

Université de Montréal

Importance de la taille et du contexte spatial des unités d'analyse
sur la structure, le pouvoir prédictif et l'extrapolation des modèles de qualité d'habitat.

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Ce mémoire intitulé :
Importance de la taille et du contexte spatial des unités d'analyse
sur la structure, le pouvoir prédictif et l'extrapolation des modèles de qualité d'habitat.

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RÉSUMÉ

Un modèle de qualité d'habitat met en relation un indicateur de la valeur écologique d'une série de sites d'échantillonnage pour une espèce ou une communauté (présence/absence, densité, production, etc.) et les conditions environnementales caractérisant ces sites (pH, composition du substrat, production primaire, etc.). L'objectif de cette étude est de voir les effets de la taille et du contexte spatial des unités d'analyse sur la structure, le pouvoir prédictif et l'extrapolation des modèles de qualité d'habitat. Pour y arriver, nous avons échantillonné une section de 14.7 km de la Rivière Sainte-Marguerite (Région du Saguenay, Québec) de façon à obtenir des séries spatiales continues de la densité de juvéniles du saumon Atlantique ainsi que de différentes caractéristiques de l'environnement de nature locale (vitesse du courant, composition du substrat, etc.) ou de contexte spatial (distance à la plus proche frayère en amont, présence de remblaiements sur la berge, etc.). Nos résultats montrent que la taille des unités d'analyse influence la structure ainsi que le pouvoir prédictif des modèles. Les modèles développés avec des unités d'analyse provenant de la fusion d'unités d'échantillonnage similaires (taches d'habitat) ou avec des unités d'analyse dont la longueur est similaire à celle de ces taches (200 m dans notre étude) ont un meilleur pouvoir prédictif et une meilleure capacité d'extrapolation que les modèles développés avec de petites unités d'analyse. Bien que les variables locales restent essentielles lors d'une modélisation d'habitat, les variables de contexte spatial contribuent à augmenter le pouvoir prédictif des modèles.

Mots clés : saumon de l' Atlantique; rivière; paysage; échelle; taches d'habitat

ABSTRACT

Habitat quality models are quantitative relationships between indicators of the ecological value of a series of sampling units (e.g. presence/absence, density, growth, survival, production, etc) and the environmental conditions prevailing at these units (e.g. temperature, substrate composition, pH, etc). The purpose of this study was to assess the effects of the size and the spatial context of analytical units on the structure, the predictive power, and the upscaling of habitat quality models. We sampled a 14.7 km section in the Sainte-Marguerite River (Saguenay region, Quebec) in a way to obtain continuous spatial series for juveniles Atlantic salmon density, and for different local habitat characteristics (flow velocity, substrate composition, etc.) and spatial context characteristics (distance to the nearest tributary upstream, presence of embankment in the shore, etc.). Our results are consistent with the expectation that changing the size of analytical units may affect the structure and the predictive ability of habitat quality models. Our analyses suggest that the merging of sampling units possessing similar environmental conditions to form habitat patches or analytical units that have a size similar to habitat patches (i.e. in our study analytical units of 200 m) may improve the predictive ability and the upscaling of habitat quality models. Our study also indicates that, while local variables often explain most of the variation of indices of habitat quality, spatial context variables may also increase the predictive power of habitat quality models.

Key words : Atlantic salmon; river; landscape; scale, habitat patches

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1 000 iterations of models developed using different sizes of analytical units (AU).

Squares represent medians of intercepts.

LISTE DES ABRÉVIATIONS

AU : Analytical unit

CI : Confidence interval

HP : Habitat patch

HQM : Habitat quality model

JAS : Juvenile Atlantic salmon

JSA : Juvénile du saumon de l'Atlantique

MAUP : Modifiable areal unit problem

MQH : Modèle de qualité d'habitat

$R^2_{adj.}$: Adjusted R^2

SMR : Sainte-Marguerite River

SU : Sampling unit

UA : Unité d'analyse

UE : Unité d'échantillonnage

Sometimes, there is just no way to hold back the river.

- Hermann Hesse, *Siddharta*

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INTRODUCTION GÉNÉRALE

Un habitat est constitué d'un ensemble de facteurs physiques et biologiques qui permettent à un organisme vivant de subvenir à ses besoins (Barbour et al. 1999). Depuis environ 200 ans, la surpopulation humaine, la surexploitation des ressources naturelles et la pollution ont entraîné une perte d'habitat pour de nombreuses espèces animales et végétales à l'échelle de la planète (Chiras et al. 2002). Selon le dernier rapport de l'Union internationale pour la conservation de la nature (IUCN; Baillie et al. 2004), la destruction, la dégradation et la fragmentation des habitats sont les plus grandes menaces pour les animaux terrestres, avec un impact sur 86 % des oiseaux et des mammifères menacés et sur 88 % des amphibiens menacés. La perte d'habitat est également la plus grande menace pour les espèces animales d'eaux douces et la deuxième plus grande menace pour les espèces animales marines, après la surexploitation. Dans cet optique, il devient très important de développer des stratégies de conservation des habitats les moins altérés et d'élaborer des plans de restauration et d'aménagement pour les habitats endommagés.

Les écosystèmes sont des mosaïques complexes d'habitats présentant différentes conditions environnementales (Dunning et al. 1992). Cette hétérogénéité spatiale suggère que les différents habitats contribuent de façon non équivalente au maintien des populations et des communautés. Le modèle de qualité d'habitat (MQH) est un outil de synthèse qui s'avère très utile lorsqu'on cherche à représenter les relations entre des individus et leur environnement. Il existe plusieurs formes de MQH. Par exemple, les courbes de préférences montrent s'il y a des associations positives ou négatives d'une

espèce avec certaines caractéristiques de l'habitat en fonction de la disponibilité de ceux-ci (Guay et al. 2000; Crook et al. 2001). L'indice de qualité d'habitat classe les habitats sur un gradient de qualité pour une espèce ou une communauté selon différents facteurs physiques, chimiques ou biologiques associés à ces habitats (Courtois 1993; Guay et al 2000). Un autre indice, développé par Karr (1981) et qui s'applique plus particulièrement aux cours d'eau, permet d'évaluer les effets des perturbations anthropiques en milieu aquatique en évaluant l'intégrité des habitats en comparant les communautés ichthyologiques (ou d'invertébrés ou autres) des habitats perturbés avec celles des habitats non-perturbés (Rioux et Gagnon 2000). Finalement, le modèle de régression met en relation un indice de la valeur écologique (ex : production, biomasse, densité, taux de croissance, taux de survie, etc.) et des conditions environnementales (ex : pH, production primaire, présence de refuges,...) dans une série d'unités d'échantillonnage (UE; ex : quadrats, parcelle, etc.). Ces modèles se présentent sous forme d'équation mathématique dont l'expression la plus simple est

$$y = b_1x_1 + b_2x_2 + b_o \quad [1]$$

où y est l'indice de la valeur écologique à un UE, x_1 et x_2 sont des variables environnementales et b_1 , b_2 et b_o sont des constantes (Turgeon et Rodriguez 2005). Dans un but de conservation et d'aménagement, les MQH devraient idéalement permettre aux scientifiques et aux gestionnaires d'identifier les habitats possédant une grande valeur écologique pour une population ou une communauté donnée et de prédire les effets de perturbations naturelles ou anthropiques sur les habitats (Gibson et al. 2004; Newbold et Eadie 2004; Woithon et Schmieder 2004; Bowman et Robitaille 2005; Klaus et al. 2005; VanManen et al. 2005).

L'étape finale du processus de modélisation est de transférer le modèle ayant été développé à partir d'observations faites sur un ensemble d'UE à une autre portion de l'écosystème où l'on souhaite identifier les habitats à haute valeur écologique. Cette extrapolation nécessite l'adoption de certaines prémisses. Cependant, les études de modélisation ne tiennent que rarement compte de celles-ci.

La première prémisses est que la taille des unités utilisées pour les analyses statistiques menant au développement de MQH, les unités d'analyse (UA; dont la taille peut différer de celle des UE, selon le design d'échantillonnage; Brind'Amour et Boisclair 2006) permet une description adéquate des processus écologiques de l'écosystème. Cependant, la taille des UE ou des UA est plus souvent déterminée par des contraintes logistiques (temps requis pour l'échantillonnage, distance entre les sites d'échantillonnage, etc.) que par des considérations écologiques. De plus, la taille des UA est reconnue pour affecter la structure, c'est-à-dire les variables environnementales incluses dans les modèles ainsi que le sens des relations entre celles-ci et l'indice de la valeur écologique, et le pouvoir prédictif des modèles empiriques (Wiens 1989; Fotheringham et Wong 1991; Jelinski et Wu 1996; Folt et al. 1998). Ce phénomène, appelé problème des unités à aires variables, a été observé dans plusieurs études empiriques. Ce problème a, selon Jelinski et Wu (1996) deux composantes : 1) le problème d'échelle, ou dépendance d'échelle, vient du fait qu'il est possible d'arriver à des résultats différents lorsque les mêmes données sont analysées à des échelles différentes. Par exemple, Bult et al. (1998) ont démontré que, à grandes échelles (> 4 m), les juvéniles du saumon de l'Atlantique (*Salmo salar*) montrent une grande préférence pour les habitats peu profonds. Par contre, des analyses à une plus petite échelle (< 1m)

à l'intérieur de ces habitats montrent que les juvéniles sont plutôt associés à des micro-habitats d'eau profonde au sein des habitats d'eau peu profondes. Une autre étude (Crook et al. 2001) suggère qu'à l'échelle du micro-habitat, la distribution de la perche dorée (*Macquaria ambigua*) est positivement associée à la présence de débris ligneux, tandis qu'à l'échelle du méso-habitat, cette association est négative. De plus, Brind'Amour et al. (2005) ont démontré qu'une communauté de poissons littoraux a une distribution spatiale structurée à plusieurs échelles et que les conditions environnementales influencent cette distribution de façon différente à toutes les échelles.

2) Le problème de zonage évoque le fait qu'une série d'UE combinées en UA qui ont la même surface mais qui sont positionnées différemment dans l'espace peut mener à des résultats différents à chaque analyse. Brind'Amour et Boisclair (2006) ont effectivement montré que, pour une communauté de poissons littoraux lacustres, le pourcentage de variance de l'indice de valeur écologique expliquée par les variables environnementales varie beaucoup pour des modèles développés avec des UA de même dimensions même avec des zonages différents.

