The effect of cloud cover on the development of habitat quality indices for juvenile Atlantic salmon (*Salmo salar*)[1]

Philippe Girard, Daniel Boisclair, and Michel Leclerc

Abstract: We tested the validity of the predictions made by a habitat probabilistic index (HPI) developed using a description of the physical conditions (depth, flow velocity, grain size) used and avoided by parrs during days of different cloudiness. Thirteen surveys were designed to estimate the number and the distribution of parrs actively foraging within a 300-m reach of a river. During these surveys, the number of parrs actively foraging ranged from 12 to 118, cloud cover ranged from 5% to 100%, and water temperature ranged from 16.5 °C to 21.7 °C. The number of parrs actively foraging was negatively related to cloud cover ($r^2 = 0.44$ to 0.88) but was independent of water temperature. HPI models developed under low (<33%) and intermediate (34–67%) cloud cover explained 82% to 98% of the local variations of fish density. The HPI model developed under high cloud cover (67–100%) was unable to predict fish distribution observed during cloudy days. Our results suggest that HPI models developed when cloudiness is >67% may have a limited predictive power.

Résumé : Nous avons testé la validité des prédictions faites par un indice probabiliste d'habitat (IPH) développé à l'aide d'une description des conditions physiques (profondeur, vélocité du courant, taille du substrat) utilisées et évitées par des tacons durant des jours de différents couverts nuageux. Nous avons effectué treize survols visant à estimer le nombre total, la distribution et les conditions utilisées et évitées par les tacons qui s'alimentent activement dans une section de 300 m de rivière. Durant ces survols, le nombre de tacons s'alimentant de façon active a varié entre 12 et 118, le couvert nuageux a varié entre 5 % et 100 % et la température de l'eau a varié entre 16,5 °C et 21,7 °C. Le nombre de tacons s'alimentant de façon active a été négativement relié au couvert nuageux ($r^2 = 0,44$ à 0,88) mais a été indépendant de la température de l'eau. Les modèles IPH développés sous un couvert nuageux faible (<33 %) et intermédiaire (34–67 %) ont expliqué 82 % à 98 % des variations locales de la densité des tacons. Le modèle IPH développé sous un couvert nuageux important (67–100 %) a été incapable de prédire la distribution des poissons lors de jours nuageux. Nos résultats suggèrent que les modèles IPH développés lorsque le couvert nuageux >67 % peuvent avoir un pouvoir prédictif limité.

Introduction

Numerical habitat models (NHM) have been developed to estimate fish habitat quality in rivers and to predict the effect of natural and anthropogenic perturbations on the quantity, quality, and distribution of habitats for fish (Bovee 1978, 1982). Biological models imbedded within NHM are intended to estimate fish habitat quality using the environmental conditions used or avoided by fish and the conditions available to fish (deGraaf and Bain 1986; Morantz et al. 1987; Guay et al. 2000). Conditions used or avoided by fish are defined by recording physical variables at locations where fish are present or at locations where fish are absent.

These data are often obtained by performing visual surveys of fish distribution. Hence, factors that determine the adoption by fish of an actively foraging or a cryptic behaviour may affect fish visibility to observers, the environmental conditions defined as used or avoided by fish, and consequently the predictions made by biological models.

The diurnal foraging behaviour of juvenile Atlantic salmon (*Salmo salar*) in the summer consists of holding a position on or above the substrate (most often a rock referred to as "home-rock") and performing frequent movements in the water column or towards the surface to capture invertebrates that drift in the flow (Kalleberg 1958; Fausch 1984). Numerous studies indicate that in the fall and winter,

P. Girard and D. Boisclair.[2] Université de Montréal, Département de sciences biologiques, C.P. 6128 Succursale Centre-ville, Montréal, QC H3C 3J7, Canada.
M. Leclerc. INRS-Eau, Université du Québec, CP 7500, Sainte-Foy, QC G1V 4C7, Canada.

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[2]Corresponding author (e-mail: Daniel.Boisclair@Umontreal.ca).

juvenile Atlantic salmon (herein referred to as parrs) exhibit a cryptic behaviour during the day and emerge from the interstices of the substrate during the night (Rimmer et al. 1983; Cunjak 1988; Bremset 2000). However, the diurnal cryptic behaviour of parrs may not occur only during the fall–winter period. Fraser et al. (1995) observed that parrs that lived in a river draining a glacial catchment (water temperature of 7.7–8.4 °C) displayed a cryptic behaviour during the day and emerged from the substrate during the night even in the summer. Manipulations of water temperature under laboratory conditions showed that parrs could be induced to adopt a diurnal cryptic behaviour when temperature is decreased below 15 °C while they continued to express a diurnal foraging behaviour at temperatures above 16 °C (Fraser et al. 1995). Adoption of a diurnal cryptic behaviour at water temperatures below 10–15 °C has been hypothesised to be a consequence of a reduced swimming performance at low temperatures (Webb 1978; Rimmer et al. 1984). The lower swimming capability has been argued to impede on the ability of fish to escape endothermic predators (Heggenes et al. 1993; Fraser et al. 1995). In situ observations performed by Gries et al. (1997) and Gries and Juanes (1998) during mid- and late summer suggest that parrs may display a cryptic behaviour during daylight hours even at temperatures above 16 °C. The effect of light intensity on the reactive distance (Benfield and Minello 1996) and the foraging efficiency (Fraser and Metcalfe 1997) of fish preying on drifting invertebrates may be invoked to explain the adoption by fish of a cryptic behaviour even during daylight hours of the summer period. Yet, the effect of light intensity on fish behaviour and on the predictions made by habitat models is not known.

The objectives of our work were (1) to assess the relative importance of water temperature and light intensity on the diurnal foraging activity of Atlantic salmon parrs during the summer and (2) to evaluate the effects of the potential interaction between water temperature, light intensity, and parr behaviour on the quality, quantity, and distribution of summer habitats predicted by biological models imbedded within NHM.

Material and methods

The approach used to attain our objective combined four operations: (1) the assessment of the number and location of parrs actively foraging under different light conditions and water temperatures; (2) the development of a hydrodynamic model to define the physical conditions used and avoided by parrs; (3) the development of biological models for different light conditions and water temperatures; and (4) the comparison between real fish distribution and habitat distribution predicted using NHM implemented with biological models developed under different conditions.

