identifié la modification ou la perte d'habitats comme menace principale à la conservation des communautés de poissons d'eau douce. Au Canada, « aucune perte nette dans la capacité productive des habitats » (NNL) est le principe directeur de la politique de gestion des habitats du ministère des Pêches et Océans. Le respect du NNL implique l'avancement des connaissances au niveau des relations entre les poissons et leurs habitats, de même que des outils pour quantifier l'impact de la modification des habitats sur les poissons. Les modèles d'utilisation de l'habitat des poissons (FHUM) sont des outils qui permettent d'améliorer nos connaissances des relations poissons – habitat, de prédire la distribution des espèces, mais aussi leurs densités, biomasses ou abondances, sur la base des caractéristiques de l'environnement.

L'objectif général de mon mémoire est d'améliorer la performance des FHUM pour les rivières des basses Laurentides, en suggérant des perfectionnements au niveau de 2 aspects cruciaux de l'élaboration de tels modèles : la description précise de la communauté de poissons et l'utilisation de modèles statistiques efficaces.

Dans un premier chapitre, j'évalue la performance relative de la pêcheuse électrique et de l'échantillonnage en visuel (plongée de surface) pour estimer les abondances des combinaisons d'espèces et de classes de taille des poissons en rivière. J'évalue aussi l'effet des conditions environnementales sur les différences potentielles entre les communautés observées par ces 2 méthodes d'échantillonnage. Pour ce faire, 10 sections de rivière de 20 m de longueur ont été échantillonnées à l'aide de ces 2 méthodes alors qu'elles étaient fermées par des filets de blocage. 3 plongeurs performèrent l'échantillonnage en visuel en se déplaçant de l'aval vers l'amont des sections, tout en dénombrant les espèces et classes de taille. Par la suite, nous avons fait 3 passages de pêcheuse électriques et les abondances furent estimées grâce à un modèle restreint de maximum de vraisemblance, basé sur la diminution des abondances observées. De plus grandes abondances de poissons furent observées en visuel qu'avec la pêcheuse électrique à tous les sites. La richesse spécifique observée en visuel était plus élevée (6/10) ou égale (4/10) à celle observée avec la pêcheuse

électrique. Les différences entre les communautés de poissons observées à l'aide de ces 2 méthodes ne purent être reliées aux conditions environnementales. Les résultats de cette expérience sont contraires à ceux de toutes les études comparant ces 2 méthodes d'échantillonnage, lesquels suggèrent une supériorité de la pêcheuse électrique. Les conditions environnementales de notre expérience étaient distinctes de celles observées dans les autres études (absence d'arbres tombés dans l'eau, très peu de substrats grossiers), mais la différence la plus marquante était en terme de communauté de poissons observée (dominance des cyprinidés et des centrarchidés plutôt que des salmonidés). Je termine ce chapitre en suggérant que les caractéristiques comportementales favorisant l'évitement de la capture (formation de bancs) et facilitant l'observation en visuel (curiosité) sont responsables de la supériorité de la plongée de surface pour échantillonner les communautés dans les rivières des basses Laurentides.

Dans un deuxième chapitre, je développe des FHUM pour des communautés de poissons de rivière ayant plusieurs espèces. Dans le but de simplifier la modélisation de telles communautés et d'améliorer notre compréhension des relations poissons – habitat, j'utilise les concepts de guilde écologique et de filtre environnemental pour explorer les relations entre les guildes formées sur la bases de différents types de traits (reproducteurs, taxonomiques, éco-morphologiques et alimentaires) et les conditions environnementales locales à l'échelle du méso-habitat. Les modèles d'habitats basés sur les guildes reproductrices ont clairement surpassé les autres modèles, parce que l'habitat de fraie reflète l'habitat de préférence en dehors de la période de reproduction. J'ai également utilisé l'approche inverse, c'est à dire définir des guildes d'utilisation de l'habitat et les mettre en relation avec les traits des espèces. Les traits reliés à l'alimentation des poissons ont semblés être les meilleurs pour expliquer l'appartenance aux groupes d'utilisation de l'habitat, mais le modèle utilisé ne représentait pas bien la relation entre les groupes. La validation de notre modèle basé sur les guildes reproductrices avec un jeu de données indépendant pourrait confirmer notre découverte, laquelle représente une manière prometteuse de modéliser les relations poissons – environnement dans des communautés de poissons complexes.

En conclusion, mon mémoire suggère d'importantes améliorations aux FHUM pour les communautés de poissons des basses Laurentides, en suggérant de prendre en compte les caractéristiques biologiques des cours d'eau dans le choix d'une méthode d'échantillonnage, et également en utilisant une méthode prometteuse pour simplifier les FHUM de communautés de poissons complexes : les guildes reproductrices.

Mots-clés : Pêcheuse électrique, plongée de surface, centrarchidé, cyprinidé, rivière, modèle d'habitat, méso-habitat, guilde reproductrice, alimentaires, éco-morphologique et taxonomique.

Abstract

Many large scale studies have identified habitat modification or habitat losses as primary threats for the conservation of freshwater fish communities. In Canada, No Net Loss (NNL) of the productive capacity of habitats is the guiding principle of the Department of Fisheries and Oceans' policy for the management of fish habitat. To respect NNL, a better understanding of fish-habitat relationships is required, as well as tools to quantify the impact of habitat modifications on fish. Fish habitat use models (FHUM) are tools that can improve our understanding of fish-habitat relationships, predict species occurrences, densities or biomass on the basis of habitat descriptors and quantify habitat requirements. They consist in relationships between biological descriptors of fish and habitat descriptors.

The general objective of my thesis is to improve the performance of FHUM for the lower Laurentian streams by suggesting refinements on 2 crucial aspects in the development of these models: a precise description of the fish community and the use of efficient statistical models.

In the first chapter, I evaluate the relative performance of electrofishing and visual surveys (snorkeling) for estimating the abundance of combinations of fish species and size classes in rivers. I also assessed the effect of environmental conditions on potential differences between the results obtained using these two sampling methods. Sampling sites consisted in 10 river sections of 20 m in length distributed in the Laurentian region of Québec. Both methods were used while sections were blocked. Three snorkelers that swam the river sections upstream while identifying and counting fish of each species and size-classes performed visual surveys. Three-pass electrofishing was performed and abundances were estimated with a maximum likelihood depletion model. Greater abundances of fish were observed by snorkeling than by electrofishing at all sites. Snorkeling species richness was higher (6/10) or equal (4/10) to electrofishing richness. Differences in the fish communities observed by both sampling methods were not related to environmental conditions. The results of our work are therefore contrary to that of most published studies

that suggested the superiority of electrofishing on visual surveys. Compared to the conditions found in previous studies, our sampling sites had different environmental characteristics (no fallen trees, insignificant cover of large cobble and boulder) but the most striking dissimilarity was in terms of fish communities (dominance of cyprinids and centrarchids instead of salmonids). Behavioural characteristics favouring capture avoidance (schooling) and facilitating underwater observation (curiosity) may be responsible for the superiority of visual surveys in our study rivers. Survey methods should be selected based on fish community composition.

In the second chapter, I develop FHUM for complex stream fish communities. In order to simplify the modelling of such communities, as well as improve our understanding of fish – habitat relationships, I used the ecological guild concept and the niche filtering hypothesis to explore the relationships between guilds based on different types of traits (eco-morphological, reproductive, alimentary and taxonomic) and local environmental descriptors, at the coarse meso-habitat scale. Reproductive guilds led to FHUM that clearly outperformed the other 3 approaches, because of the close relationship between preferred spawning grounds and non spawning habitat preferences, and also because reproductive traits are linked to habitat characteristics at the reach or coarse mesohabitat scale. We also defined guilds based on habitat-use and related them to species traits. Traits related to the feeding biology of fishes seemed to be the best at explaining the habitat-use guilds, but our model did not correctly represent the among-guild relationships. Validation of our reproductive trait model on an independent dataset would confirm our finding, which represents a promising way of modelling fish - habitat relationships in complex fish communities.

In conclusion, my thesis suggests important improvements to FHUM models in the Laurentian streams by giving new insights on the choice of a sampling method that take into account the biological characteristics of the streams targeted, and by using a promising way of simplifying FHUM for species rich communities: reproductive guilds.

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Liste des abréviations

$\cong$: approximately equal to

CCR: Correct Classification Rate

FHUM: Fish Habitat Use Models

H0: Null Hypothesis

HM: Hydraulic Model

HSI: Habitat Suitability Index

LDA: Canonical Linear Discriminant Analysis

MVCT: Multivariate Classification Tree

NM: Null Model

NNL: Not Net Loss

PC: Principal Component

PCA: Principal Component Analysis

PCNM: Principal Coordinates of Neighbour Matrices

R^2_{adj}: adjusted R square

RDA: Canonical Redundancy Analysis

RE: Relative Error

RLQ: R matrix Linked to Q matrix

SD: Standard Deviation

SE: Standart Error

SPSC: Species and Size Classes

TESS: Total Error Sum of Squares

vs.: versus

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Je tiens à remercier les personnes suivantes, car elles ont contribué tout au long de ma maîtrise à mon bonheur et à mon apprentissage. Tout d'abord, je tiens à remercier mon directeur de recherche, Daniel Boisclair, pour m'avoir permis de faire des études graduées, pour tout le temps qu'il m'a accordé, pour les connaissances et points de vue qu'il m'a partagés, ainsi que pour la grande confiance qu'il a eue en moi. Merci aux membres de mon comité, Marc Amyot et Nadia Aubin-Horth, pour avoir pris le temps de me faire des commentaires constructifs, lesquels ont permis d'améliorer significativement mon mémoire. Merci à Guillaume Bourque pour m'avoir enseigné une nouvelle langue, pour avoir grandement aidé à la collecte de mes données, pour avoir répondu à tellement de mes questions, pour son amitié, bref, pour avoir énormément contribué à mon projet de maîtrise. Je remercie aussi Gabriel Lanthier, Caroline Senay et Shannon O'Connor pour leur précieuse aide. Un gros merci à tous les « nouveaux » du labo parce qu'avec les « vieux », on est une belle gang! : Tom Bermingham, David Beauregard, Simonne Harvey-Lajoie et Camille MacNaughton. Merci à tous ceux qui m'ont aidé pour le travail de terrain : Florian Bonnaire, Jérémie Vernay, Stéphanie Massé, Olivier Houdoyer, Catherine Baltazar, Katerine Goyer, Irénée Sicard, Yohan Fittere, le personnel de la SBL et Louise Cloutier. Finalement, je tiens à dire un merci particulier à mes amis et à ma famille, que j'adore et qui m'ont soutenu tout au long de ma maîtrise, tout particulièrement Pierre-Yves Charpentier et Pierre-Luc Dézainde.

Avant propos

Ce mémoire a été rédigé sous forme d'articles dans le but éventuel de soumettre les 2 chapitres à des revues scientifiques internationales. L'auteur principal en est Jean-Martin Chamberland, lequel a élaboré en grande partie le projet, fait les revues de littératures, le travail de terrain (à l'exception des données décrivant les communautés de poissons et les conditions environnementales pour les 50 sites du chapitre 2), fait les plans d'analyse, la programmation des tests statistiques, la rédaction et la mise en page. Daniel Boisclair a encadré le projet tout au long de son avancement. Une version allongée des études est présentée dans ce mémoire, et les manuscrits devront être retravaillés par les 2 auteurs avant d'être soumis à une revue scientifique.

Introduction

Les écosystèmes aquatiques sont d'une importance capitale puisqu'ils fournissent de nombreux services, comme l'approvisionnement en nourriture, la régularisation de processus climatiques ainsi que plusieurs bénéfices non matériel tels les loisirs et le patrimoine culturel (Millenium Ecosystem Assessment 2005). Plus particulièrement, les poissons fournissent à l'ensemble de la population mondiale 16% des protéines d'origine animale (FAO 1997) et environ 1 milliard de personnes à travers le monde dépendent des poissons comme première source de protéine animale (FAO 2000). Les poissons d'eau douce constituent également une ressource renouvelable importante, puisqu'ils représentent plus de 26% des pêcheries mondiales (IUCN 2006), en plus de jouer des rôles écologiques essentiels au bon fonctionnement de ces écosystèmes, comme le stockage, le transport et le recyclage des éléments nutritifs (Vanni 2002).

En dépit de leurs importants rôles économiques, culturels et biologiques, plus de 20% des espèces de poissons d'eau douce ont subit un sérieux déclin ou se sont éteintes (Moyle et Leidy 1992). En Amérique du Nord, le nombre d'espèces de poissons d'eau douce considérées comme en danger de disparition, menacées, ou préoccupantes a augmenté de 251 à 364 dans les années 1980 (Williams et al. 1989). Plusieurs études (Miller et al. 1989; Williams et al. 1989; Noss et Cooperrider 1994; Allan et Flecker 1993; Naiman et al. 1995, Richter et al. 1997), bien qu'elles varient dans la finesse de la description des menaces à la conservation des poissons, s'accordent pour dire que les plus importantes menaces peuvent être catégorisées de la sorte : destruction et fragmentation des habitats, pollution et introduction d'espèces exotiques. Par exemple, dans une analyse portant sur l'extinction des espèces Nord Américaines de poissons, Miller et al. (1989) a conclu que l'altération physique des habitats était la cause la plus fréquente (contribuant dans 73% des cas) des extinctions d'espèces appartenant à la faune aquatique d'eau douce, suivi par l'introduction d'espèces envahissantes, l'altération chimique des habitats, l'hybridation et finalement la surpêche.

Plusieurs études à grande échelle ont donc identifié la modification ou la perte d'habitats aquatiques comme facteurs primaires menaçant la conservation des populations

et communautés de poissons d'eau douce (Williams et al. 1989; Allen et Flecker 1993; Richter et al. 1997). Au Canada, pour contrevenir à cette importante menace, le ministère des Pêches et Océans a pris le « No Net Loss of the productive capacity of habitats » (NNL; aucune perte nette en capacité productive des habitats) comme principe directeur de sa politique de gestion de l'habitat du poisson (DFO 1986). Le respect de cette politique implique d'être capable d'estimer la capacité productive en poisson d'un système non impacté, de prédire le changement en capacité productive causé par la perturbation, et finalement, que la différence entre la capacité productive avant et prédite soit de zéro. Conséquemment, le respect du NNL nécessite une excellente compréhension des relations entre les poissons et leurs habitats, de même que des outils pour quantifier les impacts des modifications de l'habitat sur la faune ichthyenne.

Les modèles de l'habitat des poissons (MHP) sont des relations mathématiques entre un descripteur biologique des poissons (e.g. biomasse, densité de poissons) et des descripteurs de l'habitat (e.g. la température de l'eau, la vitesse du courant, la profondeur de l'eau, *etc.*) (Barry 2006). Ce sont justement des outils qui permettent d'améliorer notre compréhension des relations entre les poissons et leurs habitats, ainsi que de quantifier les besoins en habitat (Ahmadi-Nedushan et al. 2006, Boisclair 2001). En milieu lotique, il est possible de prédire les effets des modifications de l'habitat sur les poissons en utilisant les prédictions d'un modèle hydrodynamique (e.g. la profondeur et la vitesse du courant) dans un MHP (Bovee et al. 1982, Nestler et al. 1989, Guay et Boisclair 2001) et ainsi obtenir une prédiction de la réponse des poissons aux modifications de leur environnement.

L'objectif général de mon mémoire est donc d'améliorer la performance des modèles de l'habitat des poissons, plus particulièrement pour les rivières des basses Laurentides. Dans chacun de mes 2 chapitres de mémoire, je montre comment améliorer un aspect d'importance particulière pour la création de ces modèles, soit la description adéquate de la communauté de poissons en place et les modèles statistiques utilisés.

Dans mon premier chapitre, je compare la performance relative de 2 méthodes d'échantillonnage communément utilisées pour décrire les communautés de poissons en

rivière : la pêcheuse électrique portative et la plongée en surface. Ces 2 méthodes présentent chacune leurs avantages et inconvénients. Par exemple, la pêcheuse électrique est moins affectée par la transparence de l'eau et la complexité de l'habitat que la plongée en surface (Gardiner 1984; Schill et Griffith 1984; Thurow et al. 2006), et elle permet aux opérateurs d'identifier précisément et de mesurer les poissons recueillis (Nordwall 1999). La plongée de surface, quant à elle, présente l'avantage d'être moins affectée par la profondeur, la vitesse du courant et la conductivité de l'eau que la pêcheuse électrique (Schill et Griffith 1984; Bonneau et al. 1995). De plus, la plongée de surface requiert beaucoup moins de temps et d'équipement que la pêcheuse électrique, ce qui la rend particulièrement appropriée pour l'échantillonnage de sites difficilement accessibles (Hankin et Reeves 1988; Thurow 1994). Cependant, lors de l'échantillonnage en plongée, il est possible de compter les poissons plus d'une fois, de même que de surestimer leur taille réelle (Griffith 1981).

Les études comparant ces 2 méthodes d'échantillonnage en rivière mènent habituellement à la conclusion que la pêcheuse électrique permet d'observer de plus grandes abondances de poissons que la plongée en surface (e.g. Cunjak et al. 1988, Hankin et Reeves 1988, Thurow et Schill 1996, Mullner et al. 1998, Wildman et Neumann 2003, Thurow et al. 2006, Roni et Fayram 2000), ce qui suggère que la pêcheuse électrique est une meilleure méthode d'échantillonnage que la plongée de surface.

Il est bien connu, cependant, que l'efficacité d'une méthode d'échantillonnage peut être reliée à la composition de la communauté de poisson, de même qu'aux conditions environnementales (Reynolds 1996). Par contre, toutes les études comparant la pêcheuse électrique portative et la plongée de surface en rivière que nous avons recensées ciblaient les communautés de poissons avec une faible richesse spécifique, dominées par les salmonidés, de même que les rivières caractérisées par une dominance de substrats grossiers et des températures froides.

Le premier objectif de mon premier chapitre est donc d'évaluer la performance relative de la pêcheuse électrique portative et de la plongée de surface pour estimer

l'abondance des espèces et classes de taille, et ce pour des communautés de poissons de rivière non dominées par les salmonidés. Le second objectif de ce même chapitre est d'évaluer l'effet des conditions environnementales sur les différences potentielles entre les communautés observées avec ces 2 méthodes.

Dans mon second chapitre, j'utilise le concept de guilde écologique (Austen et al. 1994), de même que celui des filtres écologiques agissants sur les traits fonctionnels des espèces (Smith et Powell 1971, Soutwood 1988, Zobel 1997), pour améliorer les modèles d'habitats des communautés de poissons de rivière des basses Laurentides.

La principale motivation pour appliquer ces concepts aux MHP est que le développement de tels modèles dans les communautés de poissons à forte richesse spécifique est très demandant, particulièrement en considérant que les besoins en habitat de plusieurs espèces de poissons changent tout au long de leur ontogénie (Hoagstrom et al. 2008; Weaver et al. 1997; Lamouroux et al. 2006). Une façon de simplifier l'élaboration de MHP dans de telles communautés est de grouper les espèces exploitant des ressources similaires en guildes, puisque ces espèces devraient être affectées de la même façon par des changement dans ces mêmes ressources (Roberts et O'Neil 1985).

Le concept de guilde fut originalement défini par Root (1967) comme un groupe d'espèces exploitant la même classe de ressources environnementales de façon similaire. Plus tard, Austen et al. (1994) proposèrent d'utiliser les guildes qui fonctionnent comme des « super espèces », une unité taxonomique se situant entre l'espèce et la communauté, et qui répondraient aux changements environnementaux d'une manière plus facilement prévisible que les membres individuels d'une espèce.

Le concept de filtre écologique, quant à lui, fut inspiré des idées de Southwood (1977, 1988), qui argumentait que les habitats agissent comme des cadres à l'intérieur desquels l'évolution forge les attributs phénotypiques des espèces présentes. Le concept de filtre écologique consiste donc à voir les caractéristiques des habitats comme des filtres qui imposent des contraintes aux espèces et sélectionnent ainsi les traits adaptés aux conditions environnementales présentes (Diaz et al. 1998). Ce concept suggère donc que les espèces

présentes dans les mêmes habitats seront plus semblables entre elles qu'anticipé par la chance.

Plusieurs approches existent pour former des guildes. En rivière par contre, l'utilisation des ressources par les poissons a été résumée sur la base de l'utilisation de l'habitat (Leonard et Orth 1988, Vadas et Orth 2000, Persinger et al. 2003), l'alimentation (Grossman et al. 1982, Angermeier et Karr 1983, Auster et Link 2009, Specziar et Rezsu. 2009) et les stratégies liées à la reproduction (préférence de substrat pour la fraie et comportement lors de la fraie ; Balon 1975). Une autre approche pour former des guildes consiste à grouper les espèces en se basant sur leurs traits éco-morphologiques, pour les raisons mentionnées plus haut, mais aussi parce que la morphologie reflète d'une certaine manière l'alimentation et l'utilisation de l'habitat (Bertrand et al. 2008; Reyjol et al. 2008; Bellwood et al. 2002; Wainwright 1996; Borcherding et Magnhagen 2008; Wikramanayake 1990; Chuang et al. 2006; Morinville et Rasmussen 2008).

À l'échelle du méso-habitat, la modélisation de l'habitat des poissons par guildes présente plusieurs avantages. Cette approche permet de faire des MHP plus constants, puisqu'ils sont calibrés sur des jeux de données comportant moins de zéros (Fausch et al. 1998). Lorsque utilisés conjointement avec les modèles hydrodynamiques pour déterminer les régimes hydriques nécessaires au maintien des populations, cette approche permet de protéger une plus grande proportion de l'écosystème impacté, puisqu'une plus grande proportion de la communauté de poisson est considérée (Vada et Orth 2001). Finalement, les prédictions des MHP basées sur une seule espèce sont moins précises parce que les abondances ou densités d'une espèce fluctuent beaucoup plus en fonction des changements biotiques et abiotiques que les abondances ou densités d'une guilde au complet (Orth 1995, Vadas et Orth 2000).

Le premier objectif de mon second chapitre est donc de comparer 4 différentes manières de former des guildes (par traits reproducteurs, alimentaires, éco-morphologiques et taxonomiques), et identifier la méthode qui permet de produire les meilleurs modèles d'habitat des poissons. Le second objectif est de définir *a priori* des guildes d'utilisation de

l'habitat et d'utiliser une forme de régression linéaire pour déterminer quels traits définissent le mieux ces guildes d'utilisation de l'habitat.