La seconde prémisse est que les caractéristiques environnementales estimées dans une UA spécifique permettent une représentation adéquate de l'éventail complet des conditions affectant la qualité des habitat, non seulement de cette unité, mais de toutes les unités de l'écosystème étudié. Traditionnellement, les caractéristiques environnementales utilisées dans les MQH sont des caractéristiques locales décrivant le micro-habitat. Cependant, plusieurs études conceptuels (Schlosser 1991; Kocik et Ferreri 1998) et évaluations sur le terrain (Dunning et al. 1992; Schlosser 1995; Pess et al. 2002; Brind'Amour et Boisclair 2006) suggèrent que la qualité d'un habitat n'est pas

seulement reliée à ses attributs intrinsèques mais également à ce qu'il y a autour de lui. Ces caractéristiques environnementales, faisant référence au contexte spatial des UA, représentent les interactions pouvant exister entre des habitats plus ou moins éloignés. Par exemple, Petit (1989) a bien illustré le phénomène de complémentarité en montrant qu'en hiver, les oiseaux forestiers n'utilisent pas les habitats d'alimentation qui ne sont pas situés à proximité d'un refuge contre le vent et la neige. Un autre concept, celui de la suppléantarité, fait référence à la fragmentation des habitats dans ce sens où les individus vivant dans une tache d'habitat trop petite pour subvenir à un besoin en particulier doivent avoir la possibilité de se déplacer dans une autre tache d'habitat pour combler ce besoin. Whitcomb et al. (1977) ont décrit un cas de suppléantarité d'habitats en recensant les populations d'oiseaux de plusieurs boisés dans un paysage fragmenté. Kocik et Ferreri (1998) ont démontré l'importance de tenir compte du positionnement spatial des sites de fraie et des habitats d'alimentation dans une rivière pour estimer la production de juvéniles de saumon de l'Atlantique. Enfin, l'effet de voisinage est bien démontré dans une étude de Pess et al. (2002) qui montre que l'abondance de saumons coho (*Oncorhynchus kisutch*) dans la rivière Snohomish (Washington, É.-U.) est corrélée à la nature de l'utilisation des terres à proximité du cours d'eau.

Le saumon de l'Atlantique est un bon exemple d'espèce pour laquelle les modèles traditionnels, qui ne tiennent pas compte des deux prémisses énoncées plus haut, ne parviennent pas à fournir des outils réellement utiles pour sa conservation. Jusqu'à maintenant, la grande majorité des études de modélisation d'habitat des juvéniles du saumon de l'Atlantique (JSA) se sont limitées à utiliser des UE d'au plus

une centaine de mètres, ont fait des analyses avec une seule taille d'UA et ont employé des variables caractérisant l'habitat local des JSA, comme la vitesse du courant, la profondeur de l'eau ou la composition du substrat (Wankowski et Thorpe 1979; DeGraaf et Bain 1986; Morantz et al. 1987; Heggenes et al. 1990; Bourgeois et al. 1996; Gries et Juanes 1998; Guay et al. 2000; Bélanger et Rodríguez 2002; Mäki-Petäys et al. 2002; Hedger et al. 2004; Turgeon et Rodríguez 2005). Folt et al. (1998), qui ont fait une revue de littérature pour déterminer les échelles spatiales et temporelles utilisées dans la recherche sur le saumon de l'Atlantique, montrent que plus de 85% des études utilisent plusieurs petites parcelles au sein d'une même rivière pour leurs analyses. De plus, ils remarquent que très peu d'études incluent plus d'une échelle dans leur analyses, ce qui permettrait de détecter les contradictions liés au problème des unités à aires variables et de déterminer la taille optimale d'UA. Pour leur part, Armstrong et al. (2003) ont répertorié des études sur les habitats utilisés par les JSA et ont remarqué qu'il y avait de grandes différences entre les résultats des ces études qui utilisaient pourtant toutes les même variables locales pour caractériser les habitats. Seulement quelques études théoriques (Armstrong et al. 1998; Kocik et Ferreri 1998; Bardonnnet et Baglinière 2000) ou empiriques (Bult et al. 1998; Poff et Huryn 1998) ont considéré qu'il était important de faire des analyses multi-échelle et de tenir compte d'autres variables environnementales que les variables traditionnelles locales lorsqu'on souhaite développer des MQH pour les JSA en rivière.

Le saumon de l'Atlantique est une espèce dont la majorité des populations sauvages sont en déclin depuis les dernières décennies. Quelques unes ont même été complètement éliminées (Parrish et al. 1998). Les habitats d'eau douce peuvent être une

des clés du problème de conservation des populations sauvages de saumons de l'Atlantique. Premièrement, il est plus facile d'étudier et d'intervenir au niveau des cours d'eau que dans l'océan, où les coûts associés et les difficultés techniques sont accrus. De plus, les rivières sont des habitats cruciaux pour cette espèce puisque c'est là que les juvéniles vont naître et se développer (Poff et Huryn 1998). Il est donc très important de bien connaître ces habitats pour ensuite élaborer des stratégies de conservation efficaces.

Le premier objectif de cette étude sera donc d'évaluer comment la taille des UA influence le pouvoir prédictif et le pouvoir d'extrapolation des MQH pour les JSA en rivière. Nous croyons que les modèles développés avec différentes tailles d'UA auront des pouvoirs prédictifs et d'extrapolation différents, cependant, aucun indice dans la littérature ne nous permet de prédire dans quel sens iront ces différences. Le deuxième objectif sera d'évaluer les effets du contexte spatial des UA sur la structure et le pouvoir prédictif de ces MQH. Dans, ce cas-ci, nous croyons que des variables environnementales décrivant le contexte spatial des UA auront un rôle significatif à jouer lors du développement des MQH.

Pour rencontrer nos objectifs, nous estimerons la densité de JSA et plusieurs caractéristiques environnementales dans des petites (quelques dizaines de m) UE contiguës formant une série spatiale continue de plusieurs km. Cette approche nous permettra de combiner des UE adjacents pour former des UA de différentes tailles. Cette approche permettra également de faire une description approfondie du contexte spatial des UA.

**Importance of the size and the spatial context of analytical units on the structure,
the predictive power, and the upscaling of habitat quality models.**

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INTRODUCTION

Habitat quality models (HQM) are quantitative relationships between indicators of the ecological value of a series of sites (e.g. presence/absence, density, growth, survival, production, etc) and the environmental conditions prevailing at these sites (e.g. temperature, substrate composition, pH, etc). HQM are expected to allow scientists and managers to predict the effect of changes of environmental conditions caused by natural and anthropogenic perturbations on the ecological value of habitats and to identify habitats that should be protected for conservation purposes (Gibson et al. 2004; Newbold and Eadie 2004; Woithon and Schmieder 2004; Bowman and Robitaille 2005; Klaus et al. 2005; VanManen et al. 2005).

The complete realization of the potential of HQM requires that models developed using observations performed at the scale of sampling units (SU; individual areas or volumes surveyed during sampling) can be employed to map habitat quality over large areas of an ecosystem. Such ‘upscaling’ of HQM entails the adoption of specific assumptions. First, the size of SU is assumed to permit an adequate representation of the processes that define the ecological value of sites. The size of SU, however, is often defined more by logistical constraints (size of sampling gear, time required to sample, distance between sampling sites, etc) than by ecological considerations. One approach used to circumvent the problems related to the appropriateness of the size of SU has been to adopt a sampling strategy that allows one to merge SU *a posteriori* to form larger units, hereafter referred to as analytical units (AU), which are employed during the statistical analysis performed to develop HQM (Brind’Amour and Boisclair 2006).

This approach is particularly informative in the context that the size of AU has long been recognized to affect both the structure and the predictive power of empirical models (Wiens 1989; Fotheringham and Wong 1991; Jelinski and Wu 1996; Folt et al. 1998; Crook et al. 2001). However, the effect of this situation on the upscaling of HQM has not been explored. Second, the nature of the environmental conditions employed to characterize AU is assumed to permit the adequate representation of the processes that occur not only within this unit but also in other units located anywhere in the ecosystem. Numerous conceptual models (Schlosser 1991; Kocik and Ferreri 1998) and field evaluations (Dunning et al. 1992, Schlosser 1995; Pess et al. 2002) suggest that habitat quality is not only affected by variables observed within AU but also by features observable outside AU. This situation, which refers to the spatial context of AU, has been presumed to represent the effect of the hierarchical structure of ecosystems (e.g. a microhabitat, within a riffle, within a reach, and within a watershed; Frissell et al. 1986; Hawkins et al. 1993; Imhof et al. 1996; Allan et al. 1997; Fausch et al. 2002) and the effect of the interactions that may exist among neighboring habitats (proximity of other or similar types of habitats, e.g. habitat supplementation and complementation; Schlosser 1995; Pess et al. 2002). Although the role of the spatial context on habitat quality has been quantified at the scale of few meters (Palmer et al. 2000; Silver et al. 2000; Swan and Palmer 2000), its effect on the upscaling of HQM at larger scales has not been addressed.

The purpose of this study was to assess the effects of the size and the spatial context of AU on the structure, the predictive power, and the upscaling of HQM.

METHODS

STRATEGY

The approach we employed to meet our objectives consisted in estimating fish density ($n/100m^2$; a measure of fish habitat quality) and a suite of environmental conditions in a series of small and contiguous sections of a river organized to form a spatially continuous trace. This approach allowed us to combine contiguous sections to form AU of increasing sizes, to use these different AU to develop HQM, and to test the ability of HQM developed using different AU to predict habitat quality over larger areas. Our strategy also permitted us to describe attributes of the spatial context of AU and to assess the effect of these attributes on HQM.

AREA AND SPECIES FOR STUDY

Sampling was conducted in the main branch of the Sainte-Marguerite River, (SMR; Saguenay region of Quebec, Canada; Figure 1). More specifically, the study area was a 14.7 km segment located 35 to 50 km from the river mouth. It was selected for the study because it contained a great diversity of habitats. Furthermore, it was easy to access because of a road that passed nearby, or the presence of paths in the wood when the road was farther. This segment was divided in 735 sections of 20 m distributed continuously along the downstream-upstream axis of the river. These sections were identified using georeferenced color coded fluorescent plastic markers visible from river center. Georeferenced low altitude air photographs were used to ground-truth the position of these markers. The section of the SMR surveyed consisted in sandy meanders (predominantly in the upstream part of the study area) and boulder riffles

(particularly between 39 to 41 km for the river mouth) interspersed by pools and runs. River width and maximum depth in the study area ranged from 20 to 40 m and from 0.2 to 3 m respectively. Vegetation cover was limited to 1-2 m from the banks and was provided mostly by Speckled alder (*Alnus rugosa*), Sweet gale (*Myrica gale*), and Lambkill kalmia (*Kalmia angustifolia*).