Study site and species

Sampling was conducted in the Escoumins River in the Haute-Côte-Nord Region of Quebec at ~600 km northeast of Montreal (Fig. 1). The watershed of the Escoumins River covers an area of 979.7 km². The flow of this river is controlled by dams constructed at the head of the river and on its main tributaries. The study site was a 300-m reach located 20 km from the junction of the Escoumins and St. Lawrence rivers. The width of the reach studied ranged from 21.7 m to 47.5 m. This reach consisted of a series of pools (maximum depth of 1.4 m) and riffles. The average slope of the reach was 0.2%. The substrate ranged from gravel (diameter of 4×10^{-5} to 0.032 m) to metric boulders (over 1 m in diameter). The reach did not contain areas covered by wood debris and the canopy was absent.

We studied age-1+ and age-2+ juvenile Atlantic salmon (*Salmo salar*), hereafter referred to 1+ and 2+. In our study, 1+ (7.5- to 10-cm fork length (FL)) and 2+ (9- to 11.5-cm FL) fish were treated indistinguishably because they could not be discriminated by visual observations. Parrs represented 97% of the fish observed over the reach. Other fish species observed were brook charr (*Salvelinus fontinalis*), American eel (*Anguilla rostrata*), longnose sucker (*Catostomus catostomus*), and sea lamprey (*Petromyzon marinus*).

Numerical habitat modelling

NHM consists of a hydrodynamic model and a biological model. The NHM used is a two-dimensional hydrodynamic model that predicts the variation of water depth and flow velocity over the surface area of a reach at a given flow (Leclerc et al. 1990, 1995). This model was inputted with the topographic description of the riverbed, the mapping of substrate grain size over the reach modeled, a series of physical coefficients (water viscosity and friction), and assumptions about fluid dynamics (conservation of water, mass, and momentum; Secretan et al. 2001; Secretan and Leclerc 1998). The biological model used is the habitat probabilistic index (HPI; Guay et al. 2000). This model is a multivariate logistic regression designed to distinguish the physical conditions used and avoided by fish. HPI models use depth (m), flow velocity (m·s⁻¹), and substrate grain size (m) as independent variables. HPI values range from 0 (poor habitats) to 1 (best habitats) and have been argued to represent the probability of finding a fish under given physical variables (Guay et al. 2000). NHM combines the predictions of the hydrodynamic model (water depth, flow velocity), the map of substrate grain size, and the biological model to produce a map of the spatial heterogeneity of habitat quality.

Sampling

Fish activity, light intensity, and water temperature

We assessed the number and the location of parrs actively foraging over the complete surface area of the reach studied, under different water temperature and light intensity conditions. Parrs were considered to be actively foraging when they held a position on or above the substrate or when they fed. The number and location of parrs actively foraging was estimated by snorkelling the complete surface area of our study site during a total of 13 surveys (from 29 June to 5 August 2001). Each survey began at noon and was completed within 2 to 4 h. Observers snorkelled following a zigzag trajectory extending from one shore to the other while swimming always in an upstream direction to avoid fish disturbance (Cunjak et al. 1988). Each parr that was actively foraging was recorded by marking its home-rock with a coloured stone. The observers used a gentle movement of their

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Fig. 1. Location of the study site in the province of Quebec, Canada.
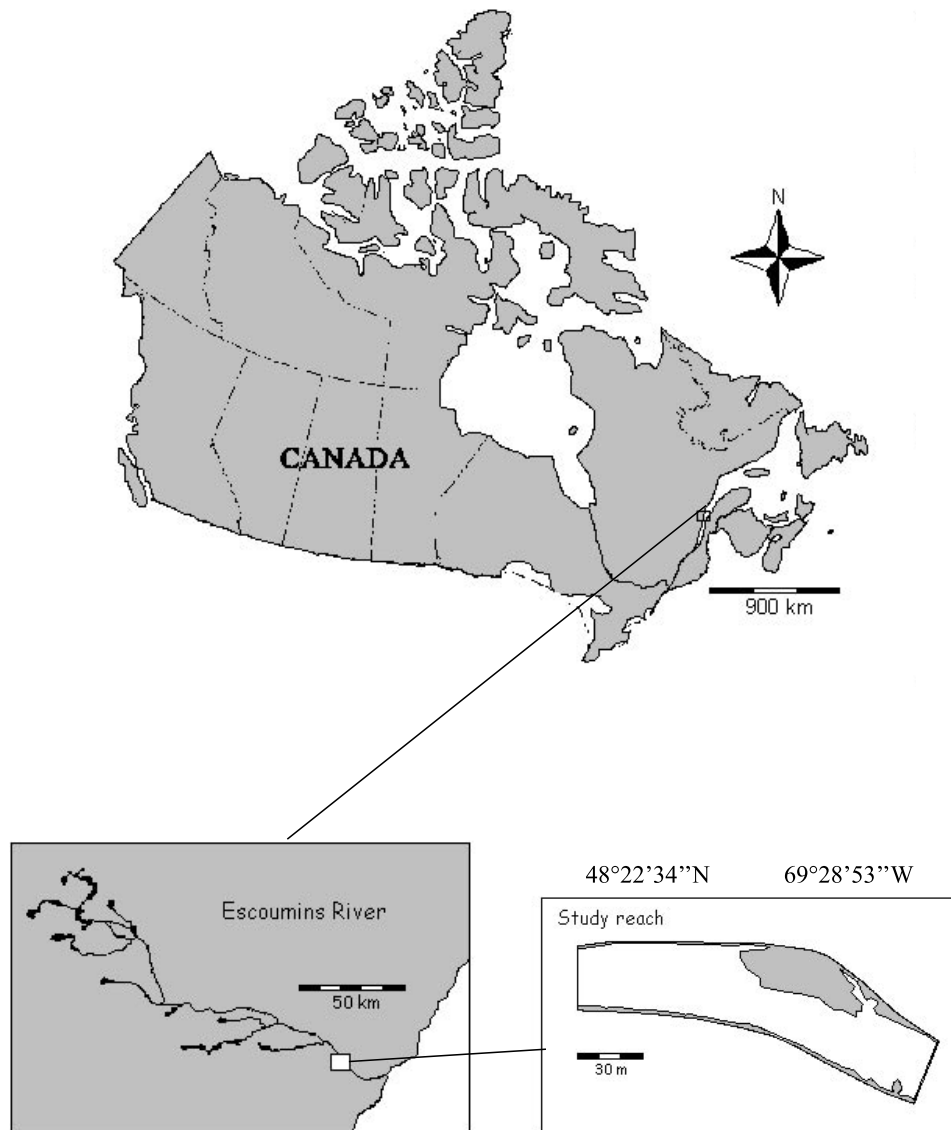
arms to direct the fish downstream and thereby avoid the recording of a second data point for a same fish. The coloured stones were georeferenced with a total station (electronic theodolite combined with an electronic distance measurement system, Sokkia SET3B; Sokkia Corp., Mississauga, Ont.) and an electronic data logger (Sokkia SDR33). Light intensity was assessed indirectly using a visual estimation of the percent cloudiness. The cloudiness and water temperature in the thalweg (measured with a hand thermometer) were noted at the beginning, middle, and end of each survey. Our surveys allowed us to count parrs and obtain precise maps of the distribution of actively foraging fish under contrasting light and water temperature conditions. Flow was noted at the beginning and end of each sampling day from the gauging station of the Ministère de l'Environnement du Québec 9 km from the river mouth. No tributaries entered the Escoumins River between the study reach and the gauging station. Flow was estimated to ensure that (*i*) each survey would be performed under a similar flow and (*ii*) the

