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Validation d'un modèle numérique de l'habitat estival des juvéniles  
de saumon atlantique (*Salmo salar*) de la rivière Sainte-Marguerite au Saguenay

par

Jean-Christophe Guay

Département de sciences biologiques

Faculté des arts et sciences

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Validation d'un modèle numérique de l'habitat estival des juvéniles  
de saumon atlantique (*Salmo salar*) de la rivière Sainte-Marguerite au Saguenay

présenté par  
Jean-Christophe Guay

a été évalué par un jury composé des personnes suivantes :

Dr Pierre Legendre, Université de Montréal

Dr Daniel Boisclair, Université de Montréal

Dr Michel Lapointe, McGill University

Michel Leclerc, INRS-eau

Dr James Grant, McGill University

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## SOMMAIRE

L'écoulement de l'eau, caractéristique propre aux milieux lotiques, est un des principaux paramètres structurant l'habitat des poissons en rivière. L'ensemble des facteurs abiotiques auxquels doivent faire face les poissons forme l'habitat physique. Il est possible de quantifier et de modéliser les préférences des poissons pour les facteurs abiotiques à l'aide de modèles biologiques. La qualité et la quantité d'habitat pour une espèce sont liées à un agencement optimum des variables abiotiques de vitesse du courant, profondeur de l'eau et type de substrat, variables elles-mêmes liées au débit. Les variations de débit entraînent des modifications rapides ou lentes des conditions auxquelles les poissons doivent faire face. La modélisation hydraulique de l'écoulement permet de prédire la vitesse et la profondeur en fonction du débit en tout lieu d'un tronçon de rivière (modèle hydraulique). En couplant le modèle hydraulique avec un modèle biologique, on peut obtenir un modèle d'habitat quantifiant la quantité et la qualité d'habitat disponible en fonction du débit.

Cette étude cherche à tester la validité et à comparer 2 modèles d'habitat pour les juvéniles de saumon atlantique (tacons) de la rivière Sainte-Marguerite.

L'écoulement a été modélisé (modèle hydrodynamique) dans un tronçon de 1,5 km de la rivière Sainte-Marguerite (région du Saguenay). Ce tronçon a ensuite été divisé en 2 sections : une section a servi à construire deux modèles biologiques (section de calibration) et l'autre a été utilisée pour la validation des modèles à l'aide d'observations géoréférencées sur la position des tacons, à deux débits différents. Le premier modèle biologique appelé Habitat Suitability Index (HSI), est basé sur des courbes de préférence. Ces courbes de préférence représentent l'utilisation faite par les tacons (n=308) de la vitesse du courant, de la profondeur de l'eau et de la grosseur du substrat dans la section de calibration. Cette utilisation des facteurs abiotiques est ensuite

pondérée par leur disponibilité dans la section de calibration. Le second modèle biologique appelé Habitat Probabilistic Index (HPI), est obtenu à l'aide de la régression logistique multiple appliquée à la matrice de présence-absence de tacons pour les trois mêmes facteurs abiotiques.

J'ai obtenu quatre cartes d'habitat, deux utilisant le HSI et deux, le HPI (débit de 2,2 et 3,2  $\text{m}^3 \cdot \text{s}^{-1}$ ). Pour les deux modèles d'habitat, l'indice varie entre 0 et 1, où 1 est l'habitat optimum et 0 l'habitat évité. Les valeurs d'habitat ont été séparées en 10 classes de 0,1 qui sont représentées par une échelle de couleurs sur les cartes. Les tacons du tronçon de validation ont été géoréférencés à des débits de 2,2 et 3,2  $\text{m}^3 \cdot \text{s}^{-1}$  en juillet et août 1997. Cela a permis de superposer les cartes de distribution spatiale des tacons sur les cartes d'habitat produites par les modèles d'habitat. Pour chaque classe de HSI et HPI, la surface et le nombre de tacons s'y trouvant ont été calculés.

Le diagramme de dispersion entre le modèle d'habitat utilisant HSI et l'abondance pour les deux débits a un  $r^2$  de 0,29. Le diagramme de dispersion a un  $r^2$  de 0,86 pour le modèle d'habitat utilisant HPI. Le modèle HPI semble mieux suivre la distribution spatiale des tacons que le HSI. Ainsi les résultats de cette recherche valident l'utilisation du modèle d'habitat et montre qu'il est préférable d'utiliser le modèle biologique HPI pour étudier les variations de quantité et de qualité d'habitat en fonction du débit.

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*À mon père, qui attend maintenant sans soucis,  
chaque printemps, le retour de l'oiseau bleu, l'arrivée d'un pays.*

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## INTRODUCTION

Le nombre d'études portant sur l'habitat des poissons s'est considérablement accru vers le début des années 80 au moment où sont apparues des menaces sérieuses de surexploitation des stocks. L'effondrement des stocks de morue de l'Atlantique, de l'esturgeon de la mer Noire ou encore du thon rouge des mers du sud ont été largement médiatisés. Dans le cas du saumon atlantique, un moratoire sur son exploitation commerciale a été décrété en 1992, suite à une baisse marquée des captures en mer et des retours en rivière. Cette espèce anadrome se reproduit essentiellement dans les cours d'eau et possède un cycle de vie complexe. Les juvéniles passent 2 à 4 années en rivière puis quittent vers la mer pour 1 à 3 ans avant de revenir frayer. Contrairement au saumon du Pacifique qui meurt après la fraie, un certain pourcentage du saumon atlantique, généralement des femelles, retourne à la mer après s'être reproduit. Les difficultés et les coûts associés aux recherches en milieu marin ont entraîné plusieurs chercheurs à se tourner vers l'étude des périodes de son cycle vital se passant en eau douce. Ainsi les gestionnaires misent beaucoup sur la recherche en rivière, dans la mesure où une intervention humaine potentielle est plus facile dans ces systèmes qu'en mer.

Les systèmes lotiques sont caractérisés par la présence d'un écoulement dynamique et très variable absent en lac et en océan. L'étude de l'habitat des populations piscicoles de tels systèmes doit donc tenir compte des variables physiques associées à l'écoulement. Les rivières subissent fréquemment des variations importantes de débit, de l'échelle journalière à l'échelle saisonnière. Ces variations affectent le niveau d'eau, sa profondeur, sa température ainsi que l'érosion des berges et du lit de la rivière (Frenette et al. 1984, Anthony and Harvey 1991, Malavoi and Souchon 1992, Fraser et al. 1995, Valentin et al. 1996, Payne and Lapointe 1997). Il a été montré que les poissons ont tendance à choisir des sites de fraie et des aires d'alimentation en fonction

des vitesses de courant, de la profondeur de l'eau et du type de substrat, confirmant ainsi l'importance des variables physiques sur la qualité de l'habitat (McCrimmon 1954, Keenleyside 1962, Saundeer et Gee 1964, Rimmer and Paim 1984, deGraaf et al. 1986, Morantz et al. 1987, Cunjak 1988, Heggenes et al. 1991, Greenberg et al. 1996, Heggenes et al. 1996, Heggenes 1996). Cette tendance des poissons à sélectionner des variables abiotiques peut être quantifiée afin de déterminer des préférences pour chacune des ces variables (Bovee 1982, Morantz et al. 1986, Heggenes et Salveit 1990, Heggenes et al. 1991, Heggenes 1996). La majorité des études portant sur la quantification des préférences suit une méthode proposée par Bovee (1978), le Habitat Suitability Index (HSI) ou indice de qualité de l'habitat.

Des modèles d'écoulement (modèles hydrauliques) ont été développés afin de prédire les variations locales de vitesses et de profondeurs dans un tronçon en fonction des fluctuations naturelles ou anthropiques du débit (Bovee 1978, Leclerc et al. 1994, Leclerc et al. 1995). Les premiers modèles hydrauliques proposés étaient unidimensionnels ce qui signifie que les variations de profondeurs et de vitesses s'établissaient principalement dans l'axe longitudinal de la rivière (sens de l'écoulement) en utilisant une méthode de partitionnement de la rivière en cellules de même taille couvrant les différents types d'habitat tels que les rapides, plats, radiers, fosses (Bovee 1982). Une approche bidimensionnelle a été développée plus récemment (Leclerc et al. 1990, Leclerc et al. 1995, Leclerc et al. 1996) permettant d'étudier les variations de vitesses et de profondeurs autant longitudinalement que latéralement par rapport à l'écoulement. Cette dernière approche consiste en un partitionnement de la rivière en parcelles triangulaires de différentes surfaces selon l'hétérogénéité du milieu. Ces parcelles sont caractérisées par leur granulométrie de surface et leur topographie. Ces dernières variables fournissent les données de base du modèle d'écoulement bidimensionnel permettant de simuler les vitesses et les profondeurs en tout lieu du tronçon modélisé, pour tout débit choisi.

La combinaison d'un modèle biologique avec un modèle hydraulique permet de prédire l'impact des variations de débit sur la qualité et la quantité des microhabitats (Bovee 1982, Souchon et al 1989, Leclerc et al. 1994, Leclerc et al. 1996, Heggenes et al. 1996). Cette combinaison devient ainsi un modèle d'habitat où la qualité anticipée d'une parcelle est définie par un index intégrant les préférences des poissons pour la grosseur du substrat, la vitesse moyenne et la profondeur de l'eau. Le principal modèle d'habitat utilisé dans la littérature est le Physical HABitat SIMulation, PHABSIM (Bovee 1982, Armour et Taylor 1991, Reiser et al. 1989, Bourgeois et al. 1996). Ce modèle, qui est associé à l'approche unidimensionnelle décrite plus haut, a souvent été utilisé lors de l'instauration de débit minimum réservé visant la conservation de l'habitat des poissons et des organismes benthiques (Leclerc et al. 1994). PHABSIM permet de déterminer des aires pondérées utiles correspondant à des surfaces possédant une certaine valeur d'habitat prédéterminée (Orth et Maughan 1982, Shirvell 1989, Bourgeois et al. 1996). Des chercheurs ont tenté de déterminer les relations entre la densité des poissons et les aires pondérées utiles, certains trouvant des relations (Stalnaker 1979, Orth et Maughan 1982), d'autres de très faibles ou aucune relation (Shirvell 1989, Bourgeois et al. 1996).

Un second modèle d'habitat, appelé modèle numérique d'habitat, découle de l'utilisation d'un modèle hydraulique bidimensionnel (Leclerc et al. 1990,1995,1996). C'est ce dernier modèle qui sera utilisé dans la présente étude.

L'utilisation de la modélisation numérique d'habitat permet de produire des cartes de qualité d'habitat où une échelle de couleurs correspond aux valeurs d'habitat déterminées par le modèle pour un certain débit (Leclerc et al. 1994). Les variations de ce dernier modifient non seulement le nombre de parcelles (surface inondée), mais aussi leur valeur d'habitat, suivant les modifications de vitesse et de profondeur à l'intérieur de celles-ci. L'intégration spatiale de ces

changements devrait soutenir l'hypothèse de l'impact des variations de débit sur la qualité et la quantité d'habitat piscicole en rivière.

