Science on the edge of spatial scales: a reply to the comments of Williams (2001)[1,2]

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

Guay et al. (2000) evaluated the ability of a numerical habitat model (NHM) to predict the spatial distribution of juveniles of Atlantic salmon (*Salmo salar*) in a river. The NHM that we used consisted of a hydrodynamic model predicting the physical characteristics (current velocity, water depth, substrate composition) of habitats under any given flow and a biological model assigning an ecological value ranging from 0 (poor habitat) to 1 (excellent habitat) to habitats using their expected physical attributes as independent variables. The main objective of Guay et al. (2000) was to compare the predictions of NHM based on two biological models to the spatial distribution of fish in a river. The new biological model that we developed, the habitat probabilistic index (HPI), predicted a significantly larger fraction of the local variations of fish density ($r^2 = 0.86$) than the traditional habitat suitability index (HSI; $r^2 = 0.39$). Williams (2001) questioned several methodological and fundamental aspects of the work of Guay et al. (2000). The points raised by Williams (2001) about Guay et al. (2000) can be grouped into problems of wording, problems of sampling sufficiency, and problems of spatial scales.

Wording

The NHM used by Guay et al. (2000) partitions the surface area of the reach modelled into a series of triangular subunits. NHM thereby represents the reach modelled as a mosaic of triangular tiles. Guay et al. (2000) mentioned that the end result of the NHM is a map describing the habitat quality index assigned to each tile at a given flow. The assignment of a habitat quality index *to each tile* was used strictly to facilitate both the writing and the reading of our paper. The comments of Williams (2001) about the spatial scales at which our model was developed, implemented, and tested suggest that we should have specified that habitat quality indices were calculated for the six points delimiting each tile (see Fig. 2 in Guay et al. 2000). These points are located at the intersection and in the middle of the sides of each of the triangular tiles making up the grid used to perform our modelling. Maps of areas of the reach having similar habitat quality indices (further referred to as habitat patches) were drawn using these points. In our maps, habitat quality indices ranged from 0 to 1 and were grouped by intervals of 0.1. Each of the ten classes of habitat quality indices was identified in our maps by a different colour shade. Williams (2001) noted that no smoothing procedure to draw our maps of habitat quality indices was described in our paper. No smoothing procedure was described because none was used. All points within a habitat patch were assigned a habitat quality index corresponding to the specified range of habitat quality index for this patch (no point was "smoothed" to become part of a patch). The locations of the limits between areas assigned with different values of habitat quality were determined by linear interpolation between the habitat quality index assigned to the points delimiting the tiles. This interpolation had no major impact on the habitat patches drawn by our modelling because of the high density of points used to perform our simulations.

Sampling sufficiency

Williams (2001) repeatedly questioned the adequacy of our sampling and of the models that we used to estimate or predict the variables required to perform the numerical habitat modelling. Sampling sufficiency and model performance should be judged relative to the objective of our study. For instance, the field measurements of current velocity made to develop our habitat quality indices and to test the predictions of the hydrodynamic model were taken over 30 s at 6/10 water depth. This approach was selected because it represents the average current velocity within a water column (Dingman 1984; Gordon et al. 1992). Williams (2001) emphasized that taking more measures of current velocity (2/10 and 8/10 water depth) for longer periods of time may provide better estimates of this variable. It is clear that taking more measurements of current velocity will increase the precision of estimates of average current velocity (Kondolf et al. 2000). It is also clear that increasing sampling intensity will necessarily require more effort and time in the field. We feel that any suggestion to further increase the already important logistical effort required to develop NHM should

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J.C. Guay,[3] D. Boisclair, and P. Legendre. Université de Montréal, Département de sciences biologiques, C.P. 6128, succursale Centre-ville, Montréal, QC H3C 3J7, Canada.
M. Leclerc. INRS-Eau, C.P. 7500, Sainte-Foy, QC G1V 4C7, Canada.
M. Lapointe. McGill University, Department of Geography, 805 Sherbrooke W, Montréal, QC H3A 2K6, Canada.

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[3]Corresponding author (e-mail: guayje@magellan.umontreal.ca).

