1	Do habitat measurements i	n the vicinity of Atlantic salmon ((Salmo salar) parr matter?
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15	Submitted to:
16	Fisheries Management and Ecology
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19 Abstract

20 Atlantic salmon (Salmo salar) parr habitat characterization is usually performed by in situ 21 measures of key environmental variables, taken at the exact fish location, or conversely, in large 22 sampling sections, often ignoring variability in the immediate vicinity around individuals. These 23 data may have a critical importance in development and validation of habitat preference models. 24 The influences of seven increasing distances of measurements, the number of considered 25 measures, and two depth of velocity measurement were tested in the calculations of HSI (Habitat 26 Suitability Index) from a multiple-experts fuzzy model. The radius of 50 cm around the fish, an 27 average measure of 6 measurements in the neighbouring environment and a velocity measured at 28 60% of the depth gave the highest HSI values. These results show some potential for the use of 29 an intermediate study scale, between micro- and mesohabitat, and questions how the fish habitat 30 conditions are currently measured.

Keywords: Fuzzy logic, Multiple-expert fuzzy modelling, Habitat model, Habitat measurement
 methods, Intermediate scale measurements, Habitat Suitability Index.

34 1 INTRODUCTION

35 In salmon habitat assessment, environmental measures characterizing this habitat are most often 36 unique focal measurements taken at the exact location of the fish (e.g. Morantz et al., 1987; Guay 37 et al., 2000), or a composite data from several measurements realized in large sampling section 38 (e.g. Hedger et al., 2005). Atlantic salmon part are territorial: they present agonistic behavior to 39 defend a territory in order to maintain the best possible place to feed, shelter and grow (Gerking, 40 1953; Heland & Dumas, 1994; Höjesjö, Kaspersson, & Armstrong, 2015). The size of this 41 territory varies according to factors such as fish size, age, habitat heterogeneity and food 42 availability (Grant, Steingrimsson, Keeley, & Cunjak, 1998; Keeley & Grant, 1995; Lindeman, 43 Grant, & Desjardins, 2015), centred on a "home rock" around which the parr moves (Guay et al., 44 2000). This behavior could interfere with the results of habitat models and characterization 45 analyses, since the data (i.e. the measurements of environmental variables) collected at the focal 46 location or in the whole section may not reflect the actual habitat being used by fish. In addition, 47 depending on the methodology and the fishing gears used to sample fish, *in situ* measurements of 48 habitat variables associated with fish presence can be done at different scales (Heggenes, 1990; 49 Wildman & Neumann, 2003). For example, sampling techniques such as direct viewing by 50 snorkeling (Flebbe & Dolloff, 1995) or detection by electronic tags can provide information on 51 the exact location of the fish and allow the researcher to associate habitat variable measurements 52 at the precise location of the fish. Alternatively, seining or electrofishing (Foldvik, Einum, & 53 Finstad, 2016; Mäki-Petäys, Erkinaro, Niemelä, Huusko, & Muotka, 2004) do not allow this 54 precision and the subsequent measurements of environmental conditions are related to a larger 55 area of capture. Finally, the protocols used to describe salmon habitat are different: the water 56 velocity can be measured at or near the bottom (e.g. Heggenes et al., 1995) or at a variable

depths according to the total depth of the water column (e.g. Morantz et al., 1987). In addition,
the habitat can be characterized by a single measurement per fish (e.g. Morantz et al., 1987) or
up to 15 measurements in the entire reach (e.g. Hedger et al., 2005).

Yet, these uncertainties may have a critical importance in habitat modeling. Indeed, before being 60 61 made available for managers, models have to be validated, i.e. they have to be tested with data 62 not used for model development and calibration. During the validation process, they have to 63 reach the required performance standards (Rykiel, 1996). In the specific case of habitat models, 64 one validation process consists in confronting the modeled predictions of habitat quantity and 65 suitability indices against field observations of presence or absence of fish (Fukuda & Hiramatsu, 2008; Mocq, St-Hilaire, & Cunjak, 2013; Mouton et al., 2008). Uncertainties in environmental 66 67 data and approximation in habitat characterization may induce errors, distort the validation, and 68 even affect the robustness of the model when the measures are used as input data.

