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Variations inter journalières dans la structure des communautés de poissons: implications pour le développement de modèles de qualité d'habitats

Gabriel Lanthier, Daniel Boisclair, Guillaume Bourque et Pierre Legendre.

Université de Montréal, Département de sciences biologiques,
C.P. 6128, Succursale Centre-ville, Montréal, Québec, Canada H3C 3J7

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maîtrise (M.Sc.) en sciences biologiques.

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Ce mémoire intitulé :

Variations inter journalières dans la structure des communautés de poissons: implications pour le développement de modèles de qualité d'habitats

présenté par :

Gabriel Lanthier

a été évalué par un jury composé des personnes suivantes :

Christopher Cameron
Président-rapporteur

Daniel Boisclair
Directeur de recherche

Pierre Legendre
Codirecteur

Normand Bergeron
Membre du jury

RÉSUMÉ

Les modèles de qualité d'habitats (MQH) sont des relations entre des descripteurs biologiques et des caractéristiques de l'habitat. Les MQH sont souvent développés à partir de données recueillies dans un nombre de sites élevé afin de couvrir adéquatement la gamme des conditions retrouvées dans l'aire d'étude. Cette approche nécessite fréquemment l'usage d'un seul échantillonnage aux divers sites étudiés. Considérant que les poissons sont des organismes mobiles, l'usage d'un échantillonnage unique pour déterminer la valeur écologique d'une série de sites pourrait induire un biais dans les relations entre les poissons et leur habitat et réduire le pouvoir explicatif des MQH. Les objectifs de cette étude étaient de quantifier l'ampleur des variations inter-journalières dans les communautés de poissons en rivière, d'évaluer l'effet de ces variations sur la capacité des MQH à : 1) expliquer la variance observée entre les sites échantillonnés et 2) sélectionner les variables appropriées pour expliquer la variance de densités observées aux sites échantillonnés. Pour atteindre ces objectifs, 18 sites situés dans les réseaux hydrographiques des rivières Rouge et de la Nord ont été échantillonnés. 24 espèces de poissons y ont été observées. Nos résultats suggèrent que, même pour une courte période de 7 semaines, certaines espèces changent suffisamment de patron de distribution pour modifier le résultat des MQH. L'usage de plusieurs échantillonnages pour représenter la valeur écologique de chaque site présente, dans certains cas, des avantages en termes de performance des MQH. L'étude de méthodologies appropriées au développement de MQH valides et fiables semble donc se révéler pertinente.

Mots-clés : Variabilité temporelle, paradigme du mouvement restreint, mouvements des poissons, modèle de qualité d'habitat, structure de communautés, rivières, poissons, Laurentides.

ABSTRACT

Habitat quality models (HQM) are relationships between biological attributes and habitat characteristics. HQM are often developed by sampling a large number of sites over a large spatial extent. This approach permits the representation of the complete range of environmental conditions found in a survey area. In order to achieve this objective, sampling sites are often sampled only once. However, fish distribution may vary over time. Among-day variations of the association between fish and their habitat may decrease the explanatory power of HQM.

The purpose of this study was to assess the magnitude of among-day variations of descriptors of fish community structures in rivers, to evaluate the effect of such variations on HQM capacity to 1) explain variance of among sampling sites density and 2) select adequate explanatory variables. To achieve these goals, 18 sites of the watersheds of the Rivière Rouge and the Rivière du Nord were surveyed. 24 species were encountered in these sites. Our results suggest that, even within a relatively small timeframe of 7 weeks, some fish species displayed enough changes in their distribution to change HQM results. The use of several samplings to represent the ecological value of each site seems to present, in certain cases, advantages in terms of performance of the MQH. The study of methodologies suited for the development of valid and reliable MQH thus seems to be relevant.

Key words: Temporal variability, restricted movement paradigm, fish movements, habitat quality models, community structure, river, fish, Laurentian region.

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%	Pourcentage
$	Dollars
≈	Approximativement égal
Adj.	Adjusted
B.P.	Before present
cm	Centimeter
CI	Confidence Interval
CV	Coefficients of variations
HQM	Habitat quality model
IUCN	International Union for Conservation of Nature
m	Meter
m^2	Square meters
MAUP	Modifiable Areal Unit Problem
MQH	Modèle de qualité d'habitat
p	Probability
r	Pearson linear correlation r
R^2	Percentage of explained variation
R^2_{adj}	Adjusted R^2
sec	Second
[s]	Number of sampled site(s)
[s · t]	Product of the number of sampled site and the number of times each site is sampled

SCV	Spatial coefficient of variation
STS	Space-for-time substitution
[t]	Number of times each site is sampled
TCV	Temporal coefficient of variation
UE	Unité d'échantillonnage
VR	Variable réponse

« Only after the last tree has been cut down,
Only after the last river has been poisoned,
Only after the last fish has been caught,
Only then will you find that money cannot be eaten. »
- *Cree Indian Prophecy*

À André, Chantal, Alex et Sari pour leur amour et leur soutien,
sans lesquels je me demande ce que je serais aujourd'hui…

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INTRODUCTION GÉNÉRALE

Les écosystèmes d'eau douce sont indispensables, au niveau mondial, à quelques 45 000 espèces (IUCN 2006). Ils fournissent plus de 26 % de la production des pêches mondiales et 4% de la protéine animale consommée sur la planète (IUCN 2006). Pourtant, selon Costanza et al. (1997), ces apports ne représentent que 2,5 % de la valeur attribuable chaque année aux lacs et rivières du globe, laquelle est évaluée à $1,7 * 10^{12}$ $.

Les systèmes d'eau douce fournissent donc à l'homme une quantité importante de biens et services, comme le mentionnent Postel et Richter (2003). Or, malgré une reconnaissance grandissante de la valeur de ces écosystèmes (Gill 1973; Wiens 2002), ceux-ci sont soumis à de fortes pressions anthropiques (Hey 1996; Imhof et al. 1996; Jorde et al. 2001; Wiens 2002). En 1999, Ricciardi et Rasmussen, en évaluant le rythme projeté des extinctions futures de la faune d'eau douce, arrivent à la conclusion que celui-ci sera cinq fois plus élevé comparativement à la faune terrestre et trois fois plus élevé que pour les mammifères marins de la côte. Déjà, en 2007, l'organisme «The Nature Conservacy» annonce que plus de 20 % des espèces connues de poissons d'eau douce sont éteintes ou menacées. Pour l'Amérique du Nord seulement, 3 genres, 27 espèces et 13 sous-espèces de poissons ont été éliminés au cours des 100 ans précédant 1989 (Miller et al. 1989).

Outre la pollution et la surexploitation, plusieurs chercheurs s'accordent sur l'idée que la perte d'habitats est une des causes principales de cette chute de diversité (Evans et al. 1996; Richter et al. 1997; Brind'Amour et Boisclair 2006). En effet, certains types d'habitats sont essentiels à la survie d'espèces et leurs caractéristiques physiques sont importantes au bon déroulement de phases critiques du cycle vital des poissons (Imhof et al. 1996).

En mettant en relation les patrons de distributions des poissons avec les caractéristiques environnementales influentes, il est possible d'identifier les zones contribuant au maintient des communautés de poissons (Boisclair 2001). Cette capacité de distinguer les habitats utiles aux différentes espèces est un atout majeur pour les efforts de préservation et de conservation (Souchon et al. 1989; Argent et al. 2003). Les études utilisant cette approche y réfèrent souvent sous les termes «modèles de qualité d'habitats» (MQH). Comme le mentionne Boisclair (2001), il existe plusieurs exemples de travaux qui, utilisant les MQH pour étudier les poissons, ont permis d'élaborer des outils utiles aux niveaux fondamental et pratique.

Cependant, les problématiques relevant du domaine de l'écologie sont habituellement complexes à interpréter, car modulées par un nombre élevé de variables dont les influences ne sont pas toujours indépendantes (Legendre et Legendre 1998). L'utilisation des MQH souscrit à cette tendance et beaucoup reste à faire pour maîtriser les concepts sur lesquels ils s'appuient. Un exemple de problème s'appliquant directement aux MQH est celui du manque de connaissances à l'égard des échelles nous permettant de bien capter le signal que représente la réponse des poissons aux variables environnementales. En effet, les caractéristiques formant les habitats de bonne qualité sont identifiées en observant ce qui distingue les UE où les abondances, densités ou autres variables réponses (VR) sont maximales (Guay et al. 2000 et 2003). Cette procédure nécessite donc de conserver une certaine variabilité entre les VR observées aux différents sites, faute de quoi aucune distinction ne peut être établie. Or, en plus d'augmenter l'effort d'échantillonnage, en augmentant la taille des unités d'échantillonnage, les variances observées entre les sites diminuent (Bellehumeur et al. 1997).

À l'inverse, en réduisant la taille des UE, nous exposons le modèle à un autre problème: la variation temporelle. En effet, dans le cas d'études portant sur des organismes mobiles, le déplacement des individus peut générer une source importante de variabilité. Plus la taille de l'UE est petite, plus la probabilité de trouver un individu dans une même zone au fil du temps diminue (Cooper 1998). Cela signifie que pour des petites UE, le temps devient une source majeure de variation qui peut être confondue avec l'information utile de la variance spatiale (entre les UE). Un exemple simple de ce type de biais serait d'attribuer un indice de qualité élevé à un site où plusieurs poissons sont observés, alors que leur présence n'est due qu'à un déplacement vers une autre zone.

Cependant, dans le contexte du développement de MQH pour poissons en rivière, la possibilité que le mouvement des individus puisse entrainer une instabilité des valeurs de VR a longuement été ignorée par une part importante de la communauté scientifique. L'une des principales sources de cette conception est certainement une étude de Gerking (1959), dans laquelle l'auteur analyse les résultats de nombreuses expériences de marquage-marque conduites en rivières. En effet, dans cette publication importante (plus d'un millier de citations) ayant guidé une part importante de la recherche sur la dynamique des populations de poissons en rivières pendant 30 ans (Gowan et al. 1994), l'auteur mentionne que les individus de 34 espèces de poissons (12 familles) de rivières possèdent des territoires (« home range »; Gerking 1959) de dimensions restreintes (ex : sections de 20m; Miller 1957) où ils demeurent pour une bonne partie ou l'entièreté de leur vie (Bachman 1984), exhibant seulement des déplacements très limités. Ce paradigme du mouvement limité (Restricted movement paradigm; Gowan et al. 1994) semble avoir été considéré par plusieurs scientifiques comme étant une indication que l'échantillonnage des poissons de rivières utilisant une seule prise de données par site pourrait être approprié pour développer des MQH en rivières.