Plusieurs autres variables, comme le taux de dérive (proies potentielles transportées par le courant), la composition de la dérive, l'abondance des compétiteurs et des prédateurs, le taux de survie hivernal et la température de l'eau affectent la qualité de l'habitat et/ou sa sélection par les poissons (Hearn et Kynard 1986, Cunjak 1988, Nakano 1995, Gelwick et al. 1997, Mäki-Petäys et al. 1999). Ainsi, la modélisation numérique d'habitat est implicitement basée sur la prémisse que l'utilisation de variables strictement physiques (vitesse, profondeur, substrat) suffit à fournir de l'information écologique pertinente sur l'habitat des poissons (Orth 1982). À ma connaissance, aucune étude n'a tenté de valider les résultats fournis par le modèle numérique d'habitat ou PHABSIM en les comparant avec la distribution des poissons.

Cette étude a porté sur l'habitat estival d'alimentation des juvéniles de saumon atlantique de 1 et 2 ans (tacons 1+2+) de la rivière Sainte-Marguerite, dans la région du Saguenay.

Les deux principaux objectifs de mon travail ont été 1) de vérifier l'existence d'une relation significative entre la distribution spatiale des tacons et les indices de qualité d'habitat fournis par le modèle numérique d'habitat, puis 2) de comparer l'approche des courbes de préférence (HSI) avec une nouvelle approche, basée sur la régression logistique multiple.

**A NEW APPROACH IN NUMERICAL RIVER HABITAT MODELLING  
FOR JUVENILES OF ATLANTIC SALMON (*SALMO SALAR*)**

**Guay, J.C.<sup>1</sup>, D. Boisclair<sup>1</sup>, D. Rioux<sup>2</sup>, M. Leclerc<sup>2</sup>, M. Lapointe<sup>3</sup>, and P. Legendre<sup>1</sup>**

<sup>1</sup>Université de Montréal, Département de sciences biologiques

C.P. 6128, succursale Centre-ville, Montréal, Québec, Canada H3C 3J7

Phone: (514) 343-6875; Fax: (514) 343-2293; e-mail: guayje@magellan.umontreal.ca  
e-mail: Daniel.Boisclair@UMontreal.ca

<sup>2</sup>INRS-Eau, C.P. 7500, Sainte-Foy, Qc Canada G1V 4C7

<sup>3</sup>McGill University, Department of Geography, 805 Sherbrooke W,  
Montréal, Qc Canada H3A 2K6

## ABSTRACT

We evaluated the validity of two physical habitat models to predict juvenile Atlantic salmon distributions in the Sainte-Marguerite River. Each model produces a habitat index based on abiotic variables. The variables were substrate size (D50), mean velocity and depth of the water column the parrs were facing. The first model was based upon the preference curve method to determine a Habitat Suitability Index (HSI). For this model, the Pearson correlation coefficient between HSI and parr distribution was 0.12. The second model was based upon a multiple logistic regression of physical variables used and avoided by fish to determine a Habitat Probabilistic Index (HPI). The Pearson correlation coefficient between HPI and parr distribution was 0.86. We conclude that HPI is a more appropriate model to describe fish preference and hence should be used in fish habitat modelling.

Nous avons évalué la capacité de deux modèles d'habitat à prédire la distribution des juvéniles de saumon atlantique de la rivière Sainte-Marguerite. Chaque modèle produit un indice d'habitat basé sur des variables abiotiques. Ces variables sont la grosseur du substrat (D50), la vitesse moyenne et la profondeur de la colonne d'eau auxquelles doivent faire face les tacons. Le premier modèle utilise des indices de préférence d'habitat (HSI) provenant de l'approche des courbes de préférence. La corrélation de Pearson entre HSI et la distribution de tacons pour ce modèle est de 0.12. Le second modèle est basé sur la régression logistique multiple des variables abiotiques utilisées et évitées par les tacons ; ce modèle produit un indice d'habitat probabiliste (HPI). La corrélation de Pearson entre HPI et la distribution des tacons est de 0.86. Il appert que la méthode de HPI discrimine mieux les préférences des poissons et devrait être utilisée dans la modélisation d'habitat de ces organismes.



## INTRODUCTION

Rivers are subjected to many natural disturbances such as changes in water levels and daily or seasonal variations of water temperature (Frenette et al. 1984, Malavoi and Souchon 1992, Fraser et al. 1995). These disturbances not only affect the flow but also the pattern of bank and riverbed erosion (Anthony and Harvey 1991, Valentin et al. 1996, Payne and Lapointe 1997, Lapointe and al. submitted). Such modifications of physical conditions in rivers are expected to have direct biological implications (Stalnaker et al. 1996). The potential importance of physical variables on habitat quality is supported by many studies indicating that fish tend to select spawning and nursery areas on the basis of substrate diameter, current speed, and water depth (Rimmer and Paim 1984, deGraaf et al. 1986, Morantz et al. 1987, Cunjak 1988, Heggenes et al. 1991, Greenberg et al. 1996, Heggenes et al. 1996, Heggenes 1996).

Hydrodynamic models have been developed to predict changes in local current speed and water depth for specified modifications of flow rates (Bovee 1978, Bovee 1982, Leclerc et al. 1994, Leclerc et al. 1995, Leclerc et al. 1996). The propensity of fish to favour specific ranges of physical variables and the ability of hydrodynamic models to predict current speed and water depth have been combined to predict the potential impact of changes in flow rate on fish habitat quality (Souchon et al. 1989, Leclerc et al. 1994, Heggenes et al. 1996). This procedure, referred to as numerical habitat modelling, generally involves the partitioning of a river in a mosaic of tiles of various surface areas (Leclerc et al. 1990). Each tile is characterised by its substrate surface composition and topography. These variables are used as input to a hydrodynamic model that predicts water depth and current speed in any given tile for a specified flow rate. The anticipated quality of a tile as a fish habitat is defined by an index that integrates predilection of fish for the substrate diameter, the water depth, and the current speed in that tile (Orth et al. 1982, Mathur et al. 1984, Leclerc et al. 1994). The end result of numerical habitat modelling is a map

describing the habitat quality index assigned to each tile at a given flow rate. Any change in flow rate not only modifies the number of tiles being modelled (by changing the wetted area of a river) but also the habitat quality index of each tile (by changing water depth and current speed over each tile). Spatial integration of changes in the number of tiles and their quality index is expected to allow the assessment of the impact of flow rate modifications on fish habitat quantity and quality in a river.

Numerous variables such as drift rate of invertebrates, size composition of the drift, and abundance of competitors and predators have been hypothesised to affect habitat quality and habitat selection by fish (Hearn and Kynard 1986, Cunjak 1988, Nakano 1995, Gelwick et al. 1997). To our knowledge, none of these variables are explicitly represented in current numerical habitat models. Numerical habitat modelling is implicitly based on the assumption that the combination of strictly physical attributes such as substrate diameter, current speed, and water depth is sufficient to yield ecologically meaningful information on fish habitat.

The purpose of our work is 1) to test the hypothesis of the existence of a significant relationship between the distribution of habitat quality predicted by numerical modelling and the distribution of fish observed in a river and 2) to propose a new approach based on the multivariate Gaussian logistic regression in the description of fish preference and incidentally in habitat modelling.

## **METHODS**

### **SITE AND SPECIES FOR STUDY**

Sampling was conducted in the main branch of the Sainte-Marguerite River in the Saguenay region of Québec. This river is adjacent to the field station of the Centre Interuniversitaire de Recherche sur le Saumon Atlantique (CIRSA). The study area was a 1.5 km reach located approximately 80 km from the junction of the Sainte-Marguerite and Saguenay rivers (Figure 1). The species selected for study was the Atlantic salmon (*Salmo salar*). Our work focussed on 1+ and 2+ parrs. In the Sainte-Marguerite river, salmon coexists with 5 other species of fish: brook charr (*Salvelinus fontinalis*), American eel (*Anguilla rostrata*), longnose dace (*Rhinichthys cataractae*), longnose sucker (*Catostomus catostomus*) and sea lamprey (*Petromyzon marinus*).

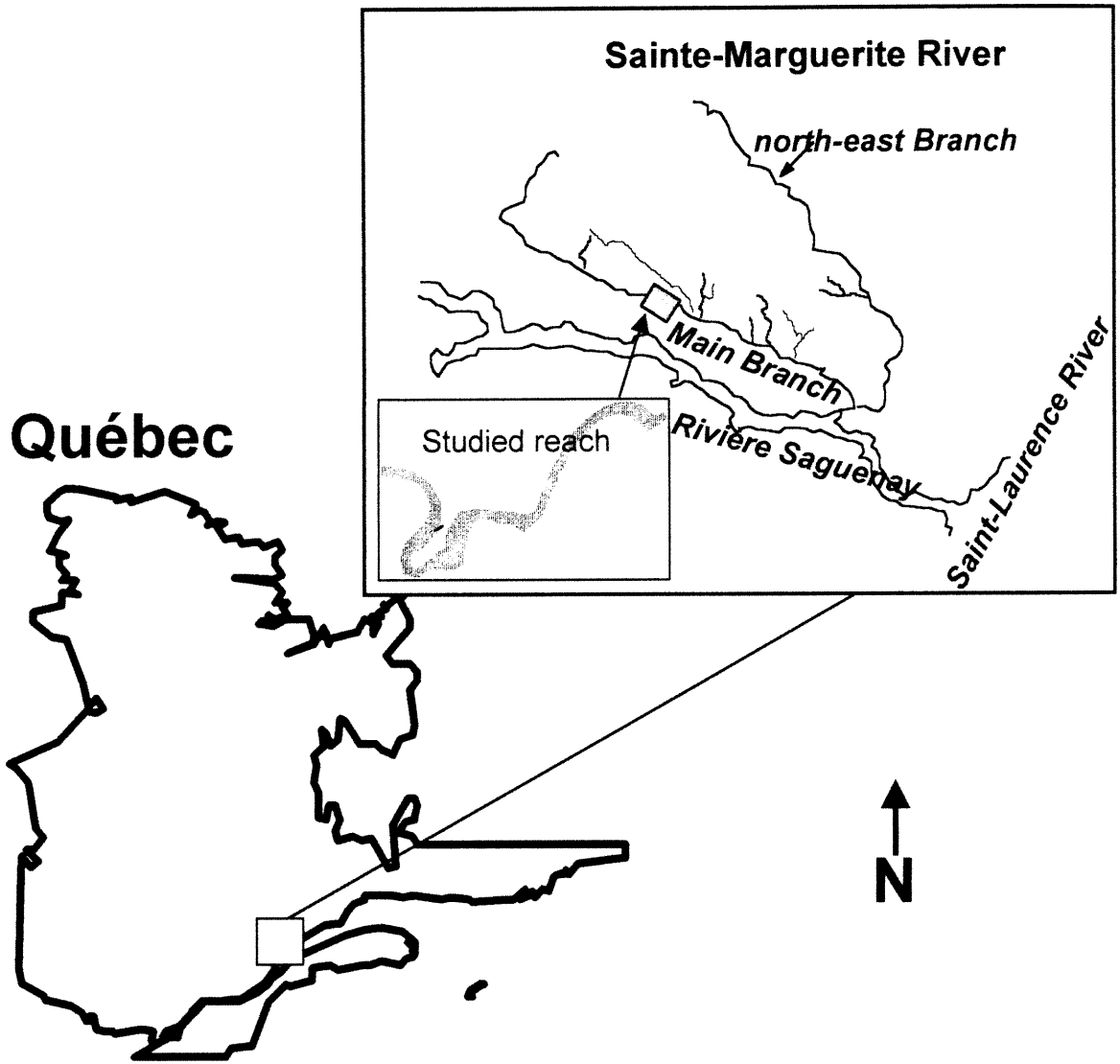
The reach studied was divided in upper, median, and lower sections. These sections were respectively 375, 750, and 375 m long and 20 to 45 m wide at bankfull conditions. The upper and lower sections, further referred to as the calibration sections, were used to assess the physical characteristics selected or avoided by parrs. The median section, further referred to as the validation section, served two purposes. First, it was used to apply a numerical model to predict habitat quality, its spatial variation, and hence, the potential fish distribution. Second, it was used to map real fish distributions and test the predictions of the numerical model.

