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ANALYSES HIÉRARCHIQUES DES COMMUNAUTÉS ET DES POPULATIONS DE POISSONS FLUVIATILES EN FONCTION DU CONTEXTE ENVIRONNEMENTAL

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RÉSUMÉ

La relation entre les poissons fluviatiles et leur environnement dans une étude peut dépendre fortement de l'échelle spatiale et du niveau hiérarchique considérés. Cependant, la majorité des études se limitent encore à examiner cette relation à une seule échelle. L'objectif général de cette thèse consistait à analyser, sous l'optique multiéchelles, l'influence du contexte environnemental sur la structure des communautés de poissons fluviatiles et la distribution de deux espèces « cibles », soit l'omble de fontaine (*Salvelinus fontinalis*) et le saumon de l'Atlantique (*Salmo salar*). Le plan d'échantillonnage était hiérarchique avec trois niveaux emboîtés : 22 ruisseaux contenant de 2 à 20 tronçons par ruisseau ($n = 120$) et 5 sections par tronçon ($n = 600$). L'abondance des poissons et les valeurs de 22 variables environnementales ont été déterminées au cours des étés 2000 à 2002 dans le bassin versant de la rivière Grande Cascapédia (Gaspésie).

L'influence du contexte environnemental sur la structure des communautés à plusieurs échelles a été examinée à l'aide des analyses de redondance et de la décomposition hiérarchique de la variation. Cette dernière a permis se séparer la variation en trois composantes « pures » : 1) entre ruisseaux, 2) entre tronçons et 3) entre sections. Par contre, les variables environnementales qui expliquaient la structure des communautés ont été sélectionnées à trois niveaux d'analyse : 1) intrabassin, incluant la variation entre ruisseaux, entre tronçons et entre sections; 2) intraruisseau, incluant celle entre tronçons et entre sections; et 3) intratronçon, incluant celle entre sections seulement. Les communautés de poissons étaient influencées par différentes caractéristiques environnementales selon le niveau d'analyse considéré. Au niveau intrabassin, la structure des communautés était principalement influencée par l'accessibilité, la largeur mouillée, la superficie du sous-bassin et la largeur des terrasses; au niveau intraruisseau par l'accessibilité, la vitesse du courant, et la distance à la rivière principale; à l'échelle intratronçon par la vitesse du courant, la profondeur et les débris ligneux.

La relation entre la densité d'ombles de fontaine et leur environnement a été examiné en fonction de trois niveaux hiérarchiques (entre ruisseaux, entre tronçons et entre sections) à l'aide des analyses multiniveaux. La densité d'ombles de fontaine ne variait pas significativement entre ruisseaux. Elle était plutôt influencée par la superficie du sous-bassin, la largeur de la vallée et la hauteur à la crue au niveau des tronçons et par la vitesse du courant, les débris ligneux et le couvert au niveau des sections. Par contre, la relation entre la vitesse du courant et la densité d'ombles de fontaine au niveau des sections variait entre les tronçons. Cet effet contextuel était expliqué en partie par une interaction entre la superficie du sous-bassin et la vitesse du courant. La présence de cette interaction suggérait que les refuges de courant étaient potentiellement moins abondants dans les grands tronçons que dans les petits. Donc, certains patrons décelés à petite échelle spatiale (niveau sections) ne pouvaient être extrapolés à plus grande échelle (niveau tronçons).

L'influence contextuelle des interventions forestières sur l'incidence et la densité du saumon de l'Atlantique a été examinée à quatre échelles spatiales à l'aide des arbres de classification (CT) et de régression (RT). Les échelles spatiales étaient délimitées par des rayons d'influence : du sous-bassin versant (~ 15 km), de 8 km, de 2 km et de 0,5 km en amont de chaque tronçon. Les CT et RT ont démontré que les effets du pourcentage cumulatif de coupes sur l'incidence étaient intégrés sur de plus longues périodes à plus grande échelle spatiale. Par contre, les effets des coupes sur la densité n'étaient détectables qu'à grande échelle. Par ailleurs, les effets des coupes étaient seulement apparents dans les grands ruisseaux pour l'incidence et dans les ruisseaux accessibles pour la densité. Ces interactions suggèrent que les sédiments fins produits par les coupes s'accumulent plus facilement dans les grands ruisseaux à faible pente; et que la faible accessibilité restreignait les ajustements locaux de densité en réaction aux effets des coupes.

La variation dans la structure des communautés et des populations de poissons fluviatiles entre les échelles considérées a permis : 1) de mieux comprendre les relations entre les communautés ou les populations en intégrant l'information obtenue à différentes échelles; 2) de suggérer des mécanismes responsables des patrons observés; 3) de souligner les limites potentielles des études à une seule échelle.

CHAPITRE I

INTRODUCTION

Les échelles spatiales

Les processus qui gouvernent les relations entre les poissons fluviatiles et leur habitat opèrent souvent à différentes échelles spatiales (Bozek et Rahel 1991; Inoue et al. 1997; Crook et al. 2001). Ainsi, les patrons observés à petite échelle ne s'appliquent pas nécessairement à plus grande échelle (Schneider 2001). Dans des ruisseaux au Japon, l'abondance de poissons est plus élevée dans les habitats ayant plus de couvert, mais seulement lorsque l'ensemble du tronçon (série de 60 à 70 habitats) a peu de couvert (Inoue et al. 1997). Par ailleurs, la relation entre les patrons observés à différentes échelles spatiales n'est pas nécessairement linéaire, ni proportionnelle (Wiens 1989; Schneider 2001). La comparaison directe entre des études menées à différentes échelles spatiales devient alors difficile, et l'extrapolation, périlleuse (Wiens 1989; Schneider 2001).

Les approches multiéchelles suscitent donc un intérêt croissant. Elles permettent une meilleure compréhension des relations entre les organismes et leur environnement et ont un pouvoir prédictif accru (Schneider 2001; Dungan et al. 2002). Les approches multiéchelles intègrent également les patrons individuels dans une vision d'ensemble (Wiens 1989; Levin 1992; Armstrong et al. 1998). Il devient alors possible d'élucider les divergences de patrons entre échelles spatiales, d'identifier les mécanismes sous-jacents et de généraliser les résultats (Folt et al. 1998). Par exemple, l'examen du microhabitat peut révéler les facteurs déterminant la position des poissons dans un tronçon, tandis que l'examen de plusieurs tronçons peut suggérer les causes de l'absence de poissons à certains endroits, malgré la présence de microhabitats convenables (Bozek et Rahel 1991).

La hiérarchie des échelles

La théorie de la hiérarchie a mis en évidence la nécessité d'utiliser des approches multiéchelles (O'Neill 1989; Wiens 1989). Selon cette théorie, les écosystèmes sont composés d'une série de sous-systèmes emboîtés qui interagissent entre eux et qui peuvent évoluer autour d'un équilibre dynamique (O'Neill 1989; Wu et Loucks 1995). Chaque niveau hiérarchique est défini par des processus qui ont une structure spécifique et qui opèrent à des vitesses spécifiques. Par exemple, les processus géologiques évoluent sur de longues échelles spatio-temporelles (de centaines à plusieurs centaines de milliers d'années; de centaine à plusieurs milliers de kilomètres), tandis que les interactions entre espèces opèrent souvent sur des échelles spatio-temporelles plus courtes (de quelques minutes à plusieurs heures, de quelques millimètres à plusieurs mètres). Par ailleurs, chaque niveau hiérarchique est limité par le contexte des niveaux supérieurs et par les mécanismes des niveaux inférieurs (O'Neill 1989).

Bien qu'il n'y ait pas de « meilleure » échelle spatiale à laquelle examiner les relations entre les poissons fluviatiles et leur environnement, il faut néanmoins choisir et caractériser celles à considérer dans une approche multiéchelles (Wiens 1989; Levin 1992). Les échelles spatiales sont souvent calquées sur la classification hiérarchique des unités physiques d'un ruisseau telles que la séquence : bassin, sous-bassin, segment, tronçon, et mésohabitat; ou la classification emboîtée de l'ordre (p. ex. Frissell et al. 1986; Hawkins et al. 1993; Bisson et Montgomery 1996; Poff 1997; Allan et Johnson 1997). L'échelle du mésohabitat est plus souvent examinée en raison du rôle central que joue l'environnement immédiat (p. ex. vitesse du courant, profondeur, substrat) dans la détermination de la structure des communautés et des populations de poissons fluviatiles (Vannote et al. 1980; Frissell et al. 1986). Cependant, ces conditions environnementales locales sont largement déterminées par l'ensemble des caractéristiques du paysage à l'échelle du sous-bassin versant (Vannote et al. 1980; Frissell et al. 1986).

Les perturbations du paysage

Les actions anthropiques de grande envergure telles que les interventions forestières peuvent fortement modifier à la fois les caractéristiques du paysage et les conditions environnementales locales. L'insolation, la température et la productivité primaire et secondaire (Murphy et Hall 1981; Davies et Nelson 1994; Kiffney et al. 2003; 2004) peuvent augmenter à l'échelle du mésohabitat à la suite de l'éclaircissement de la canopée riveraine par les interventions forestières. À l'échelle du bassin, les coupes peuvent accroître la charge de sédiments et l'amplitude des crues (Macdonald et al. 2003), ainsi que l'apport d'eau annuel et les concentrations de nutriments (Lamontagne et al. 2000; Martin et al. 2000). Les poissons ne réagissent pas à leur environnement local de la même façon qu'aux caractéristiques du bassin versant (Armstrong et al. 1998; Folt et al. 1998). Les effets des interventions forestières sur l'abondance des poissons pourraient également varier en fonction des échelles.

Le choix des échelles à considérer pour évaluer les effets potentiels des interventions forestières sur les poissons fluviatiles n'est pas clair. Certains ont suggéré que l'impact maximal des interventions forestières serait à l'échelle de dizaines ou centaines d'hectares (Carignan et Steedman 2000). À l'échelle des bassins versants de grande envergure, les effets cumulatifs des coupes forestières peuvent être mieux évaluées en intégrant une multitude de petites aires de perturbation sur une grande superficie (Hicks et al. 1991). La comparaison directe des résultats et conclusions provenant d'études à plus petite échelle peut induire en erreur puisque les patrons révélés à petite échelle ne sont pas nécessairement applicables à plus grande échelle (Wiens 1989; Hicks et al. 1991). Les approches multiéchelles peuvent donc faciliter le choix d'échelles appropriées afin d'évaluer les effets des interventions forestières sur les poissons fluviatiles.

Objectifs de l'étude et approches multiéchelles

L'objectif général du présent projet consistait donc à examiner, en fonction de différentes échelles spatiales, l'influence du contexte environnemental sur la structure des communautés de poissons fluviatiles et la distribution de deux espèces « cibles » : l'omble de fontaine (*Salvelinus fontinalis*) et le saumon de l'Atlantique (*Salmo salar*) dans le bassin versant de la rivière Grande Cascapédia (Gaspésie). Trois approches multiéchelles ont été utilisées pour traiter différents aspects de cet objectif.

La première approche (chapitre 2) visait à examiner comment l'influence du contexte environnemental sur la structure des communautés variait avec l'échelle spatiale considérée. Les objectifs spécifiques du chapitre étaient : 1) de déterminer comment variait les structures des communautés à chaque échelle 2) d'identifier les caractéristiques environnementales ayant le plus d'influence à chaque échelle et 3) de déterminer comment la variation expliquée était répartie entre les échelles. Les analyses de redondance et la décomposition hiérarchique de la variation ont été utilisées afin d'atteindre ces objectifs. Le plan d'échantillonnage était hiérarchique avec trois niveaux emboîtés : 22 ruisseaux contenant de 2 à 20 tronçons par ruisseau ($n = 120$) et 5 sections par tronçon ($n = 600$). Les trois échelles considérées étaient basées sur les niveaux hiérarchiques du plan d'échantillonnage. La décomposition de la variation a donc permis de répartir la variation des communautés et la variation expliquée en trois composantes « pures » : 1) entre ruisseaux, 2) entre tronçons à l'intérieur des ruisseaux et 3) entre sections à l'intérieur des tronçons. Par contre, les variables environnementales qui expliquaient la structure des communautés ont été sélectionnées à trois niveaux d'analyse : 1) intrabassin, incluant la variation entre ruisseaux, entre tronçons et entre sections; 2) intraruisseau, incluant celle entre tronçons et entre sections; et 3) intratronçon, incluant celle entre sections seulement. L'étendue spatiale des niveaux de décomposition et d'analyse était de ≈ 82 km (niveau intrabassin et entre ruisseaux), ≈ 8 km (niveau intraruisseau et entre tronçons) ou ≈ 0,075 km (niveau intratronçon et entre sections).

La deuxième approche (chapitre 3) visait à d'examiner comment la densité d'ombles de fontaine variait en fonction des caractéristiques environnementales à trois niveaux hiérarchiques. Les objectifs du chapitre étaient : 1) d'examiner comment la variation dans la densité d'omble de fontaine se répartissait en fonction des échelles, 2) d'identifier les variables environnementales qui influençaient la densité d'omble de fontaine à chaque échelle et 3) d'examiner si l'effet des variables environnementales aux plus bas niveaux variait entre les unités des niveaux supérieurs. Les modèles multiniveaux (modèles linéaires hiérarchiques ou modèles mixtes) ont été utilisés afin d'atteindre ces objectifs. Les niveaux hiérarchiques considérés étaient : 1) les sections à l'intérieur des tronçons, b) les tronçons à l'intérieur des ruisseaux et c) les ruisseaux.

La troisième approche (chapitre 4) visait à examiner comment l'influence contextuelle des interventions forestières sur les populations de saumon de l'Atlantique pouvait différer en fonction des échelles spatiales. Les objectifs du chapitre étaient : 1) d'identifier les variables environnementales et forestières qui influençaient l'incidence et la densité de saumons à chaque échelle, 2) de déterminer si l'influence des variables forestières était accentuée ou atténuée par certaines conditions environnementales (effets contextuels) et 3) de déterminer comment la réponse des saumons aux variables forestières variait selon les échelles. Les arbres de classification et de régression ont été utilisés afin d'atteindre ces objectifs. Contrairement aux deux premiers chapitres, les échelles spatiales utilisées dans le troisième étaient définies par des rayons d'influence en amont de chaque tronçon : le sous-bassin versant (limite naturelle ~ 15km), ainsi qu'à l'intérieur des rayons de 8 km, 2 km et 0,5 km en amont de chaque tronçon.

Intérêt de l'étude

La décomposition hiérarchique de la variation offre un cadre conceptuel simple et global qui permet à la fois d'examiner la structure d'une communauté à plusieurs échelles et d'évaluer l'importance relative des divers processus écologiques (Wiley et al. 1997). Les analyses multiniveaux permettent de prendre en considération différentes sources de variabilité sans en confondre les effets. Elles permettent donc de comprendre les relations entre les espèces et leur environnement tout en résolvant les divergences de patrons entre échelles. Les arbres de classification et de régression sont des méthodes flexibles et robustes offrant une alternative intéressante aux modèles linéaires pour l'analyse des relations espèces-habitat (De'ath et Fabricius 2000). Particulièrement, elles peuvent dévoiler des interactions complexes entre variables prédictives sans avoir à spécifier *a priori* la forme de ces interactions (Breiman et al. 1984).

Les analyses hiérarchiques proposées sont des outils puissants qui facilitent l'utilisation des approches multiéchelles en écologie fluviatile. Malgré leur utilité potentielle pour éclaircir les relations espèces-environnement, le plein potentiel des analyses hiérarchiques demeure, encore aujourd'hui, relativement sous-exploité (p. ex. Cushman et McGarigal 2002; 2004; Stadler et al. 2003; Wagner 2004; Couteron et Ollider 2005; Stoffels 2005; Rieman et al. 2006).

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CHAPITRE II

MULTI-SCALE ANALYSIS OF STREAM FISH ASSEMBLAGES BY MEANS OF HIERARCHICAL DECOMPOSITION OF VARIATION

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Substantial gains in understanding and predictive power can accrue from the use of multi-scale approaches in ecology, yet most analyses of species assemblages tend to focus on a single spatial scale. We used redundancy analyses and hierarchical decomposition of variation to evaluate how environmental effects on stream fish assemblages varied across three spatial scales: (1) among streams within a river basin (≈ 82 km); (2) among reaches, within streams (≈ 8 km); and (3) among sections, within reaches, within streams (≈ 0.075 km). Fish abundance and environmental variables describing landscape, accessibility, and local habitat, were quantified at 120 sampling sites distributed among 22 tributary streams in the Cascapedia River basin, Québec, Canada. In all, 12 environmental predictors selected by a stepwise selection procedure were included in the final models at one or more scales. Environmental influences on assemblage structure clearly varied across scales. Analysis at the within-basin scale pointed to major roles for accessibility and valley size and morphology in determining assemblage structure. Accessibility by fish and local habitat features seemed to be the main determinants of assemblage structure within streams, whereas only local habitat features had detectable influence on assemblage structure within reaches. The explained variation associated with most environmental predictors was greatest at the within-basin scale and declined progressively at smaller scales. Patterns in species-environment relationships were increasingly reliable at larger spatial scales, suggesting that models derived solely from relationships at the microhabitat scale are unlikely to yield useful understanding and prediction of large-scale distribution patterns in this system. By efficiently integrating information across spatial scales, multi-scale analyses can provide a more complete portrait of species-environment relationships than single-scale analyses and allow research and management objectives to be associated with specific spatial scales.

Introduction

Substantial gains in understanding and predictive power can accrue from the use of multi-scale approaches in ecology (Schneider 2001, Dungan et al. 2002). Aquatic ecologists have long recognized that the landscape influences waterbodies through multiple mechanisms operating at different spatial scales, and have consequently adopted conceptual schemes that organize physical units hierarchically, as in the sequence: habitat-reach-segment-subcatchment-basin, and in the nested classification of stream order (Allan and Johnson 1997). For stream fish, the processes that govern spatial distribution, habitat selection, and the relative importance of biotic interactions and abiotic influences on assemblage structure, vary across landscapes and span several spatial scales (Bozek and Rahel 1991, Inoue et al. 1997, Crook et al. 2001). Assemblage structure of stream fish generally shows predictable relationships to environmental features at regional or basin scales but seems more subject to local biotic interactions at smaller scales, such as individual habitat units (Jackson et al. 2001, Peres-Neto 2004). For example, the spatial distribution of two congeneric charrs in streams of Hokkaido Island, Japan, is governed by a temperature gradient at the island, regional, and basin scales, but dominance hierarchies structured by interspecific competition generate negative relationships in the congeners' distributions among and within pools (Fausch et al. 1994).

Analyses of stream assemblages often focus on a single spatial scale. When multiple scales are considered, the relationships between assemblages and environmental features are sometimes first examined separately at different scales and then compared across scales (Townsend et al. 1997). This procedure entails averaging patterns over the smaller scale sampling units to yield patterns at larger scales, which considerably reduces the number of observations, and thus statistical power, at larger scales. Conversely, small-scale (site-based) analyses may have greater statistical power but limited biological significance (Allan and Johnson 1997, Townsend et al. 1997). However, when species-environment relationships are analysed separately at different scales, results may be biased if large-scale variation is not accounted for in the small-scale analyses (Dunham and Vinyard 1997).

Ignoring the scale-dependence of species-habitat relationships may therefore lead to erroneous conclusions regarding habitat use and the determinants of assemblage structure (Dunham and Vinyard 1997). For example, at the scale of a pool-riffle sequence the abundance of masu salmon (*Oncorhynchus masou*) in Japanese streams is positively related to the abundance of cover, but at the scale of stream reaches (10 pool-riffle sequences) this relationship only holds when cover is rare (Inoue et al. 1997). The abundance of golden perch (*Macquaria ambigua*) in an Australian stream correlates positively with woody debris at the scale of sections (≈ 86 m), but the correlation becomes negative at the scale of the entire stream reach (450 m) (Crook et al. 2001).

Multi-scale studies are needed to elucidate differences in species-habitat relationships across scales, identify underlying mechanisms, and generalise results over time and space (Folt et al. 1998). Integrating complementary information gathered at different spatial scales can help resolve inconsistencies among studies (Folt et al. 1998). For example, microhabitat-scale analyses may detect the determinants of fish location within stream reaches, whereas habitat-scale analyses may reveal why fish are absent from reaches with suitable microhabitat (Bozek and Rahel 1991). Understanding large-scale phenomena relevant to colonization and extinction dynamics, such as dispersal capabilities, the role of barriers, and spatio-temporal patterns of connectivity at the landscape and regional scales can enhance our understanding of distribution patterns beyond that provided by a narrower focus on local habitat (Taylor and Warren 2001).

Hierarchical decomposition of variation in multivariate analyses offers a comprehensive and powerful methodological framework for examining assemblage structure at multiple scales; it is as well a working tool that can help evaluate the relative importance of various ecological processes operating at distinct spatial scales

(Wiley et al. 1997). Although the feasibility of hierarchical analyses in ecological ordination was signalled early on (ter Braak 1986, ver Hoef and Glenn-Lewin 1989), they have been used infrequently (see Cushman and McGarigal 2002, 2004, Wagner 2004, Couteron and Ollier 2005 for alternative approaches) and their considerable potential for clarifying species-environment relationships remains underexploited.

Here, we show how partial redundancy analyses based on the use of dummy variables to sequentially remove or "peel off" variation at different spatial scales allow one to apportion the variation in assemblage structure among spatial scales and explore how the magnitude and relative importance of a set of environmental effects change as one progressively "zooms in" from larger to smaller scales. The effects of environmental features on assemblage structure of stream fish were examined across spatial scales spanning three orders of magnitude. Hierarchical decomposition of variation was used to determine how species-environment relationships varied across three spatial scales: within-basin (variation among streams within a river basin: ≈ 82 km), within-streams (variation among reaches within streams: ≈ 8 km), and within-reaches (variation among sections within reaches and streams: ≈ 0.075 km). Specifically, we (1) identified the environmental features that best explained variation in fish assemblage structure at each scale, (2) quantified the variation in fish assemblage structure at each scale, and (3) examined the amount of variation in assemblage structure explained by environmental features at each scale. Although the focus here is on stream fish communities, the proposed approach to multi-scale ordination is generally applicable in ecological systems with hierarchical structure and identifiable discrete scales, such as mosses nested within leaves, branches, trees, and forest stands, or parasites nested within individual fish, lakes, and ecoregions.

Methods

Fish sampling and environmental variables

Fish abundance and environmental variables were quantified at 120 sampling sites distributed among 22 tributary streams in the Cascapedia River basin (3179 km^2), Québec, Canada (Fig. 1). Sites were visited in random sequence during low flow from mid-June to late August in 2000 (24 sites), 2001 (48 sites), and 2002 (48 sites). At each site, samples were collected from a 75-m stream reach comprising five adjacent sections, each approximately 15 m in length. No attempt was made to position sampled reaches to coincide with habitat boundaries. The nested sampling design therefore spanned three spatial scales: sections within reaches (maximum fluvial distance between sections $\approx$ 0.075 km), reaches within streams (maximum fluvial distance between reaches, averaged across streams $\approx$ 8 km), and streams within the basin (maximum fluvial distance between stream mouths $\approx$ 82 km).

Fish samples and instream environmental data were collected from an area covering the entire stream width in completely wadable reaches, and ranging 5 m from one bank, chosen randomly, towards the opposite bank otherwise. Fish were sampled by single-pass electrofishing (Smith-Root 15-D) in an upstream direction within open stream sections (Jones and Stockwell 1995). All captured fish were identified to species, measured (fork length), weighed, and returned to their section of capture. Fish densities were calculated as total captures divided by section area. Because capture efficiency was not 100%, this measure underestimates true density but should be proportional to it if efficiency is comparable across reaches. All reaches were sampled at base flow and therefore variation in depth, water velocity, cover, and substratum size among sections was limited (Table 1). Abundance estimates obtained by one-pass electrofishing have been shown to correlate well with those from multiple-pass removal experiments in homogeneous geographic areas (e.g., small mountain streams: Kruse et al. 1998; small warmwater streams: Edwards et al. 2003).