Pourtant, le RMP a été remis en cause à de nombreuses occasions. En effet, la validité des conclusions provenant d'expériences comme celle de Gerking est compromise par l'absence de considération pour les 15 à 90 % de poissons marqués qui n'ont jamais été recapturés (Fausch et Young 1995, Young 1995). Considérant que la méthode utilisée dans ce genre d'étude comporte un très faible effort d'échantillonnage à l'extérieur du site où ont eu lieu les captures, Young (1995) conclue que les résultats ainsi obtenus sont biaisés en faveur des poissons démontrant peu de mouvements. De plus, de récentes études télémétriques ont mis en évidence qu'une partie non négligeable des populations de poissons est mobile (Young 1994). Belica et Rahel (2008) ont observé que 44 % des mulets à cornes (*S. atromaculatus*) capturés se sont déplacés entre des sections de rivière différentes éloignées par plus de 600 m en 2 semaines. D'autres travaux ont mis en évidence des mouvements maximaux de cyprinidés approximant les 400 m par jour (Matthew et al. 1995) et 1 à 10 km en quelques semaines (Albanese et al.. 2004, Baade et Fredrich 2005). Des mouvements d'individus appartenant à d'autres familles allant de 8 à 40 km dans des périodes de 3 à 22 mois (Dames et al. 1989, Gatz et Adams 1994, Timmons 1999) ont aussi été observés. L'ampleur des mouvements effectués par les poissons doit cependant être comparée avec la taille du site d'échantillonnage pour déterminer la probabilité que des individus y entrent et/ou en sortent au fil du temps.

Or, considérant qu'un nombre important d'études sur les poissons de rivières utilisent des sites d'échantillonnage de longueur restreinte (50-500m, Fausch et al. 2002), il est concevable que le mouvement des poissons puisse mener à l'attribution de valeurs écologiques différentes pour un même site d'échantillonnage. Une certaine quantité de bruit est donc incorporée dans la relation entre les poissons et leur habitat. Pour augmenter la probabilité d'attribuer aux différents sites une valeur écologique représentative, il est possible d'inclure dans le plan d'expérimentation plusieurs collectes de données réparties dans le temps, et ce pour chaque site (Boisclair 2001). Cependant, comme les contraintes logistiques (temps, argent, etc.) dictent souvent les limites des travaux en écologie, plusieurs visites à chaque site impliquent une diminution du nombre de sites, lequel est directement lié à la capacité de couvrir convenablement l'aire étudiée. Il est fort probable que cette représentativité liée au nombre d'objets (sites) soit l'une des causes expliquant pourquoi la littérature scientifique en écologie des poissons contient si peu d'exemples utilisant des réplications temporelles. L'effet exact de cette procédure sur la performance des MQH générés n'a cependant jamais été testé à notre connaissance. Comme le mentionnent Gowan et al. (1994), nous croyons qu'il est inapproprié d'effectuer de la recherche, de la conservation et de la gestion sur les communautés de poissons sans considérer les effets potentiels du mouvement des poissons.

Le premier objectif de cette étude est donc de quantifier la variabilité temporelle des différentes espèces formant les communautés retrouvées dans les bassins hydrographiques des rivières Rouge et du Nord en utilisant des UE de 100 m. Notre hypothèse de base face à cet objectif est que nous devrions observer, dans une série de sites échantillonnés à 10 reprises, des différences de variabilité temporelle entre les espèces rencontrées. Nos connaissances initiales sur la composition spécifique exacte des communautés étudiées ne nous permettent cependant pas de nous avancer sur le résultat de comparaisons entre les valeurs de variabilités temporelles des différentes espèces observées.

Le second objectif de cette étude est de quantifier l'impact des variabilités temporelles mesurées sur la capacité des MQH à expliquer la variance de densité de poissons observée entre les sites. Plus précisément, nous désirons comparer la performance de MQH développés à partir de différentes stratégies d'échantillonnage, et ce pour la gamme des différentes variabilités temporelles observées. Considérant que les contraintes logistiques (temps, argent, etc.) sont constantes pour une étude donnée, chacune des stratégies d'échantillonnage comparées totalise un effort total d'échantillonnage (nombre de sites x nombre de visites par site) constant de 200 plongées. Notre hypothèse à ce sujet, en considérant l'hypothèse 1 confirmée, est que les espèces présentant des variabilités temporelles plus importantes devraient bénéficier davantage de l'usage de plusieurs visites d'échantillonnage pour attribuer une valeur écologiques aux différents sites.

Le troisième objectif de ce mémoire est d'évaluer l'impact de l'usage de différentes stratégies d'échantillonnage sur la capacité des MQH à sélectionner les variables explicatives appropriées. En effet, le développement de MQH nécessite généralement l'échantillonnage d'un nombre important de variables environnementales. Les analyses statistiques permettent ensuite de mettre en évidence les variables reliées à l'explication de la distribution observée. Cependant, comme les variables environnementales d'un site sont souvent reliées (corrélées), il est concevable que cette procédure puisse mener à des erreurs de sélection. En effet, la mobilité des poissons introduit une certaine variance dans la valeur écologique attribuée aux différents sites et cette dernière pourrait mener à la sélection de variables inappropriées et, inversement, au rejet de variables importantes. Nous désirons donc tester l'effet de différentes valeurs de variabilités temporelles sur la fréquence de sélection des variables explicatives et ce, lors de l'usage de différentes stratégies d'échantillonnage. Notre hypothèse à ce sujet est que les espèces plus variables temporellement devraient présenter des taux de sélection des variables appropriées plus élevés avec l'usage de plusieurs visites d'échantillonnage.

Enfin, le dernier objectif de cette étude consiste à évaluer si, en considérant l'ensemble des résultats obtenus dans les sections reliées aux objectifs précédents, la méthode d'échantillonnage comprenant une seule prise de données à une série de sites est appropriée pour le développement de MQH pour les poissons de rivières. Notre hypothèse à ce sujet est que les espèces présentant les plus grandes variabilités temporelles devraient bénéficier de l'usage de mesures répetées de densités à chaque site.

The effect of space-over-time precedence on the development of fish habitat quality models.

Gabriel Lanthier[1], Daniel Boisclair[1], Guillaume Bourque[1], Pierre Legendre[1], Michel Lapointe[2], and Bernard Angers[1]

[1]Université de Montréal, Département de sciences biologiques, C.P. 6128, Succursale
Centre-ville, Montréal, Québec, Canada H3C 3J7

[2]McGill University, Department of Geography, 805 Sherbrooke West, Montreal, Quebec,
Canada H3A 2K6

Contribution to the programme of GRIL (Groupe de Recherche Interuniversitaire en Limnologie et en environnement aquatique).

Author to whom all correspondence should be addressed:

Daniel Boisclair : [redacted]

Introduction

Habitat loss has been recognized as a major threat to the survival of fish populations (Evans *et al.* 1996; Richter *et al.*1997, Reed and Czech 2005). Habitats, however, may be defined by a long suite of environmental conditions (Roger *et al.* 2005, Bouchard and Boisclair 2008). One objective of conservation biology is to identify the key habitat attributes that should be preserved to ensure the survival of populations (Rosenfeld and Hatfield 2006). Habitat quality models (HQM) are particularly suitable tools to achieve this objective because they are, by definition, relationships between distributional (fish presence/absence, density, biomass, etc; Weaver *et al.* 1997, Roger *et al.* 2005, Turgeon and Rodriguez 2005) or fitness indices (growth, survival, etc.; Brandt *et al.* 1992, Tyler and Brandt 2000) of habitat quality for fish and environmental conditions (Boisclair 2001). Environmental conditions that explain a significant fraction of the variability of habitat quality indices are taken as key habitat attributes.

HQM based on distributional indices are often developed using a large number of relatively small sites (50-500 m; Fausch *et al.* 2002) selected to maximize the range of environmental conditions modelled. This strategy may be anticipated to increase the explanatory, and eventually the predictive, power of HQM and to increase the range of environmental conditions under which HQM can be applied. However, logistical constraints often imply that each site is surveyed only once over a few months (e.g. Wiley *et al.* 2004, Turgeon and Rodriguez 2005) or a few years (e.g. Wang *et al.* 2006, Heitke *et al.* 2006, Infante *et al.* 2006). The survey design used by such studies presumes that it is preferable to survey a larger number of sites once, rather than a smaller number of sites on a few occasions; the surveying of space (numerous sites) is given precedence over the surveying of time (repeated survey of sites). This survey design is here defined as the space-over-time precedence (STP).

The assumption that surveying sites only once is sufficient to develop HQM may be related to the restricted movement paradigm (RMP; Gowan *et al.* 1994). The analysis of numerous mark-recapture experiments led Gerking (1959) to note that fish from 34 species (from 12 families including centrarchids, salmonids, and cyprinids) inhabiting rivers may possess small home ranges (20 m; Miller 1957) and may display only restricted movements (distances not specified). RMP may have been taken by scientists as an indication that surveying fish only once in a series of sites may be suitable to develop HQM in rivers. However, observations in rivers of frequent and important movements by fish, belonging to numerous species, have challenged the validity of RMP (Young 1994, Fausch and Young 1995, Matthew *et al.* 1995, Albanese *et al.* 2004, Baade and Fredrich 2005, Belica and Rahel 2008). Similarly, fish community characteristics such as composition, density, and biomass within a site have been shown to vary among hours of the day (Hohausova *et al.* 2003, Imre and Boisclair 2004, Bédard *et al.* 2005), days of a season (Gowan *et al.* 1994, Schlosser 1998, Albanese *et al.* 2004), and years (Lohr and Fausch 1997). Temporal variance of distributional indices of fish habitat quality at specific sites has been identified as a threat to the development of operational HQM (Gowan *et al.* 1994, Young, 1995). Yet, the effects of this temporal variance and the consequences of STP on HQM have never been assessed.

The objectives of this study are to: 1) quantify the temporal variability of fish community characteristics estimated in a series of sites surveyed during a seven week period of a summer, 2) determine the effect of different survey design on the explanatory power of HQM developed for different fish species, and 3) evaluate the effect of different survey designs on the identity of the environmental conditions found to explain a statistically significant proportion of the variability of fish community characteristics.

Materials and methods

We repeatedly surveyed fish community characteristics (10 replicate estimates of fish density per species) and environmental conditions (1 to 10 times depending on the environmental condition) at 18 sites. The data were used for three purposes: First, to assess the difference between HQM developed for each fish species by surveying individual sites a different number of times; second, to quantify the structure of the spatial and the temporal variances of fish community characteristics and the co-variation among environmental conditions; and third to simulate the effects on HQM of different trade-offs between the number of sites [s] and the number of times sites were surveyed [t], for a constant total field effort [s x t].