69 We questioned the influence of these uncertainties in measured data in habitat models, and we 70 investigated the impact of the scale at which measurements are taken by hypothesizing that this 71 scale can affect the model results or the validation efficiency. We tested the hypothesis that focal 72 measurements (i.e. at the exact location of the fish) may not be the best representation of habitat 73 variables that determine (in part) fish presence, by using as a tool a previously developed fuzzy 74 model for Atlantic salmon (*Salmo salar*) part habitat (Mocq et al., 2013). Fuzzy logic is regularly used to model efficiently fish habitat (Muñoz-Mas et al., 2016) and this approach allows 75 76 determining a scale that provides a better habitat description according to the expert system. In 77 addition, the influences of the velocity in such a fuzzy system were assessed when it has been 78 measured at the bottom or at 60% of total depth, which is used as an estimate of average velocity 79 over the entire water column for shallow rivers. Finally, focusing on a study scale between 80 micro- and mesohabitat, we varied the number of measurements in a close neighborhood around

81 the individuals used to evaluate salmon habitat quality to highlight their impact in the model and 82 determine which numbers provide the best results, with the objective of improving the usual 83 method of sampling.

84 2 MATERIAL AND METHOD

85 2.1 Fuzzy model

86 To build the fuzzy logic Atlantic salmon parr rearing habitat model (Mocq et al., 2013), three of 87 the most important variables defining salmon distribution and abundance, i.e. depth, velocity and 88 mean substrate diameter (Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003; Bardonnet & 89 Baglinière, 2000; Heggenes, 1990) were chosen as input variables, and Habitat Suitability Index 90 (HSI) as the output variable. Each variable domain was split into three categories defined by 91 combinations of linear membership functions, which constitute the fuzzy sets. Then HSI 92 consequences of each possible combination of every category of the three variables were 93 determined with "If...Then..." fuzzy rules, i.e. 27 possible rules. A comprehensive presentation 94 of the fuzzy method and model building is provided by Mocq et al. (2013).

Since the experts' geographic range of knowledge showed influences on the fuzzy model results (Mocq, St-Hilaire, & Cunjak, 2015), only those from eastern Canada were selected. Twenty experts defined individual fuzzy sets and fuzzy rules, which were integrated and treated with the fuzzy package FuzzyToolkitUoN in R (R Development Core Team, 2016). The Mamdani inference method was used (Mamdani, 1977; Shepard, 2005) to process data from fuzzy input sets to the fuzzy output set. The defuzzyfication (i.e. the transformation from the final fuzzy sets to a crisp number) was done by the commonly used method of centre of gravity (Jorde,

102	Schneider,	Peter,	&	Zoellner,	2001),	providing	an	HSI	value	between	0	(representing	an
103	unsuitable	habitat)	ano	d 1 (repres	enting t	he most sui	tabl	e habi	itat) foi	r each exp	ert	•	

104 2.2 Sampling campaign

105 2.2.1 Study sites

Environmental measurements were taken in three Canadian Atlantic salmon rivers (Fig.1): the
Sainte-Marguerite River (Québec), the Little Southwest Miramichi River and its tributary,
Catamaran Brook (New-Brunswick).

109 Catamaran Brook flows for 20.5 km for a drainage basin of 50 km² (Cunjak, Caissie, & El-Jabi, 1990) with a mean annual discharge of 0.6 m³ s⁻¹ (Benyahya, Daigle, Caissie, Beveridge, & St-110 Hilaire, 2009). The Little Southwest Miramichi (Cunjak et al., 1990; Johnston, 1997) drains a 111 1340 km² basin with a mean annual discharge of 32.2 m³ s⁻¹ (Benvahya et al., 2009). These 112 113 streams are characterized as relatively pristine (Cunjak et al., 1993). Finally, the Sainte-114 Marguerite River is a 100 km-long river (Guay et al., 2000), with a catchment of 2100 km² and a mean annual discharge of 30.93 m³ s⁻¹ (Benyahya et al., 2009). Wild Atlantic salmon populations 115 116 are present in all three rivers.



Figure 1: Localization map of the Sainte-Marguerite River (Québec), Little Southwest Miramichi River and its tributary, Catamaran Brook (New-Brunswick).

