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Modélisation de la qualité d'habitat estival des juvéniles de saumons atlantiques (*Salmo salar*) à l'échelle d'une rivière

par

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Faculté des études supérieures

Ce mémoire intitulé :

Modélisation de la qualité d'habitat estival des juvéniles de saumons atlantiques (*Salmo salar*) à l'échelle d'une rivière

présenté par :

Judith Bouchard

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Pierre Legendre

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Daniel Boisclair

directeur de recherche

Michel Lapointe

membre du jury

SOMMAIRE

Un habitat est un milieu géographique caractérisé par des conditions physiques et biologiques particulières. Des modèles de qualité d'habitat (MQH) peuvent être développés en établissant des relations entre les indices de qualité et les conditions physiques et biologiques des habitats.

L'objectif principal de ce mémoire est de comprendre les processus déterminant la qualité d'habitat des tacons de saumons atlantiques (*Salmo salar*) le long d'une rivière. Dans le premier chapitre, nous déterminerons les tailles d'unités d'analyses (UA) fiables. Dans le second chapitre, nous déterminerons l'influence de la taille des UA et l'importance relative des variables locales, latérales et longitudinales sur le développement des MQH le long d'une rivière.

Nos résultats suggèrent d'abord que la taille des unités d'échantillonnage peut être inadéquate pour établir des relations entre l'indice de qualité d'habitat et les variables explicatives. On peut résoudre ce problème en regroupant des unités d'échantillonnage contiguës en UA plus grandes. On observe ensuite que la taille des UA influence notre perception des relations entre l'indice de qualité d'habitat des tacons et les variables physiques. Finalement, nos résultats montrent que la qualité des habitats des tacons le long d'une rivière est principalement déterminée par les variables locales : celles-ci déterminent 98% de la variation expliquée par les MQH développés.

Mots clés : modèles de qualité d'habitat, unités d'analyses, variation temporelle, variation spatiale, variables locales, variables latérales, variables longitudinales, variables contextuelles, écologie du paysage.

SUMMARY

A habitat is an area characterized by physical and biological conditions. Habitat quality model (HQM) can be developed by relating habitat quality index to physical and biological conditions of habitats.

The main objective of this master's thesis is to understand processes that influence habitat quality of parr of Atlantic salmon (*Salmo salar*) along a river. In the first chapter, we will assess which sizes of analytical units (AU) should be used to analysed parr density (which is used as habitat quality index) and physical conditions relationships. In the second chapter, we will assess the influence of the size of AU on the development of HQM, and we will quantify the relative importance of local, lateral, and longitudinal variables on HQM developed along a river.

Our results suggest that size of AU might be inadequate to establish relationships between parr density and physical variables. It is possible to solve this problem by merging adjoining sampling units into larger AU. We observed that the size of AU influence our perception of the relationships between parr density and physical variables. Finally, our results suggest that parr habitat quality along a river is mainly determined by local variables: they determined 98% of the variation explained by HQM.

Key words: habitat quality models, analytical units, temporal variation, spatial variation, local variables, lateral variables, longitudinal variables, contextual variables, landscape ecology.

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α	Seuil de probabilité
AD_AU	Area of the region drained on shores of analytical units
AU	Analytical units
b_0	Ordonné à l'origine de l'axe majeur
b_{AM}	Pente de l'axe majeur
Bedrock	Bedrock composition
Boulder	Boulder composition (B axis: 250 to 1000 mm)
cm	Centimètre
˚C	Degrés Celsius
C.I.	Confidence interval
DlinkU	Distance to the first sedimentary link upstream
Dmouth	Distance from the river mouth
Dtrib	Distance to the nearest tributary
DtribD	Distance to the first tributary downstream
FHQM	Fish habitat quality model
FRM	From the river mouth
HQM	Habitat quality model
km	Kilomètre
ln	Logarithme naturel
m	Mètre
MAUP	Modifiable areal unit problem
MQH	Modèle de qualité d'habitat
n	Taille de l'échantillon (nombre d'objets)

p	Nombres de paramètres
%	Pourcentage
r	Coefficient de corrélation de Pearson
r^2	Coefficient de détermination
R^2	Coefficient de détermination multiple
R^2_a	Coefficient ajusté de détermination multiple
s	Seconde
SD_1km	Averaged slope of the region drained on shores 1 km upstream analytical units
SMR	Sainte-Marguerite River
SU	Sampling units
SWF	Smooth water surface occurrence
UA	Unités d'analyses
V*	Coefficient de variation corrigé pour les petits échantillons
V^*_S	Coefficient de variation spatiale corrigé pour les petits échantillons
V^*_T	Coefficient de variation temporelle corrigé pour les petits échantillons
WoodD	Woody debris

À mes amis

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INTRODUCTION

Un habitat est un milieu géographique caractérisé par des conditions physiques et biologiques particulières (Ramade 1993; Morrison 1999; Morris 2003; Closs et al. 2004). Les êtres vivants peuvent tolérer une gamme de conditions physiques et biologiques. Tout au long de cette gamme de conditions se trouvent des habitats variant en qualité. Pour une espèce ou une population donnée, la qualité des habitats se mesure habituellement par l'entremise d'indices tels que : la croissance, la production, le taux de survie, le taux de reproduction, la présence ou la densités d'individus dans un milieu (Hobbs et Hanley 1990; Hayes et al. 1996; Kocik et Ferreri 1998; Porter et al. 2000). À partir de ces indices, des modèles de qualité d'habitat (MQH) peuvent être développés pour prédire la qualité et la quantité d'habitats disponibles. En outre, les MQH peuvent être utilisés pour établir des mesures de gestion et d'aménagement des habitats.

En milieux lotiques, les MQH sont généralement construits en mettant les indices de qualité d'habitat en relation avec des variables décrivant les conditions physiques à l'intérieur des sites où sont observés les poissons (variables locales). Les MQH peuvent être développés sur des segments de rivière (10^2 m; DeGraaf et Bain 1986; Bremset 2000; Beland et al. 2004; Girard et al. 2004), sur quelques kilomètres le long d'une rivière (Baglinière et Champigneulle 1982; Heggenes et Saltveit 2002) ou encore sur plusieurs rivières à la fois (Morantz 1987; Heggenes et al. 2002; Hedger et al. 2004; Johansen et al. 2005). Dans la plupart des cas, la présence et la densité des poissons, utilisées comme indices de la qualité des habitats, sont mises en relation avec des variables locales telles que la vitesse du courant, la profondeur de l'eau, la composition du substrat et la présence d'abris (Rimmer et al. 1984; Morantz 1987; Heggenes et al. 1991; Guay et al. 2000; Girard et al. 2003).

Les processus susceptibles d'être détectés par une étude doivent avoir un impact à une échelle spatiale plus grande que l'unité d'échantillonnage (la longueur, la surface ou le volume sur lesquels les variables sont mesurées), mais plus petite que l'étendue d'échantillonnage (la longueur, la surface ou le volume sur lesquelles sont distribuées les unités d'échantillonnage; Bellehumeur et Legendre1998). Il est donc possible qu'à grande échelle (à l'échelle d'une rivière par exemple) des processus autres que ceux décrits par les variables locales puissent influer sur la qualité des habitats. Récemment, l'écologie du paysage a suggéré que l'organisation spatiale des habitats le long d'une rivière pouvait avoir un impact sur la distribution et la production des organismes (Ward 1998; Fausch et al. 2002; Ward et al. 2002a; 2002b; Wiens 2002). Dans un même ordre d'idées, la théorie hiérarchique a suggéré que les systèmes fluviaux étaient organisés de façon hiérarchique (rivières, segments, sections, séquences seuil/mouille et microhabitats; Frissell et al. 1986). Les conditions des niveaux supérieurs (exemple : les rivières) contraignant les niveaux sous-jacents (exemple : les microhabitats).

De plus en plus d'études montrent d'ailleurs l'importance de considérer des variables de type contextuel (la position dans le réseau hydrographique, la végétation sur les rives, les caractéristiques du bassin versant) lorsqu'on veut développer et appliquer les MQH à des échelles plus grandes que le segment de rivière (une rivière complète, un réseau hydrographique; Fausch et al. 1994; Lammert et Allan 1999; Magalhaes et al. 2002; Rich et al. 2003; Smith et Kraft 2005). L'influence relative des variables de type local et des variables de type contextuel est toutefois mal connue. Certaines études démontrent que des MQH ne contenant que des variables contextuelles permettent de prédire correctement la distribution des poissons (Porter et al. 2000; Magalhaes et al. 2002). Par ailleurs, l'étude publiée par Bisson et al.

(2002) indique que la distribution des poissons dépend surtout des variables locales. Finalement, certaines études montrent que la distribution des poissons est influencée à la fois par des variables locales et des variables contextuelles (Fausch et al. 1994; Lammert et Allan 1999; Dovciak et Perry 2002; Argent et al. 2003; Rich et al. 2003; Smith et Kraft 2005).

Plusieurs modèles conceptuels ont été proposés pour décrire l'influence des variables contextuelles sur la distribution des organismes le long des rivières. Hynes (1975) a décrit comment les caractéristiques du bassin versant (i.e. : la composition géologique, le type de sol et le type de végétation) influençaient l'apport en matière organique et inorganique à la base de la chaîne alimentaire de la rivière. Vannote et al. (1980) ont proposé le concept de continuum fluvial. Ce concept met l'emphase sur l'influence du gradient amont-aval des conditions physiques (tel que l'apport allochtone de matière organique et la température de l'eau) sur les conditions biologiques (telles que la production primaire et la distribution des poissons) le long des cours d'eau. Rice et al. (2001) ont développé le concept de « discontinuité des maillons » qui suggère que des apports en substrats grossiers créent une série de maillons sédimentologiques le long des rivières. Les maillons sédimentologiques sont des segments de rivière délimités par du substrat grossier en amont et du substrat fin en aval. Selon Rice et al. (2001), les maillons sédimentologiques peuvent déterminer la structure amont-aval des caractéristiques physiques (particulièrement en ce qui concerne le substrat et la turbulence du courant) et biologiques d'une rivière. En résumé, ces modèles conceptuels ont démontré l'influence probable des variables contextuelles de type latéral (variables décrivant le bassin versant et les berges adjacentes aux sections de rivière échantillonnées) et de type longitudinal (variables décrivant la position des sections par rapport aux éléments de la rivière selon un axe amont-aval) sur la qualité des habitats.

Il existerait ainsi plusieurs relations potentielles entre les variables contextuelles (latérales et longitudinales), les variables locales et la distribution des poissons le long des rivières. Or, la gestion adéquate des habitats de poissons en rivière dépend de notre compréhension de ces relations. D'une part, il est primordial de comprendre les relations fonctionnelles entre les variables physiques (i.e. les processus) pour que les mesures de gestion et d'aménagement soient viables à long terme (Imhof et al. 1996; Lewis et al. 1996; Clifford 2001; Rosenfeld 2003). Pour être efficace et durable, une mesure de gestion doit traiter la variable qui est à la source du problème tout en considérant les interactions potentielles avec les autres variables physiques. D'autre part, il importe de connaître l'importance relative des différents types de variables (locales, latérales et longitudinales) dans les MQH. Ceci afin d'optimiser les efforts d'échantillonnage et de développer de puissants MQH.