Study area and survey sites

Surveys were conducted at 18 sites distributed within rivers of two adjacent watersheds (Rivière du Nord: Laurentian Region; Rivière Rouge: Outaouais Region; Figure 1) that flow into the Rivière des Outaouais. These rivers flow on the granitic bedrock of the Canadian Shield until they reach an altitude of 230 m above sea level. Below this altitude the landscape is covered by clay and silt deposited when the Champlain Sea occupied the valleys of the Rivière des Outaouais and the Fleuve St-Laurent until approximately 9 000 to 10 000 B.P. (Occhietty *et al.* 2001, Cronin *et al.* 2008). The sites surveyed were 100 m long in the upstream-downstream axis of the rivers. Sites were further divided into 10 sections of 10 m each delimited by flags positioned on shore.

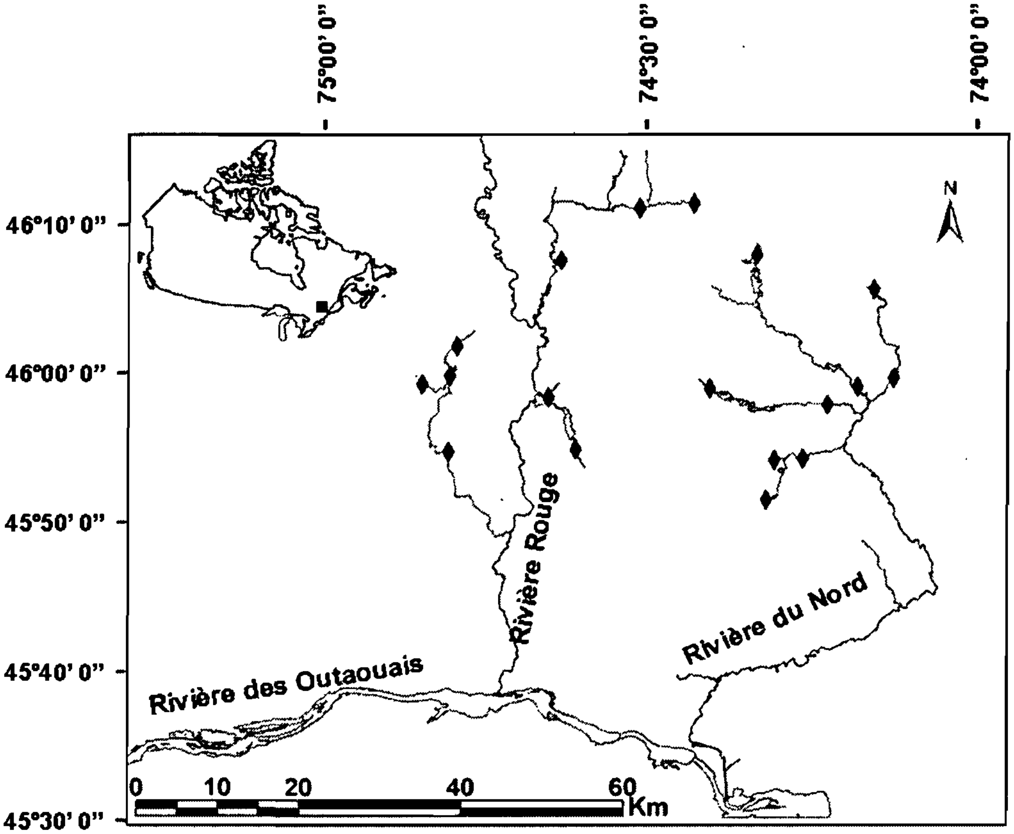

Figure 1: Distribution of the 18 sampling sites in the watersheds of Rivière Rouge and Rivière du Nord, Québec, Canada. Sites are identified by black diamonds.

Fish community characteristics

Fish community characteristics at each site were estimated 10 times between June 16th and August 10th 2007 (further referred to as the survey period). Surveys for fish community characteristics were conducted between 10:00 and 16:00 under a cloud cover ≤50% to avoid the potential effects of time of day and cloud cover on fish data (Bédard *et al.* 2005; Girard and Boisclair 2003). Fish community characteristics were collected by underwater visual observations done by three snorkellers trained for fish counts, species identification, and length assessment. One snorkeller was positioned in the thalweg (deepest part of the cross-section of the river) and the two others remained as close as possible to each shore, but at depths no shallower than 0.25 m. When no distinct thalweg could be identified, the corresponding snorkeller was positioned in the middle of the river. Snorkellers progressed upstream to minimize fish disturbance and thereby collected fish observations along three transects (left shore, thalweg, right shore) presumed to represent the complete range of environmental conditions present at a site. Snorkellers wore white polystyrene tubes on their forearm to note the number of fish observed by species at each 10 m interval. Fish <5 cm in total length were excluded from survey because their density at a location was expected to be more closely associated with the presence of a spawning site than with habitat selection. In each 10 m section, snorkellers noted the distance (by classes of 25 cm), on either side (left and right), at which fish could be counted and identified with certainty, and limited their observations to such conditions. The sum of these distances defined the width surveyed by 10 m section for each transect. The area represented as the product of 10 m and the width surveyed in a given transect is defined as a counting strip (e.g. 10 m section in which fish can be observed over 1 m left and right from the snorkeller = a 20 m^2 counting strip). The total surface area surveyed (m^2) in each 100 m site was therefore calculated as the sum of the surface area of 30 counting strips (10 sections x 3 counting strips). Fish density (abundances$\cdot m^{-2}$) in each 100 m site was estimated for each species by dividing the total number of fish observed in the 30 counting strips by the total surface area surveyed in this site. Spatial coefficients of variation (SCV = spatial standard deviation of fish density / mean fish density) of fish density were calculated for each species. The standard deviation used to calculate SCV was estimated using the variance of the mean values of fish density at each site. Temporal coefficients of variation (TCV = temporal standard deviation of fish density / mean fish density) were calculated for each combination of species and sites as the ratio of the standard deviation of fish density at a site and the mean fish density at this site.

Environmental conditions

Environmental conditions noted at each site were divided in three groups of variables that defined how many times each condition would be estimated in the field. First, 'temporally stable environmental conditions' were variables anticipated or noted not to vary significantly during the survey period. These variables were the substrate composition of the riverbed, the percentage of the riverbed covered with macrophytes, the percentage of the riverbed covered with branches, and the number of culverts, islands, offshoots, or tributaries present at each site. Macrophytes did grow in height during the survey period but the surface they covered remained relatively constant during the seven weeks of survey. These seven variables were estimated only once during the survey period. Second, 'temporally dynamic environmental conditions' were variables that were expected to vary, but within the bounds of river morphology and hydrodynamics. Temporally dynamic variables were river width, river depth, and flow velocity. These variables were estimated three times during the survey period; at the highest, intermediate, and lowest flows recorded at any given site during the survey period. Third, 'temporally unstable environmental conditions' were variables expected to vary the most from one survey to another. These variables were cloud cover and water temperature, and were recorded on each visit to a site.

Temporally stable and dynamic environmental conditions were quantified in each counting strip. Substrate composition, macrophyte cover, and branch cover were estimated visually. Substrate composition was defined as the percent contribution of nine types of substrate to the riverbed surface area (see Wolman 1954; Latulippe *et al.* 2001 for more details). Macrophyte cover and branch cover were estimated as the percentage of the riverbed surface covered by aquatic plants or branches. Culverts were counted if present within 5 meters of the limits of the sites. Islands, offshoots, and tributaries were counted in each site. River width was measured in the middle of each 10 m section (measuring tape; ±0.5 m). River depth (measuring rod; ±5 cm) and flow velocity (Gurley Pygmy flow meter; 30 seconds at 40% of the water column e.g. at 40 cm from bottom in 1 m of water) were measured in the middle of each counting strip. The thirty values of temporally stable and dynamic environmental conditions (one per counting strip) were averaged to describe the 100 m sites. One exception to this rule was river width ($n = 10$). The percentage of cloud cover was estimated visually. Water temperature was measured at a location chosen haphazardly in the trajectory of the thalweg at a depth of 15 cm with a hand thermometer held in the water for approximately 60 seconds. Habitat heterogeneity within sites was represented by the coefficient of variation (CV) of the three dominant types of substrate (silt, sand, and cobble), of flow velocity, and of water depth.

Development of habitat quality models from the field survey

HQM based on the field survey were developed for each species using multiple linear regression analyses. Fish density, observed at the 18 sites, was explained by combinations of environmental conditions. Stepwise forward selection was used to identify the explanatory variables that were significant at $p<0.05$ and that contributed to an increase in the adjusted R^2 (R^2_{adj}) of the HQM by >0.05 (Langage R, package Packfor). The R^2_{adj} was used as criterion because Ohtani (2000) has shown that it is an unbiased estimator of the contribution of a set of explanatory variables to the explanation of the response variable in multiple regressions. HQM were developed using a maximum of four explanatory variables. HQM were developed for each species using the mean fish density estimated during the 10 surveys per site as dependent variables. Five species were selected to assess the effect of the number of surveys per site on HQM. These species were chosen to represent the ranges of spatial and temporal variances of species occurrences and families (see Results). HQM for these five species were developed using the mean fish density estimated for 1 to 10 surveys per site as dependent variables. For HQM developed on less than 10 surveys per site, 5000 repetitions were used to evaluate the explanatory power (cumulative R^2_{adj}) of HQM. For each repetition, the appropriate number of surveys was randomly selected within the original dataset describing each site.

Development of a simulation domain

The 18 sites surveyed 10 times were used to assess the difference between HQM developed for each species by surveying individual sites a different number of times. However, during this exercise, the number of sites [s] used to develop HQM was always 18 (which may not be sufficient to develop HQM) and, as the number of times sites were surveyed [t] increased, the total field effort [s x t] also increased. This confounded the effect of the number of surveys per site and the effect of total field effort. We generated a framework, hereafter referred to as a simulation domain, to develop HQM with more than 18 sites and to assess the effect on HQM of increasing the number of surveys per site for a constant total field effort.