hydrodynamic simulations would be performed under the flow prevailing during the mappings of fish distribution.

Development of a hydrodynamic model

The development of the biological model (HPI) requires the description of the depth, flow velocity, and substrate grain size used and avoided by fish. These data were obtained using the hydrodynamic model and the map of substrate composition over the surface area of the reach. The hydrodynamic model was developed using the topography and the map of substrate composition of the reach. We quantified the latitude, longitude, and altitude of 2589 sampling points distributed over the riverbed and shores and above the high-water level of the reach. These points represented the complete range of morphological, topographic, and granulometric variations in the study reach. Each point was georeferenced with the total station. For each point, substrate grain size was estimated visually using the concept of $D50$ (Wolman 1954). Given that the volume of a stone is deter-

Table 1. Cloud cover (%) measured before, in the middle of, and after underwater fish surveys. Average cloud cover and water temperature (°C) for each survey are also shown.

Surveys	Cloud cover (%)				Average water temperature (°C)
	Before	Middle	After	Average	
29 June	100	100	100	100	16
30 June	90	90	100	93.3	18
1 July	100	100	100	100	16
5 July	10	5	0	5.0	20
7 July	70	50	100	73.3	19
8 July	75	70	60	68.3	18
9 July	20	30	40	30.0	20
10 July	70	85	100	85.0	19
1 August	15	70	15	33.3	20
2 August	50	100	100	83.3	21
3 August	5	10	20	11.7	21
4 August	50	20	0	23.3	21
5 August	10	20	40	23.3	20

mined by three axes (A being the longest axis, and C the shortest), $D50$ is defined as the length (in metres) of the B axis of the median stone within an area of 1 m^2. We evaluated the quality of the predictions of the hydrodynamic model by measuring depth and flow velocity (averaged over 30 s using a Price or Pygmy current meter (Gurley Precision Instruments, Troy, N.Y.) installed at 40% of the height of the water column) at 30 locations distributed over our reach. These locations represented the widest range of physical conditions available in the reach. Flow was noted at the gauging station before and after these measurements. Field measurements of depth and flow velocity were compared with predictions made by the hydrodynamic model at the 30 locations under the corresponding flow.

Calculations

Development of biological models

The 13 surveys were classified in three categories of cloud cover: low (0–33.3%), intermediate (33.4–66.7%), and high (66.8–100%). Six surveys were performed under low cloud cover, one under intermediate cloud cover, and six under high cloud cover. HPI models were developed using three of the 13 surveys (one for each category of cloud cover). The surveys used to develop HPI models under low and high cloud were selected at random within our data set. A HPI model for each of these surveys was developed by overlaying the map of fish distribution and the maps of the physical variables (i.e., depth, flow velocity, and substrate grain size). The conditions used by parrs during a survey were obtained by noting depth, flow velocity, and substrate grain size at each location where a fish was observed. The conditions avoided by parrs were taken as depth, flow velocity, and substrate grain size at points of the reach where no fish were observed within a radius of 2 m. For each survey, the number of points used to describe the conditions avoided by fish was equal to the number of fish observed during this survey. The data of the conditions used and avoided by fish were used to develop one matrix per survey. Each matrix had four columns. The first column described the presence (1) or the

absence (0) of fish. The three other columns contained water depth, current velocity, and substrate size at sites used or avoided by fish. Each matrix was subjected to a Gaussian multivariate logistic regression (Guay et al. 2000). This procedure allowed us to predict HPI with depth, flow velocity, and substrate grain size under three levels of cloud cover (0%, 50%, and 100%).
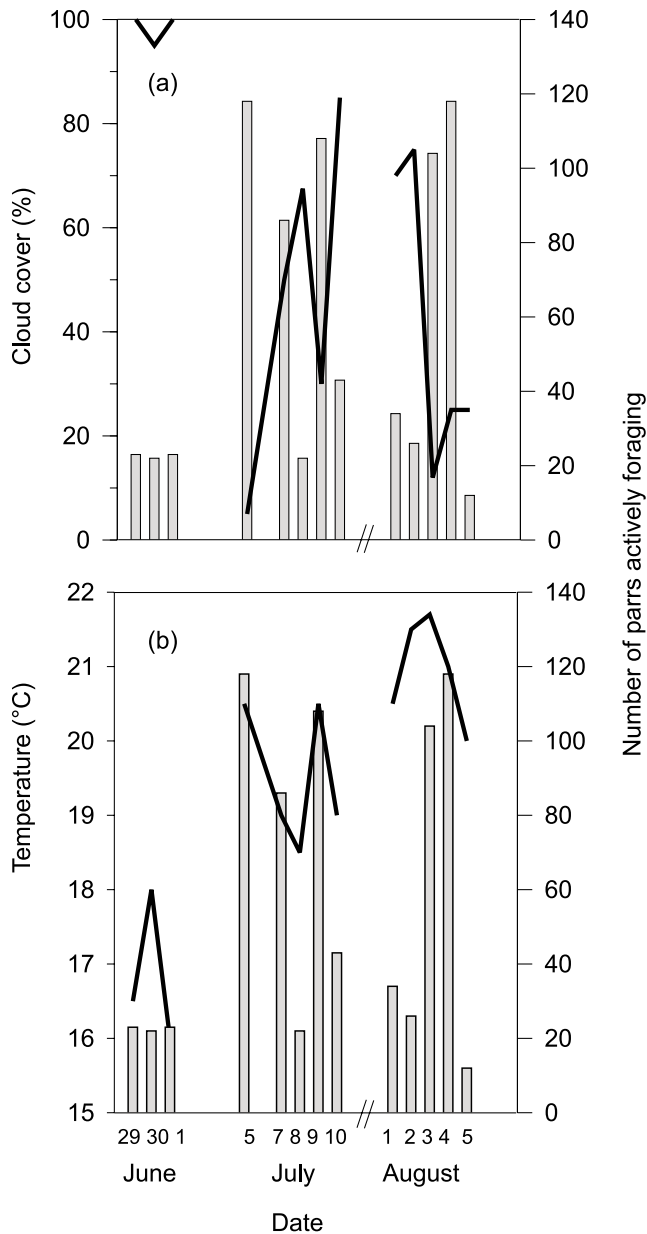
NHM partitions the surface area of the reach modelled into a mosaic of triangular tiles. NHM assigns a value of depth, flow velocity, and substrate grain size to six points that delimit each triangular tile (at the three summits and in the middle of each side of a triangle). NHM further calculates a habitat quality index for each of these points by inputting the HPI model with point-specific values of depth, flow velocity, and substrate grain size. Maps of areas of the reach having similar habitat quality indices (further referred to as habitat patches) were drawn using these points. The habitat quality predictions were grouped in 10 classes (0–1 with steps of 0.1). Three habitat maps were created, one for each HPI model developed for different cloud cover.