Comparison between electrofishing and snorkeling surveys conducted to describe fish assemblages in Laurentian Streams

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Abstract

We evaluated the relative performance of electrofishing and visual surveys (snorkeling) for estimating the abundance of combinations of fish species and size classes in rivers. We also assessed the effect of environmental conditions on potential differences between the results obtained using these two sampling methods. Sampling sites consisted of 10 river sections of 20 m in length distributed in the Laurentian region of Québec. Both methods were used while sections were blocked. Three snorkelers swam the river sections upstream while identifying and counting fish of each species and size-classes performed visual surveys. Three-pass electrofishing was performed and abundances were estimated with a maximum likelihood depletion model. Greater abundances of fish were observed by snorkeling than by electrofishing at all sites. Snorkeling species richness was higher (6/10) or equal (4/10) to electrofishing richness. Differences in the fish communities observed by both sampling methods were not related to environmental conditions. The results of our work are therefore contrary to that of most published studies that suggested the superiority of electrofishing on visual surveys. Compared to the conditions found in previous studies, our sampling sites had different environmental characteristics (no fallen trees, insignificant cover of large cobble and boulder) but the most striking dissimilarity was in terms of fish communities (dominance of cyprinids and centrarchids instead of salmonids). Behavioural characteristics favouring capture avoidance (schooling) and facilitating underwater observation (curiosity) may be responsible for the superiority of visual surveys in our study rivers. Survey methods should be selected based on fish community composition.

Keywords: Electrofishing, snorkeling, centrachid, cyprinid, stream

Introduction

Estimating the abundance of populations is crucial to assess their ecological status (endangered, threatened, *etc*; COSEWIC 2010), their potential role in food web (predator, prey, competitor; Polis and Winemiller 1996), and their capacity to sustain exploitation (fishing, hunting, harvesting; Pine et al. 2001; Krebs 2009). Electrofishing and snorkeling are two methods commonly used to estimate fish abundance in shallow areas (depth <2m) of rivers and lakes (Joyce and Hubert 2003; Mullner et al. 1998; Brind'Amour and Boisclair 2004). These methods have been used to study population dynamics (Sabaton et al. 2008; Petty et al. 2005) and to develop habitat use models (Bouchard and Boisclair 2008; Hrodey and Sutton 2008; Hedger et al. 2006).

Electrofishing has been argued to be less affected by water transparency and habitat complexity (e.g. substrate composition and macrophyte cover; (Gardiner 1984; Schill and Griffith 1984; Thurow et al. 2006) than snorkeling. Electrofishing also allows operators to precisely identify and measure the fish that are sampled and to estimate fish abundance using robust mathematical models (depletion estimates; Nordwall 1999). However, this sampling method may injure or kill fish and may have low capture efficiency, particularly for small fish (Reynolds 1996). In contrast, snorkeling has the advantages of being less affected by water depth, velocity, and conductivity than electrofishing (Schill and Griffith 1984; Bonneau et al. 1995). Nonetheless, during snorkeling, fish may be counted more than once and length estimates may be biased because of underwater magnification (Griffith 1981). Snorkeling surveys require modest equipment and less time than electrofishing, which makes it suitable to study remote locations (Hankin and Reeves 1988; Thurow 1994). Considering the importance of estimating fish abundance and the number of advantages and drawbacks associated with electrofishing and snorkeling, the identification of the most adequate survey method to estimate fish abundance in shallow waters is not a trivial problem.

Comparative studies typically lead to the conclusion that electrofishing permits the estimation of fish abundances that are higher than snorkeling. Cunjak et al. (1988) found that snorkeling underestimated the densities of juvenile Atlantic salmon (*Salmo salar*) and blacknose dace (*Rhinichtys atratulus*) compared to electrofishing. However, estimates of brook trout (*Salvelinus fontinalis*) population size were very similar between the two methods. Hankin and Reeves (1988) found that underwater surveys underestimated 1+ coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Oncorhynchus mykiss*) abundances relative to electrofishing in 13 sites out of 21, but that abundances obtained with both methods were generally well correlated (r > 0.90). Thurow and Schill (1996) concluded that snorkeling surveys were suitable for estimating the relative abundance and size structure of age 1+ bull trout (*Salvelinus confluentus*), but that snorkeling surveys underestimated abundances obtained using electrofishing by 25%. In their study on brook, rainbow (*Oncorhynchus mykiss*), and cutthroat (*O. clarki*) trouts, Mullner et al. (1998) found that trout abundances estimated with snorkeling were highly correlated (0. 90< r^2 <0.99) to values obtained using electrofishing (depletion estimates) but that snorkeling counts underestimated electrofishing counts by 35%. Wildman and Neumann (2003) compared the abundance and the size structure of brook and brown trouts (*Salmo trutta*) obtained by snorkeling and electrofishing. They found that snorkeling averaged 66% of depletion estimates obtained using electrofishing, but that overall, length–frequency distributions obtained by snorkeling were similar to those obtained by electrofishing. Thurow et al. (2006) also found that snorkeling surveys tended to underestimate counts of three salmonid species (bull, cutthroat and rainbow trout) compared to electrofishing depletion estimates, with snorkeling going up to a maximum of 33% of electrofishing estimates. Roni and Fayram (2000) compared the relative efficiency of snorkeling and electrofishing depletion estimates for estimating the abundances of juvenile coho salmon and trouts (*Oncorhynchus* spp.). Night snorkel counts were not significantly different from electrofishing estimates, although the percentage of electrofishing estimates accounted for by night snorkeling varied among streams from 50% to 175% for coho salmon and from 75% to 82% for trout. At high fish densities (>0.5fish/m^2), night snorkel counts

underestimated juvenile coho salmon abundance. However, at low densities (below 0.5 coho salmon/m^2), night snorkel counts were often equal to or higher than electrofishing estimates. Most studies conducted to date to compare electrofishing and snorkeling surveys therefore indicate that electrofishing provides higher fish abundances than snorkeling and, hence, that electrofishing may be a more suitable method to estimate fish abundance than snorkeling.

It has long been recognized that the efficiency of a sampling method may be related to the composition of the fish community sampled (species, fish size, behaviour, *etc*) and the environmental conditions that prevail at sampling sites (water conductivity, temperature, presence of cover, *etc*; Reynolds 1996). Most comparative analyses of abundance estimates based on electrofishing and snorkeling have targeted fish communities with low species richness and dominated by salmonids and rivers characterised by coarse substrate and cold water temperatures. Hence, it is presently difficult to select the most appropriate sampling method to estimate fish abundance for other types of fish communities and environmental conditions. Therefore, the objectives of this study were to (1) evaluate the relative performance of electrofishing and snorkeling for estimating the abundance of fish species and size classes for non-salmonid communities and (2) to assess the effect of environmental conditions on potential differences between the results obtained using these two methods.

Methods

Field survey

Electrofishing and snorkeling surveys were done in 10 river sections distributed in the watersheds of Rivière Rouge, Nord, and l'Assomption (Figure 1). These rivers flow in the Lower Laurentian region of Québec and eventually drain into the Saint-Lawrence River. River sections were chosen to represent the range of fish community structures and habitat characteristics found in the region (Table 1). Surveys were conducted from the 2nd to the 14th of August 2009, between 10h00 and 16h00 to avoid diel differences in fish

habitat use and also because, in species rich communities, fish identification is easier in good light conditions. Sampling was conducted on days without rain and with a cloud cover not exceeding 50%.
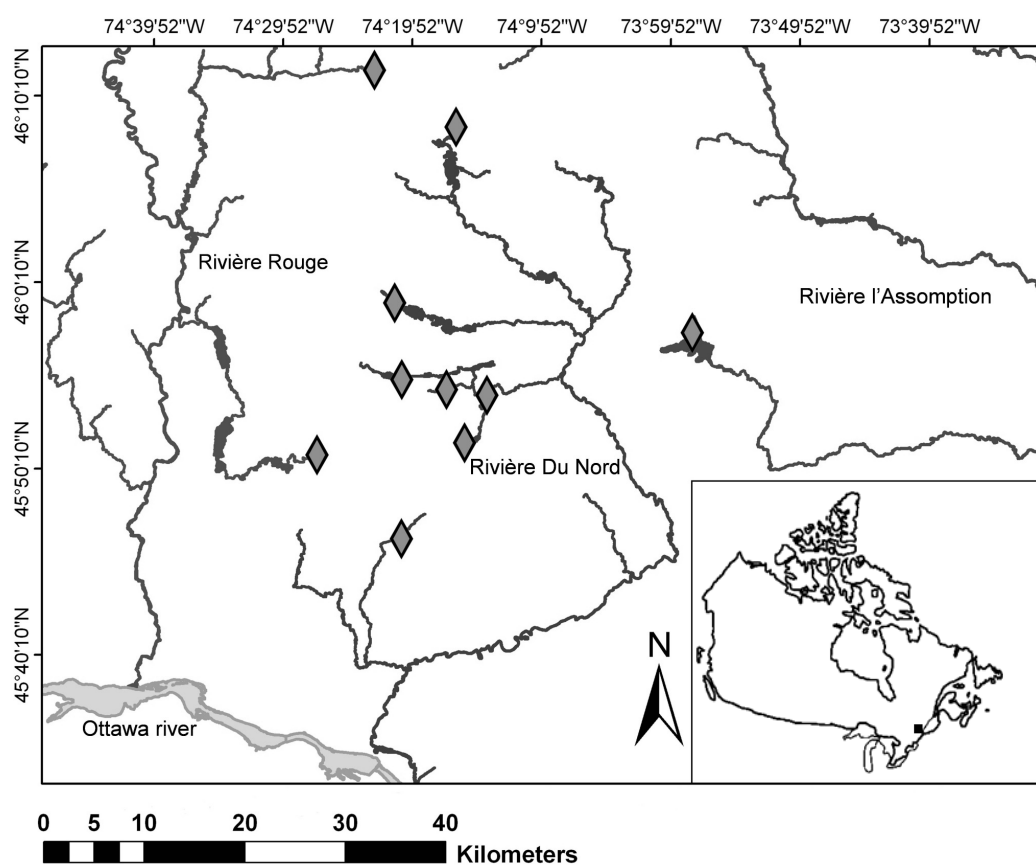
Fig. 1 Map of the study area. Grey diamonds represent sampling sites

Table 1 Main abiotic and biotic characteristics of the sampling sites

Descriptors	Mean	Range
Stream width (m)	7.9	4.2 - 12.3
Mean depth (m)	0.54	0.43 - 0.64
Flow velocity (cm/s)	24.8	14.2 - 54.0
Dominant substrates (%)		
Clay - Silt (< 2 mm)	28	1 - 90
Sand (< 2 mm)	37	5 - 88
Gravel (2-32 mm)	15	0 - 40
Macrophyte cover (%)	20	0 - 56
Trunks (number of)	6	0 - 15
Water temperature (°C)	19.9	17.3 - 21.0
Conductivity (µsiemens)	58	31- 92
Individuals belonging to (%)		
Cyprinids	75	38 - 100
Centrarchids	18	0 - 52

Surveys were performed by blocking fish passage upstream and downstream a 20 m long river section using two 20 m long by 2 m high (mesh size = 2 cm) seines set perpendicularly to river shore (from shore to shore). Seines were held in place using wooden poles stuck in the riverbed after the setting of the nets. River sections of 20 m were used because this length corresponded to the longest section that could be surveyed without excessive clogging of the seines during the surveys.

Once the block nets were set, a 30 to 45 minutes time period was allowed for fish to resume their activity and distribution patterns. Trained snorkelers moved slowly (1.0 to 1.5 m per minute) from the downstream to the upstream end of the river section, they recorded on polyvinyl chloride rolls the species and the length (size classes of 5 cm increment; Size Class 1 = 0-5 cm *etc*) of each fish observed. One snorkeler was located in

the thalweg of the river (deepest point of the cross section of a river) and the two other snorkelers were located on each shore of the river at a depth no less than 25 cm. They covered from 60 to 80% of the sampling site surface area.

A time period of 30 to 45 minutes was given after snorkeling to allow fish to resume their activity and distribution patterns. Following this time period, the three snorkeling transects were electrofished three times using a Smith-Root LR-24 backpack electrofisher, with pulsed direct current. Electrofishing was conducted over the same surface area that was surveyed by snorkeling. At each pass, the three members' crew removed, counted, and measured every fish sampled.

Main environmental conditions were quantified for the complete surface area of the site. Depth (measuring rod; ±5 cm) was measured systematically at 6 points located at 3.5 m intervals along each snorkeling transect and beginning at 1 m from the block nets. Stream width (measuring tape; ±0.5 m) and flow velocity (Gurley-Price flow meter held at 40% of the water column during 30 seconds; cm•s-1) were also estimated at these points. Stream width, depth and flow velocity were averaged for each site. The percent of the riverbed within the section surveyed covered by 7 size classes of substrate was estimated visually (Latulippe et al. 2001). The substrate classes were defined based on the length of the median axis of particles: clay (<0.002 mm), silt (0.002 mm - 0.063 mm), sand (0.063 mm - 2 mm), gravel (2 - 32 mm), pebble (32 - 64 mm), cobble (64 - 250 mm) and rocks (250 - 1000 mm). Decaying plant matter and organic debris were included in the "silt" category. Percent macrophyte cover was also estimated in each site and the number of trunks (diameter > 10 cm) was counted. Finally, the water temperature (hand held thermometer; ±0.5°C) and conductivity (Accumet AP85 Fisher Scientific conductivity meter; ±0.1 µsiemens) were measured at each site in the trajectory of the thalweg at a depth of 15 cm for respectively 60 seconds and until the measure stabilized.

Computations

Raw electrofishing counts are known to be biased (Hankin and Reeves 1988; Thurow and Schill 1996; Mullner et al. 1998). We used the maximum weighted likelihood method of Carle and Strub (1978) to estimate the total abundance of fish at each site based on the electrofishing depletion curve. Because electrofishing tends to select for larger fish (Reynolds 1996) we also used the maximum weighted likelihood method to estimate the total abundance excluding fish of Size Class 1 (less than 5 cm). For each site, we then multiplied the raw abundance per species by the ratio between estimated total abundance and raw total abundance, and rounded up to the nearest integer, to get the estimated total abundance per species. The estimates of electrofishing abundances based on the depletion curves will henceforth be referred as electrofishing abundances.

Statistical analysis

The influence of the habitat characteristics on the differences in the fish communities, observed by each sampling method, was investigated using 2 different approaches employing a forward selection of the explanatory variables (Blanchet et al. 2008) on multiple linear regressions (MLR). The "forward.sel" function available in the R "packfor" library (Dray et al. 2009) was used. The first approach consisted in performing a forward selection between the total abundance of fish observed by snorkeling (response variable) and the following standardized (mean = 0, standard deviation = 1) explanatory variables: electrofishing estimates of total abundance and environmental conditions. We also carried out the same analysis excluding fish of Size Class 1. In the second approach, we computed the Hellinger distance between the fish communities sampled by each method at each site and used it as the response variable in a forward selection of the standardized environmental conditions. The environmental descriptors used in the models were substrate composition, stream width and depth, flow velocity, macrophytes cover, number of trunks, and conductivity. In these models, substrate composition was represented by the two first principal components of a principal component (PCA) analysis on the seven substrate classes. The PCA was computed on the covariance matrix of the 7 substrate classes to

reduce the number of explanatory variables and their collinearity (Kiers and Smilde 2007). The covariance matrix was used (as opposed to the correlation matrix) because we wanted to maximize the variation explained by the 2 first principal components and also because we wanted to give more weight to the substrate classes with the most variation among the sites. Scaling type 1 was used to represent at best the relationships between the sites. The PCA was done using the "rda" function available in the "vegan" R-language library (Oksanen et al. 2010). All computations and statistical analyses were performed using R 2.11.0 (R Development Core Team 2010).

Results

A total of 17 species belonging to 7 families were recorded during the field surveys (Table 2). Cyprinids (8 species) was the most represented family, accounting for an average of 75% of individuals per site, followed by Centrarchids (4 species), accounting for an average of 18% of the individuals (Table 1). Species richness ranged from 4 to 11 for snorkeling and from 3 to 10 for electrofishing (Figure 2). Electrofishing permitted to sample 15 species (all sites combined), but was unsuccessful at sampling golden shiner (*Notemigonus crysoleucas*) and yellow perch (*Perca flavescens*). Golden shiners were only present in low abundances (1 individual) in 2 sites and yellow perch were present in 4 sites, also in very low abundances (from 1 to 12 individuals per sites). In contrast, snorkeling surveys permitted the observation of a total of 16 species, but was inefficient at detecting the presence of central mudminnows (*Umbra limi*) at any of the sites.

Table 2 Species sampled, abbreviation and method with which the species was detected.

Species	Abreviation	Method	
		snorkeling	electrofishing
Ambloplites rupestris (Rafinesque) (Rockbass)	AMru	*	*
Ameiurus nebulosus (Lesueur) (Brown bullhead)	AMne	*	*
Catostomus commersoni (Lacepède) (White sucker)	CAco	*	*
Culaea inconstans (Kirtland) (Brook stickleback)	CUin	*	*
Exoglossum maxillingua (Lesueur) (Cutlips minnow)	EXma	*	*
Lepomis gibbosus (Linnaeus) (Pumpkinseed)	LEgi	*	*
Luxilus cornutus (Mitchill) (Common shiner)	LUco	*	*
Micropterus dolomieui (Lacépède) (Smallmouth bass)	MIdo	*	*
Micropterus salmoides (Lacépède) (Largemouth bass)	Misa	*	*
Notemigonus crysoleucas (Mitchill) (Golden shiner)	NOcr	*	
Perca flavescens (Mitchill) (Yellow perch)	PEfl	*	
Phoxinus eos/neogaeus (Northern redbelly dace and/or Finescale dace)	PHsp	*	*
Pimephales notatus (Rafinesque) (Bluntnose minnow)	PIno	*	*
Pimephales promelas Rafinesque (Fathead minnow)	PIpr	*	*
Semotilus atromaculatus (Mitchill) (Creek chub)	SEat	*	*
Semotilus corporalis (Mitchill) (Fallfish)	SEco	*	*
Umbra limi (Kirtland) (Central mudminnow)	UMli		*
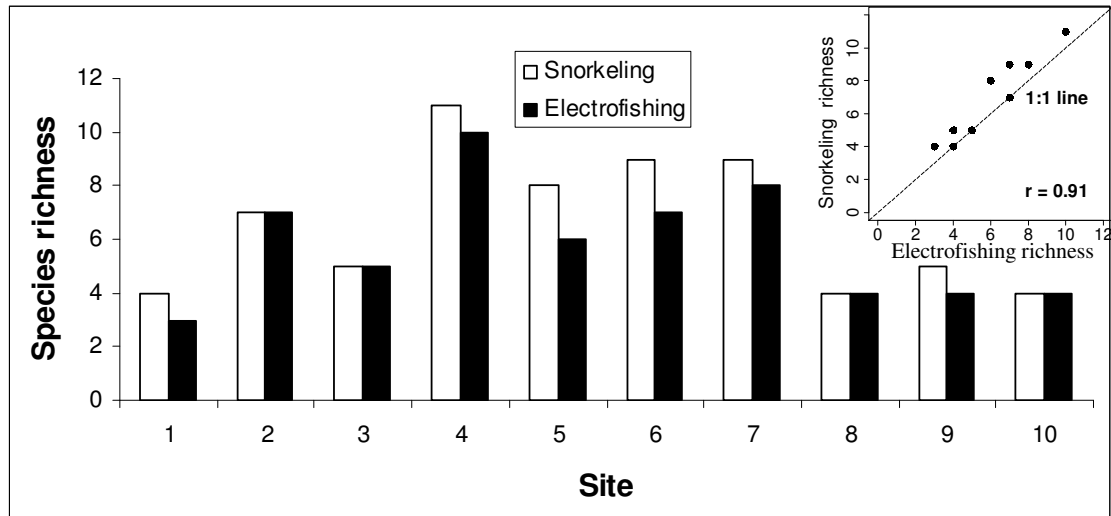
Fig. 2 Comparison of species richness observed by each sampling method at each site. Inset: graphical representation of the relationship between snorkeling and electrofishing species richness. Pearson's corrlelation was tested using 999 permutations (p=0.001).

Total abundance of fish per 20 m long river section ranged from 9 to 313 fish for electrofishing and from 17 to 387 for snorkeling and fish of Size Class 1, on average, accounted for 18% (standard deviation (sd) = 18%) of total abundance for snorkeling and averaged 26% (sd = 32%) of electrofishing abundances. The Pearson's correlation between the total abundances of fish observed by electrofishing and snorkeling was high both when fish belonging to Size Class 1 were included (r = 0.98, p = 0.001) or excluded (r = 0.99; p = 0.001) from the analysis (Figure 3). The correlations were tested using 999 permutations because the variables were not normally distributed. For most species, the average abundance per site was higher (from 0 to 26 more fish) for snorkeling than for electrofishing (Figure 4). The two exceptions in this respect were the brown bullhead (*Ameiurus nebulosus*) and the central mudminnow for which abundances were always higher (respectively 6 and 12 more fish, on average) for electrofishing than for snorkeling.