We used the mean and the variance among sites of water depth, flow velocity, substrate size, and macrophyte cover estimated for the 18 sites to generate the environmental conditions assigned to 10 000 sites comprised in the simulation domain. These four environmental conditions were used because they were anticipated to play a role in determining fish community structure in rivers (Gorman and Karr 1978, Albanese 2004). In the 18 sites surveyed, flow velocity tended to increase as water depth decreased ($r = -0.47$; $p < 0.1$), substrate grain size increased as flow velocity increased ($r = 0.79$; $p < 0.05$), and macrophyte cover increased as grain size decreased ($r = -0.82$; $p < 0.05$). The development of the environmental conditions prevailing in the simulation domain proceeded in five steps: first, we developed three probability distributions relating water depth to flow velocity (representing the probability of a given flow velocity for a specific water depth), flow velocity to grain size (representing the probability of a given grain size for a specific flow velocity), and grain size to macrophyte cover (representing the probability of a given macrophyte cover for a specific grain size). Second, we generated a frequency distribution of water depth based on the values noted in the 18 sites. Water depth was randomly assigned to each of the 10 000 sites according to this frequency distribution. Third, we assigned a flow velocity to each site given its water depth. Flow velocity for a given water depth was randomly assigned according to their joint probability distribution. For the fourth and fifth steps, the same procedure was used to assign substrate grain size (according to its joint probability with flow velocity) and macrophyte cover (according to its joint probability with grain size) to each of the 10 000 sites of the simulation domain. The environmental conditions of the simulation domain therefore respected the spatial variation and the correlations among environmental conditions estimated from field observations.

Five multiple linear regressions, one for each species subjected to a detailed analysis of HQM (see Development of habitat quality models from the field survey), were computed to obtain estimates of mean fish density in the 10 000 sites of the simulation domain using water depth, flow velocity, substrate grain size, and macrophyte cover as independent variables. The coefficients of each multiple linear regression were selected to produce fish density values that reflected the range of mean fish density observed in the field and the probability of observing species at a site. Because the mean density of a species at a given site was produced by a single multiple regression equation for all sites, the overall correlation between the density of that species and the environmental conditions in the simulation domain was expected to approach unity. Once a value of mean fish density was attributed to the 10 000 sites for each species, 10 individual values of fish density for each species (representing 10 visits to each site of the simulation domain) were produced at each site of the simulation domain such that, for each species, the mean of these values reflected the mean fish density attributed to a site and the variance of these values reflected the temporal variance of fish density values observed in the field. Finally, four simulated environmental conditions (i.e. A, B, C, D), not directly correlated to fish but correlated to depth, substrate, velocity, and macrophyte cover, were incorporated in the dataset of independent variables. A, B, C, and D were created by adding a random value to each environmental condition assigned to the sites of the simulation domain (depth, substrate, velocity, and macrophyte cover). Random values were taken from a normal distribution having a mean of zero and a standard deviation equal to 15. This standard deviation was selected because it resulted in correlations between depth, substrate, velocity, and macrophyte cover, and A, B, C and D that covered the same range as that observed between depth, substrate, velocity, and macrophyte cover and other environmental conditions noted in the field but not correlated to fish density ($r = 0.42$ to 0.77).

Development of habitat quality models from the simulation domain

HQM based on the simulation domain were developed using a statistical approach identical to that used for field data. However, the simulation domain allowed us to assess the effect of different combinations of the number of sites [s] and of the number of times sites were surveyed [t] on HQM. HQM were developed for the five fish species of the simulation domain using constant total field effort ([s x t] = 200) and five combinations of the number of sites [s] and the number of times sites were surveyed [t]: 200 sites·1 visit per site; 100 sites·2 visits per site; 67 sites·3 visits per site; 50 sites·4 visits per site; 40 sites·5 visits per site; 25 sites·8 visits per site. For each [s x t] combinations, 10 000 HQM were computed after randomly selecting sites and visits to sites from the simulation domain.

Results

Fish community characteristics

A total of 23 542 fish from 24 species were recorded during the 180 surveys (18 sites surveyed 10 times) performed over the seven week survey period. The number of species observed per site ranged from 7 to 13. The species with the highest occurrences were the pumpkinseed sunfish (*Lepomis gibbosus*) and rock bass (*Ambloplites rupestris*), which were observed at least once at every site. The common shiner (*Notropis cornutus*) and pumpkinseed sunfish (*Lepomis gibbosus*) comprised respectively 12% and 10% of the fish recorded. Mean fish density per species ranged from 1.37 x 10^{-5} (central mudminnow, *Umbra limi*) to 0.66 fish·m^{-2} (common shiner). The largemouth bass (*Micropterus salmoides*), longnose dace (*Rhinichthys cataractae*), slimy sculpin (*Cottus cognatus*), dard-perch (*Percina caprodes*), muskellunge (*Esox masquinongy*), brown bullhead (*Ictalurus nebulosus*), brook stickleback (*Culuaea inconstans*) and central mudminnow (*Umbra limi*) had a mean fish density < 0.001 fish·m^{-2} (less than two fish per site). Although the density of fathead minnow (*Pimephales promelas*), bluntnose minnow (*Pimephales notatus*), johnny darter (*Etheostoma nigrum*), redbelly dace (*Phoxinus eos*), and finescale dace (*Phoxinus neogaeus*) were noted, the identification of these species was sometimes difficult to ascertain. The records we have of these species suggest that their total density represented on mean 7% of the fish communities. Therefore, the remaining analyses focused on the eleven species for which mean fish density > 0.001 fish·m^{-2} and for which species identification was reliable (Table 1).

Spatial coefficients of variation (SCV) of fish density ranged from 1.45 (brook charr; *Salvelinus fontinalis*) to 4.11 (golden shiner; *Notemigonus crysoleucas*). Temporal coefficients of variation (TCV) of fish density per site ranged from 0.29 (brook charr) to

2.56 (common shiner). TCV varied from 2.51-fold (smallmouth bass; *Micropterus dolomieu*) to 6.5-fold (rock bass) among sites. TCV of 6 of the 11 species analysed varied > 3-fold among sites. Mean TCV across sites ranged from 0.54 (brook charr) to 1.42 (common shiner). Ranking of mean TCV indicated that species possessing similar mean TCV also tended to belong to the same families (Table 1).

Table 1: Observed fish density, number of site occurrences (/18), and spatial (SCV) and temporal (TCV) coefficients of variation of the most frequent species.

Species	Observed density (fish · m^{-2})			Number of site occurrences	SCV	TCV		
	min	max	mean			min	max	mean
Brook charr (*Salvelinus fontinalis)*	0	0.024	0.002	3	1.45	0.29	1.02	0.54
Smallmouth bass (*Micropterus dolomieu*)	0	0.049	0.007	12	3.29	0.76	1.91	0.98
Pumpkinseed sunfish (*Lepomis gibbosus)*	0.001	0.182	0.045	18	1.55	0.38	1.92	1.03
Rock bass (*Ambloplites rupestris*)	0.001	0.093	0.019	18	1.91	0.38	2.46	1.15
Yellow perch (*Perca flavescens*)	0	0.141	0.016	14	2.13	0.92	2.36	1.17
White sucker (*Catostomus commersoni*)	0	0.068	0.009	17	2.10	0.79	2.08	1.18
Cutlips minnow (*Exoglossum maxillingua*)	0	0.144	0.017	12	2.58	0.45	2.16	1.23
Creek chub (*Semotilus atromaculatus*)	0	0.226	0.036	16	2.23	0.88	2.39	1.30
Golden shiner (*Notemigonus crysoleucas*)	0	0.294	0.021	10	4.11	0.81	2.50	1.37
Fallfish (*Semotilus corporalis*)	0	0.224	0.038	16	1.54	0.53	2.42	1.40
Common shiner (*Notropis cornutus*)	0	0.228	0.066	16	1.60	1.03	2.56	1.42

The only species of Salmonidae (brook charr) had the lowest mean TCV, followed by the three species of Centrarchidae (smallmouth bass, pumpkinseed sunfish, and rock bass), the Percidae (yellow perch; *Perca flavescens*), the Catostomidae (white sucker; *Catostomus commersoni*), and the five species of Cyprinidae (cutlips minnows; *Exoglossum* *maxillingua*, creek chub; *Semotilus atromaculatus*, golden shiner, fallfish; *Semotilus corporalis*, and common shiner).

Environmental conditions

Substrate composition of the riverbed was highly heterogeneous among sites (Table 2). Silt and sand had the highest mean percent contribution to riverbed composition (35.6% and 23.4% respectively), but these types of substrate had low percent contribution to specific sites.

Table 2: Minimum, maximum, and mean values of environmental descriptors estimated at the 18 sites.

Variables	Site descriptors		
	min	max	mean
Substrate type (% cover)			
- clay	0	1.5	0.1
- silt	1.8	96.9	35.6
- sand	0	61.4	23.4
- gravel	0.4	26.9	12.6
- pebble	0	37.7	10.8
- cobble	0	48.4	13.3
- boulder	0	26.6	4.9
- metric boulder	0	12.5	1.0
- bedrock	0	1.6	0.2
Macrophyte cover (%)	0	95	22
Branch cover (%)	1	23	9
Culvert (#)	0	1	0.1
Island (#)	0	4	0.4
Offshoot (#)	0	5	1
Tributary (#)	0	3	0.5
River width (m)	7.4	24.2	15
Water depth (cm)	38	129	68
Flow velocity (cm· s^{-1})	0	56	15
Water temperature (° C)	17	25	21

In contrast, pebble, cobble, and boulder had mean percent contributions that ranged from 4.9% to 13.3%, yet they represented as much as 26.6% to 48.4% of the riverbed. Macrophyte cover was also variable among sites and ranged from 0 to 95% (average = 22%). Branch cover was less variable (1 to 23%) and less important (average = 9%). Culverts, islands, offshoots, and tributaries were relatively rare with mean values ≤ 1 per site. Mean river width at the sites ranged from 7.4 to 24.2 m, while mean river depth ranged from 0.38 to 1.29 m. Mean flow velocity ranged from 0 to 56 cm·sec^{-1}. Most sites showed relatively low flow velocities as indicated by the mean of all sites (15 cm·sec^{-1}). Mean water temperature at sites ranged from 17 to 25°C. The mean coefficients of variation (SCV) of the three dominant types of substrate (silt, sand, and cobble), of flow velocity, and of water depth, which were calculated to represent habitat heterogeneity within sites, ranged from 37 to 136 (Table 3).

Table 3: Spatial coefficients of variation (SCV) of environmental descriptors used to describe the spatial heterogeneity of the 18 sites.

	SCV		
Variables	min	max	mean
Substrate type			
- silt	5	239	107
- sand	0	140	85
- cobble	0	547	136
Water depth (cm)	25	49	37
Flow velocity (cm· s^{-1})	47	290	118

Habitat quality models based on field data

HQM developed for the eleven species for which mean density was >0.001 fish· m^{-2} and identification was reliable, explained 0% (yellow perch) to 91% (golden shiner) of the variations in fish density (average = 65%; Table 4). The most important explanatory variables were macrophyte cover (4 models; contribution to R^2_{adj} from 16 to 57%), culvert number (3 models; contribution to R^2_{adj} from 14 to 54%), flow velocity CV (3 models; contribution to R^2_{adj} from 18 to 39%), and water temperature (3 models; contribution to R^2_{adj} from 5 to 22%). The first two environmental conditions included in the HQM explained 0 (yellow perch) to 76% (golden shiner) of among-site variations in fish density (average = 52%).