In SMR, we find Atlantic salmon (*Salmo salar*), Brook trout (*Salvelinus fontinalis*), American eel (*Anguilla rostrata*), Sea lamprey (*Petromyzon marinus*), Longnose sucker (*Catostomus catostomus*), Blacknose dace (*Rhinichthys atratulus*), and Longnose dace (*Rhinichthys cataractae*). HQM developed in this study focussed exclusively on I+ and II+ juveniles of Atlantic salmon (JAS). JAS were selected because they are ubiquitous in the SMR. Others species are not enough well represented in the SMR to provide a great variability in the density between sampling sections. JAS were also selected because their fidelity to a territory during the summer (Keenleyside and Yamamoto 1962) was expected to facilitate the development of relationships between fish density, taken here as a measure of the ecological value of AU, and environmental conditions.

Sampling was conducted between June 27th and August 4th 2003. During this period, water temperature ranged from 11°C to 24°C. Water flow at a gauging station located 59.5 km from river mouth ranged from 2.5 to 23 m³·s⁻¹. However, no sampling was conducted when water flow was above 3.8 m³·s⁻¹ to minimize the effect of flow variations on our data.

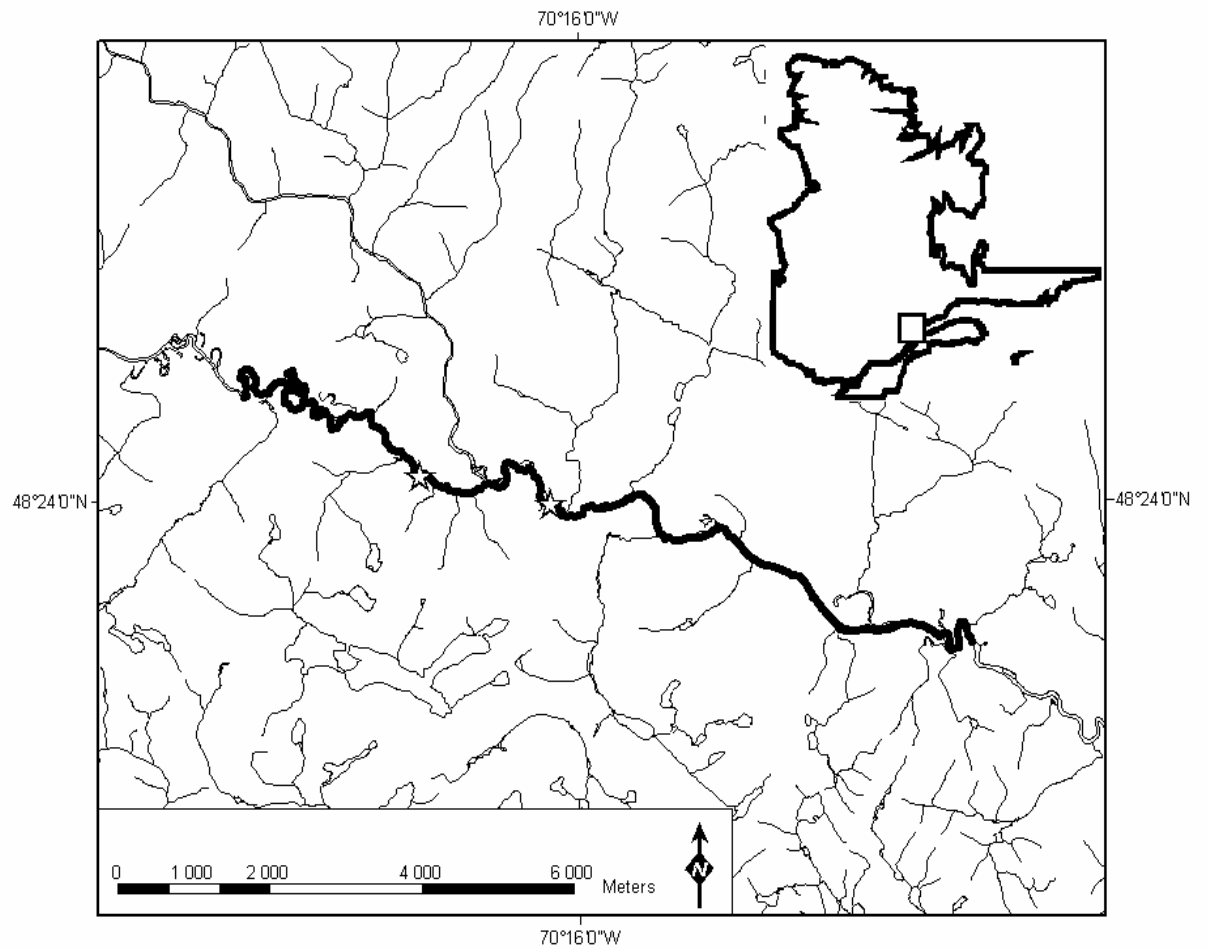


Figure 1. Study area of 14.7 km on the Sainte-Marguerite River. White stars along the Sainte-Marguerite River represent beginnings of sedimentary links.

DENSITY OF JUVENILES OF ATLANTIC SALMON

JAS density (number of JAS/100 m²) was estimated in each sections using two approximately parallel transects having a length of 20 m in the upstream-downstream axis of the river. One transect was located 1-2 m from shore and another was located approximately at half of the distance between the shore and the thalweg. The thalweg is defined by the line joining the deepest point of a river's cross section along its downstream-upstream axis. JAS density in each transect was estimated at night (22:00-03:00) because previous studies indicated that, in the SMR, estimates of JAS densities at night are 1.25 to 5 fold greater than during the day (Imre and Boisclair 2004; see also Gries et al. 1997; Johnston et al. 2004 for similar observations in other rivers). In addition, while daytime JAS density may be affected by the percent cloudiness (Girard et al. 2003), JAS density estimated at night are not significantly affected by meteorological and moon phase conditions (Imre and Boisclair 2005). Finally, Bédard et al. (2005) showed that JAS density in the SMR does not vary significantly during this period of the night for a same transect. During JAS sampling, two observers (one per transect) equipped with underwater lighting systems (UK Sunlight D4) snorkeled upstream with the light beam directed towards water surface to minimize fish disturbance (Gries et al. 1997). Each observer noted the number of JAS encountered and evaluated the maximum distance (right and left) over which they could see a fish and correctly identify it as a JAS. The maximum visibility was about 2 m on both sides of observers. The visibility varied with several conditions as the substrate size, the water depth, and the water turbidity. It was evaluated to permit the conversion of abundances of JAS into densities. A pair of observers sampled 400-700 m of the river length per night (25-35 sections of 20 m). Two pairs of observers were deployed in different parts

of the study area each night. Hence, 0.8 to 1.4 km of the SMR was surveyed each night and any given transect was sampled only once during the sampling period. JAS density in each transect was estimated by dividing the number of JAS noted by the surface area of this transect (20 m x [distance observed left + distance observed right of the observer]). JAS density within any given AU was estimated as the average of JAS densities in transects included within the AU.

ENVIRONMENTAL CONDITIONS

HQM were developed to explain variations of JAS density using two categories of environmental conditions (Table I). The local variables referred to environmental conditions that were estimated within each section (e.g. water depth, substrate composition). The spatial context variables were meant to represent the potential effect on fish density of the spatial arrangement of sections or AU relative to features observable outside these units. We defined two types of spatial context variables: lateral variables were attributes observable perpendicular to the downstream-upstream axis of the river (e.g. composition of the riverbank); longitudinal variables were attributes observable along the downstream-upstream axis of the river (e.g. distance to the closest tributary upstream of a section or an AU). Local variables were estimated in the field while spatial context variables were estimated either in the field or using a geographic information system (GIS; ArcView 8 ®). Field estimation of environmental conditions for specific section was performed in the week preceding or following sampling for fish in these sections. Maximum flow difference between observations on fish and estimation of environmental conditions in a given section was $0.15 \text{ m}^3 \cdot \text{s}^{-1}$ (or 11.5% of the mean flow during sampling).

Table I. Environmental characteristics included as potential explanatory variables in the habitat quality models.

Environmental characteristics	Units	Type	Captioning
Water depth	m	Local	Field
Water velocity	m·s ⁻¹	Local	Field
Substrate composition¹	%	Local	Field
Wood debris	p/a and relative presence (%)	Local	Field
Riverbank composition	p/a and relative presence (%)	Spatial context	Field
Drainage region area	m ²	Spatial context	GIS
Drainage region slope	°	Spatial context	GIS
Distance to the nearest tributary (up and downstream)	m	Spatial context	Field and GIS
Distance to the nearest pool (up and downstream)	m	Spatial context	Field
Distance to the nearest spawning site (up and downstream)	Km	Spatial context	Field and GIS
Relative position in a sedimentary link	%	Spatial context	Field and GIS

¹ described using 8 size classes (see Table II)

Local variables

The local variables used in our study were selected on the basis of their potential to affect JAS habitat quality (Wankowski and Thorpe 1979; DeGraaf and Bain 1986; Morantz et al. 1987; Cunjak 1988; Guay et al. 2000; Hedger et al. 2004; Turgeon and Rodriguez 2005). Water depth (± 0.05 m) was measured with a graduated rod. Water velocity ($\pm 2\%$) was estimated at 40% of the water column (at 0.4 m from the riverbed in 1 m of water) during 30 seconds with a current meter (GPI Pygmy meter). This depth was selected because it was expected to represent the average flow velocity in the water column (Gordon et al. 2004). The substrate composition of the riverbed (%) was described visually using eight classes of substrate grain size (Table II). These three variables were estimated at three locations along the river width (1-2 m from the shore, 1-2 m from the thalweg, and midway between the shore and the thalweg) at the beginning of each section of 20m. The average of the three estimates of water depth, flow velocity, and percent contribution of any given substrate grain size was used to represent the local conditions found within each section. We consider that these three estimates correctly represent the conditions prevailing in each section since they were taken at three locations covering a great variability of these environmental characteristics. Wood debris (dead trunks and branches) on the riverbed were included in our list of local variables because it may serve as a shelter for fish or a habitat for their prey. The presence (cover > 1 m²) or the absence of wood debris on the riverbed was noted over the complete river width within section.

Table II. Substrate size classes used in this study.

