Development and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*)[1]

J.C. Guay, D. Boisclair, D. Rioux, M. Leclerc, M. Lapointe, and P. Legendre

Abstract: We evaluated the ability of numerical habitat models (NHM) to predict the distribution of juveniles of Atlantic salmon (*Salmo salar*) in a river. NHMs comprise a hydrodynamic model (to predict water depth and current speed for any given flow) and a biological model (to predict habitat quality for fish using water depth, current speed, and substrate composition). We implemented NHMs with a biological model based on (*i*) preference curves defined by the ratio of the use to the availability of physical conditions and (*ii*) a multivariate logistic regression that distinguished between the physical conditions used and avoided by fish. Preference curves provided a habitat suitability index (HSI) ranging from 0 to 1, and the logistic regression produced a habitat probabilistic index (HPI) representing the probability of observing a parr under given physical conditions. Pearson's correlation coefficients between HSI and local densities of parr ranged from 0.39 to 0.63 depending on flow. Corresponding values for HPI ranged from 0.81 to 0.98. We concluded that HPI may be a more powerful biological model than HSI for predicting local variations in fish density, forecasting fish distribution patterns, and performing summer habitat modelling for Atlantic salmon juveniles.

Résumé : Nous avons évalué la capacité de deux modèles numériques d'habitat (MNH) à prédire la distribution spatiale des juvéniles de saumon atlantique (*Salmo salar*) en rivière. Les MNH comprennent un modèle hydrodynamique (pour prédire la vitesse moyenne et la profondeur de la colonne d'eau) et un modèle biologique (pour prédire la qualité d'habitat piscicole selon la profondeur, la vitesse moyenne et la composition du substrat). Nous avons utilisé les MNH avec un modèle biologique basé sur (*i*) des courbes de préférences définies par le rapport entre l'utilisation et la disponibilité de conditions physiques et (*ii*) une régression logistique multiple permettant de différencier les conditions physiques utilisées de celles évitées par les tacons. Les courbes de préférences ont fourni un indice de qualité d'habitat (IQH) variant entre 0 et 1 et la régression logistique a donné un indice probabiliste de qualité d'habitat (IPH) représentant la probabilité d'observer des tacons sous des conditions physiques spécifiques. Les coefficients de corrélation de Pearson entre IQH et les densités locales de tacons ont varié entre 0,39 et 0,63 selon le débit. Les valeurs correspondantes en utilisant IPH ont varié entre 0,81 et 0,98. Nous avons conclu que l'IPH peut être un modèle biologique plus performant que l'IQH pour prédire les variations locales de la densité des poissons, pour prédire les patrons de distribution des poissons et pour modéliser l'habitat estival des juvéniles du saumon atlantique.

Introduction

Natural and anthropogenic modifications of flow 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 (deGraaf and Bain 1986; Morantz et al. 1987; Greenberg et al. 1996; Payne and Lapointe 1997). Hydraulic models have been developed to predict changes in local current speed and water depth for specified modifications of flow rates (Bovee 1978, 1982; Leclerc et al. 1996). The propensity of fish to favour specific ranges of physical variables and the ability of hydraulic 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 (NHM), generally involves the partitioning of a river in a mosaic of tiles with similar sizes (referred to as cells by Bovee 1982; Bovee et al. 1998) or with variable surface areas (Leclerc et al. 1990; Boudreau et al. 1996). Each tile is characterised by its substrate composition and topography. These variables are used as inputs to a hydraulic 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 the predilection of fish for the substrate diameter, the water depth, and the current speed in that tile (Bovee 1978; Mathur et al. 1983; Leclerc et al. 1994). The end result of NHM is a map describing the habitat quality index assigned to each tile at a

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given flow rate. Any change in flow rate not only modifies the number of tiles 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). Changes in the number of tiles and their habitat quality index are expected to allow the assessment of the impact of flow rate modifications on fish habitat quantity and quality in a river.

The habitat suitability index (HSI) is the most commonly used index of habitat quality (Bovee 1982; deGraaf and Bain 1986; Morantz et al. 1987). This index is based on preference curves that represent the degree of preference displayed by fish over the complete range of current speed, water depth, and substrate diameter found in a river or reach. Preference for a specific range of current speed, water depth, or substrate diameter can be calculated as the ratio of percent utilisation (percentage of fish observed that used this range of variable) to percent availability (percentage of the surface area of the river characterised by this range of variable) of these environmental conditions. Preference indices range from 0 (poor habitat) to 1 (best habitat). Integration of the surface area of all tiles weighted by their HSI provides the weighted usable area (WUA) (expressed as a percentage of the total surface area or as square metres of habitat per 1000 m of river) for a river or reach at a given flow (Bovee 1982). Most attempts to validate NHM have been conducted using comparisons between WUA and fish density or standing crop. While some studies confirmed the existence of a relationship between WUA and fish density (Orth and Maughan 1982; Bovee et al. 1998), others found no such relationship (Scott and Shirvell 1987; Bourgeois et al. 1996). This situation may be related to the lack of understanding of the ecological significance of WUA. For instance, a 400-m^2 reach having an HSI value of 0.3 would have a WUA of 30% (400 × 0.3/400). The same reach having 50% of its area assigned an HSI of 0.5 and 0.1, or having 25% of its area assigned an HSI of 0.9 and 75% of its area assigned an HSI of 0.1, would also have a WUA of 30%. However, there are no indications that these habitats are indeed identical for fish (see Scott and Shrivell 1987). Boudreau et al. (1996) avoided the weighting procedure by testing for the existence of a relationship between the HSI of patches assigned a different HSI value and fish density within these patches. Their study supported the existence of a strong positive relationship between HSI and real fish density ($r^2 = 0.8$ from calculations that we performed using fig. 7 from Boudreau et al. 1996). This suggests that the spatial distribution of habitat quality predicted by NHM in a large river (Moisie River; average summer flow 130–160 $m^3 \cdot s^{-1}$, maximum depth of 6 m at these flows, up to 300 m across) corresponds closely to that of fish. However, the HSI model used by Boudreau et al. (1996) was modified according to unspecified a posteriori considerations related to differences of flow between the time the HSI model was developed and the time the HSI model was used to predict fish distribution. It is therefore presently difficult to evaluate the merits of HSI models unaffected by this problem. Furthermore, although their study indicates that HSI models have the potential to predict fish distribution, it does not allow the establishment of the value of this approach in smaller rivers.