Il n'y a pas que l'étendue d'échantillonnage qui influence les processus perçus par une étude. Il est généralement admis que la structure des relations perçues entre des variables peut être affectée par la taille des unités d'échantillonnage (Wiens 1989; Levin 1992; Bellehumeur et Legendre 1998; Folt et al. 1998; Borcard et Legendre 2002; Wiens 2002). Il en est de même pour la taille des unités d'analyses (UA; taille des UA: longueur, surface ou volume utilisés lors des analyses statistiques; Dungan et al. 2002; Brind'Amour et Boisclair 2006). D'ailleurs, selon le patron d'échantillonnage, il est parfois possible de regrouper les unités d'échantillonnage contiguës en UA de plus grandes tailles.

L'objectif principal de cette recherche de maîtrise est de comprendre les processus déterminant la qualité d'habitat des tacons (juvéniles ayant passé plus d'un hiver en rivière) de saumons atlantiques (*Salmo salar*) le long d'une rivière. Les objectifs spécifiques seront présentés en deux chapitres. Dans un premier chapitre, nous déterminerons les tailles d'UA qui peuvent être utilisées lors du développement des MQH. Et dans un second chapitre, nous déterminerons l'influence de la taille des UA sur le développement des MQH et l'importance relative des variables locales, latérales et longitudinales dans les MQH développés le long d'une rivière.

Les tacons ont été choisis comme groupe modèle pour deux raisons. Premièrement, on les observe tout au long de la rivière étudiée et ils sont réputés pour leur comportement territorial (Saunders et Gee 1964; Heggenes et Borgstrom 1991). Ces caractéristiques devraient permettre l'établissement de relations entre les densités de tacons et les variables physiques et ainsi faciliter le développement de MQH. Deuxièmement, on observe un déclin des stocks mondiaux de saumon atlantique depuis les trois dernières décennies (Parrish et al. 1998; Boisclair 2004). Les causes de ce déclin restent obscures, mais il pourrait être, en partie, imputable à la diminution de la qualité des habitats en rivière (Dodson et al. 1998). Il importe donc de bien comprendre les relations entre les tacons et leurs habitats, afin d'adopter des mesures de gestions des rivières adéquates.

Toutefois, avant de procéder au développement des MQH, les tailles d'UA fiables (i.e. les tailles d'unités pour lesquelles les estimations de densités de tacons varient peu d'un échantillonnage à l'autre) ont d'abord dû être déterminées. La densité de tacons a donc été estimée à dix reprises dans quatre segments de rivière de 200 m subdivisés en 20 sections de 10 m. D'une part, ce type d'échantillonnage permet de regrouper les unités d'échantillonnage contiguës (chaque section de 10 m) en UA de différentes tailles (i.e. : 10, 20, 40, 50, 100 et 200 m). Et d'autre part, il permet d'évaluer la variation des estimations de densités observée dans chaque unité d'analyse (variation temporelle) et la variation observée entre les UA (variation spatiale) et ce pour chaque taille d'UA.

Afin de tenir compte de l'influence potentielle de la taille des UA sur les relations perçues, nous avons développé des MQH pour toutes les tailles d'UA dont les estimations de densités de tacons sont fiables. Pour chaque taille d'UA fiable, les MQH ont été développés en mettant la densité de tacons (i.e. indicateur de la qualité d'habitat) en relation avec des variables locales, latérales et longitudinales indépendamment. Ainsi, nous avons pu déceler les variables locales, latérales et longitudinales structurant la distribution des tacons le long de la rivière tout en tenant compte de l'influence de la taille des UA sur les résultats obtenus. Ensuite, pour déterminer l'importance relative de chaque type de variables sur la qualité des habitats, nous avons combiné les MQH construits à partir des variables locales, latérales et longitudinales en un seul modèle (modèle combiné), et ce pour chaque taille d'UA considérée. Ainsi, il a été possible de procéder à des partitions de la variation sur les modèles combinés. Les partitions de variation ont permis d'établir les fractions de variation expliquées exclusivement et simultanément par les variables locales, latérales et longitudinales.

Chapitre 1

Identification of the size of analytical units required to develop fish habitat quality models

Judith Bouchard, Mariane Fradette et Daniel Boisclair

En préparation

ABSTRACT

Fish habitat quality models (FHQM) are relationships between fish presence, density, or biomass, and various environmental conditions. Among-day variations of fish distributions hamper the development of FHQM. We hypothesized that the size of the units employed to assess fish density (analytical units; AU) may affect the temporal stability of this index of habitat quality. The objective of this study was to assess the AU size(s) that should be used to minimize among-day variations of the density of parrs of Atlantic salmon (*Salmo salar* L.). Parr density was estimated in four 200-m reaches of a river during ten nights. Temporal variations of parr density represented >44% of the total variation for AU of 10-20 m and <32% of the total variation for AUs of 50-200 m (length of AU in the upstream-downstream axis of the river). For AUs of 50-200 m, at least 97% of the temporal coefficients of variation of parr density were smaller than the spatial coefficients of variation. Relationships developed between parr density and environmental conditions should use AUs of 50 to 200 m (i.e. sampling area of 100 to 400 m^2 extending over 1.2 to 2.3 times the river width) to minimize among-night variations of fish density.

INTRODUCTION

Fish habitat quality models (FHQM) are relationships between indices of habitat quality and a suite of environmental conditions. Habitat quality may be represented by indices such as the density, biomass, growth, or production of a population in a specific area (Hobbs and Hanley 1990; Hayes et al. 1996; Kocik and Ferreri 1998; Porter et al. 2000; Rosenfeld 2003). Assessment of habitat quality is a fundamental theme in ecology (Morris 2003), and numerous studies have aimed at modeling habitat quality in terrestrial and aquatic ecosystems. Ultimately, FHQM may allow scientists and managers to predict the effect of perturbations on habitat quality and identify areas that, because of their high ecological values, should be protected for conservation purposes.

Numerous theoretical and conceptual studies suggest that the ability of FHQM to adequately represent the effect of ecological processes on a population may depend on the size of the units used either during the sampling (sampling unit; SU) or the statistical analysis (analytical unit; AU) performed to develop these models (Wiens 1989; Levin 1992; Bellehumeur and Legendre 1998; Folt et al. 1998; Borcard and Legendre 2002; Wiens 2002). The effect of the size of SU or AU on the properties of models developed is referred to as the Modifiable Areal Unit Problem (MAUP; Openshaw and Taylor 1981; Holt et al. 1996; Jelinski and Wu 1996). MAUP is often perceived as a spatial problem. This situation may be related to the possibility that SU or AU of different sizes may not be equally appropriate to represent the interactions between a population and a series of ecological processes that operate at different spatial scales (Cooper et al. 1998; Lammert and Allan 1999). However, for mobile organisms, MAUP may also comprise a temporal component. For instance, although salmonids living in rivers have long been presumed to conform to the restricted movement paradigm (Gowan et al. 1994), their spatial distribution may vary among days or weeks (Gowan and Fausch 2002; Albanese et al. 2004). This situation introduces an uncertainty in FHQM based on the relationship between local fish density, which is often estimated at one specific moment and under specific prevailing physical conditions. The objectives of this study were to estimate the temporal variability of fish density in different areas of a river and to assess the effect of the AU size on this variability.

MATERIAL & METHODS

Site and species for study

The study was conducted in the main branch of the Sainte-Marguerite River (SMR) in the Saguenay region of Québec (600 km north-east of Montréal, Québec, Canada). Sampling was conducted in four reaches each having a length of 200 m (Figure 1.1). Each reach was further subdivided into 20 sections of 10 m. The four reaches were selected on the basis of their differences in substrate composition (Table 1.1). The riverbed of Reach 1 was primarily composed of pebble (16%), cobble (42%), and boulder (23%). Substrate composition of Reaches 2 and 4 was dominated by sand (respectively 35 and 24%) and gravel (respectively 53 and 69%). Reach 3 consisted mostly of a mixture of gravel (15%), pebble (32%), and cobble (38%). The reaches were therefore expected to represent different types of habitat.

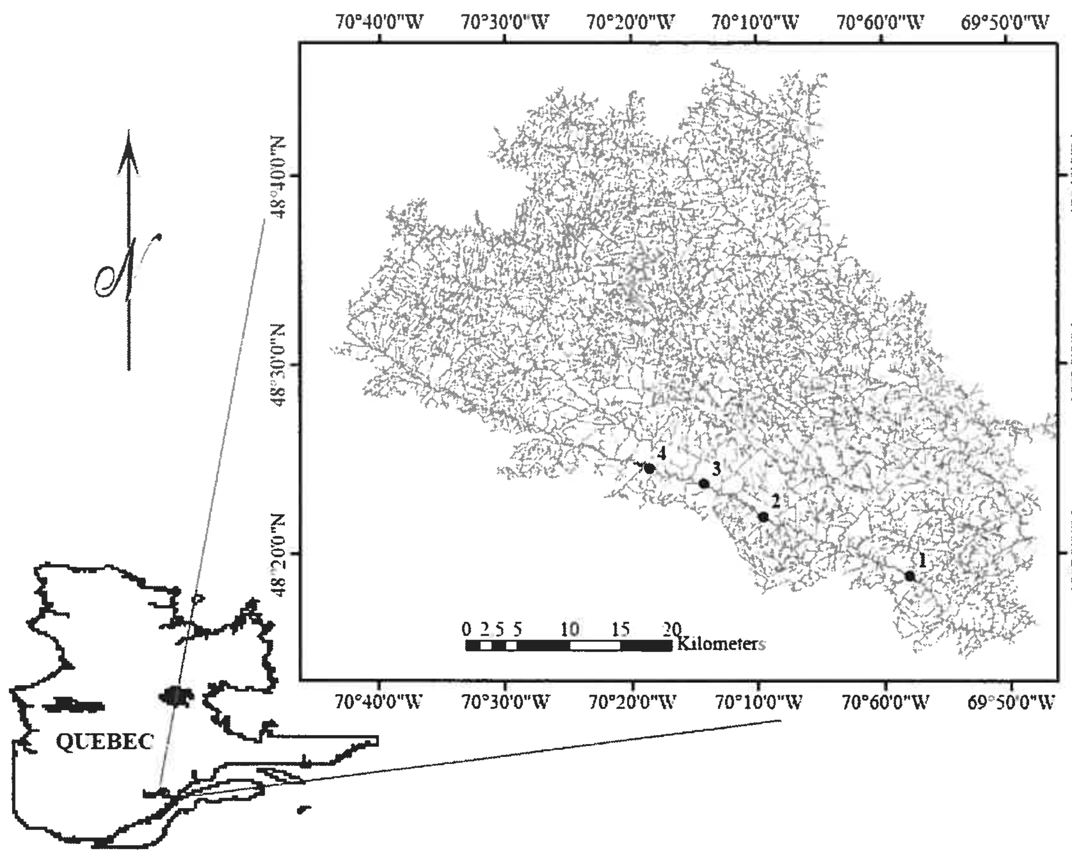

Figure 1.1 Location of the four river reaches sampled in 2004 on the main branch of the Sainte-Marguerite River.