Substrate classes	Median substrate size (mm)
Clay	*
Silt	*
Sand	*
Gravel	2-32
Pebble	32-64
Cobble	64-250
Boulder	250-1000
Metric boulder	> 1000

*These substrate classes were identified visually without estimating their median size.

Spatial context variables

Lateral variables

The nature of the terrestrial surroundings of a river can influence habitat quality (Allan and Johnson 1997; Pess et al. 2002). The form of riverbanks might therefore contribute to explain variations in JAS density in our study area. We defined four forms of riverbanks; sandy shore (gentle sandy slope $< 5^\circ$), rocky shore (shore composed of substrate > 32 mm of diameter and with a gentle slope $< 5^\circ$), eroded shore (shore composed of mixed substrate [clay - 250 mm diameter] with a steep slope [$> 35^\circ$] resulting from the effect of floods), and embankment (human made stabilizing structures composed of large substrate [> 500 mm diameter]). The presence of these forms of riverbanks were noted in the field for each section, without distinction for the right or the left shore. More, it was possible that none of these forms of riverbanks was present within a section, as it was possible that more than one were presents.

The area and the slope of the regions drained on the river's bank may potentially contribute to provide water, sediments, and nutrients to a specific section or AU and may explain variations in habitat quality (Schlosser 1995). We can define a "region drained on the river's bank" as a part of the river's watershed, corresponding to a

specific section or AU. The area (left shore + right shore) and the slope (average of the left and the right shores) of the region drained on the river's bank were calculated using a GIS, a numerical topographic maps (1:20 000) and a numerical elevation raster, used to generate the total watershed of the SMR, and divided it into regions corresponding to each section.

Longitudinal variables

Numerous conceptual studies and field tests have suggested that the proximity of a site to different features of an ecosystem might affect habitat quality at this site (Schlosser 1991; Dunning et al. 1992; Schlosser 1995; Kocik and Ferreri 1998; Pess et al. 2002; Brind'Amour and Boisclair 2006). In our study, seven longitudinal variables were employed to describe the potential interactions between AU and different features of the river, and to represent the role of these interactions in explaining variations in JAS density. The six first longitudinal variables were estimated as the distance (upstream and downstream) between sections and specific features of the river such as tributaries (point source of cool and well oxygenated water and input of invertebrates that drift in the flow; Erkinaro 1995; Bardonnet and Baglinière 2000), pools (predation and thermal refuge; Gries and Juanes 1998; Poff and Huryn 1998), and salmon spawning sites (the spatial configuration of spawning sites relative to rearing habitats may affect JAS production; Kocik and Ferreri 1998). Pools were defined as depressions of the riverbed having a minimum depth of 0.5 m, a minimum length of 20 m, and a maximum water velocity of $0.5 \text{ m}\cdot\text{s}^{-1}$. The position of the spawning sites along the SMR was determined based on the knowledge of the fishing guides of the SMR. Tributaries, pools, and spawning sites were positioned in the field, georeferenced, and the distances between

these features and any AU were estimated using a GIS and numerical topographic maps (1:20 000).

The seventh longitudinal variable represented the relative position of a section within the sedimentary links of the SMR as described by Davey (2004). A sedimentary link is defined as the area that extends between two zones dominated by coarse substrate (often boulders originating from banks, tributaries or from glacial deposition). Along the link, the substrate undergoes a process of fining such that the mean diameter of the particles of the riverbed tends to decrease from the upstream to the downstream part of a sedimentary link. Sedimentary links are thus geomorphological units at the scale of the riverscape that have been suggested to affect the spatial distribution of organisms in rivers (Rice et al. 2001). Our study area intersected three sedimentary links (Figure 1). The position of each section was described as a percentage relative to the upstream part of a link (0% = upstream part of a sedimentary link –coarse substrate; 100% = downstream part of a sedimentary link – finer substrate).

DATA ORGANIZATION

One objective of our study was to assess the effect of the size of AU on fish HQM. The spatially continuous nature of the data we collected allowed us to achieve this objective by testing the effect of different ways to group the information obtained for contiguous sections on HQM. The sections were grouped to form five different sizes of AU. Four of these sizes of AU had lengths that were multiples of the 20 m sections; AU of the size of the original section (20 m), and AU that represented the merging of three (60 m), five (100 m), or ten (200 m) contiguous sections. With the exception of

AU of 20 m, different sequences were used to merge the information of contiguous sections. For instance, for AU of 60 m, sections were merged following three sequences 1) 1-2-3, 4-5-6, 7-8-9, etc; 2) 2-3-4, 5-6-7, 8-9-10, etc; or 3) 3-4-5, 6-7-8, 9-10-11, etc. Each size of AU >20 m (60 m, 100 m, 200 m) and each possible sequence for a given size of AU required the recalculation of the dependent and the independent variables (e.g. average values of JAS density, all environmental conditions). This led to the formation of 19 datasets (one dataset for AU of 20 m, three datasets for AU of 60 m, five datasets for AU of 100 m, and ten datasets for AU of 200 m).

The fifth size of AU, like all other sizes of AU, was obtained by the grouping of contiguous 20 m sections. However, in this case, the grouping was performed with the added constraint that only sections possessing similar environmental conditions could be merged. A K-means clustering analysis (Legendre and Legendre 1998) was employed to classify sections according to the environmental conditions noted during our study. The Calinski-Harabasz pseudo-F statistics (Milligan and Cooper 1985) indicated that the optimal grouping of sections could be obtained using the percent composition of the eight classes of substrate. This procedure resulted in the definition of four types of habitats (Figure 2) and to the classification of each of the 735 sections into one of the four habitat types. Merging of contiguous sections belonging to a same habitat type led to the formation of 138 units (ranging from 20 to 1 140 m; Figure 3) further referred to as habitat patches (HP). HP formed by the merging of sections belonging to habitat type #1 were characterized by the dominance of sand (average of 60 %) whereas the substrate of HP originating from sections belonging to habitat type #2 was mostly composed of gravel (average of 70 %). In contrast, HP resulting from the merging of sections

classified as habitat type #3 consisted in a more even mixture of gravel, pebble, and cobble. HP obtained using sections belonging to habitat type #4 were defined by a higher percentage of boulders and metric boulders (average of 40%). A study by Bouchard et al. (unpublished data) suggested that, in the SMR, JAS density in AU became temporally stable when this AU was larger than 200 m² (AU 50 m long x 4 m wide [distance observed left + distance observed right of the observer]). Consequently, in addition to the data set including the 138 HP (HP1), we developed a twenty-first data set including only the 67 HP longer than 50 m (HP2). So, HP constituted the fifth size of AU and led to the formation of the twentieth and the twenty-first datasets.

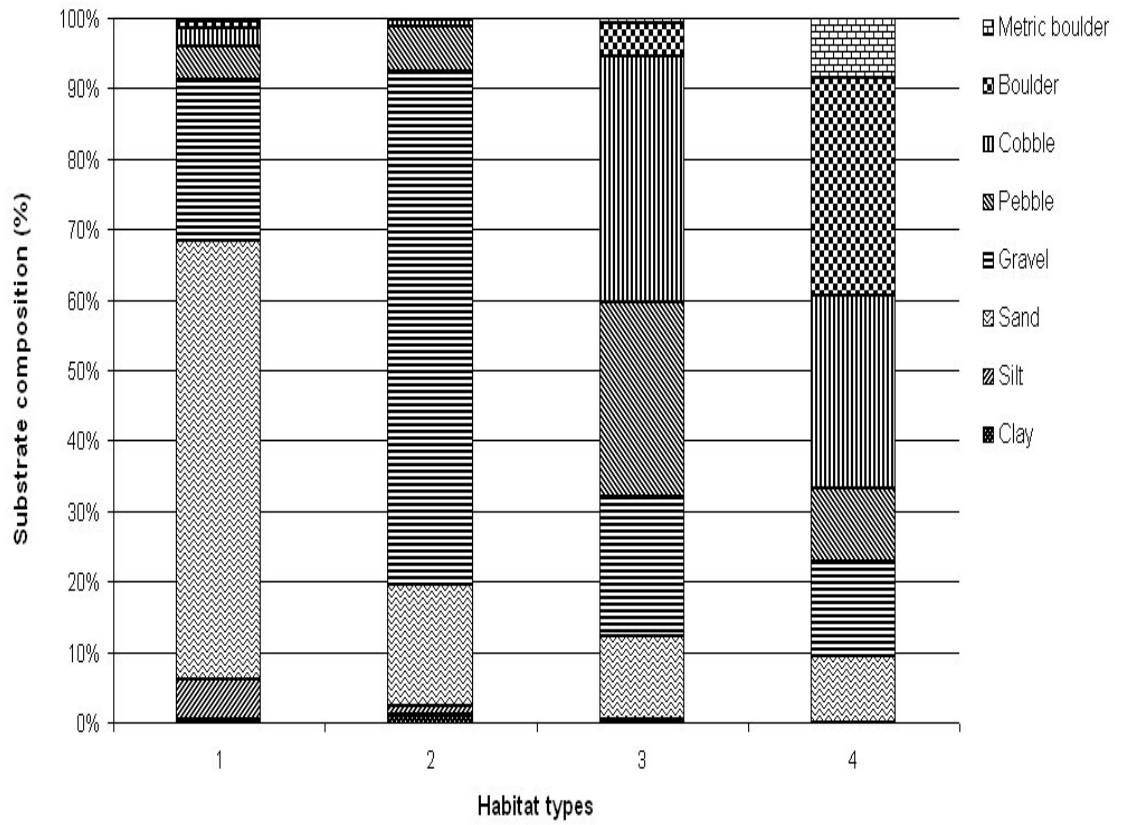


Figure 2. Substrate composition of habitat types determined by the K-means grouping method.