The objectives of our work were (*i*) to test the hypothesis of the existence of a significant relationship between the distribution of habitat quality predicted by NHM and the distribution of fish observed in a small river and (*ii*) to compare the predictions by NHM using a biological model based on preference curves with predictions by NHM implemented with a biological model consisting of a multivariate logistic regression designed to distinguish between the physical conditions used and avoided by fish.

Material and 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 (Fig. 1). The species selected for study was the Atlantic salmon (*Salmo salar*). Our work focussed on 1+ and 2+ parr. In the Sainte-Marguerite River, salmon coexists with five other species of fish: brook trout (*Salvelinus fontinalis*), American eel (*Anguilla rostrata*), longnose dace (*Rhinichthys cataractae*), longnose sucker (*Catostomus catostomus*), and sea lamprey (*Petromyzon marinus*).

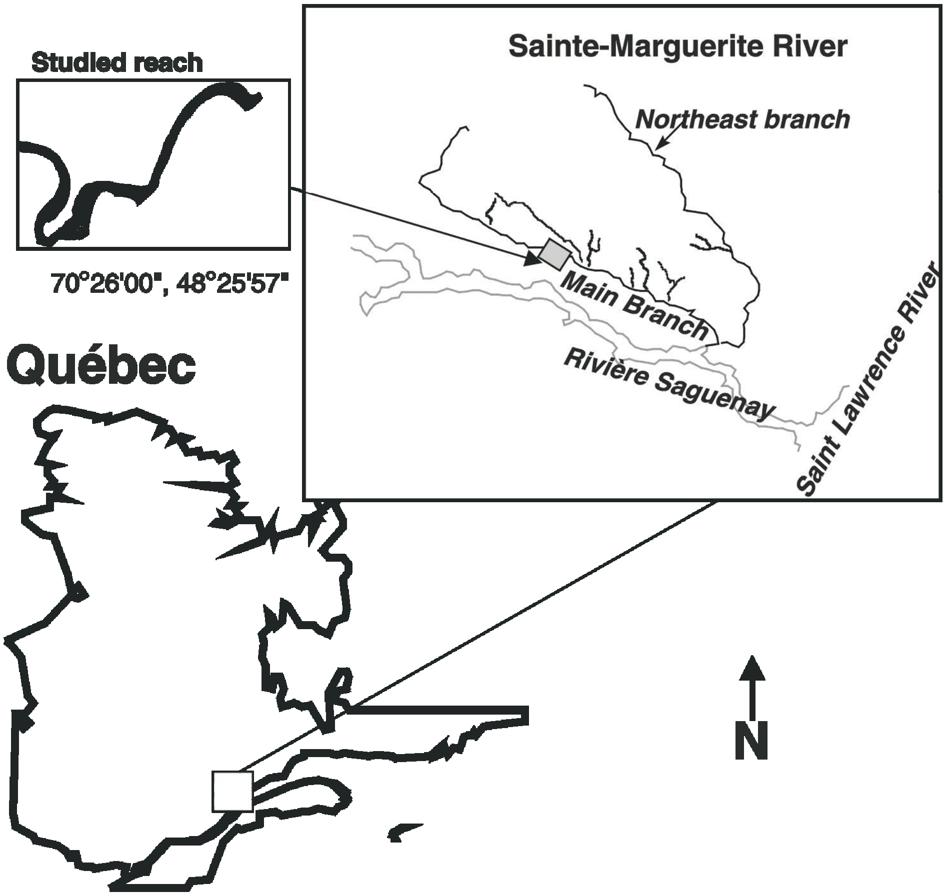
The reach studied was divided into upper, median, and lower sections characterised by similar physical conditions. These sections were 375, 750, and 375 m long, respectively. The three sections had a width ranging from 20 to 45 m at bankfull conditions and consisted of a series of shallow pools (maximum depth of 2.3 m) and small riffles. The mean slope of the three sections ranged from 0.07 to 0.7% and averaged 0.3% over the complete reach. Substrate of the riverbed in the three sections ranged from sand to boulder. The sections contained no area covered by wood debris or by patches of periphyton larger than 0.25 m^2. Canopy was absent in the three sections. The upper and lower sections, further referred to as the calibration sections, were used to assess the physical characteristics selected or avoided by parr. 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 habitat model (NHM)

The NHM adopted to predict the spatial heterogeneity of habitat quality comprised two parts: a hydraulic model and a biological model. The hydraulic model that we used, further referred as the hydrodynamic model, is a two-dimensional model that allowed us to predict current speed and water depth over the reach, i.e., on a longitudinal axis (upstream–downstream) and a transversal axis (left bank – right bank) of the river (Leclerc et al. 1990, 1994, 1995). This model requires as inputs the 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 and friction) and assumptions on fluid dynamics (conservation of water, flowing mass, and momentum), are used as inputs 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 that 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^2 locations used and not used by fish allowed us to quantify the variations in the propensity

Fig. 1. Map of the study site located on the northern shore of the Saint Lawrence River, Québec, Canada. The site is 450 km northeast of Montréal.



of fish to prefer specific conditions over the range of physical characteristics found in the reach. The biological model assumes that when fish more intensively use a specific range of substrate diameter, current speed, or water depth, this range represents a habitat of higher quality for fish. The habitat quality index assigned to a location represents a compromise between propensity of fish to prefer or avoid 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 inputs 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^2 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 prediction of current speed and water depth anywhere in the calibration and validation sections of the reach at any flow rate.

Biological models

Biological models are required to determine the physical conditions used or avoided by Atlantic salmon parr. Environmental conditions used by fish were defined by visually scanning the entire calibration section by snorkeling during two periods (July 16–24 and August 1–10). Under good weather and flow conditions, the diver could cover 50–100 m of the calibration reach per day (hereafter referred to as subsections). The diver swam upstream to minimise fish disturbance (Cunjak et al. 1988). Age 1+ (5–8 cm total length) and 2+ parr (7–10 cm total length) could not be differentiated because of their overlap in size range. Hence, the biological model that we developed described habitat use by 1+ and 2+ parr indistinguishably. Each fish encountered was observed for 2 min and georeferenced. Fish generally performed short but frequent movements upstream, presumably to capture drifting invertebrates. Between these movements, parr 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 20 coloured stones had

Table 1. Median size for substrate type used by the hydraulic model.