In all, 22 environmental variables were quantified (Table 1). For each section, water depth and substratum size (modified Wentworth scale) were measured at five equidistant points along each of four equidistant transects perpendicular to streamflow. Current velocity (pigmy-type meter, Scientific Instruments 1205) was measured at five equidistant points (60% of depth) along the second transect from the downstream end. Wetted width was measured at each transect. Abundance of submerged vegetation (moss or macrophytes) and overall availability of structural cover (rocks, woody debris, undercut bank, and overhanging vegetation) were estimated visually and assigned ordinal values reflecting areal coverage (1: ≤ 5%; 2: 6-15%; 3: 16-45%; 4: > 45%). Overhead opening (angle between riparian canopy or hilltops blocking incident sunlight at the centre of the stream) and slope over the stream reach were measured with a hand-held clinometer (Suunto MP-5). The increment in stream height and width at flood (from annual flood marks) and terrace width (distance between stream bank and piedmont) were measured on site. Water temperature (mid-point of readings from max/min thermometer, Barigo) was measured at each reach. Units of large woody debris (> 10 cm diameter) and pools were counted within each section. For each reach, entrenchment (mean gradient ≤100 m away from stream bank), sub-basin area, stream gradient (mean slope from site to headwaters), stream order (Strahler scale), and altitude were obtained from 1:20 000 topographic maps, as were distances by waterway from each section to the Cascapedia River ("distance to mainstem"), and from the mouth of each stream to the mouth of the Cascapedia River ("distance to mouth") (planimeter, Calculated Industries 6125).

Physical barriers potentially affecting upstream migration of fish along a tributary were assessed from field observations and topographic maps, and their effectiveness was coded as an integer value, *B*, ranging from 0 (no visible barrier) to 4 (insurmountable barrier for all fish in the community) and reflecting the height, type (beaver dam, log jam, culvert, fall), and configuration of the barrier (Appendix

1). An index of accessibility combining multiplicatively all potential barriers for each site was calculated as:

$$accessibility = \prod_{i=1}^{N} \left(1 - \frac{B_i}{4}\right),$$

where N is the number of visible barriers and B_i is the effectiveness of barrier i downstream from the site. Accessibility was assigned the value 1 in the absence of visible barriers. The index thus ranged from 0 to 1, taking a value of 0 if at least one barrier was insurmountable ($B_i = 4$).

As an aid to interpretation, environmental variables were categorised according to their spatial extent and grain (Dungan et al. 2002). Spatial extent comprised three categories: (1) local instream habitat, reflecting microhabitat attributes and small-scale spatial heterogeneity within the stream; (2) terrestrial landscape, reflecting intermediate-scale topographical features in the terrain adjacent to the stream; and (3) accessibility, reflecting colonization potential for fish in the regional pool of species (Table 1).

Ordination analyses and hierarchical decomposition of variation

Relationships between assemblage structure and environmental factors were examined by use of redundancy analysis (RDA) and partial RDA (pRDA). RDA directly relates assemblage structure to explanatory (usually, environmental) variables, whereas pRDA relates assemblage structure to explanatory variables after "partialling out", or statistically accounting for, the values of one or more covariables (Legendre and Legendre 1998). Graphical examination of species densities as a function of environmental variables showed that relationships were generally linear, as assumed by RDA. Linear analyses such as RDA are best suited for analyzing short community gradients (range of ordination sample scores < 2-3 standard deviations, SD; ter Braak and Šmilauer 2002). In the present study, the gradient length in a detrended correspondence analysis used to diagnose linearity in species responses was 1.8 SD. Preliminary RDA including the densities of different age classes of each species as dependent variables showed that variation among age classes was very limited relative to variation among species, i.e., all age classes of individual species had similar responses to environmental variation and these responses differed markedly among species. Therefore, all subsequent analyses were based on total densities, summed across age classes, of individual species.

Fish densities were transformed as $\ln(X + 1)$ and environmental variables were transformed by use of logarithmic or power functions to reduce the influence of extreme points and better fit statistical assumptions of linearity, normality, and homoscedasticity. The best environmental predictors in each analysis were identified by use of a forward selection procedure based on a cutoff point P=0.05 (Program CANOCO, version 4.5; ter Braak and Šmilauer 2002). Statistical significance of the individual predictors, the sum of all eigenvalues, and the ordination axes, was determined by Monte Carlo tests (1000 permutations). The nested structure of samples was maintained during resampling by use of within-block permutations, i.e., random reshuffling of samples was unrestricted for streams within the basin, but was restricted for reaches within streams and sections within reaches. To account for potential spatial autocorrelation among sections within a reach, an additional restriction was imposed at this level so that sections were reshuffled within reaches in a cyclical ("conveyor belt") pattern, rather than entirely at random (ter Braak and Šmilauer 2002). The nominal t-values of canonical coefficients were used to assess the contribution of environmental variables to individual ordination axes (ter Braak and Šmilauer 2002), and van Dobben circles (ter Braak and Looman 1994) were used to identify significant relationships of species with individual environmental variables.

Variation in fish assemblage structure was related to environmental features, and partitioned hierarchically, by use of a general model:

SPECIES = ENVIRONMENT + COVARIABLES,

in separate analyses including different combinations of environment and covariable terms, as described below. The notation [X] and [X | C] is used here to represent the RDA or pRDA models including explanatory variables X and covariables C, as well as the variation accounted for by the models.

We used a fixed-effects model to account for variation in assemblage structure at three scales: among streams, reaches, and sections. Three sets of binary (0/1) dummy variables, STREAM (31 variables), REACH (120 variables), and SECTION (600 variables), were used to assign samples uniquely to individual stream-year, reach-year, and section-year combinations (although strictly only N – 1 variables are required to distinguish among N categories, CANOCO requires specification of a full set of N variables). The last variable set, SECTION, assigns one dummy variable to each basic sampling unit (15-m stream section) and therefore exhausts the variation in assemblage structure. The dummy variable sets were used in various combinations, as nominal "explanatory" variables in RDA, or jointly with environmental variables (E) as covariables in pRDA, to obtain different components of variation. For example, in the notation given above, [SECTION] represents the total variation in assemblage structure (because variable set SECTION accounts for all the variation among samples). In practice, the total variation is given automatically by most ordination programs; variable set SECTION is therefore not directly used in the analyses but is introduced here for notational convenience.

Variation in assemblage structure can be partitioned hierarchically by systematic use of the dummy variable sets, as illustrated below. Because of the nested structure of the sampling scheme (sections within reaches within streams), variation within a given level in the hierarchy includes that at all levels below it (Fig. 2a). At the highest level, the "pure" variation among streams is given by [STREAMS], because the variable set STREAMS accounts for all of the variation among streams but none of the variation within streams. Likewise, at the lowest level, the "pure" variation among sections, within reaches and streams, is given by [SECTION] – [REACH]. Analogously, the total variation accounted for by environmental variables ("explained") is given by [E]. As with the total ("raw") variation in assemblage structure, the explained variation can be partitioned hierarchically, by joint use of the dummy and environmental variable sets. For example, the explained variation among sections is given by [E | REACH], and that among streams is given by [E] - [E | STREAM].

A first set of analyses used the dummy variable sets to partition the total raw variation in assemblage structure into three hierarchical levels: among streams within the basin (stream scale), among reaches within streams (reach scale), and among sections within reaches and streams (section scale) (Table 2A; Fig. 2b). Then, a second set of analyses used the dummy variable sets in combination with environmental variables to determine the proportion of explained variation within the basin, within streams, and within reaches (Table 2B; Fig. 2b). It is straightforward to derive the calculations for variation components in Table 2 visually by inspecting Fig. 2b, and to verify the hierarchical partitioning of components by adding terms across levels.

To determine whether the set of environmental variables that best accounted for fish assemblage structure differed across spatial scales, the best sets of environmental predictors were identified by use of forward selection at the three scales: within basin (RDA with no dummy covariables, yielding environmental predictors at the within-basin scale, E_B); within streams, following removal of the variation among streams (pRDA with STREAM as dummy covariables, yielding environmental predictors at the within-stream scale, E_S); and within reaches, following removal of the variation among streams and reaches (pRDA with REACH as dummy covariables, yielding environmental predictors at the within-reach scale, E_R). The variation in assemblage structure explained by the E_B predictors was partitioned hierarchically into within-basin, within-streams, and within-reaches components as detailed in Table 2B, and that explained by the E_S predictors was partitioned hierarchically into within-streams and within-reaches components by an analogous procedure. At the smallest scale, the variation explained by the E_R predictors was all within reaches and thus could not be further partitioned. To assess the role of individual environmental predictors, their independent contributions to explained variation were obtained by including the predictors, one at a time, as single predictors in pRDA models for each scale. In comparison, the more conventional, single-scale approach to ordination would have ended after examining the within-basin predictors E_B, possibly after adjustment of permutation tests to account for the nested structure of the data, as described above.

We compared our approach with the hierarchical decomposition of species-environment relationships proposed by Cushman and McGarigal (2002; hereafter C&M), in which the environmental variables are associated to spatial scales (landscape, patch, and plot) on the basis of grain or resolution of each variable (i.e., their measurement scale). Nested ANOVA was used to obtain variance components for each environmental variable at the stream, reach, and section scales and to assign each variable to one of three scales (Table 1). Stream-scale variables varied only across streams, reach-scale variables varied only across streams and reaches, and section-scale variables varied at all three scales. Distance to mainstem was considered a reach-scale variable because it hardly varied among sections. We selected environmental variables by the forward procedure described above. Variation in assemblage structure was partitioned following the first-tier decomposition described in C&M and the results were compared with our within-basin analysis (RDA: $[E_B]$).

Results

We collected 15 743 fish, distributed among six species: slimy sculpin (*Cottus cognatus*; 63.0% by numbers), brook trout (*Salvelinus fontinalis*; 27.1%), Atlantic salmon (*Salmo salar*; 9.8%), threespine stickleback (*Gasterosteus aculeatus*; < 0.1%), white sucker (*Catostomus commersoni*; < 0.1%), and blacknose shiner (*Notropis heterolepis*; < 0.1%). Slimy sculpin and brook trout had broad distributions (occurrence in ≈90% of sections) compared to Atlantic salmon (42%). Threespine stickleback, white sucker, and blacknose shiner are primarily lentic species and jointly accounted for < 0.1% of total captures; they were therefore omitted from subsequent analyses.

In all, 12 environmental predictors were included in the final models at one or more scales (Table 3). Of these predictors, five were selected only at the within-basin scale, four at the within-basin and within-streams scales, one at the within-streams and within-reaches scales, and two at all three scales. Environmental influences on assemblage structure varied across scales: the explained variation associated with most environmental predictors was highest at the within-basin scale and declined progressively at smaller scales. Terrestrial landscape variables accounted for relatively small amounts of variation at the within-basin and within-stream scales.

In the analysis based on variable selection at the within-basin scale (RDA: [E_B]), fish assemblage structure was significantly related to eleven environmental variables (Fig. 3a, Tables 3 and 4). The first ordination axis (accounting for 52.3% of the variation explained by environmental variables) was most strongly related to accessibility, wetted width, sub-basin area, and terrace width (Fig. 3a). The alignment of species arrows with this axis indicates that density of Atlantic salmon and slimy sculpin was highest, and that of brook trout lowest, in wide stream sections with a well-developed lateral plain and few barriers to migration. The second ordination axis (31.8%) was most strongly associated with distance from the mainstem and reflected an increase in density of brook trout and slimy sculpin, and a decline in density of Atlantic salmon, along a longitudinal gradient from the Cascapedia mainstem toward the headwaters of tributaries. Analysis at this scale therefore pointed to major roles for accessibility and valley size and morphology in determining assemblage structure.

In the analysis based on variable selection at the within-streams scale (pRDA: [E_S | STREAM]), fish assemblage structure was significantly related to seven environmental variables (Fig. 3b, Tables 3 and 4). The first ordination axis (accounting for 63.8% of the variation explained by environmental variables) was most strongly related to current velocity, accessibility, distance to the mainstem, and woody debris. Variation in assemblage structure along this axis reflected mostly changes in brook trout density, which was positively associated with woody debris and distance to the mainstem, and negatively associated with current velocity and terrace width (Fig. 3b). The second ordination axis (30.9%) was most strongly associated with mean depth and represented primarily variation in the densities of Atlantic salmon and slimy sculpin, which were highest in relatively shallow sections, free of barriers and near the Cascapedia mainstem. At this scale, accessibility and local habitat features seemed to be the main determinants of assemblage structure.

In the analysis based on variable selection at the within-reaches scale (pRDA: [E_R | REACH]), fish assemblage structure was significantly related to three environmental variables (Fig. 3c, Tables 3 and 4). Most (80.0%) of the variation explained by environmental variables was associated with the first ordination axis, which depicted an increase in density of brook trout and concomitant decline in that of slimy sculpin as current velocity declined and mean depth and woody debris increased. The second ordination axis (20.0%) reflected mainly a weak association of density of Atlantic salmon with mean depth and woody debris. At this scale, only local instream habitat influenced assemblage structure.

Individual species showed varying scale-dependence in their responses to environmental variation: brook trout was consistently associated with woody debris and current velocity at all scales, and with distance to mainstem at the two larger scales, but for slimy sculpin and Atlantic salmon, environmental influences were more variable across scales (Fig. 3) and even showed sign reversals, e.g., in the relationships between slimy sculpin and distance to the mainstem at the within-basin and within-stream scales (cf. Fig. 3a, b; Table 4). Correlations between species densities, reflected by the angles between arrows for species in the ordination plots, were scale-dependent, as shown by the varying configuration of arrows at different scales (Fig. 3). Brook trout density was negatively correlated with that of Atlantic salmon at the within-basin and within-reach scales, but showed little correlation at the within-stream scale. At all scales, the distribution of brook trout was relatively independent from that of slimy sculpin. Atlantic salmon and slimy sculpin densities showed little correlation at the within-basin scale but were correlated positively at the within-stream scale, and negatively at the within-reach scale. The contribution of individual species to patterned variation in assemblage structure also was scale-dependent, as illustrated by the differences among spatial scales in the length and alignment of species arrows. For example, Atlantic salmon showed strong correlation with axis 1 (Fig. 3a) and a host of environmental variables (Table 4) at the within-basin scale, but only weak correlation with axis 2 (Fig. 3c), and no significant relationship with environmental variables (Table 4), at the within-reach scale.

Raw variation in fish assemblage structure was greater at the stream scale (47.0%) than at the reach (35.1%) or section (17.9%) scales (Fig. 4a). Explained variation also declined from larger to smaller spatial scales. In the analysis based on variable selection at the within-basin scale (RDA: [E_B]), the environmental variables accounted for 62% of the stream-scale variation, 27% of the reach-scale variation, and 6% of the section-scale variation (Fig. 4a). Although different sets of environmental variables (E_B: 11 variables, E_S: 7 variables, and E_R: 3 variables) were selected at the three scales, the proportion of variation explained at each scale remained very similar across analyses. In the analysis based on variable selection at the within-streams scale (pRDA: [E_S | STREAM]), the environmental variables accounted for 24% of the reach-scale variation, and 6% of the section-scale variation (Fig. 4b), whereas in the analysis based on variable selection at the within-reaches scale (pRDA: [E_R | REACH]), the environmental variables accounted for 5% of the section-scale variation (Fig. 4c).

In the analysis based on C&M, 12 environmental variables were retained: one at the stream scale (distance to mouth), six at the reach-scale (accessibility index, altitude, watershed area, stream order, distance to mainstem, and entrenchment), and five at the section-scale (mean wetted width, mean current velocity, terrace width, units of large woody debris, and cover index). For all scales, explained variation shared with other scales ("confounded components" in C&M) was greater than variation explained exclusively ("independent components" in C&M) by each scale (Fig. 5). Reach-level variables accounted for the greatest proportion of exclusive variation in fish assemblage structure and stream-level variables for the least.

Discussion

The notion of faunal "screens" or "filters" is often invoked to explain nested patterns in assemblage structure. Faunal filters are a series of factors that act sequentially on a large set of species (e.g., the continental, or regional pool) and influence assemblage composition or structure at progressively smaller spatial scales by restricting the occurrence or abundance of individual species according to their susceptibility to the filters at larger scales (Tonn et al. 1990, Poff 1997, Jackson et al. 2001). Insight into the types of filter operating at each spatial scale can be gleaned from the multi-scale analysis by examining how the influence of environmental variables on assemblage structure varies across scales.

Accessibility proved to be a major determinant of assemblage structure both at the within-basin and the within-streams scales, primarily through its influence on Atlantic salmon and slimy sculpin. Barriers such as log jams, beaver dams, culverts, and waterfalls can act as filters by cutting access to spawners and preventing recolonization following local extinction, therefore leading to low density or absence at upstream sites even if local conditions are favorable at those sites. Culverts can greatly constrain the movement of stream fishes (Furniss et al. 1991, Warren and Pardew 1998). Most culverts classified as migration barriers in this study were of the corrugated-round type and lacked large substratum on the bottom, one of the least desirable configurations for fish passage because it generates high water velocities within the culvert (Furniss et al. 1991). Active beaver dams also limit upstream fish movement (Schlosser 1995, Colleen and Gibson 2001), including that of Atlantic salmon (Alexander 1998). Beavers generally seal their dams with mud and vegetation, rendering fish passage through interstices more difficult (Schlosser 1995, Alexander 1998). In addition to blocking migration of adult salmon to spawning grounds, the presence of barriers may have limited access to favorable sites for salmon parr and slimy sculpin, both of which show restricted movement in streams (Morgan and Ringler 1992, Rodríguez 2002, Petty and Grossman 2004), and may therefore have low "attempt rates" for passage through barriers (Castro-Santos 2004). In contrast to salmon parr and slimy sculpin, brook trout are highly mobile in streams (Riley et al. 1992, Gowan and Fausch 1996, Rodríguez 2002) and are able to overcome substantial barriers, such as 1.2-m-high falls (Adams et al. 1999), possibly explaining why brook trout seemed comparatively less influenced by accessibility.

The second variable reflecting accessibility, distance to the mainstem, was negatively associated with density of Atlantic salmon, and positively associated with that of brook trout, both at the within-basin and within-streams scales. This result conforms with the notion that salmon density is influenced by accessibility and further suggests that brook trout are favored in reaches distant from the mainstem, and do not strongly depend on colonization from the mainstem for maintenance of local populations. Interestingly, the association of slimy sculpin with distance to the mainstem was positive at the within-basin scale and negative at the within-streams scale, a sign reversal indicating that a longitudinal decline of sculpin density with distance to the mainstem became apparent only after the confounding effects of among-stream variation were removed statistically.

Stream size and valley morphology, as quantified by the terrestrial landscape variables, appeared to be related mostly to differences in fish assemblages among streams at a spatial scale spanning tens of kilometers and contributed little to explaining variation in fish assemblages at smaller scales, presumably because terrestrial landscape features vary little at smaller scales. Somewhat surprisingly, one of the environmental variables that we had initially classified as a descriptor of local instream habitat, wetted width, was associated with fish assemblage structure at the within-basin scale but not at smaller scales. This result suggests that the influence of wetted width is mediated through its relation with landscape-level features such as stream size, rather than on a direct effect on local habitat quality, a distinction that would not have been readily made in a single-scale analysis.

Several previously known associations between fish density and specific habitat features at the reach and smaller scales were retrieved by the multi-scale analysis. These include preference of shallow sites by Atlantic salmon (Gibson et al. 1987, Gibson et al. 1993, Rodríguez 1995), sites with fast flow by slimy sculpin (van Snik Gray and Stauffer 1999), and sites with slow flow (Gibson et al. 1987, Gibson et al. 1993, Rodríguez 1995) and woody debris (Flebbe and Dolloff 1995, Neumann and Wildman 2002) by brook trout. It is encouraging that the environmental variables that emerged as useful predictors of assemblage structure at the within-reach scale are often cited as key abiotic determinants of meso- and micro-habitat suitability for stream fish: current velocity, depth, and wood (Bjornn and Reiser 1991, Poff 1997, Jackson et al. 2001).

However, other well-known relationships at the meso- and micro-habitat scales were not detected in the multi-scale analysis; notably, the association of Atlantic salmon with fast flows (DeGraaf and Bain 1986, Gibson et al. 1987, Gibson et al. 1993) and that of brook trout with pool habitats (Gibson et al. 1987, Gibson et al. 1993, Rodríguez 1995). This omission likely arose from the sampling design of the study rather than from an inherent drawback of the multi-scale approach. The patterned variation that can be explained at the smaller spatial scale depends in part on the size of the smallest sampling unit relative to the characteristic scale of the biological pattern. Use of 15-m sections as the smallest sampling units allowed for detection of microhabitat preferences only as crude averages over all sampling units. Furthermore, although the 15-m sections roughly coincide with the meso-habitat scale corresponding to pool length in the Cascapedia River basin, no attempt was made to make the boundaries of the sections match with natural habitat boundaries at any of the scales in the study. Although matching of section and habitat boundaries was unfeasible in the present study, in which samples were taken from five adjacent sections of identical length, future multi-scale studies focusing on variation among habitats may benefit from sampling from pool-riffle pairs, or pool-riffle-run triplets, at the smallest spatial scale.

A priori identification of the spatial extent of predictors included in the analysis is useful for interpretation and can furnish insights into the processes underlying the observed patterns. In the present study, environmental predictors were assigned to three discrete categories reflecting spatial extent, but other possibilities exist, including quantification of extent as a continuous variable. Two major advantages of the multi-scale approach over single-scale ordination are that it allows for detection of differences between within- and among-group effects, as exemplified by the sign reversal for distance to the mainstem discussed above, and that it can enhance detectability and understanding of relationships at smaller scales by statistically accounting for variation at larger scales.

In contrast with the sequential removal of variation at different spatial scales by use of dummy covariables, the C&M approach did not allow for decomposition of the total nor the explained variation in species assemblage structure across spatial scales, because in that approach scale is defined by the grain of environmental variables, which does not necessarily reflect the spatial scale at which environmental influences are realised. This limitation would seem to prevent the C&M approach from detecting effects of small-grained environmental variables at larger spatial scales, or uncovering context-dependent effects, in which environmental influences vary across spatial scales.

Multi-scale analyses can efficiently integrate information across spatial scales, provide a more complete portrait of species-environment relationships than single-scale analyses, and allow researchers and managers to match their objectives to specific scales (Armstrong et al. 1998). For example, in the Cascapedia River basin, variation in fish assemblage structure was greater, and patterns in species-environment relationships increasingly reliable, at larger spatial scales, suggesting that models derived solely from relationships at the microhabitat scale are unlikely to yield useful understanding and prediction of large-scale distribution patterns in this system. As well, from a more applied perspective, the results indicate that efforts to remediate and conserve habitats should not focus exclusively on traditional approaches such as improvement of local habitat, but should also examine closely the potential impact of factors influencing stream accessibility, such as removal or creation of beaver dams and log jams, and culvert design.

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Table 1. Spatial extent (A: accessibility, T: terrestrial landscape, or I: instream local), summary statistics, and variance components, by scale (St: among streams, Re: among reaches, Se: among sections) for 22 environmental variables describing fish habitat in the Cascapedia River basin.