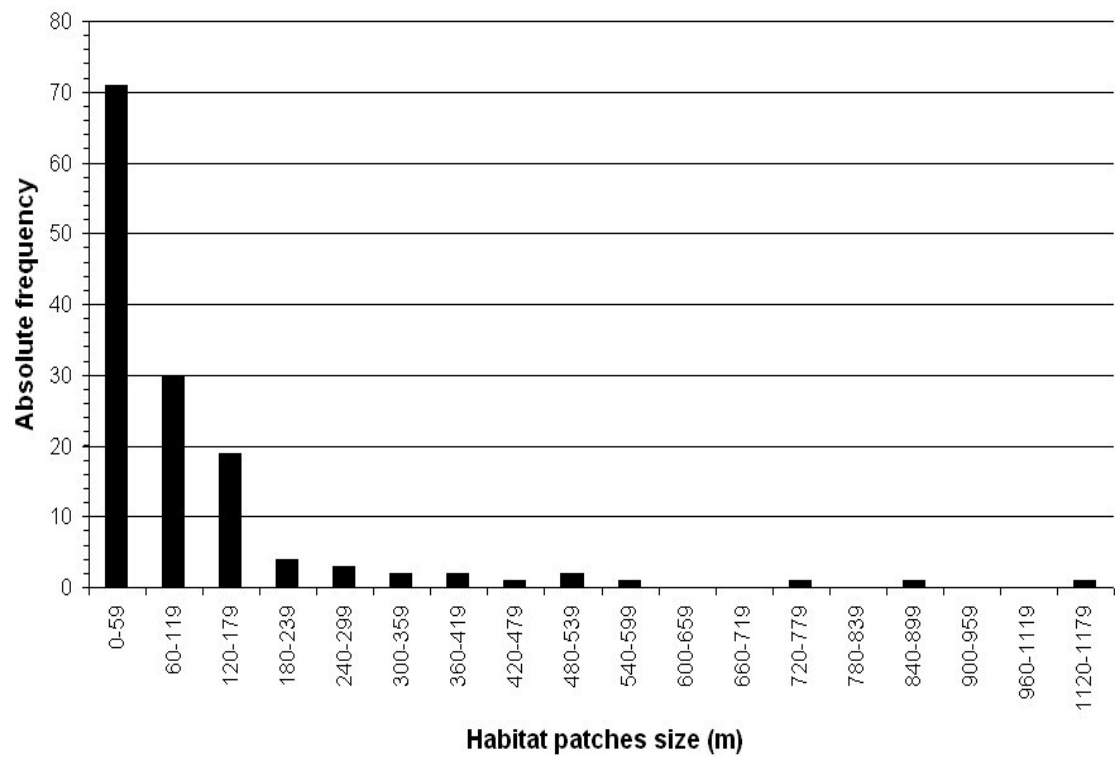


Figure 3. Frequency distribution of the size of habitat patches.

During the formation of the data sets, JAS density within each AU was represented by the average of the values obtained for the sections within these AU. The same strategy was employed for water depth, water velocity, substrate composition, drainage region slope, upstream or downstream distance to different features (the nearest tributary, pool, and spawning site), and relative position in a sedimentary link. We summed the areas of the drainage regions included in an AU. Finally, for the wood debris and the forms of riverbanks, we calculated the percentage of sections within an AU in which these attributes were present. In addition, we considered that these environmental attributes were present when they were found in at least one of the sections merged to form an AU.

STATISTICAL ANALYSIS

Description of variables

ANOVAs and Levene homogeneity of variance tests were used to describe how variables parameters (average and variance) react to the merging process. One series of those tests were made to assess changes in the average and the variance of the variables when we increased AU size (20 m to 200 m). Another series of tests were used to evaluate the effect of the HP merging method on the variables parameters.

Development of habitat quality models

HQM, in the context of our study, were relationships between JAS density and a series of environmental conditions. HQM were developed independently for the twenty-one datasets we obtained. In all cases, HQM were obtained using a forward stepwise multiple regression performed with the software Statistica6©. Dependent and

independent variables were analyzed under their linear form and, when required to insure the linearity of the relationships, were subjected to a logarithmic transformation (natural logarithm). All independent variables had to significantly contribute to a model ($p < 0.05$) to be selected and no more than four independent variables were included in the final models.

Assessment of the reliability of habitat quality models

The reliability of the models we developed was assessed using a bootstrap analysis. For each model, we randomly selected, with throw-in, a number of AU corresponding to the total number of AU in the dataset. A multiple regression was conducted to determine parameters of the relation between the dependent and independent variables included in the model. This procedure was repeated 1 000 times for each model and provided us 1 000 estimates of the adjusted R^2 (R^2_{adj}) associated with each model. The 2.5 and 97.5 percentiles of these estimates were taken as the 95% confidence intervals (CI) of the R^2_{adj} of a model.

Upscaling of habitat quality models

The models we developed were further assessed using a cross validation procedure that consisted in three steps; 1) we randomly chose one third of AU in a dataset, 2) a multiple regression analysis was conducted to determine the parameters of the relationship between the dependent and the independent variables included in the model, and 3) the resulting model was used to predict JAS density of the two thirds of the dataset. Thus, all models were validated over an area twice as large as that used to develop them. The correlation (r of Pearson), the slope, and the intercept of the

relationships between observed and predicted JAS density were calculated. This procedure was repeated 1 000 times for each model. The 2.5 and 97.5 percentile of the 1000 estimates of these parameters were taken as their 95% CI.

RESULTS

DESCRIPTION OF JAS DENSITIES AND ENVIRONMENTAL VARIABLES

Twenty nights were necessary to sample the 14.7 km of the study area. A total of 2 764 JAS were observed and 72 % of these fish (1 977 JAS) were located 1-2 m from shore. Fish density estimated with AU of 20 m ranged from 0.0 to 40.0 JAS·100 m⁻² (Figure 4) with an average of 4.6 JAS·100 m⁻² (n = 735; Table III), and a variance of 31.36 JAS·100 m⁻². Average JAS density was unaffected by the size of AU (e.g. 4.6 JAS·100 m⁻² for AU of 200 m, n = 73; ANOVA p = 0.99). However, variance of JAS density tended to decrease as the size of AU increased (15.44 JAS·100 m⁻² for AU of 200 m; Levene test p = 0.03). Averages of JAS densities estimated for HP (HP1 = 3.2 JAS·100 m⁻²; HP2 = 3.8 JAS·100 m⁻²) were slightly, but not significantly, lower than for other AU sizes (ANOVA p = 0.07). However, variances of JAS densities estimated for HP (HP1 = 11.76 JAS·100 m⁻² ; HP2 = 10.89 JAS·100 m⁻²) were significantly lower than for other AU (Levene test p < 0.0001). The averages of the local variables did not change with the increasing of AU size (Table III), but their variances decreased as AU size increased (e.g. for the water depth, Levene test p < 0.0001). Local variables estimated for HP were not all similarly affected by the size of AU. For instance, the

average contribution of boulders to the riverbed in HP1 (4.6 %) was smaller than that for other AU sizes (ANOVA $p = 0.02$). However, the average water depth for HP1 was larger (ANOVA $p = 0.002$) than for other AU. We found no significant relationship between averages or variances of spatial context variables and AU size. Averages and variances of spatial context variables estimated for HP were sometimes smaller (e.g. average and variance of the distance to the nearest pool upstream; $p < 0.001$) and sometimes larger (e.g. average and variance of the relative position in a sedimentary link $p < 0.001$) than values obtained for other AU sizes.

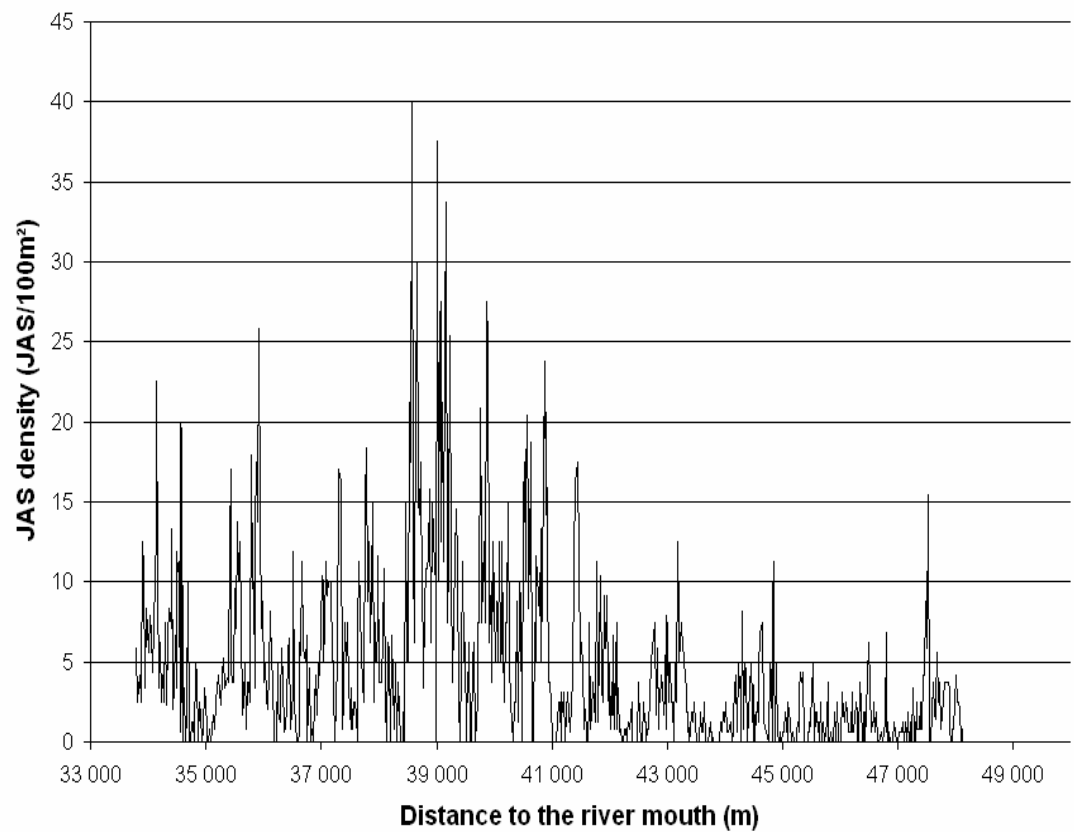


Figure 4. Spatial distribution of JAS density in the study area. The size of the sampling sections used to describe fish distribution in this figure is 20 m.

Table III. Average and variance (in parenthesis) of JAS density and selected environmental variables for each size of analytical units (AU). HP1 corresponds to the model developed with all habitat patches, and HP2 corresponds to the model developed with habitat patches > 50 m. ANOVAs and Levene tests that are statistically significant at the threshold of $p=0.05$ are marked with an * in the “pAU” column for the tests between AU sizes, and in the “pHP” column for the tests between AU sizes and HP models.

