Assessment of the transferability of biological habitat models for Atlantic salmon parr (*Salmo salar*)[1]

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Abstract: We assessed the transferability of the habitat suitability index (HSI) and the habitat probabilistic index (HPI) between two rivers. Transferability was measured by the ability of HSI and HPI models developed in the Sainte-Marguerite River to predict the distribution of Atlantic salmon parr (*Salmo salar*) in the Escoumins River. HSI and HPI were based on the pattern of utilization by fish of water depth, current velocity, and substrate size. HSI was developed using the preference curve approach, and HPI was developed using a multiple logistic regression. Predicted values of HSI and HPI in Escoumins River ranged from 0 (poor habitat) to 1 (excellent habitat). Fish density in habitat patches assigned different HSI or HPI values ranged from 0 to 1 fish·100 m^{-2}. Only HPI adequately predicted local variations in parr density ($r^2 = 0.84$) in habitat patches of Escoumins River. Our results suggest that HSI is less transferable between rivers than HPI. Differences in substrate size between the two rivers is suspected to impede the transferability of the HSI model. We also argue that the mathematical structure of HPI provides a larger degree of flexibility that facilitates its transferability and its potential generalization.

Résumé : Nous avons évalué la transférabilité d'un indice de qualité d'habitat (IQH) et d'un indice probabiliste d'habitat (IPH) entre deux rivières. Nous avons mesuré la transférabilité de ces deux modèles biologiques développés dans la rivière Sainte-Marguerite par leur habileté à prédire la distribution des tacons de saumon atlantique (*Salmo salar*) dans la rivière Escoumins. Le développement de l'IQH et de l'IPH repose sur les patrons d'utilisation par les tacons de la profondeur de l'eau, de la vitesse du courant et de la taille du substrat. L'IQH a été établi selon l'approche des courbes de préférence tandis que l'IPH a été construit en utilisant la régression logistique multiple. Les valeurs prédites d'IQH et d'IPH dans la rivière Escoumins ont varié entre 0 (mauvais habitat) à 1 (excellent habitat). Les densités de tacons dans les parcelles d'habitat auxquelles ont été attribuées différentes valeurs d'IQH ou d'IPH ont varié entre 0 et 1 tacon·100 m^{-2}. Le modèle numérique d'habitat utilisant l'IPH a été le seul qui a permis de prédire la distribution des tacons ($r^2 = 0,84$) dans les parcelles d'habitat de la rivière Escoumins. Nos résultats suggèrent que l'IQH est plus sensible au processus de transférabilité que peut l'être l'IPH. La différence de la taille du substrat entre les deux rivières semble empêcher la transférabilité de l'IQH. Nous avançons que la structure mathématique de l'IPH fournit un degré de flexibilité plus grand, ce qui facilite sa transférabilité et sa généralisation potentielle.

Introduction

Numerical habitat models (NHM) are used to evaluate the effect of variations of flow on the quantity and quality of fish habitats in rivers (Thomas and Bovee 1993; Leclerc et al. 1996; Guay et al. 2000). Numerical habitat models are divided into two parts: first, a hydrodynamic model predicting local variations of depth, current velocity, and substrate size within a reach for any given flow (Bovee 1982; Leclerc et al. 1990); and second, a biological model providing a quantita-tive estimate of the propensity of fish to use given environmental conditions (Bovee 1982; Leclerc et al. 1995). The propensity of fish to use a specific depth, current velocity, or substrate size is quantified with a habitat suitability criteria (HSC; ranging from 0 to 1). HSC may also express the utilisation ratio of a given environmental condition to its availability within a reach (Heggenes 1991). Variations in HSC over the complete range of an environmental condition define the preference curve of fish for this environmental condition (deGraaf and Bain 1986; Morantz et al. 1987;

Heggenes 1996). Knowledge of HSC values for depth, current velocity, and substrate size permit estimates of the propensity of fish to use given combinations of environmental conditions. The habitat suitability index (HSI) is a commonly used joint-suitability criteria, which is calculated as the weighted geometric product of HSC for water depth, current velocity, and substrate size (Leclerc et al. 1996; Bovee et al. 1998; Guay et al. 2000). Values of HSI generally range from 0 (poor habitat) to 1 (excellent habitat). The surface area of habitat patches assigned a given HSI value (e.g., from 0.5 to 0.6) usually range from 10^1 to 10^3 m^2 (Guay et al. 2000). Estimation of HSI values for a complete series of habitats of a reach is used to evaluate the quantity, quality, and distribution of habitats within that reach. Comparison of HSI values obtained for different flows is expected to measure the effect of flow variation on fish habitat.

The existence of a relationship ($0.63 < r^2 < 0.76$; see Guay et al. 2000) between HSI values assigned to different areas of a reach and fish density observed in these areas is supported by few studies (Boudreau et al. 1996; Guay et al. 2000). This suggests that NHM provides a biologically meaningful representation of fish habitat quantity, quality, and distribution. Although the possibility of using a HSI model developed in one river to predict attributes of fish habitat in another river would greatly facilitate the routine use of NHM, attempts to assess the validity and transferability of HSI provided mixed results (Scott and Shirvell 1987; Freeman et al. 1997; Mäki-Petäys et al. 2002). Consequently, it has been suggested that the concept of transferable models should be abandoned for a more laborious river-by-river approach in which a HSI model is developed for each river modelled (Bozek and Rahel 1992; Thomas and Bovee 1993).

The study of Guay et al. (2000) showed that a new biological model, referred to as a habitat probabilistic index (HPI), was more strongly related to fish density ($0.81 < r^2 < 0.98$) than HSI ($0.63 < r^2 < 0.71$). HPI is derived from a multivariate nonlinear logistic regression (Legendre and Legendre 1998) based on a matrix of presence–absence of fish for abiotic variables such as water depth, current velocity, and substrate size. Because of its mathematical structure, HPI has been argued to more closely represent the probability of finding fish under a given set of environmental conditions than HSI or any other model currently available (Guay et al. 2000). Interestingly, the fact that HSC such as HSI do not represent the probability of finding fish in a given habitat has been identified as a key element precluding the transferability of this kind of biological model (Scott and Shirvell 1987). The objective of our study was to assess the relative transferability of HSI and HPI by predicting the spatial distribution of fish habitat and local variations in fish density in one river using HSI and HPI developed in another river.