Substrate type	Median substrate size (cm)
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

been positioned or after 30 min of snorkeling. For each home rock, substrate composition, current speed, and water depth were noted. This information provided indications on the physical conditions used by parr. 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 (centimetres) of the *B*-axis of the median stone within a 1-m^2 area centred on the home rock. Averaged current speed (metres per second) over a 30-s 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^2 centred on the home rock (e.g., at 40 cm from the bottom when depth was 1 m). The water depth (metres) assigned to a home rock was taken to be the mean depth found within an area of 1 m^2 centred on that rock. D50 can be estimated visually to 5-mm accuracy after proper training and calibration (C. Latulipe and M. Lapointe, unpublished data) against stone count samples (Wolman 1954). Flow rate (cubic metres per second) 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 two-dimensional hydrodynamic model and the flow rate observed each day to produce maps of water depth and current speed within the 50- to 100-m subsection of the calibration section covered that day. For a given day in a subsection, we used the complete series of nodes of the subsection grid (Fig. 2) to assess abiotic conditions available to fish that day. In addition, for a given number of fish observed during 1 day in a subsection, we selected the same number of locations at random where no fish were observed (at least 2 m from the closest Atlantic salmon parr mapped). For each of these locations, substrate composition, current speed, and water depth were estimated from the maps of the subsection provided by the two-dimensional hydrodynamic model for that day and flow rate. This procedure allowed us to characterise the environmental conditions available to Atlantic salmon parr (node values of abiotic conditions of each subsection) and those avoided by fish (abiotic conditions where no fish were observed).

Fish distribution in the validation section

The distribution of Atlantic salmon parr 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 because of time limitations (i.e., the number of days per summer when sampling can be done under similar flows and good weather). 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. Snorkeling was used to visually scan the complete length of the validation section during two periods (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 biological models: a habitat suitability model and a habitat probabilistic model.

Habitat suitability model

The habitat suitability model is based on preference curves that represent the propensity of fish to prefer specific ranges of environmental characteristics expected to determine fish habitat quality (Bovee 1982; Morantz et al. 1987; Heggenes and Saltveit 1990). We constructed a preference curve of parr for substrate composition (D50), current speed, and water depth.

The relative contributions of six classes of substrate diameter to the different patches of the calibration section were transformed to D50 values. Knowing the percentage of each class of substrate diameter, we determine D50 as the substrate diameter value corresponding to the 50th percentile 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 intervals 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

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

where $\%U_{c,i}$ is the percent utilisation by fish of a specific interval *i* of an environmental condition *c* (substrate composition, current depth, or water depth) and $\%A_{c,i}$ 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 $I_{c,i}$ value was 1 (Leclerc et al. 1994). The ranged indices of preference (I_c) were used to develop an HSI following the approach proposed by Leclerc et al. (1995). First, we estimated an unweighted HSI ($\mathrm{HSI_U}$ ranging from 0 to 1 inclusively) for each fish observed within the calibration section as follows:

$$(2) \qquad \mathrm{HSI_U} = I_\mathrm{D} \times I_\mathrm{V} \times I_\mathrm{S}$$

where I_D, I_V, and I_S are the ranged index of preference for depth, current speed, and substrate composition interval, respectively. Second, a multiple regression analysis was used to explain variations in $\mathrm{HSI_U}$ using I_D, I_V, and I_S as independent variables. During this procedure, all variables were subjected to a logarithmic transformation. This allowed us to obtain partial regression coefficients for I_D (noted *X*), I_V (noted *Y*), and I_S (noted *Z*). Third, we ranged the partial regression coefficients of depth, velocity, and substrate such that $X + Y + Z = 1$ (Leclerc et al. 1995). This procedure produced a weighted HSI that could be calculated for any tile of the validation section as

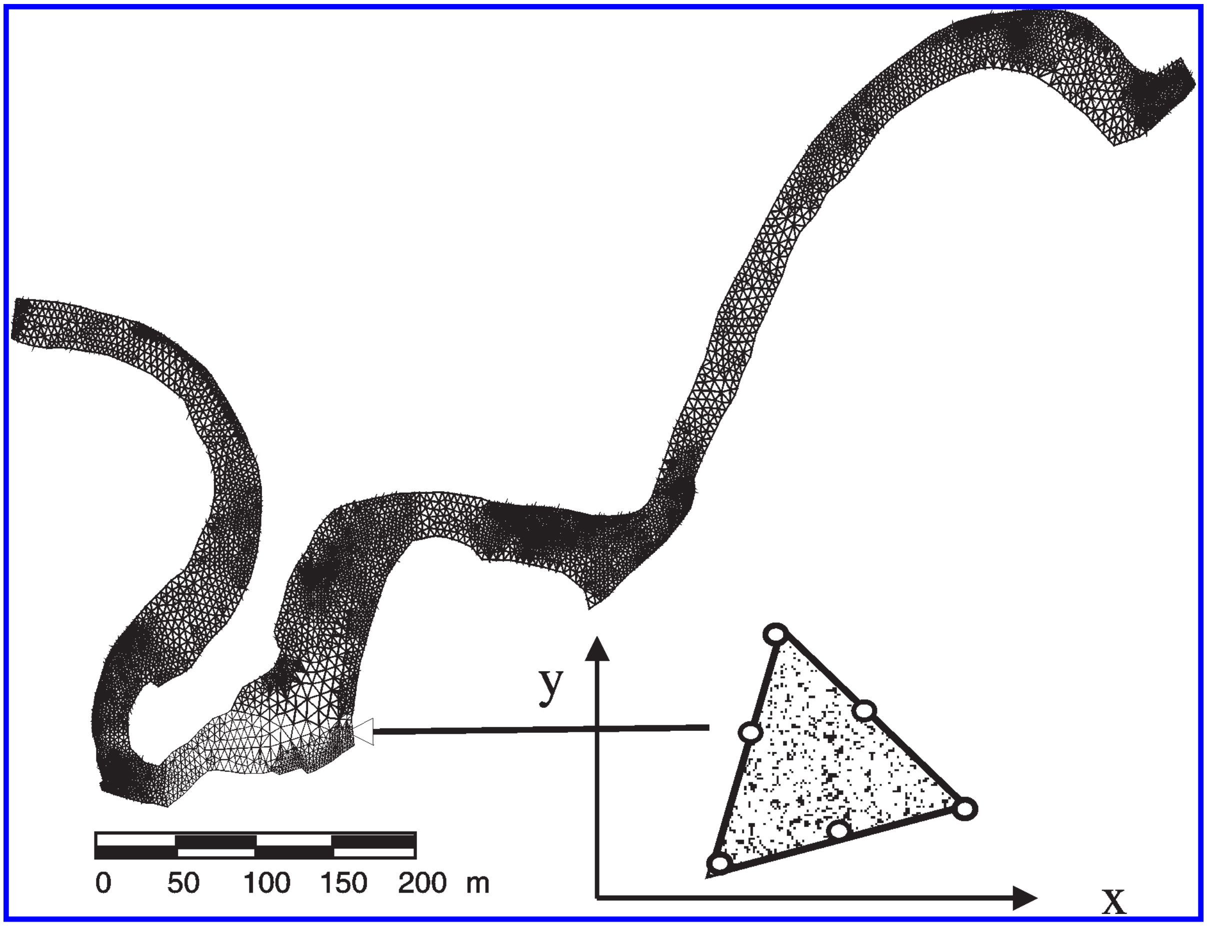
$$(3) \qquad \mathrm{HSI} = I_\mathrm{D}^X \times I_\mathrm{V}^Y \times I_\mathrm{S}^Z.$$