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118 2.2.1 Sampling method

The sampling campaign took place in July 2012, at four sites in Catamaran Brook and two sites in Little Southwest Miramichi. Two sites were sampled in the Sainte-Marguerite River, in June and September of 2012. The considered reaches were sections of length 5 times larger than the width when the width was lower than 8 m. If the width was larger than 8m, a 6x25 m subsection along the banks was sampled. The protocol was divided into three steps. First, salmon parr (1 and 2+ year-old) location was assessed by a snorkeling diver moving upstream in zigzag patterns, reaching the fish location from behind to avoid flight. Upon recognition, the diver waited motionless for a minimum of one minute to ensure that the fish position was not influenced by the observer. A painted stone was dropped onto the bottom as a position marker.

129 Environmental measurements were done for the whole reach, including in the vicinity of the 130 spotted fish. The whole reach were assessed by measurements along transects, every 2 m, with 131 nine measurements per transect, each measure constituting a coordinated node of a grid, dividing 132 the section into cells. Depth was measured with a ruler, and velocity with an electronic 133 flowmeter Flo-Mate model 2000 (Marsh-McBirney, inc.) during at least 2 min, at the bottom (i.e. 134 the position of the parr on its home-rock) and at 60% of the depth in the water column (i.e. 135 classical depth of velocity measurements). Substrate composition was assessed by evaluating the 136 proportion of the different classes of grain size according to the modified Wenthworth scale 137 (Schoeneberger, Wysocki, Benham, Soil Survey Staff, & Natural Resources Conservation 138 Service, 2012) and a mean substrate size was calculated by weighting the diameter of each class 139 by the evaluated proportion observed at the site.

Microhabitat measures were made at the precise position and in the vicinity of the located fish. Velocity and depth were measured, first at the exact location of the fish, then at distance of 10, 25 and 50 cm from it, representing respectively a circular area of 0.04, 0.2 and 0.79 m², for a total of 5 points around a circle for each radius (3 upstream, 2 downstream). The substrate was assessed by evaluating the proportion of the different classes of grain size, at the exact position of the fish first, then in a square of 10, 25 and 50 cm on each side always centered on the fish.

146 2.3 Data process and statistical analysis

147 First, for each measurement point, a mean Habitat Suitability Index (HSI) value was calculated 148 through the fuzzy inference system of each expert, providing a spatial distribution of HSI. One 149 HSI value was calculated for velocity measured at 60% of the total depth (V_{60}) and for velocity 150 measured at the bottom (V_{bot}). These two sets of mean HSI values were compared with a 151 Wilcoxon matched-pairs signed-ranks test. The variation between the two HSI values at a same 152 point were calculated for each expert and then averaged to visualize the consequence on the 153 differences of velocity measures on a map. The same process was repeated with environmental 154 measures at the exact location of fish. Since the sampled sites presented low part density, it was 155 considered that the choice of location by the parr was made regarding habitat quality only (i.e. 156 likely no density-dependence effect). The values of HSI were compared with a Wilcoxon 157 matched-pairs test with correction for multiplicity. Our hypothesis was that a fish will choose a 158 location not only because of the conditions at a focal location, but because of the conditions 159 experienced in a short-range neighborhood around the focal location. Consequently, considering 160 the neighboring environmental conditions of the fish position should improve the model results 161 by better describing habitat at a fish location, highlighted by an increase of the mean HSI and/or 162 a decrease of the variability, until a limit where the HSI mean should decrease and/or the 163 variability should increase again.



Figure 2: conceptual scheme of our study of impacts of increasing measurements distances on multiple-expert fuzzy models. (* except d310, half of combinations were performed)

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The habitat quality was also assessed within an increasing area around the fish. The unique measure realized at the exact location of the fish provided the focal data, using a mean substrate size according to the proportion of different size classes, the velocity measured at 60% of the depth and the depth measured using a ruler with a 1cm precision. The integration of measures realized at three distances (i.e. 10, 25 and 50 cm) around the fish provided the data for the areas of 0.04, 0.2 and 0.79 m². Finally, 4, 11 and 30 m², represented by circles around the fish with respective approximate radii of 113, 190 and 310 cm, were assessed by integrating the measured