Table 1.1 Description of the physical conditions observed within the four river reaches (mean value ± standard deviation).

Variables	Reach 1	Reach 2	Reach 3	Reach 4
Channel width (m)	42.5 ± 9.6	36.5 ± 2.6	27.8 ± 4.6	22.2 ± 2.8
Depth (cm)	53.7 ± 12.8	68.8 ± 11.8	45.7 ± 10.7	73.5 ± 20.6
Velocity ($m \cdot s^{-1}$)	0.46 ± 0.12	0.34 ± 0.16	0.55 ± 0.14	0.29 ± 0.23
Clay (%)	0 ± 0	3.2 ± 4.8	0 ± 0	0 ± 0
Silt (%)	2.2 ± 4.2	0 ± 0	0 ± 0	4.8 ± 9.3
Sand (%)	1.8 ± 2.4	34.7 ± 24.5	7.5 ± 2.3	24.2 ± 19.9
Gravel (%)	10.7 ± 3.5	52.6 ± 23.6	14.6 ± 3.5	68.8 ± 21.1
Pebble (%)	16.2 ± 7.5	6.5 ± 10.8	31.8 ± 9.1	2.2 ± 3.5
Cobble (%)	41.7 ± 7.1	1.5 ± 1.3	38.0 ± 7.8	0 ± 0
Boulder (%)	23.2 ± 10.7	1.5 ± 1.4	8.2 ± 4.6	0 ± 0
Metric boulder (%)	4.3 ± 4.3	0 ± 0	0.2 ± 0.5	0 ± 0

Eight fish species are present in the main branch of the SMR: Atlantic salmon (*Salmo salar*), Brook trout (*Salvelinus fontinalis*), Blacknose dace (*Rhinichthys atratulus*), Longnose dace (*Rhinichthys cataractae*), Longnose sucker (*Catostomus catostomus*), Sea lamprey (*Petromyzon marinus*), American eel (*Anguilla rostrata*), and Fallfish (*Semotilus corporalis*). However, the present study focussed on parr of Atlantic salmon (I+ and II+ indiscriminately) because they are ubiquitous in SMR and territorial during the summer (Saunders and Gee 1964; Heggenes and Borgstrom 1991). These characteristics are expected to minimize the temporal variation of parr density estimates.

Sampling

Parr density in each section was estimated by two observers who simultaneously snorkelled two 10-m long transects oriented approximately parallel to the shore. One transect was as close as possible to the shore (i.e. at a minimum depth of 25 cm), the other was located in the middle of the river (i.e. 10 to 20 m from the shore depending on the river width). Sampling took place between July 29th and August 11th 2004. During the sampling period, water temperature and discharge ranged from 14 to 22 °C, and from 3.0 to 11 $m^3 \cdot s^{-1}$ respectively. However, sampling was performed when water discharge ranged from 3.0 to 5.3 $m^3 \cdot s^{-1}$ to minimize the effect of flow variation on our data. Parr density was estimated during the night by underwater observations performed between 22h00 and 03h00. This strategy was adopted for two reasons. First, parr densities estimated by visual sampling are significantly higher during the night than during the day, presumably because most parr remain in interstices of the substrate during the day (Imre and Boisclair 2004; Johnston et al. 2004). Second, it has been shown in the SMR that parr densities estimated at night are less variable and less affected by meteorological conditions (e.g. cloud cover) than during the day (Bédard et al. 2005; Imre and Boisclair 2005). Night sampling was expected to reduce the temporal variation of parr density caused by sampling conditions.

Parr were observed using underwater lighting systems (Underwater Kinetics Light, model C4). Light was directed in an upward direction at an angle of approximately 45° relative to water surface. Hence, fish were illuminated using a diffused beam of light which is expected to minimize fish disturbance (Gries et al. 1997). For each 10-m section, the two snorkellers counted the number of parr observed and evaluated the mean visibility. The mean visibility was the average distance (ranging from 0.5 to 2 m) at which parr could be seen and correctly identified either on the left or the right hand side of the snorkellers. This sampling procedure was repeated in the four river reaches on ten nights within the 12 days sampling period.

Computations and statistical analyses

Parr density (parr · m^{-2}) along each transect (shore or middle) within any given 10-m section was obtained by dividing the number of parr observed by the surface area sampled in that transect (mean visibility · 2 sides · 10 m). Parr density in each AU was estimated as the average of the parr density estimates in 10-m sections within the AU. Because the 200-m reaches (as well as the two transects within each reach) are divided in 20 sections of 10 m each, we were able to merge adjacent 10-m sections into AUs of 10, 20, 40, 50, 100, and 200 m. The size of AUs is here defined as the length, in the upstream-downstream axis of the river, of the AUs resulting from the merging of a specific number of adjacent sections. The sampling schedule provided ten replicates of parr density for each AU.

Two statistical analyses were performed to compare the spatial and the temporal variation of parr density estimates. Firstly, coefficients of variation corrected for small sample size (V*; Sokal and Rohlf 1995) were calculated. This procedure was used to assess the range of V* that may be estimated among AU within nights (V^*_S; spatial coefficient of variation) and among nights within AU (V^*_T; temporal coefficient of variation). V^*_S was computed using the parr density of every AU sampled during a given night. V^*_T was computed using the ten nights during which parr density was estimated for each AU. V^*_S and V^*_T were calculated for every size of AU. The range of values taken by V^*_S was compared to the range of values taken by V^*_T for the different AU sizes. Secondly, the computations of a oneway analysis of variance without replication were employed to calculate the variance components and compare the percentage of variation of parr density observed among AUs (relative spatial variation) to the percentage of variation of parr density observed within AU (relative temporal variation). The mean sum of squares (MS) calculated among AUs was expected to estimate "$s^2 + n{\cdot}s^2_A$" (s^2 : error variance; n: sample size; s^2_A: added variance component due to AUs), whereas the MS calculated within AU was expected to estimate "s^2" (Sokal and Rohlf 1995). The variance due to AUs, s^2_A, was estimated by subtracting the MS within AU from the MS among AUs, and by dividing this value by "n" (in this study, n = 10). The percentages of variation among AUs (relative spatial variation) and within AU (relative temporal variation) were calculated with respect to their sum ($s^2_A + s^2$). The relative spatial and temporal variations were computed for each size of AU (i.e. 10, 20, 40, 50, 100, and 200 m).

RESULTS

Parr density estimated for the 10-m AU ranged from 0.0 to 0.3 parr · m^{-2} across reaches and sampling nights. As anticipated, parr density was affected by the size of the AU. Hence, when sections were grouped in AUs of 200 m, parr density across reaches and sampling nights ranged from 0.05 to 0.12 parr · m^{-2}. The coefficients of variation (V*) of parr density decreased from 120% to 60% as AU size increased from 10 to 200 m. Parr density varied both spatially and temporally. The narrowest and the widest ranges of parr density obtained among AUs of 10 m for any given night were respectively 0.00-0.15 parr · m^{-2} and 0.00-0.30 parr · m^{-2}. Corresponding values for AU of 200 m were respectively 0.02-0.05 parr · m^{-2} and 0.02-0.12 parr · m^{-2}. For any given AU, parr density could vary among-nights by as much as 0.30 parr · m^{-2} for AU of 10 m and by as much as 0.07 parr · m^{-2} for AU of 200 m.

Equivalent increases in AU size had a smaller effect on V^*_S than on V^*_T (Figure 1.2). As AU size increased from 10 to 200 m, the largest V^*_S decreased from 125% to 90% while the largest V^*_T decreased from 325% to 30%. For AUs of 10, 20, and 40 m, 25% to 40% of the V^*_T were larger than, or equal to, V^*_S. For AUs of 50, 100, and 200 m, V^*_T was smaller than V^*_S for at least 97% of the comparisons. Hence, these results suggest that parr density values estimated with AUs of 10, 20, and 40 m were subjected to a temporal variation that can be greater than the spatial variation. In contrast, for parr density estimates obtained using AUs of 50, 100, and 200 m, the temporal variation was almost always smaller than the spatial variation.

The increase of the size of AUs from 10 to 200 m resulted in an increase of the relative spatial variation (47.5 to 78.0%) and an equivalent decrease of the relative temporal variation (52.5 to 22.0%, Figure 1.3). The decrease in the relative temporal variation was more important between AUs of 10 to 50 m than between AUs of 50 to 200 m. From AUs of 10 m to 50 m, the relative temporal variation decreased from 7.8 to 4.3% by 10 m increases of the AU size. From AUs of 50 m to 200 m, the relative temporal variation decreased from 1.2 to 0.3% by 10 m increases of the AU size. Thus, the increase of AU size seems more efficient to reduce the parr density relative temporal variation for 10-m to 50-m AU than for 50-m to 200-m AUs.

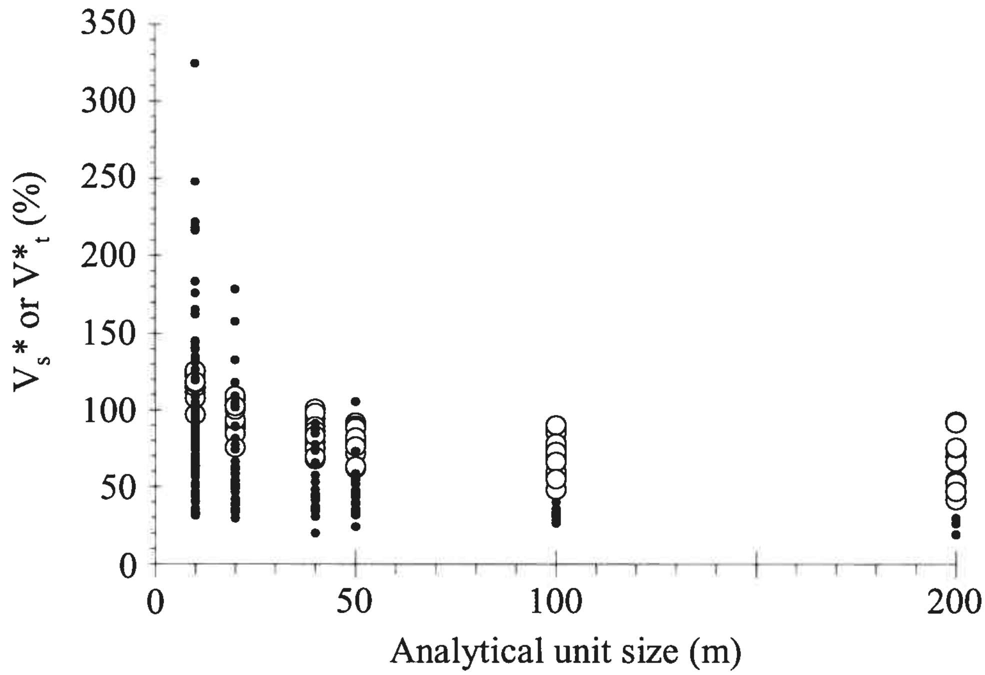

Figure 1.2 Progression of spatial (V^*_S; open circles) and temporal (V^*_T; solid circles) coefficients of variation of parr density as the size of analytical units increases.