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

Habitat probabilistic model

The habitat probabilistic model was developed by constructing a matrix containing information on the physical conditions noted where and when a parr was observed in the calibration section of

Fig. 2. Example of triangular elements grid used to perform the numerical modelling of the Sainte-Marguerite River. Velocity and depth are represented by circles and substrate type by shading.



the reach and on the physical conditions estimated where and when no fish were observed. The matrix had four 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 that 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 combinations of physical conditions. This was achieved by fitting a multivariate Gaussian logistic regression model to our presence–absence data. To our knowledge, our work represents the first attempt to use and validate the ability of a biological model based on a logistic regression to predict fish distribution patterns. Using this model, the habitat probabilistic index (HPI) of observing a fish under given physical conditions can be represented as

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

where

$$\lambda = P_0 + P_1S + P_2V + P_3D + P_4S^2 + P_5V^2 + P_6D^2 + \ldots$$

where P_n are parameters fitted by the multivariate Gaussian logistic regression and S, V, and D are substrate composition (D50), current speed, and water depth, respectively. The model was developed using a stepwise backward regression. During this procedure, we assessed the statistical significance of environmental factors raised to a power of up to 4 and all possible interaction terms (velocity × depth, velocity × D50, velocity^2 × depth, velocity × depth^2, etc.). The logistic model was intended to predict the probability (0–1) of finding fish in any tile using local substrate composition, current speed, and water depth as independent variables.

Data analysis

Physical conditions used or avoided by Atlantic salmon parr in the calibration section were defined under flow rates ranging from 1.9 to 5.5 $m^3 \cdot s^{-1}$ (average 3.7 $m^3 \cdot s^{-1}$). Real fish distribution in the validation section was described during surveys performed within two relatively narrow ranges of flow: 1.9–2.6 and 2.9–4.2 $m^3 \cdot s^{-1}$. 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 $m^3 \cdot s^{-1}$. These flows were selected because they corresponded 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 $m^3 \cdot s^{-1}$) and the daily variations in flow observed (0–8%, average 2.5%) in the reach under study were expected to have negligible influence on the riverbed, since formative bankfull discharge in the Sainte-Marguerite River is approximately 80 $m^3 \cdot s^{-1}$ (M. Lapointe, unpublished data).

The maps of physical conditions were used as inputs to the biological models (eqs. 3 and 4) to estimate HSI and HPI in all tiles of the validation section at 2.2 and 3.2 $m^3 \cdot s^{-1}$. HSI and HPI were grouped into 10 classes of habitat quality index (0–1 in increments of 0.1). This led to the production of four maps (two biological models and two flows) of the validation section. Maps were drawn using 10 colour shades, each representing one of the 10 classes of habitat quality index. Each map was taken as a prediction of expected habitat quality distribution and potential fish distribution in the validation section. We assessed the validity of these predictions by comparing HSI or HPI values with real fish densities in the validation section. This was performed using five steps. First, we overlaid the map of expected habitat quality according to one of our biological models under a specific flow and the map of observed fish distribution at that flow. Second, we calculated the total surface area of the validation section associated with each of the 10 classes of habitat quality index. Third, we counted the total number of fish observed in the areas associated with each of the 10 classes of habitat quality index. Fourth, we calculated average fish density in each of these areas (number of fish per 100 m^2, total number of fish observed within areas assigned a specific habitat quality index divided by the total surface area of the section associated with that class of habitat quality index). Fifth, we tested the existence of a significant relationship between habitat quality index and real fish density in the areas assigned different habitat quality indices using polynomial regression analysis. Although habitat quality indices and fish densities contain errors, ordinary least squares methods are appropriate for these regressions because our purpose was to obtain the best predictive model for fish densities (Legendre and Legendre 1998). This procedure was repeated for both biological models and both flows.

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^2 (Fig. 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. The surface area of the patches ranged from 25 to 1800 m^2. Patch composition ranged from being dominated by sand (50–100% in 26 of the patches covering 11% of the reach surface) to boulders (50–100% in 10 patches covering 1% of the reach surface). Gravel represented 50–100% of the surface area of 16 patches covering a total of 24% of the reach surface. Cobble dominated in 34 patches (covering 26% of the reach surface), while pebble were the principal substrate in 59 patches (50–100%) covering 38% of the reach surface (Table 2).

Table 2. Characterisation of the substrate type dominance (50% or more) of the Sainte-Marguerite River riverbed.

Dominant substrate type	Number of patches	% of surface area of the reach
Boulder	10	3.5
Cobble and pebble	93	83.0
Gravel	16	6.5
Sand	26	7.0

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 fewer than four levels of flow rate ranging from 2 to 5.6 $m^3 \cdot s^{-1}$. Although these locations were randomly selected, each one was precisely georeferenced. The hydrodynamic model was run to obtain predicted values of water depth and current speed at the 271 locations for the flow rates prevailing during field measurements. There was a strong relationship between individual depth values predicted by the hydrodynamic model and individual field measurements of depth (r^2 = 0.85). Individual water depths predicted by the hydrodynamic model were within 15% of those measured in the field. The mean, variance, and range of predicted water depths were within 2% of those calculated from field data (Table 3). Individual values of current speed predicted by the hydrodynamic model were poorly correlated with measured values (r^2 = 0.09). The hydrodynamic model tended to overestimate low velocities (<0.2 $m \cdot s^{-1}$) and to underestimate high velocities (>0.7 $m \cdot s^{-1}$). The hydrodynamic model nevertheless permitted a good representation of the mean, variance, and range of current speed values observed in the field (Table 3). The poor fit between individual values of predicted and observed current speed may not have a strong impact on our predictions of fish habitat quality because low and high velocities were associated with areas rarely used by parr (near the bank and the thalweg area). More importantly, preference curves and multivariate logistic regressions require that hydrodynamic models adequately predict the average and variance of physical conditions over an area. Biological models do not require that hydrodynamic models predict physical conditions at a specific point of a reach. Hence, the precision of the hydrodynamic model that we used was judged sufficient for our purposes.