172 data from the grid when they were located in the appropriate area. Then, for each distance and 173 for each fish, mean HSI was calculated from the fuzzy sets and rules developed by each expert, 174 for all of the combination of 5 measurements encompassed in the considered area (Fig. 2). The 175 mean depth, velocity and substrate size of all considered measurements were used as input data 176 in the fuzzy system. For the distance of 310 cm, half of the possible combinations of a set of 5 177 out of 16 measurements, randomly drawn, were used because of computational limitations, but 178 representing a final 50 344 combinations, and 1,066,880 HSI values. The accuracy of each model 179 was estimated with the kappa statistics (see for example McHugh, 2012), with a threshold of HSI 180 at 0.5 beyond which the habitat is considered suitable. Since presenting the HSI values did not 181 allow to visualize the variation of the HSI value for a same fish, the variation of value from the 182 HSI value at the focal point, and the mean HSI value for the considered distance were calculated 183 for each fish. The HSI values according to the distance, and then the variation with the focal HSI 184 values were compared with a Friedman two-way analysis of variance, the non-parametric test 185 corresponding to a repeat-measure ANOVA, with a *post hoc* analysis i.e. a Wilcoxon matched-186 pairs test with correction for multiplicity.

187 Finally, to evaluate the optimal number of environmental measurements, all measurements 188 included in a radius of 25 cm were considered for each parr (i.e. 11 measures for most of them). 189 All possible combinations of measures, including 1 to 11 measures, were averaged and a HSI 190 value was calculated for each expert fuzzy system and each fish. The accuracy of each model 191 was also estimated with the kappa statistics with a threshold of HSI at 0.5. The variation with 192 the HSI at the focal position of the fish were calculated for each expert, and then averaged for 193 each fish. The HSI variations were compared with a Friedman two-way analysis of variance with 194 a *post hoc* analysis (Wilcoxon matched-pairs test with correction for multiplicity). The optimal

- 195 number of measurements to characterize the salmon habitat was seen as the category providing
- 196 the highest HSI associated with fish presence and/or the smallest variability.

197 3 RESULTS

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198 On the 10 considered sites, a total of 1366 points were sampled, showing an overall HSI mean of

200 overall HSI mean of 0.48 ± -0.15 (range from 0.17 to 0.71) when velocity is measured at the

201 bottom (Tab. 1, Fig.3).

Table 1: Mean, minimum and maximum of Habitat Suitability Index (HSI) values from multiple-experts fuzzy system, with velocity measured at 60% of the depth (V₆₀) and at the bottom (V_{bottom}), and the calculated variation at a same point, considering the entire reach of the station.

0.42 + - 0.12 (range from 0.17 to 0.7) for the velocity measured at 60% of the depth, and an

	~ .	Year	HSI V ₆₀			HS	I V _{botto}	m	Variation		
River	Site		Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Catamaran	Div2	2012	0.35	0.17	0.59	0.37	0.17	0.66	-0.03	-0.27	0.05
Catamaran	Lor	2012	0.35	0.17	0.64	0.36	0.17	0.63	-0.01	-0.12	0.15
Catamaran	Мос	2012	0.38	0.18	0.66	0.42	0.18	0.67	-0.04	-0.25	0.16
Catamaran	Tom	2012	0.33	0.17	0.59	0.34	0.17	0.57	-0.01	-0.19	0.21
St-Marguerite	Smp	2012-06	0.51	0.29	0.69	0.59	0.31	0.71	-0.08	-0.29	0.15
St-Marguerite	Smp	2012-09	0.51	0.29	0.67	0.58	0.27	0.71	-0.07	-0.30	0.23
St-Marguerite	Smt	2012-06	0.39	0.19	0.70	0.48	0.19	0.68	-0.09	-0.25	0.13
St-Marguerite	Smt	2012-09	0.38	0.21	0.66	0.43	0.21	0.68	-0.05	-0.28	0.22
Miramichi	Alx	2012	0.53	0.30	0.69	0.65	0.30	0.71	-0.12	-0.31	0.03
Miramichi	Spm	2012	0.49	0.28	0.67	0.58	0.31	0.70	-0.09	-0.30	0.21



Figure 3: Map of HSI value distribution, after spline interpolation from measuring points (white stars), for velocity measured at the bottom (left panel) or at 60% of the depth in the water column (middle panel), and the difference between them (right panel), in the Miramichi River (Spm site).