### **STRUCTURE OF THE NUMERICAL MODEL**

The numerical model adopted to predict the spatial heterogeneity of habitat quality comprised two parts: a hydrodynamic model and a biological model. The hydrodynamic model we used is a two-dimensional model (2-D) that allows us to predict current speed and water depth over the reach, i.e. on a longitudinal (upstream - downstream) and a transversal (left bank - right bank) axis of the river (Leclerc et al. 1990, 1994, 1995). This model requires as input the

**Figure 1.**

**Study site.**



description of the topography of the riverbed and the mapping of substrate grain size. These data, together with a series of physical coefficients (water viscosity, friction), and assumptions on fluid dynamics (conservation of water, flowing mass, and momentum) are used as input to the hydrodynamic model to predict current speed (averaged over the water column) and average water depth for each tile defined during the topographic survey. Once the hydrodynamic model is developed, predictions can be computed for any specified flow rate.

The purpose of the biological model is to provide an index of fish habitat quality from the physical characteristics of the river. The only variables we employed to define habitat quality were substrate diameter, current speed, and water depth. Estimation of the physical conditions in a series of 1 m<sup>2</sup> locations used and not used by fish allowed us to quantify the variations in the propensity of fish to prefer specific conditions over the range of physical characteristics found in the river. The biological model assumes that when fish more intensively uses a specific range of substrate diameter, current speed, or water depth, this range represents a habitat of higher quality for the fish. The habitat quality index assigned to a location represents a compromise between propensity of fish for the substrate diameter, the current speed, and the water depth found at this location.

The final operation of the numerical modelling exercise is to combine the results from the hydrodynamic model at a given flow rate with the biological model. Current speed, water depth, and substrate composition predicted by the hydrodynamic model for a tile are used as input to the biological model that assigns an index of habitat quality to that tile. Estimation of an index of habitat quality for all tiles modelled produces a map of the spatial heterogeneity of expected fish habitat quality in a river for a given flow rate. This exercise can be repeated to produce predictions of habitat quality and distribution of those habitats for different flow rates.

## SAMPLING

### *Hydrodynamic model*

Data required to characterise the topography and substrate composition over the 1.5 km reach under study were collected during the first 3 weeks of June 1997 (after the spring flood). Topography was quantified by obtaining the coordinates (longitude, latitude, and altitude) of approximately 18 sampling points per 100 m<sup>2</sup> over the complete reach: in the river, on both shores, and above the high water level. Each point was georeferenced using a total station (electronic theodolite coupled with an electronic distance measurement system; SOKKIA SET3B) and an electronic data logger (SOKKIA SDR33). The reach was divided into patches of similar substrate composition. We visually estimated the percentage of the area of each patch represented by each of six classes of substrate diameter (Table 1). Those data were used in the hydrodynamic model to specify bed roughness; they allowed to predict current speed and water depth anywhere in the calibration and validation sections of the reach at any flow rate.

Table 1.

Median size of substrate types entering the hydrodynamic model.



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Substrate type	Median substrate size (cm)
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metric boulder	>100
boulder	25-100
cobble	6.4 - 25
pebble	3.2 - 6.4
gravel	0.004 - 3.2
sand	0.0005 - 0.004

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## *Biological models*

Biological models are required to determine the physical conditions used or avoided by salmon parrs. Environmental conditions used by fish were defined by visually scanning the entire calibration section by snorkelling on two occasions (July 16-24, and August 1-10). The diver covered 50-100 m of the calibration reach per day. The diver swam upstream to minimise fish disturbance (Cunjak et al. 1988). Age 1+ (5-8 cm total length; TL) and 2+ parrs (7-10 cm TL) could not be differentiated because of overlap in size range. Hence, the biological model we developed described habitat use by 1+ and 2+ parrs indistinguishably. Each fish encountered was observed for 2 minutes and georeferenced. Fish generally performed short but frequent movements upstream, presumably to capture drifting invertebrates. Between these movements, parrs came back above and slightly downstream from the centre of a particular rock referred to as the 'home rock'. Each home rock was marked with a stone coloured with fluorescent paint. The fish was then chased downstream to avoid recording two series of data for the same fish. Physical conditions were quantified at home rocks after twenty coloured stones had been positioned or after 30 minutes of diving. For each home rock, substrate composition, current speed, and water depth were noted. Substrate composition was quantified as the median diameter axis (D50) of substrate components. Given that the volume of a stone is determined by three axes (A being the longest and C the shortest axis), D50 is defined as the length (in cm) of the B-axis of the median stone within a 1 m<sup>2</sup> area centred on the home rock. Averaged current speed (m · s<sup>-1</sup>) over a 30 second period was estimated using a PRICE-GURLEY current meter. Speed was recorded 5-10 cm upstream from the home rock at a distance from the bottom equivalent to 40 % of the mean water depth within a surface of 1 m<sup>2</sup> centred on the home rock (e.g. at 40 cm from the bottom when depth was 1 m). The water depth (cm) assigned to a home rock was taken to be the mean depth found within an area of 1 m<sup>2</sup> centred on that rock. D50 can be estimated visually to 5 mm

accuracy after proper training and calibration (Latulipe and Lapointe, in press) against stone count samples (Wolman 1957). Flow rate ( $\text{m}^3 \cdot \text{s}^{-1}$ ) was estimated for every sampling date based on records from a continuous flow station located 500 m upstream from the reach under study. No tributary entered the river between the flow station and the reach or within the reach. Flow at the flow station is expected to accurately represent that of the reach.

We used the 2-D hydrodynamic model and the flow rate observed each day to produce maps of the sub-section where we work each day. Hence, we obtained the distribution of substrate composition, current speed, and water depth for each sub-section where we observed fish daily. For a given number of fish observed during one day in a sub-section, we selected a same number of location at random where no fish were observed (at least 2 m from the closest salmon parr mapped). The random selection of the locations was done using the list of the node coordinates of each sub-section grid (see Figure 2 for an example of grid). These data allowed us to characterise the environmental conditions available to salmon parrs and the environmental conditions avoided by the fish.

#### *Fish distribution in the validation section*

The distribution of salmon parrs in the validation section was obtained using a procedure identical to that used to evaluate habitat utilisation by fish in the calibration section except that no physical data other than flow rate were collected. Flow rate was noted to ensure that numerical modelling, which predicted habitat quality distribution and potential fish distribution, would be calculated at a flow rate identical to that prevailing during mapping of real fish distributions. Snorkelling was performed to scan the complete length of the validation section on two occasions (July 25-31 and August 11-17). Each fish observed was georeferenced, yielding precise maps of fish distribution in the validation section.

## MODELLING

The data collected during the two surveys in the calibration section were pooled to develop two types of models: a habitat suitability model, and a habitat probabilistic model.

### *Habitat suitability model*

Habitat suitability model is a well-known form of modelling based on the development of preference curves for a series of environmental characteristics expected to determine habitat quality for fish. We constructed a preference curve of parrs for substrate composition (D50), current speed, and water depth.

The relative contributions of 6 classes of substrate diameter to the different patches of the calibration section were transformed to D50 values. Knowing the percentage of each class, we determine D50 as the substrate diameter value corresponding to 50% of the cumulative frequencies of the classes.

The data collected in the calibration section were used to define the range of environmental conditions utilised by fish, to divide each environmental factor into a series of intervals (six intervals for substrate composition using D50, eight intervals for depth and nine for current speed), and to obtain the percentage of all fish observed during our survey of habitat utilisation within each interval of environmental conditions. The same approach was used to quantify the percentage of all locations selected at random that fell into each interval of environmental conditions. For each interval  $i$  of a given environmental condition  $c$ , we estimated an index of preference  $I_{c,i}$  as:

$$(1) \quad I_{c,i} = \% U_{c,i} / \% A_{c,i}$$

where %U<sub>c,i</sub> is the percent utilisation by fish of a specific interval i of an environmental condition c (substrate composition, current depth, or water depth) and %A<sub>c,i</sub> is the percent availability of this environmental condition in the calibration section. Each preference index for a given environmental condition was ranged such that its maximum I<sub>c,i</sub> value was 1. The ranged indices of preference (I<sub>c</sub>) were used to develop a habitat suitability index (HSI) following the approach proposed by Leclerc et al. (1995). Firstly, for each fish observed within the calibration section, we estimated an unweighted HSI (HSI<sub>U</sub>) as follows:

$$(2) \quad \text{HSI}_U = I_D \cdot I_V \cdot I_S$$

where I<sub>D</sub>, I<sub>V</sub>, and I<sub>S</sub> are, respectively, the ranged index of preference for depth, current speed, and substrate composition interval used by a given fish. HSI<sub>U</sub> is in the interval [0, 1]. Secondly, a multiple regression analysis was used after taking the log of all terms, to obtain partial regression coefficients for I<sub>D</sub> (noted X), I<sub>V</sub> (noted Y), and I<sub>S</sub> (noted Z). Thirdly, we ranged the partial regression coefficients of depth, velocity and substrate in such a way that X+Y+Z =1. This procedure produced a weighted habitat suitability index (HSI) that could be calculated for any tile of the validation section as:

$$(3) \quad \text{HSI} = I_D^X \cdot I_V^Y \cdot I_S^Z$$

A tile having a HSI value close to 0 was considered a poor habitat because it had at least one physical characteristic generally avoided by fish (low I value). A tile having a HSI value close to 1 was taken to be a good habitat because all its physical characteristics had to be close to the preferendum of fish (high I values).