Sampling sites were characterized by average flow velocities ranging from 14 to 56 cm•s-1, relatively high water temperatures (range = 18 – 22°C) and low conductivity (range = 31.0 -91.9; Table 1). The sites were also characterized by a dominance of fine substrates (65% of the sites were covered by clay, silt and sand; Table 1). The first two axes of the

PCA represented most of the variation of the percent cover of the 7 substrate classes, with the first and second axes respectively representing 60.9 and 28.6% of the variation (Figure 5). The first axis was positively correlated with silt (r = 0.958; p = 2.881e-05) and negatively correlated with pebble (r = -0.872; p-value = 0.000981) and gravel (r = -0.742; p = 0.01388) while the second axis was positively correlated with sand (r = 0.966; p-value = 5.923e-06).
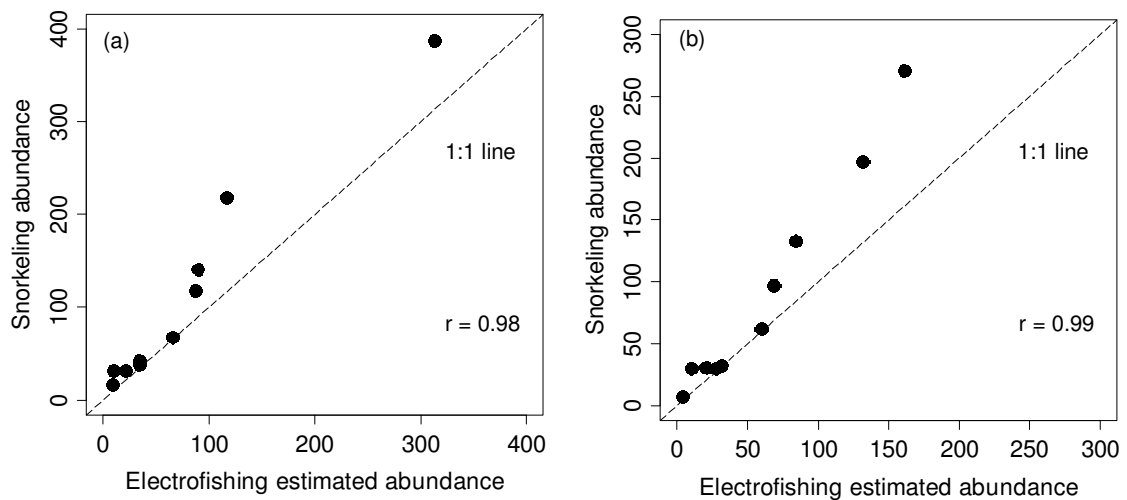
Fig. 3 Comparison of snorkeling total abundance and electrofishing estimated total abundance (a), and snorkeling abundance and electrofishing estimated total abundance excluding fish of size class 1 (b). Pearson's correlation coefficient are also shown

Forward selection based on snorkeling-derived estimates of abundance did not select for variables other than electrofishing total abundance (94.9% of the variance explained; Table 3). When using total abundance of fish observed by snorkeling excluding fish of Size Class 1, the forward selection selected electrofishing total abundance (excluding Size Class 1; 96.7% of the variance explained) and the first principal component of the PCA on the substrate classes (1.7% of the residual variance explained). The forward selection using the Hellinger distance between the fish communities observed by each sampling method as the response variable selected no explanatory variables at an alpha level of 0.05.
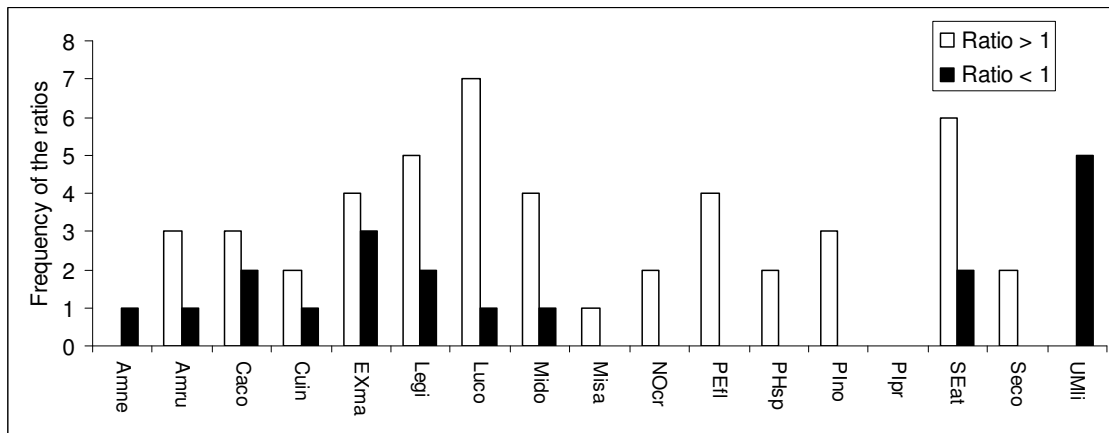
Fig. 4 Frequency of the ratio of abundances (snorkeling / electrofishing) for each species. A ratio greater than 1 means more fish of a species were observed by snorkeling than electrofishing at a sampling site. The sum of the frequencies for each species is equal to the number of sites where they were detected by either sampling method, except for the following species, for which ratios equal to 1 were observed at 1 site: AMru, CUin, EXma, LUco, MIdo, PIpr and SEat
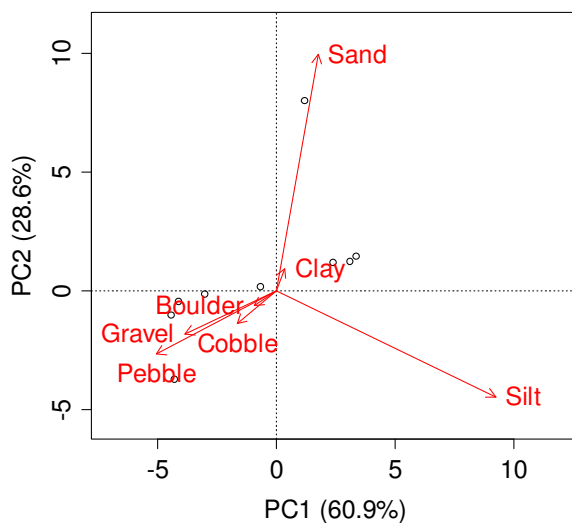
Fig. 5 Principal component analysis on the covariance matrix of the 7 substrate classes (percent cover), scaling type 1. The first axis represents 60.9% of the variation and the second 28.6%

Table 3: Cumulative adjusted r-square (R^2_{adj}), regression coefficients, standart error, t- and p-value of the forward selection of explanatory variables on MLR using snorkeling total fish abundance, snorkeling total fish abundance excluding fish of Size Class 1 and the Hellinger distance between the fish communities sampled by each method at each site as the response variables

Response	Parameters	Coefficients				
		R^2_{adj}	Estimate	Std.Error	p-value	
Snork. total fish abundance	Intercept		0.0000	0.0945	1	
	Electro. estimated total abundance	0.949	0.9595	0.0996	1.1E-05	***
Snork. total fish abundance	Intercept		0.0000	0.0405	1	
(excluding fish of size class 1)	Electro. estimated total abundance	0.967	1.0010	0.0430	6.90E-08	
	(excluding fish of size class 1)					***
	PC1 (substrate)	0.984	-0.1293	0.0430	0.0198	*
Hellinger distance	no variable selected	NA	NA	NA	NA	

significance codes: "***" p<0.001; "**" p<0.01; "*" p<0.05

Discussion

The goals of this study were to evaluate the relative performance of electrofishing and snorkeling for estimating the abundance of fish species and size classes for non-salmonid communities and to assess the effect of environmental conditions on potential differences between the results obtained using these two methods. The results showed that the two sampling methods provided similar assessment of the fish communities but snorkeling observed greater species richness than electrofishing in most of the sites (6/10; Figure 2). We haven't found any study comparing back-pack electrofishing and snorkeling for the assessment of species richness in communities with more than 3 species. However, Goldstein (1978) consistently observed more species (from 1 to 5, richness range: 9 - 18) using snorkeling than a comparable seining effort in Connecticut streams. In this study, the fish communities were dominated by catostomids, cyprinids and centrarchids (6 families represented), similarly to the ones in our study.

For most of the species (15/17), snorkeling observed more individuals per site than electrofishing (Figure 4). However, central mudminnows were never observed by snorkeling. Brind'Amour and Boisclair (2004) also failed to detect central mudminnows with visual surveys in a Laurentian lake. This species is known to burrow into the mud to escape predators (Scott and Crossman 1985), which could explain why daytime snorkeling surveys did not allow the survey of this species. The brown bullhead, observed in 1 site, was under sampled by snorkeling. This species is known to be more active at night (Scott and Crossman 1985) and we also observed it burrowed into the substrate during the daytime sampling, which could explain why more fish were electrofished than observed by snorkelers.

The correlation between electrofishing total abundance and snorkeling total abundance (Figure 3a) was high, as well as the correlation between total abundances excluding fish of Size Class 1, which could have been underestimated by electrofishing, as suggested by Reynolds (1996). 100% of the points of the relationships between electrofishing and snorkeling total abundance were above the 1:1 line, meaning that in all sites, snorkeling observed more fish than electrofishing. Snorkelers counting fish more than

once could have led to overestimation of fish abundances. However, snorkelers were rigorously trained (more than 2 months) and would never count fish escaping upstream, since they were going to be enumerated later (fish were confined in the sampling sites by the block nets). Moreover, the tendency of snorkeling surveys to observe more fish than electrofishing is consistent with the greater species richness observed in most of the sites during the snorkeling surveys. A number of studies also obtained good correlations between electrofishing and snorkeling abundances, like Hankin and Reeves (1988; r > 0.90) for 1+ coho salmon and 1+ steelhead trout, Wildman and Neumann (2003; $0.58 < r^2 < 0.93$) for brook and brown trouts, and Mullner et al. (1998; $0.90 < r^2 < 0.99$) for brook, cutthroat and rainbow trouts. However, in all these studies, the electrofishing abundances were higher than the snorkeling abundances.

Effect of abiotic conditions:

The second objective of this study was to evaluate if the environmental conditions could explain the potential differences between the fish communities observed by snorkeling and electrofishing. A forward selection of the explanatory variable using multiple linear regressions was used to model the 3 different response variables (snorkeling total abundance, snorkeling abundance excluding fish of Size Class 1 and the Hellinger distance between the fish communities observed by each sampling method; Table 3). The electrofishing abundance was found to explain most of the variation of the snorkeling total abundance. Likewise, when excluding fish of Size Class 1, the forward selection included the electrofishing total abundance (excluding Size Class 1) as the most important explanatory variables, but also selected the first principal component of the PCA performed on the 7 substrate classes. Yet, PC1 only explained 1.7% of the variation not explained by electrofishing estimates of total abundance. Finally, the forward selection using the Hellinger distance between the fish communities observed by each sampling method did not include any significant environmental characteristic, thus reinforcing the hypothesis that there is no environmental descriptor that could explain a biologically relevant portion of the differences between the fish communities described by the 2 sampling methods

among our sites. However, we are cautious to generalise our conclusions for the Laurentian streams since the sampling size was relatively small.

We do not think that the observed superiority of the snorkeling surveys is related to the low conductivity of our streams. First, this environmental descriptor was not found to be significantly related to the difference between snorkeling and electrofishing in any of the statistical models. We also visually observed the relationships to make sure there was no non-linear trend in the data. Second, it is difficult to compare our results with studies opposing snorkeling surveys and back-pack electrofishing (Table 4), because the only conductivity values mentioned were in Cunjak et al. (1988; 109 µsiemens) and Thurow and Schill (1996; 102 µsiemens), and did not vary within the study. Nonetheless, Peterson et al. (2004) found that stream characteristics were related to multipass electrofishing efficiency, but never found significant relationships with conductivity in streams where this descriptor varied from 16 to 203 µsiemens (mean = 58). Finally, many studies performed electrofishing surveys in low-conductivity streams (Kanno et al. 2009; Habera et al. 2010) and proper setting of voltage (to maintain power) should compensate for this drawback (Reynolds 1996).

Wildman and Neumann (2003) found that woody debris variables could improve the prediction of electrofishing depletion estimates based on snorkel counts. Mullner et al. (1998) reported that regression models predicting electrofishing depletion estimates from snorkel counts for three trout species were improved with the addition of visibility and instream cover variables (fallen trees, woody debris, large cobble, and boulders). Our sampling sites had different environmental characteristics from those observed in the 2 previous studies (no fallen trees, insignificant cover of large cobble and boulders, the most important instream cover descriptor being aquatic plants), but the most striking dissimilarity is between the fish communities observed.

Effect of biotic descriptors of fish communities:

Our study is different from the others since the comparison between back-pack electrofishing and snorkeling surveys was carried out in streams dominated by cyprinids and centrarchids, as opposed to salmonid dominated streams (Table 4), while the environmental conditions were suitable for both methods. Vulnerability to electrofishing varies according to the species sampled (Reynolds 1996) and a few studies reported that cyprinids and centrarchids had lower electrofishing capture efficiencies than other families. For instance, Meador et al. (2003) mentioned that cyprinids and centrarchids were the 2 most likely families (among the 7 most common) to be missed on the first electrofishing pass. Bayley and Dowling (1990) obtained very low capture efficiency with electrofishing for cyprinids (< 0.25), and Kimmel and Argent (2006) observed that small percids (e.g., darters) and schooling fish (e.g., cyprinids) avoided capture more frequently than other common families. Also, Reynolds (1996) mentioned that salmonids tend to be more vulnerable to electroshocking than cyprinids.

Table 4: Previous studies comparing snorkeling surveys with electrofishing (NI = not identified in the reference)

Authors	Families (# sp)	T° range (°C)	Depth range (cm)	Dominant substrate
Cunjak et al. 1988	Salmonid (2) Cyprinid (1)	15 - 20	7 - 80	Boulder, Cobble
Hankin and Reeves (1988)	Salmonid (2)	15	10 - 130	Cobble, Gravel
Heggenes et al. (1990)	Salmonid (2)	6 - 18	28 - 87	Gravel, Pebble
Rodgers et al. (1992)	Salmonid (1)	10 - 16	61 - 123	Sand, Silt
Thurow and Schill (1996)	Salmonid (1)	9.0 - 13.5	40 - 110	Boulder, Bedrock
Mullner et al. (1998)	Salmonid (3)	3.6 - 9.9	>30	NI
Roni and Fayram (2000)	Salmonid (3)	3.0 - 6.5	NI	Gravel, Cobble
Joyce and Hubert (2003)	Salmonid (2)	5 – 9	NI	NI
Wildman and Neumann (2003)	Salmonid (2)	NI	6 - 81	Pebble, Cobble
Peterson et al. (2005)	Salmonid (2)	5.7 - 12.5	7 - 23	Boulder, Cobble
Thurow et al. (2006)	Salmonid (3)	3 - 16.8	?	Boulder, Cobble

The lack of relationship between the differences in the fish communities observed by the 2 sampling methods and environmental conditions in our study could be explained

by the behaviour of the fish encountered. Salmonids may show territorial and cryptic behaviours (Thurow and Schill 1996; Peterson et al. 2004), which could explain why the inclusion of habitat complexity descriptors can help predict the electrofishing depletion estimates based on snorkeling surveys (Mullner et al. 1998; Peterson et al. 2004; Wildman and Neumann 2003). Cyprinids and centrarchids do not tend to show these types of behaviours (except for territoriality during reproduction, particularly for Centrarchids from May to mid-July; Moyle and Cech 2004), but tend to show schooling behaviours (Kimmel and Argent 2006; McCartt et al. 1997). Schooling fish may show group fright response and evade capture more frequently than non-schooling species (Kimmel and Argent 2006; Reynolds 1996). It may also be more difficult to capture all fish from a school using electrofishing than for snorkelers to estimate the abundance of fish in such schools. We also frequently observed centrarchids remaining stationary and facing the snorkeler. This behaviour, also reported by Goldstein (1978), could facilitate the snorkeling counts.

In conclusion, electrofishing and snorkeling surveys were found to be two complementary methods for sampling fish communities in the lower Laurentian streams. Snorkeling, however, observed more fish species in six of the ten sites and higher abundances in all of the sampling sites. Snorkeling also allowed for a more cost-effective enumeration of species and abundances since the same sampling units could be surveyed in a fifth of the time needed to conduct 3 pass depletion electrofishing. Our results also suggest that, in some streams where the environmental conditions are suitable for both sampling methods, fish communities may be more important than environmental descriptors at determining the efficiency of snorkeling surveys relative to back-pack electrofishing. Finally, we would like to remind that snorkeling efficiency highly relies on the field assistants' expertise and that proper training is a key element for the success of such field surveys.

Aknowledgements

Comparison among different fish functional classification methods to develop habitat use models

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Abstract

Fish habitat use models (FHUM) are quantitative relationships between biological descriptors of fish (biomass, abundance, density) and environmental descriptors (depth, flow velocity, substrate type, etc.). In species rich communities, developing FHUM for every species and ontogenetic stage can be quite challenging. In order to simplify the modelling of such communities, as well as improve our understanding of fish – habitat relationships, we used the ecological guild concept and the niche filtering hypothesis to explore the relationships between guilds based on different types of traits (eco-morphological, reproductive, alimentary and taxonomic) and local environmental descriptors, at the coarse meso-habitat scale. Reproductive guilds led to FHUM that clearly outperformed the other 3 approaches, because of the close relationship between preferred spawning grounds and non spawning habitat preferences, and also because reproductive traits are linked to habitat characteristics at the reach or coarse mesohabitat scale. We also defined guilds based on habitat-use and related them to species traits. Traits related to the feeding biology of fishes seemed to be the best at explaining the habitat-use guilds, but our model did not correctly represent the among-guild relationships. Validation of our reproductive trait model on an independent dataset would confirm our finding, which represents a promising way of modelling fish - habitat relationships in complex fish communities.

Keywords : Fish habitat use models, centrarchid, cyprinid, guild, reproductive, alimentary, eco-morphological and taxonomic traits, stream, meso-habitat

Introduction

Many large scale studies have identified habitat modification or habitat losses as primary threats for the conservation of freshwater fish communities (Williams et al. 1989; Allan and Flecker 1993; Richter et al. 1997; Dudgeon et al. 2006). In North America, 73% of freshwater fish extinctions can be attributed to habitat modifications (Miller et al. 1989). In Canada, No Net Loss (NNL) of the productive capacity of habitats is the guiding principle of the Department of Fisheries and Oceans' policy for the management of fish habitat. The respect of NNL implies to be able to estimate the productive capacity of the unimpacted system, to predict the change in productive capacity caused by the perturbation, and that the difference between the unimpacted and predicted productive capacity of the habitats be zero. Hence, to respect NNL, a better understanding of fish-habitat relationships is required, as well as tools to quantify the impact of habitat modifications on fish.

Fish habitat use models (FHUM) consist in relationships between biological descriptors of fish (e.g., density, abundance, biomass and diversity) and habitat descriptors (e.g., water temperature, substrate size, water depth). They are tools that can improve the understanding of fish-habitat relationships, predict species occurrences, densities or biomass on the basis of habitat descriptors and quantify habitat requirements (Ahmadi-Nedushan et al. 2006; Boisclair 2001). In lotic systems, it is possible to predict the effect of habitat modifications on fish by using the output of hydraulic models (HM; predict changes in habitats based on different modifications of flow rates) with the biological FHUM (Bovee et al. 1982; Nestler et al., 1989), and then compare with the observed fish community.

Species have different habitat requirements throughout their ontogeny (Hoagstrom et al. 2008; Weaver et al. 1997; Lamouroux et al. 2006). In species rich communities, developing FHUM for every species and life stage can be challenging. One way to simplify the understanding of species-rich communities is to group species exploiting similar resources, like habitat, because they should be affected similarly by the alteration of those resources (Roberts and O'Neil 1985). Guilds were originally defined as species exploiting the same class of environmental resources (Root 1967). Austen et al. (1994) further developed the guild concept and proposed the use of guilds

that function as "super species", a unit that would respond to environmental changes in a more predictable manner than any individual member of a species.

The niche filtering hypothesis (Zobel 1997) stipulates that the species found in the same habitats will be more similar than expected by chance because the environment acts as filters, letting the species with the adapted traits pass through these filters. Similarity between species can be assessed by looking at different aspects of fish biology. Functional traits can either indicate an ecological function (e.g., trophic level, habitat preference, growth rate) or a way in which a resource is used (e.g., mouth position, body length – body depth ratio, *etc.*). Hence, fish guilds can be defined based on traits describing resource use.

Many approaches exist to form guilds. In streams, however, resource use by fishes has been summarized on the basis of habitat use (Leonard and Orth 1988; Vadas and Orth 2000; Persinger et al. 2003), feeding (Grossman et al. 1982; Angermeier and Karr 1983; Auster and Link 2009; Specziar and Rezsu. 2009), and reproduction strategy (preferred spawning grounds and behaviour; Balon 1975). Another approach to form guilds consists in grouping fish species based on their eco-morphological traits, because morphology is known to reflect some aspects of feeding behaviours and habitat use (Bertrand et al. 2008; Reyjol et al. 2008; Bellwood et al. 2002; Wainwright 1996; Borcherding and Magnhagen 2008; Wikramanayake 1990; Chuang et al. 2006; Morinville and Rasmussen 2008).

At the meso-habitat scale, the guild concept presents several advantages. Modelling habitat use by guilds allows for more constant FHUM, because they are usually calibrated on larger sample sizes (Fausch et al. 1998). FHUM used with HM to determine flow regimes necessary to maintain fish populations usually lead to a better protection of stream ecosystem, because more of the available fish assemblage is considered (Vadas and Orth 2001). Finally, predictions of FHUM based on single species are less accurate, because species can fluctuate more depending on biotic and abiotic factors than whole guilds (Orth 1995; Vadas and Orth 2000).

Many authors have defined guilds based on habitat use (Elliott and Dewailly 1995; Lamouroux and Souchon 2002) but at the meso-habitat scale, the only studies we found were the ones of Vadas and Orth (2000, 2001). These authors defined seven habitat use guilds based on a cluster analysis of the species correlation matrix. They then separately modelled the habitat use of those guilds using habitat suitability indices

(HSI). Developing multivariate habitat use models, where both the response and explanatory variables are matrices, may be more appropriate because they take into account the co-varying structure of the descriptors and avoid the problem of multiple testing (Legendre and Legendre 1998), especially in the context of species-rich fish communities (i.e. not dominated by salmonids).

Our study is focused on the relationships between different ways of forming fish guilds and the modelling of habitat use in Laurentian streams. More specifically, the first objective of this study is to compare four approaches used in the literature to form guilds (reproductive, alimentary, eco-morphology and taxonomy) and identify the one that produces the best multivariate fish habitat use models. The second objective is to define habitat use guilds and to find which specific traits (diet, reproduction or eco-morphology) or taxonomy could have been used to define those habitat use guilds.

Methods

In order to accomplish the study objectives, five data matrices (row by columns) were required: (1) site by fish densities (species and size class; SC), (2) site by local environmental conditions, (3) species and SC by trophic traits, (4) species and SC by reproductive traits and (5) species and SC by eco-morphological trait. Matrices 1 and 2 were obtained from the 2008 field work campaign, matrices 3 and 4 were obtained from the literature and matrix 5 was obtained by taking pictures of fishes on the field and doing image analyses. For the remaining of this manuscript, the expression species and Size Classes, referring to the subdivision of the species present in the fish community into species and Size Classes (SC), will henceforth be known as SPSC.