Material and methods

Study sites and species

The rivers covered by our study are the Sainte-Marguerite (70°26′E, 48°25′N) and the Escoumins (69°28′E, 48°21′N) rivers. These rivers are located in two adjacent watersheds on the northern shore of the St. Lawrence River, approximately 600 km north–northeast of Montreal (Quebec, Can-

ada; Fig. 1). Summer low water flow in the Sainte-Marguerite and Escoumins rivers range from 2.0 to 3.0 $m^3 \cdot s^{-1}$ and from 5.5 to 7.5 $m^3 \cdot s^{-1}$, respectively. HSI and HPI were developed in a 750-m reach of the Sainte-Marguerite River located 80 km from its discharge into the Saguenay River (Guay et al. 2000). These two models were used to predict fish distribution in a 350-m reach of the Escoumins River 25 km from its discharge at the St. Lawrence River. Our work focussed exclusively on juveniles (ages 1+ and 2+) of Atlantic salmon (*Salmo salar*). Both rivers were dominated by Atlantic salmon (>95% of observations) but shared five other fish species: brook charr (*Salvelinus fontinalis*), American eel (*Anguilla rostrata*), longnose dace (*Rhinichthys cataractae*), longnose sucker (*Catostomus catostomus*), and sea lamprey (*Petromyzon marinus)*.

Numerical habitat model

NHM consist of a hydrodynamic model and a biological model (Leclerc et al. 1996; Bovee et al. 1998). The methods and computations that we used to develop the hydrodynamic and biological models have been described in detail by Guay et al. (2000). Briefly, the hydrodynamic model used is a two-dimensional model designed to predict water depth and current velocity for any combination of longitudinal (upstream–downstream axis) and transversal coordinates (left bank – right bank axis) of a river (Leclerc et al. 1994, 1996). This hydrodynamic model requires a topographic and granulometric representation of a riverbed. Coordinates of the locations used to assess river topography are used to construct a grid of triangular elements that serve as a spatial framework on which to perform the numerical habitat simulations. The hydrodynamic model is inputted with a user-defined flow and combines topographic measurements, substrate information, and a series of physical coefficients and assumptions (water viscosity and friction, equations of energy conservation and momentum). This procedure allows the hydrodynamic model to assign a value of average water depth, current velocity, and substrate size to the points located at the summit and in the middle of the sides of each of the triangular elements of the grid extending over the complete surface area of the reach modelled. Hydraulic conditions in the Escoumins River were modelled at a flow of 6.0 $m^3 \cdot s^{-1}$ because it corresponded to the average flow prevailing during the mapping of fish distribution in this river (range = 5.5–6.5 $m^3 \cdot s^{-1}$). The hydrodynamic model that we used is not appropriate to predict current velocity at very small spatial scales (i.e., point measures of current velocity as taken in the field). The hydrodynamic model that we used predicts a single current velocity in a patch of 10^1–10^3 m^2, whereas in reality, current velocity may vary 10- or 100-fold from one point to another within this patch (e.g., from 1 m upstream of a large rock to a few centimetres downstream of the same rock). Although the hydrodynamic model that we used is not able to predict current velocity variations at fine spatial scales, the current velocity value predicted in a patch corresponds to the average current velocity value within this patch (Guay et al. 2000, 2001). Hence, the hydrodynamic model used is capable of expressing variations of current velocity and, consequently, of habitat quality between patches of 10^1–10^3 m^2. We therefore limited interpretation of the predictions of NHM to this spatial scale. The ability of hydro-

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Fig. 1. Location of the Sainte-Marguerite and Escoumins rivers in Québec, Canada.

dynamic models to predict current velocity at different spatial scales has been discussed by Williams (2001) and Guay et al. (2001).

Water depth, current velocity, and substrate size obtained from the hydrodynamic model are used as inputs to the biological models to assign HSI or HPI values to the summit and the middle of the sides of each of the triangular elements. The results of the modelling exercise are maps of local variations in HSI or HPI values over the reach modelled. These maps are expected to represent patches of habitats with different ecological values and, consequently, patches of habitats potentially characterized by different fish densities. These maps are drawn using colours representing 10 classes of presumed habitat quality values (0–1 by increments of 0.1).

Sampling

Hydrodynamic model

The topographic map of the Escoumins River required to perform the hydrodynamic simulation was developed by measuring the X, Y, and Z coordinates (longitude, latitude, and altitude) of the riverbed at 2116 locations distributed throughout the reach studied. These coordinates were obtained using an electronic theodolite coupled with an electronic distance measurement system (Sokkia SET3B; Sokkia Corp., Mississauga, Ont.). The granulometric representation of the riverbed was obtained by estimating the mean size of the substrate ($D50$) at every location. Given that the volume

of a stone is determined by three axes (A being the longest, B the intermediate, and C the shortest axis), $D50$ is defined as the length (in cm) of the B axis of the median stone within the 1-m^2 area centred on each location. $D50$ was estimated visually by observers trained during 2 days of calibration (Latulippe and Lapointe 2001).

Biological models

The two biological models used in our study were developed in the Sainte-Marguerite River using a description of the prevalent environmental conditions in a series of 1-m^2 areas used by fish (where fish were found), available to fish (selected at random regardless of the presence or absence of fish), and avoided by fish (where no fish were observed). The HSI model used requires a description of the environmental conditions used by fish and the availability of these conditions in a river. The HPI model requires data on the environmental conditions used and avoided (instead of available to fish) by fish in a river. The environmental conditions used by fish were assessed by snorkelling a 750-m reach of the Sainte-Marguerite River during two periods of the summer (16–24 July and 1–10 August 1997). Sampling was performed during mid-day (between 10:00 and 16:00) and only during days when the cloudiness was lower than 25%. Flow rate ($m^3 \cdot s^{-1}$) was recorded for every sampling day from a continuous flow station located 500 m upstream from the reach under study. Flow ranged from 1.9 $m^3 \cdot s^{-1}$ to 4.1 $m^3 \cdot s^{-1}$ in July and from 2.3 $m^3 \cdot s^{-1}$ to 5.5 $m^3 \cdot s^{-1}$ in August (both months averaged 3.7 $m^3 \cdot s^{-1}$). Water temperature during our

surveys ranged from 15 °C to 23 °C in July and from 14 °C to 21 °C in August.

