## Short communication

# Improving models of juvenile Atlantic salmon habitat use through high resolution remote sensing 

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#### Abstract

The effect of spatial variation in substrate size on juvenile Atlantic salmon density in the Sainte-Marguerite, a major salmon-spawning river in QC, Canada, was investigated using ground surveys and remote sensing. Densities of both fry and parr were determined by single-pass electro-fishing at up to 48 sites along the length of the river in August of each of the years from 1997 to 2004. Substrate size was determined by two techniques. Firstly, a ground survey of median substrate size (D50) was conducted concurrently with the electrofishing, providing information on the substrate actually experienced by the salmon at the point of capture (a parcel area of $5 \mathrm{~m} \times 20 \mathrm{~m}$ for each site). Secondly, an airborne survey was conducted along the length of the river in August 2002 using a helicopter-mounted digital camera. Images from this survey were then processed to show the mean D50 in the area of each image (an area from bank to bank, 60 m in length along the river) encompassing each parcel. Relationships between juvenile salmon density and substrate size were determined using preference models where the model partitioning had been determined by regression tree analysis. For comparison, preference models were also produced where the model partitioning was determined arbitrarily. The shape of the relationships between juvenile salmon density and parcel D50 were similar to those between juvenile salmon density and mean image D50. However, the relationship was stronger with mean image D50, suggesting that the habitat surrounding the location in which juvenile salmon were found had a direct influence on their density. Additionally, preference models determined from regression tree analysis had greater explanatory power than those determined using an arbitrary partitioning approach. These results suggest that remote sensing, alongside a robust approach for determining preference models, may be an effective tool in modelling juvenile Atlantic salmon habitat use.


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## 1. Introduction

The dominant method for determining fish habitat use within rivers is by in situ ground survey, in which habitat characteristics are sampled concurrently and at the same locations within the river as the sample of fish density. A variety of approaches are then used for analysing relationships between the habitat and fish density data including regression analysis (Terrell et al., 1996), artificial neural nets (Reyjol et al., 2001) and generalised additive models (Hedger et al., 2005). One of the most established approaches is that of empirical preference modelling, often using some variant on the method outlined by Jacobs (1974), which shows the change in habitat use as a function of availability, usually by a step function in which the habitat is subjectively partitioned into a series of distinct classes. For example, substrate size is a key determinant of habitat selection by juvenile Atlantic salmon (Salmo salar L.) in rivers (Gries and Juanes, 1998). Empirical preference modelling has shown that juvenile salmon prefer moderately coarse substrates of pebbles ( $0.4-6.4 \mathrm{~cm}$ ), cobbles ( $6.4-25.6 \mathrm{~cm}$ ) and boulders (greater than 25.6 cm ) (Bardonet and Baglinière, 2000), with fry dominating the pebble to cobble range and parr dominating the cobble to boulder range (Klemetsen et al., 2003).

The limitation of the habitat modelling approach of measuring the habitat solely where the fish are found is that this approach ignores spatial patterns of habitat use, in which fish move throughout a home range (Martin-Smith et al., 2004) to exploit multiple habitats (Heggenes et al., 1999). Thus, fish density will be dependent not solely on the habitat characteristics in which they may be found but on surrounding characteristics-an area of optimal habitat may not support a high fish density if it is surrounded by an area of sub-optimal habitat. The application of remote sensing may increase coverage of the river habitat (Mertes, 2002; Lane et al., 2003; Gilvear et al., 2004; Legleiter et al., 2004) and overcome the spatialcoverage limitations associated with ground sampling. The dominant method for analysing remote sensing imagery has been through qualitative analysis, but the use of quantitative
techniques has increased in recent years (Whited et al., 2002; Carbonneau et al., 2004).

In this paper, we use high resolution remote sensing in the modelling of juvenile Atlantic salmon habitat use of different bed substrates in the Sainte-Marguerite River, QC, Canada. In particular, we examine how the synoptic coverage provided by remote sensing compares with the limited coverage available from ground sampling in terms of explaining substrate use by juveniles. We do this using preference models in which the partitions have been determined using the bilinear recursive partitioning technique of regression tree analysis-the rationale being that allowing the data to determine the partitioning will lead to a greater explanatory power than would be achieved through an arbitrary user-determined partitioning.