Biological models

Physical attributes used by the fish were defined by measuring substrate composition, current speed, and water depth at 308 locations where parr were observed. Eighty-five percent 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 $m \cdot s^{-1}$ and at depths ranging from 0.12 to 1.2 m (Table 4; Fig. 3). Substrate available under flows observed during sampling in the calibration section had D50 values ranging from 0.002 to 1.5 m (Fig. 3*a*). Maximum current speed predicted by the hydrodynamic model at flows prevailing during calibration ranged from 1.1 to 1.2 $m \cdot s^{-1}$ (Fig. 3*b*). Corresponding values for maximum water depth were 2.37–2.40 m (Fig. 3*c*). 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 those used (Fig. 3). These conditions were employed to develop the habitat probabilistic model and hence to differentiate between habitat characteristics used and avoided by fish. Fish expressed distinct preferences for the three physical variables under study (Fig. 4). Fish preferentially used depth ranging from 0.3 to 0.7 m (Fig. 4*a*), current speeds ranging from 0.60 to 0.75 $m \cdot s^{-1}$ (Fig. 4*b*), and substrate composition characterised by D50 values of 3.0–4.5 cm (Fig. 4*c*).

The multiple regression equation (n = 308, p < 0.0001) that best represented variations in HSIs was

Table 3. Comparison of velocity and depth predicted by the hydrological model with field measurements.

	Mean current velocity ($m \cdot s^{-1}$)		Mean water depth (m)	
Statistic (n = 271)	Predicted	Field	Predicted	Field
Mean	0.389	0.487	0.491	0.488
Variance	0.040	0.056	0.049	0.059
Minimum	0.044	0.0085	0.038	0.13
Maximum	0.93	1.21	1.16	1.23

Table 4. Total range of utilisation and range of dominant utilisation (in which 80% of the fish were found) of abiotic factors.

Abiotic factor	Total range of utilisation	Range of dominant utilisation
Water depth (m)	0.12–1.2	0.24–0.72
Current velocity ($m \cdot s^{-1}$)	0.05–1.2	0.15–0.75
Substrate size (D50) (m)	0.012–0.09	0.03–0.06

$$\mathrm{HSI} = I_{\mathrm{D}}^{0.30} \times I_{\mathrm{V}}^{0.38} \times I_{\mathrm{S}}^{0.32} \ .$$

The simplest statistically significant logistic model developed to estimate HPIs was

$$\mathrm{HPI} = 1/(1 + e^{-\lambda})$$

where

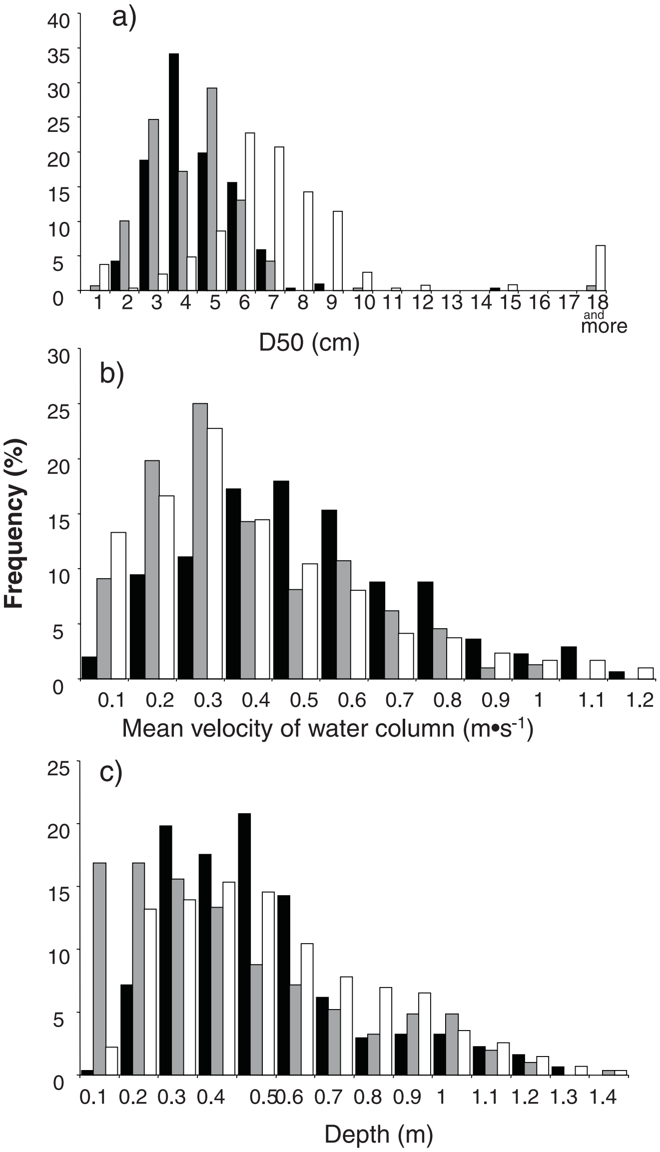
$$\lambda = -3.067 + 8.461D + 2.86V + 0.093S - 6.203D^2.$$

Predictions made by the NHM

The NHM was used to predict the spatial distribution of habitat quality within the validation section at two flow rates (2.2 and 3.2 $m^3 \cdot s^{-1}$) using alternatively HSI or HPI as a 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 $m^3 \cdot s^{-1}$) (Fig. 5*a*). 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) habitat quality indices. Only 16.4% (2750 m^2 at 2.2 $m^3 \cdot s^{-1}$) to 16.7% (2820 m^2 at 3.2 $m^3 \cdot s^{-1}$) of the surface area of the validation section were assigned HSI values higher than 0.7. HSI values assigned to the tiles of the validation section were only slightly affected by changes in flow rates. 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 that 0.7 represented 1513 m^2 or 9.0% of the surface area of the validation section at 2.2 $m^3 \cdot s^{-1}$. Corresponding values were 1633 m^2 and 9.7% at 3.2 $m^3 \cdot s^{-1}$ (Fig. 5*b*). HPI values assigned to the validation section were relatively stable within the range of flow covered by our study and simulations.