### *Habitat probabilistic model*

The habitat probabilistic model was developed in the course of the present work by constructing a matrix containing information on the physical conditions noted where and when a parr was observed in the calibration section of the reach and on the physical conditions estimated where and when no fish were observed. The matrix had 4 columns that described whether or not a fish was observed (presence or absence of fish noted as 1 or 0), and associated water depth, current speed, and substrate composition (D50). Since we randomly selected as many locations without fish as there were fish observed, the matrix had twice as many lines as the total number of fish we observed in the calibration section of the reach. This matrix was used to develop a model to estimate the probability of observing a fish under given physical conditions. This was achieved by fitting a multivariate Gaussian logistic regression model to our presence-absence data. Using this model, the habitat probability index (HPI) of observing a fish under given physical conditions can be represented as:

$$(4) \quad \text{HPI} = 1/(1 + e^{-\lambda})$$

where,

$$\lambda = P_0 + P_1 S + P_2 V + P_3 D + P_4 S^2 + P_5 V^2 + P_6 D^2 + \dots$$

where  $P_n$  are parameters fitted by multivariate Gaussian logistic regression and S, V, and D are, respectively, the substrate composition (D50), current speed and water depth. During a stepwise backward regression procedure, we explored the possibility of entering in the Gaussian logistic model environmental factors raised to powers up to 4 in order to allow expression of complex forms of relationships. The logistic model permitted to predict the probability (0 to 1) of finding a

fish in any tile using local substrate composition, current speed, and water depth as independent variables.

## **DATA ANALYSIS**

Physical conditions used or avoided by salmon parrs in the calibration section were defined under flow rates ranging from 1.9 to 5.5  $\text{m}^3 \cdot \text{s}^{-1}$  (average=3.7  $\text{m}^3 \cdot \text{s}^{-1}$ ). Similarly, fish distribution in the validation section was described during surveys that corresponded to two relatively narrow ranges of flow: 1.9 to 2.6  $\text{m}^3 \cdot \text{s}^{-1}$  and 2.9 to 4.2  $\text{m}^3 \cdot \text{s}^{-1}$ . Hence, our sampling yielded two maps that represented observed fish distributions. We used the numerical model to produce maps of substrate composition, current speed, and water depth in the validation section at 2.2 and 3.2  $\text{m}^3 \cdot \text{s}^{-1}$ . These flows were selected to correspond to the mean flows for which observed fish distributions were available. Hydrodynamic models may be implemented only within a range of discharge that does not have a marked effect on river topography and substrate distribution and composition. The range of flow (2-6  $\text{m}^3 \cdot \text{s}^{-1}$ ) and the daily variations of flow observed (0-8 %, average 2.5 %) in the reach under study were expected to have negligible influence on the river bed since formative bankfull discharge in the Sainte-Marguerite river is 80  $\text{m}^3 \cdot \text{s}^{-1}$  (Lapointe, unpublished data).

The maps of physical conditions were used as input to the biological models to estimate HSI and HPI in all tiles of the validation section at 2.2 and 3.2  $\text{m}^3 \cdot \text{s}^{-1}$ . HSI and HPI were grouped in ten classes of habitat quality (0 to 1 by increments of 0.1). This led to the production of four maps (2 biological models and 2 flows) defined by 10 intervals of habitat quality represented by ten colour shades on the maps. Each map was taken as a prediction of expected habitat quality distribution and potential fish distribution in the validation section.

We used the maps of expected habitat quality distribution in the validation section to estimate fish densities (number of fish/100 m<sup>2</sup>) in the areas associated with each class of expected habitat quality index. Polynomial regression was used to assess the predictive power of each model, by comparing the model predictions to observed fish distributions.



## RESULTS

### HYDRODYNAMIC MODEL

The topography of the complete reach was defined by estimating the easting, northing and elevation at 9470 survey points. The topographic survey represented the study reach as a mosaic of tiles ranging from 1 to 25 m<sup>2</sup> (Figure 2). The difference in bed elevation from the upstream to downstream limits of the reach was 4.1 m. The mean slope of the river, calculated over 100 m stretches, ranged from 0.07 % to 1.2 %. The reach was divided into a total of 145 patches of relatively homogenous substrate composition (Figure 3). The surface area of the patches ranged from 25 to 1800 m<sup>2</sup>. Patch composition ranged from being dominated by sand (50 to 100 % sand in 26 of the patches, covering 11 % of the reach surface) to boulders (50 to 100 % boulders in 10 patches, covering 1 % of the reach surface). Gravel was dominating in 16 patches (50 to 100 %) covering 24 % of the reach surface. Cobble dominate in 34 patches (covering 26 % of the reach surface) and pebble dominated in 59 patches (50 to 100 %) covering 38 % of the reach surface (Table 2).

We evaluated the ability of the hydrodynamic model to predict current speed and water depth by measuring these values at 271 locations in the field and under 4 levels of flow rate ranging from 2 to 5.6 m<sup>3</sup> · s<sup>-1</sup>. Although locations were randomly selected, each one was precisely georeferenced. The hydrodynamic model was then run to obtain predicted values of current speed and water depth at the 271 locations for the flow rates prevailing during field measurements. Individual values of current speed predicted by the hydrodynamic model were poorly correlated with the measured values ( $r^2=0.09$ ; major axis regression, Figure 4). The slope of the relationship between predicted and observed current speeds differed significantly from 1 but its intercept was not significantly different from 0. Visual analysis of the major axis regression (figure 4), show

**Figure 2.**

**Section of the Sainte-Marguerite River under study and example of a triangular grid element (tile) used by the hydrodynamic model.**

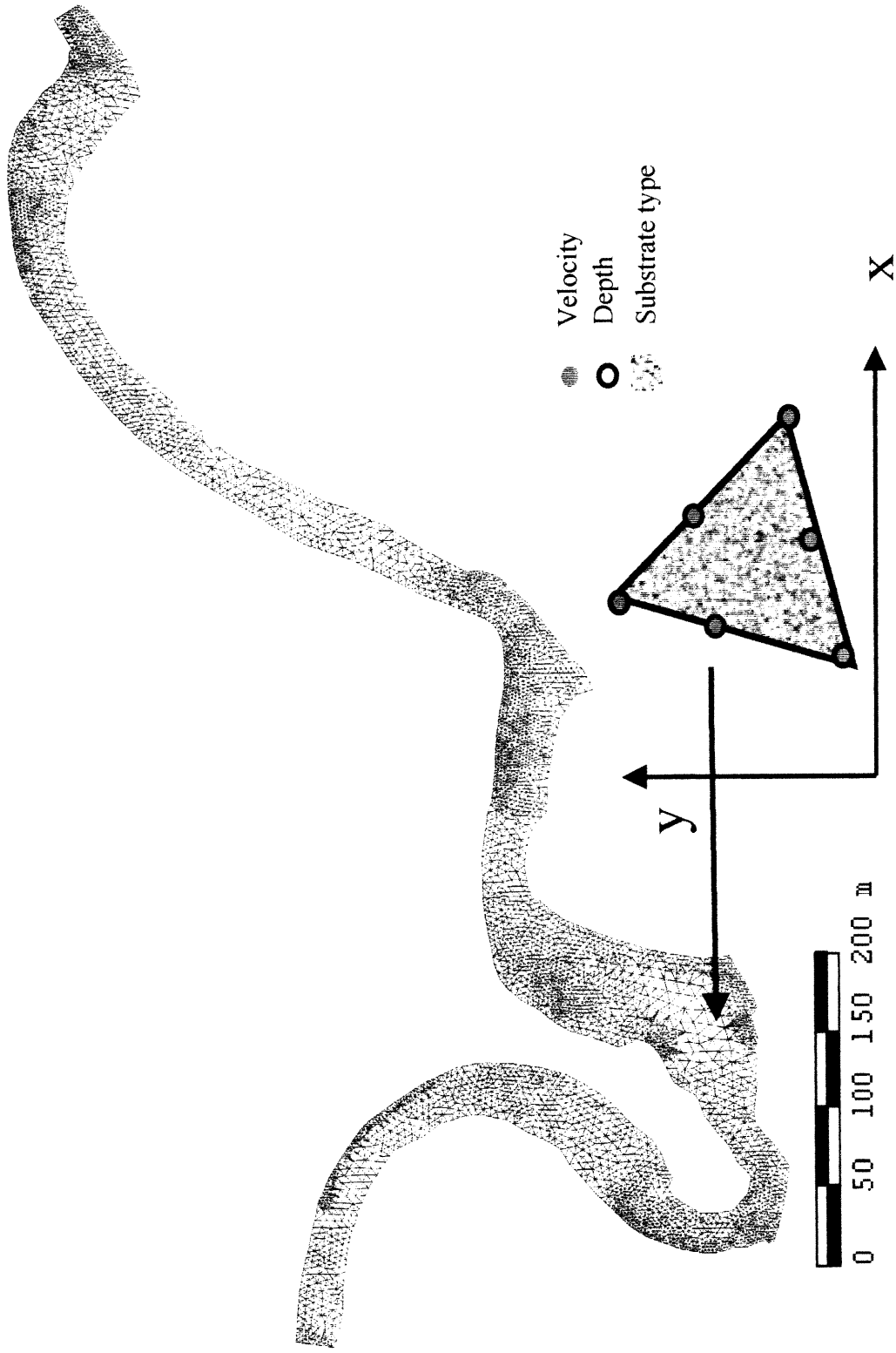


Figure 3.

Patches of substrate types along the entire reach, and view  
of the validation section.

D50 (cm)