## 2. Study area and data analysis

The Sainte-Marguerite River ( $48^{\circ} 09^{\prime} 21^{\prime \prime} \mathrm{N}, 69^{\circ} 33^{\prime} 51^{\prime \prime} \mathrm{W}$ ) is a cobble-bed river located on the north coast of the SaintLawrence estuary in Québec, eastern Canada (Fig. 1) (Talbot and Lapointe, 2002). It drains a basin of $2130 \mathrm{~km}^{2}$, through its principle branch ( 98 km in length) and its north-east branch ( 97 km in length). The mean width of the principle branch is approximately 22 m at peak discharge in the spring. Width varies greatly: $25 \%$ of the river course has a width greater than approximately 30 m and the maximum width is greater than 60 m . Mean monthly discharge of the principle branch is approximately $25 \mathrm{~m}^{3} \mathrm{~s}^{-1}$ and the maximum daily discharge during peak flow may exceed $70 \mathrm{~m}^{3} \mathrm{~s}^{-1}$. The banks of the river are covered by either riparian vegetation, consisting of scrub or trees, or non-vegetated substrates (particularly at low flows). Given the width of this river, shading by riparian vegetation accounts for less than $10 \%$ of the river surface.

A ground survey of juvenile Atlantic salmon density was conducted on the principle branch of the Sainte-Marguerite in August of each year from 1997 to 2004. Forty-eight survey stations were sited along the length of the principle branch, with their positions being determined by a hand-held GPS in 2004.


Fig. 1 - The River Sainte-Marguerite. Survey station positions on the principle branch are shown by super-imposed filled circles.

Due to operational constraints related to the difficulty of sampling the river habitat, the actual position of the sites where juvenile densities were measured (parcels) varied from year-to-year within a range of approximately 30 m around each of the survey station positions. Additionally, samples were not made at every survey station in every year (measurements were made at only 21 stations in the year of minimum sampling effort). In each parcel (of dimension $5 \mathrm{~m} \times 20 \mathrm{~m}$ ), juvenile salmon density was estimated using single-pass electrofishing (see Jones and Stockwell, 1995) and were categorised on the basis of length as being either fry or parr. Single-pass electro-fishing has been used in habitat modelling (Rahel and Nibbelink, 1999; May and Brown, 2002; Paller, 2002) but produces less accurate estimates than multi-pass electro-fishing (Meador, 2003). Given this, the relative accuracy of single pass electro-fishing in the Sainte-Marguerite was determined by analysis of multi-pass samples obtained at 22 stations in a survey conducted by Ministère des Ressources naturelles et de la Faune, Québec, in this river in 1994. Densities in these stations were estimated by a maximum likelihood method (Junge and Libosvàrsky, 1965).

A ground survey of substrate size was conducted concurrently with the electro-fishing. A Wolman count (Gibson et al., 1998) of the substrate was acquired from each parcel, the length of the secondary axis of each particle was measured and a D50 (the median length) was determined. Remotely sensed imagery of the principle branch of the river was obtained between 10:00 and 15:00 h on 17 and 18 August 2002 (giving a solar elevation angle varying between $42^{\circ}$ and $52^{\circ}$ above the horizon) using a helicopter-mounted XEOS truecolour digital camera (GENIVAR Inc.). From an above-river elevation of 155 m , this provided a ground spatial resolution of 3 cm . The centre of each image was geo-referenced by a helicopter-mounted GPS, allowing cross-registration with the
survey station positions. Each image covered a ground area of $90 \mathrm{~m} \times 50 \mathrm{~m}$ so despite the variation in parcel positions around a single survey station all the parcels from a single station were included within a single image. D50 was estimated for each pixel using the semi-automated image analysis method outlined by Carbonneau et al. (2004), which used local variogram analysis of the images, calibrated with 'ground-truth' measurements of D50, to provide remotely sensed estimates of D50. Carbonneau et al. (2004) found that remotely sensed measurements explained $96 \%$ of the variance in the D50s determined by ground samples. D50s were estimated for both the wet bed (beneath the water level in the imagery acquired in August) and the dry bed (above the water level) because the mean water level of the river changed throughout the year. Thus, areas of dry bed would have been submerged when the mean river water depth was greater than in August, and may have had an impact on juvenile salmon habitat use. An example of the remotely sensed imagery can be seen in Fig. 2. A visual inspection of the data showed that some D50 estimates of greater than 40 cm were actually the result of features on the water surface, such as 'white water' induced by rapids rather than coarse substrates. Additionally, riparian vegetation, river debris and shadows from vegetation or debris caused spurious estimates. Such areas were removed from further analysis. The mean D50 of each image, using the entire wet and dry substrate, was then estimated.