Study area

Sampling sites consisted in 50 river sections distributed across the watersheds of Rouge, Nord, and Assomption Rivers (Figure 1). These rivers flow in the Lower Laurentian region of Québec and eventually drain into the Saint-Lawrence River. The sampling sites had a thalweg (deepest part of the cross-section of the river) depth ranging between 0.25 and 1.5 m, because snorkeling could not be performed adequately outside this range. Sampling sites were 100m long in the upstream-downstream axis, and the sites were further divided into 10m sub-sections delimited by flags positioned on shore. Surveys were conducted in July 2008 between 10h00 and 16h00, on days without rain and with a cloud cover not exceeding 50%.
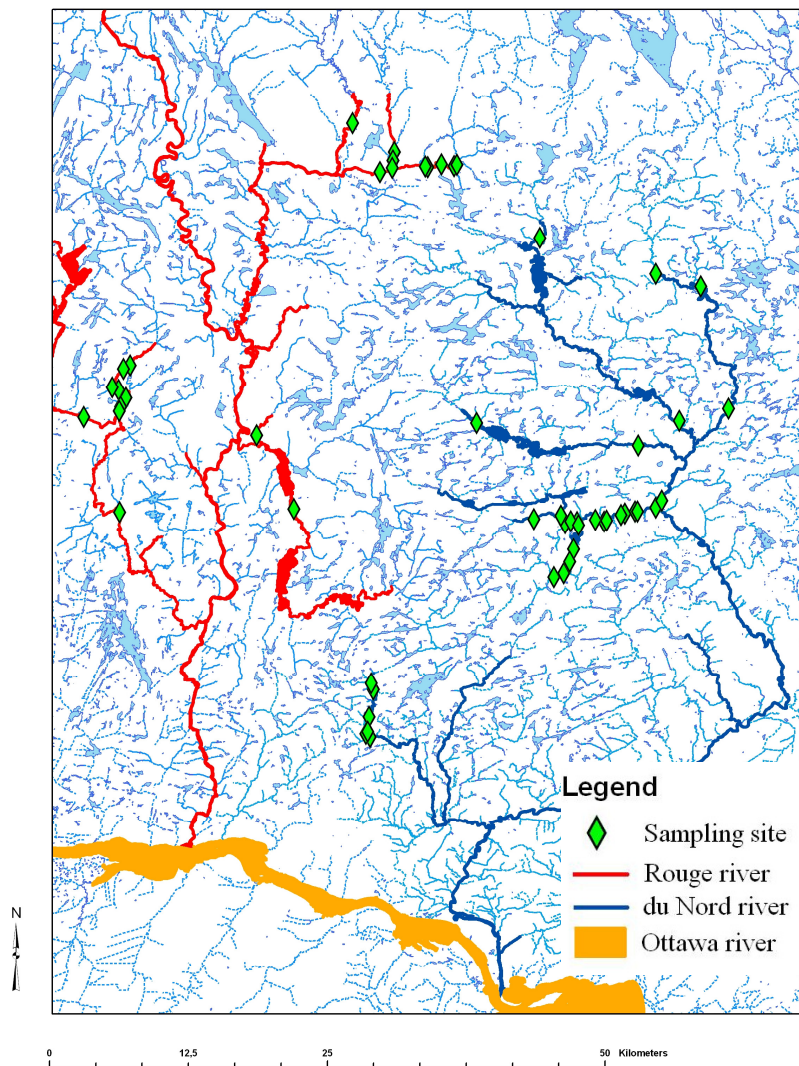
Fig. 1: Distribution of the 50 sampling sites in the watersheds of Rivière Rouge and Rivière du Nord, Québec, Canada. Sites are identified by green diamonds.

Sampling protocol

Fish community. - Snorkeling surveys were performed by 2 to 3 experienced snorkelers moving slowly (1.5 to 2 m per minute) from the downstream to the upstream end of the river sections. One snorkeler was located in the thalweg of the river and the two other snorkelers were located on each shore of the river, at a depth no less than 25 cm. When two snorkelers could survey more than 75% of the stream wetted width, each one was located near the shores and the thalweg snorkeler was not required. For each 10 m sub-section, the snorkelers recorded on polyvinyl chloride rolls the species and the length (Size Classes of 5 cm increment; Size Class 1 = 0-5 cm, *etc*.) of each fish observed. The snorkelers also recorded the maximum distance (classes of 0.25 m), on

each of their sides, at which fish could be counted and identified with certainty. The observations were limited to that surface area. The sum of these two maximum distances, multiplied by 10 m, represents the surface area sampled for each sub-section. The total surface area sampled at a site was obtained by summing all these surface areas for the 2 or 3 snorkeling transects. To allow better inter-site comparisons, the fish community characterizing each site was compiled in densities (number of fish per m^2) by dividing the total number of fish per SC by the total sampled surface area. The fish community characteristics were averaged for sites where more than one visit had been performed (Lanthier 2009).

Local habitat descriptors. - Local environmental conditions were measured at 2 different times, depending on the temporal stability of the descriptors. The habitat descriptors expected to vary temporally were measured systematically after each dive, whereas the more temporally stable habitat descriptors were measured after the snorkeling campaign, in August or October 2008. The habitat descriptors expected to vary temporally were: flow velocity, depth, water temperature and stream wetted width. Flow velocity (Gurley-Price flow meter held at 40% of the water column during 30 seconds; $cm \cdot s^{-1}$) and depth (measuring rod; ±5 cm) were measured in the middle of each of the 20 or 30 (depending on the number of snorkeling transects) 10 m sub-sections. Water temperature (hand held thermometer held at a depth of 15 cm for 60 seconds; ±0.5 C) was measured after each dive at one point in the thalweg of the site and stream wetted width (measuring tape; ±0.5 m) was measured systematically 10 times per site.

The more temporally stable habitat descriptors were percent of the riverbed covered by different substrate classes, percent macrophyte cover, percent branch cover, the number of trunks and 2 habitat heterogeneity indices. They were measured or estimated for each of the 20 or 30 sub-sections per site. The percent of the riverbed, within the sections surveyed, covered by 9 size classes of substrate, was estimated visually (Latulippe et al. 2001). The substrate classes were defined based on the length of the median axis of particles: clay (<0.002 mm), silt (0.002 mm - 0.063 mm), sand (0.063 mm - 2 mm), gravel (2 - 32 mm), pebble (32 - 64 mm), cobble (64 - 250 mm) and rocks (250 - 1000 mm), boulders (> 1000mm) and bedrock. Percent macrophyte cover was also estimated for each sub-section, as well as the percent of the surface of the section covered by branches (diameter < 10 cm). The percent cover of the substrate classes always summed up to 100%, and were independent from the surface area covered by branches and macrophytes. The number of trunks (wood logs with a

diameter > 10 cm) was also counted in all 10 m sub-sections. All these local environmental descriptors were averaged for each of the 50 sampling sites, except for the number of trunks, which was summed for each site. Hence, the same trunks could be counted more than once (e.g. when crossing more than one snorkeling transect), but still represented the surface area of the habitat influenced by this type of structure. Finally, because habitat heterogeneity is known to influence the fish community characteristics (Weaver et al. 1997; Eadie and Keast 1984), we also included two descriptors of within site heterogeneity: standard deviation (SD) of flow velocity and SD of the percent cover of gravel. The gravel was the substrate type chosen because it showed the highest within-site variations. SD was used as an index of within site heterogeneity, instead of the coefficient of variation because the latter includes the effect of the average site condition, which was already considered by the descriptors "flow velocity" and "percent gravel cover".

SPSC traits matrices

Alimentary traits. - To describe the diet of the fish SPSC, we used the categories considered in Brind'Amour et al. (2011), which had been found to be significantly related to habitat use. They consisted in the presence or absence of the following food items: plant material, zoobenthos (defined as organisms living in or on the substrate, excluding insect larvae), zooplankton, insect larvae (odonata or chironomids living in or on the substrate or in the mid-water) and fish or crayfish. Since many fish species usually show high plasiticity in their diets (Chabot and Maly 1986; Johnson and Dropkin 1995; Hajisamae and Ibrahim 2008; Mendes et al. 2009), we did a vast literature review and included a food item if it represented more than 20% of the summer diet of the SPSC (either in % weight, % volume, number of organisms or relative importance index (George and Hadley 1979) in at least one reference. The references are found in the Appendix 2 (p.86).

Reproductive traits. - Reproductive traits consisted in the preferred spawning substrate type as well as spawning behaviours, following Balon (1975). Preferred substrate types consisted in coarse substrate, vegetation, no particular substrate or cavity. Nesting behaviours consisted in nesting and parental care. The choice of the reproductive traits was based on Poff (1997) hypothesis that such traits would be linked to habitat use at the meso-habitat scale. The reproductive traits were also coded in a presence-absence matrix, in order to allow for creation of reproductive guilds based on a

clustering method rather than arbitrary choices. Even if reproductive traits vary within a species, this information was not included in the reproductive matrix, because of the impossibility to distinguish males and females for many species while snorkeling. Since reproductive traits were the same for the different SC of a same species, reproductive guilds always included all the SC of a species.

Eco-morphological traits. - To describe the morphology of each fish species and Size Class, we used eight quantitative traits and five qualitative traits, taken from Reyjol et al. (2008) and Dumay et al. (2004). Quantitative traits were estimated by taking measurements on approximately 20 pictures per fish SPSC. Pictures were taken from fish captured on the field and imported in the TPS DIG 2 software (Integrated Morphometrics Packages) where the landmarks were positioned in a Cartesian system. The geometric positioning of the landmarks was then imported in R statistical language to calculate the quantitative traits, which were averaged by SPSC. Quantitative traits were shape factor, swim factor, relative insertion distance of the dorsal fin, relative eye diameter, relative pectoral fin length, relative insertion height of the pectoral fin, ratio between pectoral fin length and depth and the ratio between caudal fin length and caudal fin depth. Figure 2 shows the position of the landmarks used to calculate these traits and table 1 defines each trait in terms of landmark distances, using the law of cosines. The qualitative traits were mouth position (ventral, sub-terminal, terminal or superior), presence of silvery body coloration (presence or absence), mottled or vertical stripe patterns on the body (presence or absence), lateral stripe (presence or absence) and presence of spiny dorsal fin rays.
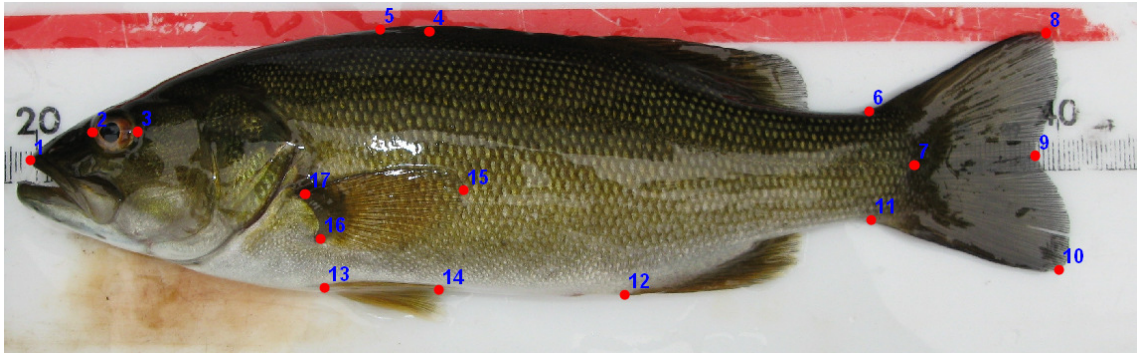
Fig. 2: Position of the 17 the landmarks used to calculate the 8 quantitative morphological traits.

Table 1: Definition of the eco-morphological traits. See figure 2 for the position of the landmarks

Eco-morphological trait	Calculation
Shape factor (ShapeF)	dist(1,9) / dist(4,14)
Swim factor (SwimF)	dist(6,11) / dist(8,10)
Relative insertion distance of the dorsal fin (DorsDist)	dist(1,5) * COS(angle 5,1,9) / dist(1,9)
Relative eye diameter (EyeDiam)	dist(2,3) / dist(1,9)
Relative pectoral fin length (PectLength)	dist(mean(16,17), 15) / dist(1,9)
Relative insertion height of the pectoral fin (PectHeight)	dist(14,17) * COS(angle 4,14,17) / dist(4,14)
Ratio between pectoral fin length and depth (pL_pd)	dist(mean(16,17), 15) / dist(16,17)
Ratio between caudal fin length and caudal fin depth (cL_cd)	dist(7,10) * SIN(angle 7,10,8) / dist(8,10)

Computations and statistical analysis

Relationship between guilds based on the diet, reproduction, eco-morphology and taxonomy, and habitat use. - In order to compare the strength of the relationship between the guilds formed with different trait matrices and habitat use, the following general procedure was followed: (1) group SPSC using K-means partitioning on each of the trait matrices, (2) sum fish densities (from the fish density matrix) per site for each group, following the groups created at step 1, (3) use canonical redundancy analyses (RDA) to relate fish group matrices to local environmental conditions. The last step (4) consisted in comparing the models formed at step (3) with null models of community composition (see Figure 3 for graphical representation of the analytical framework).

More precisely, step 1 consisted in performing a K-means partitioning, a non hierarchical iterative clustering method that looks for groups of objects minimizing the TESS (Total Error Sum of Squares), on each of the SPSC trait matrices: alimentary, reproductive and eco-morphological. For each of the trait matrices, we defined 2 to 12 groups of SPSC using the K-means in cascade ("cascadeKM" function, from the

"vegan" library; Oksanen et al. 2010). For the taxonomic guild approach, however, we grouped SPSC into the following taxonomic levels: order, family and species.

The second step consisted in using the 36 different partitions of the fish species and SC defined at the previous step to re-organize the fish density matrix into as many fish guild matrices. At each of the 50 sampling sites, fish densities were summed by guilds to create new fish guild matrices that had from 2 to 12 columns. We chose to extend the analysis to 12 groups, the total number of species, in order to have a better comparison with the taxonomic guild approach.

The third step consisted in relating the new fish guild matrices to the environmental descriptors using RDA. Prior to RDA, the fish guild matrices were transformed using Hellinger's transformation. The Euclidean distance computed on these transformed matrices is equal to the Hellinger distance computed on the untransformed data. The transformed data is hence suitable for RDA (Legendre and Gallagher 2001). Since the goal was to explore which fish community partition maximized the variance explained, the RDAs were computed with all the local environmental descriptors (no variable selection procedure; Legendre and Legendre 1998). The "rdaTest" package (Legendre and Durant 2010) was used the compute the adjusted R square (R^2_{adj}), an unbiased estimate of the variance explained by the environmental descriptors and assess the model significance.

Fig. 3 (next page)**:** Analytical framework. Part (A) consists in comparing the relationship between guilds based on the diet, reproduction, eco-morphology and taxonomy, and habitat use. (1) Use each trait matrices in a K-means partitioning to define 2 to 12 groups of species. (2) In the fish density matrix, sum the densities by site, according to the groups defined in (1). (3) Extract the R^2_{adj} from the RDA. Part B) is the building of the Null models. (1) Assign the species randomly to one of the 2 random groups. (2) In the fish density matrix, sum the densities by site, according to the groups defined in (1). (3) Extract the R^2_{adj} from the RDA and repeat step 1 and 2 many times, in order to create a distribution of random R^2_{adj}. (3) Redo the same operations for 3 to 12 groups.

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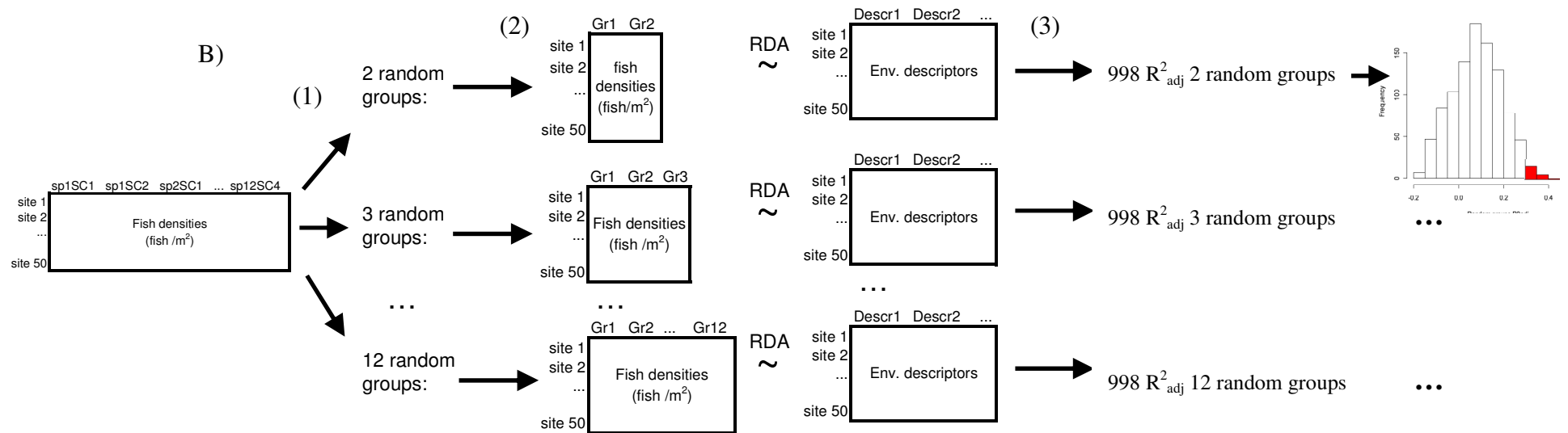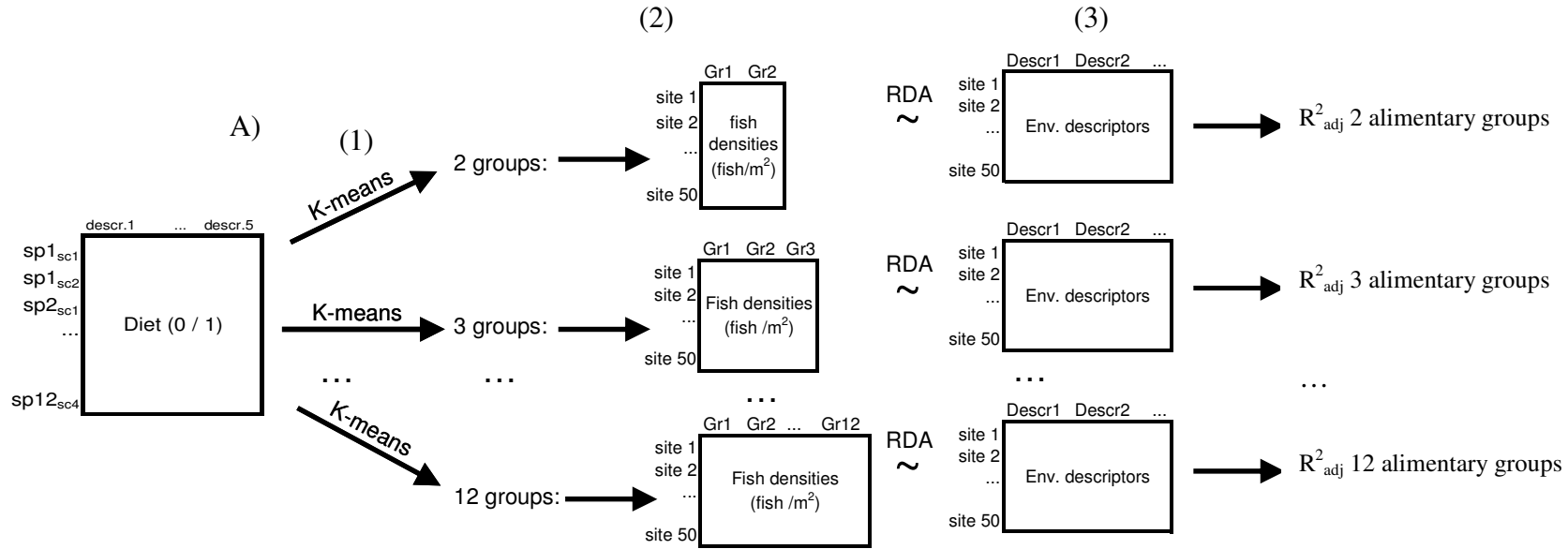
The environmental descriptors in these models were stream flow velocity, depth, water temperature, stream wetted width, substrate composition, macrophyte cover, branch cover, number of trunks, within-site SD of flow velocity and within-site SD of gravel cover. A Pearson's correlation matrix was computed to identify the most highly collinear environmental descriptors. Descriptors with one or more correlation coefficients greater or equal to 0.7 ($r \geq 0.7$) were removed. In these models, substrate composition was represented by the principal components (PC) of a principal component (PCA) analysis on the nine substrate classes, in order to reduce the number of explanatory variables and minimize collinearity (Kiers and Smilde 2007). The PCA was computed on the covariance matrix of the 9 substrate classes (as opposed to the correlation matrix) because we wanted to maximize the variation explained by the principal components, and also because we wanted to give more weight to the substrate classes with the most among site variation. Scaling type 1 was used to best represent the relationships between the sites. The PCA was done using the "rda" function available in the "vegan" R-language library (Oksanen et al. 2010). All the environmental descriptors were standardized (mean = 0, standard deviation = 1) before computing the models.

Since we created a large number of fish community matrices defined with the K-means partitioning on the traits matrices and with taxonomy, we compared the models created with a large number of random models. These random models, called null models in community ecology, consist in statistical methods comparing observed patterns with a large number of randomly permuted models, and can include constraints in the permutational framework (Peres-Neto et al. 2001). In our case, we created two sets of random models. The first one consisted in randomly partitioning the SPSC (columns of the fish community matrix) into 2 groups, using the new fish community matrix to perform the global RDA with all the environmental descriptors, extract the R^2_{adj} and repeat the operations 998 times. The R^2_{adj} of the alimentary and eco-morphological guilds was then compared with the distribution of the random group models 1000 R^2_{adj}. This procedure was then repeated for 3 to 12 groups. The second set of random models was similar to the previous one, except that the models were constrained to put all the size classes of a species in the same group, in order to compare with the reproductive and taxonomic guild approaches. The different alimentary, reproductive, eco-morphological and taxonomic

guild models were considered significant only if their R^2_{adj} was greater than 95% of the null models to which they were compared.

Finally, the last step of the analyses consisted in exploring the relationships between the fish guilds and the environmental descriptors in the best model. To do so, we selected the RDA model with the highest R^2_{adj} and performed a forward selection of the explanatory variables following the modifications suggested by Blanchet et al. (2008). To do so, we used "forward.sel" function (packfor library; Dray et al. 2009). The global model R^2_{adj} computed with "RdaTest" at the third step was used as a threshold in the forward selection. The "RDA" function (Oksanen et al. 2010) was used to compute the final model parameters.

Habitat use guilds and relationship with SPSC traits. - Similarly to Vadas and Orth (2000), we defined habitat use guilds with species association analyses. More specifically, we used Ward's agglomerative clustering on a species distance matrix (1-Pearson correlation matrix of the Hellinger transformed fish density matrix). We then used Kendall's coefficient of concordance following Legendre (2005) to identify significantly associated groups of SPSC. This analysis is described in details in Appendix 1A and B.

The next step consisted in determining the species traits explaining the previously identified habitat-use guilds. To do so, we performed two types of analyses, a stepwise canonical linear discriminant analysis (LDA) and a multivariate classification tree (MVCT), both relating the vector defining the habitat use guilds for each species (response variable) to the matrices of species traits (explanatory variables).

The stepwise stepwise canonical linear discriminant analysis was performed using the "stepclass" function from the "klaR" library (Weihs et al. 2005), in combination with a self programmed bootstrapping procedure to select to best model based on the cross-validation Correct Classification Rate (CCR). Details on the model selection and computation of the final model parameters are shown in Appendix 1C. We also computed classification functions for each of the 7 habitat-use guilds, which are linear equations that can be used for the purpose of assigning objects to groups. The coefficients of the

explanatory variables (traits) in each function indicate the relative importance of the traits to assign an object to that group. Likewise, we used MVCT to relate habitat-use guilds to SPSC traits. The best model was also selected using cross-validated CCR. Details on the method are described in Appendix 1C.