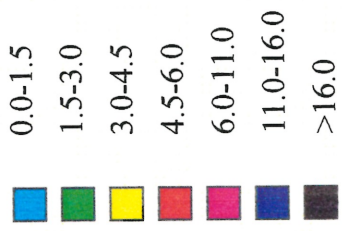


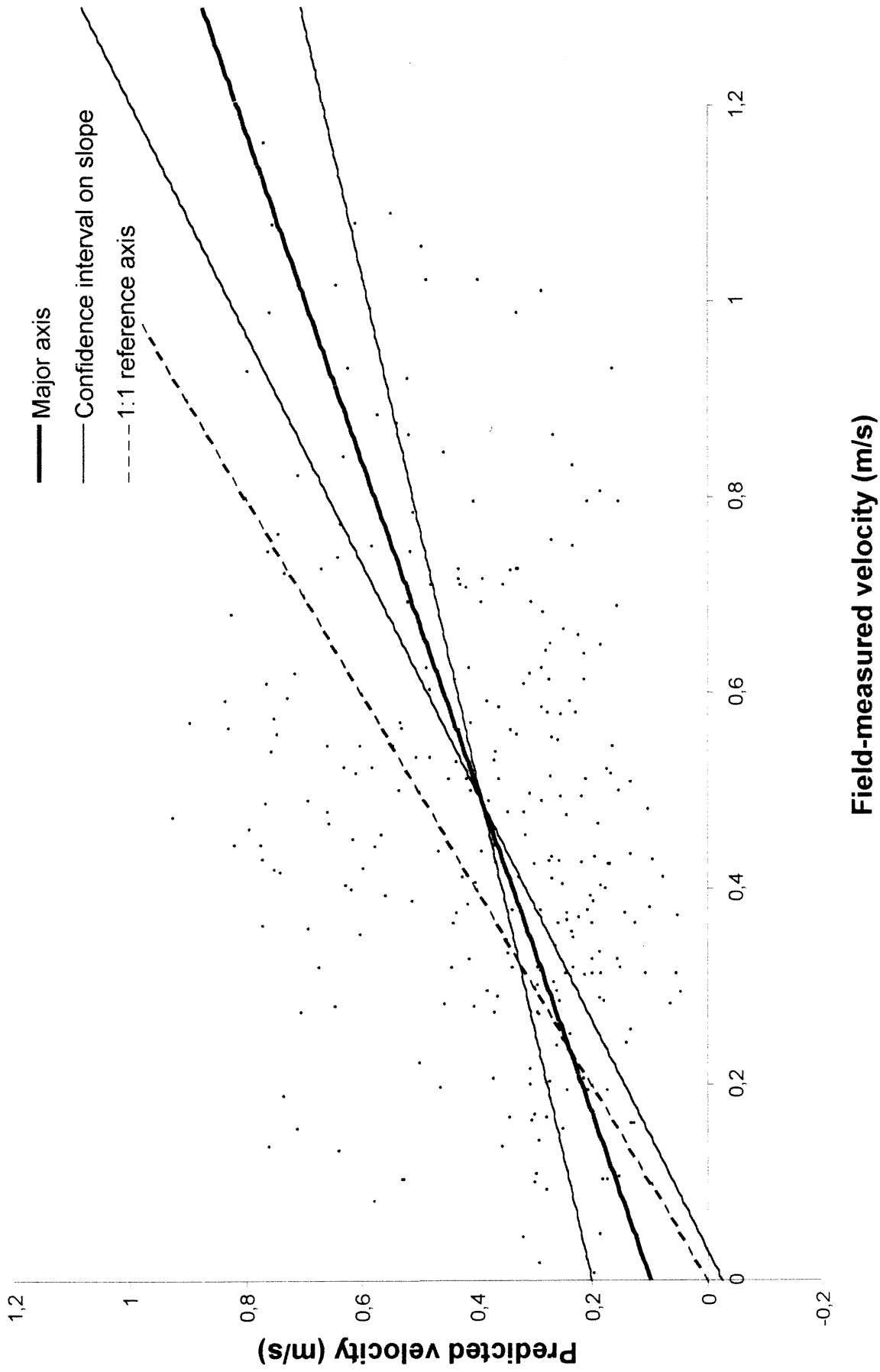
Table 2.  
Substrate type dominance (50% or more) in the  
Sainte-Marguerite River bed.

Dominant substrate	Number of patches	% of total wetted area
boulder	10	1
cobble	34	26
pebble	59	38
gravel	16	24
sand	26	11

Figure 4.

Difference between the predicted and observed velocities.  
Slope (a) = 0.5957, 95 % confidence interval = [0.386, 0.852],  
intercept (b) = 0.0985, 95 % confidence interval = [-0.027, 0.201].





that the hydrodynamic model mostly tended to overestimate low velocities ( $< 0.2 \text{ m} \cdot \text{s}^{-1}$ ) and underestimate high velocities ( $>0.6 \text{ m} \cdot \text{s}^{-1}$ ). Low and high velocities were mainly associated with, respectively, the areas near the bank and the thalweg area. As parrs rarely choose those sites, and since the main goal is to describe a general trend in velocity preference, we think that it is still adequate to use the results of the 2-D hydrodynamic model despite errors on extreme predicted velocities. A fish is not facing a velocity at a precise location but all around its homerock, as it is moving around or over it. Individual water depths predicted by the hydrodynamic model were within 15 % of the measurements made under field conditions, with only a 2 % difference between the mean values (Table 3a). There was a strong relationship between individual depth values predicted by the hydrodynamic model and individual field measurements of depth ( $r^2=0.85$ ).

## **BIOLOGICAL MODELS**

Physical attributes used by the fish were defined by measuring substrate composition, current speed, and water depth at 308 locations where parrs were observed. 85 % of the fish observed in the calibration section used substrate characterised by D50 values between 3 and 6 cm. Those fish were found under current speeds ranging from 0.05 to  $1.20 \text{ m} \cdot \text{s}^{-1}$ , and at depths ranging from 0.12 to 1.2 m (Table 3b; Figure 5a,b,c). Substrate available under flows observed during sampling in the calibration section had D50 values ranging from 0.002 m to 1.5 m (Figure 5a). Maximum current speed predicted by the hydrodynamic model at flows prevailing during calibration ranged from 1.1 to  $1.2 \text{ m} \cdot \text{s}^{-1}$  (Figure 5b). Corresponding values for maximum water depth were 2.37 to 2.4 m (Figure 5c). These conditions were defined as the physical conditions available to fish to develop the preference indices.

Physical variable values avoided by fish (defined where and when no fish were observed during the calibration survey) were quite similar to the ones they used (Figure 5a,b,c). These conditions were employed to develop the habitat probabilistic model, and hence, to differentiate habitat characteristics used and avoided by fish. Fish expressed distinct preferences for the three physical variables under study. Fish preferentially used substrate composition characterised by D50 values of 3.0 to 4.5 cm (Figure 6a) and current speeds ranging from 0.60 to 0.75 m · s<sup>-1</sup> (Figure 6b). The preference curve for water depth was bimodal with higher preference indices at depths around 45-60 cm (Figure 6c).

Table 3.

- a) Comparison of simulated velocities and depths with field measurements.
- b) Range and dominant utilisation of abiotic factors where fish were encountered.

a)

Sample size = 271	Current velocity (m/s)		Water depth (m)	
	simulated	field	simulated	field
mean	0.389	0.487	0.491	0.488
variance	0.040	0.056	0.0493	0.0585
min	0.044	0.0085	0.038	0.13
max	0.93	1.21	1.16	1.23

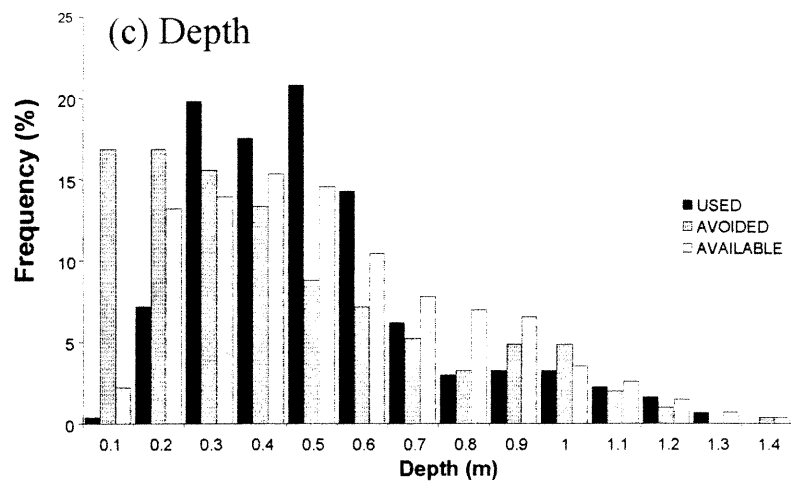
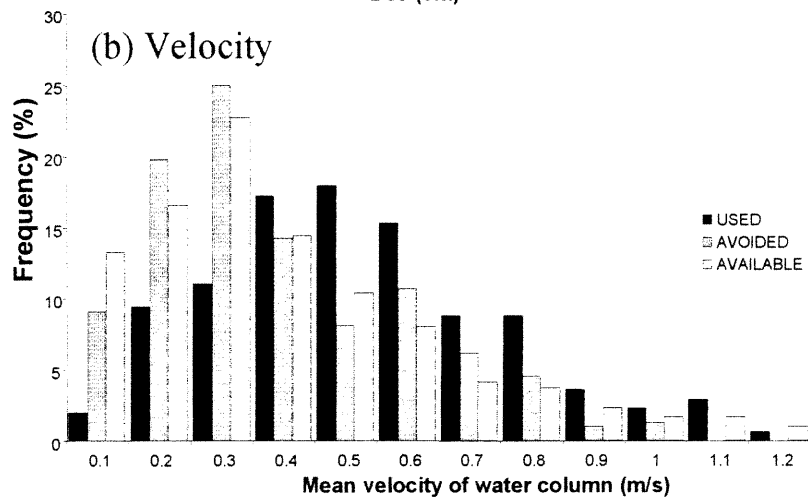
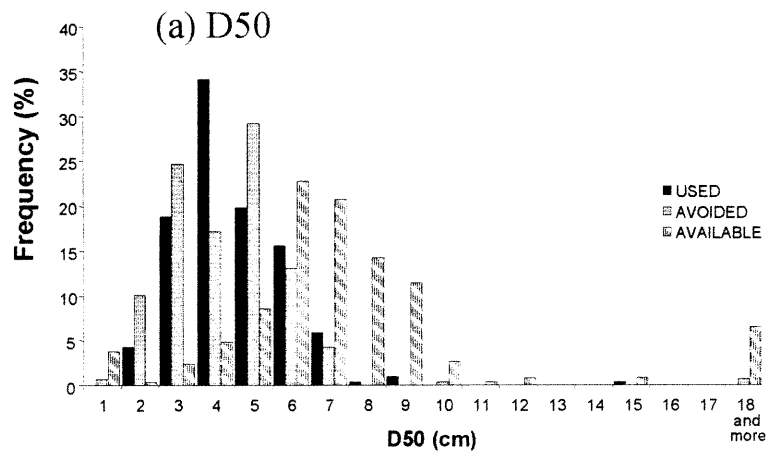
b)

Abiotic factors	Total range of utilisation	Dominant utilisation (%)	Dominant range
depth	0.12 m - 1.2 m	80%	0.24 - 0.72 m
velocity	0.05- 1.2 m · s <sup>-1</sup>	80%	0.15 - 0.75 m · s <sup>-1</sup>
D50	0.012 m - 0.09 m	80%	0.03 m - 0.06 m

Figure 5.