The two sets of HSI were significantly different (Wilcoxon matched-pairs signed-ranks test with correction for multiplicity, *p-value* < 2.2e-16). The variations of HSI values were ranged from -0.30 to +0.23 (mean= -0.06 +/-0.09).

In the three rivers, 93 fish were observed. HSI were calculated at the focal location of the fish, using the velocity measured at the bottom, then at 60% of depth (Fig.4). The resulting HSI values were significantly higher (Wilcoxon matched-pairs signed-ranks test, *p-value* <0.001), when the velocity was measured at 60% of the depth (mean= 0.47 + 0.11) than at the bottom



210 (mean= 0.42 + 0.1).

Figure 4: Distribution of HSI values with velocity measured at the bottom (left panel) or at 60% of the depth (right panel) at the exact fish location. Asterisks (*) indicate significant difference (Wilcoxon matched-pairs signed-ranks test, p-value <0.001).

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212 Regarding the influence of increasing area of measures around the fish, 7 distances were tested: 0 213 (focal measure), 10, 25, 50, 113, 190 and 310 cm around the parr (Tab.2, Fig.5). The focal 214 measures provided the lowest mean HSI and the largest variability (mean= 0.47 + 0.11). The 215 HSI increased slowly until d50, and decreased afterward, while the variability decreased 216 progressively. Regarding the variation of HSI by fish, the highest positive difference with the focal HSI value occurred at d50 (mean= $+3.92.10^{-2} + -6.35.10^{-2}$) and the highest kappa value is 217 218 reached at the same distance ($\kappa = 0.66$ at d50; Tab.2). Friedman's test was significant for the HSI 219 values and for the variations with the focal value (both *p*-value <0.01). The post hoc analysis 220 found only a significant difference between d0 and all other distance (all *p-value* <0.01) but no

other significant difference was found afterwards. The same analysis on the variation with the focal values highlighted significant differences between every distances (all *p*-value <0.05) but d113 and d190 (*p*-value= 0.28).

Table 2: mean values and standard deviation (SD) for HSI values, and for the variation from the focal HSI values for each parr, provided by a multiple-expert fuzzy system on every possible combination of 5 measures encompassed in seven increasing distances (0, 10, 25, 50, 113, 190 and 310 cm) around the considered parr.

Distance	Mean HSI	SD HSI	Mean variation with focal values	SD variation with focal values
d0	0.475	0.112	0	0
d10	0.499	0.106	0.024	0.058
d25	0.506	0.105	0.031	0.062
d50	0.514	0.099	0.039	0.064
d113	0.514	0.095	0.039	0.07
d190	0.514	0.096	0.039	0.08
d310	0.512	0.096	0.037	0.082

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Figure 5: Distribution of HSI values calculated with a multiple-experts fuzzy model (left panel) and the variation of this HSI values with the focal HSI value for each parr (right panel), according to the distance inside which measures were considered as input data for the model; the HSI values (lines) of a selection of 6 (out of 93) different fish are provided. Asterisks (*) indicate a significant difference with the other categories. Daggers (†) indicate non-significant difference between the two categories, all other differences are significant (both post hoc Wilcoxon matched-pairs signed-ranks test).

For the number of measurements to include in the models, the HSI provided by the different categories of included measures were averaged for each fish and for each expert. All HSI calculated showed an increase compared with the value calculated from the focal position 0*. The maximum is reached with 11 measures but the Cohen's kappa was the highest with 6 measures ($\kappa = 0.66$), providing 94% of the maximum improvement of HSI values (Tab. 3, Fig. 6). The variations of HSI values between categories were significantly different from each other (Friedman rank sum test, *p-value* < 0.01). Only the categories of 9, 10 and 11 measures showed

- significant differences with each other (Wilcoxon matched-pairs signed-ranks test, *p-value* <0.01
- for these three categories, p-value >=0.42 for the other combinations).

Table 3: Means and standard deviations of differences in values of calculated HIS, between focal environmental measures of Salmon parr location (0*) and averaged HSI from every combination of measures, including from 1 to 11 measures.