Variables	AU 20m	AU 60m	AU 100m	AU 200m	pAU	HP1	HP2	pHP
JAS Density (JAS·100m⁻²)	4.6 (31.36)	4.6 (22.56)	4.6 (19.01)	4.6 (15.44)	*	3.2 (11.76)	3.8 (10.89)	*
Water Depth (m)	0.67 (0.06)	0.67 (0.04)	0.67 (0.03)	0.67 (0.03)	*	0.75 (0.05)	0.70 (0.06)	*
Water velocity (m·s⁻¹)	0.43 (0.05)	0.43 (0.04)	0.43 (0.04)	0.43 (0.03)	*	0.33 (0.03)	0.39 (0.03)	*
Percent of sand (%)	20.5 (465.26)	20.5 (331.24)	20.5 (288.66)	20.6 (221.12)	*	31.8 (569.78)	24.0 (492.40)	*
Percent of pebbles (%)	15.3 (155.50)	15.3 (130.64)	15.3 (118.81)	15.3 (104.65)		10.6 (95.84)	12.6 (109.62)	*
Percent of boulders (%)	8.3 (164.35)	8.3 (151.78)	8.3 (145.93)	8.3 (134.56)		4.6 (73.44)	5.9 (97.61)	*
Wood debris (%)	31.4 (1626.51)	31.4 (1382.35)	31.4 (1338.10)	31.3 (1246.80)	*	47.5 (1592.81)	40.5 (1409.25)	*
Embankment (%)	11.4 (439.74)	11.4 (375.97)	11.4 (340.77)	11.4 (246.80)	*	9.9 (316.84)	10.7 (254.40)	*
Drainage region area (m²)¹	3.6x10 ⁵ (2.50x10 ⁷)	1.1x10 ⁶ (2.25x10 ⁷)	1.9x10 ⁶ (3.80x10 ⁷)	3.9x10 ⁶ (7.62x10 ⁷)	*	1.9x10 ⁶ (4.08x10 ⁷)	3.9x10 ⁶ (8.35x10 ⁷)	*
Drainage region slope (°)	10.0 (56.10)	10.0 (56.10)	8.2 (24.90)	8.1 (19.27)	*	9.8 (43.96)	9.3 (34.34)	*
Distance to the closest pool upstream (m)	669.7 (7.88x10 ⁵)	656.0 (7.99x10 ⁵)	620.4 (7.79x10 ⁵)	573.0 (7.45x10 ⁵)		360.3 (3.58x10 ⁵)	389.1 (3.57x10 ⁵)	*
Distance to the closest pool downstream (m)	601.4 (7.41x10 ⁵)	580.9 (7.27x10 ⁵)	563.8 (7.30x10 ⁵)	510.2 (6.93x10 ⁵)		358.5 (5.33x10 ⁵)	465.1 (7.56x10 ⁵)	*
Relative position in a sedimentary link (%)	45.0 (1267.36)	45.0 (1270.92)	44.9 (1272.35)	46.1 (1302.49)		60.2 (1007.43)	51.4 (1188.87)	*

¹ High values because of an extreme value (7.84x10⁷ m²).

HABITAT QUALITY MODELS

The twenty-one datasets obtained following our sampling allowed us to develop twenty-one HQM. Bootstrap analyses indicated that the predictive power of HQM tended to increase as the size of AU increased from 20 (average $R^2_{adj.} = 0.31$) to 200 m (average $R^2_{adj.} = 0.61$; Figure 5). The 95% CI of the $R^2_{adj.}$ showed that the predictive power of HQM increased significantly as the size of AU increased from 20 ($R^2_{adj.} = 0.25-0.37$) to 100 m ($R^2_{adj.} = 0.39-0.67$). Although the $R^2_{adj.}$ of models developed using AU of 200 m ($R^2_{adj.} = 0.42-0.81$) was higher than with AU of 100 m, the gain in predictive power was not statistically significant. In addition, the range of the 95% CI of $R^2_{adj.}$ associated with HQM tended to increase as the size of AU increased. The predictive power of HQM developed using all habitat patches (HP1) was similar to that of models based on AU of 60 m but lower than that of HQM developed using only habitat patches >50 m (HP2; Figure 5). $R^2_{adj.}$ of HQM developed using HP2 were similar to those based on AU of 200 m.

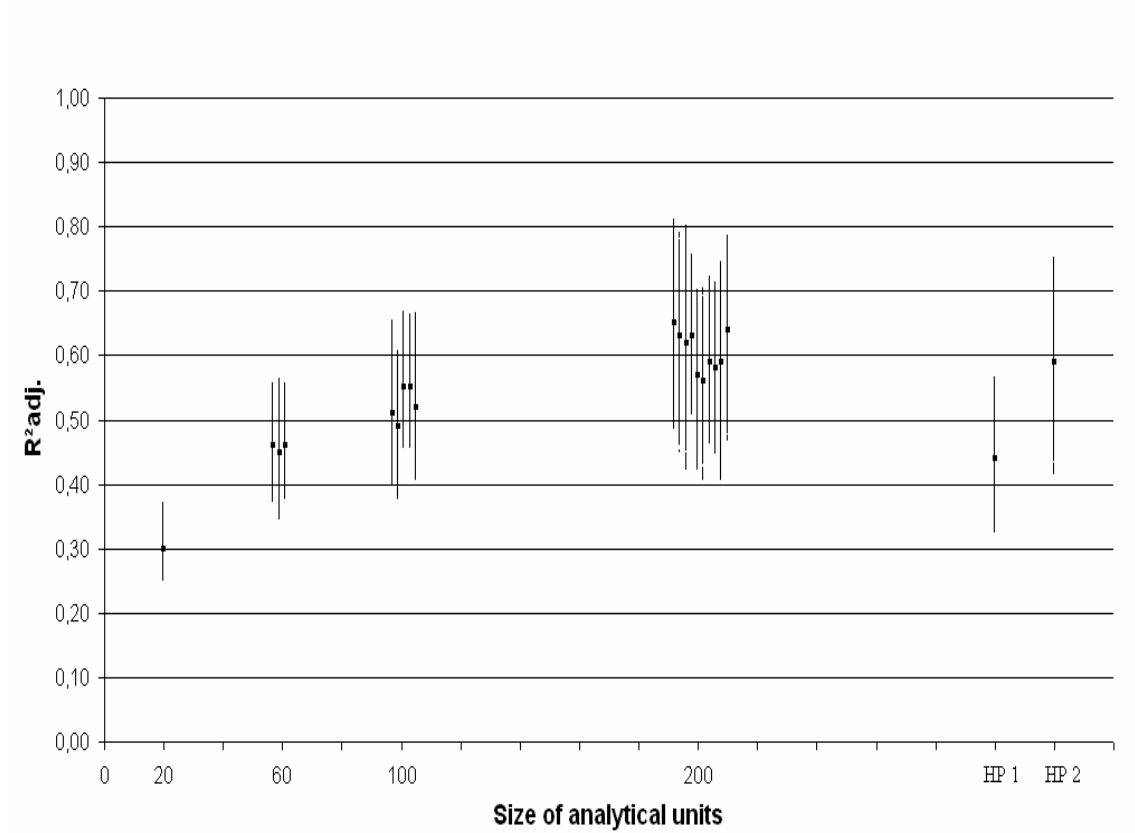


Figure 5. Results of the bootstrap analysis. Bars represent 95% confidence intervals of $R^2_{adj.}$ for 1 000 iterations of models developed using different sizes of analytical units (AU). Squares represent original values of $R^2_{adj.}$.

The cross-validation of the models we developed suggested that the upscaling of HQM was affected by the size of AU. Pearson correlation coefficients of relationships between JAS densities predicted using HQM based on AU of 20 m and observed values ranged from 0.51 to 0.58 (Figure 6). Corresponding values for HQM developed using AU of 200 m ranged from 0.64 to 0.86. This range extended from 0.56 to 0.71 for models developed using all HP, and from 0.67 to 0.83 for those based on HP >50 m. However, models developed using AU of 200 m and HP >50 m (HP2) were the only HQM for which the slopes and the intercepts of the relationship between predicted and observed JAS densities always had 95% CI that included, respectively, the value of 1 (Figure 7) and the value of 0 (Figure 8). Hence, only eleven of the twenty-one HQM developed explained significant proportions of the variation of JAS densities and could be upscaled to adequately predict JAS densities (Table IV).

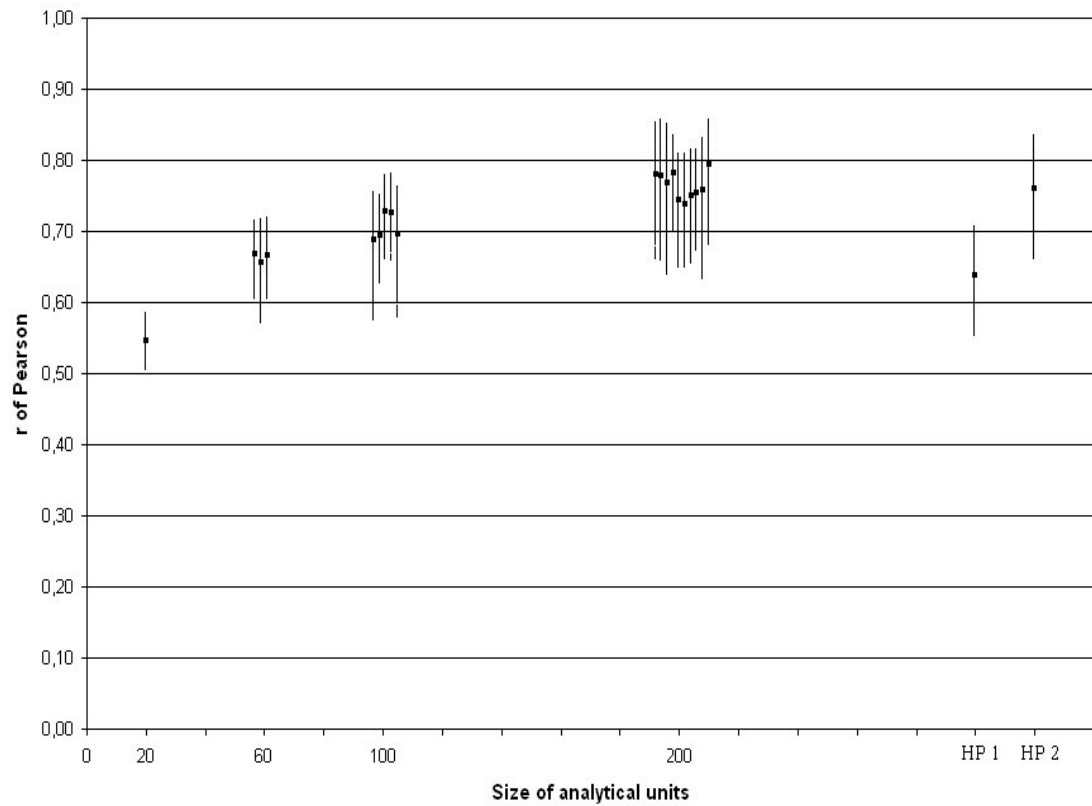


Figure 6. Results of the cross-validation analysis. Bars represent 95% confidence intervals of r of Pearson of the relation between observed and predicted JAS density for 1 000 iterations of models developed using different sizes of analytical units (AU). Squares represent medians of r of Pearson.