Table 4: HQM developed for 11 species, using the mean of 10 surveys, to describe the fish community at each site. R^2_{adj}: change in R^2_{adj} associated with the addition of the variable.

Species	**Models**					**Cum. adj. R2**
Brook charr	1.2e-05 (FV CV) R^2_{adj} = 0.39	+ 2.7e-04 (SD CV) R^2_{adj} = 0.05	- 2.6e-03			0.44
Smallmouth bass	0.071(FV) R^2_{adj} = 0.40	- 0.0018 (ST) R^2_{adj} = 0.20	- 0.0013 (BR) R^2_{adj} = 0.14	+ 0.0017 (WT) R^2_{adj} = 0.05	+ 0.069	0.79
Pumpkinseed sunfish	0.066 (BC) R^2_{adj} = 0.29	+ 0.0027 (WT) R^2_{adj} = 0.22	+ 0.0023 (MC) R^2_{adj} = 0.19	+ 0.0029 (TB) R^2_{adj} = 0.11	- 0.26	0.81
Rock bass	- 0.057 (SD CV) R^2_{adj} = 0.28	- 0.00040 (CB) R^2_{adj} = 0.26	- 0.036 (OF) R^2_{adj} = 0.16	- 0.0017 (ID) R^2_{adj} = 0.10	+ 0.16	0.80
Yellow perch	NULL					0
White sucker	6.3e-05 (OF) R^2_{adj} = 0.24	+ 2.9e-02 (WP) R^2_{adj} = 0.14	- 1.4e-04 (HB) R^2_{adj} = 0.09	- 9.9e-03 (BR) R^2_{adj} = 0.07	- 1e-02	0.54
Cutlips minnow	0.00018 (FV CV) R^2_{adj} = 0.38	+ 0.0096 (MB) R^2_{adj} = 0.35	- 0.0010			0.73
Creek chub	0.036 (CU) R^2_{adj} = 0.54	- 0.012 (WT) R^2_{adj} = 0.16	+ 0.084 (BC) R^2_{adj} = 0.08	+ 0.00033 (DT) R^2_{adj} = 0.06	+ 0.23	0.84
Golden shiner	0.0028 (MC) R^2_{adj} = 0.57	- 0.052 (SD) R^2_{adj} = 0.19	- 0.011 (HB) R^2_{adj} = 0.09	+ 0.024 (TB) R^2_{adj} = 0.06	+ 0.019	0.91
Fallfish	-0.0015 (ST CV) R^2_{adj} = 0.29	- 0.0018 (MC) R^2_{adj} = 0.28	- 0.0012 (SD) R^2_{adj} = 0.06	+ 0.23		0.63
Common shiner	0.22 (WP) R^2_{adj} = 0.35	+ 0.28 (FV CV) R^2_{adj} = 0.18	- 0.069 (MC) R^2_{adj} = 0.16	+ 0.047		0.69

Silt = ST, Sand = SD, Cobble = CB, Metric boulder = MB, Bedrock = BR, Macrophyte cover = MC, Branches cover = BC, Culvert = CU, Island = ID, Offshoot = OF, Tributaries = TB, Depth= DT, Flow velocity = FV, Water temperature = WT, Hydrographic basin = HB, Coefficient of variation = CV.

The five species selected to assess the effect of the number of surveys per site on HQM were the brook charr, the smallmouth bass, the pumpkinseed sunfish, the white sucker, and the common shiner. The explanatory power of HQM tended to increase as the number of surveys per site (1 to 10) and the total field effort increased (from 18 to 180; Figure 2). However, the magnitude of this effect varied among species. Increasing the number of surveys per site from 1 to 10 or the total field effort from 18 to 180 increased the explanatory power of HQM by 7% for brook charr and by 43% for pumpkinseed sunfish. Intermediate increases in explanatory power of HQM were noted for common shiner (26%), smallmouth bass (19%), and white sucker (16%).

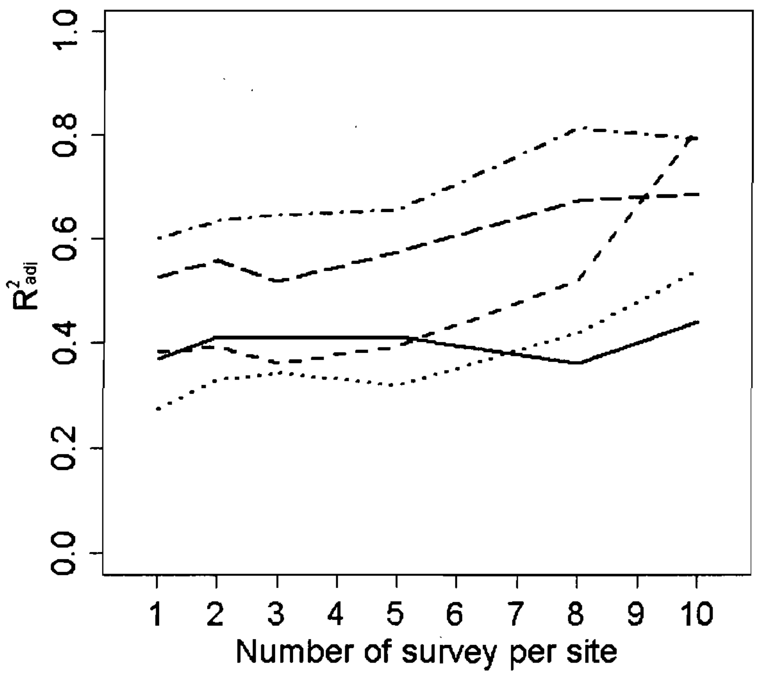

Figure 2: Effect of the number of survey per site on the explanatory power (R^2_{adj}) of habitat quality models developed for brook charr (solid line), smallmouth bass (dashed-dotted line), pumpkinseed (small broken line), white sucker (large broken line), and common shiner (dotted line).

Simulation domain

The mean explanatory power of the 10 000 HQM developed for the five species of the simulation domain increased asymptotically as the number of surveys per site increased (Figure 3). The increase in mean R^2_{adj} of HQM ranged from 5% (brook charr) to 42% (common shiner) as the number of surveys per site increased from 1 (200 sites surveyed) to 8 (25 sites surveyed). This increase for the other species was 27% (smallmouth bass), 33% (pumpkinseed sunfish), and 34% (white sucker). On average, 48% (from 40 to 68%) of the increase in the mean R^2_{adj} of HQM occurred as the number of surveys per site increased from 1 to 2. A corresponding value as the number of surveys per site increased from 1 to 3 was 67% (from 62 to 75%). Hence, most of the potential increase in mean R^2_{adj} of HQM occurred as the number of surveys per site increased from 1 to 3.

The 95% confidence intervals (CI) of the explanatory power of HQM, developed using the simulation domain for the five species, tended to increase as the number of surveys per site increased (Figure 3). This situation, which may be related to the decrease of the number of sites used to develop HQM (total field effort being kept constant at [s x t] = 200), varied among species. The lower and the upper limits of the 95% CI of the R^2_{adj} of HQM developed for brook charr, using 200 sites surveyed once, were respectively 73% and 90% (CI = 17%). In contrast, the CI for HQM developed for this species using 8 surveys to 25 sites was 42%. Thus, the CI of the R^2_{adj} of HQM for brook charr increased by 145% ([42%-17%]/17%) as the number of surveys per site increased from 1 to 8. Under the same range of survey design, the CI of the R^2_{adj} of HQM for other species was less affected and increased by 57% (pumpkinseed sunfish), 43% (common shiner), 42% (white sucker), and 28% (smallmouth bass). The mean CI of the R^2_{adj} of HQM (all species combined) increased

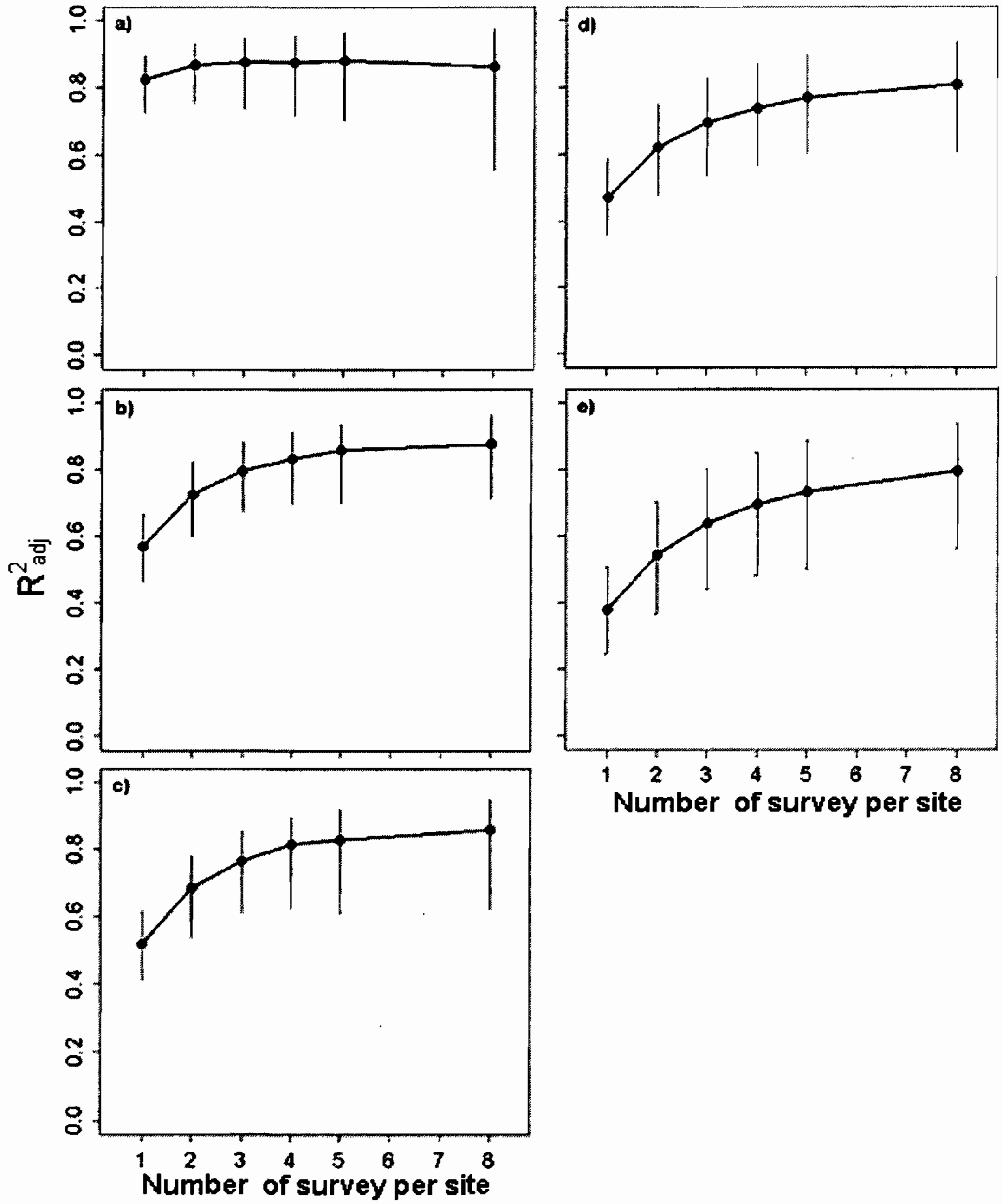

Figure 3: Mean explanatory power (R^2_{adj}) of habitat quality models developed using different combinations of number of sites and number of surveys per site with a constant field effort (200 fish surveys). Habitat quality models were developed following 10 000 simulations for (a) brook charr, (b) smallmouth bass, (c) pumpkinseed, (d) white sucker and (e) common shiner. Vertical lines represent 95% CI of R^2_{adj}.