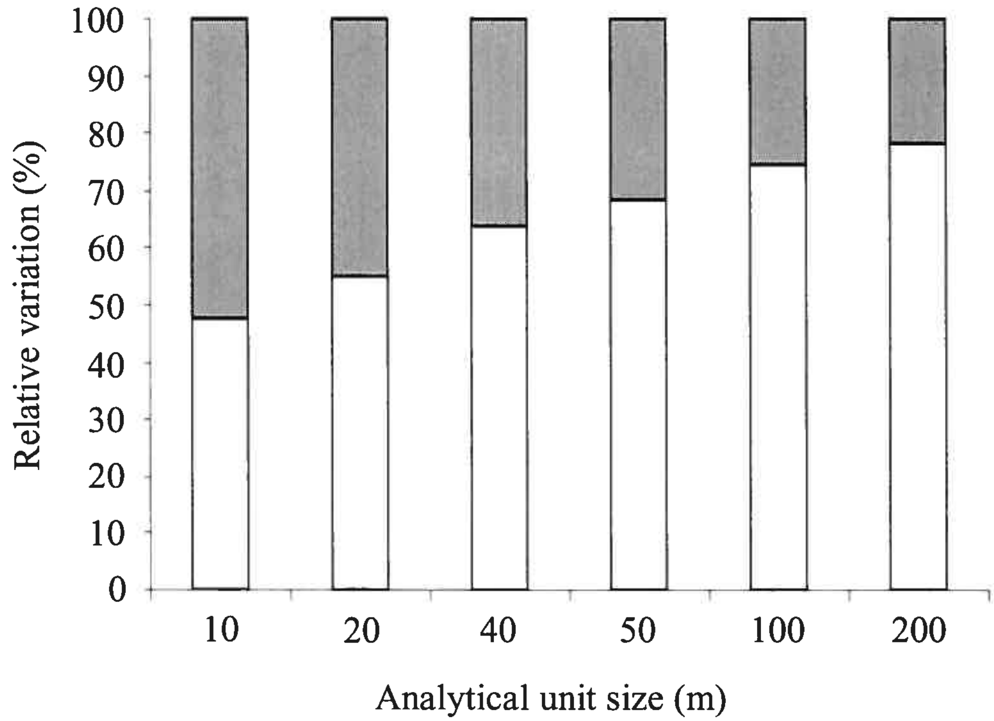

Figure 1.3 Relative spatial (white) and temporal (grey) variation of parr density for different sizes of analytical units.

DISCUSSION

This study indicates that parr density in any given AU of 10 m (excluding the AUs where no parr were observed) may change 1.2- to 14-fold among ten nights. In contrast, parr density estimated in AUs of 200 m varied 0.7- to 1.5-fold among these same nights. Although parr are generally perceived as territorial fish, they are also known to explore their habitat during the summer months (Armstrong et al. 1997; Metcalfe et al. 1997). Atlantic salmon parr may move 208 to 862 m within a 13-day period in the summer and fall (Økland et al. 2004). The larger temporal variations observed for AUs of 10-40 m than for AUs of 50-200 m are consistent with the suggestion that these fish may occupy habitats separated by tens of meters within a few days. However, the data of the present study do not permit to exclude the possibility that the observed variation of parr density may be caused by among-night changes in the cryptic behaviour of parrs. Such among-night changes may introduce noise in density estimates, particularly in small AUs. In addition, observations performed during this study support the suggestion of Gries et al. (1997) that parr of Atlantic salmon are less territorial during the night than during the day. Approximately 18% of the parr observed along the shore transects were observed in groups of 8 to 13 individuals. In this context, sampling by transects instead of sampling 100% of the surface area of a site may mean that, depending on the position of the transect relative to the distribution of parr, in some 10-m sections, all parr present may be counted while in other sections of the same length, none of the parr present will be surveyed. The probability of observing or missing all groups of parr in AUs of 10 m appears larger than in AUs of 200 m. This may contribute to inflate the variance of parr density in small relative to large AUs. Consequently, the decrease of the maximum values of V^*_T from 325% to 30%, when the AUs increased from 10 to

200 m, could be the results of the dilution of extreme values of parr density in larger AUs (Bellehumeur et al. 1997).

The relative temporal variation of parr density observed within units and among nights decreased when the AUs increased in size. This observation could have been influenced by the simultaneous decrease of the number of AUs analysed as their size increased. To ensure that the relative spatial and temporal variation observed for each AU size was not a mathematical artefact of the sample size, we recalculated them after permuting the AUs. We proceed to 1000 permutations for each size of AU (i.e. 10, 20, 40, 50, and 100 m; Figure 1.4). The 95% confidence intervals (C.I.) of the relative temporal and spatial variation were estimated by calculating the 2.5 and 97.5 percentiles of the 1000 values obtained from the permutations. Contrary to observations made on real data (Figure 1.3), we did not observe a decrease of the relative temporal variation in AUs larger than the size of AUs that have been permuted (Figure 1.4). Thus, it appears that the decrease of relative temporal variation for larger AUs was not influenced by the simultaneous decrease of the number of AUs analysed. The permutation of AUs of a given size destroys the spatial structure of parr density at scales larger than that of this AU. Hence, it seems that the decrease of relative temporal variation for larger AUs depends on the spatial structure of parr densities at smaller scale.

We observed that V^*_S is generally larger than V^*_T for AUs of at least 50 m and that the increase of AU size induces a more important decrease of the relative temporal variation for AUs of 10 to 50 m than for AUs of 50 to 200 m. These results suggest that studies aimed at developing relationships between parr density and physical conditions should use AUs longer than 50 m in order to minimize the

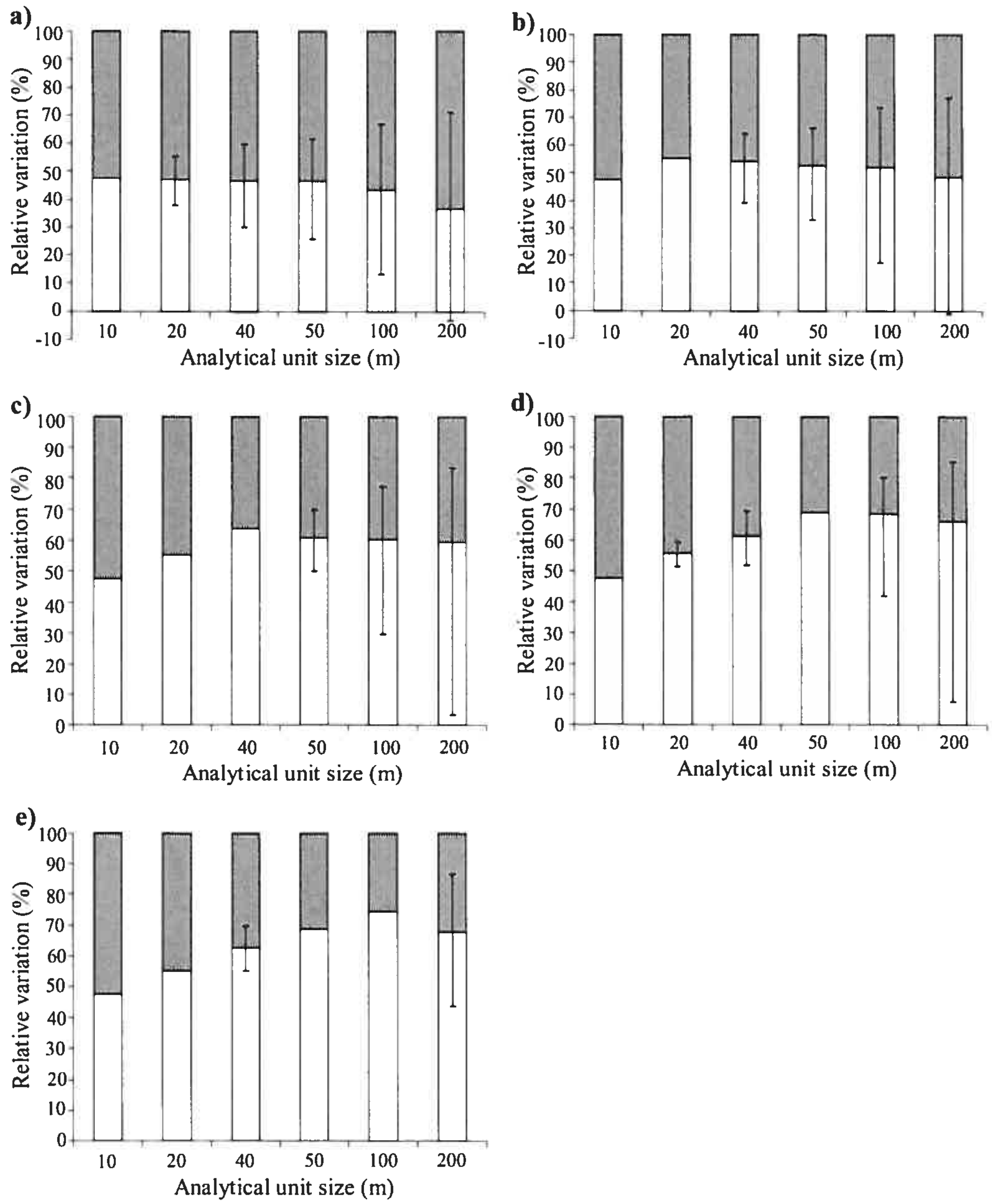

Figure 1.4 Effect of the permutation of AUs of a) 10 m, b) 20 m, c) 40 m, d) 50 m, and e) 100 m on the median percentages of spatial (white) and temporal (grey) relative variation of parr density for different sizes of analytical units. Vertical bars correspond to the 95% confidence intervals.

temporal variation. Such AUs, in our study, corresponded to 1.2 to 2.3 times the river width and to sampling areas ranging from 100 to 400 m^2 depending on visibility. Whether or not the suggestion to develop FHQM using analytical units of 100 to 400 m^2 is specific to parr of Atlantic salmon, to the sampling procedure used (visual surveys performed via linear transects snorkelled during the night), or to the river sampled (SMR) remains to be evaluated. However, our work does suggest that the temporal and spatial structure of the variation of fish densities should be assessed before trying to develop FHQM.

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Chapitre 2

The relative importance of local, lateral, and longitudinal variables on the development of habitat quality models for a river

Judith Bouchard et Daniel Boisclair

En préparation

ABSTRACT

Fish habitat quality models (FHQM) developed for rivers often consist of relationships between fish density and physical conditions prevailing within a series of sites (local variables). However, FHQM may be affected by the size of the units employed to develop these models (analytical units; AU). Application of FHQM over complete rivers may require the inclusion in FHQM of variables that operate at spatial scales larger than local variables. The objectives of this study were to assess the influence of the AU size and quantify the relative importance of local, lateral (characteristics of the shores), and longitudinal (attributes along the upstream-downstream axis of the river) variables on FHQM developed for parr of Atlantic salmon (*Salmo salar*). Parr densities, local, lateral, and longitudinal variables were estimated in 32 reaches of 200 m. FHQM were developed using AUs of 50, 100, and 200 m (length of AU in the upstream-downstream axis of the river). The structure and predictive power of FHQM were affected by AU size. In the river under study, 98% of the predictive power of FHQM may be imputed to the effect of local variables.