Variable name	Extent	Median (25%-75% quartiles)	Variance component (%)		
			St	Re	Se
Accessibility index	A	0.75 (0.25-1.00)	39.7	60.3	0.0
Distance to mouth (km)	A	75.5 (52.8-83.2)	100.0	0.0	0.0
Distance to mainstem (km)	A	9.1 (2.4-21.8)	53.3	46.6	0.1
Altitude (m)	T	240 (167-315)	80.2	19.8	0.0
Entrenchment (%)	T	20 (15-25)	35.4	64.6	0.0
Height increment at flood (m)	T	0.5 (0.4-0.7)	42.5	38.9	18.7
Stream gradient (°)	T	2.1 (0.6-3.3)	88.2	11.8	0.0
Stream order	T	3 (3-4)	66.0	34.0	0.0
Terrace width[a] (m)	T	105 (78-175)	29.6	59.4	11.0
Watershed area (km^2)	T	70.1 (25.5-155.9)	60.9	39.1	0.0
Width increment at flood[a] (m)	T	2 (1.5-4.0)	7.9	54.8	37.3
Mean temperature (°C)	I	10.5 (9.0-12.0)	51.0	49.0	0.0

Table 1 (continued and concluded).

Stream slope (°)	I	1.0 (0.6-1.3)	26.0	74.0	0.0
Canopy opening (°)	I	95 (76-114)	19.6	57.6	22.8
Cover index	I	2 (1-3)	30.0	43.7	26.3
Mean current velocity (cm s^{-1})	I	36.1 (22.6-50.1)	12.6	48.0	39.4
Mean depth (cm)	I	23.4 (17.8-30.9)	18.0	44.5	37.4
Mean substratum size index	I	5.4 (4.9-5.9)	17.6	52.4	30.0
Mean wetted width (m)	I	9.6 (6.0-14.1)	63.4	30.5	6.1
Pools (number)	I	0 (0-0)	13.3	19.4	67.3
Units of large woody debris (number)	I	0 (0-2)	23.6	28.7	47.7
Vegetation abundance index	I	1 (1-2)	11.9	67.3	20.7

[a] Sum of measures from right and left margins

Table 2. Decomposition of the total variation and the explained variation in fish assemblage structure among streams (stream scale); among reaches, within streams (reach scale); and among sections, within reaches, within streams (section scale). See Methods: *Ordination analyses and hierarchical decomposition of variation* for explanation of model notation

Source of variation	Model accounting for the variation component	Numerical label in Figure 2
A) Decomposition of the total variation		
All scales combined	[SECTION]	1
Stream	[STREAM]	2
Reach	[REACH] – [STREAM]	3
Section	[SECTION] – [REACH]	4
B) Decomposition of the explained variation		
All scales combined	[E]	5
Stream	[E] - [E | STREAM]	6
Reach	[E | STREAM] – [E | REACH]	7
Section	[E | REACH]	8

Table 3. Standardized canonical coefficients for environmental variables (with associated *t*-values in parentheses) in RDA or pRDA based on variable selection at the within-basin, within-streams, and within-reaches scales. The total variation explained by environmental variables (sum of all canonical eigenvalues), $[E_B]$, $[E_S \mid \text{STREAM}]$, and $[E_R \mid \text{REACH}]$, is given for each analysis. For all analyses, the Monte Carlo probability for significance of the sum of eigenvalues is ≤ 0.001. Eigenvalues and Monte Carlo probabilities for individual axes are reported also

Environmental variable	Scale of variable selection					
	Within basin ($[E_B] = 0.391$)		Within streams ($[E_S \mid \text{STREAM}] = 0.094$)		Within reaches ($[E_R \mid \text{REACH}] = 0.010$)	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
	Standardized canonical coefficients					
Accessibility index	-0.243 *(-11.3)*	-0.176 *(-7.3)*	-0.045 *(-1.5)*	-0.145 *(-4.9)*		
Mean wetted width	-0.177 *(-5.0)*	-0.034 *(-0.6)*				
Distance to mainstem	0.012 *(0.6)*	-0.228 *(-10.2)*	0.157 *(4.7)*	0.074 *(2.3)*		
Stream order	0.073 *(3.0)*	-0.320 *(-12.0)*				
Sub-basin area	-0.006 *(-0.2)*	0.356 *(8.4)*				

Table 3 (continued and concluded).

Mean current velocity	-0.085	0.044	-0.141	0.099	-0.101	0.024
	(-4.5)	*(2.1)*	*(-6.9)*	*(5.0)*	*(-4.6)*	*(1.2)*
Terrace width	-0.185	-0.058	-0.119	-0.004		
	(-8.5)	*(-2.4)*	*(-5.2)*	*(-0.2)*		
Large woody debris	0.051	-0.066	0.128	-0.035	0.060	-0.039
	(2.6)	*(-3.0)*	*(6.2)*	*(-1.9)*	*(3.1)*	*(-2.2)*
Entrenchment	-0.107	-0.067				
	(-5.2)	*(-2.9)*				
Mean substratum size	-0.037	-0.034				
	(-1.8)	*(-1.5)*				
Height increment at flood	-0.072	-0.010	-0.109	0.035		
	(-3.7)	*(0.4)*	*(-4.4)*	*(1.5)*		
Mean depth			0.008	0.120	0.081	0.060
			(0.4)	*(6.1)*	*(3.6)*	*(2.9)*
	Eigenvalue for individual axes					
	0.207	0.126	0.060	0.029	0.008	0.002
	Monte Carlo probability for individual axes					
	0.001	0.001	0.001	0.001	0.001	0.028

Table 4. Independent contributions of individual environmental variables to explained variation in fish assemblage structure at three spatial scales. Empty cells indicate that a variable had no significant influence on assemblage structure at a given scale. The selected environmental variables collectively explained 39.6% of the total variation at the within-basin scale (E_B), 17.7% at the within-streams scale (E_S), and 5.6% at the within-reaches scale (E_R) (see Fig. 3). Significant positive ($^{+}$) and negative ($^{-}$) associations of each environmental variable with Atlantic salmon (A), brook trout (B), and slimy sculpin (S) are reported also

Spatial extent	Environmental variable	Contribution of variable and associations with fish species, by scale								
		Within basin			Within streams			Within reaches		
		Expl. var.	% of tot. var.	Species assoc.	Expl. var.	% of tot. var.	Species assoc.	Expl. var.	% of tot. var.	Species assoc.
Accessibility	Accessibility index	0.118	11.8	$A^{+}S^{+}$	0.026	4.9	$A^{+}S^{+}$			
Accessibility	Distance to mainstem	0.047	4.7	$A^{-}B^{+}S^{+}$	0.025	4.7	$A^{-}B^{+}S^{-}$			
Landscape	Sub-basin area	0.102	10.2	$A^{+}B^{-}S^{-}$						
Landscape	Terrace width	0.065	6.5	$A^{+}S^{+}$	0.011	2.1	$A^{+}B^{-}S^{+}$			
Landscape	Stream order	0.042	4.2	$A^{-}B^{+}S^{+}$						
Landscape	Entrenchment	0.018	1.8	$A^{+}S^{+}$						

Table 4 (continued and concluded).

Landscape	Height increment at flood	0.011	1.1	A^+S^+	0.005	0.9	B^-			
Instream local	Mean wetted width	0.114	11.4	A^+S^+						
Instream local	Large woody debris	0.042	4.2	A^-B^+	0.014	2.6	B^+	0.002	1.1	B^+
Instream local	Mean current velocity	0.039	3.9	A^+B^-	0.026	4.9	A^-B^-	0.005	2.7	B^-S^+
Instream local	Mean substratum size	0.008	0.8	S^+						
Instream local	Mean depth				0.012	2.3	A^-S^-	0.004	2.2	S^-

Figure captions

Figure 1. Location of the 120 sampling sites distributed among 22 tributary streams on the Cascapedia River basin, Gaspésie, Québec.

Figure 2. Conceptual framework for hierarchical decomposition of variation. a) Variation in assemblage structure within a given level in the hierarchy includes that at all levels below it: within the river basin (i), the total variation (1) includes variation among streams (stream scale, 2); among reaches, within streams (reach scale, 3); and among sections, within reaches and streams (section scale, 4). Successive removal of variation components by use of covariables in pRDA leaves only within-stream (ii) or within-section (iii) variation. b) Partitioning of the total variation (1-4) and the explained variation (5-8) into stream, reach, and section scales.

Figure 3. Ordination diagrams for RDA or pRDA based on variable selection at three spatial scales: a) within basin ($[E_B]$), b) within streams ($[E_S \mid \text{STREAM}]$), and c) within sections ($[E_R \mid \text{REACH}]$). Left: biplots of species and environmental variables; right: unlabeled triplots of species, environmental variables, and stream sections (circles). Arrow origins coincide with mean values of the transformed variables.

Figure 4. Hierarchical decomposition of the total variation and the explained variation in assemblage structure for RDA or pRDA based on variable selection at three spatial scales: a) within basin, b) within streams, and c) within sections. The total explained variation is $[E_B]$ in a), $[E_S \mid \text{STREAM}]$ in b), and $[E_R \mid \text{REACH}]$ in c). Rectangle areas are proportional to the amount of variation represented. Numbers for the stream-, reach-, and section-scale variation are percentages relative to the total variation for each analysis, with corresponding eigenvalues in parentheses. Values for explained variation (in italics) are percentages relative to the explained variation for each

analysis, with corresponding eigenvalues in parentheses. Eigenvalues are scaled so that the total ("raw") variation equals one.

Figure 5. Decomposition of explained variation in assemblage structure among stream, reach, and section scales following the approach of Cushman and McGarigal (2002). Variance components are given as percentages of total variation in assemblage structure. Shaded components are exclusive to each scale; white components are shared among scales.

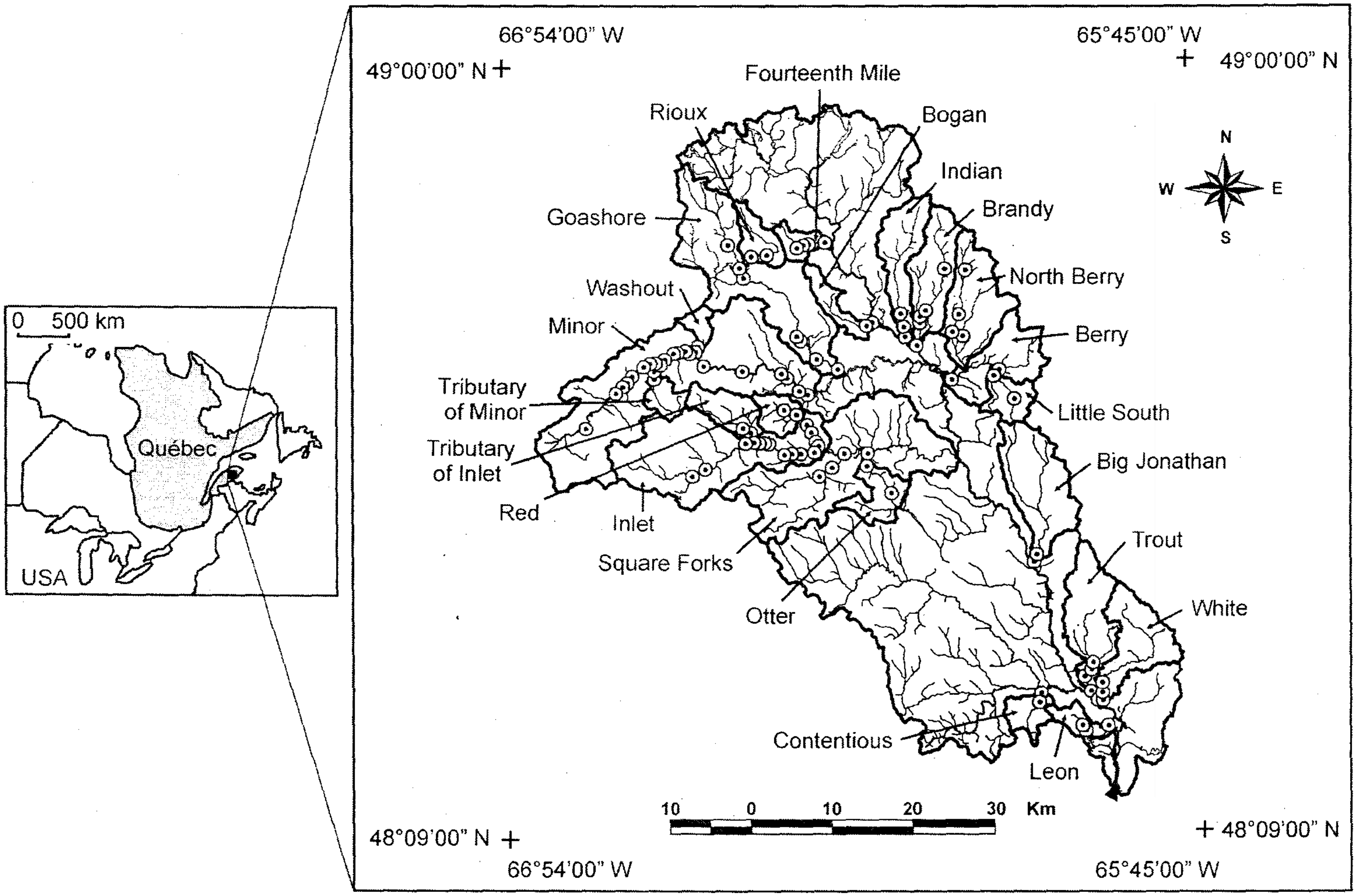
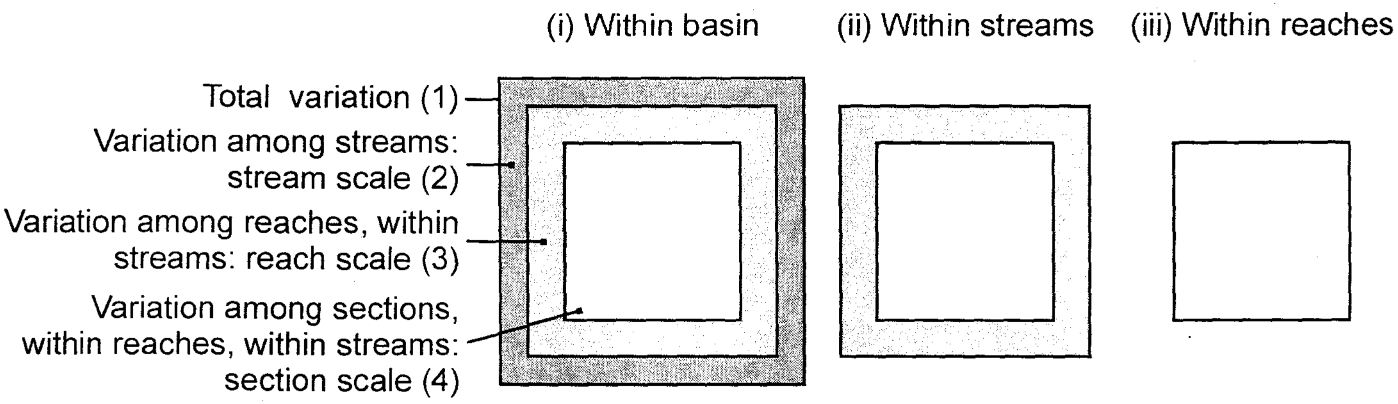


Figure 1. Deschênes and Rodríguez

a) Nested structure of variation at different scales



b) Partitioning of total and explained variation among scales

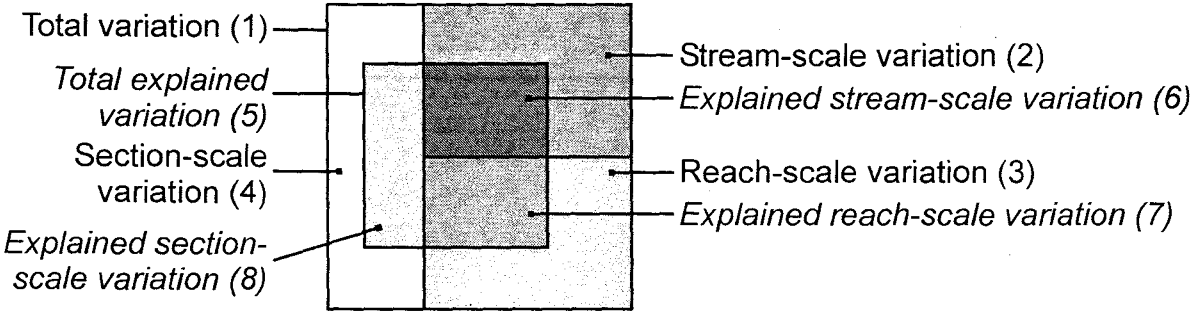


Figure 2. Deschênes and Rodríguez

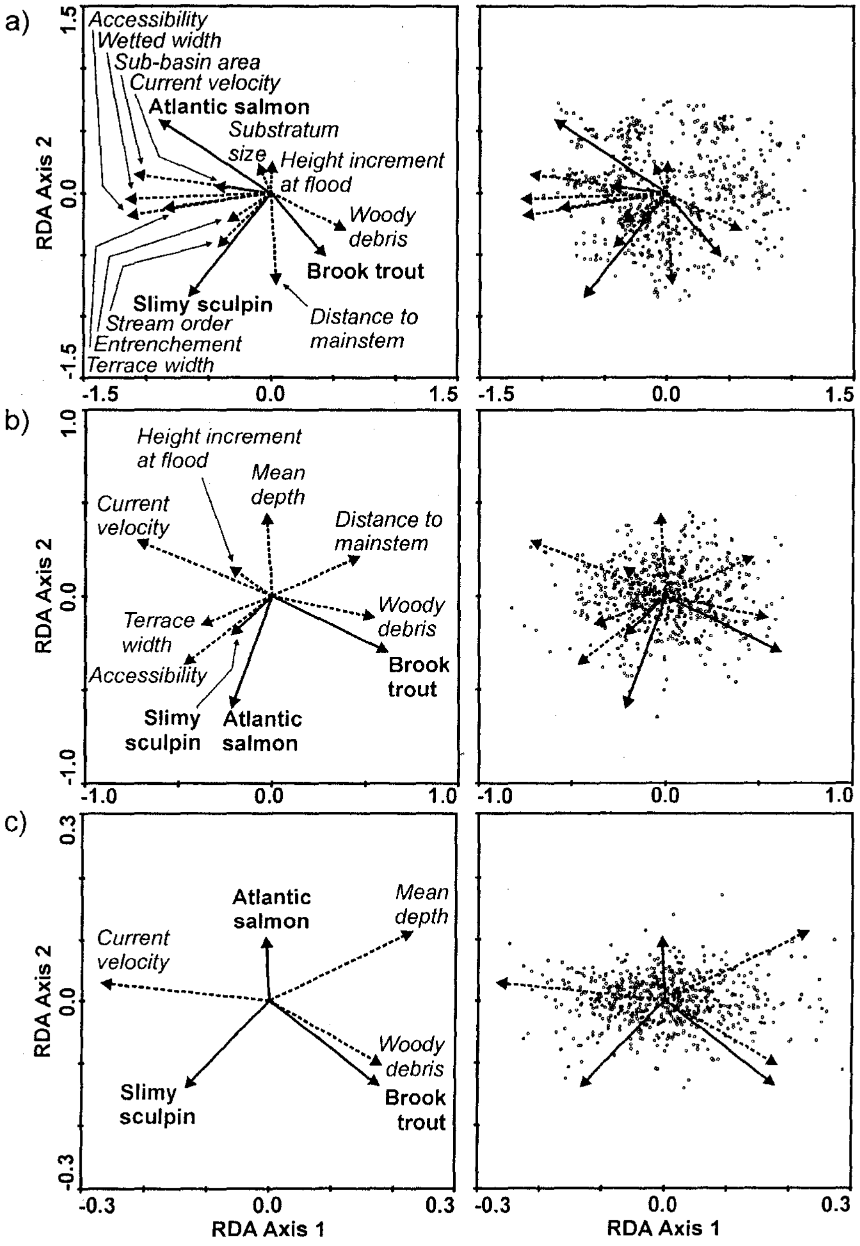
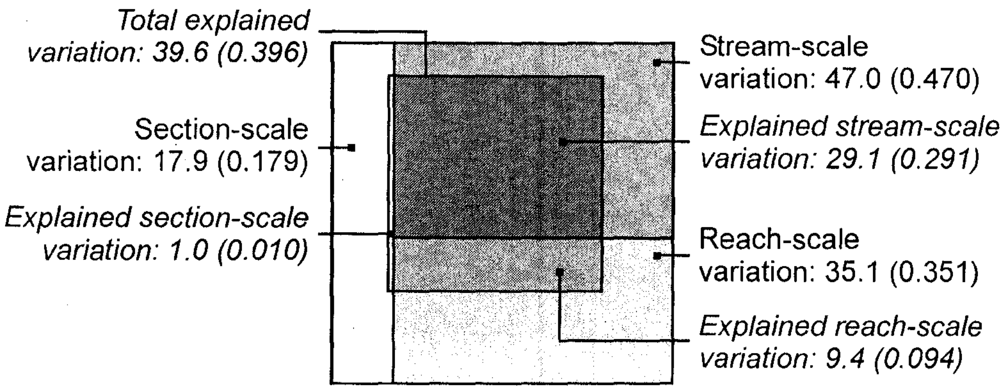
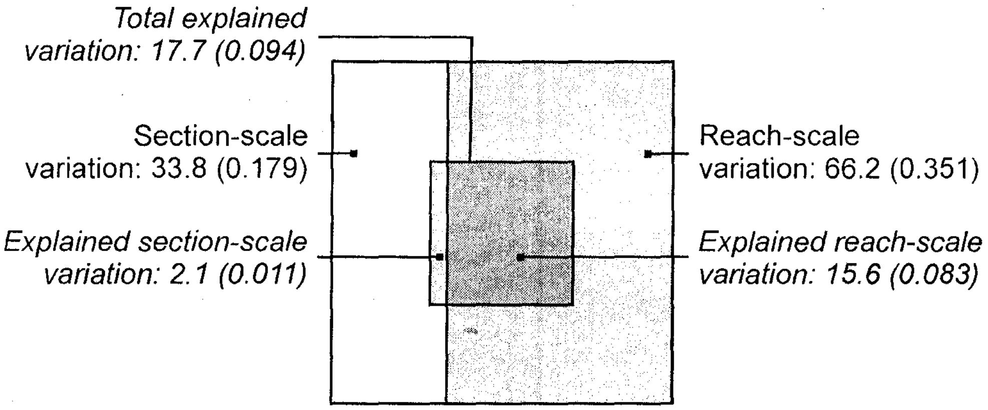