Number of												
included	0*	1	2	3	4	5	6	7	8	9	10	11
measures												
Mean	0	0.023	0.03	0.032	0.037	0.034	0.033	0.033	0.033	0.031	0.032	0.034
SD	0	0.07	0.073	0.072	0.07	0.072	0.073	0.073	0.073	0.069	0.068	0.066



Wilcoxon matched-pairs signed-ranks test).

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238 4 DISCUSSION

Highlighting and calculating the radial distance from the fish defining a circle in which measurements could be taken to describe accurately the physical habitat is one possible way to improve habitat characterization and subsequent habitat modeling. Seven different distances

242 were tested for each presence. The null distance, i.e. the focal measure taken at the exact location 243 of the fish, gave globally the lowest HSI values and the highest variability. This is potentially 244 explained by the fact that only one measurement of each habitat variable may introduce an important bias: assuming the fact that the parr may chose a suboptimal focal location with good 245 246 vicinity, if the exact location did not present good conditions for the fish, the error is not 247 attenuated by other measurements. Consequently, despite the geographic proximity of their 248 measures, the multiple-measures 10 cm-distance and the unique focal measure showed 249 significant differences in their calculated HSI, the 10 cm-distance providing a slightly better HSI 250 than focal measurements. Then, increasing the distance improved the model performance: for a 251 same fish, the HSI calculated by the fuzzy system reached a peak at a distance of 50 cm, which 252 corresponded with an area of 0.79 m², consistent with previous assessment of parr territory sizes 253 (Keeley & Grant, 1995; Lindeman et al., 2015). Beyond this distance, the calculated HSI values 254 tend to remain constant, the loss of variability in HSI values being the sign of a homogenization 255 of the measures at a large scale instead of a model improvement, as proved by the large 256 variability of HSI values at large distance.

257 Our protocol gave the opportunity to explore the influence of the location of the velocity 258 measurements in an expert fuzzy system. As expected, the data highlighted the fact that the 259 velocities at the bottom were slower than at 60%, because of frictions with the substrate, and 260 sometimes even counter-currents were observed. Near the bottom, parr can save some energy 261 while having access to the drifting food, the habitat quality should be consequently higher there 262 than further up in the water column. The HSI values were slightly lower when the velocities 263 were measured at the bottom than at 60% of total depth. In addition, with the measurements 264 taken at the fish location, our result showed an improvement of the model with higher HSI when 265 the velocity is measured at 60% of the depth. Thus, having better calculated HSI at 60% of the depth instead of at the bottom for a benthic fish is unexpected and raises some questions. It is unclear if the experts unconsciously referred to the velocity in the middle of the water column when they built their memberships functions and rules, or if they consider the 60%-depth velocity is more representative of the velocity associated with the drifting food.

270 It is usual, when characterizing salmon habitat, to take one measure of velocity and depth, and 271 an assessment of the substrate at the exact location of the fish. Our results showed that the values 272 of HSI provided by one measure at the exact location of the fish were generally lower than 273 several measures realized in its direct environment. The average highest HSI value was obtained 274 when all the measurements of each habitat variable, at randomly selected locations (within a 275 radius of 25 cm), were aggregated, but 6 measurements provided the best model. More than 6 276 measurements improved marginally the model outputs and the extra time and efforts required is 277 not warranted in this case. However, a fixed number of measurements to describe the 278 environmental conditions cannot be applicable to every circumstance and should be adapted to 279 local habitat complexity. In addition, our results exhibit a snapshot of habitat suitability, for a 280 short time period and the integration of flow dynamics would be important to model adequately 281 the salmon habitat (Boavida, Harby, Clarke, & Heggenes, 2017). Nevertheless, our study shows 282 a clear difference in the models outputs, highlighting the needs to take into consideration 283 multiple measurements in a close range around the individuals.