The snorkelling diver could cover all of the surface area of a 50- to 100-m reach (further referred to as sections) in one day. The diver swam upstream to minimise fish disturbance (Cunjak 1988). Each fish encountered was observed for 1–2 min to confirm that it displayed site fidelity. The position of each fish that displayed site fidelity was then marked with a stone coloured with fluorescent paint and was later georeferenced. The fish was then chased downstream to avoid recording two series of data for the same fish. For each fish location, water depth, mean current velocity of the water column, and substrate size ($D50$) were noted. A total of 308 fish were used to assess the environmental conditions used by parr of Atlantic salmon. Our visual observations indicated that fish behaviour was qualitatively comparable between the sampling surveys of July and August. Furthermore, overall parr abundance in the reach used to develop our biological models was relatively stable between both months (159 parrs in July, 149 parrs in August) for an average density of 0.75 parr·100 m^{-2}. These observations suggest that parr do not perform important behaviour or habitat shifts during this period of the summer.

Water depth and current velocity available to fish during a specific sampling day were predicted using the hydrodynamic model implemented with the flow rate observed in the section surveyed that day. Hence, the hydrodynamic model was used to predict water depth and current velocity at the summit and in the middle of the sides of each of the triangular elements making up the hydrodynamic grid during a given sampling day (total of 1500–2500 points). Substrate size at these points was taken directly from a mapping of substrate composition performed over the complete study reach. This procedure was used to minimize the sampling effort deployed in the field and to maximize the proportion of the reach for which physical conditions were obtained. A frequency distribution of water depth, current velocity, and substrate size over the complete length of the section surveyed for fish during a day was taken as an adequate representation of the environmental conditions available to fish during that day.

Environmental conditions avoided by fish during a sampling day were described using the hydrodynamic model, the flow rate, and the map of fish distribution observed in the section surveyed that day. The map of fish distribution during one day was overlaid on the maps of predicted water depth and current velocity and on the map of substrate size for the section surveyed that day at the proper flow. This allowed us to randomly select a total of 308 points (sum across all sampling days) in which no fish were observed (at least 2 m from the closest georeferenced parr). Water depth, current velocity, and substrate size at these 308 locations where no fish have been observed were taken as an adequate description of the environmental conditions avoided by fish.

Mapping of the spatial distribution of fish

Mapping of fish spatial distribution in the Escoumins River was performed by snorkelling the 350-m reach between 10:00 and 16:00 on two consecutive days during which cloud cover was <25% (14–15 July 1999). Flow dur-

ing these days ranged from 5.5 m^3·s^{-1} to 6.5 m^3·s^{-1}. Water temperature during the mapping of parr ranged from 14 °C to 21 °C. Fish were observed and georeferenced following an approach identical to that used to develop HSI and HPI models. However, no additional physical data were collected during the mapping of fish in the Escoumins River. Hence, fish mapping was performed during a period of the summer that was within 1 month of the sampling done to develop the biological models that we used. Furthermore, both samplings were performed under almost identical meteorological and water temperature conditions except for flow, which was 1.6 times greater in the Escoumins River than in the Sainte-Marguerite River. This situation had relatively little effect on the difference in water depth and current velocities available to fish in these rivers (see Results, Predictions of NHM).

Computations

Habitat suitability model

The habitat suitability model was developed using the environmental conditions used by fish and those available to fish in the Sainte-Marguerite River. This model requires the calculation of the propensity of fish to select given intervals of water depth, current velocity, and substrate size (see Guay et al. (2000) for a complete description of the computations). The propensity of fish to select an environmental condition, c, was estimated using a preference index I_c (ranging from 0 to 1). We used weighted preference indices for water depth (I_D), current velocity (I_V), and substrate size (I_S) to develop our HSI model (Guay et al. 2000):

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

The weight of each preference index is represented by their respective exponent and is estimated using a multiple regression analysis (Guay et al. 2000).

Habitat probabilistic model (HPI)

The model of HPI was calculated by fitting a multivariate Gaussian logistic regression model to the presence–absence fish data set of the Sainte-Marguerite River. This data set was organised as a matrix containing four columns. The first column identified if the associated environmental conditions were observed for the presence (1) or absence of a fish (0). The three other columns contained the water depth, current velocity, and substrate size at sites characterized by the presence or absence of fish. The logistic equation derived using these data produced our HPI model (Guay et al. 2000):

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

where

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

and where D, V, and S are water depth (m), current velocity (m·s^{-1}), and substrate size ($D50$; cm), respectively.

The models of HSI and HPI allowed us to produce predictions of habitat quality for parr at any point of a reach for which water depth, current velocity, and substrate size can be estimated. In our study, water depth and current velocity were estimated using the hydrodynamic simulation of the

study reach of Escoumins River, and substrate composition was extracted from the field-derived map of riverbed substrate size.