Figure 3. Deschênes and Rodríguez

a) Variable selection within basin



b) Variable selection within streams



c) Variable selection within reaches

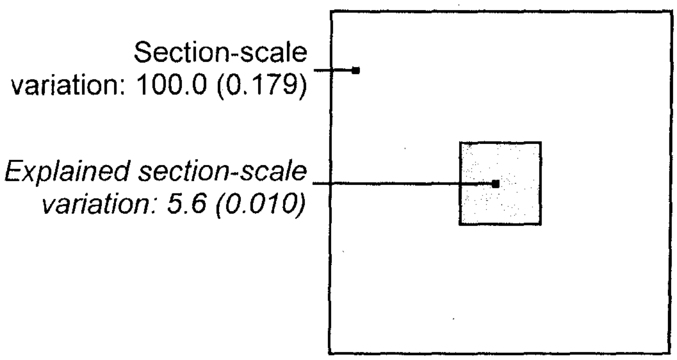


Figure 4. Deschênes and Rodríguez

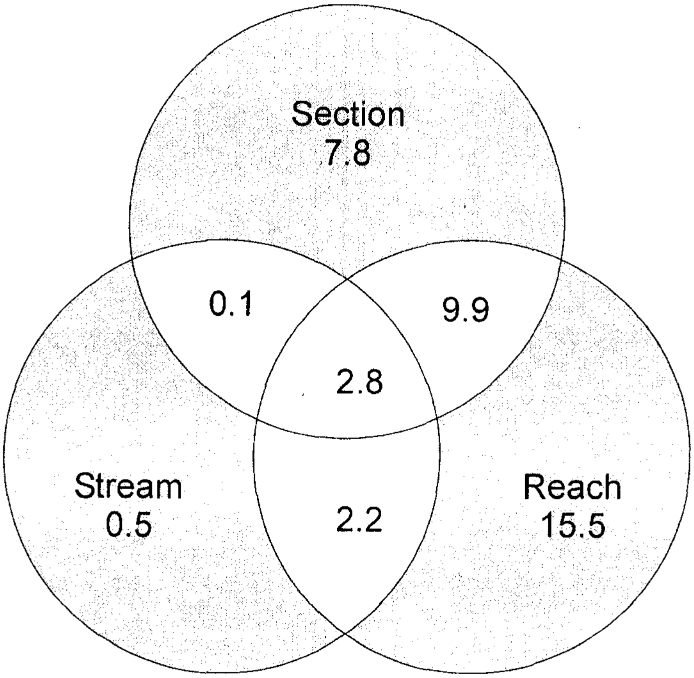
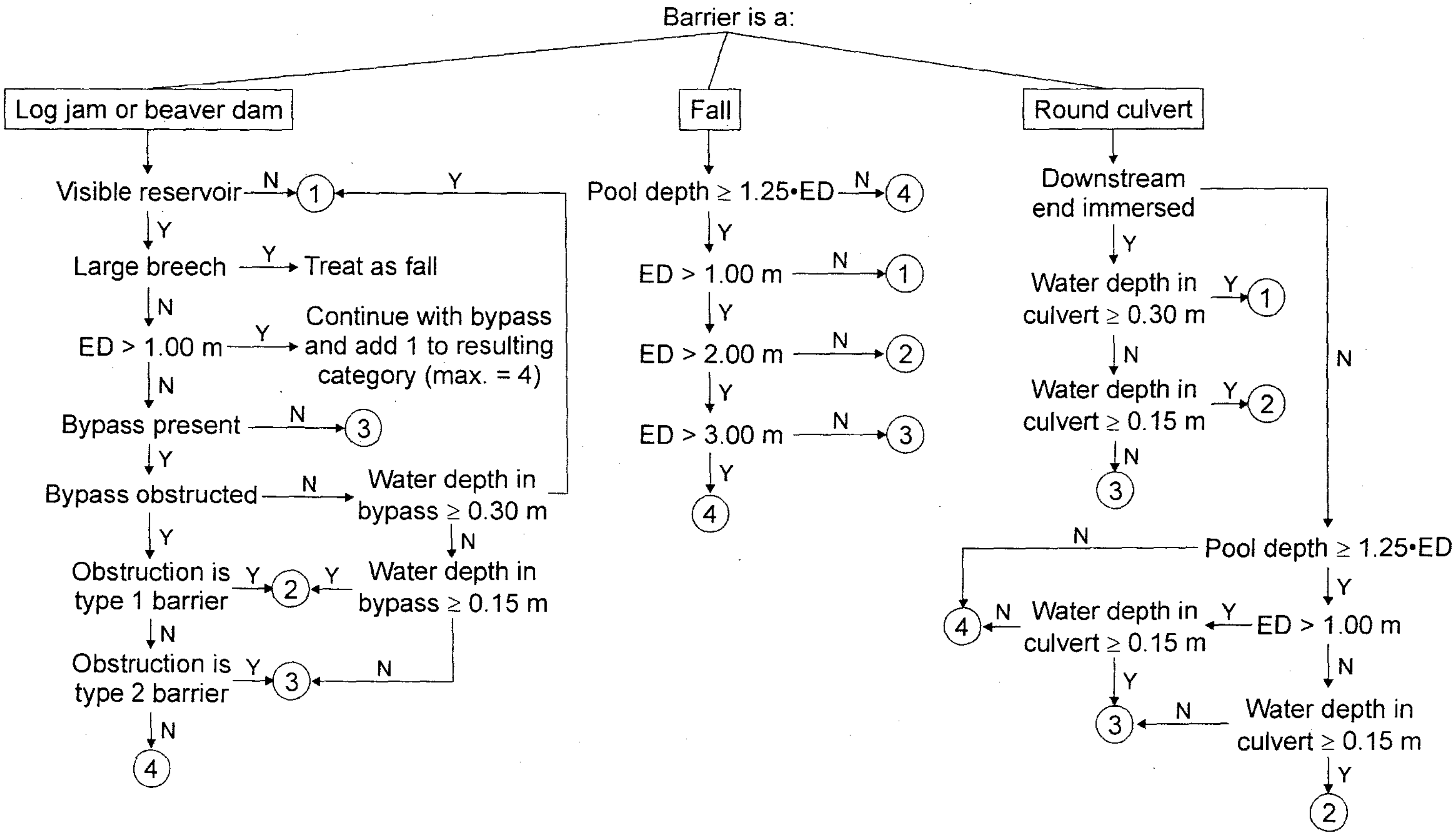


Figure 5. Deschênes and Rodríguez.



Appendix 1. Decision tree used to classify the effectiveness (circled values) of three types of barrier (rectangles). Barriers spanning less than 75% of stream width are not considered barriers. Each step in a fall with multiple steps is considered as an independent barrier. Elevation difference (ED) denotes the difference between water levels immediately upstream and downstream of a barrier. Adapted from Bjorn and Reiser (1991) and Furniss et al. (1991).

CHAPITRE III

HIERARCHICAL ANALYSIS OF RELATIONSHIPS BETWEEN BROOK TROUT DENSITY AND STREAM HABITAT FEATURES[2]

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Abstract: We used hierarchical linear regression to examine relationships between brook trout density and habitat features nested at three levels: sections within reaches, reaches within streams, and streams within a basin. Brook trout density and environmental variables were quantified at 600 stream sections distributed among 120 reaches and 22 streams in the Cascapedia River basin, Quebec. Decomposition of variance showed that variation in density among streams was small relative to that among sections or reaches, and not statistically significant. Density was influenced by habitat variables at both the section (current velocity, woody debris, cover) and reach (sub-basin area, height increment at flood, valley width) levels. A cross-level interaction between current velocity and sub-basin area pointed to a "contextual" effect: density showed stronger decline with current velocity in larger sub-basins than in smaller sub-basins. This result suggests that there was no single "best scale" for examining fish-environment relationships. Accounting for contextual effects by use of hierarchical models can enhance our understanding of how habitat features influence fish densities at multiple spatial scales.

Résumé : La régression linéaire hiérarchique nous a permis d'examiner les relations entre la densité d'ombles de fontaine (*Salvelinus fontinalis*) et les caractéristiques environnementales emboîtées à trois niveaux hiérarchiques : les sections à l'intérieur des tronçons, les tronçons à l'intérieur des tributaires et les tributaires à l'intérieur d'un bassin. Nous avons échantillonné les poissons et les variables environnementales dans 600 sections réparties sur 120 tronçons et 22 tributaires de la rivière Cascapédia, Québec. La décomposition de la variance montrait que la variation de la densité entre tributaires n'était pas significative et était plus faible que celle entre sections ou entre tronçons. La densité était influencée par des caractéristiques environnementales aux niveaux des sections (vitesse du courant, débris ligneux, couvert) et des tronçons (superficie du sous-bassin, augmentation de la hauteur à la crue, largeur de la vallée). L'interaction entre la vitesse du courant et la superficie du sous-bassin suggérait l'existence d'un effet contextuel : l'influence négative de la vitesse du courant sur la densité était plus forte dans les grands sous-bassins que dans les petits sous-bassins. Les résultats indiquent qu'il n'y avait pas d'échelle « optimale » pour l'analyse des rélations poissons-environnement. L'examen des effets contextuels à l'aide des modèles hiérarchiques peut améliorer notre compréhension des relations poissons-environnement à plusieurs échelles spatiales.

Keywords: contextual effects, cross-level interaction, hierarchical linear models, multiple spatial scales, nested habitat features

Introduction

Ecological data often have clustered or nested structure that arises from observations made on sampling units grouped at different hierarchical levels. Because sampling levels can be chosen to correspond to spatial scales of analysis, nested sampling designs can be useful in examining fish-habitat relationships at multiple spatial scales. The hierarchical structure in data from such designs can be exploited to address questions about the scale-dependence of patterns and responses, such as: do environmental features influence fish distribution similarly across channel units nested within reaches, reaches nested within streams, or streams nested within a basin? (Dunham and Vinyard 1997; Inoue et al. 1997; Watson and Hillman 1997).

By explicitly considering hierarchical structure, one can also examine potential "cross-level" interactions between environmental variables characterising units at different spatial scales. Such interactions may result in contextual effects, in which the influence of a local environmental variable is contingent upon the level of another, larger-scale, variable. For example, in Japanese streams, the influence of cover on the abundance of masu salmon (*Oncorhyncus masou*) within a small-scale channel unit (pool, riffle, glide, cascade, or rapid) differs across large-scale geomorphic channel types comprising groups of 60 to 70 channel units (Inoue et al. 1997). At the scale of a pool-riffle sequence, salmon density is positively related to the abundance of cover, but at the scale of stream reaches (10 pool-riffle sequences) this relationship only holds when cover is rare (Inoue et al. 1997).

Patterns and processes detected at local spatial scales do not necessarily apply also at larger scales (Inoue et al. 1997; Folt et al. 1998; Schneider 2001). Examples of apparent inconsistencies in patterns and processes across scales include differences in habitat preference of fish species across river sections or reaches (Poizat and Pont 1996), fish response to environmental features across basins (Watson and Hillman 1997; Dunham and Vinyard 1997), and longitudinal distribution of mesohabitats across hydro-ecoregions (Cohen et al. 1998). These examples hint at potential outcomes of cross-level interactions and suggest that the above inconsistencies may be resolved by explicitly considering such interactions.

Nested sampling designs can yield useful insights into processes operating at multiple spatial scales, yet few studies in stream ecology seem to have fully exploited this potential. One technical obstacle has been that, in nested samples, units within a group usually tend to be more similar to other units within their group than to units in other groups. Thus, individual observations are not entirely independent as required by conventional regression models.

This potential drawback is addressed by hierarchical regression modelling, a statistical approach that copes effectively with nested data structures and allows for inclusion of effects operating at several levels, as well as cross-level interactions, in a single model (Hox 2002; Goldstein 2003). In this study, we use hierarchical linear (HL) regression to examine the relationships between brook trout (*Salvelinus fontinalis*) density and environmental features nested at three spatial scales: across sections within reaches and streams, across reaches within streams, and across streams within a basin.

Methods

Fish sampling and environmental measurements

Brook trout density and environmental variables were quantified at 600 sections distributed among 120 sampling sites and 22 tributary streams in the Cascapedia River basin (3179 km^2), Québec, Canada (Fig. 1). Sites were selected to maximize spatial coverage of the basin subject to accessibility constraints. Sites were visited in random sequence during low flow from mid-June to late August in 2000 (24 sites), 2001 (48 sites), and 2002 (48 sites). At each site, samples were collected from a 75-m stream reach comprising five adjacent sections, each approximately 15 m in length. No attempt was made to position sampled reaches to coincide with habitat boundaries. The nested sampling design therefore spanned three spatial scales:

sections within reaches (maximum distance between sections ≈ 0.075 km), reaches within streams (maximum distance between reaches, averaged across streams ≈ 8 km), and streams within the basin (maximum distance between streams ≈ 82 km).

Sampled areas covered the entire stream width in completely wadable reaches and ranged five meters from one bank, chosen randomly, towards the opposite bank otherwise. Fish were sampled by single-pass electrofishing (Smith-Root D-15) in an upstream direction within open stream sections (Lobón-Cerviá and Utrilla 1993; Crozier and Kennedy 1994; Jones and Stockwell 1995). All captured fish were identified, measured, weighed, and returned to their point of capture. Brook trout density was calculated as total captures divided by section area (numbers•100^{-1}•m^{-2}). Because capture efficiency is not 100%, this measure underestimates true density but should be proportional to it if efficiency is comparable across sampling units, an assumption that seems tenable given that all sites were sampled under base flow conditions.

In all, 21 environmental variables were quantified at the section, reach, or stream scales (Table 1). For each section, water depth and substratum size (modified Wentworth scale) were measured at five equidistant points along each of four equidistant transects perpendicular to stream flow. Current velocity (pigmy-type meter, Scientific Instruments 1205) was measured at five equidistant points along the second transect from the downstream end. Wetted width was measured at each transect. Abundance of submerged vegetation (moss or macrophytes) and overall availability of structural cover (rocks, woody debris, undercut bank, and overhanging vegetation) were estimated visually and assigned ordinal values reflecting areal coverage (1: ≤ 5%; 2: 6-15%; 3: 16-45%; 4: > 45%). Overhead opening (angle between riparian canopy or hilltops blocking incident sunlight at the centre of the stream; Table 1) and slope over the stream reach were measured with a hand-held clinometer (Suunto MP-5). The increment in stream height and width at flood (from annual flood marks) were measured on site for each section and averaged by reach. Water temperature was measured at each section (hand-held thermometer, Barigo).

Entrenchment (mean gradient ≤ 100 m away from stream bank), valley width (distance between piedmonts on each side of the stream), stream order (Strahler scale), and altitude were obtained from 1:20 000 topographic maps, as were distances by waterway from each section to the Cascapedia River ("distance to mainstem"), and from the mouth of each stream to the mouth of the Cascapedia River ("distance to mouth") (planimeter, Calculated Industries 6125). Sub-basin surface area and stream gradient (mean slope from sampling reach to source) were obtained from 1:20 000 maps (Ministère des Ressources naturelles du Québec) by use of a geographic information system (ArcView 3.2). Units of large woody debris (> 10 cm diameter) and pools were counted within each section. Physical barriers potentially affecting upstream migration of fish along a tributary were assessed from field observations and topographic maps, and their effectiveness was coded as an integer value, B, ranging from 0 (no visible barrier) to 4 (insurmountable barrier) and reflecting the height, type (beaver dams, log jams, culverts, falls), and configuration of the barrier. An index of accessibility combining multiplicatively all potential barriers for each site was calculated as:

$$accessibility = \prod_{i=1}^{N} \left(1 - \frac{B_i}{4}\right),$$

where N is the number of visible barriers and B_i is the effectiveness of barrier i downstream from the site. Accessibility was assigned the value 1 in the absence of visible barriers. The index thus ranged from 0 to 1, taking a value of 0 if at least one barrier was insurmountable ($B_i = 4$).

Quantitative analyses

The relationships between brook trout density and habitat features nested at different hierarchical levels were examined by use of HL regression (program

MLwiN, version 2.0; Rasbash et al. 2004), a model known as linear mixed effects in the statistical literature and multilevel regression in the social sciences. The description that follows is largely drawn from Hox (2002) and Goldstein (2003). The HL model relates observations made on *i* units clustered within *j* groups to one or more predictor variables (X_{ij}). For a single predictor:

$$Y_{ij} = \beta_{0j} + \beta_{1j}X_{ij} + \varepsilon_{ij},$$

where β_{0j} is the intercept and β_{1j} is the group-specific slope for the predictor. Departure of observation *i* from the predicted regression line of group *j* is represented by the random term ε_{ij}, the level-one residuals. In contrast to ordinary least-squares (OLS) regression, HL regression assumes that groups are randomly sampled from a larger population of groups, and sampling units within groups need not be independent. Variation among groups in the intercept β_{0j} and slope β_{1j} is characterized as:

$$\beta_{0j} = \beta_0 + u_{0j}$$

$$\beta_{1j} = \beta_1 + u_{1j},$$

where the random effects u_{0j} and u_{1j} represent departures of the intercept and slope of group *j* from the fixed terms β_0 (overall mean intercept) and β_1 (overall mean slope). The random effects u_{0j} and u_{1j}, which represent level-two residuals, explicitly allow for the hierarchical structure of the data and constitute a fundamental difference between OLS and HL regressions. The terms u_{0j}, u_{1j}, and ε_{ij} are assumed to follow normal distributions with zero mean and variances to be estimated (σ^2_{u0}, σ^2_{u1}, and σ^2_{ε}). The random effects u_{0j} and u_{1j} are assumed to be independent from the level-one residuals ε_{ij}, but generally not from each other.

The intercepts and slopes of the HL regression are weighted averages of OLS estimates for each group and the overall regression estimate for all similar groups. As a result, residuals are shrunken back towards the overall mean. The amount of shrinkage depends on the reliability of the estimate for a group, which is determined by the number of units within the group and the difference between the estimate for the group and the overall mean. Therefore, less reliable estimates are shrunken closer to the mean.

Among-group variation in both intercept and slope can be accounted for by introducing level-two predictors (Z_j):

$$\beta_{0j} = \beta_0 + \beta_{01} Z_j + u_{0j}$$

$$\beta_{1j} = \beta_1 + \beta_{11} Z_j + u_{1j},$$

The full model, including fixed and random terms, is then:

$$Y_{ij} = \beta_0 + \beta_1 X_{ij} + \beta_{01} Z_j + \beta_{11} X_{ij} Z_j + u_{0j} + u_{1j} X_{ij} + \varepsilon_{ij},$$

where $X_{ij}Z_j$ is a cross-level interaction between level-one and level-two predictors. The regression model was produced by a forward selection procedure in which individual terms were selected according to the significance of changes in deviance between models (log-likelihood ratio tests; $\alpha = 0.05$). A stepwise sequence similar to that proposed by Hox (2002) was followed in building the final model. In the first step, the total variance in brook trout density was decomposed and apportioned among hierarchical levels by use of the classical model for variance components:

$$Y_{ijk} = \beta_0 + u_{0jk} + v_{0k} + \varepsilon_{ijk},$$

where

$$u_{0jk} \sim \mathcal{N}(0, \sigma^2_{u0}),\ v_{0k} \sim \mathcal{N}(0, \sigma^2_{v0}),\ \varepsilon_{ijk} \sim \mathcal{N}(0, \sigma^2_{\varepsilon}),$$

and the σ^2 terms represent variances at the stream (σ^2_{v0}), reach (σ^2_{u0}), and section (σ^2_{ε}) levels. To determine whether random intercepts were needed at the reach and stream levels, we examined whether brook trout density varied significantly at those levels, by use of one-sided tests for the corresponding variance terms (Snijders and Bosker 1999; Hox 2002). Because brook trout density did not vary significantly at the highest level, across streams (Table 2), only two-level models reflecting variation at the section and reach levels were considered in subsequent analyses. In the second step, section-level (level-one) predictors were tested one at a time, and the predictor accounting for the greatest change in deviance was added to the model if the change in deviance was significant. This procedure was repeated until no significant reduction in deviance could be attained by including any of the remaining potential predictors. In the third step, the slope coefficients of the selected predictors were tested for significant reach-level (level-two) variation to determine whether random slopes were required for those predictors. In the fourth step, reach-level predictors were tested similarly to the section-level predictors in step 2. In the fifth step, all first-order interaction terms between section- and reach-level predictors already in the model were tested and included in the model if significant.

To account for serial correlation potentially arising between first level residuals because of the proximity between sections within a reach, a first-order autoregressive (AR1) covariance structure with equal spatial intervals was included in the model:

$$\mathrm{cov}(\varepsilon_{ij}, \varepsilon_{i-s,j}) = \sigma^2_{\varepsilon}\, e^{-\alpha s},$$

where s is the standardized distance between two sections in the same reach and α is a decay coefficient for the spatial autocorrelation, which is given by $e^{-\alpha s}$ (Yang et al.

2001; Hox 2002; Goldstein 2003). The section-level R^2 was obtained by squaring the Pearson correlation between observed values and values predicted by the full model. Prior to analysis, brook trout density was transformed as $\ln(X + 1)$; environmental variables were transformed by use of logarithmic or power functions when necessary to reduce the influence of extreme points and better fit statistical assumptions of linearity, normality, and homoscedasticity. All variables were standardized to their grand mean to avoid non-essential colinearity between predictors and facilitate the interpretation of the intercept (Hox 2002).

Results

Brook trout were found in 89% of sections, 98% of reaches, and all streams. The decomposition of variance showed that variation in brook trout density among streams was small (5.2% of total variance) in relation to that among sections (35.3%) or reaches (59.5%), and not statistically significant (Table 2). The 21 potential predictors were not strongly inter-correlated: only 8 of 210 pairwise correlations were > 0.5 in absolute value and all of the tolerances were ≥ 0.06. The final regression model included three section-level predictors (current velocity, units of woody debris, and cover index), three reach-level predictors (sub-basin area, valley width, and height increment at flood), and a cross-level interaction between current velocity and sub-basin area. Although the spatial autocorrelation term was not statistically significant ($p = 0.075$), it was nevertheless kept in the model to adjust for the spatial relationship between sections. The tolerance for predictor variables in final models was always ≥ 0.75, indicating only mild colinearity among the predictors. Graphical analyses showed no apparent deviations from the assumptions of normality, homogeneity of variance (residual plots for the section and reach levels; Fig. 2), and linearity (scatterplot of observed vs. predicted values; Fig. 3).

Brook trout density was positively related to woody debris and cover, and negatively related to height increment at flood, valley width, and current velocity, but the relationship between brook trout density and current velocity varied markedly across reaches, as shown by the variation in the slope coefficients for current velocity (Fig. 4). This variation was related systematically to sub-basin area, as revealed by the significant cross-level interaction between current velocity and sub-basin area (Table 3). A graphical display of the cross-level interaction showed stronger decline with current velocity in larger sub-basins than in smaller sub-basins (Fig. 5).

Discussion

In the Cascapedia River basin, brook trout density did not vary significantly among streams, but varied substantially both among sections within reaches and among reaches. Although multiscale studies often examine the proportion of variation explained by environmental features at different spatial scales (Milner et al. 1995; Watson and Hillman 1997) only a few of these studies have specifically quantified variation in fish abundance at each scale (e.g., Dunham and Vinyard 1997). Yet, the decomposition of variation in fish abundance can identify those scales at which populations vary most and can therefore guide the choice of environmental features and measurement grain needed in an analysis. In the present study, the results from the decomposition of variation motivated the use of a simplified hierarchical model focused on variation only at the section and reach scales.

The relationship between brook trout density and current velocity varied across reaches as a function of sub-basin area. Brook trout density was weakly related to current velocity in reaches within smaller sub-basins, but declined markedly with current velocity in reaches within larger sub-basins. This contextual effect may be linked to stream size, because sub-basin area was positively related to stream width (Spearman rank correlation: $r_s = 0.85$) and stream order ($r_s = 0.63$), two measures of stream size. Velocity refugia are used by stream salmonids to maximise energy intake and minimise swimming costs (Grant and Noakes 1987; Fausch 1993; McLaughlin and Noakes 1998). Instream structures that create velocity refugia, such as boulders, provide energetically suitable locations for salmonids, resulting in greater population density (Fausch and Northcote 1992; McLaughlin and Noakes 1998). Structures such as boulders and woody debris tend to be less abundant in larger streams (Benke and Wallace 1990; Jowett et al. 1998; Wing and Skaugset 2002). Because of their greater depth, larger streams also have lower relative roughness, and thus smoother flow near the stream bed, than smaller streams (Leopold et al. 1964). Water velocity may therefore have had greater influence on brook trout density in larger streams as a result of the lower availability of velocity refugia in those streams.

Within reaches, brook trout density was greater in sections with more woody debris and cover. Large woody debris and cover are thought to enhance the habitat suitability of streams for salmonids by providing low-velocity refugia during floods, profitable feeding positions of low velocity next to high-velocity patches, and visual isolation that reduces interference competition and risk of predation (McMahon and Hartman 1989; Fausch 1993; Inoue et al. 1997). Woody debris acts as additional substratum for macroinvertebrates, usually resulting in higher food abundance for fish (Harmon et al. 1986; Dolloff 1986). Large woody debris is also associated with the development of pools (Andrus et al. 1988; Carlson et al. 1990), a preferred habitat for brook trout (Gibson et al. 1993; Rodríguez 1995; Bélanger and Rodríguez 2002).