Statistical analyses

Fish activity, light intensity, and water temperature

The relationship between the number of parrs actively foraging, cloud cover, and water temperature was evaluated with a multiple regression. This analysis was performed using the average cloud cover and the average water temperature noted at the beginning, in the middle, and at the end of our surveys as independent variables. Average cloud cover was always within 10% of the cloud cover observed in the middle of our surveys except on 7 July and 1 August (Table 1). On these dates, average cloud differed by 25–40% from cloud cover in the middle of the surveys. The relationship between the number of parrs actively foraging, water temperature, and cloud cover was evaluated using either the average cloud cover or, for 7 July and 1 August, the cloud cover observed in the middle of the survey. Average water temperature varied by less than 1 °C during any given survey. The partial regression coefficients were quantified with

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Fig. 2. Variations of the number of actively foraging fish (shaded bars) with (*a*) cloud cover (black line) and (*b*) water temperature (black line).
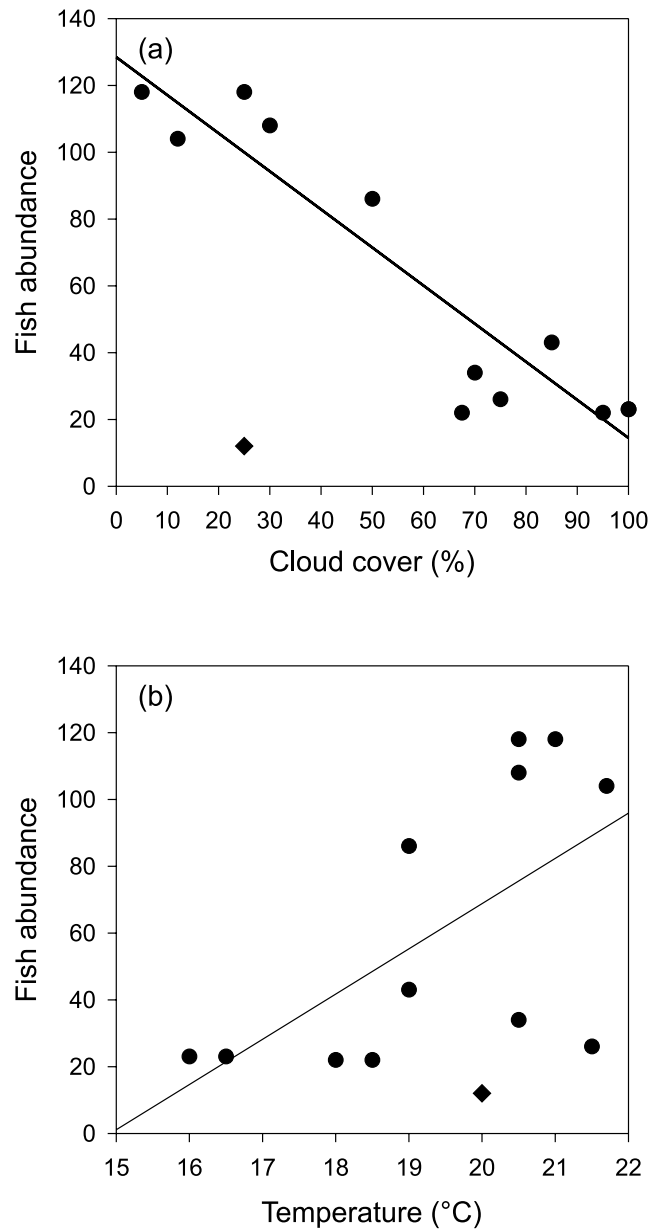

Fig. 3. Relationship between the number of parrs actively foraging and (*a*) cloud cover ($r^2 = 0.88$) or (*b*) water temperature ($r^2 = 0.37$). The sampling performed on 5 August is represented by a diamond. The regression lines were estimated without the sample of 5 August.

a multiple linear regression and permutation tests (Anderson and Legendre 1999).

Validity of the predictions made by the hydrodynamic model

We evaluated the predictive power of our hydrodynamic model by comparing the values of depth and flow velocity predicted by the hydrodynamic model to 30 real measures taken under the same flow. Predicted and measured values of depth and velocity were compared using a type II regression model (Mesplé et al. 1996). The predictions of the hydrodynamic model were considered valid if the 95% confidence intervals (CI) of slope and the intercept of the relationships between predicted and measured values included unity and

zero, respectively. Mean and variance of predicted and measured values were compared with t and F statistics.