by 33% as the number of surveys per site increased from 1 to 2, and by 45% as it increased from 1 to 3. Hence, for most species modelled, the greatest increase in CI of the R^2_{adj} of HQM occurred when the number of surveys per site increased from 3 to 8 (the number of sites surveyed from 67 to 25).

The frequency of selection of the four appropriate explanatory variables (those used to generate fish density values in the simulation domain) tended to decrease as the number of sites decreased and the number of surveys per site increased. This tendency varied among species. For brook charr, the frequency of selection of the appropriate explanatory variables decreased by 2 to 56%, depending on the variable (mean = 21%), as the number of sites decreased from 200 to 25 and as the number of surveys per site increased from 1 to 8 (Figure 4). Equivalent changes in the survey design reduced the frequency of selection of the appropriate explanatory variables, on average, by 13%, 5%, and 4% for smallmouth bass, pumpkinseed sunfish, and white sucker respectively. Common shiner was the only species for which the selection of the appropriate explanatory variables was not affected by the survey design. Similarly, the frequency of selection in HQM of variables related to depth, substrate, velocity, and macrophyte cover, but not to fish density (inappropriate variables), tended to decrease as the number of sites decreased and the number of surveys per site increased. The mean decreases (four variables combined) of the frequency of selection in HQM of inappropriate variables were: 11% (brook charr), 4% (smallmouth bass), 3% (pumpkinseed), 3% (white sucker), and 0% (common shiner). The effect of the number of surveys per site on the frequency of selection of inappropriate variables was therefore less pronounced than for appropriate explanatory variables.

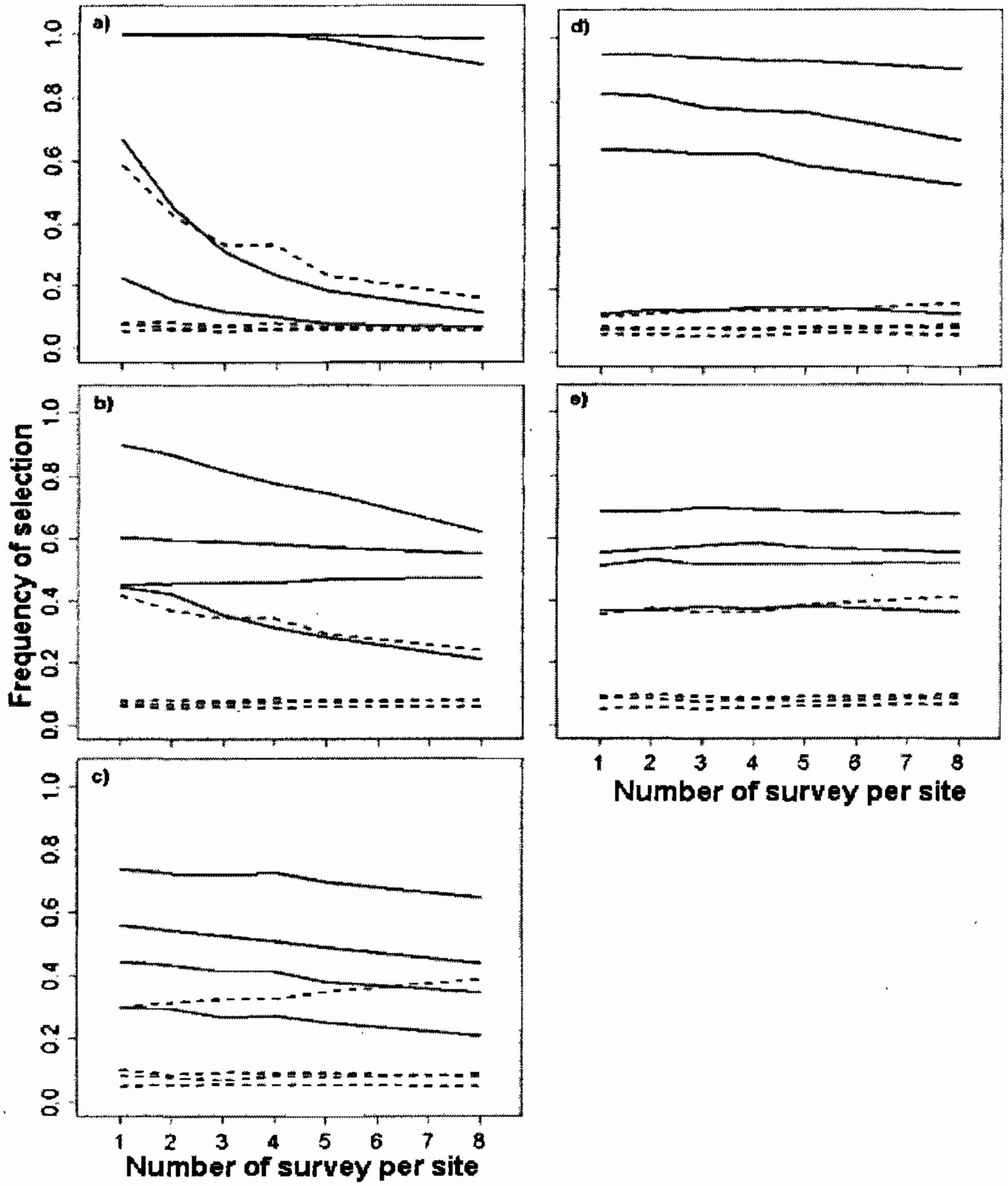

Figure 4: Frequency of selection of appropriate (broken lines) and inappropriate (solid lines) variables for habitat quality models developed using different combinations of number of sites and number of surveys per site with a constant field effort (200 fish surveys). Habitat quality models were developed following 10 000 simulations for (a) brook charr, (b) smallmouth bass, (c) pumpkinseed, (d) white sucker, and (e) common shiner.

Discussion

This study showed that fish density can vary substantially (temporal coefficients of variation, TCV, up to 2.56) among surveys to a series of sites. It has long been recognized that fish density at a site can vary through time. However, most studies focus on inter-annual variation of fish density that may be attributed to processes related to population dynamics (Moyle and Vondracek 1985, Danehy *et al.* 1998, Oberdorff 2001). Studies that document variation in fish density over shorter time intervals are often based on groups of species (e.g. Gorman and Karr 1978; 33 to 68% changes in total fish community density between June and September, Schlosser and Ebel 1989; 6- to 10-fold changes in total cyprinids density between May and June). In addition, the precise time of survey (day, night, dusk, dawn; mean over 24 h) and the meteorological conditions (percent cloudiness, rain), which may affect estimates of fish density (Gaudreau and Boisclair 2000, Girard *et al.* 2003, Bédard *et al.* 2005), are rarely documented or considered. Comparison of TCV estimated by the present study, with published values calculated over similar time intervals, is further complicated by the expected negative relationship between TCV and the size of the sites which often varies among studies (Imre and Boisclair 2004, 10 m; Moyle and Vondracek 1985, 30-40 m; Oberdorff 2001, >100m; Danehy *et al.* 1998, 30 times bankfull width ≈ 90-200m). One contribution of the present study is therefore to show that the density of individual species can vary substantially among surveys to a series of sites even when data are collected over a relatively well defined period of the summer (7 weeks), under standardized times of day (from 10:00 to 16:00) and meteorological conditions (<50% cloudiness).

TCV estimated during the present study differed among species and appeared related to taxonomy. The ranking of TCV resulted in the grouping of species by families.

Brook charr had the lowest mean TCV (0.54), while species of cyprinids had the largest mean TCV (1.23 to 1.42). Low TCV for the only salmonid species observed is consistent with the suggestion that this family contains species that may display site fidelity or territoriality (Bridcut *et al.* 1993, Bridger *et al.* 2001, Steingrímsson 2003). However, this should not be taken as an indication that all salmonids display site fidelity or territoriality. Similarly, the present study should not be taken as an indication that riverine salmonids do not perform significant movements. In the present study, fish were not marked and their movements were not assessed. Recent studies designed to assess fish movements indicate that salmonids populations may be composed of both mobile and sedentary individuals in variable proportions (Heggenes *et al.* 1991, Rodriguez 2002, Scruton *et al.* 2003). The present study may suggest, however, that despite potential movements, the density of brook charr may be consistently (from one survey to another) higher at certain sites than others. The higher TCV associated with species of cyprinids may be related to a common observatory bias. The species of cyprinids present at the sites all have small body size that makes them more difficult to observe than fish belonging to other families. Small fish such as cyprinids may be more prone to cryptic, evasive, or gregarious behaviours. The difference between the presence and the absence of a shoal of cyprinids at a site may have a strong effect on its TCV. Notwithstanding the cause of the high TCV for cyprinids, our study suggests that accurate assessment of the density of cyprinids may require more surveys per sites than is needed for other families.