Fig. 3. Frequency of (*a*) D50, (*b*) velocity, and (*c*) depth used (solid bars), avoided (stippled bars), or available (open bars) for 1+ and 2+ Atlantic salmon parr.



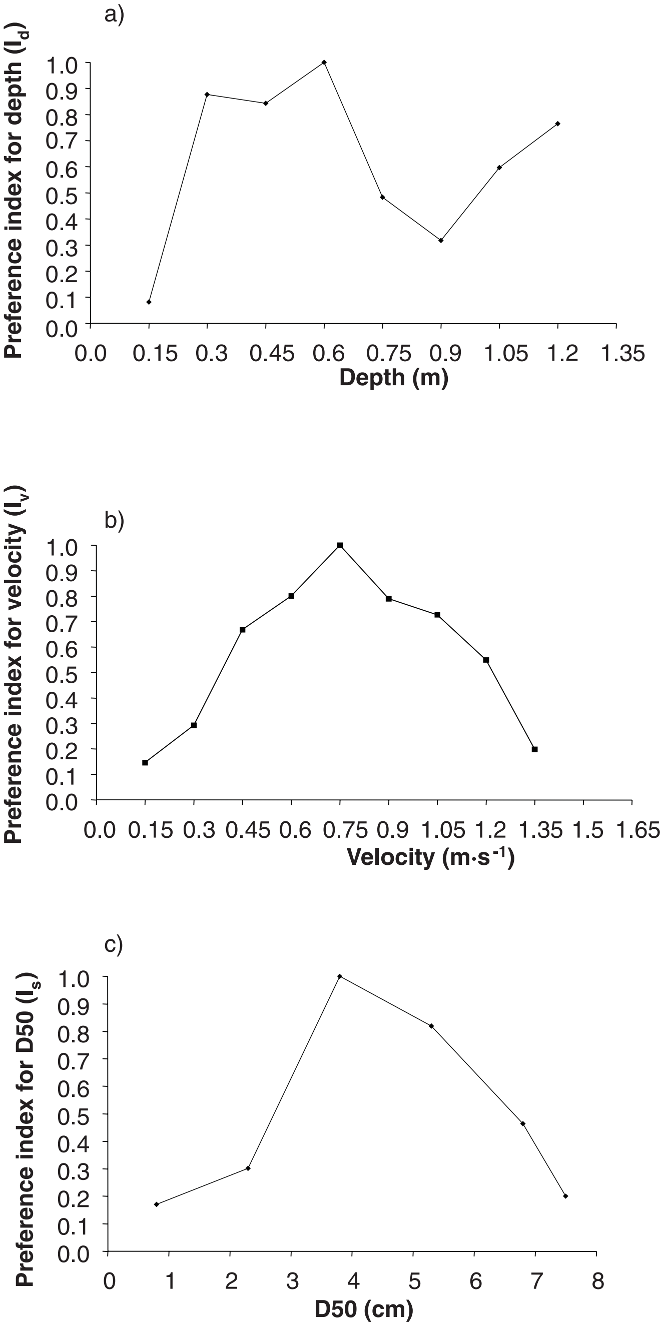
Observations of fish distribution

The distribution of 1+ and 2+ Atlantic salmon parr in the validation section was heterogeneous. Survey-specific parr densities calculated for 17 randomly chosen and distinct subsections (625–995 m^2, adding to 78% of the surface area of the validation reach at a flow of 3.2 $m^3 \cdot s^{-1}$) ranged from 0 to 2.01 fish·100 m^{-2} and had a mean of 0.76 fish·100 m^{-2} (variance = 0.26). There was no relationship between the density of fish and the surface of the subsections (r^2 = 0.003), indicating that densities were not scale dependent for the 17 subsections that we defined.

Relationship between observed fish densities and predictions made by the NHMs

Fish density estimated for each of the 10 areas of the validation section assigned HSI values of 0–1 in increments of

Fig. 4. Preference curves for (*a*) depth, (*b*) current speed, and (*c*) substrate size (D50).



0.1 (0–0.10, >0.10–0.20, >0.20–0.30, etc.) ranged from 0.4 to 1.2 fish·100 m^{-2} at 2.2 m^3·s^{-1} and from 0.1 to 1.6 fish·100 m^{-2} at 3.2 m^3·s^{-1}. The 10 areas of the validation section associated with different HPI values were characterised by fish densities from 0 to 2.5 fish·100 m^{-2} at 2.2 m^3·s^{-1} and from 0 to 2.0 fish·100 m^{-2} at 3.2 m^3·s^{-1}.

There was a statistically significant and positive relationship between real fish densities and habitat quality indices predicted by habitat numerical models. Such relationships were observed for NHM implemented with either biological model and for both flow rates. Predictions of NHM based on HSI explained from 63% (2.2 m^3·s^{-1}) to 71% (3.2 m^3·s^{-1}) of local variations in real fish density ($p < 0.0001$) (Fig. 6*a*). When data from the two flow rates were combined, HSI explained 39% of variations in real fish density. Corresponding values for NHM based on HPI were 98% (2.2 m^3·s^{-1}) and 81% (3.2 m^3·s^{-1}). The use of HPI allowed us to explain 86% of the variations in real fish density when data from both flows were combined ($p < 0.0001$) (Fig. 6*b*). Hence, our results suggested that local fish densities were higher in areas of the validation section for which the NHM predicted higher habitat quality indices. However, predictions of NHM based on HPI for the two flows or with both flows combined explained a larger fraction of local variations in fish density than NHM based on HSI.