Frequency of D50, velocity and depth used, avoided and available for

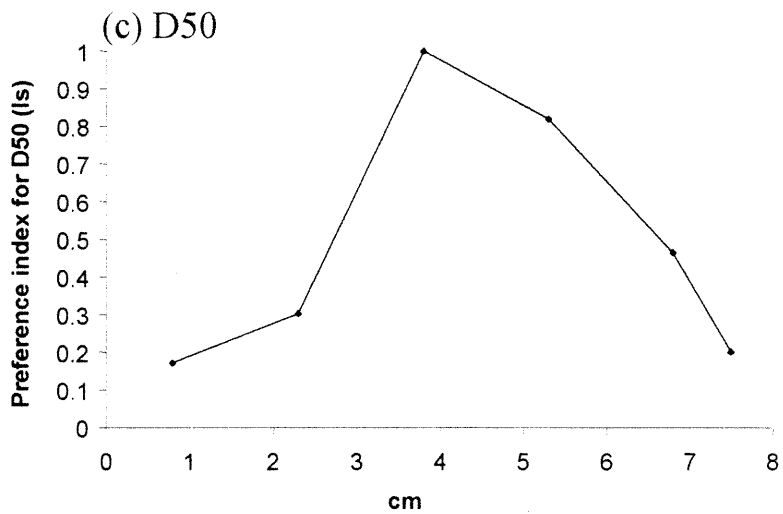
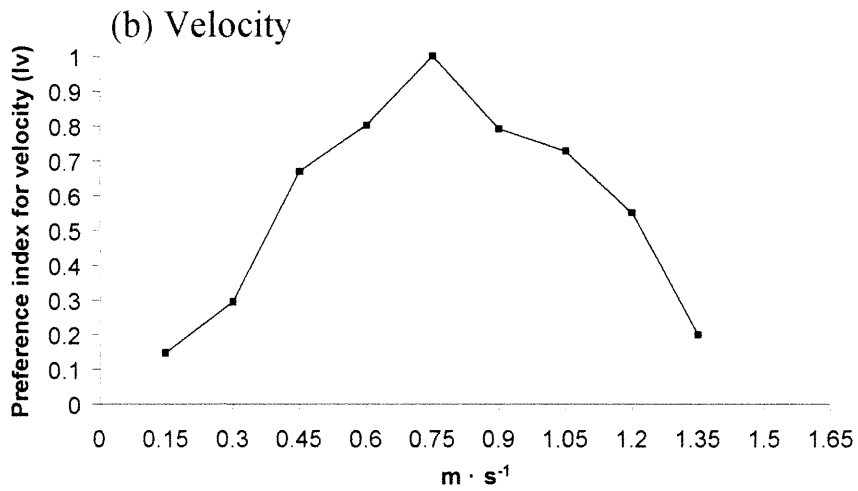
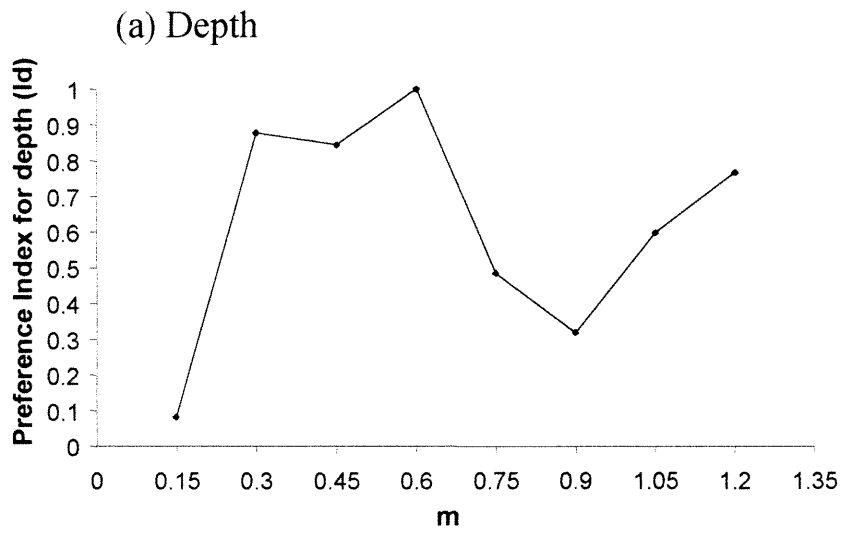
1+2+ parrs of Atlantic salmon.



**Figure 6.**

**Preference curves for a) depth, b) mean velocity and c) substrate size.**





The multiple regression equation (n=308; p<0.0001) that best represented variations of habitat suitability indices (HSI) was:

$$\text{HSI} = (I_D^{0.30}) \times (I_V^{0.38}) \times (I_S^{0.32})$$

The logistic model developed to predict habitat probabilistic indices was:

$$\text{HPI} = 1 / 1 + e^{-\lambda}$$

where  $\lambda = -3.067 + 8.461 D + 2.86 V + 0.093 S - 6.203 D^2$

#### **PREDICTIONS MADE BY THE NUMERICAL HABITAT MODEL**

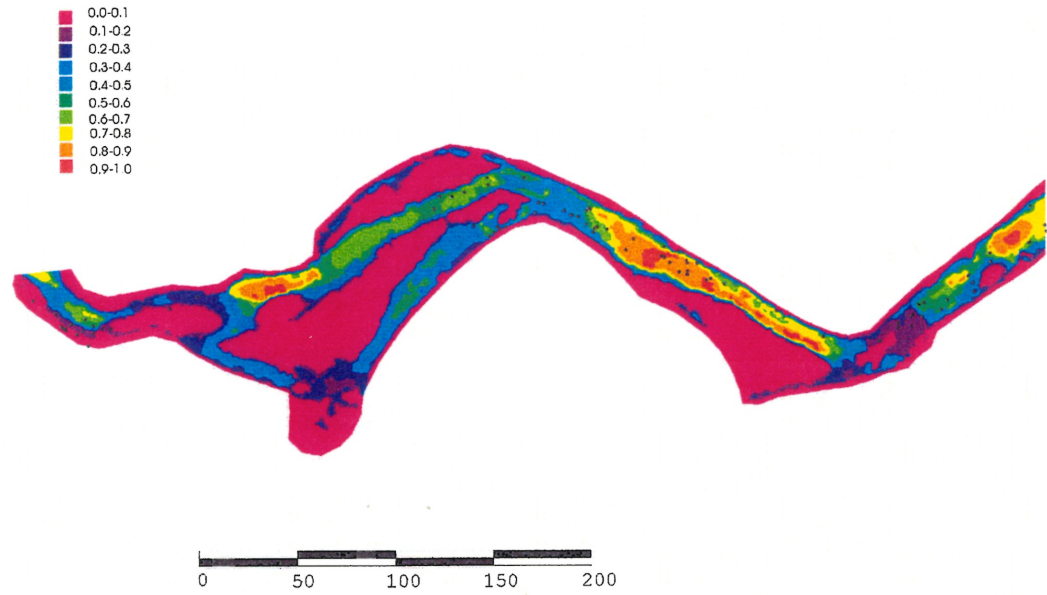
The numerical habitat model was used to predict the spatial distribution of habitat quality within the validation section at two flow rates (2.2 and 3.2 m<sup>3</sup> · s<sup>-1</sup>) using alternatively HSI or HPI as the biological model. These predictions represented expected spatial distributions of fish at these specific flow rates.

HSI values predicted by numerical modelling in the validation section ranged from 0 to 0.97 for the two flows (2.2 and 3.2 m<sup>3</sup> · s<sup>-1</sup>; Figure 7a,b). The results predicted highly heterogeneous fish distribution patterns including areas with very low (HSI values close to 0) and very high (HSI values close to 1) fish densities. Only 16.4 % (2750 m<sup>2</sup> at 2.2 m<sup>3</sup> · s<sup>-1</sup>) to 16.7 % (2820 m<sup>2</sup> at 3.2 m<sup>3</sup> · s<sup>-1</sup>) of the surface area of the validation section were assigned to HSI values

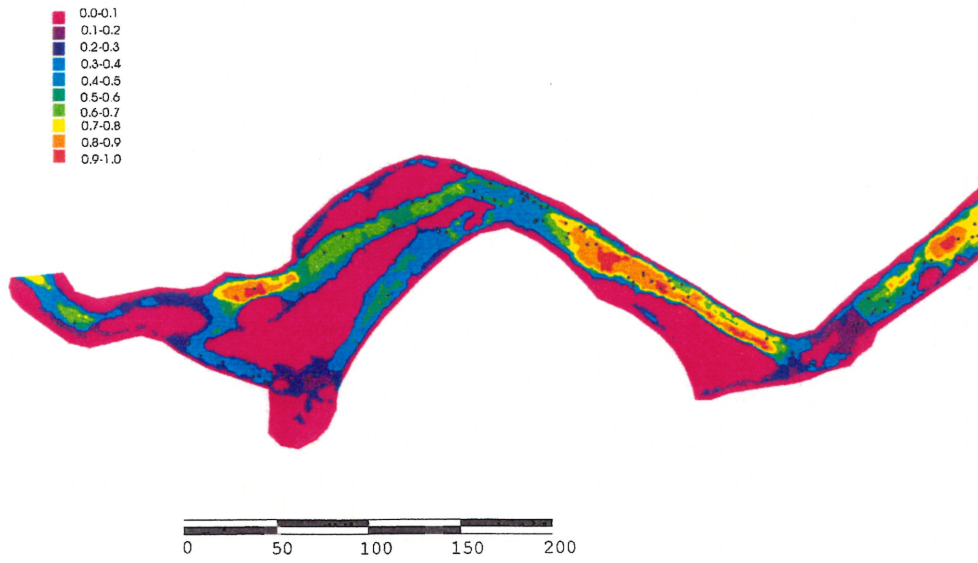
**Figure 7.**

**Maps of Habitat Suitability Index and fish  
distribution for 2.2 and 3.2 m<sup>3</sup> · s<sup>-1</sup>.**

(a) HSI  $2.2 \text{ m}^3 \cdot \text{s}^{-1}$



(b) HSI  $3.2 \text{ m}^3 \cdot \text{s}^{-1}$



higher than 0.7. The two flow rates modelled had a relatively small influence, absolute or relative, on the HSI values assigned to the validation section.

HPI values predicted by numerical modelling in the validation section at the two flow rates ranged from 0 to 0.86. Tiles assigned to HPI values higher than 0.7 represented 1513 m<sup>2</sup> or 9.0 % of the surface area of the validation section at 2.2 m<sup>3</sup> s<sup>-1</sup> (Figure 8a). Corresponding values were 1633 m<sup>2</sup> and 9.7 % at 3.2 m<sup>3</sup> · s<sup>-1</sup> (Figure 8b). HPI values assigned to the validation section were relatively stable within the range of flow covered by our study and simulations.

### **OBSERVATIONS OF FISH DISTRIBUTION**

The distribution of 1+ and 2+ parrs of Atlantic salmon in the validation section was heterogeneous. Survey-specific parr densities calculated for 17 randomly chosen and distinct sub-sections (625 m<sup>2</sup> to 995 m<sup>2</sup>; adding to 78 % of the surface area of the validation reach at a flow of 3.2 m<sup>3</sup> · s<sup>-1</sup>) ranged from 0 to 2.01 fish / 100 m<sup>2</sup> and had a mean of 0.76 fish / 100 m<sup>2</sup> (variance = 0.264). There was no relationship between the density of fish and the surface of the sub-sections ( $r^2 = 0.003$ ), indicating that densities were not scale dependant in our study.