Relationships between juvenile salmon density and D50 were determined using preference models in which the partitioning of the D50 range into distinct partitions was determined by regression trees. Regression trees use binary recursive partitioning to split a numeric response variable into increasingly homogeneous subsets (partitions) at partitioning nodes as a step function of one or more predictor variables (in this study, the predictor variable was parcel D50 or mean


Fig. 2 - Sample remotely sensed images: (a) panchromatic representation of the true colour images and (b) images processed to show D50. Parcel positions for 2004 have been overlaid on the D50 images.

D50 of the image). The advantage of using regression trees is that, being non-parametric, they make fewer restrictions on the type of variables that may be used. For example, they allow for modelling relationships between response and predictor variables where the variance of the response variable is a function of the predictor variable-a common occurrence in the relationship between fish densities and the environment (Terrell et al., 1996; Dunham et al., 2002).

Firstly, regression trees were fitted separately between each of fry and parr density and (i) the parcel D50 of the ground survey and (ii) the mean D50 of each remotely sensed image (mean image D50) encompassing the parcel. Regression trees were then pruned using cross-validation as a means of determining at what size (in terms of terminal nodes) the minimum deviance was achieved. Additionally, any partition nodes, which appeared to have resulted from over-fitting of the data were removed. Preference models were then fitted according to the method of Jacobs (1974) (Eq. (1)):
$P_{i}=\frac{S_{i}-A_{i}}{\left(S_{i}+A_{i}\right) \times 2\left(S_{i} \times A_{i}\right)}$
where $P$ is the preference for partition $i, S$ the proportional utilisation by juveniles of that partition and $A$ is the proportional availability of habitat in that partition. Preference mod-
els were fitted to each of parcel D50 and mean image D50 separately, and to parcel D50 and mean image D50 together. Models expressed preferences as varying from -1 (strongly avoided), through 0 (neutral preference) to 1 (strongly selected). To identify the relative strength of using regression trees for determining the partitioning, additional preference models were created where the partitioning had not been determined by regression trees, but instead had been arbitrarily set as being of equal width-firstly, using preference models with three partitions (partition breaks at 12.1 and 24.2 cm ) and secondly, using preference models with six partitions (partition breaks at 6.05, 12.1, 18.5, 24.2 and 30.25 cm ).

## 3. Results

In the multi-pass electro-fishing sample of 1994, the density estimates from the first pass explained, respectively, $75 \%$ and $77 \%$ of the variation in fry and parr density that was obtained from three-passes using a maximum likelihood method. Given this, it is reasonable to infer that a singlepass electro-fishing approach was sufficient for determining the relationship between juvenile density and substrate size.

Parcel D50


Mean image D50


Fig. 3 - Regression trees of fry and parr density against parcel D50 and mean image D50. Values shown in bold above each partition node show the D50 where partitioning results in minimum deviance; values at each terminal node show the mean juvenile density of the respective partition.


Fig. 4 - Preference models of fry and parr for parcel D50 and mean image D50. Partition breaks have been derived from the respective regression trees. Preferences may vary from -1 (strongly avoided), through 0 (neutral preference) to 1 (strongly selected).