Data analysis

We tested the ability of HSI or HPI models developed in the Sainte-Marguerite River to predict the distribution of parr habitat and density in the Escoumins River by comparing the strength of the relationship between real fish density and predicted HSI or HPI values. This was performed in five steps. First, we overlaid the map of expected habitat quality according to HSI or HPI and the map of observed fish distribution in the reach. Water depth and current velocity required to calculate HSI and HPI in the Escoumins River were obtained using a hydrodynamic model. The procedure by which the hydrodynamic model was used to predict water depth and current velocity (and to obtain substrate composition) within the reach studied in the Escoumins River was identical to that used to obtain these predictions in the Sainte-Marguerite River. Second, we calculated the total surface area of the reach associated with each of the 10 classes of HSI or HPI (increments of 0.1 from 0 to 1). Third, we counted the total number of fish observed in the areas associated with each of the 10 classes of HSI or HPI. Fourth, we calculated the average fish density in each of these areas (number of fish·100 m^{-2}). Finally, we tested the existence of a significant relationship between HSI or HPI and real fish density using regression analysis.
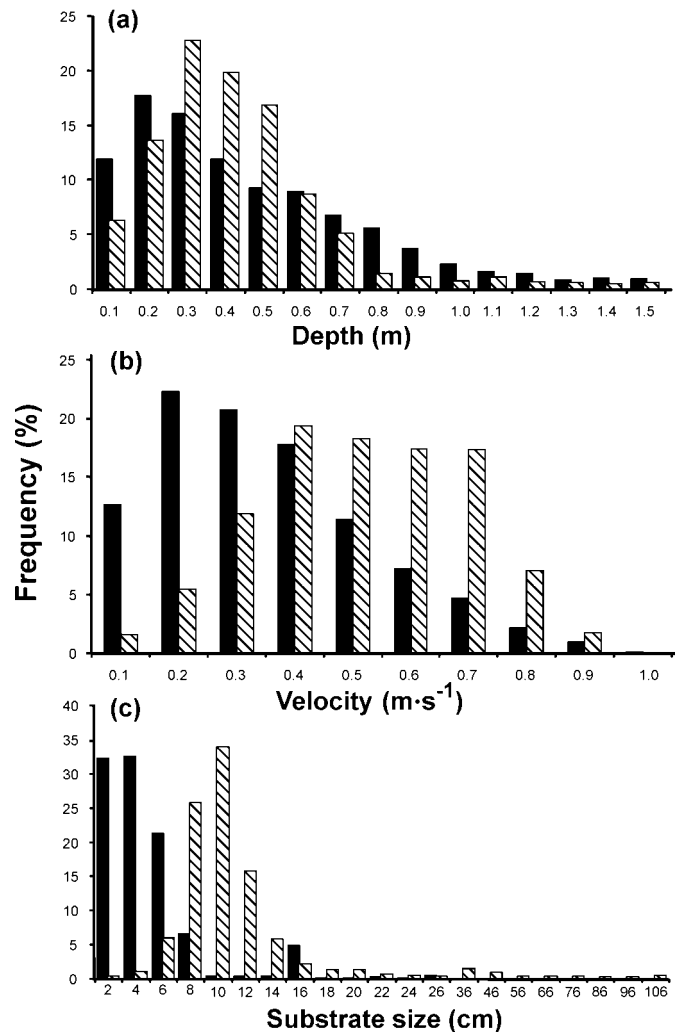
Results

Predictions of NHM

The depth and velocity values observed in the Sainte-Marguerite River during the development of our biological models covered a range similar to that found in the Escoumins River when these models were applied (Fig. 2). However, substrate grain size in the Sainte-Marguerite River never exceeded $D50$ values of 25 cm, whereas the maximum $D50$ values observed in Escoumins River attained 106 cm. The frequency distributions of water depth, current velocity, and substrate size in the reach used in the Sainte-Marguerite River to develop our biological models were statistically different from the study reach in the Escoumins River (Kolmogorov–Smirnov two-sample test, $p < 0.001$; Fig. 2). Despite the statistical significance of these findings, average water depth and average current velocity varied only 13–16% between the two reaches (Table 1). The key difference between our sites was the average substrate size that varied threefold between reaches (average $D50$ of 4.0 cm in the Sainte-Marguerite River and 11.5 cm in the Escoumins River). Hence, in general, the Sainte-Marguerite River was characterized by slightly shallower depths and slower current velocities but threefold smaller average substrate grain size than the Escoumins River.

The surface area of the 350-m reach studied in the Escoumins River was 13 320 m^2 with a flow of 6.0 m^3·s^{-1}. NHM predictions of both biological models differed in the relative proportions of the reach surface area covered by specific intervals of habitat quality values. The map produced using HSI indicated that 7.5% (1004 m^2) of the reach could

Fig. 2. Frequency distribution of (*a*) water depth, (*b*) current velocity, and (*c*) substrate size predicted by the hydraulic model for the Sainte-Marguerite River (solid bars) and the Escoumins River (hatched bars) at 6 m^3·s^{-1}.