Comparison between fish distribution and predicted distribution pattern of habitats

We compared real fish distribution with the distribution of habitats predicted by NHM implemented with the three HPI models using two surveys (one low and one high cloud cover) selected at random from the 10 remaining surveys. A polynomial regression was used to assess the positive relationship between fish density and predicted HPI values assigned to habitat patches. This was done six times (combinations of three HPI models and two surveys). Because predictions of

Table 2. The mean and the variance of the two physical variables predicted by the hydrodynamic model (depth and flow velocity) and corresponding values measured in the field ($n = 30$).

| | Depth (m) | | Flow velocity (m·s⁻¹) | |
	Predicted	Field	Predicted	Field
Mean	0.434	0.366	0.440	0.434
Variance	0.038	0.031	0.033	0.036

Table 3. Lower and upper limits of the 95% confidences intervals of slope and intercept of the relationship (major axis) between predicted and measured depths and flow velocities for a discharge of 4.5 m³·s⁻¹.

| | Depth (m) | | Flow velocity (m·s⁻¹) | |
Limits	Slope	Intercept	Slope	Intercept
Lower	0.821	–0.00052	0.712	–0.088
Upper	1.176	0.14392	1.217	0.131

HPI models were tested with a fish distribution taken from the same reach and, potentially, with the same fish used to develop HPI models, it can be expected, because of an autocorrelation between our dependent and independent variables, that HPI models will be adequate to predict fish distribution in the reach in which HPI models were developed. Hence, our procedure should not be interpreted as an attempt to validate HPI models, but as an attempt to identify invalid HPI models.

Results

Fish activity, light intensity, and water temperature

The number of fish observed over the complete reach during the different surveys ranged from 12 to 118 (average = 57 fish; Fig. 2). Cloud cover ranged from 5% to 100% and water temperature ranged from 16.5 °C to 21.7 °C among the surveys (Table 1). Multiple regression analysis showed that average cloud cover explained 44% of the variability of the number of fish actively foraging during our surveys ($p = 0.001$). Water temperature had no statistically significant effect on the number of fish observed ($p = 0.48$). A similar analysis using cloud cover in the middle of our surveys on 7 July and 1 August (for which the average was not within 10% of the cloud cover observed in the middle of the survey) suggested that cloud cover explained 58% of the variability of the number of fish observed ($p = 0.001$). Hence, the number of fish actively foraging decreased with cloud cover (Fig. 3a) but was unaffected by water temperature (Fig. 3b) in the range of conditions observed among the surveys. The last sampling point of the summer (5 August) was characterized by a very low number of fish observed ($n = 12$), despite the low cloud cover (25%; Fig. 3a) and the warm water temperature (20 °C; Fig. 3b). Elimination of the last sampling point of the summer from our analysis had no effect on our interpretation other than increasing the percentage of the variance of the number of fish observed explained by average cloud cover to 88% (using cloud cover in the middle of the surveys for 7 July and 1 August). We found a statistically significant relationship between average cloud cover (middle of survey values used for 7 July and 1 August) and water temperature ($p < 0.05$ tested by permutations). Water temperature tended to increase as cloud cover decreased ($r = –0.64$).

Validity of the predictions made by the hydrodynamic model

The mean (depth, $t = –1.22$, $p = 0.15$; flow velocity, $t = 0.28$, $p = 0.90$) and the variance (depth, $F = 1.18$, $p = 0.59$; flow velocity, $F = 1.59$, $p = 0.83$) of the predictions made by the hydrodynamic model were not significantly different

from the mean and the variance of the measures taken in the field at a comparable flow (Table 2). Furthermore, predicted and measured values were correlated ($r^2 = 0.84$ for depth; $r^2 = 0.62$ for flow velocity). The slope of both major axes calculated between measured and predicted depth or velocities was not significantly different from 1 (Table 3). In addition, the intercept of these axes was not significantly different from 0 (Table 3). Our results, together with arguments provided by Guay et al. (2001), suggest that the precision of the hydrodynamic model was sufficient for our purposes.

The average discharge measured at the gauging station during sampling days of summer 2001 was 6.8 m³·s⁻¹ (range = 5.0 to 8.1 m³·s⁻¹). The hydrodynamic simulation used in this work was implemented at this average flow. According to this simulation, the maximum water depth for a discharge of 6.8 m³·s⁻¹ was 1.40 m and the maximum flow velocity was 1.09 m·s⁻¹. A complete description of the depths, flow velocities, and substrate grain size available to fish over the study reach according to the NHM are presented in Table 4.

Biological models

The surveys selected for the development of HPI were 5 July (flow of 6.1 m³·s⁻¹, 5% cloud cover, number of fish observed = 141), 7 July (flow of 6.3 m³·s⁻¹, 50% cloud cover, number of fish observed = 105), and 29 June (flow of 8 m³·s⁻¹, 100% cloud cover, number of fish observed = 32). The following multivariate logistic regression model (Guay et al. 2000) was used to predict HPI values under different combinations of depth, flow velocity, and substrate grain size:

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

The three λ equations obtained using data collected under low (λ_L), intermediate (λ_I), and high cloud cover (λ_H) were

$$(2) \qquad \lambda_L = –2.39 + 5.73D + 3.03V + 0.52S – 6.29D^2$$

$$(3) \qquad \lambda_I = –3.06 + 9.88D + 3.31V – 4.13S – 9.68D^2$$

$$(4) \qquad \lambda_H = –11.25 + 27.65D + 4.21V + 61.34S$$
$$– 31.43D^2$$

where D is the depth (m), V is the flow velocity (m·s⁻¹), and S is the substrate grain size (m). The maps of habitat quality obtained using the three different HPI models always predicted relatively low habitat quality indices near the shores (HPI values from 0 to 0.1; Fig. 4). Furthermore, the maps of habitat quality indices predicted by HPI models developed under different cloud cover shared a common feature for rel-

Table 4. Depth (m), flow velocities (m·s^{-1}), and substrate grain size (m) available over the study reach at a discharge of 6.8 m^{-3}·s^{-1}. The availability of each physical condition is expressed as a percentage of the wetted surface of the reach.