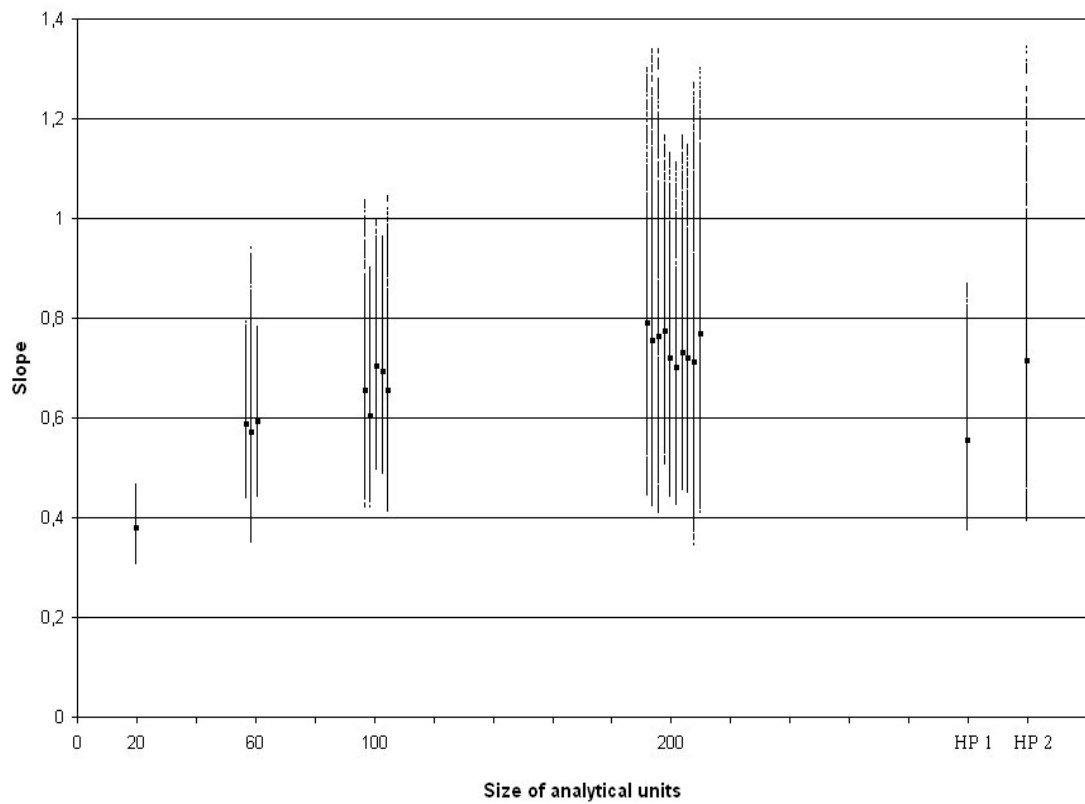


Figure 7. Results of the cross-validation analysis. Bars represent 95% confidence intervals of the slope of the relation between observed and predicted JAS density for 1 000 iterations of models developed using different sizes of analytical units (AU). Squares represent medians of slopes.

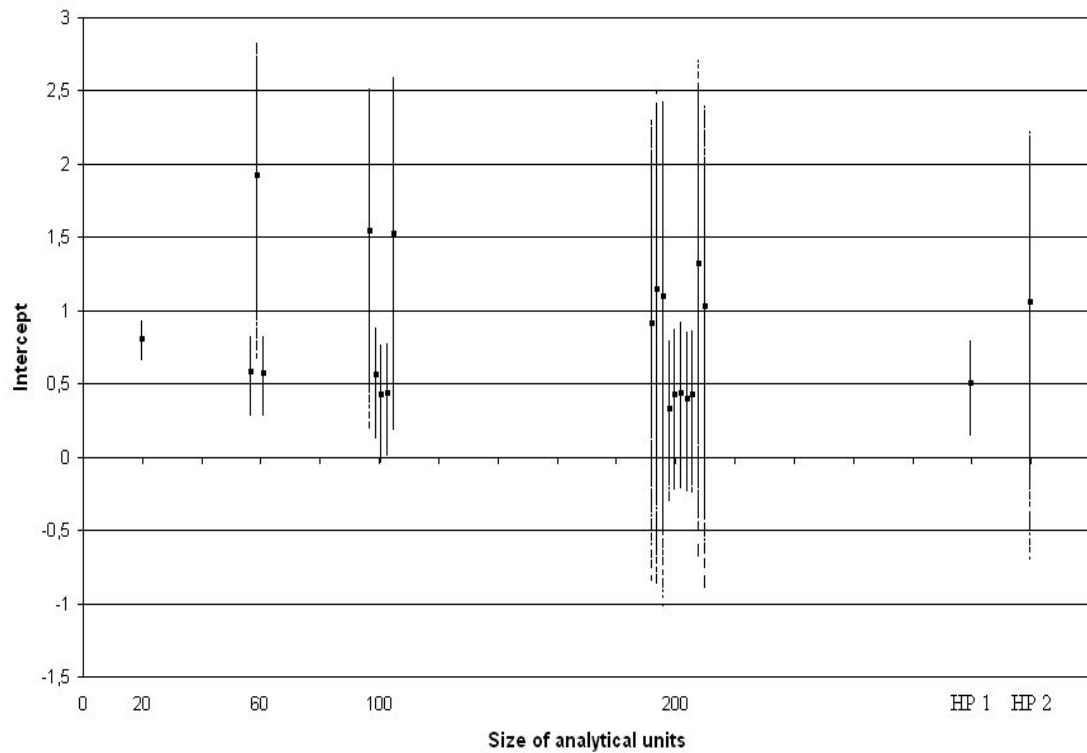


Figure 8. Results of the cross-validation analysis. Bars represent 95% confidence intervals of the intercept of the relation between observed and predicted JAS density for 1 000 iterations of models developed using different sizes of analytical units (AU). Squares represent medians of intercepts.

Table IV. Habitat quality models that successfully predicted JAS density variations during the cross-validation exercise. Numbers in bold are partial $R^2_{adj.}$. Numbers in italic are the beta coefficients of each variable in the regression models.

Size of analytical units	200 m										HP
	1	2	3	4	5	6	7	8	9	10	2
Data set											
$R^2_{adj.}$	0.65	0.63	0.62	0.63	0.57	0.56	0.59	0.58	0.59	0.64	0.59
Dependant variable	JAS	JAS	JAS	Ln JAS	Ln JAS	Ln JAS	Ln JAS	Ln JAS	JAS	JAS	JAS
Boulders (%)	0.58 <i>+0.208</i>	0.58 <i>+0.222</i>	0.58 <i>+0.229</i>						0.56 <i>+0.230</i>	0.59 <i>+0.228</i>	
Ln boulders (%)				0.58 <i>+0.315</i>	0.54 <i>+0.299</i>	0.54 <i>+0.305</i>	0.54 <i>+0.240</i>	0.55 <i>+0.311</i>			
p/a of wood debris	0.02 <i>-1.390</i>										
Wood debris (%)				0.03 <i>-0.006</i>	0.03 <i>-0.005</i>	0.02 <i>-0.004</i>		0.03 <i>-0.005</i>			
p/a of embankment	0.05 <i>+1.832</i>	0.05 <i>+2.076</i>							0.03 <i>+1.630</i>	0.05 <i>+2.062</i>	0.05 <i>+1.847</i>
Ln embankment (%)			0.04 <i>+0.615</i>								
Sandy shore (%)							0.03 <i>-0.013</i>				
Ln dist. to the closest pool downstream (m)				0.02 <i>-0.039</i>							
Distance to the closest spawning site upstream (km)							0.02 <i>-6.3x 10⁻⁵</i>				
Ln relative position in a sedimentary link (%)											0.54 <i>-1.847</i>
Intercept	+2.965	+1.781	+1.847	+1.384	+1.219	+1.202	+1.542	+1.194	+1.896	+1.673	+9.688

The percent contribution of boulders to the riverbed explained the majority the variance of parr density in all models developed using AU of 200 m ($0.54 < \text{partial } R^2_{\text{adj}} < 0.59$). Wood debris, another local variable, was selected in half of the HQM developed using AU of 200 m ($0.02 < \text{partial } R^2_{\text{adj}} < 0.03$). Embankment, a lateral variable, was included in half of the 200 m models. Embankment was always as the second most important variable in the model ($0.03 < \text{partial } R^2_{\text{adj}} < 0.05$). The percentage of sandy shore (lateral variable) also contributed to explain a fraction of the variations of JAS density (partial $R^2_{\text{adj}} = 0.03$). Finally, the distance to the nearest pool downstream ($R^2_{\text{adj}} = 0.02$), and the distance to the nearest spawning site upstream ($R^2_{\text{adj}} = 0.02$) were the two longitudinal variables that explained a significant fraction of JAS density in models developed using AU of 200 m.

Contrary to the models developed with AU of 200 m, the HP2 model exclusively included spatial context variables. In this model, the variable that had the most significant effect on JAS density (partial $R^2_{\text{adj}} = 0.54$) was the relative position of a AU in a sedimentary link. The other spatial context variable included in this model was the presence or the absence of embankment (partial $R^2_{\text{adj}} = 0.05$).