be assigned habitat quality values ranging from 0.7 to 1.0 (Fig. 3*a*). The maps that resulted from the use of HPI showed that 69% (9193 m^2) of the surface area of the reach could be given a habitat quality value ranging from 0.7 to 1.0 (Fig. 3*b*). Conversely, NHM implemented with HSI predicted that 82% (10 902 m^2) of the reach should be assigned habitat quality values <0.3 compared with only 4.5% (602 m^2) with HPI.
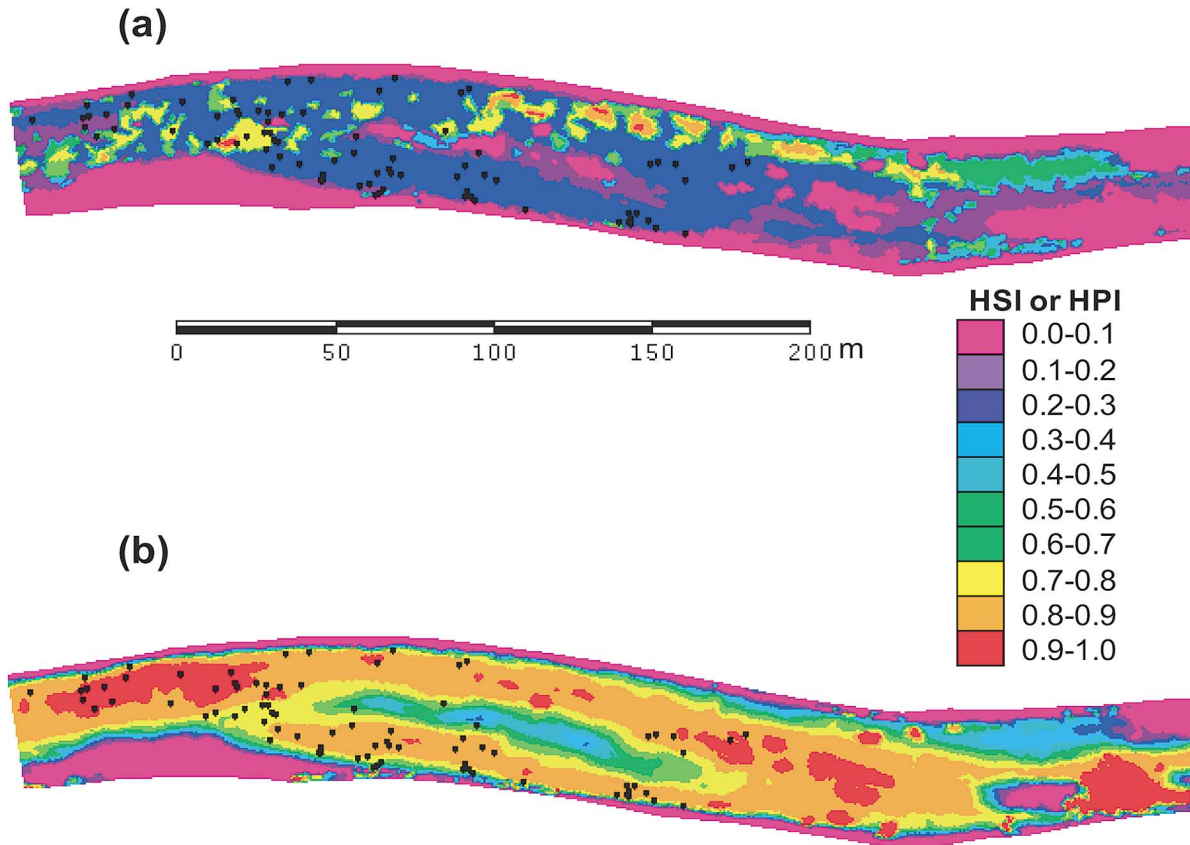
Fish distribution

We georeferenced and mapped 82 Atlantic salmon parr in the 350-m reach of the Escoumins River (Fig. 3). The average density of parr within the total wetted area of the reach was 0.63 parr·100 m^{-2} (standard deviation = 0.67). However, parr density was spatially heterogeneous. Fish density in 16 adjacent areas of relatively similar sizes (22- to 25-m sections; 560–933 m^2) indicated that parr density ranged from 0 to 2 parr·100 m^{-2}.

Table 1. Mean, standard deviation (SD), and maximum values (max.) of water depth (m), current velocity (m·s^{-1}), and substrate size ($D50$; cm; minimum (min.) size included) for the reaches sampled in the Sainte-Marguerite River (hydraulic conditions predicted at a flow of 3 m^3·s^{-1}) and the Escoumins River (hydraulic conditions predicted at a flow of 6 m^3·s^{-1}).

River	Depth			Velocity			Substrate size			
	Mean	SD	Max.	Mean	SD	Max.	Mean	SD	Min.	Max.
Sainte-Marguerite	0.44	0.36	2.37	0.30	0.18	0.87	4.0	3.88	0.3	25
Escoumins	0.39	0.27	2.00	0.46	0.18	0.95	11.5	11.89	0.2	>50

Fig. 3. Maps of (*a*) habitat suitability index (HSI) and (*b*) habitat probabilistic index (HPI) for a flow of 6 m^3·s^{-1}. The colour scale is used to identify HSI and HPI values. Fish distribution is overlaid on the maps. Each black dot represents a single fish.

Comparison between the predictions by NHM and fish distribution

There was a poor correspondence between the prediction of the distribution of fish habitats obtained by NHM implemented with HSI and the distribution of fish within the reach of the Escoumins River. Only seven of the 82 fish mapped occurred in habitats assigned values >0.5 (presumably the best habitats according to HSI). However, 68 of the fish were found in habitats given HSI values ranging from 0.2 to 0.4. Hence, 83.9% of the parr observed in the field were located in areas representing some of the worst habitats predicted by NHM inputted with HSI. In contrast, 81 of the 82 fish were found in areas allotted HPI values >0.5. Furthermore, 89% of the fish observed were located in areas assigned HPI values ranging from 0.7 to 1.0.

Fish densities in each of the 10 classes of habitat quality values (0 to 1 by increments of 0.1) predicted by either HSI or HPI ranged from 0 to 1 fish·100 m^{-2}. We found no statistically significant relationship between the fish densities observed in the patches of habitats assigned different values of HSI ($r^2 = 0.25$; Fig. 4*a*). However, fish densities estimated at the level of patches were strongly correlated to HPI ($r^2 = 0.84$; Fig. 4*b*).

Discussion

Our results indicate that it may be possible to use a biological model developed in one river to assess fish habitat quality and to predict fish distribution pattern in another river. The possibility of using a biological model developed in one river to predict habitat quality in another river defines the term "transferability". Many authors (Thomas and Bovee 1993; Freeman et al. 1997; Leftwich et al. 1997) have used this definition of transferability. In this context, our work supports the hypothesis that biological models may be transferable from one river to another. Our analyses suggest that