Depth (m)	Percent available	Velocities (m·s^{-1})	Percent available	Substrate (m)	Percent available
0.0–0.3	31.4	0.0–0.2	7.1	Gravel (4 × 10^{-5}–0.032)	5.2
0.3–0.6	54.6	0.2–0.4	28.7	Pebble (0.032–0.064)	40.4
0.6–0.9	10.4	0.4–0.6	43.7	Cobble (0.064–0.25)	51.8
0.9–1.2	3.3	0.6–0.8	14.5	Boulder (0.25–1)	2.5
>1.2	0.3	>0.8	6.0	Metric boulder (>1)	0.1

atively high HPI values (0.6–0.7 or 0.9–1.0 depending of the model). The three HPI models predicted high HPI values just upstream of an island in the middle of the reach and relatively low HPI values near the upstream limit of this reach. Differences in HPI values predicted by these models were most obvious between HPI models developed with cloud cover <67% (low and intermediate cloud cover) and the HPI model developed with cloud cover >67% (high cloud cover). According to the models developed with <67% cloudiness, the study reach did not contain any habitat with a HPI index higher than 0.8. The surface area of habitat patches assigned the HPI values ranging from 0.9 to 1.0 represented 15% of the reach when using the HPI model developed with >67% cloudiness (near the left bank of the midsection of the reach; Fig. 4). The HPI values predicted by the models developed with <67% cloudiness in this same area were relatively low (0–0.1 or 0.4–0.5). Despite these differences, the HPI values averaged over the complete reach were very similar regardless of the model used (0.51, 0.54, and 0.51 for HPI models developed under low, intermediate, and high cloud cover, respectively).

Comparison between fish distribution and predicted distribution pattern of habitats

The maps of habitat quality predicted using NHM implemented with our three HPI models (Fig. 4) were compared with the real fish distribution during two surveys selected at random among days of low (9 July, 30% cloud cover, flow = 8.1 m^3·s^{-1}; Fig. 5a) and high (1 July, 100% cloud cover, flow = 5.5 m^3·s^{-1}; Fig. 5b) cloud cover. We found statistically significant and positive relationships ($p < 0.005$) between real fish densities in habitat patches under low cloud cover and HPI predictions for all HPI models (Fig. 6). However, the HPI models developed under low and intermediate cloud cover explained a larger fraction of the local variations of fish density at low cloud cover (94% and 98%, respectively) than the model developed under high cloud cover (82%). Relationships between fish densities under high cloud cover and predicted habitat quality were positive and statistically significant only for the HPI models developed under low and intermediate cloud cover ($p < 0.005$, $r^2 = 0.88$ and 0.79, respectively). The HPI model developed under high cloud cover was unable to predict fish distribution during the day of high cloud cover ($p > 0.1$; Fig. 6).

Discussion

Our results indicate that the number of fish adopting an actively foraging behaviour during the day may vary 5- to 10-fold among consecutive days of a summer. Our analyses further suggest that under the range of physical conditions found in our study, this variation is mostly related to the percent cloud cover ($0.44 < r^2 < 0.88$) and, by extension, to light intensity. Variations of water temperature did not explain a significant fraction of the among-day variations of the number of parrs adopting a diurnal foraging behaviour. Because increases in water temperature positively influence chemical and physiological processes in fish such as digestion rates and, thus, potential consumption rates (Elliott 1972; He and Wurtsbaugh 1993), it is possible that fish could increase their foraging activities during days when digestion rate and consumption rates are less limited by water temperature. This possibility is consistent with the studies of Fraser et al. (1995) and Bremset (2000), who found a clear positive relationship between the number of actively foraging parrs and water temperature. The lack of relationship between the foraging activity of parrs and water temperature in our study may be related to the small range of water temperature that we observed (16.5–21.7 °C) relative to Fraser et al. (1995; 2–18.5 °C) and Bremset (2000; 0–18 °C). The effect of the temperature range on the interpretation of our results is confirmed by the observation of Jonsson et al. (2001), who found that consumption rates of parrs in the lab at 16 °C did not differ from those estimated at 21 °C. Although fish foraging behaviour may be affected by water temperature in the range of 0 –18 °C, our results suggest that this effect is not statistically significant in the temperature range observed during our study.

One approach that can be used to interpret the relationship found between the number of actively foraging fish and cloud cover is to hypothesize that foraging strategies, like many other traits, have evolved to maximize fitness (Metcalfe and Steele 2001). It has been suggested that foraging strategies are chosen by fish on the basis of selective pressures defined by food availability or feeding rate (Lampert 1987; Reiriz et al. 1998; Metcalfe et al. 1999) and predation risk (Sih 1987; Eklöv 1997; Warburton and Brown 1997). In this context, fish may be hypothesized to select a foraging strategy that maximizes the ratio of food intake to predation risk. Our results are consistent with the hypothesis that factors decreasing the food intake – predation risk ratio may induce a larger proportion of a population of parrs to adopt a cryptic behaviour. Food intake is directly related to conditions that affect the capture efficiency of fish (Metcalfe and Steele 2001). Mechanistic models suggest that the capture efficiency of fish that hold a sit-and-wait position on or above the substrate partly depends on their ability to detect a food item and react sufficiently quickly to capture a prey before it is