HQM developed using the field data were affected by survey design defined by different combinations of the number of sites and the number of surveys per site. The mean R^2_{adj} of HQM based on field data tended to increase with the number of surveys per site. The smallest increase (7%) was noted for brook charr and the largest increase (43%) with pumpkinseed sunfish. This analysis does not permit an appropriate evaluation of the effect of survey design on HQM because of an insufficient number of sites. This problem was circumvented by developing a simulation domain that possessed the four attributes necessary to test the effect of STP on HQM: a large number of sites, a large number of surveys per site, spatial and temporal variations (and co-variations) in dependent variables (fish density), and spatial variations (and co-variations) of independent variables (environmental conditions) similar to those observed in the field. HQM developed based on the simulation domain confirmed the analyses of field surveys by indicating that the mean R^2_{adj} of HQM increased with the number of visits per survey design and that the intensity of this effect could vary among species (Figures 2 and 3). Both analyses, however, differed on particular points. For instance, the specific HQM that benefited most from the increase in the number of surveys per site and the magnitude of this effect differed slightly between the analyses based on field data and those based on the simulation domain. Field-based HQM of pumpkinseed sunfish showed the largest increase of mean R^2_{adj} as the number of surveys per site increased from 1 to 8. Analyses based on the simulation domain suggested that the HQM of common shiner had the largest increase in mean R^2_{adj} for a similar increase in the number of surveys per site. Three elements may be suggested to explain these differences. First, when developing field-based HQM, the total field effort increased as the number of surveys per site increased. In contrast, when developing HQM based on the simulation domain, the total field effort was kept constant and the number of sites decreased as the number of surveys per site increased. Second, the HQM developed using the field data were based on the re-surveying of a much smaller number of sites (18) than for the simulation domain (10 000). Third, the field dataset comprised more environmental conditions than the simulation domain (Table 2). These elements can affect the exact progression of the mean R^2_{adj} of HQM as the number of surveys per site increases (Figures 2 and 3). It is useful to emphasize that while the HQM developed using the field data may have an ecological meaning (accurate relationship between fish density and environmental conditions for the 18 sites), the HQM developed using the simulation domain have no ecological meaning (they do not represent the absolute or relative effects of environmental conditions on fish density in nature). The simulation domain was created to reflect the spatial and the temporal structures of the variation and the co-variation of specific variables observed in the field, to produce a dataset in which relationships between fish density and environmental conditions (HQM) are imbedded, and to evaluate the effect of the number of sites and the number of surveys per site on our ability to recover these relationships. Hence, HQM developed using the simulation domain have a mathematical meaning useful to identify the proper survey design given specified variation and co-variation structures that reflect those found under natural conditions.

HQM developed using the simulation domain indicated that an increase of the number of surveys per site increased the CI of R^2_{adj} of HQM. Given that the total field effort was kept constant when developing HQM based on the simulation domain, this observation suggests that HQM developed with fewer sites are more variable. The amplitude of CI differences between 1 and 8 surveys per site was tightly correlated with SCV. This result suggests that species having low SCV are more affected by the use of fewer sites than species having high SCV.

Differences in survey design affected the capacity of HQM to identify the adequate environmental conditions that explained variations in fish density (Figure 4). The effect of survey design varied among species and appeared related to TCV. The selection of appropriate explanatory variables by HQM developed for species having low TCV was more directly related to the number of sites than to the number of surveys per site. In contrast, the probability of selecting the appropriate explanatory variables was unaffected by the survey design for the common shiner (highest TCV).

The present study explored the assumption of space-over-time precedence which suggests that, to maximise the explanatory and eventually the predictive power of HQM, it may be preferable to survey a large number of sites once rather than to survey fewer sites repeatedly. STP is an implicit component of survey design used to develop HQM, particularly when total field effort is a limiting factor. The comparative analyses and simulations indicated that survey design should not be applied broadly and that the validity of survey design based on STP may depend on the interaction between SCV and TCV. In this context, the present study suggests that the validity of survey design based on STP may vary among species. HQM developed for species characterized by low TCV may benefit from surveying a large number of sites only once. For such species, distributing a specified total field effort towards the repeated survey of sites might, in fact, have a negative effect on HQM. This situation is best illustrated by the analyses aimed at developing HQM for brook charr (lowest SCV; lowest TCV). Increasing the number of surveys per site (and decreasing the number of sites) produced HQM with marginally higher R^2_{adj} (related to low TCV) but markedly larger CI of R^2_{adj} (related to low SCV). The probability of developing HQM based on the appropriate explanatory variables also decreased as the number of surveys per site increased (related to low TCV). The present study therefore suggests that the development of HQM based on single surveys to a larger number of sites may be valid for salmonids (e.g. Turgeon and Rodriguez 2005). In contrast, HQM developed for species characterized by high TCV may benefit from the repeated survey of fewer sites. For instance, the R^2_{adj} of HQM developed for common shiner (intermediate SCV; highest TCV) increased noticeably as the number of surveys per site increased from 1 to 3 (26%), and this with relatively small changes in CI of R^2_{adj} and the probability of selecting the appropriate explanatory variables. For species possessing similar SCV and TCV, surveying 66 sites thrice may be preferable to 200 sites once. However, even for such species, more than 3 surveys per site may not be useful given that the majority of the benefits for HQM (increase in R^2_{adj}) occurred as the number of surveys per site increased from 1 to 3, and the majority of the disadvantages associated with such increase (increase in CI of the R^2_{adj} related to a decrease in the number of sites) occurred as the number of surveys per site increased from 3 to 8. Finally, for species such as smallmouth bass (highest SCV; second lowest TCV), surveying 100 sites twice instead of 200 sites once may increase the R_{adj}^2 of HQM by 19% with minimal effects on CI of R_{adj}^2 and the probability of selecting the appropriate explanatory variables.

The comparative analyses of the present study are admittedly subjected to the legitimacy of the criteria used to assess the relative performance of different survey design (R^2_{adj}, 95% CI of R^2_{adj}, and frequency of selection of appropriate variables). It may also be expected that the absolute effects on HQM of different combinations of the number of sites and the number of surveys per site may vary with the size of the sites. The length of river segment surveyed (100 m per site) is similar to that commonly used to develop HQM (100 m; Zampella and Bunnell 1998, Diana *et al.* 2006, Moerke and Gary 2006), and hence, from this perspective, the findings of the present study may be useful to plan future studies. Generalization may be limited by the range of combinations of SCV and TCV observed for the river, and for the species, surveyed. Similar additional work may be needed to confirm the results of the present study. However, the linkage unveiled here among fish taxonomy, TCV, and survey design may serve as a framework to simplify the search of solutions to one of the logistical problems associated with the development of operational and reliable HQM.

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CONCLUSION GÉNÉRALE

Le premier objectif de notre étude était de quantifier la variabilité temporelle des espèces de poissons formant les communautés de poissons rencontrées dans les rivières formant les bassins hydrographiques des rivières Rouge et du Nord. Notre hypothèse à ce sujet concernait la présence de différents degrés de variabilité temporelle chez les espèces de poissons. Cette hypothèse est confirmée puisque nos résultats mettent en évidence d'importantes différences inter spécifiques de TCV. Ainsi, la valeur moyenne de variabilité temporelle obtenue pour le mené à nageoires rouges (*Notropis cornutus*; TCV le plus élevé) est plus de 2,22 fois supérieure à son équivalent pour la truite mouchetée (*Salvelinus fontinalis*; TCV le plus faible). Ces mêmes résultats nous ont aussi permis d'observer que l'importance de la variabilité temporelle pouvait être reliée à l'appartenance aux familles taxonomiques. Bien qu'imprévue, cette constatation nous semble d'un intérêt majeur puisqu'elle semble indiquer les bases d'une méthode simple permettant d'évaluer la variabilité temporelle des espèces d'intérêt lors d'études futures. Cependant, une évaluation juste des TCV des différentes espèces présente une complexité supplémentaire. En effet, les TCV que nous avons obtenus diffèrent aussi, au sein des espèces, entre les différents sites d'échantillonnage étudiés. Ainsi, nous avons observé des différences de variabilités temporelles inter sites pouvant atteindre, chez une même espèce, un facteur de 6,5 (*Ambloplites rupestris*, voir Annexe 1). Différentes études ont cependant suggéré que certaines caractéristiques environnementales telles la variabilité du débit (Schlosser and Ebel 1989, Freeman et al. 2001, Oberdorff 2001), les conditions d'hivernation et de nidification (Moyle and Vondracek 1985), la présence de refuge (Roberts 2007) ou la position longitudinale (Danehy et al. 1998) puissent expliquer ces différences inter sites de variabilité temporelle. Nos résultats portent donc à croire que l'importance de la variabilité temporelle des communautés de poissons pourrait être estimée à partir de critères combinant la composition spécifique et les caractéristiques environnementales des sites à échantillonner.

Le second objectif était de quantifier l'impact des variabilités temporelles observées sur la capacité des MQH à expliquer les variances de densités observées entre les sites. Pour ce faire, nous avons comparé la performance de MQH développés à partir de différentes stratégies d'échantillonnage et ce pour la gamme des différentes variabilités temporelles observées. Notre hypothèse à ce sujet était que les espèces présentant des variabilités temporelles plus importantes bénéficieraient davantage de l'usage de plusieurs visites d'échantillonnage pour attribuer une valeur écologique aux différents sites. Cette hypothèse est confirmée puisque nos résultats montrent un appariement parfait entre un ordre croissant des TCV et celui de l'ampleur des gains de R^2 (ajusté cumulé) reliés à l'usage de stratégies d'échantillonnage impliquant un nombre croissant de visites à chaque site.

Le troisième objectif visait à évaluer la capacité des MQH à sélectionner les variables explicatives appropriées. Notre hypothèse à ce sujet était que les espèces plus variables temporellement devraient présenter des taux de sélection des variables appropriées plus élevés avec l'usage de plusieurs visites d'échantillonnage par site. Cette hypothèse est infirmée par nos résultats. En effet, ceux-ci mettent plutôt en évidence que la majorité des espèces étudiées ont des fréquences de sélection des variables appropriées diminuées lorsque la stratégie d'échantillonnage inclue davantage de prises de données à chacun des sites. Seul le mené à nageoires rouges (TCV le plus élevé) n'a pas souscrit à cette tendance, présentant des taux de sélection constants avec les différentes stratégies d'échantillonnage.

Enfin, le dernier objectif de cette étude était d'évaluer si, en considérant l'ensemble des résultats obtenus, la méthode d'échantillonnage comprenant une seule prise de données à une série de sites est appropriée pour le développement de MQH pour les poissons de rivières. Notre hypothèse à ce sujet, laquelle stipulait que les espèces présentant les plus grandes variabilités temporelles devraient bénéficier de l'usage de mesures répétées de densités à chaque site, est partiellement confirmée. En effet, nos résultats suggèrent que les différents critères étudiés des MQH (pouvoir explicatif, stabilité du modèle et fréquence de sélection des variables) ne réagissent pas de la même façon aux changements de stratégie d'échantillonnage. Ainsi, pour une espèce donnée, le même changement de stratégie peut mener à des gains et à des pertes selon le critère considéré. La méthode jugée la plus performante peut donc varier selon l'importance relative et l'intérêt qu'accorde le chercheur aux différents critères du modèle.