INTRODUCTION

Fish habitat quality models (FHQM) developed for rivers often consist in relationships between fish presence or density, which are used as indices of habitat quality, and physical conditions prevailing at a series of sites (i.e. local variables; Rimmer et al. 1984; Heggenes et al. 1991; Girard et al. 2003). The structure of relationships between the biological and physical variables may be affected by the size of the sampling units (the area or the volume of the units over which variables are sampled; Wiens 1989; Bellehumeur and Legendre 1998; Folt et al. 1998). Problems related to the ignorance of the effect of the size of the sampling units may be circumvented by using a sampling strategy that allows one to merge sampling units to form larger analytical units (AU; units employed during the statistical analysis performed to develop models; Dungan et al. 2002; Brind'Amour and Boisclair 2006). Such a sampling strategy permits not only the assessment of the effect of the AU size on the structure of FHQM but also the identification of the AU sizes that should be used to develop potentially more efficient FHQM.

Local variables have been used to model fish habitat quality in river reaches (10^2 - 10^3 m; Guay et al. 2000; Heggenes and Saltveit Svein 2002). These variables have also been used to model habitat quality at the scale of segments and complete rivers (10^3 – 10^6 m; Baglinière and Champigneulle 1982; Heggenes et al. 2002; Johansen et al. 2005). However, many studies suggest that the application of FHQM over complete rivers may require the inclusion in FHQM of variables that better describe processes that operate at that scale (Porter et al. 2000; Magalhaes et al. 2002; Smith and Kraft 2005). Several conceptual models have been proposed to represent the structure of physical and biological components along complete rivers. Hynes (1975) emphasized the effect of land-water interactions on stream attributes. Vannote et al. (1980) proposed the river continuum concept which focuses on the upstream-downstream gradient of physical and biological properties of rivers. Rice et al. (2001) developed the link discontinuity concept which suggests that the input of coarse substrate from tributaries or other lateral sources creates a series of sedimentary links (segments delimited upstream by coarse substrate and downstream by finer substrate) that may determine the spatial structure of the physical and biological variables along the upstream-downstream axis of rivers. Some scientists have also proposed that the spatial organisation among different habitats along a river may influence the distribution and the production of the biota (Fausch et al. 2002; Ward et al. 2002a; Wiens 2002). These models suggest that habitat quality at a series of sites may not be determined only by the conditions found within these sites (local variables), but also by conditions found on the shore (lateral variables) and along the upstream-downstream axis of a river (longitudinal variables). Although local, lateral, and longitudinal variables may contribute to explain the variation of fish habitat quality at the scale of complete rivers, little is known about the relative importance of these variables. The objectives of this study are to assess the influence of the AU size and quantify the relative importance of local, lateral, and longitudinal variables on FHQM developed for a river.

MATERIAL & METHODS

Sampling area and species for study

The study was conducted in the main branch of the Sainte-Marguerite River (SMR) in the Saguenay region of Québec (Figure 2.1). The SMR consists of a succession of sedimentary links caused by inputs of coarse substrate from glacial deposits and dry lateral sources (Davey 2004). Typical pool-riffle sequences are superimposed on the succession of sedimentary links. Meanders are particularly developed 13 to 23 km and 41 to 52 km from the river mouth (FRM). Features such as cascades (85 km FRM) and rapids (40 km FRM) are also present. The SMR was perturbed by the rectification of meanders (41 to 52 km FRM) during the construction of a highway in 1966. Consequently, embankments were made to stabilize the shores. Except for this highway, the watershed of the SMR is relatively free of anthropogenic perturbation.

Eight fish species are present in the main branch of the SMR: Atlantic salmon (*Salmo salar*), Brook trout (*Salvelinus fontinalis*), Blacknose dace (*Rhinichthys atratulus*), Longnose dace (*Rhinichthys cataractae*), Longnose sucker (*Catostomus catostomus*), Sea lamprey (*Petromyzon marinus*), American eel (*Anguilla rostrata*),

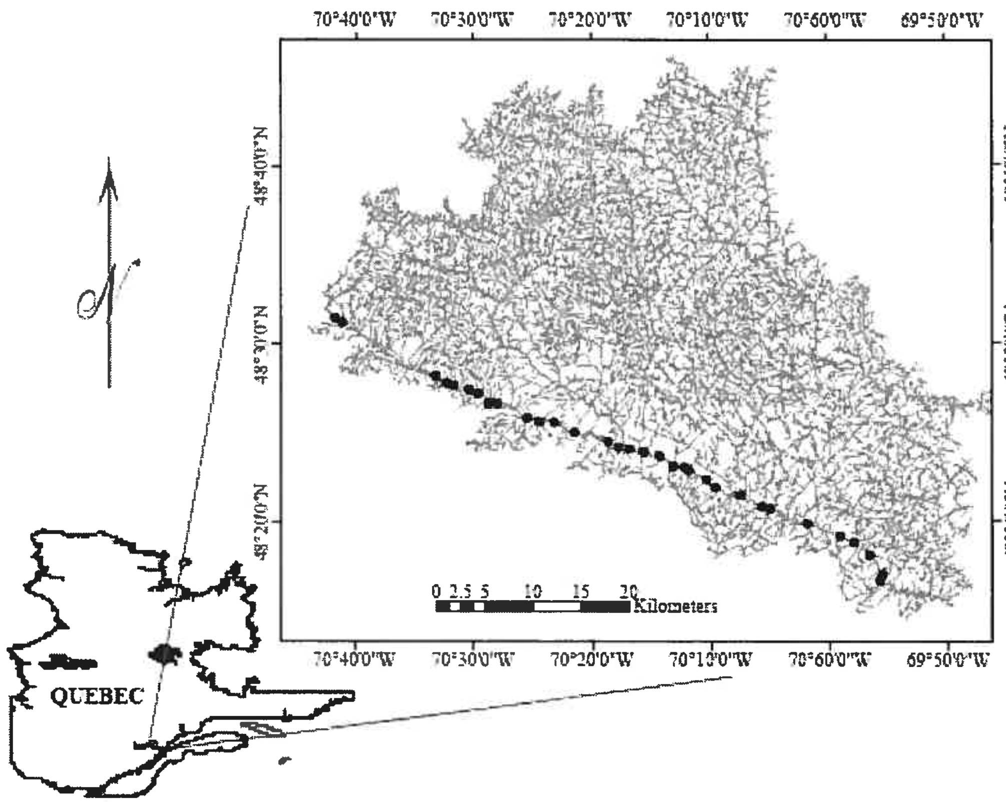

Figure 2.1 Map of the watershed of the Sainte-Marguerite River. The reaches sampled during the present study are represented by black dots.

and Fallfish (*Semotilus corporalis*). This study focussed on parr of Atlantic salmon (I+ and II+ indiscriminately) because they are ubiquitous in SMR and because they are territorial during the summer (Saunders and Gee 1964; Heggenes and Borgstrom 1991). These characteristics were expected to facilitate the establishment of relationships between fish density and the physical conditions along the SMR.

Spatial and temporal context

Field work was performed in 32 reaches each measuring 200 m in the downstream-upstream axis of the river (Figure 2.1). These reaches were distributed in an 88-km segment of the SMR limited upstream by a fall and downstream by the junction of the Sainte-Marguerite and Saguenay Rivers. Each reach was divided in 20 sections of 10 m. This approach allowed us to merge contiguous 10-m sections to form AUs of 50, 100, and 200 m. The size of AUs is here defined as the length, in the upstream-downstream axis of the river, of the AUs resulting from the merging of a specific number of adjacent sections. Sampling was conducted between June 27th and August 5th 2003. During this period, water temperature and discharge ranged from 11 to 28°C, and from 2.5 to 23 $m^3 \cdot s^{-1}$ respectively. However, sampling was done when discharge ranged from 2.5 to 4.5 $m^3 \cdot s^{-1}$ to minimize the effect of flow variation on our data.

Densities of parr of Atlantic salmon

Parr density in each section was estimated by two observers who simultaneously snorkelled two 10-m long transects oriented approximately parallel to the shore. One transect was located as close as possible to the shore (min. depth of 25 cm), and another was located in the middle of the river (5 to 40 m from shore depending on river width). Parr densities were estimated during the night (22h00-03h00) by underwater observations. This strategy was adopted for two reasons. First, the densities of Atlantic salmon parr estimated by visual sampling are significantly higher during the night than during the day because most parr may remain in interstices of the substrate during the day (Imre and Boisclair 2004; Johnston et al. 2004). Second, it has been shown in the SMR that parr densities estimated at night are less variable and less affected by meteorological conditions than during the day (Bédard et al. 2005; Imre and Boisclair 2005). Hence, FHQM developed from night data may be more robust than models developed for daytime data.

Parr were observed using underwater lighting systems (Underwater Kinetics Light, model C4). Light was directed in an upward direction at an angle of approximately 45° relative to the water surface. Hence, fish were illuminated using a diffused beam of light which was expected to minimize fish disturbance (Gries et al. 1997). For each 10-m section, the two snorkellers counted the number of parr observed and evaluated the mean visibility (m). The mean visibility was the average distance (m) at which parr could be seen and correctly identified either on the left or the right hand side of the snorkellers. Parr density (parr $\cdot$ m^{-2}) in a specific transect (shore or middle) of any given 10-m section was obtained by dividing the number of parr observed by the surface area sampled in that transect (mean visibility $\cdot$ 2 sides $\cdot$ 10 m). The average parr density in any AU was obtained by averaging parr densities of transects within the unit.

Sampling and computations of physical variables

The variation of parr densities was modeled using three categories of physical variables: local, lateral, and longitudinal. Local variables described the conditions observed within the AUs. For each 10-m section, we took three estimates of water depth, averaged velocity (at 40% of the water column from the bottom of the river), substrate composition (within an area of 1.5 m^2, as percent contribution of eight size classes of substrate determined by their median axis, also known as their B axis; Table 2.1), and flow type present within the section (smooth water surface: flat water surface or presence of waves up to 3 cm without air bubbles; and rough water surface: uneven water surface with waves ranging from 5 to 10 cm and air bubbles). These estimates were taken at three locations between the thalweg and the farthest shore from the thalweg. These locations corresponded approximately to 1) the thalweg, 2) a point between the thalweg and the farthest shore, and 3) a point in the middle of a line joining point 2) to the farthest shore. The average depth, velocity, and substrate composition were calculated for each AU. Smooth and rough water surfaces were transformed into two binary variables representing the presence (1) or

Table 2.1 Description of the dependent and independent variables estimated for analytical units of 50 m. V* is the coefficient of variation corrected for small sample size (Sokal and Rohlf 1995).