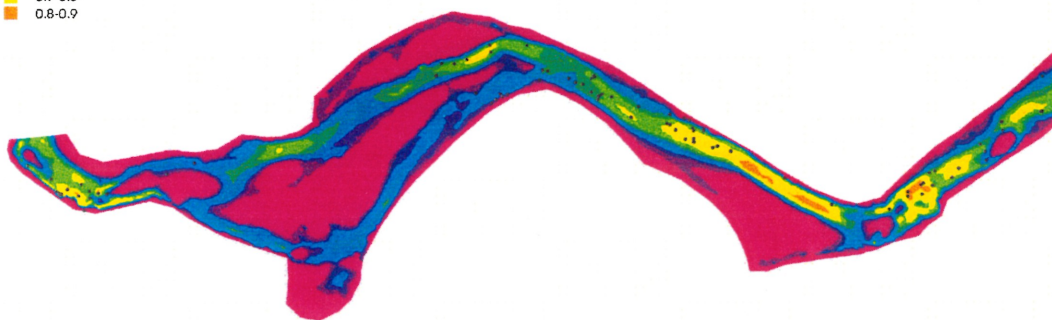
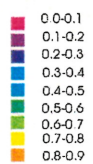
### **RELATIONSHIP BETWEEN OBSERVED FISH DENSITIES AND PREDICTIONS MADE BY THE NUMERICAL HABITAT MODELS**

Fish densities estimated over each of the ten areas of the validation section assigned to HSI values of 0 to 1 by increments of 0.1 (0 to 0.10, >0.10 to 0.20, >0.20 to 0.30, etc) ranged from 0.4 to 1.2 fish / 100 m<sup>2</sup> at 2.2 m<sup>3</sup> · s<sup>-1</sup>, and from 0.1 to 1.6 fish / 100 m<sup>2</sup> at 3.2 m<sup>3</sup> · s<sup>-1</sup>. The ten areas of the validation section associated to different HPI values were characterised by fish densities from 0 to 2.5 fish / 100 m<sup>2</sup> at 2.2 m<sup>3</sup> · s<sup>-1</sup>, and from 0 to 2.0 fish / 100 m<sup>2</sup> at 3.2 m<sup>3</sup> · s<sup>-1</sup>.

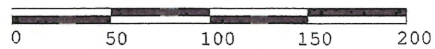
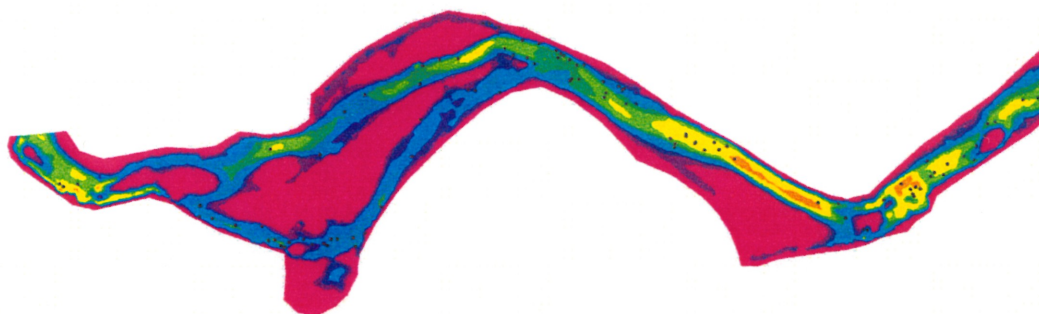
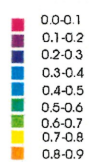
**Figure 8.**

**Maps of Habitat Probabilistic Index and fish  
distribution for  $2.2 \text{ m}^3 \cdot \text{s}^{-1}$  and  $3.2 \text{ m}^3 \cdot \text{s}^{-1}$ .**

(a) HPI  $2.2 \text{ m}^3 \cdot \text{s}^{-1}$



(b) HPI  $3.2 \text{ m}^3 \cdot \text{s}^{-1}$



There was a statistically significant and positive relationship between real fish densities and habitat quality indices predicted by the numerical model for both biological models. This suggested that local fish densities were higher in areas of the validation section for which the numerical model predicted higher habitat quality indices. However, predictions of the numerical model based on HSI for the two flows explained only 12.4 % of the variation of local fish densities ( $p < 0.0001$ ; Figure 9a) compared to 86 % using HPI for the two flows ( $p < 0.0001$ ; Figure 9b). Despite the fact that both variables contain error, ordinary least squares (OLS) are appropriate for these regression because the purpose is to obtain the best predictive model for fish densities (Legendre and Legendre 1998).

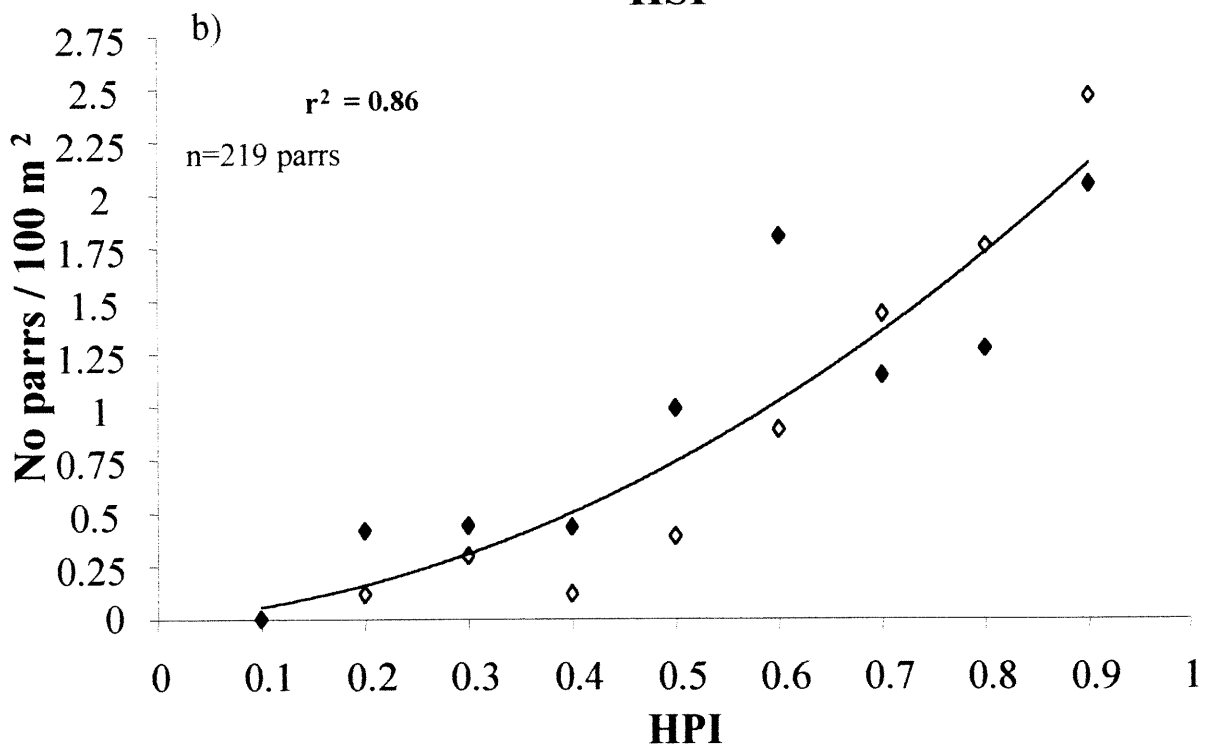
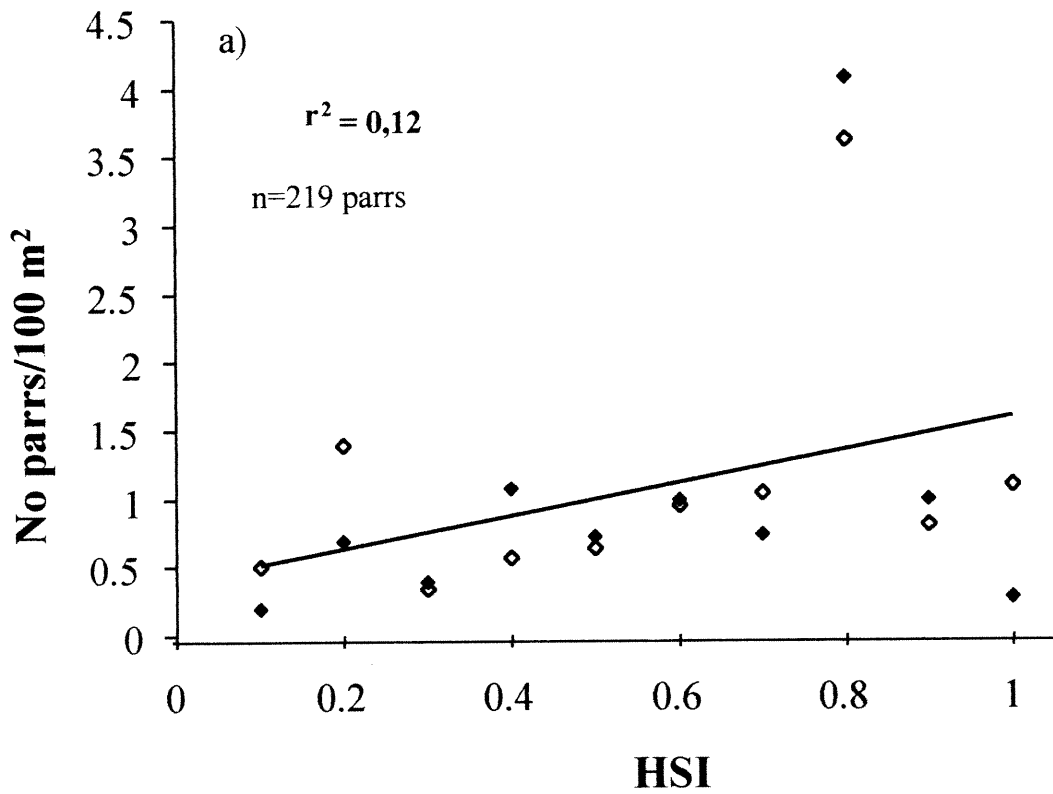


**Figure 9.**

**Distribution of parrs (expressed as densities) in relation with:**

**a) HSI for 2.2 (◊) and 3.2 (◆)  $\text{m}^3 \cdot \text{s}^{-1}$**

**b) HPI for 2.2 (◊) and 3.2 (◆)  $\text{m}^3 \cdot \text{s}^{-1}$**



## DISCUSSION

Our study indicates that numerical modelling strictly based on abiotic factors is appropriate to predict summer distribution patterns of Atlantic salmon parrs in rivers. However, our analyses also indicate that the type of biological model used is important in determining the quality of the predictions obtained from the habitat numerical model. In our study, fish distribution was better predicted by a biological model based on the Habitat Probabilistic Index (HPI;  $r^2 = 0.86$ ) than on a Habitat Suitability Index (HSI;  $r^2 = 0.12$ ).