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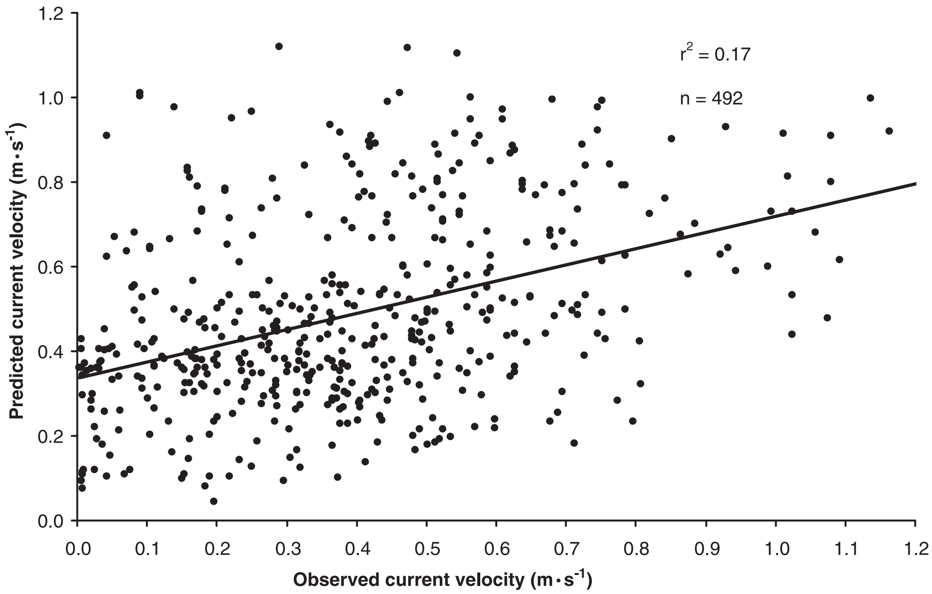
Fig. 1. Relationship between current velocities predicted by the hydrodynamic model used by Guay et al. (2000) at specific points of the Sainte-Marguerite River and observed current velocities at these points. Predictions and observations of current velocities were performed at a flow of 3.2 $m^3 \cdot s^{-1}$.



be justified with very convincing arguments. The strategy of increasing the quantity and the quality of data collected to estimate speed is absolutely correct if the ultimate objective of the sampling is to obtain more accurate data of current velocity. However, our ultimate objective was to model and predict fish habitat and fish distribution. We could not find in the references cited by Williams (2001), or anywhere else, a support for the proposition that the approach that he proposes is better at predicting something useful about fish and their habitats than the approach used by Guay et al. (2000). Furthermore, measuring average current velocity at a given point with a precision of, for instance, 10% appears futile when available hydrodynamic models used to predict current velocity during habitat modelling cannot discriminate instantaneous velocities that vary by an order of magnitude within the range of current velocity observed in the river that we studied. This can be visualized with the relationship between current velocities predicted by the hydrodynamic model for a series of sampling points at a given flow and current speed observed at these points for this flow (Fig. 1). As requested by Williams (2001), we added a total of 221 new data points to develop this relationship to the results presented by Guay et al. (2000). The poor performance of the hydrodynamic model to predict instantaneous current velocity in our study is no doubt related to our use of this model in extreme conditions defined by highly turbulent currents, shallow waters, complex riverbanks, and a riverbed of highly variable roughness on a small spatial scale. The hydrodynamic model that we used has been known to perform better in larger rivers (Leclerc et al.1995, 1996). As such, we recognize that our application of NHM and, in particular, of hydrodynamic models may be "at the edge" of what is scientifically possible with the models presently available. We doubt that increasing the sampling effort to estimate any of the physical variables would significantly affect this performance under the conditions studied. Williams (2001) underlined that Guay et al. (2000) did not show how well the hydrodynamic model predicted the average depth and velocity within the tiles. Unfortunately, we do not have the data to test the performance of the hydrodynamic model at the scale of individual tiles. However, our prediction is that the performance of the hydrodynamic model at the scale of individual tiles would be only marginally better than that found for point estimates.

The strategy used by Guay et al. (2000) was not to improve methods or models to measure or predict current velocity or any other physical variable. Rather, the strategy used was to test if simple and common methods of measurements together with hydrodynamic models currently available could allow us to predict something useful about fish and their habitat. We showed that the level of precision of the approach used to estimate current velocity (and all other variables) was sufficient to explain 86% of the variations in fish density at the scale of habitat patches. We are looking forward to new approaches to measure and model current velocity (or any other variable) that would further improve the predictive power of such NHM.

Spatial scale

The spatial scale for which a model is developed and tested depends on the objective of the modelling. In contrast with the interpretation of Williams (2001), our purpose was not to test the existence of a relationship between habitat quality predicted by NHM and fish density at the scale of 1 m^2 or individual tiles. While we recognize that the wording of our paper could have been more precise, it is not because habitat values are calculated at the scale of specific points, areas of 1 m^2, or tiles that the testing of the relationship between predicted habitat quality and fish density had to be performed at any of these scales. To our knowledge, all fish habitat models use data collected at different spatial scales (points, fish territories, etc.) to assess habitat quality

Table 1. Minimum, mean, and maximum percentage change in habitat probabilistic index resulting from a 20% or a 50% increase (+) or decrease (–) in water velocity (m·s^{-1}), water depth (m), and substrate size (cm).