Variables	Code	Unit	Type	Mean	Min	Max	V* (%)
Dependent variable							
Atlantic salmon parr density	Density	Parr*m^{-2}	continuous	0.078	0.000	0.340	89
Independent variables							
Local variables							
Clay composition (B axis: < 0.004 mm)	Clay	%	continuous	1	0	33	398
Silt composition (B axis: 0.004 to 0.06 mm)	Silt	%	continuous	1	0	12	220
Sand composition (B axis: 0.06 to 32 mm)	Sand	%	continuous	14	0	86	130
Gravel composition (B axis: 2 to 32 mm)	Gravel	%	continuous	29	0	92	71
Pebble composition (B axis: 32 to 64 mm)	Pebble	%	continuous	19	0	48	65
Cobble composition (B axis: 64 to 250 mm)	Cobble	%	continuous	22	0	61	74
Boulder composition (B axis: 250 to 1000 mm)	Boulder	%	continuous	12	0	58	147

Variables	Code	Unit	Type	Mean	Min	Max	V* (%)
Metric boulder composition (B axis: > 1000 mm)	MetricB	%	continuous	1	0	13	258
Water depth	Depth	m	continuous	0.47	0.22	0.96	35
Water velocity	Velocity	m/s	continuous	0.40	0.07	0.73	40
Smooth water surface occurrence	SWS	%	continuous	93	0	100	19
Rough water surface occurrence	RWS	%	continuous	22	0	100	167
Woody debris presence	WoodD	-	binary	0.65	0	1	-
Pool presence	Pool	-	binary	0.11	0	1	-
Island or mid-channel bar presence	Island	-	binary	0.23	0	1	-
Lateral variables							
Area of the region drained on shores of AU	AD_AU	km²	continuous	4	0.002	471	1095
Averaged slope of the AD_AU	SD_AU	degrees	continuous	10	0.4	26	70
Area of the region drained on shores 500 m upstream AU	AD_500m	km²	continuous	5	0.1	472	865

Variables	Code	Unit	Type	Mean	Min	Max	V* (%)
Averaged slope of the AD_500m	SD_500m	degrees	continuous	15	4	23	26
Area of the region drained on shores 1 km upstream AU	AD_1km	km²	continuous	8	0.5	472	508
Averaged slope of the AD_1km	SD_1km	degrees	continuous	14	8	21	19
Distance to a road	Droad	m	continuous	251	15	2107	187
Overhanging vegetation	Overveg	-	binary	0.73	0	1	-
Sandy shore	Ssand	-	binary	0.52	0	1	-
Shore composed of pebble and/or cobble	Spebble	-	binary	0.69	0	1	-
Cliff	Cliff	-	binary	0.17	0	1	-
Embankment	Embank	-	binary	0.05	0	1	-
Tributary junction	Trib	-	binary	0.07	0	1	-
Longitudinal variables							
Distance from the river mouth	Dmouth	m	continuous	42465	3056	85739	55
Distance to the first tributary downstream	DtribD	m	continuous	309	0	1714	117
Distance to the first tributary upstream	DtribU	m	continuous	439	0	2790	132

Variables	Code	Unit	Type	Mean	Min	Max	V* (%)
Distance to the nearest tributary	Dtrib	m	continuous	177	0	1300	129
Distance to the nearest spawning site	Dspawn	m	continuous	1917	0	7820	101
Distance to the nearest island	Disland	m	continuous	2375	0	10628	119
Distance to the next sedimentary link downstream	DlinkD	m	continuous	9791	0	28748	89
Distance to the next sedimentary link upstream	DlinkU	m	continuous	7631	0	29353	97
Distance to the nearest sedimentary link	Dlink	m	continuous	4062	0	14586	97
Relative distance to the next sedimentary link upstream	RDlinkU	-	continuous	0.45	0	1	67
Relative distance to the nearest sedimentary link	RDlink	-	continuous	0.23	0	0.50	65

the absence (0) of these types of flows in at least one of the three locations within each 10-m section. Because smooth water surface was almost always present once within every AU, we calculated the percentage (%) of smooth and rough water surface within each AU. In addition, we visually assessed the presence of woody debris (wood debris consisted of wood fragments longer than 30 cm that covered at least 1 m^2 of the riverbed), pool (section of river deeper than 200% of the upstream and downstream sections; the depth of pools ranged from 0.5 to 2 m with an average of 1 m), and island or mid-channel bar in each 10-m section. These variables were coded 1 (presence) if they were present in at least one 10-m section of an AU; otherwise they were coded 0 (absence). River features (pool and island or mid-channel bar) were coded 'present' in every contiguous 10-m sections where they occurred. Local variables were estimated at a site a maximum of three days before or after parr densities were estimated at this site. Water discharge varied by less than 0.8 $m^3 \cdot s^{-1}$ (21% of average flow) over this interval.

Lateral variables referred to characteristics of the shore. The presence of sand, pebble, cliff, embankment, tributary junction (every tributary seen was considered, no matter its size) or overhanging vegetation (covering at least a surface of 1 m^2 above the water) were visually assessed from the river. Other lateral variables were estimated with a GIS software (ArcGIS 8.3) and numerical topographic maps (1:20 000). For each AU, the distance to a paved road was estimated. The area and average slope of the valley side draining to the river were calculated from a numerical elevation raster (raster resolution: 10 m by 10 m). These attributes were estimated in three ways, for the valley side area draining to the length of bank 1) corresponding to the AU, 2) from the AU and extending 500 m upstream, and 3) from the AU and extending 1 km upstream.

Longitudinal variables described the position of the AU relative to features along the upstream-downstream axis of the river (distance to river mouth, tributaries, spawning sites, islands, boundaries of sedimentary link). River mouth, tributaries and islands were localised on topographic maps (1: 20 000). Spawning sites and boundaries of sedimentary link were localised by Davey (2004). Longitudinal variables were estimated using GIS software in which the river was represented by a line that corresponded to the trajectory of the thalweg. For each AU, we estimated the distance to the nearest feature. In the case of tributaries and boundaries of sedimentary links, we estimated the distance between an AU and the first feature upstream and downstream. In addition, because the lengths of sedimentary links are variable in the SMR (1.5 to 26.5 km; Davey 2004), we calculated the relative distance between an AU and the boundaries of a sedimentary link. Relative distances were estimated by dividing the distance to the boundary of the sedimentary link (upstream and closest) by the total length of the sedimentary link considered.

Selection of multiple regression models

FHQM were developed using multiple regression analysis. Parr densities were modelled using physical variables from one category (local, lateral or longitudinal) at a time. Physical variables and their natural logarithm (in the case of continuous variables) were selected with a forward selection procedure. We employed two approaches to eliminate FHQM that did not correctly predict parr densities. First, we tested multiple regression models with unrestricted permutation tests (10 000 permutations of the estimates of parr densities; permutation tests are described in some textbooks, including Legendre and Legendre 1998). We eliminated models that were not significant or that included variables that did not significantly contribute to the model at an α level of 0.05. Second, we proceeded to the cross-validation of each significant model to eliminate models that did not correctly predict statistically independent data and to select the model with the highest potential to predict such data. The cross-validation was performed as follows: 1) we randomly split our data into a learning set and a testing set of the same size; 2) we used the learning set to develop a multiple regression model based on the independent variables found to have a significant effect during the analysis of the complete data set; 3) we used the model developed with the learning set to predict parr density of the testing set; 4) we compared the predictions made by the model to the observation in the testing set; 5) we repeated steps 1 to 4 10 000 times. We assessed the quality of the predictions (step 4) by calculating the major axis slope (b_{MA}), the major axis intercept (b_0), and the coefficient of determination (r^2) between predictions and observations (Mesplé et al. 1996). The 95% confidence intervals (C.I.) of these parameters were estimated by calculating the 2.5 and 97.5 percentiles of the 10 000 values obtained for each parameter in step 5. A model was rejected whenever the 95% C.I. of its b_{MA} included the value 0 or excluded the value 1, or the 95% C.I. of b_0 excluded the value 0. We then selected models with the highest median r^2 value estimated by cross-validation for each combination of AU size (50, 100, and 200 m) and variable category (local, lateral, and longitudinal). Hence, nine habitat quality models could be obtained (3 AU sizes x 3 categories of variables). The fraction of parr density variation explained by the multiple regression models was determined by computing the adjusted coefficient of multiple determination (R^2_a; Legendre and Legendre 1998). R^2_a is the coefficient of multiple determination (R^2) corrected for the sample size (n) and the number of parameters (p) in the model.

$$R^2_a = 1 - (1 - R^2) \cdot (n-1) \cdot (n-p-1)^{-1} \quad (1)$$

We evaluated the relative importance of local, lateral, and longitudinal variables, using two steps. First, we developed the model that represented the relationship between parr densities estimated at any given AU size and every local, lateral, and longitudinal variable shown to have a significant effect during the cross-validation analysis performed for that AU size. The three resulting models (one for each AU size) are hereafter referred to as the combined models for a given AU size. Second, we proceeded to a variation partitioning for each combined model (Borcard et al. 1992; Legendre and Legendre 1998). Variation partitioning permits to separate the exclusive contributions of different categories of variables (in our case local, lateral, and longitudinal variables) to the model obtained for each AU size. In addition, it permits to determine the part of the variation of parr density explained simultaneously by two or three categories of physical variables. This analysis was complemented by the computation, for each AU size, of a correlation matrix (Pearson r) describing the relationship between the physical variables.

RESULTS

Parr densities and physical conditions

Parr densities estimated for AUs of 50 m ranged from 0.0 to 0.34 parr · m^{-2} (Table 2.1). For AUs of 200 m, parr densities ranged from 0.007 to 0.26 parr · m^{-2}. Coefficients of variation (V*) of parr densities ranged from 89% (AUs of 50 m) to 77% (AUs of 200 m). Physical conditions (local, lateral, and longitudinal) estimated for different AU sizes varied to different degrees depending on the specific variables within each category of physical conditions (Table 2.1). Local variables estimated for AUs of 50 m were associated with V* that ranged from 19% (smooth water surface; SWS) to 710% (Bedrock). Lateral variables for this AU size had the largest range of variation with V* of 19% for slope of the drainage region within 1 km upstream of the AU (SD_1km) and 1095% for the area of the drainage region at the AU

(AD_AU). In contrast, longitudinal variables covered the smallest range of V* with 55% for the distance to the river mouth (Dmouth) to 129% for the distance to the closest tributary (Dtrib). Local and lateral variables had V* that decreased by as much as 10-fold as the AU size increased from 50 to 200 m. For instance, V* of the area of the region drained on the river shores 500 m upstream the AU decreased from 865% (AU of 50 m) to 85% (AU of 200 m). In contrast, the V* of longitudinal variables increased by at most 1.5-fold as the AU size increased (V* of the distance to the first tributary downstream, DtribD, increased from 117 to 170% as AU sizes increased from 50 to 200 m).

Fish habitat quality models and the influence of the size of the analytical units

No statistically significant model using local variables was developed for AUs of 50 m. Models developed using local variables for other sizes of AU explained from 50% (100 m) to 65% (200 m) of the parr density variation (Table 2.2). The predictive power of these models therefore tended to increase as the size of the AUs increased. For AUs of 100 m, three variables were selected: Boulder, Woody debris (WoodD), and Smooth water surface (SWS). However, for AUs of 200 m, only two variables significantly contributed to explain variations of parr densities: Boulder and WoodD. For all sizes of AU analysed, the first local variable selected during the forward stepwise procedure was always Boulder. This variable alone explained from 41% (AUs of 100 m) to 47% (AUs of 200 m) of the parr density variation (R^2_a). Other local variables increased the R^2_a by 9% (100 m) to 18% (200 m). Independently of the AU size, parr densities were positively correlated with all local variables selected. The coefficient of ln(Boulder +1) in the model based on local variables was unaffected by the AU size. However, the coefficient of WoodD increased from 0.036 to 0.085 and the intercept of the model increased from -0.32 to -0.064 as the AU size

Table 2.2 Habitat quality models selected for the three categories of physical variables and the three different sizes of analytical units. R^2_a is the adjusted coefficient of determination of the models. See Table 2.1 for the codes of the variables.