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Fig. 4. Relationship between fish densities and values of (*a*) habitat suitability index (HSI) and (*b*) habitat probabilistic index (HPI). For HSI, $r^2 = 0.12$, $p > 0.1$; for HPI, $y = 0.68x^2 + 0.49x - 0.21$, $r^2 = 0.84$, $p < 0.001$.
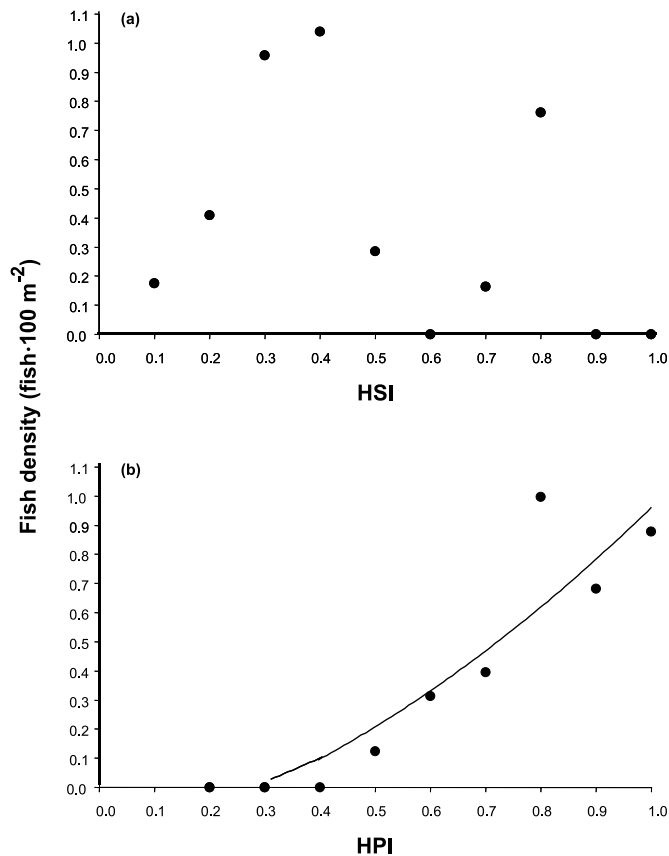
transferability may not be achievable for all biological models. The HPI model developed in the Sainte-Marguerite River was able to explain 86% of the local variation in Atlantic salmon parr density in this river (Guay et al. 2000). This same model explained 84% of local variation in fish density in the Escoumins River. Hence, the HPI model developed in the Sainte-Marguerite River could adequately rank habitat quality in the Escoumins River. The HSI model developed in the Sainte-Marguerite River was able to explain 39% of local variation in fish density in this river (Guay et al. 2000). However, HSI from the Sainte-Marguerite River could not explain a significant proportion of fish density variation in the Escoumins River. Our results suggest that HSI models may not be as transferable as HPI models. We recognise that the low fish density of the Escoumins (0.63 parr·100 m^{-2}) and Sainte-Marguerite (0.76 parr·100 m^{-2}) rivers may affect the applicability of our findings to more densely populated rivers. As such, the transferability of HPI models developed in rivers characterized by low fish densities to densely populated rivers remains to be tested. However, the low fish densities that we observed do not explain the difference between the transferability of HSI and HPI models in our study (both rivers had low fish densities).

Three hypotheses can be invoked to explain the relative transferability of the HSI and HPI models. First, for a simi-

lar number of observations about the environmental conditions used by fish, a HPI model contains more specific information than a HSI model. HSI contains information about the environmental conditions used by and available to fish. The conditions used by fish are necessarily, and completely, included within those available to fish, which creates an overlap in the information contained in both variables. The availability of the environmental conditions is, to some extent, implicitly included in HPI. However, HPI explicitly refers to conditions that are fundamentally more contrasting (those that define the presence or the absence of fish) than HSI (conditions available to fish and those used by fish). Although the conditions used and avoided by fish do overlap, the fact that both variables are potentially more contrasted may contribute to the better performance of HPI models (Guay et al. 2000). For instance, mean water depth, mean current velocity, and mean substrate size used by fish in the Sainte-Marguerite River differed from conditions available in this river by 2.3, 5.9 and 1.5%, respectively. Corresponding differences between conditions used and avoided by fish were 4.0, 18.6, and 0.97%. We performed a series of Kolmogorov–Smirnov tests to assess the difference between environmental conditions used by fish and available to fish and between conditions used and avoided by fish in the Sainte-Marguerite River. These tests indicated that the frequency distributions of water depth and current velocity used by fish did not differ significantly from those of water depth and current velocity available to fish ($p > 0.1$). The frequency distribution of substrate size used by fish was statistically different from that available to fish ($p < 0.01$). In contrast, the frequency distribution of water depth, current velocity, and substrate size used by fish were all significantly different from those avoided by fish ($p < 0.05$). Consequently, these result confirm our contention that the difference between habitat variables used by fish and those avoided by fish is larger than the difference between habitat variables used by fish and available to fish. Hence, HPI is effectively based on more contrasting variables which, we argue, allows HPI models to better differentiate good from poor habitats.

Second, the structure of HSI models may not allow one to represent the interactions among physical variables used to estimate habitat quality as well as HPI. HSI models are based on preference curves (in our study, on three preference curves or three HSC) that are developed separately and independently. For instance, a specific range of substrate size is given a high or low preference index independently of water depth or current velocity. However, it is realistic to believe that the preference of fish for one substrate size may vary with water depth and current velocity. The HSI does not allow modifying the preference index for one environmental condition with the two other conditions. In contrast, because of their structure, HPI models do not allow one to estimate a preference index for a single environmental condition, the two other conditions must be specified. Because of the statistical characteristics of multivariable logistic regressions, HPI models are developed using physical variables and the interactions that may exist among them. Explicit and structural inclusion of the interaction between environmental conditions may explain the better performance of HPI relative to HSI models in rivers for which both models are developed

(Guay et al. 2001). Our study suggests that this attribute may also provide HPI models a larger degree of flexibility, which facilitates their transferability.