Fig. 4. Maps of habitat quality indices predicted by habitat probabilistic index (HPI) models developed under (*a*) low, (*b*) intermediate, and (*c*) high cloud cover in the reach studied. HPI values ranging from 0 to 1 by intervals of 0.1 are represented using 10 shades of colour. Shores and islands are represented in grey. Simulations were performed for a flow of 6.8 $m^3 \cdot s^{-1}$.
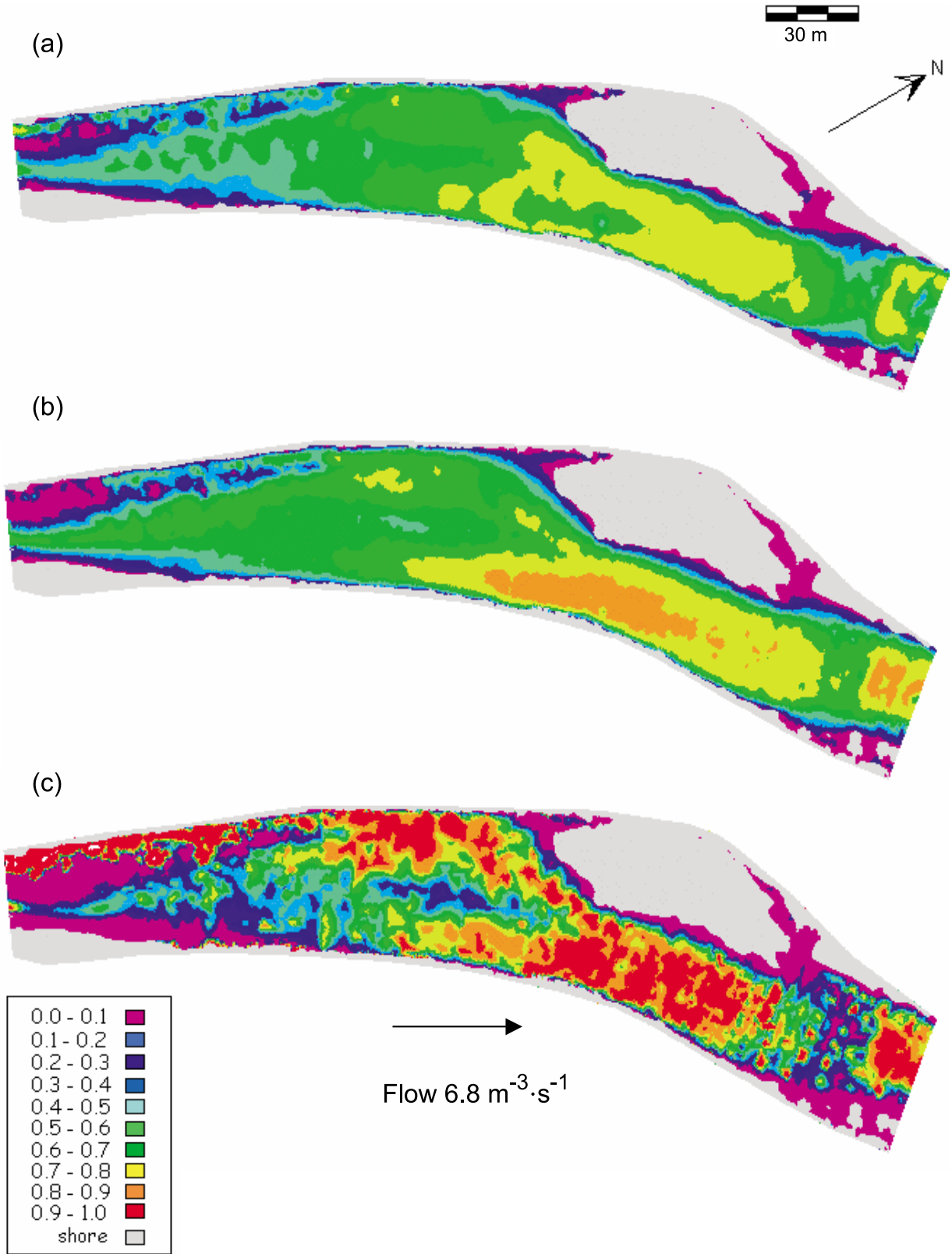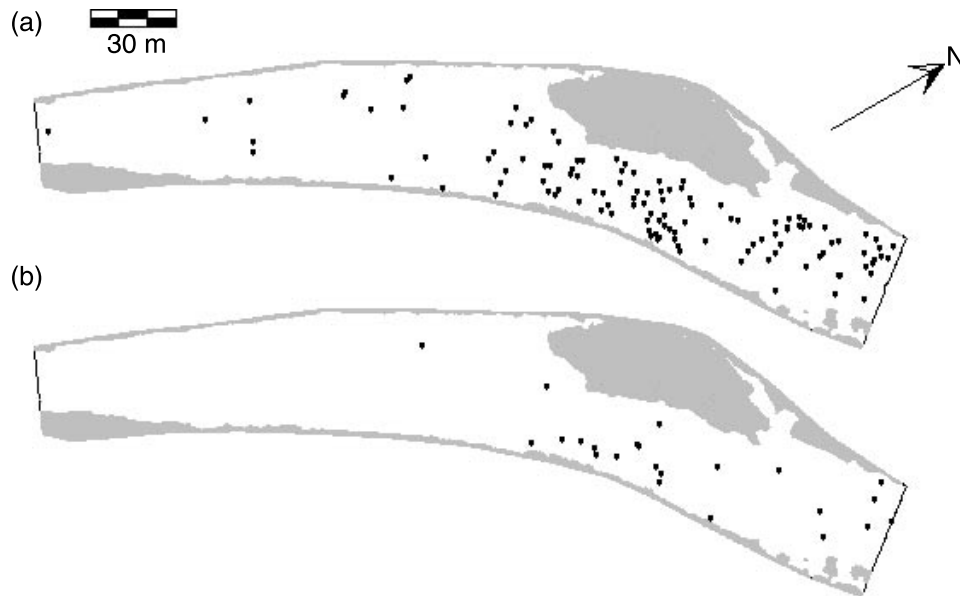
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Fig. 5. Observed fish distribution under (*a*) low and (*b*) high cloud cover in the reach studied. Each point represents the location of a single fish. The scale is in metres.

carried downstream (Hughes and Dill 1990; Metcalfe et al. 1997). Hence, any condition that will influence the reactive distance of the fish will also influence the time available to capture a prey and, therefore, the capture efficiency and food intake. It has been demonstrated that in low turbidity conditions, such as those encountered in Escoumins River, light intensity positively influences the reactive distance of parrs to preys and, consequently, their food intake (Benfield and Minello 1996). Light intensity may also affect the predation risk of parrs. The common merganser (*Mergus merganser*), the most important predator of parrs in Escoumins River, is a visual feeder. The efficiency of this predator is highest during daylight hours (Cramp and Simmons 1977). However, there are indications that light intensity may decrease predation risks affecting parrs. To detect fish, the common merganser submerges its head and visually scans areas underneath the water surface (Alvo 1995). This strategy is useful where depth is relatively important (<4 m) and flow velocity is moderate. In the Escoumins River, where mean depth is nearly 0.4 m and mean flow velocity is >0.8 m·s^{-1}, prey detection directly from the surface is more common (as used by the juvenile mergansers; Foreman 1976). Hence, cloud cover, which directly influences light reflection on water surface, may improve the efficiency of mergansers to detect parrs. One interpretation of our results is that the negative relationship found between the abundance of actively foraging parrs and cloud cover may be driven simultaneously by the two selective pressures that determine fish foraging strategies. Under low cloud cover, higher light intensity may improve the ability of parrs to capture their prey and may diminish the risk of predation of parrs by mergansers. As cloud cover increases, the food intake – predation risk ratio may decrease (food intake decreases and predation risk increases), and consequently, as exemplified by our results, fewer fish adopt an actively foraging behaviour. The number of fish adopting an actively foraging behaviour was more strongly related to estimates of

cloud cover in the middle of the surveys (when these were >20% different from estimates at the beginning or end of surveys) than to average cloud cover (including estimates noted at the beginning and end of surveys). This may suggest that the evaluation by fish of the benefits and costs associated with a certain level of cloud cover is done within minutes of a sudden change of cloud cover. Although our observations are consistent with the hypothesis that fish may select a foraging strategy (active or cryptic behaviour) that maximizes the food intake – predation risk ratio, we do not have any data (consumption or predation rates) allowing us to directly test this hypothesis.