Physical variables	**Analytical units size**	**Models of Parr density**	R^2_a
local	50 m	No model selected	-
	100 m	- 0.32 + 0.040*ln(Boulder+1) + 0.036*WoodD + 0.069*ln(SWS +1)	0.50
	200 m	- 0.064 + 0.040*ln(Boulder+1) + 0.085*WoodD	0.65
lateral	50 m	No model selected	-
	100 m	No model selected	-
	200 m	No model selected	-
longitudinal	50 m	No model selected	-
	100 m	0.22 - 0.017*ln(DlinkU+1)	0.20
	200 m	0.19 - 0.014*ln(DlinkU+1)	0.19

increased from 100 to 200 m. Lateral variables did not permit the development of statistically significant models to explain the variation of parr density, and this, regardless of the size of the AU. No statistically significant model using longitudinal variables was developed for AUs of 50 m. For larger AUs, models developed using longitudinal variables explained from 19% (200 m) to 20% (100 m) of the variation of parr densities. Hence, the size of the AUs did not have a marked effect on the predictive power of the models developed using longitudinal variables. Parr density for AUs of 100 and 200 m decreased as the distance between AU and the upstream boundary of a sedimentary link (DlinkU) increased. Regression coefficients (-0.014 to -0.017) and intercepts (0.19 to 0.22) of models based on longitudinal variables did not vary significantly as the AU size increased from 100 to 200 m. The cross-validation indicated that FHQM based on local variables have an ability to predict independent data ($0.47 < r^2 < 0.64$) that is 2- to 3-fold higher than models based on longitudinal variables ($0.22 < r^2 < 0.24$; Figure 2.2). In addition, the median r^2 of models developed using local variables increased as the AU size increased from 100 m (0.47) to 200 m (0.64).

Relative importance of local, lateral, and longitudinal variables

The combined models based on local and longitudinal variables explained 51% (100 m) to 65% (200 m) of the variations of parr density (Figure 2.3). Variation partitioning indicated that the variance of parr density explained by the combined model could be divided in three fractions. The first and most important fraction was the part of the variance explained exclusively by local variables. This fraction ranged from 31% (AUs of 100 m) to 47% (AUs of 200 m). The second fraction was the part of the variance explained exclusively by longitudinal variables. This fraction never explained more than 1% of the variation of parr density (AUs of 100 m). The third fraction was the variation explained simultaneously by the local and longitudinal variables. The joint effect of these variables on combined FHQM models ranged from 18% (AUs of 200 m) to 19% (AUs of 100 m).

DISCUSSION

Influence of the size of the analytical units

Our analyses are consistent with the expectation that the AU size may affect specific attributes of the relationships between the biological and physical variables

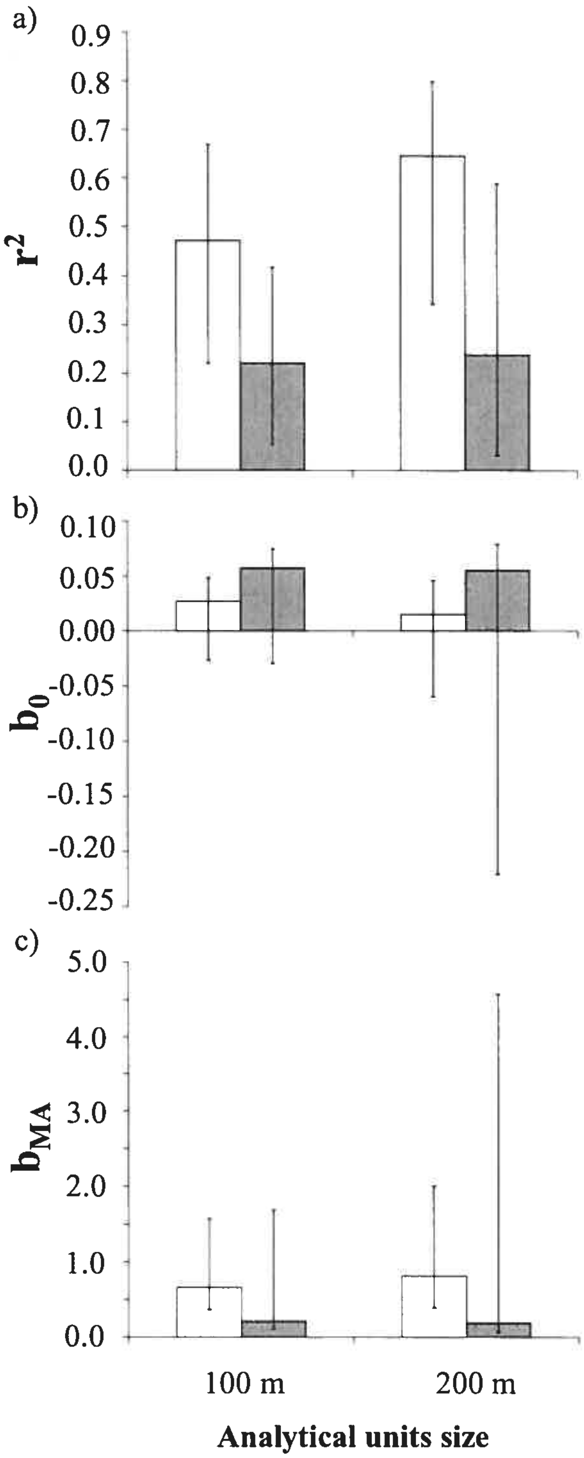

Figure 2.2 Distributions of the slopes (b_{MA}), the intercepts (b_0), and the coefficients of determination (r^2) of the relationships between predicted and observed parr density obtained following the cross-validation of the models developed using local (white) and longitudinal variables (grey) for analytical units of 100 and 200 m.

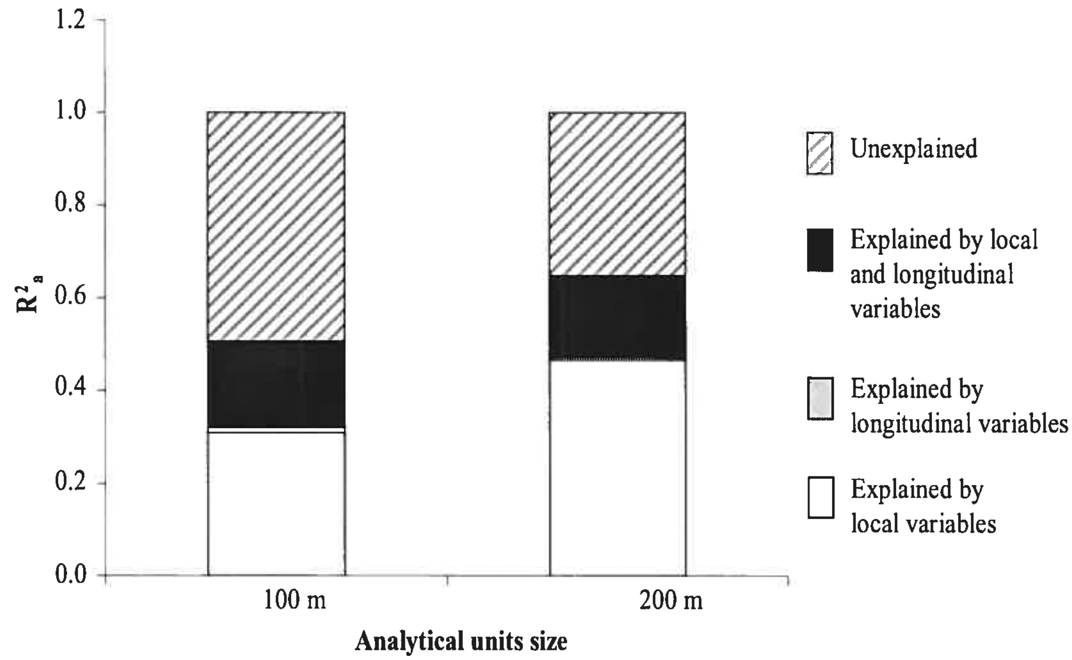

Figure 2.3 Explained and unexplained portions of the variance of parr density in combined models developed using AU of 100 and 200 m. Explained variance is further divided in portions explained exclusively by local and longitudinal variables, and simultaneously by local and longitudinal variables. R^2_a is the adjusted coefficient of determination of the models.

(Levin 1992). However, our results indicate that the influence of the AU size may vary among categories of physical variables and among physical variables within a category. The number of local variables having a significant effect on parr density decreased from three to two as the AU size increased from 100 to 200 m. In contrast, the number of variables included in the model developed using longitudinal variables remained constant for these AU sizes. The nature of the variables that significantly contributed to FHQM was more stable among the sizes of AU than their number. For instance, ln(Boulder+1) and WoodD both contributed to the FHQM based on local variables using AUs of 100 and 200 m. Similarly, DlinkU contributed to the models based on longitudinal variables using AUs of 100 and 200 m. The effect of the AU size on the regression coefficients associated with the variables that significantly contributed to explain the variation of parr density and on the intercepts of the FHQM also varied among categories of variables and variables within a category. The regression coefficients of a local variable such as ln(Boulder+1) in the model based on AUs of 100 m did not differ from that of the model based on AUs of 200 m. Other parameters of models based on local variables (the regression coefficient of WoodD and the intercept of the FHQM) varied 2.4- to 5-fold respectively between models developed using AUs of 100 and 200 m. This situation may be related to the difference between the number of variables included in the models developed for AUs of 100 m (3 variables) and that developed for AUs of 200 m (2 variables). We reanalysed our data to obtain FHQM for AUs of 100 and 200 m that comprised only two variables (ln(Boulder+1) and WoodD). Although the new '2-variable' model based on local variables was slightly different from the original '3-variable' model (parr density = 0.034 * (ln(Boulder + 1)) + 0.041 * (WoodD) - 0.008), this reanalysis confirmed that changing the AU size may have little effect on the regression coefficient of some variables (ln(boulder+1); 1.17-fold difference) but caused a 2- (regression coefficient of WoodD) to 8.4-fold difference (intercept) for other parameters of FHQM based on local variables. In contrast, the parameters of the models developed using longitudinal variables for AUs of 100 m did not vary by more than 1.21-fold from those of models developed for AUs of 200 m. The fraction of parr density variation explained by FHQM (R^2_a) based on local variables increased from 0.50 to 0.65, and the ability to predict independent data during a cross-validation exercise (r^2) increased from 0.47 to 0.64 as the AU size increased from 100 to 200 m. However, the R^2_a (0.19 to 0.20) and the r^2 (0.22 to 0.24) of FHQM developed using longitudinal variables remained relatively constant for the two AU sizes.