Results

Fish communities and local habitat descriptors

Sampling sites were snorkeled from 1 to 3 times, from July 1 to 17. A total of 23 species belonging to 11 families was observed during the field surveys, for a total of 16 760 individuals. Cyprinids (9 species) was the most represented family, accounting for 73% of the individuals, followed by centrarchids (4 species), accounting for 19.6% of the individuals. Site species richness ranged from 2 to 14 and averaged 8.4 species. Because of logistic and time constraints, we restricted our analyses to the species representing more than 1% of the individuals observed. The species removed from the analyses were the following: banded killifish (*Fundulus diaphanus*), brook trout (*Salvelinus fontinalis*), brown bullhead (*Ictalurus nebulosus*), central mudminnow (*Umbra limi*), fathead chub (*Pimephales promelas*), johnny darter (*Etheostoma nigrum*), logperch (*Percina caprodes*), muskellunge (*Esox masquinongy*), northern pike (*Esox lucius*), northern redbelly dace or finescale dace or their hybrids[1] (*Chrosomus* sp.) and slimy sculpin (*Cottus cognatus*). This led to a new fish community matrix of 12 species (34 SPSC), belonging to 5 families (Table 2). The new fish community matrix (hereafter referred as fish density matrix) accounted for 92.9% of the individuals observed. SC 2 common shiner (*Notropis cornutus*), SC 2 creek chub (*Semotilus atromaculatus*) and pumpkinseed (*Lepomis gibbosus*) were the three most abundant species and had an average site density of respectively 0.153, 0.056, 0.049 fish·m^{-2}.

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[1] Northern redbelly dace and finescale dace cannot be differentiated from their hybrids with external morphological characteristics (Doeringsfeld et al. 2004).

Sites were characterized by relatively low flow velocity (mean = 17 cm·s⁻¹), but high within-site flow velocity variations (sd = 9 cm·s⁻¹; Table 3). Water temperatures ranged from 17 to 22°C, while stream wetted width ranged from 6.9 to 26.2 m (Table 3). Substrate composition was dominated by fine substrate classes (clay, silt and sand covered 60% of the sites on average). Aquatic vegetation also covered a significant portion of the sites (18% on average; Table 3). In contrast, branch cover was less important and less variable among sites.

Table 2: Fish community characteristics. Size Class, mean, minimum and maximum observed densities and number of occurrences of the 12 more abundant observed species.

Species	Size Class	Observed density (fish·m⁻²)			Number of site occurences
		min	max	mean	
Exoglossum maxillingua (Lesueur) (Cutlips minnow)	1	0	0.141	0.011	27
	2	0	0.214	0.039	30
Notemigonus crysoleucas (Mitchill) (Golden shiner)	1	0	0.009	0.001	5
	2	0	0.274	0.012	20
Semotilus atromaculatus (Mitchill) (Creek chub)	1	0	0.154	0.009	26
	2	0	0.380	0.056	40
	3	0	0.252	0.016	33
Luxilus cornutus (Mitchill) (Common shiner)	1	0	0.413	0.051	39
	2	0	1.727	0.153	48
	3	0	0.080	0.013	34
Semotilus corporalis (Mitchill) (Fallfish)	1	0	0.020	0.002	12
	2	0	0.408	0.031	26
	3	0	0.108	0.010	21
	4	0	0.061	0.004	15
Pimephales notatus (Rafinesque) (Bluntnose minnow)	1	0	0.080	0.007	18
	2	0	0.115	0.014	28
Micropterus dolomieu (Lacépède) (Smallmouth bass)	1	0	0.268	0.008	12
	2	0	0.045	0.002	13
	3	0	0.029	0.002	14
	4	0	0.024	0.002	16
Ambloplites rupestris (Rafinesque) (Rockbass)	1	0	0.090	0.010	30
	2	0	0.079	0.014	34
	3	0	0.036	0.007	32
Lepomis gibbosus (Linnaeus) (Pumpkinseed)	1	0	0.086	0.005	24
	2	0	0.828	0.049	39
	3	0	0.115	0.012	29
Culaea inconstans (Kirtland) (Brook stickleback)	1	0	0.088	0.005	10
Catostomus commersoni (Lacepède) (White sucker)	1	0	0.015	0.001	13
	2	0	0.035	0.003	14
	3	0	0.040	0.004	18
	4	0	0.065	0.005	22
Perca flavescens (Mitchill) (Yellow perch)	1	0	0.169	0.004	5
	2	0	0.088	0.006	13
	3	0	0.100	0.007	18

Table 3: Main environmental conditions

Environmental descriptors	min	max	mean
Flow velocity (cm/s)	3	58	17
Depth (cm)	49	102	75
Water temperature (°C)	17	22	20
Stream wetted width (m)	6.9	26.2	15.1
Substrate type (% cover)			
- clay	0	18	1
- silt	0	63	20
- sand	6	88	38
- gravel	0	51	22
- pebble	0	19	6
- cobble	0	57	8
- rocks	0	33	4
- boulders	0	12	1
- bedrock	0	10	0
Macrophyte cover (%)	0	90	18
Branch percent cover (%)	1	28	8
Number of trunks	7	206	66
Within-site standard deviation of flow velocity (cm/s)	1	16	9
Within-site standard deviation of % gravel cover (%)	4	87	24

Relationship between guilds based on the diet, reproduction, eco-morphology and taxonomy, and habitat use.

Before relating the different guilds formed using the trait matrices or taxonomy to the local environmental descriptors, a screening of the environmental descriptor was done to remove highly collinear variables, which could have biased the estimation of the models' parameters (Legendre and Legendre 1998). Percent silt cover and percent macrophyte cover were the only two highly collinear descriptors ($r = 0.740211$, p-value < 0.0001). Consequently, percent silt cover was removed from the principal component analysis on the substrate classes (Figure 4). The three first axes of the PCA on the 8 remaining substrate classes respectively represented 65.4, 19.0 and 9.6% of the variation. PC3 (not shown in Figure 4) was included because it represented a gradient between mid-size substrate classes (pebble-cobble) and rocks, not perceivable on the 2 first PC.
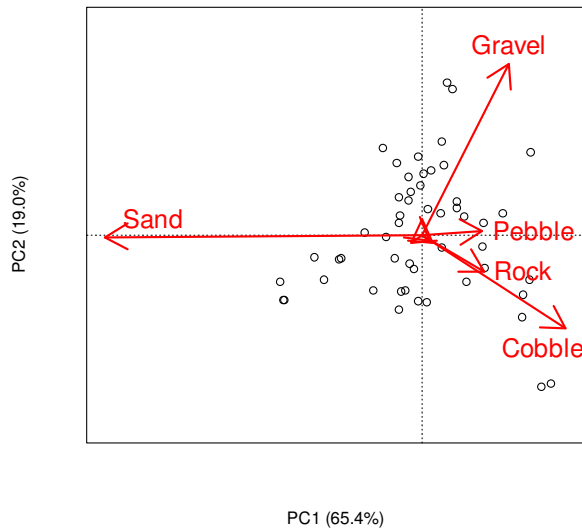
Fig. 4: Principal component analysis performed on the covariance matrix of the percent cover of the 9 substrate classes. Silt was removed because it was collinear to percent macrophyte cover (r = 0.740211, p-value < 0.0001). Scaling type 1.

The K-means partitioning of the species and SC on the alimentary and eco-morphological trait matrix led to the formation of 2 to 12 groups. The reproductive trait matrix (6 binary traits), however, could only be partitioned from 2 to 8 groups, because there was a maximum of 8 combination of traits. The taxonomic approach partitioned the fish community either in 3 orders (cypriniform, perciform and gasterosteiform), 5 families (*cyprinidae, centrarchidae, catostomidae, percidae, gasterosteidae*) or 12 species (Table 2).

The strength of the relationship between fish guilds and habitat use is summarized in Figure 5. Guilds based on the alimentary trait matrix produced poor FHUM, except for the partition of the fish community into 2 groups, as can be seen on Figure 5. In all cases, however, the diet guild models were not significantly different from NM 1 (Figure 5). Eco-morphological guilds also produced poor models, as most of the R^2_{adj} were not significantly different than 0 and hence, not better than NM 1. Guilds based on reproductive traits produced the best models, as most of them were significantly different than NM 2. The best model was when partitioning the fish community into 3 groups, based on reproductive

traits. The taxonomic guild approach led to poor models ($R^2_{adj} = 0$) when partitioning the community into 3 orders or 5 families. When using the more traditional species – environment approach, the RDA explained 18.5% of the variation, which was significantly different than 0, but not significantly better than NM 1.

The best model (3 guilds based on reproductive traits) explained 32.3% of the variance in the fish community. When forward selecting the environmental descriptors, the model explained 28.5% of the variance. The significant local environmental descriptors were selected in the following order: coarse substrate (PC1 of the PCA on the substrate classes, Figure 6), percent macrophyte cover and stream section average depth. They respectively explained 12.4, 7.6 and 8.5 % of the variance. Group 1 consisted in species building a nest for the reproduction and giving parental care (e.g. pumpkinseed, bluntnose minnow and brook stickleback). Group 2 was defined by species not building nests and not giving parental care (e.g. golden shiner, white sucker and yellow perch), two of which use aquatic vegetation to spawn. Group 3 was defined by species using gravel or coarser substrate classes to build nests (lithophils, e.g. centrarchids, excluding pumpkinseed, and cutlips minnow). Group 1 was well correlated with finer substrate classes, group 2 was well correlated with macrophyte cover and group 3 was well correlated with coarser substrate classes (Figure 6).
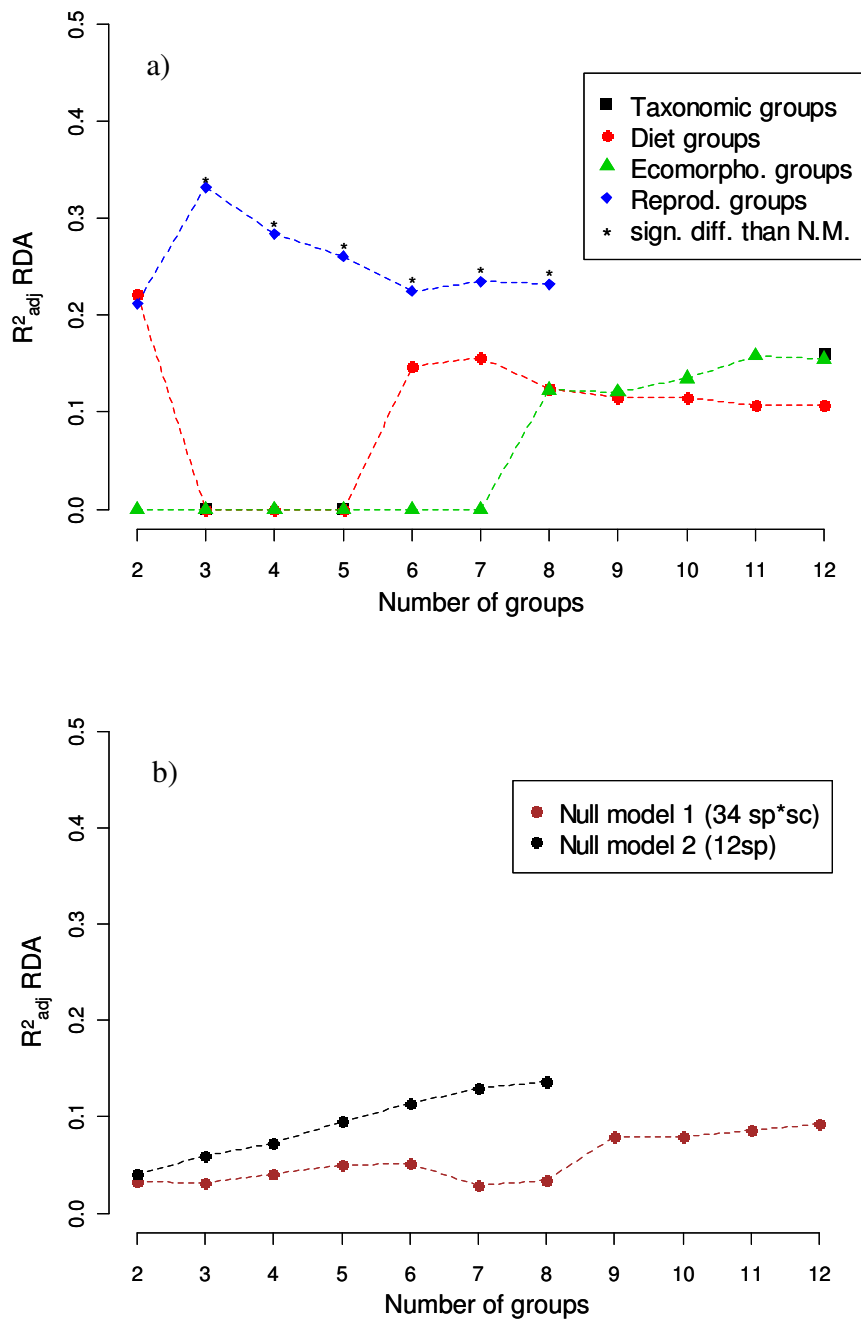
Fig. 5a: R^2_{adj} of the relationship between the guilds formed based on alimentary, reproductive, eco-morphological or taxonomic similarities (A). Points with and asterisk (*) are models with a significantly different R^2_{adj} than the null models. (B) Average null models R^2_{adj}. Null models 1 consisted in totally randomized groups, whereas null models 2 consisted in randomized groups with the SC of a same species always in the group.
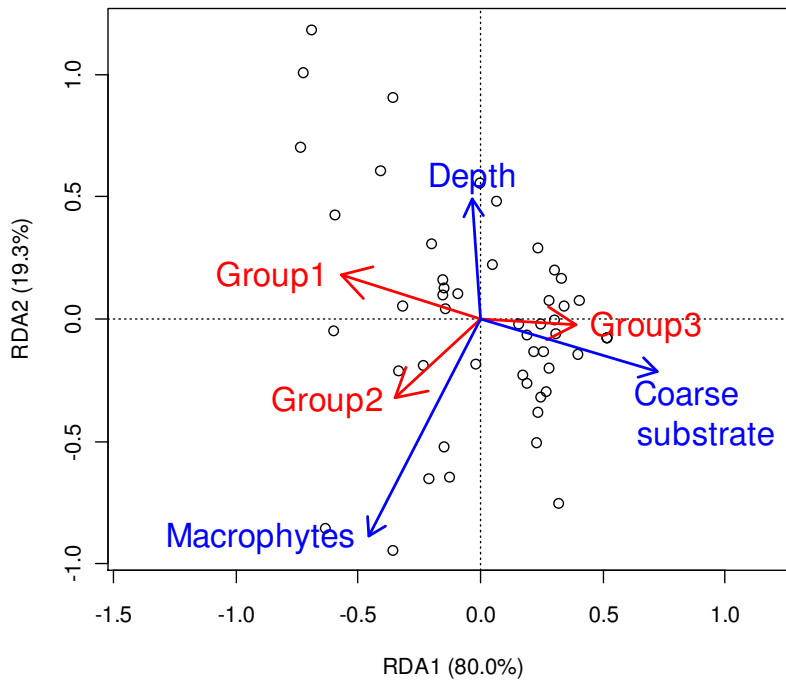
Fig. 6: Triplot of the rda relating the 3 guilds based on reproductive traits to the forward selected local environmental descriptors. Scaling type 2. First and second canonical axis represent respectively 80% and 19.3% of the variance explained (28.5%). Arrows represent guild densities (red) or environmental descriptors (blue) and circles represent the sampling sites.

Habitat use guilds and relationships with species trait matrices

The Ward's agglomerative clustering coupled with Kendall coefficient of concordance tests identified seven significant habitat use guilds (Figure 7). When cutting the tree at k = 6 groups, 3 species were not significantly associated to their group (LUco_3, PEfl_1, CAco_1; *a posteriori* test, $\alpha = 0.05$), while when cutting the tree at k = 7 groups, all species were significantly associated with their groups, except for SC 1 yellow perch (p = 0.053). We had to go up to k = 9 groups to have all species significantly associated with their groups, with the SC 1 yellow perch in their own group. Consequently, we decided that seven groups was the most relevant habitat-use guild structure, specifically since SC 1 yellow perch were not very abundant and therefore were more hardly significantly associated with their group.
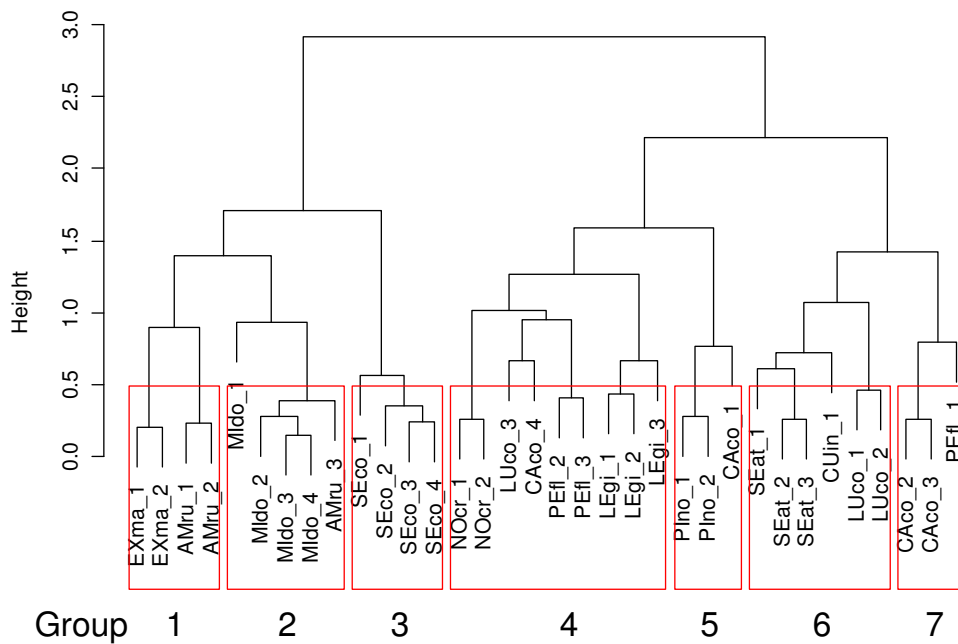
Fig. 7: Habitat use guilds. The dendrogram represents a Ward's agglomerative clustering done on the Hellinger transformed fish sp and SC 1-correlation matrix. The 7 groups are all composed of significantly associated SPSC, except for PEfl_1 ($p = 0.053$).

Group 1 consisted in cutlips minnows and rockbass, group 2 smallmouth bass and large rock bass, group 3 was only represented by fallfish, group 4 consisted in golden shiners, yellow perch (except for juveniles), pumpkinseed and large common shiner and white suckers. Group 5 included bluntnose minnow and small white suckers, group 6 included creek chub, brook stickleback and common shiners. Finally, group 7 consisted in medium sized white suckers and juvenile yellow perch (Figure 7).

Many Size Classes of a same species were found to be in the same habitat-use guilds, more strikingly for cyprinids species (Figure 7). The exception to that were SC 1 rock bass (they were however located close to the rest of its species), SC 1 yellow perch, and SC 1 and 4 white suckers. SC 3 common shiner were the only SC of cyprinid species not significantly associated with its species.

There also seemed to be 2 very distinct fish communities identified in the dendrogram (group 1, 2 and 3 vs. groups 4 to 7), that could be interpreted as fish preferring coarser substrate and faster current (on the left hand side of the dendrogram) as opposed to fish communities characterizing finer substrate, higher macrophyte cover and lower current velocity habitats (right hand side of the dendrogram).

The LDA final model, relating fish habitat-use guilds to eco-morphological traits, included 4 explanatory variables (Zoobenthos, sub-terminal mouth position, Insect larvae and Silver; Figure 8), whereas the classification tree had a much complex structure: 7 splits including different explanatory variables and at least 1 surrogate variable at 3 splits (Figure 9). LDA apparent CCR was 76.9% and was 88.2% for MVCT but ten fold cross-validation CCR was 73.3% for LDA and 30.2% for MVCT. Considering the complexity and poor cross-validation CCR of the MVCT, we chose to work only with LDA for interpretation of the habitat-use guilds. This result is not surprising, however, since LDA allows for linear combinations of traits to discriminate between groups, and not MVCT.

The ordination of the LDA (Figure 8) represented 85% of the among-group variation on the first two canonical axes (63.0 and 22.1% on respectively the first and second axes). The standardized canonical coefficients for the first two canonical axes (Figure 8) indicate that the descriptors that best accounted for the among-group variation are Zoobenthos, Sub-terminal mouth position, Insect larvae. Groups 4 and 7 are close to each other in the canonical space and hence, were not well discriminated.
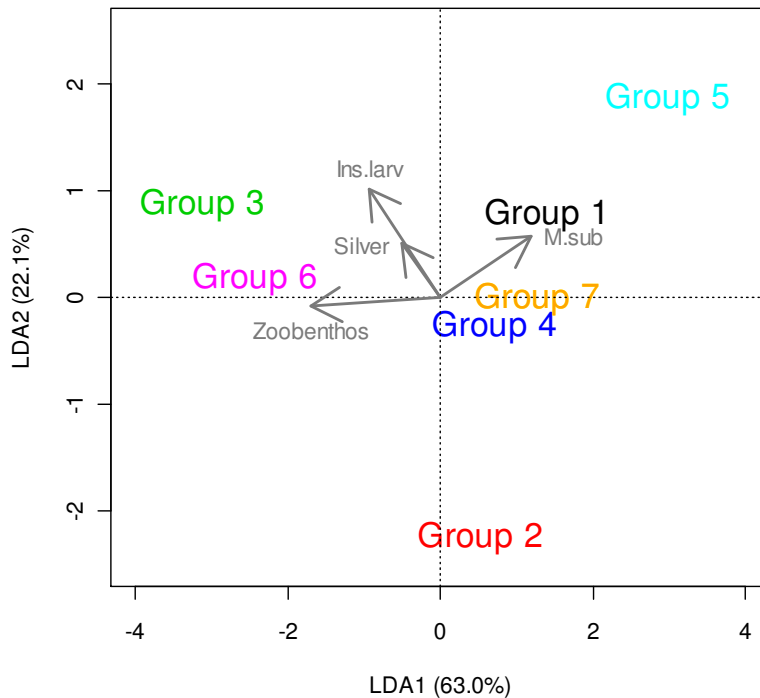
Fig 8: Position of the habitat-use group centroids in the space of the 2 first linear discriminant axes (LDA1 and LDA2). First axis (LDA1) represents 63.0% of the explained among-group variation, whereas LDA2 represents 22.1% of this variation. Zoobenthos : presence of zoobenthos in the diet; Ins.larv : presence of insect larvae in the diet; Silver : silvery coloration pattern; M.sub : subterminal position of the mouth.