	Velocity			Depth			Substrate		
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum
+20%	–0.2	–5.0	–22.9	–0.06	9.5	82.4	–0.01	–2.1	–19.9
–20%	0.4	6.0	22.3	–0.03	–3.1	–133.6	0.01	2.3	19.9
+50%	–0.3	–10.9	–57.5	–0.08	25.7	99.7	–0.03	–4.7	–47.8
–50%	1.2	17.1	53.0	0.14	–3.5	–195.0	0.03	6.4	47.9

at the scale of complete reaches (Boudreau et al. 1996; Heggenes et al. 1996). Consequently, it is not appropriate to conclude from our text that the testing of the relationship between predicted habitat quality and fish density was done (or had to be done) on a tile-by-tile basis. It is also inappropriate to interpret that we tested the prediction of NHM using randomly chosen points (Williams 2001). In fact, the Data analysis section of Guay et al. (2000) described that we tested the prediction of our NHM at the scale of ten habitat patches assigned quality indices ranging from 0 to 1 and grouped by intervals of 0.1. Because our purpose was to test the existence of a relationship between predictions made by NHM and fish density at the scale of habitat patches defined by the NHM, we believe that it is most important that hydrodynamic models should adequately predict physical conditions at this scale. Our study showed that, at the spatial scale of habitat patches, the hydrodynamic model that we used was able to discriminate average current velocities that differed by approximately 20%. Williams (2001) presumed that a 20% error of mean current velocity at the scale of habitat patches might be biologically significant. Although Williams (2001) provides no support for this presumption, our data and models suggest otherwise. We performed a sensitivity analysis to show the effect of modifying water depth, current velocity, or substrate composition by 20% or 50% on our estimates of HPI. The sensitivity analysis consisted of three steps. First, we estimated HPI with 8–12 classes of the three physical variables covering the complete range of these variables and of their combinations in the reach studied. This provided us with 1152 estimates of HPI further referred to as nominal HPI values (12 classes of depth × 12 classes of current velocity × 8 classes of substrate diameter). Second, one of the three physical variables was increased by 20% and the effect of this change on the corresponding nominal HPI values was noted. Third, this physical variable was also decreased by 20% to assess the effect of such a change on nominal values of HPI. The same procedure was used to assess the effect of a 50% increase or decrease of any physical variable. The effect of a 20% or 50% increase or decrease was tested independently for the three key physical variables to assess the relative sensitivity of our HPI model to these variables. These simulations indicated that a 20% and 50% change in current velocity resulted in a mean change of 6% and 17.5% in HPI, respectively (Table 1). Interestingly, for specific combinations of physical variables, a 20% change in water depth could affect HPI by as much as 133%. However, a 20% variation in current velocity and substrate composition never affected HPI by more than 22.9% and 19.9%, respectively. Hence, our sensitivity analysis tends to suggest that our HPI is most sensitive to water depth. This may partly explain why NHM performed relatively well despite the poor performance of hydrodynamic models at predicting current velocity at the scale of points. Taken together, our sensitivity analyses suggest that a 20% error in current velocity would result, at most, in a 23% change in HPI (e.g., at most, a change of HPI value from 0.4 to 0.5). As can be judged from our Results (Fig. 6*b* in Guay et al. 2000), this degree of variation has no effect on our finding of the existence of a strong relationship between the predictions of NHM and fish density at the scale of habitat patches. Williams (2001) suggested that considering the poor precision of available hydrodynamic models on an instantaneous basis, habitat modelling should be performed using an empirical approach such as proposed by Lamouroux et al. (1998). Although this approach appears promising, we believe that it should be tested in a manner similar to that used by Guay et al. (2000) before judging the relative merits of NHM based on empirical and hydrodynamic models.

We can only partly agree with Williams (2001) that the ability of two-dimensional hydrodynamic models to estimate the depth and flow fields well enough for numerical modelling remains to be tested. This evaluation depends on the definition of "well enough" and on the modelling objective (spatial and temporal scales). The only way to evaluate if the precision of hydrodynamic models is sufficient to assess fish habitat quality is to compare the predictions of NHM based on these hydrodynamic models with real fish distribution patterns at the desired scale(s). Although our models were developed using data collected and processed at the scales of 1 m^2 and individual tiles, we have not performed the comparison between predictions of NHM and fish density at these scales because, as we have shown, hydrodynamic models cannot adequately predict physical conditions at these small spatial scales. Furthermore, we do not feel that such comparison is useful in our case. Considering the average density of fish in the river studied (1–3 parrs/100 m^2), we would be correct in predicting that there are no fish in a given area of 1 m^2 in more than 96% of the cases. We are not sure, however, that this sort of prediction has much practical value in a decision-making process. Finally, even if it were possible, we would question the practical utility of predicting habitat quality at the scale of 1 m^2 on the basis that it may be difficult to adopt and implement management decisions on such a small spatial scale. At the scale of habitat patches, however, we found that habitat quality predicted by our NHM explained 86% of variations of fish density. Consequently, our work suggests that NHM allows us to predict something ecologically useful about fish habitats and at a spatial scale that is practically manageable. Hence, we agree with Williams (2001) that the question of the ability of two-dimensional hydrodynamic models to estimate key variables at the scales of 1 m^2 or individual tiles remains open.

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