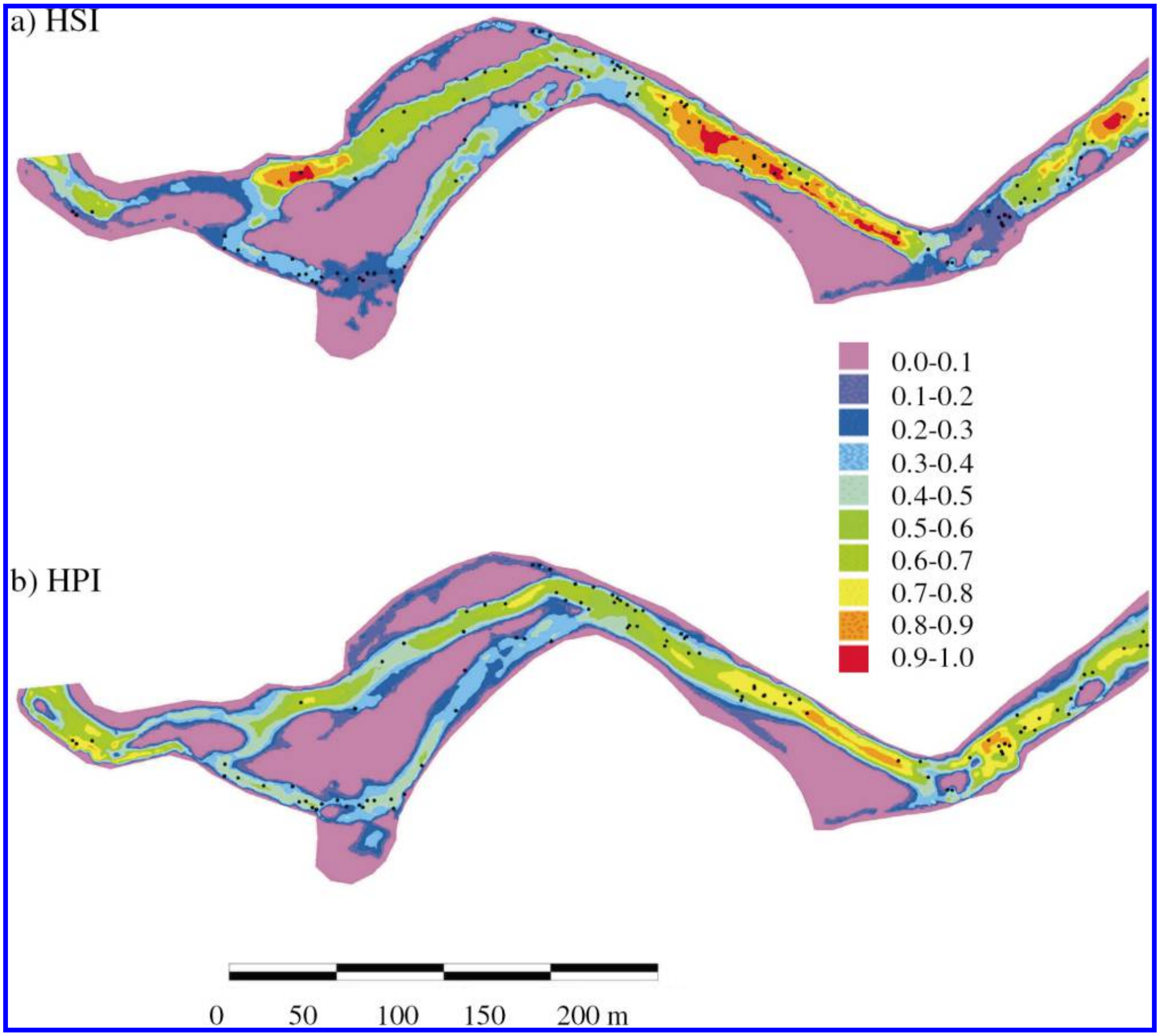
Discussion

Our study suggests that numerical modelling may be appropriate for predicting distribution patterns of Atlantic salmon parr in rivers. Although our study suggests that strictly abiotic variables may allow the prediction of the distribution pattern of Atlantic salmon parr, it is important to note that these variables have also been argued to implicitly represent important biotic variables. For instance, water depth could represent a protection against aerial predators and provide larger search volume during feeding (Wankowski and Thorpe 1979; Metcalfe et al. 1997). Current speed has been hypothesised to modify the costs of habitat utilisation and the drift rate of invertebrate preys in the vicinity of fish (Morantz et al.1987; Heggenes 1996). Finally, substrate granulometry has been suggested to affect cover from predators and from adverse physical conditions during summer or winter (Rimmer et al. 1984; Cunjak 1988; Heggenes et al. 1991).

Our analyses indicate that the quality of the predictions made by numerical modelling is determined by the type of biological model used. In our study, fish distribution was better predicted by a biological model based on an HPI (with both flows combined, $r^2 = 0.86$) than on an HSI (with both flows combined, $r^2 = 0.39$). Although the removal of one point that could be considered as an outlier (1.0, 0.5) improved the relationship between fish density and HSI ($r^2 = 0.46$), it did not affect our observation that NHM performed better when implemented with HPI than with HSI. Two hypotheses can be invoked to explain the different performance of the two biological models that we used.

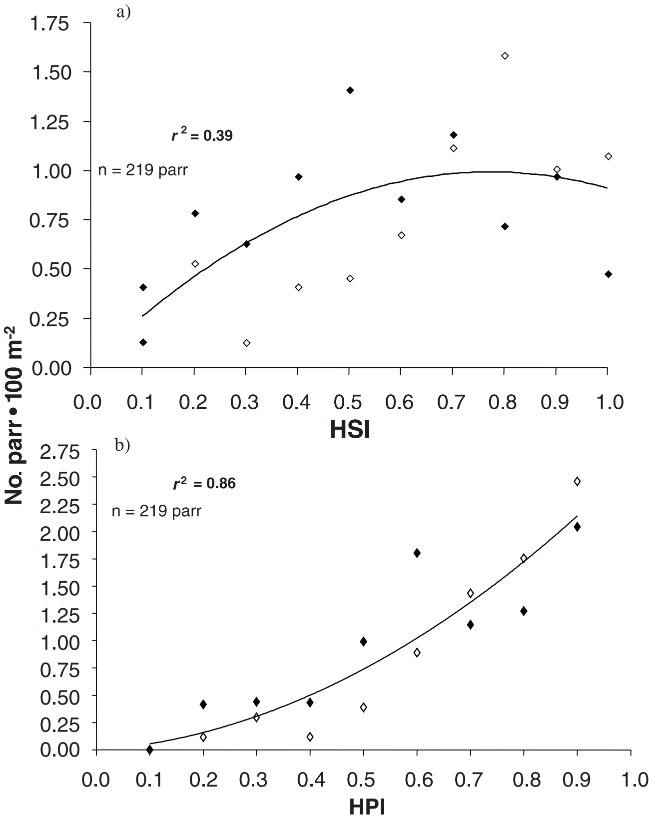
The first hypothesis is that HSI may be more sensitive to the quantity of data required than HPI in developing appropriate models. In our study, we developed our preference curves and indices using observations performed on 308 fish. Since this value represents our complete data set, it is presently impossible for us to assess the effect of increasing the number of fish observed to, for instance, 500 or 600 fish on the quality of the predictions made by HSI models. However, the number of fish that we observed corresponds to the average number of fish generally used to define preference indices. For instance, deGraaf and Bain (1986) developed preference indices using from 123 (North Arbour River) to 215 (North Arm River) parr. Morantz et al. (1987) constructed preference curves by pooling data collected on 538 parr observed over 3 years. Cunjak (1988) and Whalen and Parrish (1999) described winter habitat utilisation of parr using data on 148 and 127 fish, respectively. At the other end