Brook trout density was negatively related to height increment at flood and valley width. Negative effects of high flows on stream fish abundance are well documented (Freeman et al. 2001; Roghair et al. 2002; Lobón-Cerviá and Rincón 2004). High flows may increase egg and yearling mortality or displace juvenile and older fish (Erman et al. 1988; McMahon and Hartman 1989; Carline and McCullough 2003). Brook trout displaced experimentally in a natural stream tended to settle in preferred habitats away from their home site (Bélanger and Rodríguez 2001); in the absence of effective homing, population density may remain low for extended periods in stream reaches where brook trout are displaced by high flow events. The negative relation between brook trout density and valley width may be mediated by geomorphic processes related to longitudinal variation. Valley width was related negatively to entrenchment (r_s = -0.57) and stream gradient (r_s = -0.38). Other studies have found greater fish density (Rabeni and Sowa 1996) or better spawning substratum (Coulombe-Pontbriand and Lapointe 2004) in narrower, more entrenched, upstream segments than in wider downstream segments, which have shallower slopes, a greater proportion of gravel and sand, and a smaller proportion of cobbles and boulder in the streambed (Rabeni and Sowa 1996; Isaak and Hubert 2000). This result suggests that large-scale fluvial dynamics contributed to determining brook trout density at the reach scale.

Hierarchical models account for the intra-group correlation inherent to nested sampling designs and can therefore properly assess the statistical significance of potential predictors, hence improving the reliability of these models relative to conventional approaches such as multiple regression based on ordinary least squares. In many studies, the problem of intra-group correlation has been dealt with by aggregating observations at the higher levels and working with group means, examining small-scale (lower-level) patterns separately for each higher-level group, or a combination of both (e.g., Inoue et al. 1997; Watson and Hillman 1997; Angermeier and Winston 1999). However, these approaches usually leave among-group differences in small-scale patterns unexamined, and can also lead to loss of information and statistical power (Hox 2002; Goldstein 2003).

Although hierarchical models are often used in aquatic ecology to account for spatial or temporal correlation between sampling units, their potential to enhance our understanding of patterns of species distribution at multiple spatial scales still remains largely untapped. The relationships between brook trout density and individual environmental features in this study are broadly in agreement with findings from previous studies; however, the hierarchical modelling approach additionally allowed for detection and proper statistical treatment of the effect of reach-level variables and the contextual effect of section-level variables on brook trout density. By accounting for the nested sampling design and simultaneously using the information available at all spatial scales, the hierarchical model allowed us to detect a cross-level interaction between environmental predictors at the section and reach levels which by definition would not have been detectable had we aggregated the data by averaging observations from individual sections. The presence of a cross-level interaction illustrates that patterns uncovered at smaller scales can not always be extrapolated to larger scales, and supports the notion that there is no single "best scale" at which to examine the relationships between fish distribution or abundance and environmental features (Schneider 2001).

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Table 1. Hierarchical level, median, and interquartile range for 21 environmental variables describing fish habitat in 600 sections distributed among 120 reaches and 22 streams of the Cascapedia River basin. The hierarchical level indicates the scale at which measurements varied among sampling units.

Variable name	Hierarchical level	Median	Interquartile range
Overhead opening (°)	Section	95.7	75.4-113.5
Cover index	Section	2.4	1.4-3.0
Mean depth (cm)	Section	24.6	18.8-29.4
Mean current velocity (cm•s^{-1})	Section	34.9	26.0-48.9
Mean substratum size index	Section	5.3	4.9-5.8
Mean wetted width (m)	Section	9.3	6.3-14.1
Large woody debris (number)	Section	3.5	1.0-8.5
Vegetation abundance index	Section	1.0	1.0-1.8
Accessibility index	Reach	0.8	0.3-1.0
Altitude (m)	Reach	240.0	167.5-315.0
Distance to mainstem (km)	Reach	9.1	2.5-21.7
Entrenchment (%)	Reach	10.0	5.0-15.0
Height increment at flood (m)	Reach	0.5	0.4-0.7
Mean temperature (°C)	Reach	10.5	9.0-12.0
Stream slope (°)	Reach	1.0	0.6-1.3
Stream gradient (°)	Reach	2.1	0.6-3.3
Stream order	Reach	3.0	3.0-4.0
Valley width (m)	Reach	180.0	95-350

Table 1 (continued and concluded).

Sub-basin area (km^2)	Reach	70.1	25.5-151.0
Width increment at flood[a] (m)	Reach	2.6	1.9-4.0
Distance to mouth (km)	Stream	75.5	52.8-82.4

[a] Sum of measures from right and left margins

Table 2. Random-effects decomposition of the total variance in brook trout density, by hierarchical level: sections (σ^2_ε), reaches (σ^2_{u0}), and streams (σ^2_{v0}). Variance among sections corresponds to the error term and has no associated *p* value.

Hierarchical level	Variance term	Estimate (s.e.)	Total variance (%)	*p*
Sections	σ^2_ε	0.349 (0.023)	34.9	
Reaches	σ^2_{u0}	0.597 (0.096)	59.7	< 0.001
Streams	σ^2_{v0}	0.051 (0.060)	5.1	0.102

Table 3. Coefficient estimates, standard errors, and p values for the fixed and random components of the hierarchical linear model. The coefficients for the intercept and current velocity have a fixed and a random part, i.e., $\beta_{0j} = \beta_0 + u_{0j}$, $\beta_{1j} = \beta_1 + u_{1j}$, with $u_{0j} \sim \mathcal{N}(0, \sigma^2_{u0})$ and $u_{1j} \sim \mathcal{N}(0, \sigma^2_{u1})$. The covariance between u_{0j} and u_{1j} is σ_{u01}. The autocorrelation decay coefficient is α.

Model term	Estimate	Standard error	P
Predictor variable (*fixed coefficient*)			
Intercept (β_0)	0.018	0.063	
Current velocity (β_1)	-0.221	0.044	<0.001
Large woody debris (β_2)	0.160	0.034	<0.001
Cover index (β_3)	0.103	0.042	<0.001
Sub-basin area (β_4)	-0.164	0.069	0.008
Height increment at flood (β_5)	-0.226	0.070	<0.001
Valley width (β_6)	-0.129	0.068	0.003
Current velocity x sub-basin area (β_7)	-0.093	0.043	0.032
Random components			
σ^2_ε	0.325	0.046	
σ^2_{u0}	0.360	0.066	<0.001
σ^2_{u1}	0.054	0.026	0.034
σ_{u01}	-0.050	0.028	0.034
Decay coefficient for spatial autocorrelation			
α	2.378[a]	0.521	0.075

[a] Implies a spatial correlation of 0.186 between adjacent sections

Figure Captions

Figure 1. Location of the 120 sampling sites distributed among 22 tributary streams in the Cascapedia River basin, Québec.

Figure 2. Residual plots for section-level and reach-level residuals. Section-level residuals (a) are the differences between observed values and values predicted by reach-level regressions. Reach-level residuals refer to the regression parameters for current velocity. Reach-level residuals for the intercept (b) are the differences between the estimated intercepts for each reach and the overall mean intercept. Reach-level residuals for the slopes (c) are the differences between the estimated slope for each reach and the overall mean slope. Residuals are plotted against the standardized density predicted by the fixed-effects part of the model.

Figure 3. Scatterplot of observed vs. predicted densities of brook trout (*Salvelinus fontinalis*). Densities are standardized to zero mean and unit variance. Predicted values are from the full model including both fixed and random effects. One-to-one (solid) and regression (dashed) lines are shown also. The horizontal row of values at the bottom of the figure represents sections where no fish captured.

Figure 4. Plot of predicted densities of brook trout (*Salvelinus fontinalis*) vs. current velocity at each of the 120 reaches. Densities and current velocity are standardized to zero mean and unit variance. Predicted values are from the model including both fixed and random effects for the intercept and current velocity.

Figure 5. Contour plot illustrating the effect of the cross-level interaction between current velocity, a section-level predictor, and sub-basin area, a reach-level predictor, on density of brook trout (*Salvelinus fontinalis*). Contour lines represent density of brook trout (numbers•100^{-1}•m^{-2}) as predicted by the fixed-effects part of the HL

model. The circles represent observed combinations of current velocity (cm•s^{-1}) and sub-basin area (km^2) at individual sections; the dispersion of the circles reflects the joint variability in these two variables.

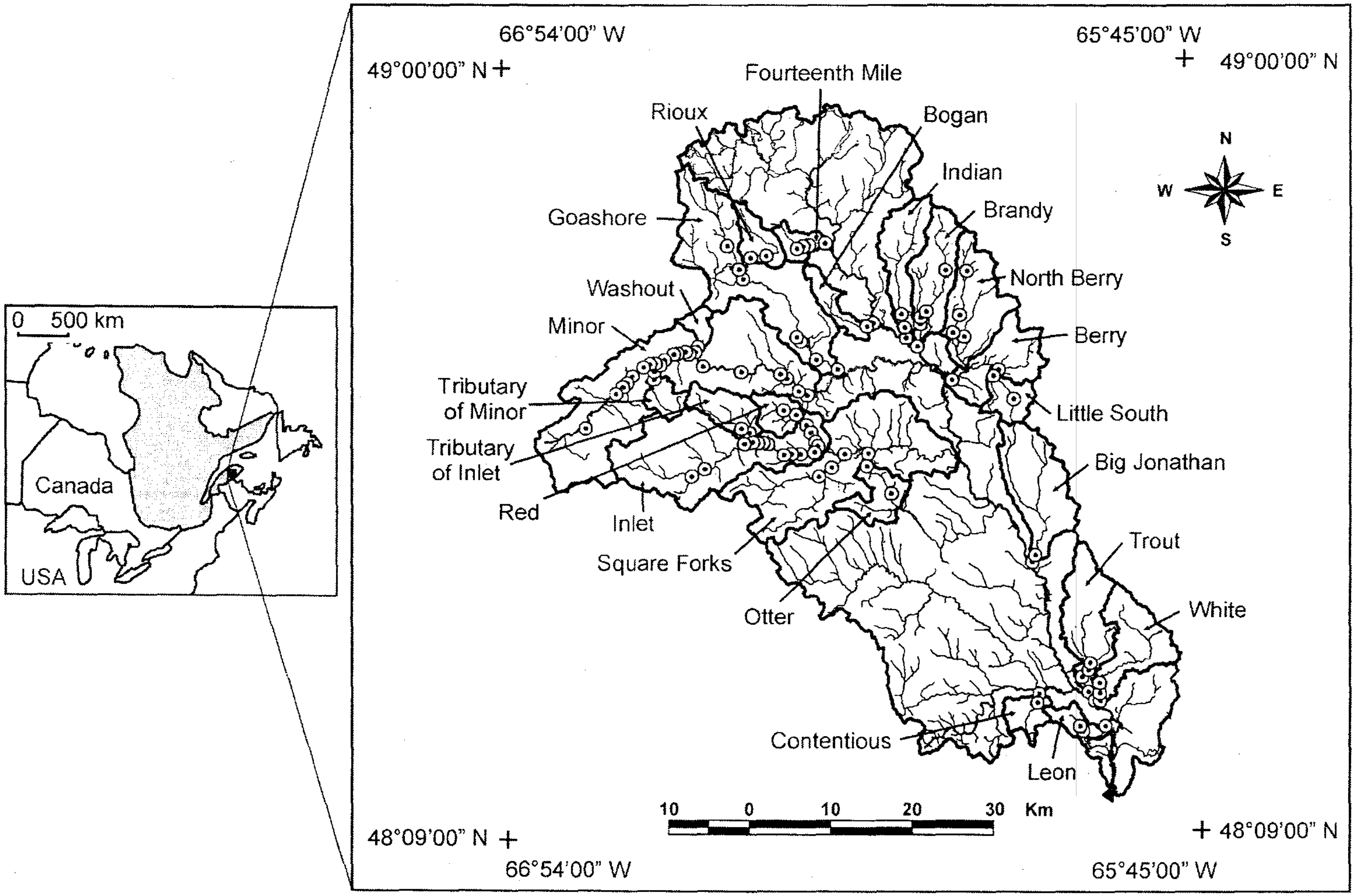

Figure 1. Deschênes and Rodríguez

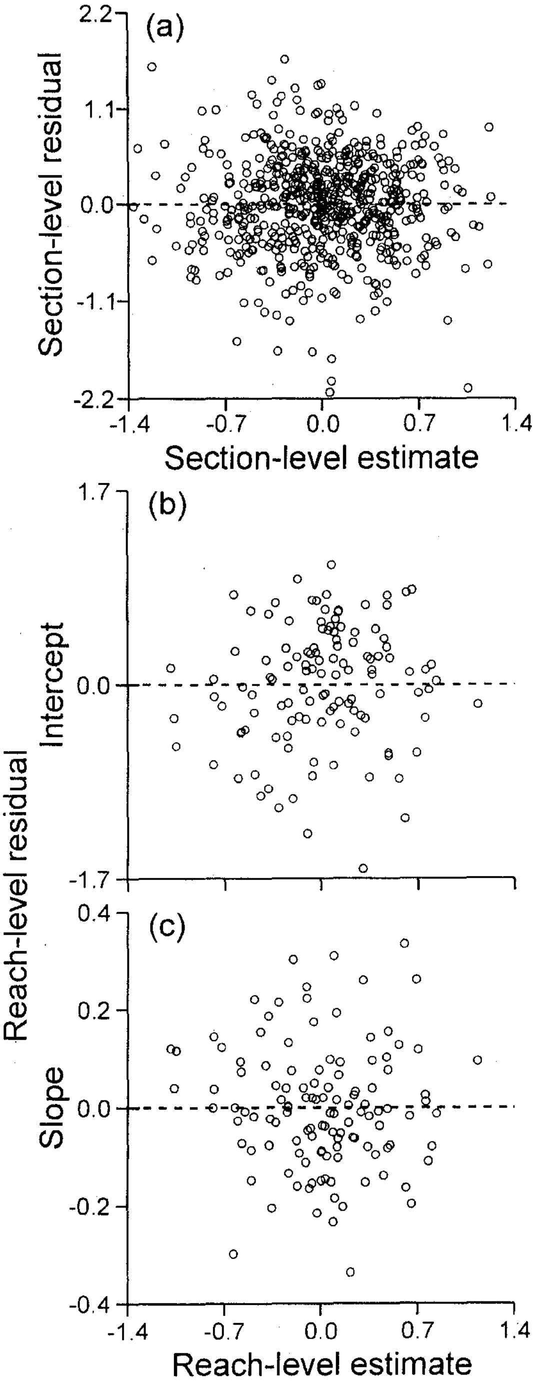

Figure 2. Deschênes and Rodríguez

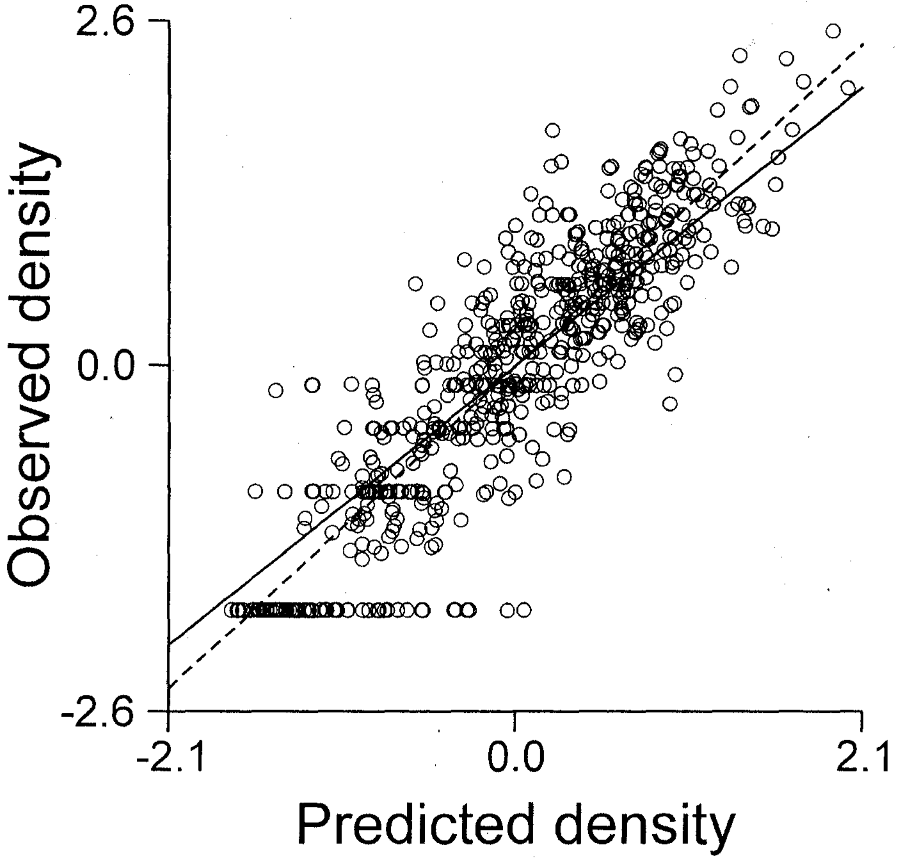

Figure 3. Deschênes and Rodríguez

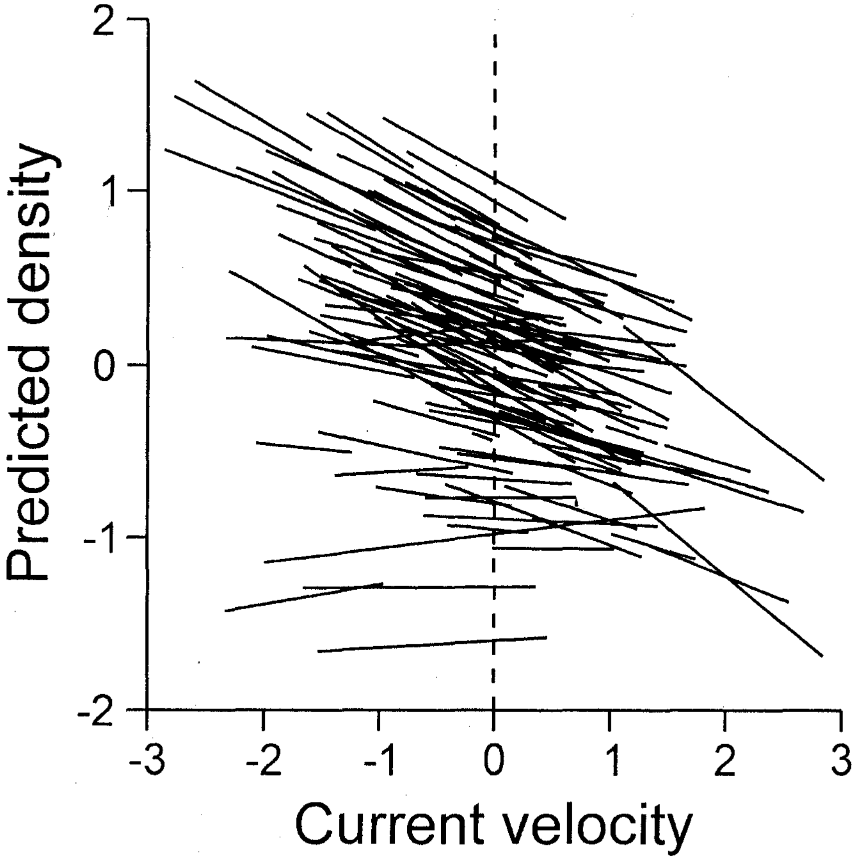

Figure 4. Deschênes and Rodríguez

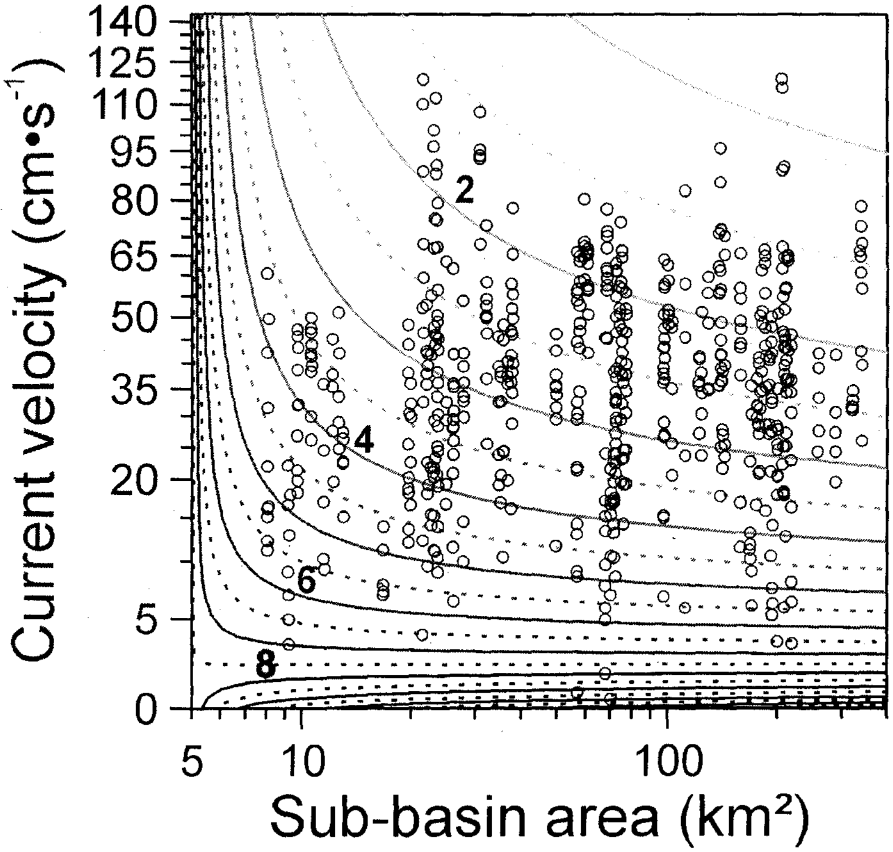

Figure 5. Deschênes and Rodríguez

CHAPITRE IV

CONTEXT-DEPENDENT RESPONSES OF JUVENILE ATLANTIC SALMON (*SALMO SALAR*) TO FORESTRY ACTIVITIES AT MULTIPLE SPATIAL SCALES WITHIN A RIVER BASIN[2]

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Abstract: We used classification trees and regression trees to relate the incidence and density of juvenile Atlantic salmon (*Salmo salar*) to forestry activities measured at four spatial scales (sub-basin, and 8-, 2-, and 0.5-km radii upstream of study sites) and environmental features in 120 stream reaches of the Cascapedia River basin, Québec, Canada. At all scales, incidence increased with reach size and accessibility to the reach from the river mainstem. Incidence declined with areal coverage of logging at all scales, but only in larger reaches. The time horizon over which logging effects were detected increased with spatial scale. At all scales, density in salmon-bearing reaches increased with accessibility. Density in more accessible reaches was negatively related to logging over the preceding nine years at the sub-basin and 8-km scales, but no effects of logging on density were detected at the 0.5- and 2-km scales. Overall, apparent effects of logging activities on salmon incidence and density were mostly negative and strong, but were both markedly scale-dependent and conditional on environmental context.

Résumé : Nous avons utilisé les arbres de classification et de régression pour relier l'incidence et la densité de saumons de l'Atlantique (*Salmo salar*) à l'environnement et aux activités forestières quantifiées à quatre échelles spatiales (le sous-bassin et des rayons de 8, 2, et 0,5 km en amont de chaque tronçon) dans 120 tronçons du bassin versant de la rivière Cascapédia, Québec, Canada. A toutes les échelles, l'incidence de saumon augmentait avec la taille des tronçons et l'accessibilité depuis la rivière principale et diminuait avec une augmentation du pourcentage de superficie coupée. Les effets des coupes étaient détectables sur des horizons temporels croissants avec l'augmentation de l'échelle spatiale. La densité de saumons augmentait avec l'accessibilité à toutes les échelles. Dans les tronçons plus accessibles, la densité diminuait avec une augmentation du pourcentage de superficie coupé au cours des neuf années précédentes aux deux plus grandes échelles. Aucun effet des coupes sur la densité de saumons n'était détectable aux deux plus petites échelles. Les effets apparents des coupes sur l'incidence et la densité de saumons juvéniles étaient forts et négatifs, mais dépendant de l'échelle spatiale et du contexte environnemental.