Third, our HSI model may be more sensitive than our HPI model to physical variables that differ between the rivers for which transferability was attempted. Indeed, the transferability of any biological model depends on the magnitude of the difference between the rivers for which transferability is performed or assessed. Summer flows (3 $m^3 \cdot s^{-1}$ for the Sainte-Marguerite River and 5.5 $m^3 \cdot s^{-1}$ for the Escoumins River) and maximum width (15–40 m) varied, respectively, 1.8- and 2.7-fold between the reaches studied. These variables are probably meaningless in the context of among-river transferability because they may not explain among-river differences in the conditions affecting fish. Fish may experience the same conditions of depth and current velocity in two rivers that vary 10-fold in flow if the width of the high-flow river is much larger than that of the low-flow river. More importantly, frequency distributions of water depth, current velocity, and substrate size in the reach that we used in the Sainte-Marguerite River to develop our biological models were statistically different from those of the study reach in the Escoumins River. Because the range of water depth and current velocity was identical between these reaches and average values for these variables differed only 13–16% between the two reaches, the key difference between our sites may be substrate size, which differed threefold. This threefold variation in substrate size may indicate the among-river or among-site differences for which HSI is not transferable and for which HPI remains transferable. We have no field data to evaluate the degree of variability of physical variables required to impede the transferability of HPI. However, we performed a sensitivity analysis to assess the relative effect of modifying water depth, current velocity, or substrate composition by 20% on predictions made by HSI and HPI models (Table 2). This sensitivity analysis was performed in five steps. First, we calculated 1000 HSI values and 1000 HPI values with combinations of water depth, current velocity, and substrate size covering the complete range observed in the Sainte-Marguerite River. These are defined as nominal HSI or HPI values. Second, we alternatively increased water depth, current velocity, or substrate size by 20% and calculated the percent change in HSI or HPI values relative to the nominal values. Third, we decreased the value of each physical condition by 20% and calculated the percent change in HSI or HPI values relative to the nominal values. Fourth, we noted the maximum (largest increase) and the minimum (largest decrease) percent change in HSI or HPI value relative to the nominal values. Fifth, we calculated the mean of the absolute percent change in HSI or HPI values caused by a 20% increase or decrease in the physical conditions. This analysis indicated that HSI is 1.7- to 5.2-fold more sensitive than HPI to a ±20% change in depth, flow velocity, or substrate size. For instance, the absolute value of the average variation resulting from a 20% decrease in water depth was 21% for HSI compared with 10.2% for HPI. Similarly, a 20% increase in water velocity produced a 19.5% variation in HSI and a 5% variation in HPI. Furthermore, a 20% decrease in substrate size caused a 11.8% variation in HSI and only a 2.3% variation in HPI. Our analyses also showed that with one exception (20% decrease in water

Table 2. Minimum, mean of absolute values, and maximum percent change in habitat suitability index (HSI) and habitat probabilistic index (HPI) resulting from a 20% increase (+20%) or decrease (–20%) in water depth (m), current velocity (m·s⁻¹), and substrate size (D50; cm).

	HSI		HPI	
	+20%	–20%	+20%	–20%
Depth				
Minimum	–118.8	–119.4	–19.3	–133.6
|Mean|	25.7	21.0	15.3	10.2
Maximum	45.4	17.7	82.4	19.8
Velocity				
Minimum	–76.1	–69.8	–22.9	1.2
|Mean|	19.5	12.4	5.7	6.8
Maximum	47.7	7.3	–0.6	22.3
Substrate size				
Minimum	–11.4	–34.4	–16.5	0.01
|Mean|	8.0	11.8	2.2	2.3
Maximum	19.9	11.6	–0.01	15.0

depth), the range of variation (increase or decrease) caused by a 20% change in any of the physical variables is smaller for HPI than for HSI. Hence, the sensitivity of HPI to 20% changes in depth, water velocity, and substrate size is not only generally smaller than for HSI (i.e., in mean absolute percent changes), its direction (increase or decrease of HPI) is also more stable and predictable than that of HSI. We can only speculate that the mathematical structure of HPI, which allows a better representation of the interaction between environmental conditions, may act as a buffer against frequently large and unstable predictions. Regardless of the ultimate cause of the apparent sensitivity of the HSI model, the greater sensitivity of HSI to substrate size than HPI, together with the fact that the study reaches of the Sainte-Marguerite and the Escoumins rivers differed mostly in substrate size, contribute to explain the difficulty of transferring the HSI model.
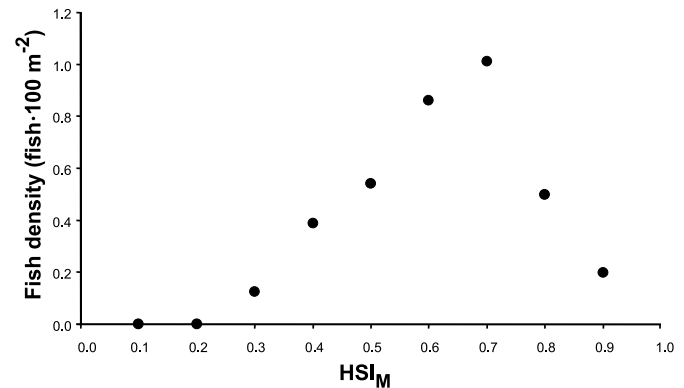
It is conceptually reasonable to expect that developing HSI or HPI models based on data obtained using a wide range of environmental conditions from one or many rivers may allow one to obtain more general and more transferable models. This expectation was tested by Mäki-Petäys et al. (2002) using data on habitat use by Atlantic salmon parr and habitat availability in four Finnish rivers. They developed a general HSI model (HSI_M; geometric mean of HSC for water depth, current velocity, and substrate size) based on HSC for water depth, current velocity, and substrate size combining data from the four rivers that they studied. They also compared their HSC and the predictions of their HSI_M with similar models developed by Heggenes and Saltveit (1990; HSI_{HS}). Mäki-Petäys et al. (2002) used a two-sided χ^2 test to compare the observed proportions of fish encountered in given ranges of habitat quality predicted by their HSI_M with those expected if fish selected habitats according to their availability. HSI_M and HSI_{HS} were declared successful and transferable when these models demonstrated the nonrandom selection of habitats by fish (significant difference between observed and expected habitat use). They achieved this goal for nine of the 11 comparisons performed with HSI_M and

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Fig. 5. Frequency distribution of predicted habitat values in the Escoumins River using the habitat suitability index of Mäki-Petäys et al. (2002; HSI_M). Opened bars are for habitats available ($n = 2116$); solid bars are for habitats used ($n = 82$).