Fig. 5. Maps of (*a*) HSI and (*b*) HPI for a flow of 3.2 $m^3 \cdot s^{-1}$ and fish distribution. The same colour scale gives the values of HSI and HPI.



of the spectrum of sample sizes, Heggenes and Salveit (1990) established habitat preferences using 1454 parr observed over a period of 2 years. However, in that study, observations for young-of-the-year fish were combined with parr, and summer and fall observations were pooled. Our sample size was in the range of those found in the literature. Hence, sample size cannot be invoked to explain differences between the preference indices that we calculated and published values. Our preference curve for water depth had maximum values between 30 and 60 cm. This range is similar to that found for maximum preference for depth observed by deGraaf and Bain (1986) (15–55 cm) and Morantz et al. (1987) (30–55 cm). However, in the Sainte-Marguerite River, we estimated the maximum preference index for current speeds of approximately 60–70 $cm \cdot s^{-1}$. These values are higher than most current speeds found in the literature for Atlantic salmon parr. Morantz et al. (1987) observed maximum preference indices at current speeds ranging from 20 to 50 $cm \cdot s^{-1}$, and Heggenes and Saltveit (1990) found corresponding values between 10 and 30 $cm \cdot s^{-1}$. Despite the apparent difference between the preferred speed range that we found and those presented in other studies, it is important to note that parr for different studies have very similar maximum utilisation ranges for that variable (our study: 35–65 $cm \cdot s^{-1}$; other studies 20–60 $cm \cdot s^{-1}$). Utilisation by fish of a range of environmental condition is defined strictly by the number of fish using this condition, while preference for a specific range of environmental conditions is the utilisation weighted by availability of a condition. Hence, the difference between the preference indices for current speed that we found and those of other studies may not be related to the utilisation of habitat by parr but to different levels of availability of specific ranges of current speed among rivers. A similar situation may also occur for preference indices of substrate composition. Preference curves for substrate are generally based on substrate type (sand, cobble boulder, etc.) instead of D50 values. In our study, maximum preference indices for substrate were between D50 values ranging from 30 to 60 mm, which, according to the Wentworth scale, correspond to the size range of gravel (see Bovee 1982). Gravel

Fig. 6. Polynomial regression between real fish density and (*a*) HSI and (*b*) HPI. Solid diamonds, 3.2 $m^3 \cdot s^{-1}$; open diamonds, 2.2 $m^3 \cdot s^{-1}$.



has been described as optimal for parr by deGraaf and Bain (1986) and Morantz et al. (1987), although maximum preference obtained by Heggenes and Saltveit (1990) was for large cobble (256–384 mm). Discrepancies between their results and ours could again be partly explained by the different availability of substrate in the two studies. In the river studied by Heggenes and Saltveit (1990), the percent occurrence of particles larger than 128 mm was 67 compared with 9% in our study. Hence, the parr studied by Heggenes and Saltveit (1990) may have had no other choice, compared with fish from the Sainte-Marguerite River, than to "select" larger substrate as a habitat. Our examination of published studies indicates that HSIs are very sensitive to the availability of a series of abiotic variables found in different rivers. It is difficult to assess the stability of HPIs or of the logistic model that we developed among rivers because, to our knowledge, no such model has yet been produced to define habitat quality for parr in other rivers. The only other logistic model developed for habitat analysis purposes has been produced to predict spawning site quality for golden trout (*Oncorhynchus mykiss aguabonita*) (Knapp and Preisler 1999). Interestingly, that study also illustrates the ability of logistic models to predict habitat quality.

A second hypothesis that could explain the different performance of HSI and HPI may be related to the underlying assumptions of both models. The equation used to calculate HSI considers that the three physical variables water depth, current speed, and substrate composition contribute to affect habitat quality. However, it also assumes that these variables affect fish, to some extent, independently. For instance, a specific range of current speed is given a high or low preference index independently of water depth or substrate composition. Furthermore, one range of current speed is always given a preference index of 1, even if this range may not constitute a biologically optimum condition whether this variable is considered alone or together with the two other variables. While the relative effect of water depth, current speed, and substrate composition is represented by the weighting of each variable using an exponent (X, Y, Z of eq. 3), it is important to note that the weighting is done after indices of preference have been assigned to the different range of variables. This procedure may not fully reflect the interdependence among the variables. In contrast, HPI is calculated from a multivariate approach in which all variables are considered simultaneously and with no arbitrary correction (no environmental condition is considered a priori better and given a preference index of 1 or worse). In addition, the polynomial approach that we used to model our logistic equation and to assess HPI (allowing linear and no-linear interactions) may be more appropriate for accounting for the possibility that a below-average current speed, from a preference index perspective, may provide above-average habitat conditions when associated with specific combinations of depth and substrate composition. Hence, the mathematical structure that we employed to estimate HPI may allow a better representation of the statistical as well as biological interaction among the physical variables used to estimate habitat quality than that used to estimate HSI.

We tested the validity of the predictions made using our numerical modelling by assessing the existence of a relationship between HSI or HPI values assigned to specific areas of the river and observed fish densities within these areas. The correlation that we obtained may be taken as a measure of the success of numerical modelling to predict local differences in fish density at a given level of global fish density (in our study, the total number of fish present in the complete validation reach divided by the surface area of this section). However, we do not believe that our study can be taken as an indication of the ability of numerical modelling to predict global differences in fish density among rivers or temporal variations in global fish density within a river. This limit of numerical modelling is illustrated by the difficulty of finding a relationship between predictions made by NHM and fish densities on a larger temporal or spatial scales than used in our study (Milhous et al. 1989; Bourgeois et al. 1996). It is tempting to speculate that while strictly physical variables may determine local distribution patterns of Atlantic salmon parr, both biotic and abiotic conditions may determine the number of parr living in a river at a given time.

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