Keywords: classification and regression trees, incidence, logging effects, population density, stream fish

Introduction

The responses of aquatic organisms to human activities such as logging can be conditional on environmental context. For example, removal of riparian vegetation by logging in Oregon streams led to greater increase of periphyton and invertebrate abundance in small reaches than in large ones, apparently because riparian forest had greater influence on stream production in the small reaches (Murphy and Hall 1981). Logging also had a context-dependent effect on winter abundance of salmonid fry in Alaskan streams: fry abundance at logged sites declined if woody debris was removed, but increased otherwise (Murphy et al. 1986). Accounting for environmental context can lead to clearer understanding of the impacts of logging on stream fish populations and help develop preventive or remedial measures tailored to specific environmental conditions. Nonetheless, few studies have explicitly considered potential interactions between logging and the environmental context when assessing impacts of logging on fish populations (e.g., Murphy and Hall 1981, Murphy et al 1986).

Logging activities affect stream fish populations by modifying key environmental features that structure these populations at various spatial scales. At the local habitat scale, removal of riparian canopy by logging can increase water temperature and light penetration (Davies and Nelson 1994), resulting in increased invertebrate abundance (Kiffney et al 2003). At the drainage basin scale, logging can increase the load of suspended sediments and the magnitude of freshet discharge (Macdonald et al. 2003), as well as water yield and nutrient concentrations (Martin et al. 2000, Lamontagne et al 2000). Because fish relate to their local or proximal environment differently than to larger-scale characteristics of the basin (Folt et al. 1998, Armstrong et al. 1998), effects of logging on fish abundance may also differ across scales.

It is not clear which scale, local habitat or drainage basin, is most useful for understanding potential context-dependent effects of logging on fish populations.

Logging has been suggested to have maximum impact at a scale of tens to hundreds of hectares (Carignan and Steedman 2000). However, basin-wide studies at larger scales may allow for more effective assessment of the cumulative effects of logging, by integrating a multitude of small disturbances over a large basin (Hicks et al 1991). Direct comparison of results and conclusions from studies conducted at different spatial scales can be misleading because patterns found at smaller scales do not necessarily extrapolate to larger scales (Wiens 1989, Hicks et al 1991). Multi-scale studies can therefore help identify the most appropriate spatial scales for understanding the impacts of logging activities on fish stream populations.

Logging effects on stream ecosystems have been examined mostly by comparing biotic or physical features of streams between logged and unlogged sites (e.g., Rowe et al. 2002, Death et al. 2003, Latterell et al. 2003). However, the areal coverage of logged patches within different age-classes may be a more precise and informative measure of impact than simply the presence or absence of logging. For example, population densities of smaller fish species in Oregon streams declined with increases in coverage of recent (1 - 3 year) logging, whereas larger species declined with increase in coverage of older (4 - 8 years) logging (Rutherford et al. 1992).

This study examines responses of juvenile Atlantic salmon (*Salmo salar*) to forestry activities occurring 1-19 years prior to the study, measured at four spatial scales (sub-basin, and 8-, 2-, and 0.5-km radii upstream of study sites). Two biological metrics, incidence and population density in salmon-bearing reaches, were used as measures of population responses. Specifically, we compared the usefulness of proximate and larger-scale measurements of forestry activity for understanding the impacts of forestry on Atlantic salmon, and examined whether those impacts were mitigated or accentuated by specific combinations of environmental conditions (i.e., whether forestry effects were context-dependent).

Methods

The incidence and population density of Atlantic salmon and a host of environmental variables were quantified at 120 sampling sites distributed among 22 tributary streams in the Cascapedia River basin (3179 km^2), Québec, Canada (Fig. 1). The basin topography is hilly: 49% of the basin area has terrain slopes ≤15°; 28% has slopes >30°, and 23% has intermediate slopes. Plant cover consists primarily of fir-spruce forest (conifers: 66 %; mixed: 23 %; scattered deciduous: 2 %), with the remaining area accounted for by shrubs, rocks, and other non-forest cover (9 %; includes 2% in agricultural and urban land). The basin is sparsely populated but is subject to intensive forestry activities. Of the 120 sites in the present study, 116 were in sub-basins exposed to logging in the 19 years preceding the study. Substantial portions of the sub-basins upstream from the study sites (sub-basin area: median = 70.1 km^2; range = 8.1-337.9 km^2) were affected by intensive logging (percentage of upstream area covered by cuts: median = 18.0%; range = 0.0-37.6%) over this period. Governmental regulations have required forestry operations in the basin to leave unharvested a 20-m buffer strip (60-m when Atlantic salmon is present) along permanent streams since 1988.

Sites were visited in random sequence during low flow from mid-June to late August in 2000 (24 sites), 2001 (48 sites), and 2002 (48 sites). Sampled areas covered the entire stream width in completely wadable reaches and ranged 5 m from one bank, chosen randomly, towards the opposite bank in deeper reaches. Fish were sampled by single-pass electrofishing (Smith-Root D-15) in an upstream direction within open stream sections (Lobón-Cerviá and Utrilla 1993; Jones and Stockwell 1995). All captured fish were identified, measured, weighed, and returned to the stream site of capture. Salmon density was calculated as total captures divided by section area (numbers•100^{-1}•m^{-2}). Because capture efficiency was not 100%, this measure underestimates true density but should be proportional to it if efficiency is comparable across reaches. All reaches were sampled at base flow and therefore variation in depth, water velocity, cover, and substratum size among reaches was limited (Table 1). Abundance estimates obtained by one-pass electrofishing have been shown to correlate well with those from multiple-pass removal experiments in homogeneous geographic areas (e.g., small mountain streams: Kruse et al. 1998; small warmwater streams: Edwards et al. 2003), including estimates for juvenile Atlantic salmon in areas similar to those sampled in the present study (Hegder et al. 2005; M.A. Rodríguez, unpublished data).

In all, 25 environmental variables were quantified (Table 1). Water depth and substratum size were recorded at five equidistant points along each of sixteen transects perpendicular to streamflow (Fig. 2a). Substratum size was assigned a numerical code reflecting the dominant size category (modified Wentworth scale; 1: ≤ 0.0625 mm; 2: 0.0625 - 2 mm; 3: 2 - 16 mm; 4: 16 - 32 mm; 5: 32 - 64 mm; 6: 64 - 256 mm; 7: > 256 mm; 8: bedrock). Current velocity (pigmy-type meter, Scientific Instruments 1205) was measured at five equidistant points along every third transect starting with the second transect from the downstream end. Wetted width was measured at each transect. Abundance of submerged vegetation (moss or macrophytes) and overall availability of structural cover (rocks, woody debris, undercut bank, and overhanging vegetation) were estimated visually and assigned ordinal values reflecting areal coverage (1: ≤ 5%; 2: 6 - 15%; 3: 16 - 45%; 4: > 45%). Overhead opening (angle between riparian canopy or hilltops blocking incident sunlight at the centre of the stream; Fig. 2b) and slope over the stream reach were measured with a hand-held clinometer (Suunto PM-5). The increment in stream height and width at flood (from annual flood marks) and terrace width (distance between stream bank and piedmont) were measured on site (Fig. 2c). Water temperature (midpoint of maximum and minimum recorded while electrofishing) was measured with a max/min thermometer (Barigo). Entrenchment (mean gradient ≤ 100 m away from stream bank), sub-basin area, stream order (Strahler), and altitude were obtained from 1:20 000 topographic maps, as were distances by waterway from each reach to the Cascapedia River ("distance to mainstem"), and from the mouth of each stream to the mouth of the Cascapedia River ("distance to mouth") (planimeter, Calculated Industries 6125). Units of large woody debris (> 10 cm diameter) and pools were counted within each reach. Physical barriers potentially affecting upstream migration of fish along a tributary were assessed from field observations and topographic maps, and their effectiveness was coded as an integer value, B, ranging from 0 (no visible barrier) to 4 (insurmountable barrier) and reflecting the height, type (beaver dams, log jams, culverts, falls), and configuration of the barrier. An index of accessibility combining multiplicatively all potential barriers for each site was calculated as:

$$accessibility = \prod_{i=1}^{N} \left(1 - \frac{B_i}{4}\right),$$

where N is the number of visible barriers and B_i is the effectiveness of barrier i downstream from the site. Accessibility was assigned the value 1 in the absence of visible barriers. The index thus ranged from 0 to 1, taking a value of 0 if at least one barrier was insurmountable ($B_i = 4$).

A geographic information system (ArcGIS, v. 8.2) was used to measure logging activities at four spatial scales: sub-basin, and semi-circular zones of 8-, 2-, and 0.5-km radii upstream of each site (Fig. 3a), as well as the total sub-basin area upstream of the site, and stream gradient (mean slope from the site to upstream boundary), the percentage of the sub-basin area affected by spruce budworm outbreaks, and the density of roads (primary, secondary, tertiary, and total; km•km^{-2}). GIS maps were based on 1:20 000 forest maps (Ministère des Ressources naturelles du Québec), annual logging records, and photo-interpretation (Société de la faune et des parcs du Québec). All but 25 of the study reaches had sub-basins that extended beyond the 8-km radius (Fig. 3b). Logging activities were grouped into three categories reflecting the harvesting procedures employed by forestry companies: intensive (clear-cut harvesting, protection of regeneration, seed tree, and patch cutting), partial (partial harvesting, thinning, strip harvesting, selection cutting, harvesting within green strips, and diameter-limit cutting), and combined (intensive plus partial) logging. The logging variables used in the analyses quantified the percentage of the total land area at a given distance upstream that was logged (either intensively, partially, or combined) in the following time intervals preceding the study: 0-1, 0-2, 0-3, 0-4, 0-9, 0-14, and 0-19 yr (Table 2).

We used classification trees (CT) and regression trees (RT) to examine the context-dependent response of salmon populations to forestry variables measured at multiple scales. CT and RT are robust tools for ecological modelling that can effectively represent non-linear relationships between a single response variable (qualitative in CT and quantitative in RT) and a set of predictor variables. Additionally, they can reveal non-additive effects and complex interactions between predictors without requiring *a priori* specification of the form of these interactions (Breiman et al 1984, De'ath and Fabricius 2000). This ability to detect interactions is particularly relevant in studies focusing on context-dependent effects, which by definition are interactive. CT and RT use binary recursive partitioning (Breiman et al. 1984) to split the data into progressively smaller and more homogeneous subgroups. Beginning with the entire data set, at each step this algorithm examines all possible splits for each possible value of the predictor variables and selects the candidate split (the "splitting value") that maximizes the homogeneity within the two resulting subgroups with respect to the response variable. Similar to parametric methods such as multiple regression, in CT and RT strong collinearity among predictor variables can complicate the interpretation of effects of individual predictors. However, in CT and RT only one predictor is allowed to enter the model at any given split, and as the data are split into smaller subgroups, the relations among predictors may change. Therefore, predictors that are highly correlated over the whole data set may not be as strongly correlated in subgroups of the data (Lawler and Edwards 2002).

Salmon incidence and density were treated separately because salmon were absent from 51 of the 120 reaches. CT were used to analyse salmon incidence in all 120 reaches, whereas RT were used to analyse salmon density only in the 69 salmon-bearing reaches. Although RT are invariant to the distribution of predictor variables, they are not invariant to the distribution of the response variable (Atkinson and Therneau 2000). Salmon density was therefore transformed as ln(*X*) to reduce the potential influence of outliers. CT and RT were produced for each spatial scale separately.

Model specification and cross-validation followed Turgeon and Rodríguez (2005). The Rpart software library (Atkinson and Therneau 2000) was used for all calculations (S-PLUS program, v.7.2). Because recursive partitioning sometimes leads to excessive splitting, producing trees that are too large and overfit the data, we used "pruning" and cross-validation (an alternative to conventional parametric inference for model assessment) to select optimal trees (Atkinson & Therneau, 2000; De'ath & Fabricius, 2000). First, we generated a sequence of trees of increasing size, using a cost-complexity parameter, CP, to eliminate ("prune off") splits that were obviously not worthwhile, i.e., that did not improve the fit by at least the value of CP (= 0.01 for all trials) (Atkinson & Therneau, 2000). Then, 10-fold cross-validation was used to estimate prediction error, and final tree size was determined by the 1-SE rule, which favours the largest tree for which the cross-validated error falls within one standard error of the minimum relative error determined by cross-validation (Atkinson & Therneau, 2000). The influence of individual predictor variables was gauged by the proportional reduction in error (PRE, a measure of the variation accounted for by the splits associated with each predictor in the tree), an approach similar to the use of partial R^2 to assess the contribution of individual predictors in multiple regression. Additionally, we used the correct classification rate (CCR; percentage of all cases correctly predicted), sensitivity (percentage of observed presences correctly predicted), and specificity (percentage of observed absences correctly predicted) to evaluate the accuracy of CT. Empirical odds ratios, calculated as:

$$OR = \frac{P_1 A_2}{P_2 A_1},$$

where P_x and A_x represent numbers of reaches where salmon was present (P) or absent (A) under condition x, were used to compare salmon incidence under different environmental conditions determined by the CT, e.g., in reaches with wetted width < 8.7 m vs. reaches with wetted width ≥ 8.7 m. A small constant (0.5) was added to values of P and A to avoid null denominators.

We conducted a preliminary principal components analysis (PCA; based on the correlation matrix) to examine the relationships between the environmental and forestry variables (measured at the sub-basin scale) and check for multicollinearity among these variables. Variables were transformed as required to reduce the influence of outliers and linearize relationships. We did not retain a reduced set of components from the PCA for subsequent inclusion as predictors in CT and RT because of the difficulties in interpreting composite variables and because using linear composites of variables as predictors can reduce predictive power and mask interactions among the original variables (Muñoz and Felicísimo 2004).

Results

The PCA of environmental and forestry variables showed little relationship between the areal coverages of intensive and partial logging in the Cascapedia River basin (Fig. 4). Combined logging, given by the sum of intensive and partial logging, was positively related to both these variables, as would be expected. Within each of these three sets of logging variables, correlations reflected the overlap in temporal coverage between pairs of variables, e.g., strong correlation between 0-14 and 0-19 yr cuts (14-yr overlap), but weaker correlation between 0-14 yr and 0-1 yr cuts (1-yr overlap). Among the environmental variables, the strongest correlations were between wetted width and sub-basin area (Pearson $r_p = 0.86$), altitude and distance to mouth ($r_p = 0.84$), altitude and distance to mainstem ($r_p = 0.77$), stream gradient and sub-basin area ($r_p = -0.74$), and stream gradient and wetted width ($r_p = -0.70$) (Fig. 4); all other correlations were ≤ 0.63. The strongest correlation between environmental and logging variables was between stream gradient and 0-19 yr combined cuts ($r_p = -0.62$). Logging variables were generally related positively to sub-basin size and wetted width, and negatively to stream gradient (Fig 4), perhaps reflecting greater accessibility and ease of manoeuvring for forestry equipment in large expanses of flat lowland terrain.

A total of 1539 salmons were captured over the three years of sampling. Salmon were present in 69 of the 120 reaches and 14 of the 22 streams sampled. The ability of final CT models to classify reaches correctly on the basis of incidence (CCR) differed little across scales, and ranged from 88.3% at the sub-basin scale to 90.0% at the 8-km scale (Table 3). All models had a greater ability to correctly classify salmon-bearing reaches (sensitivity) than reaches without salmon (specificity). For CT models, the proportional reduction in error varied little across scales (72.5 - 76.5%).

Although CT models were built for each spatial scale separately, two environmental predictors, wetted width and distance to the mainstem, were retained in the final models at all scales (Fig. 5). Smaller reaches (wetted width < 8.7 m) had lower incidence than larger reaches (odds-ratio, OR = 11.4). Among smaller reaches, salmon incidence was greater in reaches nearer (< 2.7 km) to the Cascapedia River mainstem than in more distant reaches (OR = 29.8) (Fig. 5).

Among larger reaches(wetted width ≥ 8.7 m), salmon incidence was negatively related to logging at all scales (Fig. 5a-d). Salmon incidence was negatively related to combined logging in the preceding 14 years both at the sub-basin (OR = 24.3) and 8-

km scales (OR = 17.8) (Fig. 5a,b). Salmon incidence also was negatively related to intensive logging in the preceding 9 years at the 2-km scale (OR = 41.4) and to intensive logging in the preceding 4 years at the 0.5-km scale (OR = 24.3) (Fig. 5c,d). At the two smaller scales, declines in salmon incidence were apparent at relatively low threshold values for intensive logging (17.0% at the 2-km scale; 10.6% at the 0.5-km scale). The fact that salmon incidence was negatively related to logging only in larger reaches points to an interaction between logging and stream size that is independent of scale (Fig. 5).

Final RT models for salmon density in salmon-bearing reaches retained only two or three predictor variables. The proportion of variation in salmon density accounted for by the models increased with spatial scale, ranging from 49.1% at the 0.5-km scale to 68.7% at the sub-basin scale (Table 3). Accessibility was a major predictor of salmon density at all scales (Fig. 6). Mean salmon density in readily accessible reaches (accessibility ≥ 0.625) was approximately twice that in less accessible ones (Fig. 6).

Relationships between salmon density and logging were only detected in readily accessible reaches, at the two largest spatial scales (Fig. 6). At the sub-basin scale, mean salmon density in reaches having < 21.3% of combined logging in the preceding 9 years was twice that in reaches with greater values of combined logging (Fig. 6a). Among the former reaches, those having wetted width ≥ 10.9 m had greater salmon density than narrower ones. At the 8-km scale, mean salmon density in reaches having < 5.2% of intensive logging in the preceding 9 years was twice that in reaches with greater values of intensive logging (Fig. 6b). At this scale, mean salmon density was greatest in reaches having < 5.2% of intensive logging in the preceding 9 years and wetted width ≥ 10.5 m. Final RT models were similar for the 2-km and 0.5-km scales. At these scales, salmon density was greatest in readily accessible reaches subject to spruce budworm outbreaks having areal coverage > 28 - 29.1% (Fig. 6c,d). Similar to the models for incidence, an interaction involving logging and an environmental predictor was apparent. Salmon density was negatively related to logging only in readily accessible reaches, but, contrary to the models for incidence, only at the two largest spatial scales (Fig. 6c,d).

Discussion

At all spatial scales, logging appeared to have context-dependent effects: incidence declined only in large reaches and density declined only in readily accessible reaches. Logging impacts on periphyton, invertebrates, and physical characteristics in Oregon streams varied as a function of stream width and gradient and resulted in greater abundance of periphyton and invertebrates in small, high-gradient reaches than in large, low-gradient ones (Murphy and Hall 1981). Canopy removal resulted in a smaller reduction in shading, and thus less enhancement of primary production, in large reaches than in small reaches. Furthermore, sediment deposition was greater in large reaches because of their lower gradient and transport capacity relative to small reaches. Increased sedimentation offset any beneficial effect of increased light exposure in larger reaches (Murphy and Hall 1981). In the Cascapedia River basin, the effect of logging on salmon incidence in large reaches may have been linked to decline in habitat quality mediated by increased deposition of fine sediments. Because reach width and gradient were negatively correlated (Spearman rank correlation: $r_s = -0.66$), small reaches likely were less susceptible to accumulation of fine sediments than large ones, possibly explaining why no effect of logging on salmon incidence was apparent in small reaches. The proportion of silt increased with logging in larger reaches but not in smaller ones (Fig. 7; ANCOVA term for the interaction between stream width and logging: $p = 0.007$), lending support to this interpretation. The apparent context-dependent effect of logging on salmon density may be a consequence of restriction of fish movement by barriers such as log jams, beaver dams, culverts, or waterfalls in less accessible reaches, which may hinder adjustment of local densities to match spatial differences in habitat quality induced by logging. In contrast, salmon in accessible reaches may move more freely and avoid areas impacted by logging, creating density differentials that better reflect habitat quality.

The cumulative effects of logging on salmon incidence seemed to be integrated over longer time horizons at larger spatial scales. Fine sediments produced by logging have been reported to rapidly increase in reaches immediately downstream of the logged area and subsequently decline within one to three years after the disturbance (Macdonald et al. 2003, Haggerty et al. 2004). However, redistribution and transport of deposited sediments to reaches further downstream may continue for many years. For example, in the Big Beef Creek basin (USA), mass influx of sediments arising from forestry activities between 1850 and 1930 produced a sediment wave which was transported over 18 km of main stream channel and an artificial lake (≈ 1 km in length) (Quinn and Peterson 1996) before arriving near the downstream limit of the creek by 1970 (Madej 1982). This wave was then transported over a distance of 6 km between 1970 to 1976, (Madej 1982). Logging effects on downstream reaches may therefore be detectable for many decades after the actual disturbance (e.g. Madej 1982, Swank et al. 2001). Transport of fine sediments from upstream to downstream reaches over a span of decades may explain why logging effects appeared to be integrated over longer time periods at larger spatial scales. These long-term effects seem akin to the "ghost of the land use past", where past agricultural activity in North Carolina basins determined present-day fish and invertebrate diversity, independently of riparian reforestation (Harding et al. 1998).

In contrast with salmon incidence, logging effects on salmon density were only apparent at the two largest spatial scales. When fine sediments from multiple headwater sources accumulate in downstream reaches, effects of logging on fish populations may be magnified in those reaches, which receive the impact of distant upstream sources, and thus be apparent only at larger spatial scales. Salmon density was positively related to areal coverage of spruce budworm outbreaks at the two smaller scales, 2 km and 0.5 km. Loss of riparian canopy caused by defoliation can result in increased light exposure, local temperature, and productivity (Swanston 1991, Kiffney et al. 2003, 2004). The influence of defoliation on salmon density seems to be local (Swanston 1991) and may thus be more readily detectable at smaller spatial scales.

In summary, apparent effects of logging activities on salmon incidence and density were mostly negative and strong, but were both markedly scale-dependent and conditional on environmental context. The two biological metrics used to quantify the responses to logging, incidence and density, differed in their sensitivity to spatial scale, capacity to detect logging impacts, and integration of effects over time. Examining the variation in salmon incidence and density over multiple spatial scales helped us understand the context-dependent responses of salmon populations to logging, and pointed to potential limitations of studies focusing on single scales and biological metrics. For example, the apparent absence of logging effects on salmon density at the two smaller spatial scales suggests that future study designs should consider the possibility that large-scale disturbances arising from logging may not be detectable at smaller spatial or temporal scales. Potential effects of logging should therefore be examined with a view to detection of downstream effects, particularly as concerns transport of sediments from headwaters to downstream reaches. Because biotic responses to logging can differ across geomorphic settings, future studies may benefit from considering environmental context explicitly when assessing the effects of logging on fish populations.

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Table 1. Median, interquartile range, and variable codes for 25 environmental variables describing fish habitat at 120 sites in the Cascapedia River basin. Variable codes for figure 4 are also given.

Variable name	Median	25-75% quartiles	Code
Accessibility index	0.8	0.3-1.0	AI
Altitude (m)	240.0	167.5-315.0	AL
Overhead opening (°)	95.7	75.4-113.5	OO
Cover index	2.4	1.4-3.0	CI
Distance to mainstem (km)	9.1	2.5-21.7	DM
Distance to mouth (km)	75.5	52.8-82.4	DO
Entrenchment (%)	10.0	5.0-15.0	EN
Height increment at flood (m)	0.5	0.4-0.7	HI
Mean current velocity ($cm \cdot s^{-1}$)	34.9	26.0-48.9	MC
Mean depth (cm)	24.6	18.8-29.4	MD
Mean substratum size	5.3	4.9-5.8	MS
Mean temperature (°C)	10.5	9.0-12.0	MT
Mean wetted width (m)	9.3	6.3-14.1	MW
Pools (number)	0.0	0.0-1.5	PO
Stream gradient (°)			
Sub-basin	2.1	0.6-3.3	SG
8 km	1.1	0.5-2.3	
2 km	1.0	0.5-1.7	
0.5 km	1.1	0.3-2.0	

Table 1 (concluded).