Our results suggest that the best description of the parr rearing habitat during summer diurnal period to be used in the fuzzy logic model described by Mocq et al. (2013) is reached by taking into consideration the neighboring conditions, i.e. measuring variables at 50 cm from the fish and adding them to calculate a mean value. In addition, this multiple-points sampling protocol could improve the models. Moreover, the fuzzy model is based on expert knowledge and it is possible that they defined the fuzzy sets and rules using characteristics of parr habitat that include all or a 290 part of its territory instead of only its home-rock, as our results indicate. Our hypothesis about 291 the model efficiency was that a high calculated HSI for a presence indicated that habitat 292 description used in the calculations was accurate and consequently, led to a more efficient model. 293 However, parr were frequently present in habitats with calculated HSI under 0.5, while the 294 reaches presented large bands of good quality. Field observations indicate that, in the three 295 sampled rivers, densities extended from 0.5 to 13.5 ind/100 m², were too low to force some parr 296 to use poor-quality habitat. Therefore, density dependence-related biases are not the likely cause 297 of presence of fish in relatively poor habitat. This observation can more likely be explained by 298 expert's unsure or ill-translated knowledge in the fuzzy sets and rules. These biases are found in 299 the fuzzy sets and rules definition: the unsure or ill-defined knowledge could be represented in 300 fuzzy logic by an important overlap between successive categories or by membership functions 301 limits irrelevant with ecological reality. Indeed, accurate codification of the expert knowledge is 302 an important obstacle. The difficulties could come from the expert (unwanted forgetting of 303 information, difficulty of expression or abstraction, fear of personal knowledge disclosure and 304 use; Chevrie and Guély, 1998, Drescher et al., 2013), or from the method (poor ergonomics of 305 the worksheet used to collect data, lack of precision in words or concepts description; Knol et al., 306 2010). In addition, the growth of the part evolves quickly in few months, especially for the 307 youngest parr, modifying their habitat preferences and complicating the definition of the related 308 fuzzy sets. Finally, another explanation could be related with the physical factors that were not 309 included in the model: indeed, the habitat selection by parr is under the influences of multiple 310 factors (Armstrong et al., 2003), generally of lesser importance than the three selected variables 311 but sufficiently important to modify substantially the habitat selection of some of the fish.

This study is linked to the problematic study of scale, i.e. the spatial and temporal dimension of a process or an entity (Lewis et al., 1996). Considering the Atlantic salmon (*Salmo salar*)

314 physical habitat, some studies work at the microhabitat scale, measuring environmental physical 315 variables in the vicinity of the fish, on the order of the cm² (Armstrong et al., 2003; Heggenes et 316 al., 1995; Heggenes, Bagliniere, & Cunjak, 1999). By contrast, other studies are concerned with 317 the mesohabitat scale, from m² to some tens of m², equivalent to Channel Morphological Units 318 (CMU, e.g. riffle, glide, pool; Folt et al., 1998). For the habitat characterization, the mesohabitat 319 is too large to precisely describe salmon needs and preferences, while the microhabitat neglects 320 environmental elements which could influence the selection and the occupation of the habitat by 321 the fish (Shirvell, 1994). An intermediate scale, considering the exact location of the fish and its 322 close environment as potential used habitat, could be useful to describe more precisely the 323 habitat and improve the model predictions. Moreover, lots of scientific studies and protocols 324 about fish habitat are based, for their field data, on the measures of environmental variables at 325 the exact location of the fish: our results suggest a change in this protocol may be needed, in 326 order to improve the habitat description.

327 Acknowledgements

328 The authors wish to acknowledge every expert who agreed to participate in this study: 329 Alfredsen K., Belles-Isles M., Belzile L., Bergeron N., Bérubé M., Boivin A., Breau C., Buoro 330 M., Caron F., Clément M., Cuerrier D., Cunjak R., Dauphin G., Dumont R., Gauthier C., 331 Guérard N., Heggenes J., Johnston P., Lapointe A., Lesvesque F., Linnansaari T., Milner N., 332 Moore D., Murdock M., Noak M., Prevost E., Riley B., Rodriguez M., Sabourin F., Saltveit S.J. 333 and their respective organizations. We thank Genivar Consulting for hydraulic model outputs, 334 and A. Maheu, A. Blanchette, M. Samsom-Do and the crew of the UNB for their help on field. 335 Additionally, we thank C. Gignac for his help in GIS and V. Ouellet for graphical advices.

- 336 Funding: This work was supported in part by NSERC, Hydro-Québec and the Institut National
- 337 de la Recherche Scientifique (INRS).

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