Considérant que l'usage de visites multiples aux différents sites impliquait un nombre diminué de sites pour maintenir l'effort d'échantillonnage total constant, ces résultats montrent à notre avis les effets antagonistes des facteurs nombres de sites et nombre de visites. En effet, l'usage de visites multiples aux différents sites vise à attribuer à chaque site une valeur écologique aussi juste que possible afin de minimiser l'impact des mouvements de poissons sur la valeur écologique attribuée aux différents sites. D'une perspective mathématique, cette procédure a donc comme objectif de préciser la position de chaque point (ici, les sites) décrivant la relation entre la valeur écologique et les caractéristiques environnementales des différents sites étudiés. Ce faisant, l'entrée de variables inappropriées devrait être réduite au profit des variables expliquant la relation. Cependant, la hausse du nombre d'objets favorise aussi la détection de relations telles que celles recherchées dans le développement de MQH (Sokal and Rohlf 1995.). Notre interprétation des résultats obtenus est donc que la variance temporelle des espèces étudiées n'était pas toujours suffisamment importante pour générer un bruit dont l'impact aurait justifié l'usage de réplicats au détriment du nombre de sites échantillonnés. Considérant qu'il est possible que certaines espèces de poissons ou certains types de milieux présentent des variances temporelles plus élevées que celle que nous avons observées, il demeure cependant possible que l'usage d'une seule visite par site ne soit pas toujours optimal.

Nous reconnaissons d'ailleurs que plusieurs facteurs limitent la généralisation possible des résultats obtenus. En effet, en mettant en évidence que la variabilité temporelle diffère entre les espèces et entre les sites, nous croyons avoir aussi indiqué que la portée des résultats obtenus se limite présentement aux sections de rivières étudiées. Une connaissance plus exhaustive des valeurs observables dans d'autres systèmes nous semble nécessaire à toute extrapolation. De plus, la méthode d'échantillonnage utilisée (méthode visuelle) pourrait être considérée comme un second facteur limitant les possibilités de généralisation de nos résultats. En effet, différentes études ont mis en évidence que les méthodes d'échantillonnage visuel, de pêche électrique et de l'usage de seines mènent à des résultats différents (Roni and Fayram 2000, Thurow et al. 2006, Jordan et al. 2008). Enfin, il importe de rappeler l'importance de l'effet de la longueur des sites utilisés sur la variabilité temporelle observée. En ce sens, nous croyons que la taille restreinte de nos sites d'échantillonnage (UE =100m) peut être vue comme un facteur expliquant les variabilités temporelles mesurées, donc les résultats obtenus. En effet, l'usage de sites d'échantillonnage plus vastes (ex: tributaire entier) réduit la variance temporelle et permet d'éviter les problèmes potentiels reliés à la variance temporelle lors du développement de MQH (Lohr et Fausch 1997). Néanmoins, nous croyons que le choix de cette taille d'UE est approprié pour deux raisons. Tout d'abord, de tels sites d'échantillonnage sont fréquemment utilisés pour étudier les poissons de rivières (Zampella and Bunnell 1998, Diana et al. 2006, Moerke and Gary 2006). Ensuite, les différentes échelles spatiales contiennent des informations complémentaires et la compréhension globale des besoins des poissons nécessite de développer notre capacité à étudier convenablement les phénomènes se déroulant à chacune de ces échelles (Jackson et al. 2001). Par exemple, les approches à grandes échelles sont certainement appropriées pour évaluer l'effet des changements de conditions environnementales à grande échelle (ex : utilisation des terres, effet de barrages, changements climatiques) et des modifications à long terme dans les communautés de poissons (ex : variations annuelles), mais peuvent être moins appropriées pour comprendre les effets de conditions environnementales plus locales (ex: importance du rôle joué par les cycles seuil-mouille, les tributaires, ou par les patchs de macrophytes) sur des communautés de poisson. Le présent travail s'est donc concentré sur l'étude de méthodes appropriées permettant de capter efficacement l'information contenue dans l'échelle du méso-habitat. Nous espérons qu'il puisse servir de cadre de référence à de futurs travaux dont l'objectif serait de consolider les bases méthodologiques sur lesquelles s'appuie l'outil de conservation et de gestion prometteur qu'est le MQH.

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ANNEXE 1

Tableau des variances temporelles (TCV) de chaque espèce de poissons à chacun des sites d'échantillonnage. Les cellules noires représentent les valeurs maximales de chaque espèce et les cellules grises, les valeurs minimales.

Species	Sampling sites																		Mean	Max / min ratio
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18		
Brook charr						1.02	0,29							0,32					0,54	3,52
Smallmouth bass	0,82	0,89	0,76	1,01	0,85	0,86	0,78			1,19	0,91	0,95	1.91					0,88	0,98	2,51
Pumpkinseed sunfish	0,79	0,53	0,86	0,97	1,01	1,02	0,72	1,59	1.92	1,53	1,61	1,43	0,75	1,19	0,98	0,38	0,61	0,69	1,03	5,05
Rock bass	0,64	1,21	0,38	0,72	0,39	0,86	1,67	2,39	2,09	0,82	1,26	1,05	1,50	2.46	1,61	0,71	0,49	0,40	1,15	6,47
Yellow perch	0,97		1,42	1,01		2.36		1,37	1,12		1,10	1,13	0,96	1,09	0,97	0,95	0,92	1,07	1,17	2,57
White sucker	1,17	0,79		0,89	0,80	1,97	0,91	1,94	0,91	2.08	1,19	1,81	0,88	0,84	1,22	0,89	0,87	0,82	1,18	2,62
Cutlips minnows	2.16	0,91	2,08	0,45	0,56	0,88	0,45		1,30		2,02		1,63	0,68			1,70		1,23	4,80
Creek chub	1,02	1,06	2.39	0,99	0,96	1,91	0,88	1,91	1,98	1,36			0,90	0,92	1,34	1,33	0,88	0,97	1,30	2,72
Golden shiner	1,14	2,09		2.50	1,94		1,09						0,94	0,97		0,81	0,81	1,40	1,37	3,10
Fallfish	1,20	0,90	1,00	0,67	1,41	1,79		2,10	2.42	0,72	0,89	1,07	1,50		2,32	1,70	2,21	0,53	1,40	4,57
Common shiner	1,23	1,13		1,07	1,08	1,84	1,08	1,55	2,02	1,49	1,99		1,20	1,03	1,09	1,35	1,05	2.56	1,42	2,49

ANNEXE 2

Tableau des valeurs par site pour les différents descripteurs environnementaux utilisés dans cette étude. (Partie 1, sites 1 à 9)

Variables	**Sites**								
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Substrate type (% cover)									
- clay	1,5	0	0	0	0	0	0	0	0
- silt	28,2	1,8	20,0	81,5	29,6	14,1	65,8	24,4	26,0
- sand	60,8	9,1	5,8	0	11,5	14,2	32,7	23,0	35,3
- gravel	9,3	8,8	10,1	3,3	24,1	9,9	1,4	26,9	24,2
- pebble	0,2	17,2	34,6	5,6	12,3	2,5	0	22,0	5,3
- cobble	0	48,5	24,5	6,9	10,0	20,2	0,1	3,5	2,7
- boulder	0	14,3	4,4	2,6	9,6	26,6	0	0,1	6,5
- metric boulder	0	0	0,6	0	2,2	12,5	0	0	0
- bedrock	0	0,3	0	0	0,7	0	0	0,1	0
Macrophyte cover (%)	24,9	0	3,3	29,2	6,7	1,5	55,2	2,9	23,1
Branch cover (%)	11,3	0,8	13,9	6,1	11,9	4,3	6,3	5,3	5,2
Culvert (#)	0	0	0	0	1,0	0	0	0	0
Island (#)	0	0	0	0	0	0	0	2,0	0
Offshoot (#)	0	0	1,0	2,0	1,0	0	5,0	1,0	0
Tributary (#)	0	0	1,0	0	0	0	1,0	0	0
River width (m)	13,7	19,2	10,0	17,6	18,4	16,2	10,3	24,2	9,2
Water depth (cm)	86,2	66,8	54,9	80,1	80,3	68,3	50,4	38,0	64,2
Flow velocity (cm· s^{-1})	8,3	25,8	5,4	4,7	0,4	6,2	3,3	10,9	19,2
Water temperature (° C)	23	24	25	20	22	21	19	20	18

ANNEXE 2 (suite)

Tableau des valeurs par site pour les différents descripteurs environnementaux utilisés dans cette étude. (Partie 2, sites 10 à 18).

Variables	Sites								
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Substrate type (% cover)									
- clay	0	0	0,4	0	0	0	0	0	0
- silt	2,7	16,4	35,7	52,1	39,1	39,4	96,9	54,4	7,1
- sand	9,8	46,2	61,4	30,7	13,8	22,0	0,0	27,3	18,9
- gravel	20,3	21,6	2,4	13,0	5,9	13,0	0,4	18,1	16,6
- pebble	13,2	15,1	0	2,1	20,6	9,6	0,8	0,2	37,7
- cobble	41,4	0,7	0	2,1	15,4	10,3	0,3	0	17,3
- boulder	10,9	0	0,1	0,1	5,2	4,3	0,6	0	2,3
- metric boulder	0,2	0	0	0	0,2	1,1	1,0	0	0
- bedrock	1,6	0	0	0	0	0,3	0	0	0
Macrophyte cover (%)	0,1	3,0	29,8	19,1	18,3	3,5	95,2	43,3	8,0
Branch cover (%)	2,7	5,3	19,7	22,9	12,2	10,2	0,7	8,7	8,0
Culvert (#)	0	0	0	0	1,0	0	0	0	0
Island (#)	1,0	1,0	4,0	0	0	0	0	0	0
Offshoot (#)	0	0	0	0	0	0	2,0	0	3,0
Tributary (#)	0	1,0	0	3,0	1,0	0	0	0	1,0
River width (m)	20,7	8,9	11,2	22,3	7,4	12,8	16,5	10,9	17,4
Water depth (cm)	45,9	52,0	61,6	129,0	85,6	63,4	89,1	54,6	56,8
Flow velocity (cm· s^{-1})	55,7	15,4	15,0	8,3	1,8	5,3	1,8	3,3	31,8
Water temperature (° C)	20	17	17	24	25	20	24	19	21