The ordination could be used to interpret the importance of the traits in the determination of the habitat-use guilds, but we preferred to use the classification functions (Table 4) since the coefficients gave a more precise idea of the importance of each trait in the determination of the habitat-use guilds. Group 1 was mostly determined by sub-terminal mouth position, group 2 mostly characterized by the absence of the selected traits, group 3 was determined by presence of zoobenthos and insect larvae in their diet, as well as silvery coloration, group 4 was not well discriminated, group 5 was mostly determined by sub-terminal position of the mouth and the absence of zoobenthos in the diet of the SPSC belonging to that group. Group 6 was mostly determined by presence of zoobenthos and insect larvae in their diet and finally, group 7 was not well discriminated by any trait.
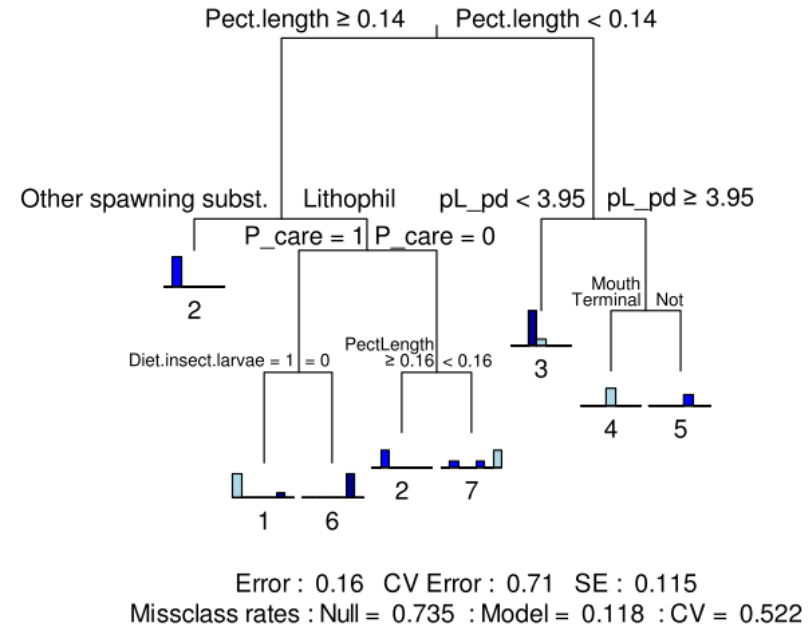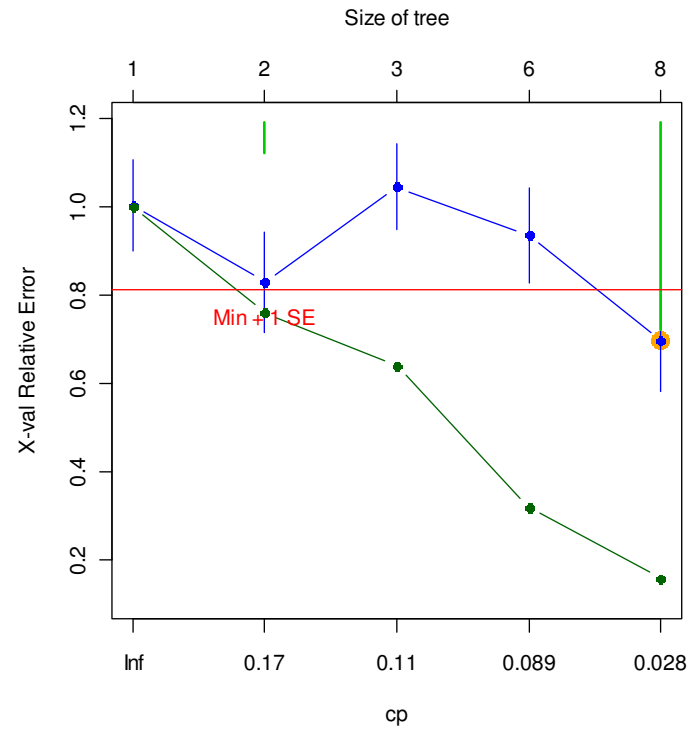
Fig. 9: (a) Multivariate classification tree 10 fold cross-validation relative error (±standard error; blue). The red horizontal line represents the x-val relative error (RE) of the best tree plus 1 sd of this x-val RE. (b) multivariate classification tree selected following the Min + 1 SE rule (8 leaves). Refer to table 1 for definition of abbreviations.

Table 4: Classification functions for each habitat-use guild. Coefficients were calculated from standardized descriptors, so that their value can be interpreted as the relative contribution to the definition of the group.

Group	Constant	Diet.Zoobenthos	Diet.Insect.larvae	Mouth_po_D	Silver
1	-2.36	-1.32	0.01	2.99	-1.66
2	-2.84	-0.30	-3.05	-0.15	-1.29
3	-5.68	4.86	3.26	-3.31	2.92
4	-0.60	-1.81	-0.99	0.06	0.06
5	-6.55	-5.22	-1.49	4.88	0.17
6	-3.22	4.53	2.84	-2.54	0.58
7	-1.49	-2.62	-0.49	0.68	-1.05

Discussion

The goals of this study were to identify, within four approaches found to form guilds (reproductive, alimentary, eco-morphology and taxonomy), which one produces the best fish habitat models, and to evaluate if specific traits (diet, reproduction or eco-morphology) or taxonomy could differentiate habitat-use guilds. Reproductive guilds led to the best fish habitat models, most probably because of the relationship between fish preferred spawning grounds and habitat use. On the other hand, traits related to the feeding biology seemed to be the best at discriminating the *a priori* defined habitat use guilds. The analysis used to explain habitat use guilds did not, however, reflect the among habitat use guilds relationships, while the reproductive guild model was supported by the literature. Validation of the reproductive guild model could confirm our findings, and be used to predict changes in the productive capacity of habitats.

Comparison of the different guild to develop fish habitat models

Taxonomic groups led to poor habitat-use models and this is not surprising since many species within an order or a family are known to have distinct habitat preferences. For instance, within the centrarchid family, some species are known to prefer habitats with coarse substrate and the absence of macrophytes (rock and smallmouth bass; Weaver et al. 1997), while others like pumpkinseed or bluegill (*Lepomis macrochirus*) are known to prefer vegetated areas and soft substrates (Bernatchez and Giroux 2000; Weaver et al. 1997; Randall et al. 2004). The same reasoning holds for cyprinid species, like fallfish and golden shiner for instance, which are respectively found in greater densities in fast flowing river sections and densely vegetated areas (Lanthier 2009; Scott and Crossman 1985;

Bernatchez and Giroux 2001). It is hence proposed that taxonomic guilds be used with caution, especially when studying fish-habitat relationships at the meso-habitat scale in the Laurentian streams. The term taxonomic guild has been more extensively used in extremely diverse fish communities, like the ones found in coral reefs (Bean et al. 2002), for very diverse groups of organisms (e.g. insects, phytoplankton; Kruger et al. 2010; Vadrucci et al. 2003) or for very large scale studies (Read et al. 2010) and we recognize that this appellation can be useful in such circumstances.

Alimentary groups led to a few good models (for 2 and 8 to 12 groups), but none of them were significantly different than null model 1, and did not outperform the taxonomic (12 species) approach (Figure 5). Many authors had stressed the importance of size-related diet changes in structuring fish communities (Specziar and Rezsu 2009; Garrison and Link 2000), and we expected that the inclusion of such details in the description of the diet would help create better fish-habitat models. This result was even more surprising considering that (Brind'Amour et al. 2011) had found significant associations between the feeding-oriented traits and the environmental characteristics in very similar lake fish communities. We could, however, relate this result to a certain lack of precision in the determination of the ontogenetic diet shift. The Size Classes (5 cm increments) were defined in order to facilitate underwater fish identification and the ontogenetic diet shift occurred, for many species, within a SC. Consequently, SC of some species had more food items since, for instance, both plankton and benthos feeders were found in the same SC (e.g. SC 1 pumpkinseed and SC1 white sucker). Another reason why this approach may not have led to good models is the high flexibility observed in the diet of many fish species (Pusey et al. 1995; Specziar and Rezsu 2009; Wennhage and Pihl 2002). Fish diets are known to change depending on season (Hajisamae and Ibrahim 2008), ontogenetic stage (Specziar and Rezsu 2009; Garrison and Link 2000) and, to a certain level, habitat type (Wennhage and Pihl 2002). It may consequently be harder to precisely describe fish diet and to relate it to habitat-use, especially when considering a wide range of habitat types.

Eco-morphological groups led to poor fish-habitat models (Figure 5). When looking more precisely at the groups formed with this approach (not shown), it appeared that they

largely reflected taxonomy. This is not surprising since species with a common ancestor are known to share many morphological characteristics (Campbell 1995). Taxonomic guilds produced poor habitat-use models, and eco-morphological groups could have led to poor models because of their similarity with the latter approach and the reasons mentioned previously. Moreover, Poff (1997), in his niche model to filter species traits at different spatial scales, hypothesized that eco-morphological traits would respond to habitat features like flow velocity or water depth at the micro-habitat scale. Our sampling was done at a coarse meso-habitat scale, which could partly explain why eco-morphological groups did not led to good habitat-use models.

A number of authors have, however, successfully related morphology to habitat-use like Reyjol et al. (2001) who individually regressed 11 morphological traits against main environmental characteristics, Morinville and Rasmussen (2008) who used discriminant analysis to relate brook trout habitat-type specialist to morphologic traits, or Brind'Amour et al. (2011) who used the fourth corner and RLQ analyses to directly relate fish feeding traits to environmental descriptors. One of the major differences with these studies is that we did not directly relate each fish morphological trait to habitat use. We used a clustering method based on the average (over many traits) morphological distances between SPSC, to create groups of eco-morphologically similar species, and then related the densities of these groups to local habitat features. It is thus possible that the average of all the morphological traits blurred the relationship between traits and environmental conditions, since all the information has been used at the same time in the analysis.

Reproductive groups clearly outperformed the other models and were significantly different than both Null Model 1 and 2 (for 3 to 8 groups; Figure 5). When looking more in detail at the best of the reproductive group models (for three groups; Figure 6), the RDA triplot showed concordant relationships between preferred spawning grounds and habitat use. Group 1 (nest builders giving parental care; e.g. pumpkinseed, bluntnose minnow and brook stickleback) was well correlated with finer substrate, which is consistent with other studies showing that pumpkinseed, the species largely driving the variation in this group (Table 2), prefers fine substrate (Bernatchez and Giroux 2000; Weaver et al. 1997; Randall

et al. 2004). Group 2 (no nests, no parental care; e.g. white sucker, golden shiner, and yellow perch) was well correlated with macrophyte cover, which is also consistent with the literature about those species (Lanthier 2009; Bernatchez and Giroux 2000). Moreover, 2 species in this group (golden shiner and yellow perch) use aquatic vegetation to spawn. Group 3 (lithophils, e.g. centrarchids, excluding pumpkinseed, and cutlips minnow) was well correlated with coarser substrate type, which is also confirmed by the literature (Scott and Crossman 1985).

The good fit between reproductive guild densities (largely based on spawning ground habitat) and local environmental conditions could be explained in part by the temporal proximity of the sampling campaign with the reproductive period of many of the species. Indeed, most species modeled were late spring or early summer spawners and the sites were sampled soon after this time period (from July 1 to 17). Precise information about spawning periods is hard to find in the literature, because of high regional variability (Scott and Crossman 1985), but in three years of field work, we have never observed signs of reproduction in our streams after June 24. It is thus possible that the superiority of the reproductive guild model be seasonal, and that other guild models perform better later in the summer. The superiority of the reproductive guild model could also be related to the similarity between spawning and nonspawning habitat preference for many riverine species (Aarts and Nienhuis 2003). In addition to the above mentioned explanations, the superiority of the reproductive group models is concordant with Poff (1997) hypotheses that fish reproductive traits would respond to environmental filters such as substrate composition at the reach and meso-habitat scale.

Even if the superiority of the reproductive guilds model was supported by the literature (Aarts and Nienhuis 2003; Poff 1997), and that it explained significant proportions of the variance, we are cautious with the interpretation of this result because our analytical framework could be improved. First, when comparing the strength of the relationship between each different approach to form guilds and the local environmental conditions, we did not remove the spatially structured component of the environmental descriptor matrix, so that the variance explained by the environment could have been over

estimated (Legendre et al. 2002; Legendre and Legendre 1998). Partial RDA with PCNM as covariate could have been used to this purpose (Dray et al. 2006). Second, the use of K-means partitioning led to species and SC groups that were not easily defined by the traits, even if the algorithm is supposed to create the most homogenous groups as possible. A hierarchical method such has Ward's agglomerative clustering could have led to more easily interpretable groups. Finally, we did not include any validating procedure to compare the models, so that the variance explained by the different models could have been overestimated (Olden et al. 2002). Calculation of R^2_{adj} on an independent dataset or inclusion of a cross-validation procedure could have improved the analysis.

Habitat-use guilds and relationships with species traits

The second objective of this study was to create habitat-use guilds based on observed correlations and to explain those guilds with the species trait matrices. Habitat-use guilds were represented in Ward's agglomerative clustering dendrogram (Figure 7), and identified two distinct fish communities. The first one (group 1, 2 and 3) consisted in species known to prefer coarser substrate types (cobbles, rocks and boulders) or faster flow velocities, as opposed to species known to prefer areas of sedimentation (finer substrate classes) and the cover provided by aquatic vegetation (group 4, 5, 6 and 7). Additional regression analysis could provide more insight into the interpretation of the habitat-use guilds.

Another interesting finding is that many SC of the same species were found into significantly associated groups. A number of studies have had similar results, like Weaver et al. (1997) who found that all sizes smallmouth and rock bass were associated with unvegetated habitats structured by very coarse substrate types, which is concordant with our results (Figure 7). All cyprinid SC of a same species were found in significantly associated groups, with the exception of SC 3 common shiner. Similarly, Chuang et al. (2006) found that juvenile and adults of 2 morphologically similar stream cyprinid species had very similar habitat preferences, at the meso-habitat scale. Hoagstrom et al. (2008), however, found differences in flow velocity preferences in relation with body size for a

small-bodied riverine minnow, but his analysis was performed at the micro-habitat scale. It could hence be possible that the detection of within species differences in habitat preference for cyprinids be related to the spatial scale at which observations are taken.

Few Size Classes were not significantly associated the other SC of their species, like SC 1 yellow perch. This finding is contrary to Weaver et al. (1997), who found that both the yearling and adult yellow perch dominated the community in abundant and species rich macrophyte beds. This difference ought to be related to the fact that our study was done in streams (as opposed to the latter study) and that such environment may impose more important constraints to small sized fish, especially since both studies were done at the same spatial scale ($\cong$100m long sampling sites). Aadland (1993) also found differences in habitat-use patterns between young of the year and adult white suckers, which could be related to the strong ontogenetic shift in the diet occurring in their first year (Lalancette 1977; Johnson and Dropkin 1995). As for midsize (SC 2 and 3) and large (SC 4) white sucker, we found no explanation why they were not in the same habitat-use guild.

A number of reasons could explain that we found most Size Classes of a same species in the same habitat-use groups. First, as mentioned previously, the spatial scale at which this study was performed could be too coarse to detect such subtle differences. It is also possible that our definition of size classes (5cm increment; in order to facilitate field work) did not match the ontogenetic change in habitat use for many of the species present in this study. This definition could have blurred the ontogenetic change in habitat use by placing species of different life stages in the same Size Class. Finally, it is also possible that many species of the Lower Laurentian streams do not show a strong ontogenetic habitat use shift. It is unfortunately not possible to test the support for these hypotheses for now.

We related the habitat-use guilds to species trait matrices with LDA and MVCT. Both models had good apparent CCR, but when comparing the complexity of their structure and their cross-validation CCR, the LDA model was clearly superior to the classification tree. This result is contrary to some studies comparing these two methods, like Olden and Jackson (2002) as well as Karels et al. (2004), who obtained better models

with classification trees. Our study was distinct, however, in that the response variable was multi class (as opposed to binary in the latter studies), and the LDA forward selection procedure was modified in order to be very similar to the one employed in MVCT.

The 2 first discriminant functions (Figure 8) explained most of the among group variation (85%) with a linear combination of 4 binary traits: zoobenthivorous, sub-terminal mouth position, diet including insect larvae and silvery coloration patterns. Three of these selected traits are related to the feeding biology of fishes, which is inconsistent with the results of the analysis for the first objective (Figure 5). On the other hand, when looking at the LDA ordination (Figure 8), the relative position of the group centroids did not reflect the structure of the dendrogram. For instance, group 1 and 2 are closer to each other than group 1 and 7 in the dendrogram, which is not the case in the LDA ordination. The underlying reason is that the only information included in the analysis was the species and SC group membership, reflecting the within group correlations, and that the among-group correlations was not taken into account. Other multivariate models, like extensions of the co-inertia analysis (Dray et al. 2003), could improve our understanding of the habitat-use groups.

The 3 reproductive guilds identified in the first section had a different structure than the habitat-use guilds. In the reproductive guilds, all the SC of a species were in the same group, whereas it was not always the case in the habitat use guilds. Habitat use groups 1, 2 and 3 (Figure 7), similarly to reproductive group 3, included cutlips minnow, fallfish, smallmouth and rock bass. Reproductive group 3, however, also included the two most common species: common shiner and creek chub. The other 2 reproductive groups had no similarities with habitat use groups 4 and 5, or 6 and 7. This leads us to doubt the validity of our reproductive guilds model, even if it was supported by the literature and that variance explained was significantly different than zero and from the null models. As mentioned above, a good way to assess if the reproductive guild model is valid and did not overfit the data would be to use it, as well as the habitat-use guild models, on an independent dataset.

Conclusion

In the first part of this study, we concluded that reproductive traits were the best at delineating fish guilds to produce multivariate fish habitat models, and that a 3 reproductive guilds model seemed to perform particularly well. In the second part of the study, we did the opposite analysis: delineate fish habitat use guilds and relate them to species traits. We found that traits oriented towards the feeding ecology of fish seemed to be the best at explaining habitat use guilds. Even if these result are somehow discordant, they do support the niche filtering hypothesis (Zobel 1997), stipulating that species co-occuring will be more similar than expected chance, because the environment acts as filters to select for the species with the adapted traits. We showed that it was possible to improve multivariate fish habitat models by grouping species based on different types of traits, and in that sense, our approach is promising for modelling the productive capacity of stream fish habitats in the context of NNL.

Aknowledgements

Conclusion générale

Le premier objectif de mon premier chapitre était d'évaluer la performance relative de la pêche électrique et de la plongée de surface pour estimer les abondances des espèces et classes de taille pour des communautés de poissons non dominées par les salmonidés. Notre étude a démontré que les 2 méthodes d'échantillonnages décrivent de façon semblable les communautés de poissons présentes aux sites. L'échantillonnage en plongée de surface a cependant permis d'observer de plus grandes richesses spécifiques, de même que de plus grandes abondances que la pêcheuse électrique, même si elle a sous-estimé les abondances de 2 espèces aux comportements cryptiques ou nocturnes. Une étude de Goldstein (1978) comparant la seine de rivage et la plongée de surface dans des rivières aux communautés de poissons très semblables a également observé une supériorité de l'échantillonnage en plongée. Il est possible que les plongeurs aient surestimé les abondances de poissons en les comptant plus d'une fois. Cependant, les plongeurs furent entraînés rigoureusement (plus de 2 mois) et avaient pour directive de ne jamais compter les poissons qui fuyaient vers l'amont, puisqu'ils étaient confinés à l'intérieur des sites par des filets de blocage et qu'ils allaient donc être énumérés plus tard. De plus, la forte tendance de l'échantillonnage en plongée de surface à observer de plus grandes abondances de poissons est concordante avec la plus grande richesse spécifique observée par cette même méthode.

Le second objectif du premier chapitre de mon mémoire était d'évaluer l'impact des conditions environnementales sur les différences potentielles entre les communautés de poissons observées par ces 2 méthodes. Les 3 modèles utilisés pour tester cette hypothèse n'ont pu identifier de caractéristique environnementale expliquant la différence entre les communautés observées avec la pêcheuse électrique et celles observées en plongée de surface. Nous avons cependant émis une certaine réticence à extrapoler ces résultats à toutes les rivières des Laurentides étant donné que la taille de notre échantillon n'était pas très importante. D'autre part, certaines études comparatives entre ces 2 méthodes d'échantillonnage ont réussi à expliquer la différence observée à l'aide de descripteurs environnementaux, comme Wildman et Neumann (2003), ainsi que Mullner et al. (1998). Nos sites d'échantillonnage avaient des conditions environnementales distinctes de ces 2

études, mais la différence la plus marquante est en terme de communautés de poissons observées.

Notre étude est donc très différentes de toutes les autres que nous avons recensées dans la littérature puisque la comparaison entre la pêcheuse électrique et la plongée de surface a eu lieu dans des cours d'eau dominés par les cyprinidés et les centrarchidés, plutôt que les salmonidés, tout en ayant des conditions environnementales favorables aux 2 méthodes. Il est reconnu dans la littérature que la probabilité de capture des poissons à la pêcheuse électrique varie en fonction des espèces (Reynolds 1996), et certains auteurs mentionnent que les poissons formant des bancs, comme les cyprinidés, et les centrarchidés pourraient être moins facilement capturés que d'autres groupes de poissons (Reynolds 1996, Meador et al. 2003, Kimmel et Argent 2006).

L'absence de relation entre les différences dans les communautés de poissons observées par les 2 méthodes d'échantillonnage et les conditions environnementales de notre étude pourrait être expliquée par le comportement des poissons rencontrés. Les salmonidés sont reconnus pour montrer certaines formes de comportements territoriaux ou cryptiques (Thurow et Schill 1996; Peterson et al. 2004), ce qui pourrait expliquer pourquoi l'inclusion de descripteurs de la complexité de l'habitat puisse contribuer à expliquer les différences entre les 2 méthodes d'échantillonnages en question. Les cyprinidés et les centrarchidés, quant à eux, ne montrent généralement pas ce genre de comportements (à l'exception de la territorialité pour les centrarchidés en période de reproduction ; Moyle et Cech 2004), mais tendent plutôt à former des bancs de poissons (Kimmel et Argent 2006; McCartt et al. 1997). La formation de bancs facilite la détection des risques potentiels, ce qui favorise les comportements de fuite en groupe et pourrait contribuer à diminuer leur probabilité de capture (Kimmel et Argent 2006; Reynolds 1996). Nous avons également régulièrement observé, lors de l'échantillonnage en plongée de surface, des centrarchidés demeurant stationnaires tout en faisant face aux plongeurs. Ce comportement, également observé par Goldstein (1978), de même que la formation de bancs, pourrait favoriser l'échantillonnage des communautés de poissons en plongée de surface, au détriment de la pêche électrique.