Stream order	3.0	3.0-4.0	SO
Stream slope (°)	1.0	0.6-1.3	SS
Sub-basin area (km^2)	70.1	25.5-151.0	SA
Terrace width[a] (m)	107.8	81.3-163.5	TW
Units of large woody debris (number)	3.5	1.0-8.5	UW
Vegetation abundance index	1.0	1.0-1.8	VA
Width increment at flood[a] (m)	2.6	1.9-4.0	WI

[a] Sum of measures from right and left margins

Table 2. Median and interquartile range for 35 forestry variables measured at four spatial scales in the Cascapedia River basin. Road densities are expressed as km•km^{-2}. Spruce budworm outbreaks and logging data are given as % of total sub-basin area. Variable codes for figure 4 are also given.

Variable name	Spatial scale				
	Sub-basin	8 km	2 km	0.5 km	Code
Spruce budworm outbreaks	22.6 (18.8-27.8)	25.8 (17.3-32.2)	21.3 (6.5-37.8)	9.7 (0.0-23.4)	sb
Road density					
Total	1.9 (1.4-2.3)	1.8 (1.5-2.1)	1.5 (1.0-2.2)	1.6 (0.6-2.8)	rt
Primary	0.2 (0.1-0.3)	0.1 (0.0-0.3)	0.0 (0.0-0.4)	0.0 (0.0-0.9)	r1
Secondary	0.8 (0.2-1.6)	0.4 (0.1-1.2)	0.2 (0.0-0.8)	0.0 (0.0-0.0)	r2
Tertiary	0.6 (0.2-1.0)	0.8 (0.3-1.4)	0.8 (0.2-1.4)	0.0 (0.0-1.6)	r3
Intensive logging					
0-1 yr	1.0 (0.0-2.8)	0.3 (0.0-4.6)	0.0 (0.0-2.3)	0.0 (0.0-0.0)	i1
0-2 yr	2.5 (0.0-3.5)	1.9 (0.0-5.4)	0.0 (0.0-5.8)	0.0 (0.0-0.0)	i2
0-3 yr	2.8 (0.7-4.3)	2.4 (0.0-5.6)	0.0 (0.0-9.0)	0.0 (0.0-2.2)	i3
0-4 yr	3.1 (0.8-5.6)	2.3 (0.0-7.9)	0.0 (0.0-10.0)	0.0 (0.0-4.0)	i4

Table 2 (continued).

0-9 yr	8.6 (2.9-14.2)	5.1 (2.2-18.9)	2.4 (0.0-24.5)	0.0 (0.0-5.4)	i9
0-14 yr	13.1 (4.0-22.4)	11.4 (4.0-23.8)	6.3 (0.3-25.1)	0.0 (0.0-11.5)	i14
0-19 yr	16.4 (4.5-23.8)	17.8 (4.8-25.6)	8.7 (1.3-25.5)	0.0 (0.0-17.4)	i19
Partial logging					
0-1 yr	0.1 (0.0-2.2)	0.0 (0.0-0.3)	0.0 (0.0-0.0)	0.0 (0.0-0.0)	p1
0-2 yr	0.6 (0.0-3.1)	0.1 (0.0-1.6)	0.0 (0.0-0.0)	0.0 (0.0-0.0)	p2
0-3 yr	0.9 (0.0-3.9)	0.1 (0.0-2.8)	0.0 (0.0-0.0)	0.0 (0.0-0.0)	p3
0-4 yr	1.5 (0.0-5.8)	1.0 (0.0-5.1)	0.0 (0.0-0.5)	0.0 (0.0-0.0)	p4
0-9 yr	3.8 (0.8-8.5)	2.3 (0.1-6.9)	0.0 (0.0-3.1)	0.0 (0.0-0.0)	p9
0-14 yr	6.1 (0.9-11.1)	4.3 (0.1-9.0)	0.0 (0.0-6.7)	0.0 (0.0-0.0)	p14
0-19 yr	7.2 (0.9-13.4)	4.9 (0.1-9.1)	0.0 (0.0-7.2)	0.0 (0.0-0.3)	p19
Combined logging					
0-1 yr	2.7 (0.3-5.5)	2.7 (0.0-6.3)	0.0 (0.0-7.1)	0.0 (0.0-1.5)	c1
0-2 yr	3.9 (2.6-7.2)	4.0 (2.1-8.4)	0.0 (0.0-13.2)	0.0 (0.0-3.6)	c2
0-3 yr	5.1 (2.9-8.9)	5.5 (2.5-9.4)	0.0 (0.0-16.2)	0.0 (0.0-4.4)	c3

Table 2 (continued and concluded).

0-4 yr	7.8 (3.7-12.5)	5.8 (3.3-13.4)	5.1 (0.0-17.1)	0.0 (0.0-9.7)	c4
0-9 yr	15.4 (6.7-23.0)	10.6 (5.7-22.6)	8.8 (0.6-31.1)	0.0 (0.0-11.7)	c9
0-14 yr	18.3 (10.3-29.5)	18.5 (7.3-30.0)	12.6 (1.8-31.9)	3.9 (0.0-21.4)	c14
0-19 yr	21.5 (11.1-35.4)	23.6 (7.7-31.2)	18.7 (2.9-34.5)	4.4 (0.0-24.5)	c19

Table 3. Classification success (CCR, specificity, and sensitivity) and proportional reduction in error (PRE) of classification tree models, and PRE of regression tree models, by spatial scale. All values are percentages.

Spatial	Classification trees				Regression
	CCR	Specificity	Sensitivity	PRE	PRE
Sub-basin	88.3	84.3	91.3	72.5	68.7
8 km	90.0	84.3	94.2	76.5	68.4
2 km	89.2	84.3	92.8	72.5	57.5
0.5 km	88.3	84.3	91.3	72.5	49.1

Figure Captions

Figure 1. Location of the 120 sampling sites distributed among 22 tributary streams in the Cascapedia River basin, Québec.

Figure 2. Schematic views illustrating field measurements of: (a) depth and substratum size, recorded at sampling points (circles) along all transects, and current velocity, recorded at sampling points along every third transect starting from the second most downstream transect; (b) overhead opening (angle between structures blocking direct sunlight); (c) terrace width, height increment at flood, and width increment at flood.

Figure 3. (a) Schematic representation of zones used to quantify landscape features and forestry activities at four spatial scales: sub-basin, and 8-, 2-, and 0.5-km radii upstream of the sampling sites. The concentric curves are delimited by watershed boundary lines; (b) Frequency distribution of the radius from the study reach to the most distant upstream point within the sub-basin of the reach (km).

Figure 4. Loadings from a principal component analysis of environmental (black arrows, uppercase codes) and forestry (grey arrows; lowercase codes) variables measured at the sub-basin scale. Plots are presented for: (a) axes 1 (30.6% of total variance) and 2 (13.8%) and (b) axes 1 and 3 (11.6%). Linear correlations between variables are represented approximately by the length and alignment of their respective arrows. Variable codes are as in Tables 1 and 2.

Figure 5. Classification tree models for salmon incidence. Models are composed of a common part (top, left) and a part specific to each scale (open boxes; bottom): (a) sub-basin, (b) 8 km, (c) 2 km, and (d) 0.5 km. Vertical bars represent the number reaches with (black) or without (white) salmon at each node. Splitting rules and

proportional reduction in error (PRE) are given on the branches of each tree. The number of reaches with and without salmon are given alongside the boxes for each node.

Figure 6. Regression tree models for population density in salmon-bearing reaches (*X* axis). Models are composed of a common part (top) and a part specific to each scale (open boxes; bottom): (a) sub-basin, (b) 8 km, (c) 2 km, and (d) 0.5 km. Vertical bars represent the density distribution of salmon at each node. Splitting rules and proportional reduction in error (PRE) values are given on the branches of each tree. Density (numbers$\bullet 100^{-1} \bullet m^{-2}$) is transformed as ln(*X*). The mean density (s.d.) and the number of observations (in italics) are given alongside the boxes representing terminal nodes.

Figure 7. Relative abundance of silt (particle size < 0.0625 mm; transformed as arcsine square-root) vs. percent areal coverage of 0-14 yr combined logging, at the sub-basin scale. Lines are lowess regression curves for reaches in two categories of wetted width derived from CT models (Fig. 4): ≥ 8.7 m (solid) and < 8.7 m (dotted). A small amount of random jitter was added to improve the visibility of overlapping symbols.

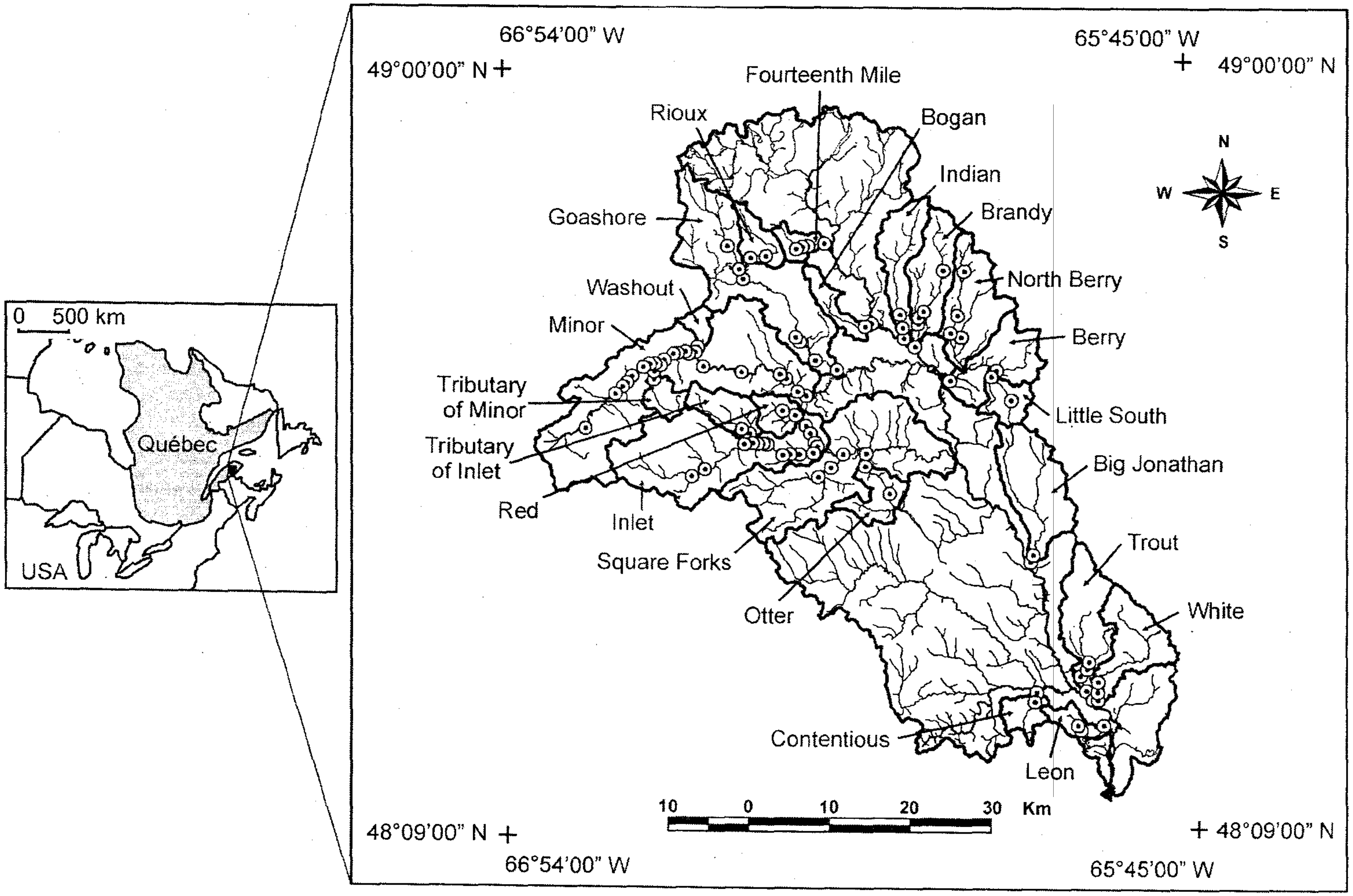
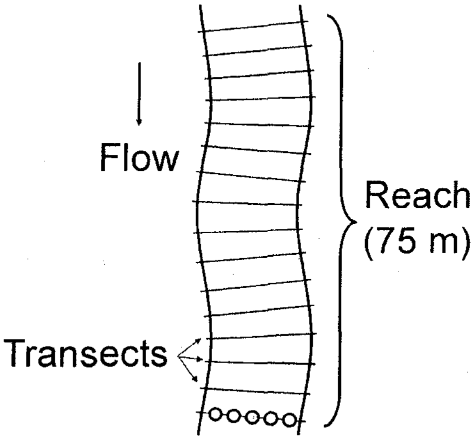
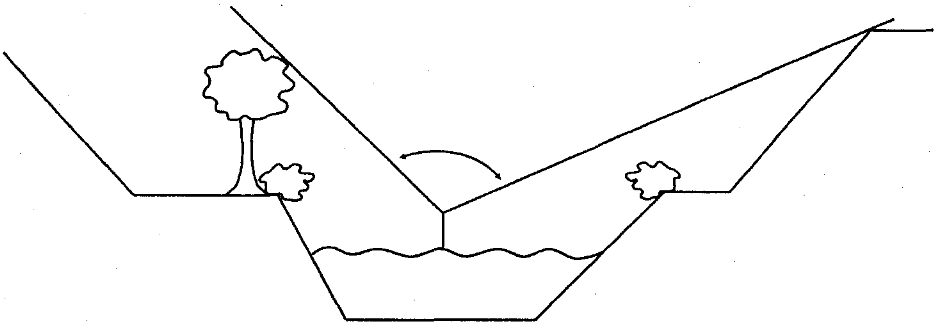