Our study suggests that FHQM based on local variables are structurally (number, nature and coefficient of variables, intercepts of models) and functionally (predictive power; R_a^2 and r^2) more sensitive to changes in the AU size than models based on longitudinal variables. Two hypotheses may be proposed to explain that models based on local variables have a better predictive power for AUs of 200 m than for AUs of 100 m. First, it may be hypothesized that the model based on local variables for AUs of 200 m has a higher predictive power than the FHQM developed for AUs of 100 m because it comprised fewer variables (two explanatory variables for AUs of 200 m instead of three for AUs of 100 m). It has been shown that model complexity (the number of independent variables) may induce an "over fit" of the data (Gong 1986) and may increase the prediction error (Mac Nally 2000). However, the R^2_a (0.46) and r^2 (0.45) of a new FHQM based on two local variables using AUs of 100 m remained lower than models developed using AUs of 200 m. The relative performance of FHQM based on local variables and developed using AUs of 100 and 200 m may therefore be independent of the number of variables comprised in the models. Second, it may be hypothesized that the temporal uncertainty related to fish density in individual AUs may affect the strength of the relationship between parr density and environmental conditions. In our study, parr density was estimated only once per 200-m reach and in each AU. It is conceivable that parr density in any given AU may vary among nights. Although parr are generally perceived as territorial fish, they are also known to explore their habitats during the summer months (Armstrong et al. 1997; Metcalfe et al. 1997). Atlantic salmon parr may move 208 to 862 m within a 13-day period in the summer and fall (Økland et al. 2004). The possibility that the temporal variability of parr density due to fish movement may decrease with the AU size may explain that FHQM based on AUs of 200 m may perform better than those based on 100 m. One consequence of our second hypothesis, for which we presently have no support, is that if the movement of fish or the average size of home range of parr changes among rivers, the AU size that should be used to develop FHQM may also vary among rivers.

The structural and functional stability of FHQM developed using longitudinal variables with different AU sizes may be related to the spatial extent over which longitudinal variables exert their influence (Levin 1992; Folt et al. 1998). The length of sedimentary links in the SMR ranged from 1.5 to 26.5 km (Davey 2004). Hence, the effect of such large structures is destined to be expressed over large scales. We may not have perceived differences in coefficients of regression, intercepts, R^2_a, and r^2, among AU sizes because the influence of DlinkU occurs at a much larger scale (10^3 to 10^4 m) than the AU sizes for which FHQM were developed (100 to 200 m).

Relative importance of local, lateral, and longitudinal variables

Variation partitioning showed that local and longitudinal variables shared a lot of information and hence are interrelated (Table 2.3). The fact that local and longitudinal variables shared information supports the suggestion of Rice et al. (2001) that sedimentary links may influence local variables as well as the longitudinal distribution of organisms. Parr density was negatively related to DlinkU; this was expected because the percent contribution of boulders to the riverbed is expected to decrease as the distance upstream to a sedimentary link increases. However, DlinkU explained less than 20% of the parr density variation, whereas local variables explained 44 to 65% of that variation. Consequently, in the SMR, sedimentary links may have contributed to structure local variables but other processes may have played a larger role in determining local variables and, in particular, the percent contribution of boulders to the riverbed.

Table 2.3 Correlations matrix among physical variables selected to model parr densities for analytical unit of a) 100 m and b) 200 m. See Table 2.1 for the codes of the variables. Significant correlations are noted as follows: **p≤0.01; *p≤0.5.

a) Analytical unit of 100 m

	WoodD	ln(SWS+1)	ln(DlinkU+1)
ln(Boulder+1)	-0.39**	-0.55**	-0.48**
WoodD		0.32**	0.00
ln(SWS+1)			0.30*

b) Analytical unit of 200 m

	WoodD	ln(DlinkU+1)
ln(Boulder+1)	-0.48**	-0.53**
WoodD		-0.12

We observed that lateral and longitudinal variables contained very little new information about habitat quality in the river. No lateral variables could correctly predict parr density. Variation partitioning indicated that regardless of the AU size employed, at least 98% of the predictive power of FHQM developed by combining local and longitudinal variables was imputable to the effect of the local variables (alone or jointly with longitudinal variable). This, in turns, means that the information contained in lateral and longitudinal variables contributed for less than 2% of the variation of parr density explained by FHQM developed in our study. Concepts of landscape ecology suggest that the spatial organisation of ecosystems might influence habitat quality (Fausch et al. 2002; Ward et al. 2002a; Wiens 2002). Our analyses indicate that habitat quality is mainly determined by local conditions. While our results do not support the expectation of hypotheses about the role of the spatial organisation of habitats within the SMR ecosystem, they are consistent with studies that found that stream macro-invertebrate and fish are more strongly related to local conditions than to landscape conditions (Lammert and Allan 1999; Dovciak and Perry 2002).

Our study suggests that local variables are sufficient to model parr habitat quality. It would be premature to generalize this finding to other salmon rivers. The relative effect of local, lateral, and longitudinal variables may be contextual. In the SMR, tributaries, which are known to represent a source of food and a potential refuge against unfavorable environmental conditions (Erkinaro 1995; Bardonnet and Bagliniere 2000), are observed at 0.1 to 88 km FRM (only tributaries downstream the fall have been considered here) at intervals of 0.02 to 2.9 km (average = 0.52 km). Spawning sites, which may also affect parr distribution (Kocik and Ferreri 1998), are observed at 11 to 85 km FRM at an interval of 0.07 to 16 km (average = 2 km). Hence, our analyses may indicate that the number and the spatial organisation of longitudinal variables that characterize the SMR do not affect parr habitat quality. Whether or not other patterns of spatial distribution of longitudinal variables may affect parr density and be considered limiting to parr habitat quality remains to be elucidated. In this context, it may be hypothesized that, although landscape attributes may not always be useful to explain habitat quality variations within a river, they may be relevant to explain habitat quality variations among rivers.

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CONCLUSION

L'objectif principal de ce projet de maîtrise était de comprendre les processus modulant la distribution des tacons de saumons atlantiques le long d'une rivière. Pour l'atteindre, nous avons d'abord déterminé les tailles d'unités d'analyses (UA) fiables (i.e. pouvant être utilisées pour développer des MQH). Nous avons ensuite déterminé l'influence de la taille des UA fiables sur le développement des MQH et l'importance relative des variables locales, latérales et longitudinales dans les MQH développés le long d'une rivière.

Souvent, les unités d'échantillonnage sont directement utilisées comme UA. Or, selon les organismes étudiés et la méthode d'échantillonnage choisie, la taille des unités d'échantillonnage peut être inadéquate pour répondre aux questions posées. Par exemple, pour établir des relations entre des densités de tacons de saumons atlantiques et des variables physiques, il est souhaitable de minimiser la variabilité temporelle des estimations de densité de tacons. Nous avons donc estimé à dix reprises les densités de tacons dans quatre segments de rivière de 200 m. Cet échantillonnage nous a permis d'estimer la variation spatiale et la variation temporelle pour différentes tailles d'UA. Nos résultats montrent qu'il est possible de diminuer la variation temporelle des estimations de densités de tacons en regroupant les unités d'échantillonnage contiguës en UA plus grandes. Pour des UA de 10, 20 et 40 m, les estimations de densités de tacons peuvent être plus variables temporellement que spatialement. Alors que, pour les UA de 50, 100 et 200 m, on obtient des estimations de densités de tacons relativement peu variables temporellement tout en étant variables spatialement. Caractéristique nécessaire pour mettre en évidence les relations entre les tacons (ou tout autre organisme) et les conditions physiques de leur habitat, ainsi que pour développer des MQH puissants.

Pour les tacons de saumons atlantiques et la méthode d'échantillonnage utilisée, nos résultats suggèrent donc qu'on devrait développer des MQH à partir d'UA ≥50 m.

Chacune des tailles d'UA fiables (50, 100 et 200 m) a le potentiel de produire des MQH différents. Les processus pouvant être détectés par une étude sont en partie déterminés par la taille des UA. Nous avons, par ailleurs, remarqué que la variation perçue dans une variable dépend de la taille d'UA utilisée. Pour les variables locales et latérales, la variation observée entre les UA diminue (d'un facteur maximal de 10) avec leur augmentation en taille; alors que, pour les variables longitudinales, la variation peut augmenter légèrement (d'un facteur maximal de 1.5). L'influence de la taille des UA sur la variation perçue est différente pour chaque catégorie de variables et, même, pour chaque variable physique. Nous avons donc construit des MQH en utilisant chaque taille d'UA fiable. Nous avons d'abord remarqué que la taille des UA influence les caractéristiques (nombre de variables sélectionnés, coefficients de régression, ordonnés à l'origine) des MQH développés différemment selon les variables physiques considérées. Nos résultats suggèrent que l'influence de la taille des UA est plus grande sur les MQH développés à partir des variables locales (blocs, courant uniforme et débris de bois) que ceux développés à partir d'une variable longitudinale (DlinkU; distance à un maillon sédimentologique en amont de l'UA). Nos résultats montrent également qu'il est possible d'améliorer la puissance prédictive des MQH développés à partir des variables locales en augmentant la taille des UA de 50 à 200 m. Il semble que l'effet de la taille des UA sur les caractéristiques des MQH développés à partir des variables locales puisse dépendre de la taille des territoires utilisés par les tacons de saumons atlantiques. Bien que cette étude ne permette pas de corroborer cette hypothèse, il serait important de l'étudier. En effet, si la taille des territoires des tacons est variable d'une rivière à une autre, alors la taille des UA à utiliser pour développer des MQH pourrait aussi être variable d'une rivière à une autre. Il est aussi possible que l'influence de la taille des UA sur les MQH dépende de l'échelle spatiale à laquelle les variables physiques sont structurées. En effet, nous avons remarqué une plus grande influence de la taille des UA sur les MQH développés à partir des variables locales que sur les MQH développés à partir des variables longitudinales. Le peu d'influence de la taille des UA sur les MQH développés à partir de la variable longitudinale, DlinkU, est peut être dû au fait que les maillons sédimentologiques sont des segments variant de 1.5 à 26.5 km dans la rivière Sainte-Marguerite, alors que les variables locales sont vraisemblablement structurées à une plus petite échelle spatiale.

Indépendamment de la taille des UA, nos résultats montrent que les variables locales (particulièrement l'abondance relative de blocs) suffisent pour prédire adéquatement la qualité des habitats de tacons le long de la rivière étudiée. Aucune variable latérale n'a permis d'expliquer ou de prédire correctement la distribution des tacons le long de la rivière étudiée. Et bien que la variable longitudinale, DlinkU, explique dans une certaine mesure la distribution des tacons, l'information qu'elle apporte est grandement redondante à celle fournie par les variables locales. Notons, cependant, que cette étude a été menée sur une seule rivière du Québec. L'importance relative des variables locales, latérales et longitudinales pourrait être différente dans d'autres rivières dont les caractéristiques contextuelles (variables latérales et longitudinales) diffèrent de la rivière étudiée. Par ailleurs, il est possible que des variables latérales et longitudinales puissent améliorer la puissance des MQH développés sur plusieurs rivières à la fois. Par conséquent, il serait intéressant de mener des études similaires à celle-ci sur des rivières présentant des organisations spatiales différentes de la rivière Sainte-Marguerite.

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