Dans ce premier chapitre, nous avons donc observé que la pêcheuse électrique portative et la plongée de surface étaient 2 méthodes d'échantillonnage complémentaires pour décrire les communautés de poissons dans les rivières des basses Laurentides. La plongée de surface, cependant, a permis d'observer plus d'espèce (dans 6 sites sur 10) et de plus grandes abondances de poissons dans tous les sites. Mais encore, cette même méthode d'échantillonnage a permis une description des communautés de poissons beaucoup plus efficace que la pêcheuse électrique, puisque les mêmes sites ont pu être échantillonnés en un cinquième du temps requis pour le faire à la pêcheuse électrique. Conséquemment, significativement plus de sites auraient pu être visités en plongée de surface qu'en pêcheuse électrique. En terminant, nous croyons que cette étude pourrait permettre d'améliorer les modèles d'habitat des poissons en permettant de choisir la technique d'échantillonnage la plus appropriée pour décrire la communauté de poissons ciblée, ainsi que, dans le cas où nous recommandons l'utilisation de la plongée de surface, en permettant d'échantillonner plus de sites.

Le premier objectif de mon second chapitre est de comparer 4 différentes manières de former des guildes (par traits reproducteurs, alimentaires, éco-morphologiques et taxonomiques), et identifier la méthode qui permet de produire les meilleurs modèles d'habitat des poissons. Les groupes taxonomiques ont mené à de mauvais modèles d'habitats, ce qui n'est pas tout à fait surprenant en considérant que plusieurs espèces à l'intérieur d'un ordre ou d'une famille évoluent dans différents habitats. À l'intérieur de la famille des centrarchidés, par exemple, le crapet de roche, comme sont nom l'indique, préfère les habitats à substrat grossiers et l'absence de plantes aquatiques (Weaver et al. 1997). D'autres espèces de cette famille, comme le crapet soleil (*Lepomis gibbosus*) ou le crapet arlequin (*Lepomis macrochirus*) sont reconnus pour habiter les zones où la végétation aquatique est abondante et conséquemment où les substrats sont dominés par les particules fines et/ou organiques (Bernatchez et Giroux 2000, Weaver et al. 1997, Randall et al. 2004).

Les guildes basées sur l'alimentation des poissons ont également mené à des modèles d'habitat de moindre performance. Plusieurs auteurs avaient identifié des changements de diète en fonction de l'ontogénie des poissons (e.g. Speeziar et Rezsu 2009; Garrison et Link 2000), et nous croyions que l'inclusion de cette information aurait contribué à faire de meilleurs modèles. Ce résultat était d'autant plus surprenant puisque Brind'Amour et al. (2011) avait trouvé des associations significatives entre les traits alimentaires des poissons et les caractéristiques environnementales dans une communauté de poissons similaire. Ce résultat peut cependant être mis en relation avec le fait que nos classes de tailles n'étaient pas divisées de façon à refléter parfaitement les changements ontogéniques de diète, puisqu'elles avaient d'abord été conçues pour faciliter l'échantillonnage en plongée de surface. De plus, certains auteurs suggèrent que l'utilisation de guildes alimentaires ne soit pas une bonne manière de simplifier l'analyse des relations entre les poissons et leurs habitats, puisque ceux-ci sont reconnus pour avoir une grande flexibilité alimentaire (Welcomme et al. 2006) et que plusieurs espèces sont opportunistes (Elliott et al. 2007).

Les guildes basées sur les traits éco-morphologiques ont également mené à des modèles expliquant peu de variance. En regardant plus précisément les groupes formés, il a été possible de voir qu'ils ressemblaient beaucoup aux groupes taxonomiques, ce qui fait un certain sens puisqu'il est connu que les espèces d'un même groupe taxonomique partagent plusieurs traits morphologiques (Campbell 1995). La pauvre performance de ces modèles peu donc être reliée à leur ressemblances avec les modèles par guildes taxonomiques, pour les raisons évoquées précédemment. Bien que plusieurs études aient réussi à montrer des liens entre la morphologie des poissons et leur utilisation de l'habitat (Reyjol et al. 2001, Morinville et Rasmussen 2008, Brind'Amour et al. 2011), j'attribue ce résultat à l'approche statistique indirecte que j'ai employée, de même qu'à l'échelle spatiale à laquelle nous avons étudié les relations entre les poissons et leur habitat.

La supériorité des modèles par guildes basées sur les traits reproducteurs des poissons, lesquels représentaient bien l'habitat de fraie, peut être expliquée par les raisons suivantes. D'abord, la période d'échantillonnage pour cette étude a eu lieu du 1er au 17

juillet, soit peu après la fraie pour la majorité des espèces présentes dans cette étude. Il est très difficile de trouver de l'information précise sur la période de reproduction des espèces présentes dans cette étude en raison d'une grande variabilité régionale et de l'absence d'études dans notre région (Scott et Crossman 1985). Cependant, en 3 ans d'échantillonnage dans ces systèmes, nous n'avons jamais observés de signes de reproduction après le 24 juin. Cependant, il est bien connu que la totalité des espèces modélisées dans cette étude se reproduisent au printemps ou tôt dans l'été (Scott et Crossman 1985). Il est donc possible que la supériorité du modèle par guildes reproductrices soit saisonnière, et que d'autres modèles performent mieux plus tard dans l'été. Également, Aarts and Nienhuis (2003) mentionnent que plusieurs espèces de milieu lotique ont des habitats de préférence semblables pour la reproduction et l'alimentation. La figure 6 semble supporter cette hypothèse. Finalement, ces résultats concordent avec supportent l'hypothèse de Poff (1997) qui stipule que les traits reproducteurs des poissons sont liés à l'utilisation de l'habitat à l'échelle du méso habitat ou de la section de rivière.

Il est difficile de dire quels auraient été les changements dans mes résultats si j'avais inclus toutes les espèces rares. Pour les raisons mentionnées ci haut, il se pourrait que l'inclusion des espèces rares améliorent ou détériorent mes modèles par guildes. Cependant, étant donné que plus de 92% des poissons ont été inclus, il est fort probable que les espèces exclues aient une influence mineure sur la performance de ces modèles.

Par contre, l'inclusion des espèces rares dans un modèle d'habitat ordinaire (une analyse canonique de redondance entre toutes les espèces et les conditions environnementales, par exemple) aurait fort probablement eu pour effet de diminuer le pourcentage de variance expliqué. En effet, les données d'abondances pour les espèces rares ou peu communes contiennent typiquement plus de 0 qu'il serait prédit en utilisant des distributions statistiques unimodales, telles qu'utilisées dans les RDA (Cunningham and Lindenmayer 2005). Ce type de données est souvent appelée « zero inflated data » et nécessite des méthodes statistiques particulières pour être modélisées, lesquelles n'ont pas encore d'équivalents multivariés, du moins pour les RDA. Relativement à un modèle multivarié ordinaire, l'inclusion des espèces rares aurait donc fait mieux paraître mes

modèles par guildes, puisque ceux-ci présentent l'avantage de grouper les espèces rares avec d'autres espèces et ainsi diminuer le nombre de zéro.

Le second objectif du deuxième chapitre de mon mémoire était de définir *a priori* des guildes d'utilisation de l'habitat et d'utiliser une forme de régression linéaire pour déterminer quels traits définissent le mieux ces guildes. La représentation en dendrogramme des guildes d'utilisation de l'habitat a permis d'identifier 2 éléments importants. Tout d'abord, l'analyse a mis en évidence 2 communautés bien distinctes caractérisées d'une part par les espèces préférant les substrats grossiers et les courant plus élevés, et d'autres part les espèces d'herbier aquatique et/ou préférant les substrats fin. Ensuite, plusieurs classes de tailles appartenant à la même espèce se sont retrouvées dans la même guilde d'utilisation de l'habitat, particulièrement pour la famille des cyprinidés. 3 hypothèses pourraient expliquer cette dernière découverte : les classes de tailles n'étaient pas définies de façon à représenter un changement ontogénique dans l'utilisation de l'habitat ; l'échelle spatiale utilisée ne permettait pas de déceler des différences d'utilisation de l'habitat, et finalement, dans les communautés de poissons de rivière dominées par cyprinidés et les centrarchidés, un changement ontogénique dans l'utilisation de l'habitat est rarement observé. Il n'a malheureusement pas été possible de préciser laquelle de ces hypothèses s'avérait la plus probable.

J'ai par la suite tenté de mettre en relation ces guildes d'utilisation de l'habitat avec les traits reproducteurs, alimentaires, éco-morphologiques et taxonomiques des espèces. Une analyse discriminante canonique a mis en évidence que ces guildes semblaient plus facilement définissables en utilisant des traits reliés à l'alimentation des poissons. Je n'ai pas donné beaucoup d'importance à ce résultat quelque peu surprenant, considérant ce qui a été dit précédemment sur la formation de guildes alimentaires de poissons. De plus la représentation graphique de l'analyse reflétait bien peu la relation entre les guildes d'utilisation de l'habitat.

J'ai constaté qu'il y avait peu de ressemblances entre les 3 guildes basées sur les traits reproducteurs (le modèle « gagnant » identifié dans la première partie du second

chapitre) et la structure du dendrogramme représentant les guildes d'utilisation de l'habitat. Cela m'a permis de douter de la validité du modèle par guildes reproductrices, bien qu'il soit supporté par la littérature. D'autres analyses, en utilisant un jeu de donnée indépendant par exemple, pourraient permettre de vérifier la validité du modèle.

Les objectifs de mon second chapitre étaient donc d'identifier, parmi 4 approches pour former des guildes (reproductives, alimentaires, éco-morphologiques et taxonomie), laquelle permettait de produire les meilleurs modèles d'habitat des poissons, ainsi qu'évaluer si les traits des espèces pouvaient permettre de définir des guildes d'utilisation de l'habitat définies *a priori*. Les guildes se basant sur les traits reproducteurs produirent les meilleurs modèles d'habitat, probablement en raison de la bonne relation entre l'habitat de fraie des poissons et l'utilisation de l'habitat à l'échelle du méso-habitat. En revanche, une majorité de traits reliés à l'alimentation des poissons furent sélectionnés par une analyse discriminante pour expliquer l'appartenance des espèces et des classes de taille à leur guilde d'utilisation de l'habitat. Par contre, la représentation graphique de cette dernière analyse ne reflétait pas la relation entre les guildes d'utilisation de l'habitat, alors que notre modèle par guildes reproductives était supporté par la littérature. La validation de ce modèle sur un jeu de données indépendant pourrait confirmer cette innovation potentielle dans le domaine de la modélisation de l'habitat du poisson.

Dans le contexte d'aucune perte nette de la capacité productive des habitats du poisson, notre modèle par guildes reproductrices (figure 6, chapitre 2) pourrait s'avérer utile pour prédire un changement de communauté de poissons causé par un impact anthropique. Par exemple, la construction d'un seuil sur une rivière de notre aire d'étude aurait tendance à diminuer les vitesses du courant à l'amont de celui-ci. Cette diminution du courant favoriserait les dépôts de substrats fins, favorisant ainsi les espèces du groupe 1 et potentiellement du groupe 2 au détriment des espèces du groupe 3. Avec des valeurs précises de descripteurs environnementaux, telles que prédites par les modèles hydrodynamiques (Guay et al.2000), il serait même possible d'entrer ces données dans le modèle et d'obtenir une prédiction quantitative de la communauté. Outre ce changement dans la communauté de poissons, les impacts sur la capacité productive pourraient être

modélisés en calibrant le modèle sur des biomasses plutôt que des densités de poissons.

Il est cependant important de mentionner que notre modèle ne pourrait pas prédire les impacts de l'ouvrage sur la reproduction des poissons, de même que l'impact d'une perte de connectivité, des facteurs importants dans la dynamique des populations. De même, notre modèle ne pourrait pas prédire des impacts environnementaux trop importants, c'est-à-dire à l'extérieur des conditions sur lesquelles il a été calibré. Bien que les modèles d'habitat des poissons soient très utiles, leur utilisation doit être faite de manière rigoureuse.

En conclusion, je crois avoir réussi à atteindre l'objectif général de mon mémoire, qui visait à améliorer les modèles de l'habitat du poisson pour les rivières des basses Laurentides, en apportant de nouvelles connaissances au sujet de 2 composantes essentielles à ce domaine de l'écologie aquatique : le choix d'une méthode d'échantillonnage adéquate, dont on connaît les forces et les faiblesses, pour décrire la communauté de poissons, ainsi que le développement d'un modèle statistique utilisant le concept de guilde écologique pour mieux décrire les besoins en habitat des communautés poissons.

Références

Aadland, L. P. 1993. Stream Habitat Types: Their fish assemblages and relationship to flow. North American Journal of Fisheries Management 13:790-806.

Aarts, B. G. W. and P. H. Nienhuis. 2003. Fish zonations and guilds as the basis for assessment of ecological integrity of large rivers. Hydrobiologia 500:157-178.

Ahmadi-Nedushan, B., A. St-Hilaire, M. Bérubé, E. Robichaud, N. Thiémonge, and B. Bobée. 2006. A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. River Research and Applications 22:503-523.

Allan, J. D. and A. S. Flecker. 1993. Biodiversity conservation in running waters. Bioscience 43:32-43.

Austen, D. J., P. B. Bayley, and B. W. Menzel. 1994. Importance of the guild concept to fisheries research and management. Fisheries 19:12-20.

Balon, E. K. 1975. Reproductive guilds of fishes: a proposal and definition. Journal of the Fisheries Research Board of Canada 32:821-864.

Barry S, Elith J. 2006 Error and uncertainty in habitat models. Journal of Applied Ecology 43 (3):413-423

Bayley, P. B. and D. C. Dowling. 1990. Gear efficiency calibrations for stream and river sampling. Illinois Natural History Survey, Aquatic Ecology Technical Report 90/08, Champaign, Illinois.

Bean, K., G. P. Jones, and M. J. Caley. 2002. Relationships among distribution, abundance and microhabitat specialisation in a guild of coral reef triggerfish (family Balistidae). Marine Ecology-Progress Series 233:263-272.

Belica, L. A. T. and F. J. Rahel. 2008. Movements of creek chubs, Semotilus atromaculatus, among habitat patches in a plains stream. Ecology of Freshwater Fish 17:258-272.

Bellwood, D. R., P. C. Wainwright, C. J. Fulton, and A. Hoey. 2002. Assembly rules and functional groups at global biogeographical scales. Functional Ecology 16:557-562.

Bertrand, M., D. J. Marcogliese, and P. Magnan. 2008. Trophic polymorphism in brook charr revealed by diet, parasites and morphometrics. Journal of Fish Biology 72:555-572.

Blanchet, F. G., P. Legendre, and D. Borcard. 2008. Forward selection of explanatory variables. Ecology 89:2623-2632.

Boisclair, D. 2001. Fish habitat modeling: from conceptual framework to functional tools. Canadian Journal of Fisheries and Aquatic Sciences 58:1-9.

Bonneau, J. L., R. E. Thurow, and D. L. Scarnecchia. 1995. Capture, Marking, and Enumeration of Juvenile Bull Trout and Cutthroat Trout in Small, Low-Conductivity Streams. North American Journal of Fisheries Management 15:563-568.

Borcherding, J. and C. Magnhagen. 2008. Food abundance affects both morphology and behaviour of juvenile perch. Ecology of Freshwater Fish 17:207-218.

Bouchard, J. and D. Boisclair. 2008. The relative importance of local, lateral, and longitudinal variables on the development of habitat quality models for a river. Canadian Journal of Fisheries and Aquatic Sciences 65:61-73.

Bovee, Ken D. & Western Energy and Land Use Team. Instream Flow and Aquatic Systems Group. & U.S. Fish and Wildlife Service. & United States. Environmental Protection Agency. & United States. Soil Conservation Service. & Geological Survey (U.S.) 1982 A guide to stream habitat analysis using the Instream Flow Incremental Methodology [microform] / by Ken D. Bovee Western Energy and Land Use Team, Office of Biological Services, Fish and Wildlife Service, U.S. Dept. of the Interior : [Supt. of Docs., U.S. G.P.O., distributor], Washington, D.C.

Brind'Amour, A. and D. Boisclair. 2004. Comparison between two sampling methods to evaluate the structure of fish communities in the littoral zone of a Laurentian lake. Journal of Fish Biology 65:1372-1384.

Brind'Amour, A., D. Boisclair, S. Dray, and P. Legendre. 2011. Relationships between species feeding traits and environmental conditions in fish communities: a three-matrix approach. Ecological Applications 21:363-377.

Carle, F. L. and M. R. Strub. 1978. A new method for estimating population size from removal data. Biometrics 34:621-630.

Chuang, L.-C., Y.-S. Lin, and S.-H. Liang. 2006. Ecomorphological comparison and habitat preference of 2 cyprinid fishes, *Varicorhinus barbatulus* and *Candidia barbatus*, in Hapen Creek of northern Taiwan. Zoological Studies 45:114-123.

Coleman, K. and D. S. Wilson. 1996. Behavioral and ecological determinants of home range size in juvenile pumpkinseed sunfish (*Lepomis gibbosus*). Ethology 102:900-914.

COSEWIC. 2010. COSEWIC'S assessment process and criteria.

Cunjak, R. A., R. G. Randall, and E. M. P. Chadwick. 1988. Snorkeling versus electrofishing: a comparison of census techniques in Atlantic salmon rivers. Naturaliste Canadien:89-93.

Cunningham, R. B. and D. B. Lindenmayer. 2005. Modeling count data of rare species: some statistical issues. Ecology 86:1135-1142.

De'ath, G. and K. E. Fabricius. 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. Ecology 81:3178-3192.

DFO (Fisheries and Oceans Canada).1986. Policy for the management of fish habitat. Ottawa, Ontario, 28 pp.

Doeringsfeld, M. R., I. J. Schlosser, J. F. Elder, and D. P. Evenson. 2004. Phenotypic consequences of genetic variation in a gynogenetic complex of *Phoxinus eos-neogaeus* clonal fish (*Pisces : Cyprinidae*) inhabiting a heterogeneous environment. Evolution 58:1261-1273.

Doherty, C. A., R. A. Curry, and K. R. Munkittrick. 2010. Spatial and temporal movements of white sucker: Implications for use as a sentinel species. Transactions of the American Fisheries Society 139:1818 - 1827.

Dray, S., D. Chessel, and J. Thioulouse. 2003. Co-inertia analysis and the linking of ecological data tables. Ecology 84:3078-3089.

Dray, S., P. Legendre, and F. G. Blanchet. 2009. packfor: Forward Selection with permutation.

Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196:483-493.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81:163-182.

Dumay, O., P. S. Tari, J. A. Tomasini, and D. Mouillot. 2004. Functional groups of lagoon fish species in Languedoc Roussillon, southern France. Journal of Fish Biology 64:970-983.

Eadie, J. M. and A. Keast. 1984. Ressource heterogeneity and fish species diversity in lakes. Canadian Journal of Zoology-Revue Canadienne De Zoologie 62:1689-1695.

Elliott, M. and F. Dewailly. 1995. The structure and components of European estuarine fish assemblages. Aquatic Ecology 29:397-417.

Food and Agriculture Organisation of the United Nations (FAO). 1997. Review of the State of World Aquaculture. FAO Fisheries Circular No. 886, Rev. 1. Rome, Italy.

Food and Agriculture Organisation of the United Nations (FAO). 2000. The state of world fisheries and aquaculture 2000. FAO, Rome, Italy.

Framing Committee of the Global Water System Project (FCGWSP). 2004. Humans transforming the global water system. Eos, Transactions of American Geophysical Union 85, 513–514.

Gardiner, W. R. 1984. Estimating population-densities of salmonids in deep-water in streams. Journal of Fish Biology 24:41-49.

Garrison, L. P. and J. S. Link. 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. Marine Ecology-Progress Series 202:231-240.

Goldstein, R. M. 1978. Quantitative comparison of seining and underwater observation for stream fishery surveys. Progressive Fish-Culturist 40:108-111.

Griffith, J. S. 1981. Estimation of the age-frequency distribution of stream-dwelling trout by underwater observation. Progressive Fish-Culturist 43:51-53.

Guay, J. C., D. Boisclair, D. Rioux, M. Leclerc, M. Lapointe, and P. Legendre. 2000. Development and validation of numerical habitat models for juveniles of Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 57:2065-2075.

Habera, J. W., M. A. Kulp, S. E. Moore, and T. B. Henry. 2010. Three-pass depletion sampling accuracy of two electric fields for estimating trout abundance in a low-conductivity stream with limited habitat complexity. North American Journal of Fisheries Management 30:757-766.

Hajisamae, S. and S. Ibrahim. 2008. Seasonal and spatial variations of fish trophic guilds in a shallow, semi-enclosed tropical estuarine bay. Environmental Biology of Fishes 82:251-264.

Hankin, D. G. and G. H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45:834-844.

Hedger, R. D., J. J. Dodson, J. F. Bourque, N. E. Bergeron, and P. E. Carbonneau. 2006. Improving models of juvenile Atlantic salmon habitat use through high resolution remote sensing. Ecological Modelling 197:505-511.

Hoagstrom, C. W., J. E. Brooks, and S. R. Davenport. 2008. Recent habitat association and the historical decline of *Notropis simus pecosensis*. River Research and Applications 24:789-803.

Hrodey, P. J. and T. M. Sutton. 2008. Fish community responses to half-log additions in warmwater streams. North American Journal of Fisheries Management 28:70-80.

Internation Union for the Conservation of Nature (IUCN). 2006: The World Conservation Union 2006. IUCN Red List of Threatened Species. www.iucnredlist.org

Jackson, C. A. L. and J. Zydlewski. 2009. Summer movements of sub-adult brook trout, landlocked Atlantic salmon, and smallmouth bass in the Rapid River, Maine. Journal of Freshwater Ecology 24:567 - 580.

Johnson, J. H. and D. S. Dropkin. 1995. Diel feeding chronology of six fish species in the Juniata river, Pennsylvania. Journal of Freshwater Ecology 10:11-18.

Johnston, C. E. and M. J. Maceina. 2009. Fish assemblage shifts and species declines in Alabama, USA streams. Ecology of Freshwater Fish 18:33-40.

Joyce, M. P. and W. A. Hubert. 2003. Snorkeling as an alternative to depletion electrofishing for assessing cutthroat trout and brown trout in stream pools. Journal of Freshwater Ecology 18:215-222.

Kanno, Y., J. C. Vokoun, D. C. Dauwalter, R. M. Hughes, A. T. Herlihy, T. R. Maret, and T. M. Patton. 2009. Influence of rare species on electrofishing distance when estimating species richness of stream and river reaches. Transactions of the American Fisheries Society 138:1240-1251.

Karels, T. J., A. A. Bryant, and D. S. Hik. 2004. Comparison of discriminant function and classification tree analyses for age classification of marmots. Oikos 105:575-587.

Kiers, H. A. L. and A. K. Smilde. 2007. A comparison of various methods for multivariate regression with highly collinear variables. Statistical Methods and Applications 16:193-228.

Kimmel, W. G. and D. G. Argent. 2006. Efficacy of two-pass electrofishing employing multiple units to assess stream fish species richness. Fisheries Research 82:14-18.

Krebs, C. J. 2009. Ecology. The Experimental Analysis of Distribution and Abundance. 6th edition. Benjamin Cummings, San Francisco.