DISCUSSION

INFLUENCE OF THE SIZE OF ANALYTICAL UNITS

The results of our analyses are consistent with the expectations associated with the modifiable areal unit problem (MAUP; Jelinski and Wu 1996), also referred to as the

scale dependence problem (Wiens 1989; Folt et al. 1998). The size of AU had a significant effect on attributes of HQM. For instance, the average R^2_{adj} of HQM increased as the AU size increased from 20 m to 200 m. Two hypotheses may be used to explain effects of AU size on HQM attributes. First, the nature of the independent variables used during this study to develop HQM may hamper the ability of these models to explain JAS density variations when AU are small (e.g. 20-60 m) and facilitate the finding of more powerful models when AU are large (200 m, HP2). In the present study, only physical variables were employed to model JAS density variations because they are generally easier to estimate than biological variables such as prey availability, competition, and predation. Yet, it has been suggested that, as the size of AU decreases, the magnitude of the effect of biological variables on the distribution of the biota increases while that of physical variables decreases (Legendre 1993; Jackson et al. 2001; Brind'Amour et al. 2005). Our findings that the development of powerful HQM based on small AU is difficult without biological variables and that the predictive power of HQM based on physical variables increases as AU size increases are consistent with this suggestion. Second, it may be more difficult to develop strong predictive models with small AU (e.g. 20-60 m) because the error associated with JAS density in small AU may be larger than that in large AU (200 m; HP2, habitat patches > 50 m). In our study, JAS density was estimated only once in any given AU. Bouchard et al. (unpublished data) estimated JAS density on ten occasions in four 200 m reaches of the SMR using a sampling method identical to that used in the present study. They found that the coefficient of variation of JAS density decreased from 120% to 60% as AU size increased from 10 to 200 m. They attributed this situation to the possibility that, although JAS are generally described as territorial fish, they may move tens to hundreds

of meters over few days (Armstrong et al. 1997; Metcalfe et al. 1997; Økland et al. 2004; Booker et al. 2004) Hence, this interpretation and our findings are consistent with the suggestion of Bellehumeur and Legendre (1997) that the use of larger AU may diminish the noise found in spatial data and increase the ability to develop statistically significant models.

The performance of HQM based on relatively large AU was also expressed during the upscaling of the models we developed. HQM based on AU of 200 m and HP2 model taken from one third of the segments were the only models that could be effectively upscaled to the other two thirds of the segments. We would argue that two elements contribute to the similar performance of HQM developed using AU of 200 m and HP > 50 m. First, the size of habitat patches in the HP2 data set averaged 193 m (range from 60 m to 1 140 m) which confers to HP larger than 50 m the same kind of statistical advantage (lower coefficients of variation) as AU of 200 m. Second, the fact that the size of 200 m AU is similar to that of the average HP confers to AU of 200 m the same ecological advantages as HP. HP, which are spatially continuous units possessing relatively homogeneous environmental characteristics, may represent more ecologically meaningful AU than AU of an arbitrary size defined irrespective of any environmental variable (Brind'Amour and Boisclair 2006). In this context, one may expect that HP >50 m would allow the development of HQM more powerful than AU of 200 m. However, we found that the R^2_{adj} of HP2 model (0.59) was slightly lower than that of HQM based on AU of 200 m (average = 0.61). Whether this is caused by the presence of smaller patches (50 to 200 m) in HP2 cannot be evaluated because of an insufficient number of patches >200 m in this data set (17; Figure 3).

INFLUENCE OF THE SPATIAL CONTEXT OF ANALYTICAL UNITS

The HQM we developed potentially included the effect of local variables (environmental conditions observed within AU) and spatial context variables (environmental conditions observed outside AU). However, the models that had the best predictive abilities (AU of 200 m and HP >50 m) differed in their structure and, in particular, in the relative importance of these types of variables for HQM. Seven of the ten HQM based on AU of 200 m included the combined effects of local ($0.02 < \text{partial } R^2_{\text{adj}} < 0.59$) and spatial context variables ($0.02 < \text{partial } R^2_{\text{adj}} < 0.05$). Among the local variables, the percentage of boulders contributed most to explain the variations in JAS density ($0.54 < \text{partial } R^2_{\text{adj}} < 0.59$). The effect of this variable may be related to the expectation that the size of JAS territory should decrease as the contribution of boulders to a riverbed increases due to a visual isolation between them (Kalleberg 1958; Dolinsek 2004). Wood debris is a local variable included in half of the 200 m models. Wood debris tended to have a negative effect on JAS density. However, Bouchard et al. (unpublished data) found a positive relationship between wood debris and JAS density in the SMR. We explain this inconsistency by the study extend difference existing between their study and ours. Their data have been collected in sites located all along the SMR, where wood debris are found in all habitat types. In contrast, our data were concentrated in a specific 14.7 km section where wood debris were particularly associated with the meanders sections. Indeed, in our study, there is a positive relationship between the percentage of sand and the presence of wood debris (with AU of 200 m; r of Pearson = 0.30, $p < 0.05$). Furthermore, in the 200 m datasets, only 20 % of the AU contain wood debris and boulders (> 15 %). It is thus possible that, in our study, the effect of wood debris on JAS density was masked by the effect of substrate.

Yet, wood debris were particularly found in habitats where JAS were already less abundant.

Among the spatial context variables, the variables that described attributes of the shore (lateral variables) explained, on average, 3 % (negative effect of the presence of sandy beaches) to 5 % (positive effect of the presence of embankments) of JAS density variations. Both variables confirmed the positive effect of the presence of large substrate on JAS density. Longitudinal variables that expressed the effect of the distance between AU and specific features of the river explained 2 % (distance of the nearest pool downstream, and distance to the nearest spawning site upstream) of JAS density variations. Gries and Juanes (1998) documented that pools represent daytime sheltering habitats against high water temperatures, highly turbulent flows, intra-specific competition, and predation. Our analyses, suggest that JAS also tend to be associated with pools at night. This observation, together with the expectation that intra-specific competition and predation should be lower at night (Poff and Huryn 1998), indicate that physical conditions such as cooler water temperatures and less turbulent flows may be the primary conditions attracting JAS to pools and that, if there is any structure to this behaviour, parr tend to move upstream of a pool at night. However, further studies may be needed to confirm this behaviour. JAS density was negatively related to another longitudinal variable; the distance to the closest spawning site, this time, upstream of AU. This relationship may be related to sedentary behaviour that favour the use of nursery habitats close to the spawning site and, when movements do occur, to a passive behaviour that transport JAS, particularly during their first year of life, towards the closest nursery areas downstream of spawning sites (Beall et al. 1994).

In contrast with models based on AU of 200 m, the only HQM based on HP >50 m comprised exclusively spatial context variables. The position of AU within a sedimentary link (longitudinal variable) explained 54 % of the variation of JAS density while the presence of embankment (lateral variable) explained 5 % of this variation. Our analyses therefore suggest that JAS density tended to decrease as the distance from AU to the upstream limit of a sedimentary link increased. Hence, the identity of the variables that explained the largest fraction of JAS density differed between models developed using AU of 200 m (percent contribution of boulders) and HP >50 m (position within a link). However, the percent contribution of boulders to the riverbed is related to the position of habitat patches within a sedimentary link (r of Pearson = 0.68 for HP2). The elimination of the variable ‘position within a sedimentary link’ from the analysis performed to develop HQM based on HP2 resulted in the finding of a new model in which the percent contribution of boulders to the riverbed (partial $R^2_{adj} = 0.45$) and the presence of embankment (partial $R^2_{adj} = 0.07$) explained 52% of the variations of JAS density. These analyses, together with the knowledge that the upstream limits of sedimentary links are characterized by the dominance of boulders (Rice et al. 2001) suggest that models developed for HP2 using either local or spatial context variables may basically emphasize the same biological relationship between JAS and boulders.

CONCLUSION

Taken together, our study is consistent with the expectation that changing the size of AU may affect the structure and the predictive ability of HQM. Our analyses

suggest that the merging of SU possessing similar environmental conditions to form HP or AU that have a size similar to HP (i.e. in our study AU of 200 m) may improve the predictive ability and the upscaling of HQM. Our study also indicates that, while local variables often explain most of the variation of indices of habitat quality (in our study, JAS density), spatial context variables may also increase the predictive power of HQM.

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CONCLUSION GÉNÉRALE

Cette étude a suggéré que la taille des UA a effectivement un effet sur le développement et l'extrapolation des MQH. Dans notre, étude, le pouvoir prédictif des modèles augmentait avec la taille des UA. Le modèle développé à partir des taches d'habitat de plus de 50 m et les modèles développés à partir des AU de 200 m se sont avérés les seuls à permettre l'extrapolation. Les taches d'habitat sont des entités homogènes pour ce qui est de leur caractéristiques environnementales. Chaque tache a donc une valeur écologique intrinsèque uniforme pour les JSA. Au contraire, les UA formées à partir d'un nombre systématique d'UE peuvent contenir des UE qui ont des valeurs écologiques différentes pour les JSA, ce qui peut cacher ou déformer certaines relations existant entre les individus et leur environnement. Pour ce qui est des modèles développés à partir d'UA de 200 m, leur capacité d'extrapolation similaires à celle du modèle de taches d'habitat s'explique par le fait que la longueur de ces UA correspond à la longueur moyenne des taches d'habitat dans notre site d'étude. Il est donc souhaitable, lorsqu'on veut développer des MQH pour une population une communauté, d'utiliser des UA homogènes parce que celles-ci ont un réel sens écologique. Toutefois, si des contraintes logistiques s'imposent, il est également possible d'utiliser des UA systématiques qui auraient une taille similaire à celle des taches d'habitat. Par contre, encore faut il connaître cette longueur critique pour l'espèce ou le groupe d'espèces étudié.

Notre étude a également laissé entendre que le contexte spatial des UA influence la structure et le pouvoir prédictif des MQH. Nos modèles suggèrent que le substrat

grossier a un effet positif très fort sur les JSA. Plusieurs variables, soit locales ou de contexte spatial, qui ont été impliquées dans l'un ou l'autre de nos modèles exprimaient cette réalité : blocs dans le lit de la rivière, remblais ou sable sur les berges et position relative dans un lien sédimentologique. Même si les variables locales sont restées essentielles lors du développement de MQH, plusieurs variables de contexte spatial ont été impliquées dans l'un ou l'autre des modèles développés dans cette étude. Ces résultats appuient l'hypothèse qui suggère que la valeur d'un habitat ne se réduit pas à ses caractéristiques intrinsèques, mais implique également ce qui l'entoure.

Cette étude a montré que lorsqu'on veut développer des MQH, il est important de se questionner quant à la taille des UA que l'on va employer, ainsi que sur les caractéristiques environnementales que l'on veut utiliser pour décrire l'habitat. Cette réflexion devient d'autant plus importante si les MQH sont développés dans une optique de conservation. En effet, il est essentiel de choisir une taille d'UA qui soit pertinente pour l'espèce ou le groupe d'espèces que l'on cherche à protéger, sinon, l'exercice peut s'avérer inefficace. De plus, il devient primordial de tenir compte du contexte spatial autant que des caractéristiques locales d'un habitat lorsqu'on cherche à le conserver ou à le restaurer. La conservation ou la restauration d'un habitat devrait non pas se concentrer seulement sur l'habitat en tant que tel, mais aussi sur ce qui l'entoure et qui est susceptible de contribuer à son intégralité.

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