Figure 1. Deschênes, Rodríguez, and Bérubé

(a) Sampling reach



(b) Overhead opening



(c) Stream cross-section

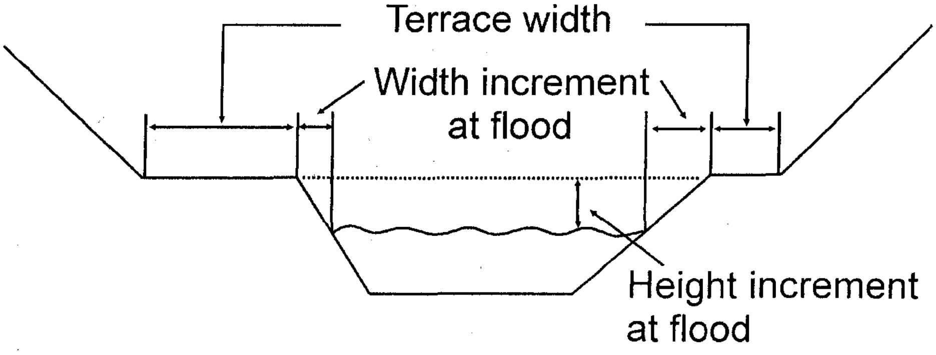


Figure 2. Deschênes, Rodríguez, and Bérubé

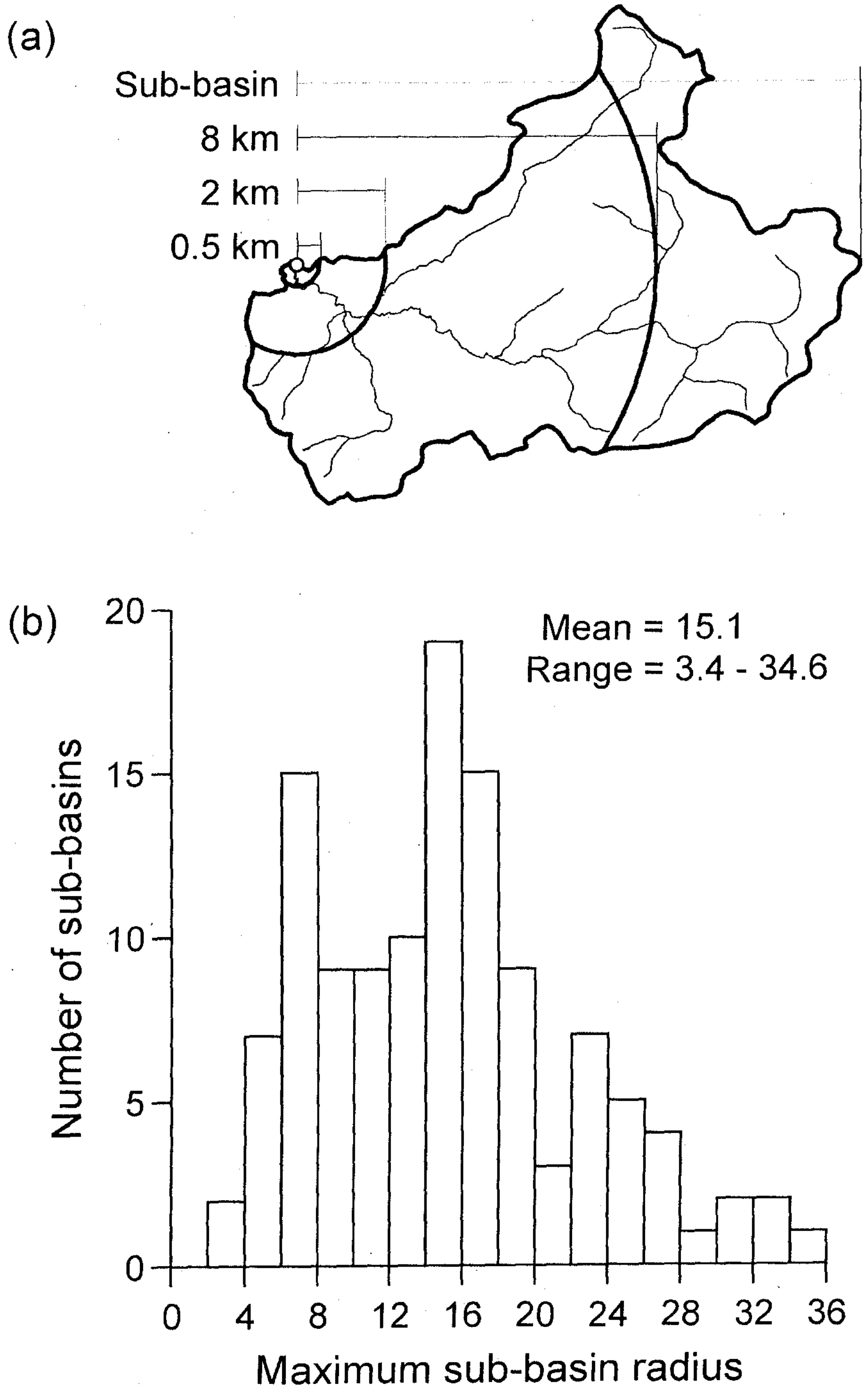


Figure 3. Deschênes, Rodríguez, and Bérubé

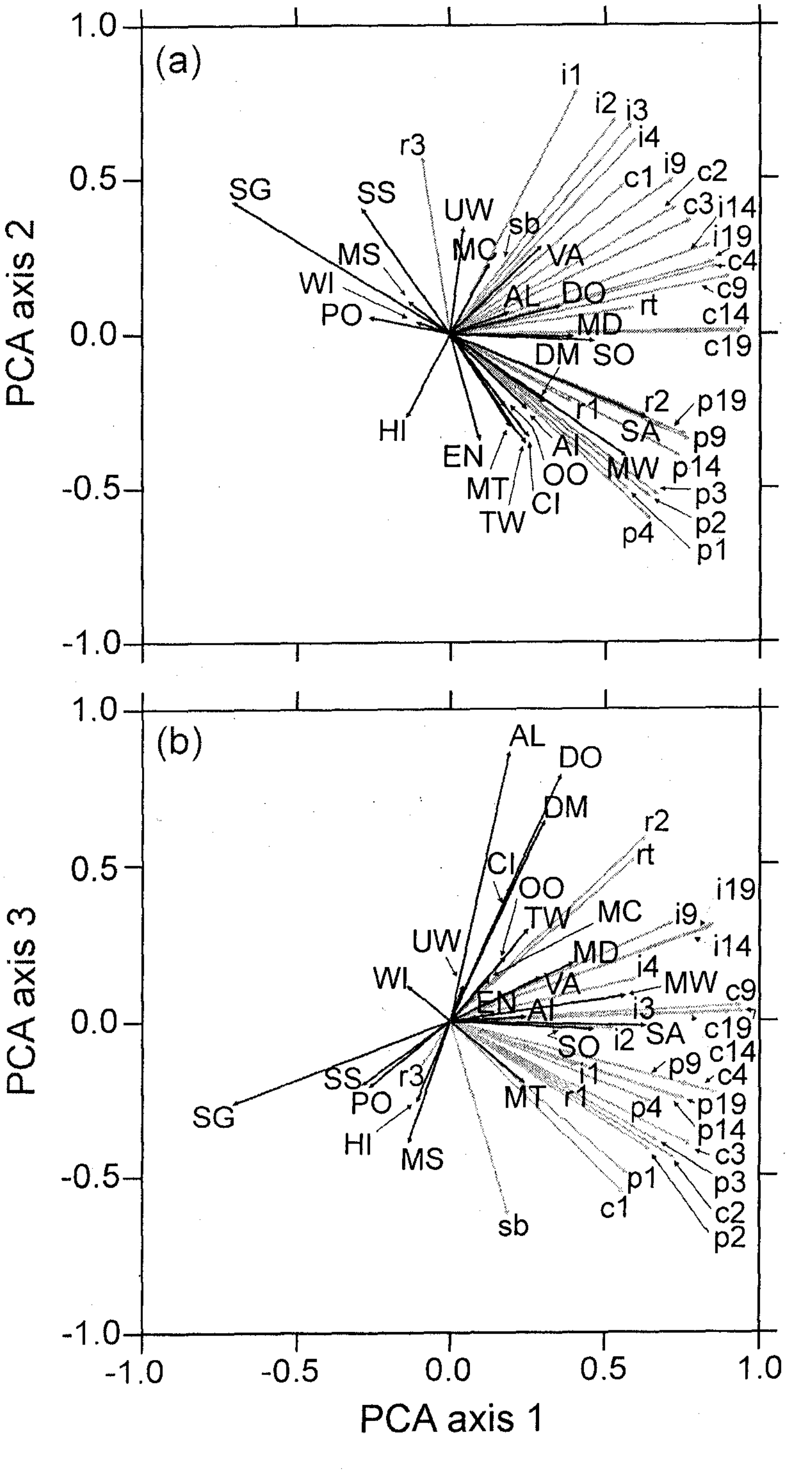


Figure 4. Deschênes, Rodríguez, and Bérubé

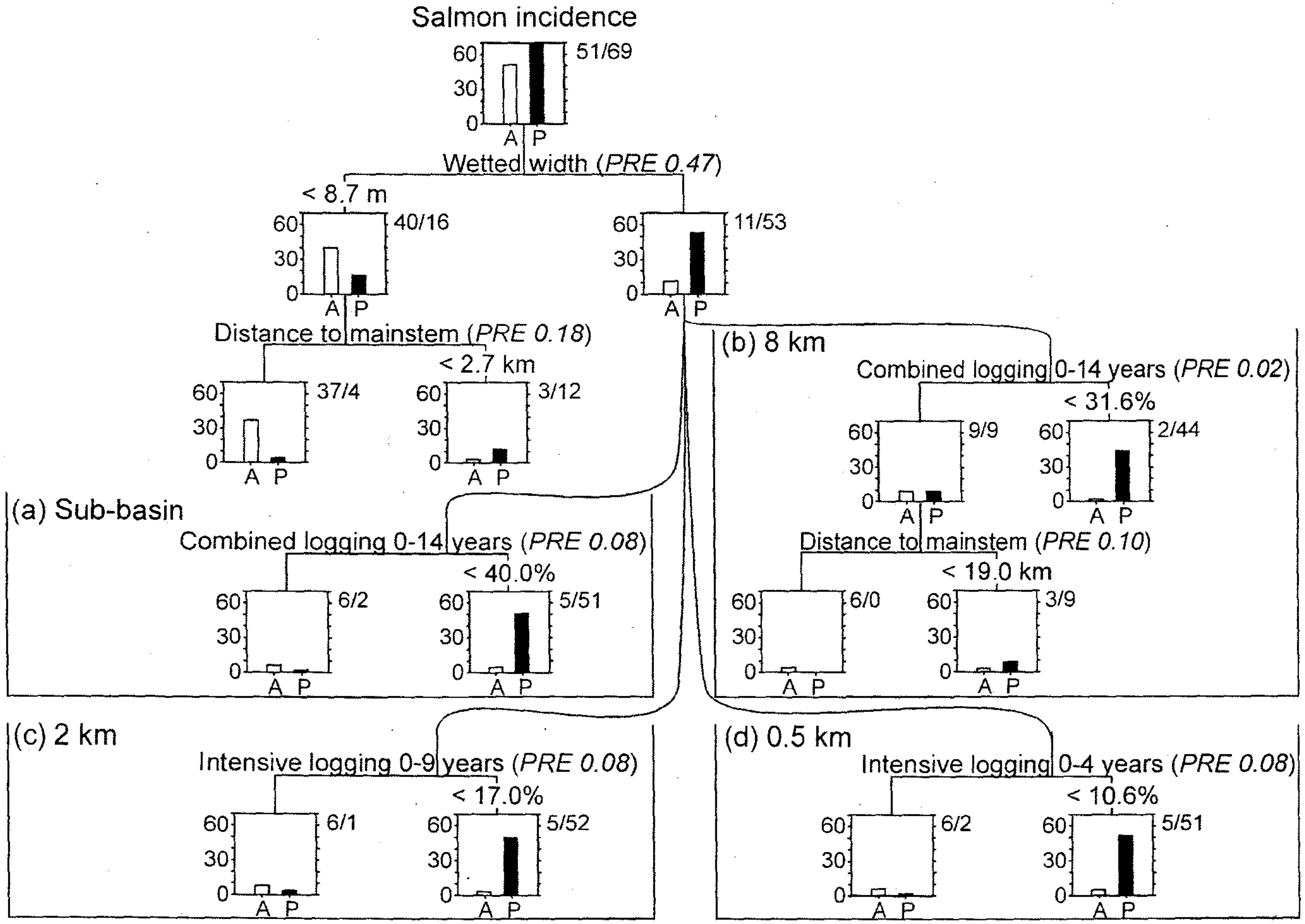


Figure 5. Deschênes, Rodríguez, and Bérubé

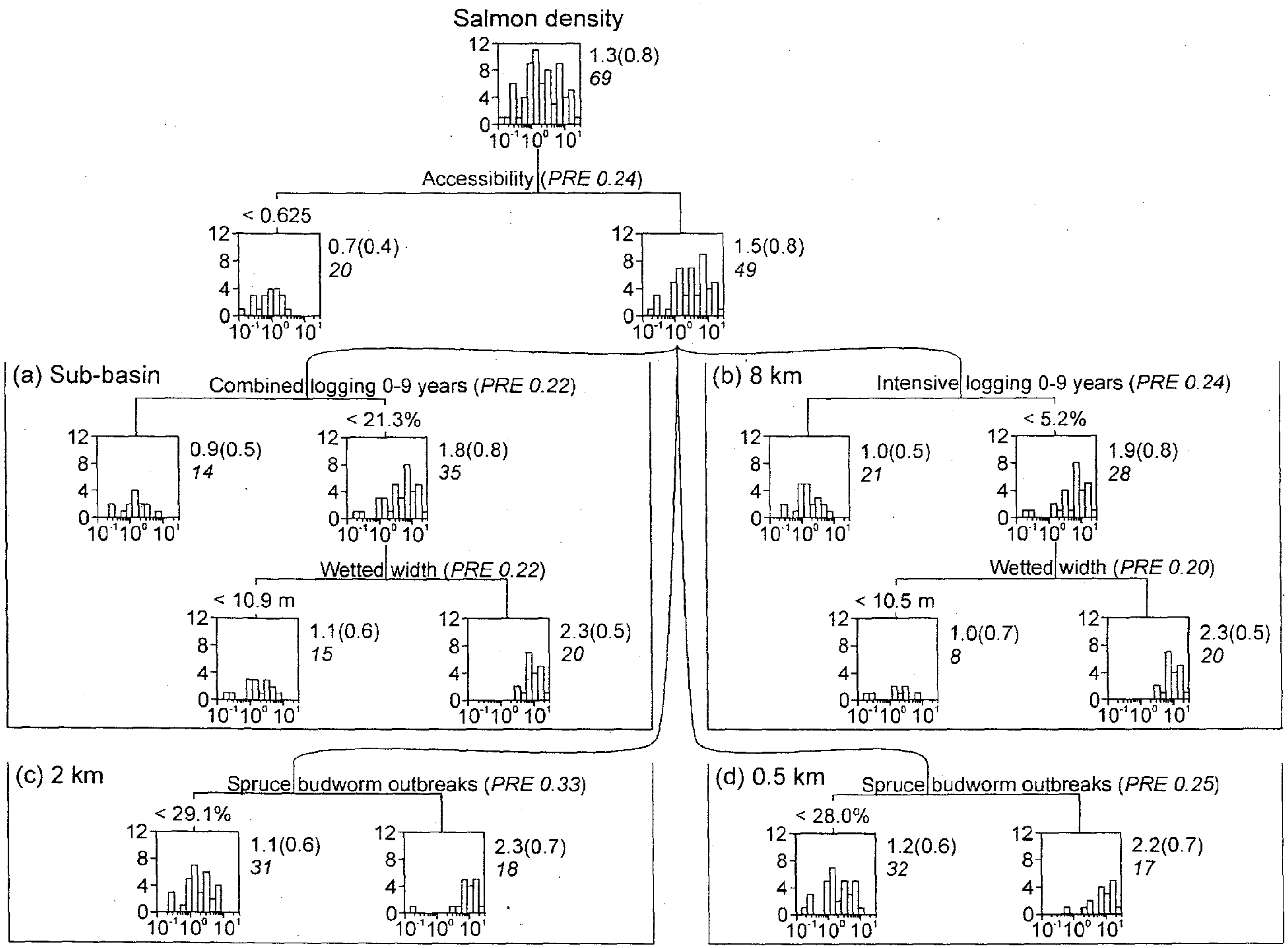


Figure 6. Deschênes, Rodríguez, and Bérubé

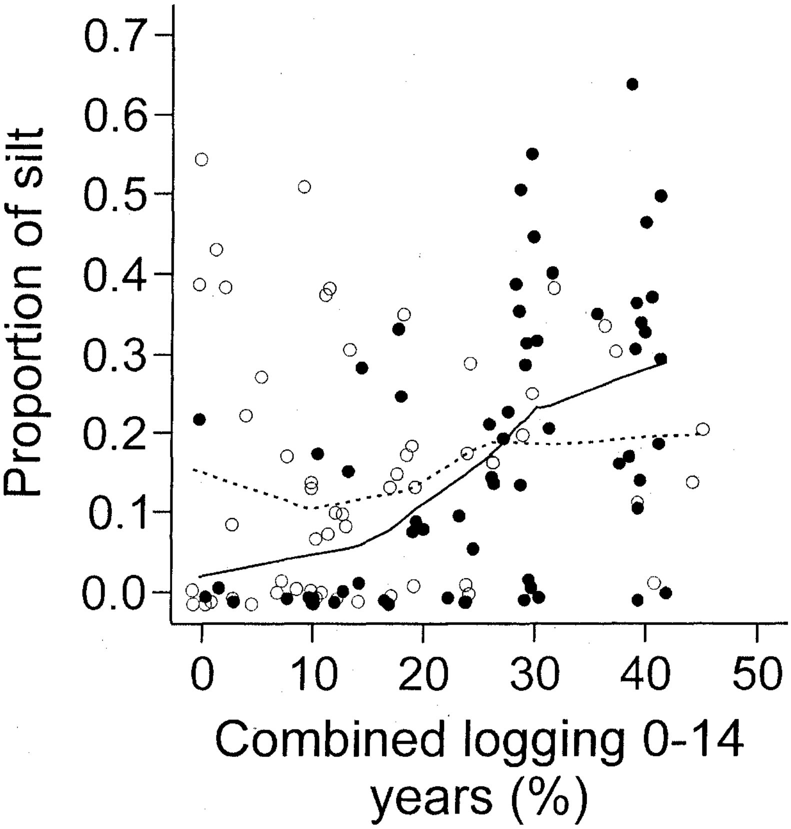


Figure 7. Deschênes, Rodríguez, and Bérubé

CHAPITRE V

CONCLUSION

Le principal objectif de ce projet était d'examiner l'influence du contexte environnemental sur la structure des communautés de poissons fluviatiles et la distribution de deux espèces « cibles », l'omble de fontaine et le saumon de l'Atlantique, à différentes échelles spatiales. Trois approches multiéchelles ont été utilisées pour traiter différents aspects de cet objectif. Premièrement, la relation entre la structure des communautés et le contexte environnemental a été examinée à trois niveaux hiérarchiques à l'aide d'analyses de redondance et de décomposition de la variation. Deuxièmement, la relation entre la distribution de l'omble de fontaine et les caractéristiques environnementales à trois niveaux hiérarchiques a été examinée à l'aide des modèles multiniveaux. Troisièmement, la réponse contextuelle du saumon de l'Atlantique aux variables forestières et aux conditions environnementales a été examinée à quatre échelles spatiales à l'aide des arbres de classification et de régressions.

Les relations espèces-environnement : une question d'échelle

Les résultats des trois approches multiéchelles ont démontré que les communautés de poissons fluviatiles et populations d'ombles de fontaine et de saumons de l'Atlantique étaient influencées par différentes caractéristiques environnementales ou forestières selon le niveau hiérarchique ou l'échelle spatiale considéré.

Les analyses de redondance (chapitre 2) à l'échelle intrabassin démontraient que la structure de la communauté était largement déterminée par l'accessibilité, ainsi que la taille et la morphologie de la vallée. À l'échelle intraruisseau, la structure de la communauté était principalement influencée par l'accessibilité et les caractéristiques de l'habitat local. À l'échelle intratronçon, seulement les caractéristiques de l'habitat local influençaient la structure des communautés. Certaines caractéristiques environnementales peuvent être considérées comme étant des filtres hiérarchiques à travers lesquels doit passer la communauté régionale afin de former la communauté locale (Poff 1997; Jackson et al. 2001). Chaque filtre permet de déterminer la composition et l'abondance des espèces à une échelle particulière. L'accessibilité semblait donc jouer un rôle déterminant dans la structure de la communauté à grande échelle en agissant comme « filtre », surtout en ce qui concerne l'abondance du saumon et du chabot visqueux. Bien que les sections étaient grossièrement basées sur les mésohabitats (p. ex. fosses, rapides, seuils), les limites des sections ne correspondaient pas toujours à celle des mésohabitats. Les analyses de redondance ont tout de même démontré que la structure des communautés était influencée par les caractéristiques de l'habitat local l'échelle intratronçon. Ces caractéristiques étaient souvent citées comme étant importantes dans la sélection du micro ou mésohabitat pour les poissons (Frissell et al. 1986; Jackson et al. 2001), particulièrement chez les salmonidés (Bjornn et Reiser 1991; Swanston 1991; Hicks et al. 1991).

Les résultats démontraient également que la variation dans la structure de la communauté diminuait progressivement des ruisseaux (λ 47%), aux tronçons (λ 35%) aux sections (λ 18%). Un patron similaire, mais plus prononcé, a été décelé pour la variation expliquée par les variables environnementales (ruisseaux λ 60%; tronçons λ 25%; sections λ 5%). Les patrons observés aux plus grandes échelles étaient donc plus fiables que ceux observés à l'échelle intratronçon. Les modèles développés à partir des relations à l'échelle du microhabitat risquent de fournir peu d'informations utiles sur la composition des communautés à grande échelle.

L'analyse détaillée de la distribution de l'omble de fontaine (chapitre 3) a révélé que les densités ne variaient pas significativement entre ruisseaux. La densité d'omble de fontaine était plutôt influencée par les caractéristiques de l'habitat local (vitesse du courant, abondance de débris ligneux, abondance de couvert) au niveau des sections, ainsi que par la taille (superficie du sous-bassin) et la forme (largeur de la vallée et augmentation de la hauteur à la crue) des tronçons. Toutefois, la vitesse du courant avait un effet différentiel sur la densité d'ombles de fontaine en fonction des tronçons. La superficie des sous-bassins versants était systématiquement reliée à cet effet différentiel (contextuel) par l'intermédiaire d'une interaction avec la vitesse du courant. Dans les petits sous-bassins, la vitesse du courant n'influençait pas la densité d'omble. Dans les grands sous-bassins, la densité d'ombles de fontaine diminuait fortement avec une augmentation de la vitesse du courant. L'interaction était non seulement entre deux variables de niveaux différents, mais également entre deux échelles spatiales. La relation entre la vitesse du courant et la densité d'ombles à l'intérieur d'une étendue d'environ 0,075km (entre sections), variait sur une étendue d'environ 8 km (entre tronçons). Cette interaction confirmait donc que certains patrons décelés à plus petite échelle ne pouvaient pas être extrapolés à grande échelle (Folt et al. 1998; Schneider 2001).

Les arbres de classification (CT) et de régression (RT) ont également démontré que les effets apparents des coupes forestières sur les populations de saumons variaient selon l'échelle spatiale et la métrique biologique utilisée (chapitre 4). Les effets cumulatifs des coupes sur l'incidence de saumons étaient intégrés sur de plus longues périodes et à plus grande échelle spatiale. Les sédiments produits par les coupes forestières peuvent s'accumuler rapidement dans les tronçons à proximité des aires de coupes, mais ils seraient également exportés rapidement vers l'aval (Swank et al. 2001; Macdonald et al. 2003). Les effets des coupes forestières sur les tronçons à proximité seraient donc transitoires. Par contre, le transport subséquent des sédiments vers l'embouchure des ruisseaux s'échelonne parfois sur plusieurs décennies, selon la taille du réseau hydrographique et l'apport de sédiments fins (Madej 1982; Swank et al. 2001; Ripley et al. 2005). La durée de ce transport pourrait expliquer l'intégration temporelle progressive de l'influence des coupes forestières aux plus grandes échelles spatiales. Ces effets à long terme sur l'incidence de saumon suggèrent que la structure des populations actuelle reflète l'utilisation antécédente des terres plutôt que son utilisation actuelle (Harding et al. 1998). Contrairement à l'incidence, les coupes forestières n'avaient pas d'influence apparente sur la densité de saumons aux plus petites échelles spatiales. Lorsque les tronçons en aval accumulaient les sédiments provenant des ruisseaux de tête, les effets des coupes forestières pouvaient être amplifiés et donc plus facilement repérables à grande échelle.

Interactions révélatrices

L'effet contextuel de la vitesse du courant sur la densité d'ombles de fontaine (chapitre 3) suggérait qu'il y avait un manque de refuges de courant dans les plus grands sous-bassins, refuges particulièrement exploités par l'omble de fontaine (Cunjak et Power 1987; McLaughlin et Noakes 1998). Les structures qui créent des refuges de courant augmenteraient la quantité d'emplacements énergétiquement profitables, résultant en une augmentation de densité (Fausch et Northcote 1992; McLaughlin et Noakes 1998). Ces structures, telles que les débris ligneux et les blocs, tendent à être moins abondantes dans les ruisseaux plus larges (Benke et Wallace 1990; Jowett et al. 1998; Wing et Skaugset 2002). Puisque la taille du sous-bassin était corrélée à la largeur du tronçon, les sous-bassins plus grands pourraient donc contenir moins de refuges de courant, rendant les sections moins rapides plus attrayantes pour l'omble de fontaine.

Les CT et RT montraient également des interactions entre les coupes forestières et le contexte environnemental (chapitre 4). Le pourcentage de coupes semblait affecter différemment les populations de saumons selon le contexte environnemental : l'incidence était réduite seulement dans les tronçons larges et la densité seulement dans les tronçons facilement accessibles. L'effet apparent des coupes forestières sur l'incidence de saumon dans les tronçons plus larges suggère que la qualité de l'habitat était réduite par l'accumulation de sédiments fins. Les tronçons plus larges avaient également des pentes plus faibles, réduisant leur capacité de transport des sédiments fins (Murphy et Hall 1981). Par conséquent, ces sédiments pourraient s'accumuler plus facilement que dans les petits tronçons pentus. Ceci expliquerait l'absence d'effet apparent des coupes forestières sur l'incidence de saumons dans les petits tronçons. L'effet contextuel des coupes sur la densité de saumons dans les tronçons moins accessibles suggère qu'il y a eu une restriction des déplacements. Les barrières à la migration telles que les embâcles, les barrages de castors, les ponceaux et les chutes restreindraient les ajustements locaux de densité en réponse à la réduction dans la qualité des habitats découlant des coupes forestières. Dans les tronçons plus accessibles, les saumons pourraient se déplacer plus facilement. En évitant les zones plus fortement affectées par les coupes, ils créeraient des gradients de densité correspondant à la qualité des habitats. Les caractéristiques environnementales jouaient donc un rôle primaire dans la détermination de l'influence des coupes forestières sur l'incidence et la densité de saumons.

Les interactions décelées par les analyses hiérarchiques permettent de mieux comprendre les réponses de l'omble de fontaine aux gradients environnementaux et du saumon de l'Atlantique aux effets apparents des interventions forestières. Par ailleurs, elles permettent d'émettre certaines hypothèses au sujet des mécanismes qui sous-tendent ces réponses.

Les analyses hiérarchiques

Les approches utilisées dans ce projet sont des procédures d'analyse générales. Les analyses de communautés, la décomposition de la variation et les analyses multiniveaux peuvent facilement s'appliquer des structures d'échantillonnage hiérarchique avec ou sans composante temporelle, en milieu terrestre, aquatique ou autre. Par rapport aux analyses conventionnelles (sans séparation des échelles), les analyses de communauté et la décomposition de la variation ont l'avantage de déceler l'influence des conditions environnementales sur la structure des communautés à petite échelle après avoir explicitement pris en considération la variation à plus grande échelle (Dunham et Vinyard 1997).

Les analyses multiniveaux ont permis de généraliser les relations entre les poissons et leur environnement à grande échelle spatiale tout en conservant une haute résolution grâce à l'utilisation simultanée de toute l'information disponible à chaque niveau. Cette haute résolution a permis de déceler l'effet différentiel de la vitesse du courant sur la densité d'ombles de fontaine entre tronçons, ce qui n'aurait pas été possible si l'agrégation avait été faite au niveau des tronçons. L'importance potentielle des refuges de courant pour l'omble de fontaine dans les grands ruisseaux n'aurait donc pas été mise en évidence. Jusqu'à présent, les études multiéchelles ont souvent agrégé les observations au niveau des groupes ou analysé les patrons à l'intérieur de chaque groupe séparément (Inoue et al. 1997; Watson et Hillman 1997; Angermeier et Winston 1999). L'agrégation peut réduire considérablement la puissance statistique des analyses (Hox 2002; Goldstein 2003). Même si l'analyse séparée par groupe peut révéler des différences de patrons et processus entre groupes, ces différences demeurent souvent inexpliquées (Poizat et Pont 1996; Dunham et Vinyard 1997; Watson et Hillman 1997; Cohen et al. 1998). En prenant en considération l'emboîtement des données et en utilisant simultanément l'information disponible à tous les niveaux, les analyses multiniveaux sont particulièrement bien adaptées pour résoudre de telles différences de patrons entre niveaux.

Alors que l'omble de fontaine était présente dans tous les ruisseaux, 98 % des tronçons et 89 % des sections, le saumon de l'Atlantique n'était, lui, présent que dans 73 % des ruisseaux, 58 % des tronçons et 42 % des sections (chapitre 2). Par ailleurs, les analyses de communautés (chapitre 2) ont suggéré qu'aucune caractéristique de l'habitat local ne pouvait expliquer la variation dans la densité du saumon de l'Atlantique au niveau intratronçon (entre sections). Contrairement aux chapitres précédents (2 et 3), les densités de saumons (chapitre 4) ont donc été agrégées au niveau des tronçons (moyenne des sections pour chaque tronçon). Les arbres de classifications et de régressions étaient néanmoins particulièrement utiles pour déceler des interactions entre variables prédictives sans préalablement spécifier leur forme.

Limites et perspectives de recherche

L'examen des variations dans la structure des communautés et des populations de poissons fluviatiles à différentes échelles spatiales a permis, entre autres, de souligner les limites potentielles des études à une seule échelle spatiale ou une seule métrique, ainsi que de suggérer des mécanismes potentiellement responsables des patrons observés.

La difficulté à prédire la structure des communautés à bas niveau hiérarchique pourrait être en partie le résultat de l'échantillonnage à une seule passe en sections ouvertes (chapitre 2). Par ailleurs, les limites des sections n'étaient pas calquées sur celles des mésohabitats (p. ex. fosses, rapides, seuils). La capacité de prédiction était donc sous-estimée à l'intérieur des tronçons. Les études ultérieures pourraient potentiellement accroître cette capacité en choisissant des niveaux plus « naturels » tels que plusieurs séquences fosse-rapide le long de segments de ruisseaux.

Par ailleurs, l'absence apparente d'effet des coupes forestières sur les densités de saumons aux plus petites échelles suggérait que les perturbations de grandes envergures n'étaient pas nécessairement détectables en examinant une seule échelle spatiale restreinte (chapitre 4). Les effets potentiels des coupes forestières sur les populations de poissons devraient également être examinés dans une perspective plus globale en considérant que ces effets peuvent être exportés vers l'aval. Puisque les réponses biotiques aux coupes forestières peuvent varier selon la structure géomorphologique des ruisseaux, le contexte environnemental devrait donc être pris en considération dans les études ultérieures.

L'accessibilité était un filtre particulièrement important dans la répartition des espèces entre ruisseaux et entre tronçons (chapitre 2). Elle influençait particulièrement la distribution du saumon de l'Atlantique (chapitre 4) et sa réponse aux coupes forestières. L'accessibilité pourrait donc affecter le déplacement des poissons en obstruant des voies de migration. Cependant, il n'est pas clair si l'accessibilité affectait plus la migration des adultes ou les déplacements des juvéniles. Par ailleurs, le rôle exact et l'importance de l'accessibilité dans la réponse des saumons aux coupes forestières reste à vérifier.

L'effet contextuel de la vitesse du courant sur la densité d'ombles de fontaine en fonction de la superficie des sous-bassins (chapitre 3) suggère que les refuges de courant étaient importants pour l'omble de fontaine, particulièrement dans les grands ruisseaux. Ces effets contextuels avaient donc le potentiel d'élucider les différences de patrons entre échelles spatiales emboîtées.

Tel que le démontrent les trois chapitres précédents, les relations entre les communautés ou les populations de poissons fluviatiles et leur environnement peut changer à la fois selon les niveaux hiérarchiques, les échelles spatiales et les métriques biologiques considérés. Les approches multiéchelles, en général, demeurent donc nécessaires pour mieux comprendre les processus et mécanismes qui structurent les communautés et les populations de poissons fluviatiles.

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