Kruger, R. F., C. J. B. de Carvalho, and P. B. Ribeiro. 2010. Assembly rules in Muscid Fly assemblages in the grasslands Biome of Southern Brazil. Neotropical Entomology 39:345-353.

Lalancette. 1977. Feeding in white suckers (*Catostomus commersonii*) from Gamelin lake, Québec, over a twelve month period. Naturaliste Canadien 104:369-376.

Lamouroux, N., J.-M. Olivier, H. Capra, M. Zylberblat, A. Chandesris, and P. Roger. 2006. Fish community changes after minimum flow increase: testing quantitative predictions in the Rhône River at Pierre-Bénite, France. Freshwater Biology 51:1730-1743.

Lamouroux, N. and Y. Souchon. 2002. Simple predictions of instream habitat model outputs for fish habitat guilds in large streams. Freshwater Biology 47:1531-1542.

Lanthier, G. 2009. Variations inter journalières dans la structure des communautés de poissons: implications pour le développement de modèles de qualité d'habitats. Université de Montréal, Montréal.

Latulippe, C., M. F. Lapointe, and T. Talbot. 2001. Visual characterization technique for gravel-cobble river bed surface sediments; Validation and environmental applications. contribution to the Programme of CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique). Earth Surface Processes and Landforms 26:307-318.

Legendre, P. 2005. Species associations: The Kendall coefficient of concordance revisited. Journal of Agricultural Biological and Environmental Statistics 10:226-245.

Legendre, P., M. R. T. Dale, M. J. Fortin, J. Gurevitch, M. Hohn, and D. Myers. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography 25:601-615.

Legendre, P and S. Durand (2010). rdaTest: Canonical redundancy analysis. R package version 1.7.

Legendre, P. and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271-280.

Legendre, P. and L. Legendre. 1998. Numerical Ecology. 2nd English edition. Elsevier Science BV, Amsterdam.

Maechler, M. 2011. The cluster package.

McCartt, A. L., W. E. Lynch, and D. L. Johnson. 1997. How light, a predator, and experience influence bluegill use of shade and schooling. Environmental Biology of Fishes 49:79-87.

Meador, M. R., J. P. McIntyre, and K. H. Pollock. 2003. Assessing the efficacy of single-pass backpack electrofishing to characterize fish community structure. Transactions of the American Fisheries Society 132:39-46.

Meybeck, M. 2003. Global analysis of river systems: from Earth system controls to Anthropocene syndromes. Philosophical transactions of the Royal Society of London 358:1935-1955.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-being: Synthesis. Island Press, Washington, DC.

Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions of North American fishes during the past century. Fisheries 14:22-38.

Morgan, M. J. and P. W. Colgan. 1987. The effects of predator presence and shoal size on foraging in bluntnose minnows, *Pimephales notatus*. Environmental Biology of Fishes 20:105-111.

Morinville, G. R. and J. B. Rasmussen. 2008. Distinguishing between juvenile anadromous and resident brook trout (*Salvelinus fontinalis*) using morphology. Environmental Biology of Fishes 81:171-184.

Moyle, P. and J. Cech. 2004. Fishes: an introduction to ichthyology. 5th edition. Pearson Prentice Hall.

Moyle, P. and R.A. Leidy. 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. Pages 127-169 in P.L. Fielder and S.K. Jain, editors. Conservation Biology: the Theory and Practice of Nature Conservation, Preservation, and Management. Chapman and Hall, New York.

Mullner, S. A., Hubert, W. A., and Wesche, T. A.. 1998. Snorkeling as an alternative to depletion electrofishing for estimating abundance and length-class frequencies of trout in small streams. North American Journal of Fisheries Management 18:947-953.

Nordwall, F. 1999. Movements of brown trout in a small stream: Effects of electrofishing and consequences for population estimates. North American Journal of Fisheries Management 19:462-469.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2010. Vegan: Community Ecology Package. R package.

Olden, J. D. and D. A. Jackson. 2002. A comparison of statistical approaches for modelling fish species distributions. Freshwater Biology 47:1976-1995.

Olden, J. D., D. A. Jackson, and P. R. Peres-Neto. 2002. Predictive models of fish species distributions: A note on proper validation and chance predictions. Transactions of the American Fisheries Society 131:329-336.

Peres-Neto, P. R., J. D. Olden, and D. A. Jackson. 2001. Environmentally constrained null models: site suitability as occupancy criterion. Oikos 93:110-120.

Peterson, J. T., R. F. Thurow, and J. W. Guzevich. 2004. An evaluation of multipass electrofishing for estimating the abundance of stream-dwelling salmonids. Transactions of the American Fisheries Society 133:462-475.

Petty, J. T., P. J. Lamothe, and P. M. Mazik. 2005. Spatial and seasonal dynamics of brook trout populations inhabiting a central Appalachian watershed. Transactions of the American Fisheries Society 134:572-587.

Pine, W. E., M. S. Allen, and V. J. Dreitz. 2001. Population viability of the Gulf of Mexico sturgeon: Inferences from capture-recapture and age-structured models. Transactions of the American Fisheries Society 130:1164-1174.

Poff, N. L. 1997. Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16:391-409.

Polis, G. A. and K. O. Winemiller. 1996. Food webs - Integration of patterns and dynamics. Chapman and Hall.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Randall, R. G., C. K. Minns, and C. M. Brousseau. 2004. Coastal exposure as a first-order predictor of the productive capacity of near shore habitat in the Great Lakes. Canadian Science Advisory Secretariat.

Reyjol, Y., P. Lim, A. Belaud, and S. Lek. 2001. Modelling of microhabitat used by fish in natural and regulated flows in the river Garonne (France). Ecological Modelling 146:131-142.

Reyjol, Y., M. A. Rodriguez, N. Dubuc, P. Magnan, and R. Fortin. 2008. Among- and within-tributary responses of riverine fish assemblages to habitat features. Canadian Journal of Fisheries and Aquatic Sciences 65:1379-1392.

Reynolds, J. B. 1996. Electrofishing. Pages 221-253 in B. R. Murphy and D. W. Willis, editors. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

Rezsu, E. and A. Specziar. 2006. Ontogenetic diet profiles and size-dependent diet partitioning of ruffe *Gymnocephalus cernuus*, perch *Perca fluviatilis* and pumpkinseed *Lepomis gibbosus* in Lake Balaton. Ecology of Freshwater Fish 15:339-349.

Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology 11:1081-1093.

Roberts, T. H. and L. J. O'Neil. 1985. Species selection for habitat assessments. Transactions of the North American Wildlife and Natural Resources Conference 50:352-362.

Roni, P. and A. Fayram. 2000. Estimating winter salmonid abundance in small western Washington streams: a comparison of three techniques. North American Journal of Fisheries Management 20:683-692.

Sabaton, C., Y. Souchon, H. Capra, V. Gouraud, J. M. Lascaux, and L. Tissot. 2008. Long-term brown trout population responses to flow manipulation. River Research and Applications 24:476-505.

Schill, D. J. and J. S. Griffith. 1984. Use of underwater observations to estimate Cutthroat trout abundance in the Yellowstone River. North American Journal of Fisheries Management 4:479-487.

Scott, W. B. and E. J. Crossman. 1985. Freshwater fishes of Canada. 2nd edition. Fisheries Research Board of Canada. Bulletin 184.

Smith, C.L. and C.R. Powel. 1971. The summer fish communities of Brier Creek, Marshall County Oklahoma. American Museum Novitates, vol. 2458, p.1-30.

Specziar, A. and E. T. Rezsu. 2009. Feeding guilds and food resource partitioning in a lake fish assemblage: an ontogenetic approach. Journal of Fish Biology 75:247-267.

Thurow, R. E. and D. J. Schill. 1996. Comparison of day snorkeling, night snorkeling, and electrofishing to estimate Bull trout abundance and size structure in a second-order Idaho stream. North American Journal of Fisheries Management 16:314-323.

Thurow, R. F. 1994. Underwater methods for study of Salmonids in the Intermountain West. General Technical Report INT-GTR-307, United States Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.

Thurow, R. F., J. T. Peterson, and J. W. Guzevich. 2006. Utility and validation of day and night snorkel counts for estimating bull trout abundance in first- to third-order streams. North American Journal of Fisheries Management 26:217-232.

Vadas, R. L. 1990. The importance of omnivory and predator regulation of prey in fresh-water fish assemblages of North-America. Environmental Biology of Fishes 27:285-302.

Vadas, R. L., Jr. and D. J. Orth. 2000. Habitat use of fish communities in a Virginia stream system. Environmental Biology of Fishes 59:253-269.

Vadrucci, M. R., F. Vignes, A. Fiocca, A. Basset, I. Santarpia, G. C. Carrada, M. Cabrini, and S. F. Umani. 2003. Space–time patterns of co-variation of biodiversity and primary production in phytoplankton guilds of coastal marine environments. Aquatic Conservation: Marine and Freshwater Ecosystems 13:489-506.

Vanni MJ. 2002. Nutrient cycling by animals in freshwater ecosystems. Annu Rev Ecol Syst 33:341-370

Verbyla, D. L. and J. A. Litvaitis. 1989. Resampling Methods for Evaluating Classification Accuracy of Wildlife Habitat Models. Environmental Management 13:783-787.

Wainwright, P. C. 1996. Ecological Explanation through Functional Morphology: The Feeding Biology of Sunfishes. Ecology 77:1336-1343.

Weaver, M. J., J. J. Magnuson, and M. K. Clayton. 1997. Distribution of littoral fishes in structurally complex macrophytes. Canadian Journal of Fisheries and Aquatic Sciences 54:2277-2289.

Wennhage, H. and L. Pihl. 2002. Fish feeding guilds in shallow rocky and soft bottom areas on the Swedish west coast. Journal of Fish Biology 61:207-228.

Wikramanayake, E. D. 1990. Ecomorphology and biogeography of a tropical stream fish assemblage: evolution of assemblage structure. Ecology 71:1756-1764.

Wildman, T. L. and R. M. Neumann. 2003. Comparison of snorkeling and electrofishing for estimating abundance and size structure of brook trout and brown trout in two southern New England streams. Fisheries Research 60:131-139.

Williams, J. E., J. E. Johnson, D. A. Hendrickson, S. Contrerasbalderas, J. D. Williams, M. Navarromendoza, D. E. McAllister, and J. E. Deacon. 1989. Fishes of North-America: endangered, threatened, or of special concern. Fisheries 14:2-20.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends in Ecology & Evolution 12:266-269.

Annexe 1 : Détails sur les options de programmation des analyses pour le chapitre 2, le second objectif.

A) Grouping of SPSC based on habitat use.

Similarly to Vadas and Orth (2000), we defined habitat use guilds with species association analyses. More specifically, we used Ward's agglomerative clustering (also called Ward's minimum variance method) on a species distance matrix (1-Pearson correlation matrix of the Hellinger transformed fish density matrix). It was performed using the function "agnes" from the "cluster" package (Maechler 2011). Ward's agglomerative clustering is a hierarchical clustering method. The algorithm starts with as many clusters as the number of objects (observations or SPSC in this case) and groups SPSC while minimizing the total error sum of squares (TESS, same objective function as in K-means partitioning) at each step (Legendre and Legendre 1998). The results can be represented in a dendrogram. We then used Kendall's coefficient of concordance following Legendre (2005) to identify significantly associated groups of SPSC. This analysis is described in details in Appendix 1.

B) Identification of significantly associated groups of SPSC: Kendall's coefficient of concordance.

We used Kendall's coefficient of concordance following Legendre (2005) to identify significantly associated groups of SPSC. The procedure consisted in repeating the following steps for 2 to k groups: (1) compute Kendall's global test of significance, where the null hypothesis (H0) is that SPSC within a group are independent and differ in the way they rank the objects (sites). The rejection of H0 means that at least one of the SPSC is concordant with at least one other SPSC in its group. When the global test is significant, one can look for groups of associated SPSC. We then (2) perform *a posteriori* tests to determine which of the individual SPSC are concordant with one or several of the other SPSC within their group. If some SPSC were not significantly related to their group, we

refined the groups, following the hierarchical structure of the dendrogram produced by Ward's agglomerative clustering, until each SPSC was significantly associated with its group. We used the function "kendall.global" and "kendall.post" from the library "vegan" (Oksanen et al. 2010) to respectively perform global and *a posteriori* tests of significance of the groups.

C) Determination of the species traits explaining the previously identified habitat-use guilds.

To determine the species traits explaining the habitat-use guilds, we performed two types of analyses, a stepwise canonical linear discriminant analysis (LDA) and a multivariate classification tree (MVCT), both relating the vector defining the habitat use guilds for each species (response variable) to the matrices of species traits (explanatory variables).

Linear discriminant analysis

LDA looks for linear combination of descriptors maximizing the among group variation while minimizing the within group variation of the explanatory variables. The explanatory variables were standardized and tested for multivariate homogeneity of within-group variances before building the model (with all traits) and for the final model (forward selected traits), using Marti Anderson's "betadisper" function from the "vegan" library (Oksanen et al. 2010). The model selection algorithm (forward selection) consisted in starting with no explanatory variables (traits) and finding, at each step, the trait with the highest averaged cross-validation correct classification rate (CCR; number of correct classifications divided by the number of observations). The ten fold cross-validation procedure was chosen because it gives more precise estimates of the classification accuracy than the over optimistic apparent CCR (Verbyla and Litvaitis 1989). The "stepclass" function from the "klaR" library (Weihs et al. 2005) was used in combination with a self programmed bootstrapping procedure, because the function could not perform more than

one ten fold cross-validation (one formation of 10 random groups of observation and exclude each group, one at a time, for independent assessment of the CCR) at each step of the model variable selection procedure. Consequently, when using the "stepclass" function alone, the final model selected was not always the same when repeating the same analysis. The bootstraped ten fold cross-validation forward selection procedure thus consisted in the following steps: run 100 times the "stepclass" function with no specified model structure and select the first explanatory variables entering the model the most often. We then ran another 100 times the "stepclass" function while constraining the model to start with the variable selected at the previous step and retained the second explanatory variable that had been selected the most often. We repeated the procedure until the model could not be improved by the inclusion of new explanatory variables. The ten fold cross-validation CCR of the final model consisted in the average of 100 ten fold CCR.

To compute the parameters of the final LDA model, we used the "lda" and "predict.lda" functions from the "MASS" library (Venables and Ripley 2002). We also computed classification functions for each of the 7 habitat-use guilds, which are linear equations that can be used for the purpose of assigning objects to groups. See Legendre and Legendre (1998; p.625) for details. The coefficients of the explanatory variables (traits) in each function indicate the relative importance of the traits to assign an object to that group.

Multivariate classification trees

We also used MVCT to relate habitat-use guilds to SPSC traits. MVCT is a non linear classification method that looks for binary splits in the explanatory variables (1 at a time) that maximize the within group homogeneity of the response variable (vector defining habitat-use guilds), which is equivalent to maximizing the CCR. The tree is grown up until no improvement in CCR is observed. The tree was then pruned with 100 ten fold cross-validation procedure to avoid over fitting of the model (De'ath and Fabricius 2000), similarly to the procedure described above for the LDA. We then used the "1-SE" rule to pick the best tree. This rule consists in choosing the most parsimonious tree (less leaves) that falls within 1 standard deviation of the cross-validation relative error (RE; 1-CCR) of

the tree having the smallest cross-validation RE (De'ath and Fabricius 2000). The "mvpart" function from the "mvpart" library (De'ath 2001) was used.

Annexe 2: Literature used to define the alimentary traits of all fish species and Size Class.

Table 1: Literature used to describe the diet of every fish species and size class.

Species	Size Class	Reference
Exoglossum maxillingua (Lesueur) (Cutlips minnow)	1	Johnson (1981); Pappantoniou et al. (1984)
	2	Johnson (1981); Pappantoniou et al. (1984)
Notemigonus crysoleucas (Mitchill) (Golden shiner)	1	Keast (1985)
	2	Keast (1968)
Semotilus atromaculatus (Mitchill) (Creek chub)	1	Barber and Minckley (1971); McMahon (1982); Magnan and FitzGerald (1984)
	2	Dinsmore (1962); Barber and Minckley (1971); Moshenko and Gee (1973); McMahon (1982); Magnan and FitzGerald (1984)
	3	McMahon (1982); Magnan and FitzGerald (1984)
Luxilus cornutus (Mitchill) (Common shiner)	1	Keast (1968); Scott and Crossman (1985)
	2	Page and Magnin (1978); Scott and Crossman (1985)
	3	Page and Magnin (1978); Scott and Crossman (1985)
Semotilus corporalis (Mitchill) (Fallfish)	1	Reed (1971); Johnson and Dropkin (1991)
	2	Reed (1971); Johnson et al. (2009)
	3	Johnson et al. (2009)
	4	Johnson et al. (2009)
Pimephales notatus (Rafinesque) (Bluntnose minnow)	1	Magnin et al. (1978); Keast (1985)
	2	Keast (1968)
Micropterus dolomieu (Lacépède) (Smallmouth bass)	1	Lachner (1950); Scott and Crossman (1985)
	2	Lachner (1950); Scott and Crossman (1985)
	3	Doan (1940); Clady (1974); Scott and Crossman (1985)
	4	Doan (1940); Clady (1974); Scott and Crossman (1985)

Table 1 (continued)

Ambloplites rupestris (Rafinesque) (Rockbass)	1	Magnin et al. (1978); Keast (1985)
	2	Magnin et al. (1978); Keast (1985)
	3	Magnin et al. (1978); Keast (1985)
Lepomis gibbosus (Linnaeus) (Pumpkinseed)	1	Sadzikowski and Wallace (1976); Rezsu and Specziar (2006)
	2	Sadzikowski and Wallace (1976); Rezsu and Specziar (2006); Brind'Amour et al. (2010)
	3	Sadzikowski and Wallace (1976); Rezsu and Specziar (2006); Brind'Amour et al. (2010)
Culaea inconstans (Kirtland) (Brook stickleback)	1	Keast (1968); Tompkins and Gee (1983); Scott and Crossman (1985)
Catostomus commersoni (Lacepède) (White sucker)	1	Keast (1968); Lalancette (1977)
	2	Lalancette (1977)
	3	Lalancette (1977); Johnson and Dropkin (1995)
	4	Lalancette (1977)
Perca flavescens (Mitchill) (Yellow perch)	1	Keast (1977)
	2	Clady (1977); Keast (1977)
	3	Clady (1977); Keast (1977)

Annexe 1 (suite)

Reference cited in table 1:

Barber, W. E. and W. L. Minckley. 1971. Summer foods of the cyprinid fish Semotilus atromaculatus. Transactions of the American Fisheries Society 100:283-289.

Brind'Amour, A., D. Boisclair, S. Dray, and P. Legendre. 2011. Relationships between species feeding traits and environmental conditions in fish communities: a three-matrix approach. Ecological Applications 21:363-377.

Clady, M. D. 1974. Food habits of yellow perch, smallmouth bass and largemouth bass in two unproductive lakes in Northern Michigan. American Midland Naturalist 91:453-459.

Dinsmore, J. J. 1962. Life history of the creek chub. Proceedings of the Iowa Academy of Science 69:296-301.

Doan, K. H. 1940. Studies of the smallmouth bass. The Journal of Wildlife Management 4:241-266.

Johnson, J. H. 1981. The summer diet of the cutlips minnow, *Exoglossum maxillingua*, in a central New York stream. Copeia 1981:484-487.

Johnson, J. H. and D. S. Dropkin. 1991. Summer food-habits of spotfin shiner, mimic shiner, and subyearling fallfish in the Susquehanna river basin. Journal of Freshwater Ecology 6:35-42.

Johnson, J. H. and D. S. Dropkin. 1995. Diel feeding chronology of six fish species in the Juniata river, Pennsylvania. Journal of Freshwater Ecology 10:11-18.

Johnson, J. H., C. C. Nack, and M. A. Chalupnicki. 2009. Predation by fallfish (*Semotilus corporalis*) on Pacific salmon eggs in the Salmon River, New York. Journal of Great Lakes Research 35:630-633.

Keast, A. 1968. Feeding of some Great Lakes fishes at low temperatures. Journal of the Fisheries Research Board of Canada 25:1199-1218.

Keast, A. 1977. Diet overlaps and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). Environmental Biology of Fishes 2:53-77.

Keast, A. 1985a. Development of dietary specializations in a summer community of juvenile fishes. Environmental Biology of Fishes 13:211-224.

Keast, A. 1985b. The piscivore feeding guild of fishes in small fresh-water ecosystems. Environmental Biology of Fishes 12:119-129.

Lachner, E. A. 1950. Food, growth and habits of fingerling northern smallmouth bass, *Micropterus dolomieu dolomieu* Lacépède, in trout waters of western New York. The Journal of Wildlife Management 14:50-56.

Lalancette. 1977. Feeding in white suckers (*Catostomus commersonii*) from Gamelin lake, Québec, over a twelve month period. Naturaliste Canadien 104:369-376.

Magnan, P. and G. J. Fitzgerald. 1984. Ontogenetic changes in diel activity, food-habits and spatial distribution of juvenile and adult creek chub, Semotilus atromaculatus. Environmental Biology of Fishes 11:301-307.

Magnin, É., M. E., and A.-M. Clément. 1978. Régime alimentaire de sept poissons littoraux de la grande anse de l'île Perrot, sur le lac Saint-Louis, près de Montréal, Québec. Naturaliste Canadien 105:89-101.

McMahon, T. E. 1982. Habitat suitability index models: Creek chub U.S.D.I. Fish and Wildlife Service.

Moshenko, R. W. and J. H. GEE. 1973. Diet, time and place of spawning, and environments occupied by creek chub (*Semotilus atromaculatus*) in the Mink River, Manitoba. Journal of the Fisheries Research Board of Canada 30:357-362.

Page, G. and E. Magnin. 1978. Some aspects of the biology of the common shiner, *Notropis cornutus* (Mitchill), in a Laurentian lake, Québec. Naturaliste Canadien 105:301-308.

Pappantoniou, A., R. E. Schmidt, and G. Dale. 1984. Aspects of the life-history of the cutlips minnow, *Exoglossum-maxillingua* (*pisces, Cyprinidae*), from the Titucus river, Westchester county, New-York. Annals of the New York Academy of Sciences 435:325-327.

Reed, R. J. 1971. Biology of the fallfish, *Semotilus corporalis* (*Pisces, Cyprinidae*). Transactions of the American Fisheries Society 100:717 - 725.

Scott, W. B. and E. J. Crossman. 1985. Freshwater fishes of Canada. 2nd edition. Fisheries Research Board of Canada. Bulletin 184.

Specziar, A. and E. T. Rezsu. 2009. Feeding guilds and food resource partitioning in a lake fish assemblage: an ontogenetic approach. Journal of Fish Biology 75:247-267.

Tompkins, A. M. and J. H. Gee. 1983. Foraging behaviour of brook stickleback, Culae inconstans (Kirtland): optimization of time, space, and diet. Canadian Journal of zoology 61:2482:2490.