The abiotic factors probably integrate other variables, since they have influence on other life stages and biotic factors. For instance, substrate granulometry is a key determinant of the quality of spawning sites for many fish species. Granulometry has also been suggested to affect cover from predators and from adverse physical conditions during summer or winter (Rimmer and Paim 1984, Cunjak 1988, Heggenes et al. 1991, Heggenes 1996, Whalen and Parrish 1999). Current speed has been hypothesised to modify the cost of habitat utilisation and the drift rate of invertebrate preys in the vicinity of fish (Morantz et al. 1987, Heggenes 1996). Finally, greater water depth could represent a protection against aerial predators and provide larger search volume for feeding (Wankowski and Thorpe 1979, Metcalfe et al. 1997).

Three hypotheses can be invoked to explain the different performances of the two biological models we used. The discrepancies between the two models are related to three points: the assumptions of the models, the mathematical form of the models and the sample size.

Two assumptions stand at the foundation of the HSI model, assumptions that are absent from the HPI model: the transformation of abiotic factors into indices does not reduce the quality of the data, and the abiotic factors are independent of one another. HSI is based on three independent preference curves that are transformed values of abiotic factors. These curves provide a quantification of the effects of the abiotic factors on fish preferences. There is no such

transformation in the construction of the HPI, avoiding the loss of information inherent to normalised or transformed data.

There are fundamental differences in the mathematical structure of the two models. The HSI model assumes the presence of an optimum for each of the factors taken separately. The preference curves of the HSI model are weighted in such a way that the value 1 is arbitrarily given to the highest frequency of a variable. On the contrary, the HPI model is based on a matrix of fish presence-absence. For each presence (308), the values of the abiotic factors of velocity, depth and D50 are noted. To obtain data on fish absence, an identical number of locations (308) were randomly chosen where no fish were present within a circle of 1.5 m in diameter. This procedure is a multivariate approach allowing us to study the segregation of the habitat by fish, comparatively to the HSI model which is based on habitat preference curves. The polynomial form of the HPI equation is more flexible than the commonly used geometric mean of HSI, allowing the equation to follow more accurately subtle changes in habitat features. It potentially permits to describe multiple optima resulting from the interaction of the factors. For example, velocity should have different values of optimum depending on depth. The use of a polynomial (multimodal) approach is clearly more appropriate to describe habitat features from the fish point of view, since they never encounter an abiotic factor alone. Finally, the HPI model produces a value which represents the probability of observing a fish, compared to HSI that is a weighted ratio of conditions used on conditions available. The consequences of such a construction is that the output of the HSI model is not a predicted value, i.e. a probability of presence or a predicted number of fish.

The sensitivity of the two models could potentially differ for the same sample size of fish. In the HPI model, the absence of a fish is an information related to fish preferences, compared to

the measure of availability in the HSI model, which does not provide this type of information. Actually, the sample size in our work should be considered to be 308 fish for HSI and 616 locations for HPI. This could explain in part the differences between the two models, since HSI would necessitate more fish presence data than HPI to reach the same power. The preference curves were determined using a moderate number of fish (308), but this number is comparable with those found in the literature. DeGraaf and Bain (1986) worked with 215 parrs in North Arm River and 123 in North Harbour River. Morantz et al. (1986) used 538 parrs collected over 3 years. Heggenes and Salveit (1990) established habitat preferences using 1454 parrs over 2 years and they included some values for young-of-the-year and other values taken during autumnal conditions. Finally, Cunjak (1988) described winter habitat utilisation using data on 148 fish.

Our preference curve for depth had its optimum (30-60cm; Figure 6a) within the range of the values found in the literature. For example DeGraaf and Bain (1986) find an optimum for depth between 15 and 55 cm while Morantz (1986) finds it between 30 and 55 cm.

Our results show some differences with the literature for the velocity and substrate optima. Our preference curve for mean velocity (Figure 6b) had an optimum around 60-70  $\text{cm} \cdot \text{s}^{-1}$ . This is much higher than in the literature: Heggenes and Saltveit (1990) found a preference optimum for parrs at much lower velocity (10-30  $\text{cm} \cdot \text{s}^{-1}$ ) while Morantz et al. (1986) obtained a mean velocity optimum between 20 and 50  $\text{cm} \cdot \text{s}^{-1}$ . Looking now at parr utilisation of mean water velocity, the use of velocity by our fish (Figure 5b) had an optimum between 35 and 65  $\text{cm} \cdot \text{s}^{-1}$ . These results are about the same as reported by Heggenes and Saltveit (1990) who found the optimum for parr velocity utilisation to be between 20 and 60  $\text{cm} \cdot \text{s}^{-1}$ . The discrepancy between our results and those of Heggenes and Saltveit (1990) about velocity preference can be explained by differences in the velocities available in the rivers. Heggenes and Saltveit found that 21 % of the velocities were higher than 0.6  $\text{m} \cdot \text{s}^{-1}$  and 23 % were lower than 0.2  $\text{m} \cdot \text{s}^{-1}$ . In the present

study, we found 14 % of velocities higher than  $0.6 \text{ m} \cdot \text{s}^{-1}$  and 30 % lower than  $0.2 \text{ m} \cdot \text{s}^{-1}$ . These results support the idea that differences between rivers could lead to very different interpretations of preferences. For about the same utilisation of mean velocities, the optimum preference for velocity was substantially higher in the Sainte-Marguerite River. Finally, an error on preference may have been introduced by the fact that we had few values of availability for the high velocities. Velocity classes with few values could lead to an overestimation of the relative importance of these classes because the velocity used is divided by a small number of observations.

The preference curve for substrate cannot really be compared to data from the literature since we used an uncommon approach (D50). However, our preference optimum values for D50 (35-55 mm; Figure 6c) is within the range of classes of the modified Wentworth scale (Bovee 1982) of substrate commonly used by parrs in river habitat studies. This class is considered to be a substrate preference optimum for parrs by some authors (deGraaf and Bain 1986, Morantz et al. 1986). The parr preference optimum for substrate in Heggenes and Saltveit (1990) was large cobble (256-384 mm). Discrepancies between their results and ours could partly be explained by the different availability of substrate types in the two studies. In mean, Heggenes and Saltveit had substrate higher than 128 mm diameter in 67 % of their study sites comparatively to 9% in our study. Differences in granulometry may lead to changes in preference curves and then also in HSI.

HSI may be well related to the river where it has been computed but it cannot be transferred to other rivers where the availability and use of abiotic factors are different. Transferring preference curves and HSI from a river to another would depend on the assumption that there is no important difference between the rivers. Since the logical structure of HPI is based on fish presence-absence data rather than on a river description (availability of factors), the

HPI model is less river-dependant than HSI and differences in river characteristics should have less impact on HPI than on HSI. Further investigations are needed to verify this deduction.

Some studies tried to validate the relationship between weighted usable area given by the PHABSIM method (Milhous et al. 1989) and fish density; some studies found a positive relationship while others have not (Bourgeois et al. 1996). Particular attention should be paid to the meaning of our models. They are not density-prediction models but fish-distribution models. We used density as an indicator of parr distribution; the values of density found should not be interpreted as predictions of the models. The summer density of salmon parrs in a river is more influenced by biotic factors such as inter-specific competition, predation and food supply than by parr distribution. The density of parrs is also related to the number and survival rate of eggs and fry and it varies a lot from year to year in most rivers.

In view of the fact that most of the rivers are now used and altered by man, habitat modelling based on multiple Gaussian logistic regression is an important and efficient tool to predict the potential impact of anthropic flow variation on fish habitat.

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## CONCLUSION

Cette étude suggère que la modélisation numérique d'habitat permet de prédire les patrons de distribution des juvéniles de saumon atlantique en rivière de façon satisfaisante. Cependant, la qualité des prédictions dépend du modèle biologique choisi. Dans cette étude, la distribution spatiale a été prédite plus correctement en utilisant l'indice HPI ( $r^2 = 0,86$ ) comparativement à l'indice HSI ( $r^2 = 0,124$ ). L'utilisation de l'approche logistique gaussienne (HPI) dans la modélisation d'habitat semble ainsi mieux refléter les préférences d'habitat que la méthode des courbes de préférence (HSI).

Bien qu'il m'ait été possible de valider le modèle numérique d'habitat pour des faibles débits ( $2-3 \text{ m}^3 \text{ s}^{-1}$ ), je n'ai pas recueilli de données à débit plus élevé afin de vérifier si le débit avait un impact sur les modèles d'habitat HSI et HPI. Ainsi, les prédictions possibles du modèle pour des débits éloignés de ceux ayant présidé à sa construction, i.e.  $2 \text{ à } 3 \text{ m}^3 \cdot \text{s}^{-1}$ , n'ont toujours pas été vérifiées.

Il est nécessaire de demeurer vigilant dans l'interprétation des résultats pouvant être obtenus par le modèle numérique d'habitat. Malgré une quantité appréciable d'habitats possédant un indice HPI élevé ( $\text{HPI} > 0,7$  ;  $1513 \text{ m}^2$ ), la densité de poissons, de l'ordre de  $0,02 \text{ m}^{-2}$  dans ces sections, demeure faible si on considère la densité maximale prédite par la théorie de la taille du territoire (Grant and Kramer, 1990) qui prévoit jusqu'à 1 tacon par  $\text{m}^2$  pour des tacons de 10 cm. Des densités de 30 tacons par  $100 \text{ m}^2$  ont par ailleurs été observées dans des tributaires de la rivière Sainte-Marguerite (Burton F., communication personnelle). À ce jour, aucune étude, à ma connaissance, n'a pu établir de lien entre la productivité d'une rivière et un modèle d'habitat. L'utilisation d'un modèle doit donc être confinée à l'étude de la répartition spatiale; les valeurs de

densité qui lui sont associées ne doivent pas être utilisées dans des calculs de productivité piscicole.

Dans l'immédiat, il me semble important de vérifier si le modèle d'habitat demeure valide pour différentes valeurs de débit ou de densité. Une hypothèse que j'émetts ici est que les facteurs abiotiques utilisés dans cette étude sont les principaux déterminants de la répartition spatiale estivale tandis que les différences de densité de tacons inter-sites et inter-rivières relèvent de plusieurs autres facteurs biotiques et abiotiques tels que le nombre de sites de fraie, le régime thermique, les conditions hivernales, la prédation et la compétition interspécifique. Ainsi, les modèles d'habitat actuels demeureraient applicables essentiellement à leur rivière d'origine.

Plusieurs autres questions sont intimement liées à la modélisation d'habitat. Est-ce qu'un modèle d'habitat peut être transféré à une autre rivière ? Est-ce que d'autres variables telles que la turbulence, l'hétérogénéité du substrat ou encore la température ne devraient pas être intégrées au modèle d'habitat? Est-il possible de transformer les indices d'habitat en indices de croissance potentielle?

Malgré ces interrogations, la modélisation numérique demeure un outil utile pour les gestionnaires qui tentent d'établir des liens entre le débit et l'habitat. Cependant, l'utilisation des résultats de la modélisation pour l'étude de la dynamique des populations de saumons ne devrait être envisagée que dans le cadre d'une compréhension globale de l'ensemble des facteurs influençant le cycle de vie de l'espèce.

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