Our analyses show that the quality of the predictions made by a habitat quality model such as HPI depends on the cloud cover prevailing during the collection of the data used to develop this biological model. HPI models developed under low to intermediate cloud cover could adequately predict habitat quality and fish distribution under any cloud cover. This is expected as HPI models were applied to the reach in which it was developed. Furthermore, many of the fish georeferenced to produce the map of fish distribution against which NHM predictions were tested may have been the same fish used to develop the HPI models. As such, our work cannot be interpreted as a statistically appropriate validation of HPI models. However, it is our contention that the inability of the HPI model developed under high cloud cover to predict fish distribution under these cloud conditions, despite the autocorrelation that exists within our data, is an indication that HPI models developed under high cover may be flawed. One alternate hypothesis that could explain the difficulty of a HPI model developed under high cloud cover to predict fish distribution is that this model was also developed using fewer fish (*n* = 64) than models under low and intermediate cloud cover (*n* = 210–282). We tested this hypothesis by assessing the performance of HPI models developed under low and intermediate cloud cover with a sample size identical to that used under high cloud cover conditions.

Fig. 6. Relationship between fish densities in habitat patches assigned different habitat probabilistic index (HPI) values during (*a*, *c*, e) low or (*b*, *d*, *f*) high cloud cover, and HPI values predicted by HPI models developed under (*a*, *b*) low, (*c*, *d*) intermediate, or (*e*, *f*) high cloud cover.
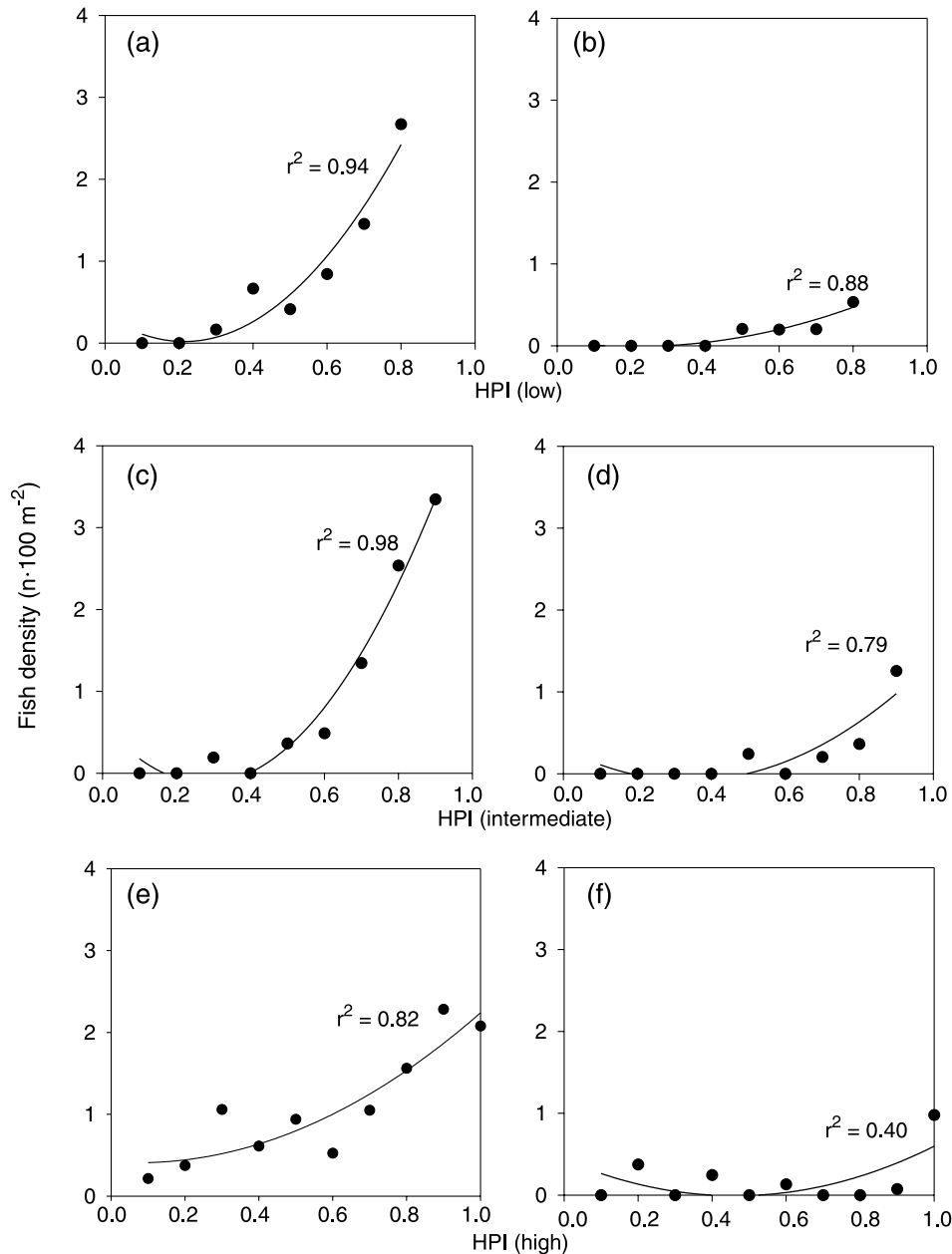
During this process, locations where fish were present or absent were selected at random within our data sets. These analyses showed that despite the lower sample size ($n = 64$), HPI models developed under low and intermediate cloud cover could adequately predict local variations of habitat quality and fish density within habitat patches ($r^2 = 0.85$–0.95), regardless of cloud cover. These simulations confirm that biologically meaningful and robust HPI models of parrs of Atlantic salmon may be developed only when cloud cover is <67%.

Acknowledgments

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