Fig. 6. Relationship between fish density and the habitat suitability index of Mäki-Petäys et al. (2002; HSI_M).
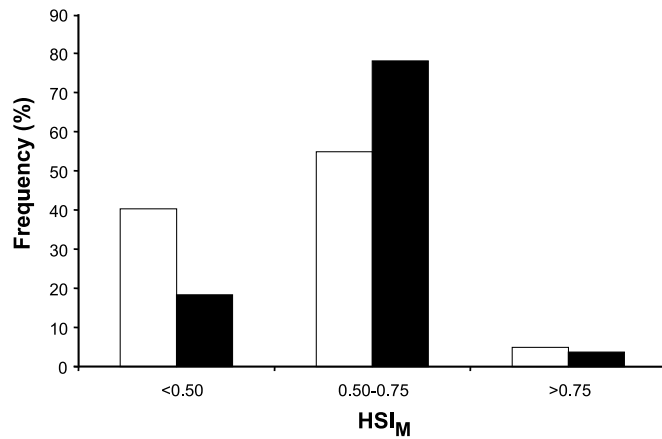
HSI_{HS}. Two points are worth noting about the work of Mäki-Petäys et al. (2002). First, technically speaking, the confirmation by these authors that HSI_M adequately determines the nonrandom habitat selection by fish is not a true test of transferability among rivers because the HSI_M was tested in the same rivers that were used to develop this model. The procedure that they adopted is closer to a test of the generality of a model (conceptually different but equally, if not more, interesting). The test that they performed with HSI_{HS} conforms to the definition of transferability generally used (Thomas and Bovee 1993; Freeman et al. 1997; Leftwich et al. 1997). Second, their study illustrates that whether or not a model is declared successful or transferable may depend on the statistical approach used to test the transferability. We calculated that for two of the nine successful comparisons performed with HSI_M and for two of the nine successful comparisons performed with HSI_{HS}, fish showed a preference for intermediate ($0.5 < HSI < 0.75$) rather than high ($HSI > 0.75$) quality habitats. Their approach was, however, capable of differentiating poor ($HSI < 0.5$) from good ($HSI > 0.5$) habitats. The procedure that we used to test the transferability requires that fish density increases continuously with habitat quality indices. The presence of peaks of fish density at intermediate habitat quality values would cause the acceptance of the null hypothesis (no significant relationship between fish density and habitat quality values) and the rejection of the hypothesis of the transferability of our models. Our statistical approach may therefore be more stringent than that used by Mäki-Petäys et al. (2002). This point can be illustrated by testing the transferability of HSI_M to the Escoumins River. For this purpose, we extracted the data from the HSC curves presented by these authors and adjusted a polynomial regression to each of their HSC. HSI_M was estimated as described by Mäki-Petäys et al. (2002). A two-sided χ^2 test confirmed that HSI_M was able to determine nonrandom habitat selection by fish (Fig. 5). However, we found no statistically significant relationship between fish density and HSI_M (Fig. 6), again because of the tendency of this model to underestimate the frequency of fish in excellent habitats. It must be recog-

nised, however, that although HSI_M underestimated fish density for $HSI_M > 0.7$, it performed remarkably well otherwise. Water depth (mean ± standard deviation; 0.27 m ± 0.17 to 0.47 m ± 0.22 depending on the rivers) and current velocity (0.28 m·s^{-1} ± 0.28 to 0.39 m·s^{-1} ± 0.31) in the Finnish rivers did not differ significantly from those conditions in the Escoumins River. However, the mean substrate size in three of the Finnish rivers was larger than 18 cm in diameter and, hence, larger than that found in either of our rivers. Whether the difficulty of HSI_M to predict fish density in excellent habitat is caused by the mathematical structure of this sort of biological model or by the difference that appears to exist between the substrate size of Escoumins River and the Finnish rivers studied by Mäki-Petäys et al. (2002) is difficult to establish. Interestingly, the reasons that explain why HSI from Sainte-Marguerite River could not be transferred to Escoumins River may be the same as those explaining the difficulty of transferring HSI_M to the Escoumins River. Our work suggests that the development of the kind of general model proposed by Mäki-Petäys et al. (2002) using HPI instead of HSI may further improve the potential for developing more transferable biological models.

In the same manner as differences that may exist between rivers limit transferability, our data suggest that there are also limitations to the predictions made by biological models. Our work indicates the existence of a strong relationship between HPI and fish density in both reaches for which transferability was attempted. It is possible that the HPI model developed in one reach of a river may allow for the prediction of fish distribution and density in another reach of the same river if both reaches are characterised by similar environmental conditions; however, this remains to be tested. In this sense, HPI may have a relative meaning among rivers (allow one to discriminate good from poor habitats) and an absolute meaning within a river (allow one to predict fish density). Both strategies are useful to assess, for instance, the effect of flow variations on the quantity and quality of habitats for fish. However, our analyses indicate that a HPI model structurally similar to that used in our study may not have an absolute meaning among rivers. It appears reasonable to expect that there may be more fish in habitats assigned HPI values of 0.8 than in habitats assigned HPI values of 0.4. This was true in the river in which our HPI model was developed and remained true in the river to which

we attempted the transfer of our biological model. This characteristic allowed us to successfully transfer the HPI model from the Sainte-Marguerite River and to predict fish distribution patterns in the Escoumins River. However, it is not be realistic to predict fish density in one river using HSC developed in another river. For instance, HPI values of 0.4 and 0.8 in the Sainte-Marguerite River were associated with fish densities of 0.5 and 1.5 fish·100 m^{-2} (Guay et al. 2000). Yet, these same HPI values were associated with fish densities of 0.0 and 1 fish·100 m^{-2} in the Escoumins River. In fact, there is no relationship between fish densities assigned identical HPI values in both rivers ($r^2 = 0.26$, $p = 0.13$). Considering the existence of among-river relationships between fish biomass or abundance and phosphorus, food biomass, and the availability of winter habitats (Symons 1971; Randall et al. 1995; Cunjak 1996), we can only speculate that the inclusion of such variables in the framework of HPI models may improve the value of these models among rivers. Much remains to be done to confirm this possibility. However, the prospect of using one HPI model in many rivers may facilitate the achievement of the ultimate objective of NHM — to evaluate the potential impact of variations of flow regime on fish habitat quality and quantity within a river.

Acknowledgements

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