The initial partition nodes of the regression trees differed depending upon whether parcel D50 or mean image D50 was used: 3.4 cm (fry) and 10.5 cm (parr) for parcel D50; 19.2 cm (fry) and 4.8 cm (parr) for mean image D50 (Fig. 3). However, preference models with the partitioning determined from the regression trees were similar regardless of the method used to determine D50 (Fig. 4). In both cases, fry selected finer substrates than parr. There were some difference in ranges of optimal D50 (defined as the range of D50 where preference was greatest): for fry, optimal parcel D50 was from 9.8 to 10.6 cm and optimal mean image D50 was from 7.1 to 7.4 cm ; for parr, optimal parcel D50 was greater than 10.6 cm and optimal mean image D50 was 14.9-18.9 cm. The most obvious difference was that preference models fitted between parr and mean image D50 showed a negative preference at D50s greater than 18.9 cm , a feature that was absent in the model for parcel D50.

Mean image D50 explained a greater proportion of the variance in juvenile preference ( $r^{2}$ of 0.18 for fry and $r^{2}$ of 0.29 for parr) than parcel D50 ( $r^{2}$ of 0.11 for fry and $r^{2}$ of 0.22 for parr). This suggested that the mean D50 of the habitat surrounding the juveniles was more important that than the D50 of the precise location where they were found. This was further confirmed by preference models fitted between juvenile density and the D50s of the parcel and image together (Tables 1 and 2). For example, greatest parr preferences were found where optimal parcel D50 (greater than 10.6 cm ) coincided with optimal image D50 (14.9-19.9 cm), but preferences decreased when image D50 was sub-optimal (either by being less than 14.9 cm or greater than 18.9 cm ). Additionally, greater preferences were found when image D50 was optimal and par-

Table 1 - Fry preference according to optimal and sub-optimal parcel and image D50s

|  | Mean image D50 |  |  |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- |
|  | $0-4.6$ | $4.6-7.1$ | $7.1-7.4$ | $7.4-19.2$ | $>19.2$ |
| Parcel D50 |  |  |  |  |  |
| $0-3.4$ | -0.63 | -0.71 | NA | 0.24 | NA |
| $3.5-5.8$ | -0.03 | 0.28 | 0.47 | -0.02 | -0.39 |
| $9.8-10.6$ | NA | NA | 0.40 | 0.59 | -1.00 |
| $>10.6$ | NA | -0.63 | NA | 0.08 | -0.62 |

Optimal ranges are shown in bold. Preferences may vary from -1 (strongly avoided), through 0 (neutral preference) to 1 (strongly selected).

Table 2 - Parr preference according to optimal and sub-optimal parcel and image D50s

|  | Mean image D50 |  |  |  |  |  |
| :---: | :--- | :--- | :--- | :--- | :--- | :---: |
|  | $0-3.5$ | $3.5-4.8$ | $4.8-14.9$ | $14.9-18.9$ | $>18.9$ |  |
| Parcel D50 |  |  |  |  |  |  |
| $0-3.4$ | -0.94 | -0.66 | -0.82 | NA | NA |  |
| $3.4-10.6$ | NA | -0.09 | -0.08 | 0.34 | -0.27 |  |
| $>10.6$ | NA | NA | 0.29 | 0.55 | 0.08 |  |

Optimal ranges are shown in bold. Preferences may vary from - 1 (strongly avoided), through 0 (neutral preference) to 1 (strongly selected).
cel D50 was sub-optimal (less than 10.6 cm ) than when parcel D50 was optimal and image D50 was sub-optimal.

Preference models with partitioning determined by regression trees had a greater explanatory power than preference models created using arbitrary partitioning. Using preference models with three partitions of equal length, the proportion of variance explained was 0.02 (fry and parcel D50), 0.10 (parr and parcel D50), 0.03 (fry and mean image D50) and 0.04 (parr and mean image D50); using preference models with six partitions of equal length, the proportion of variance explained was 0.03 (fry and parcel D50), 0.13 (parr and parcel D50), 0.06 (fry and mean image D50) and 0.09 (parr and mean image D50). That is, the proportion of variance explained increased with an increase in the number of partitions, but was still less than that explained using preference models with partitioning determined by regression trees.

## 4. Discussion and conclusions

The shape of the preference models was consistent with those that have been found in other studies, with parr selecting coarser substrates than fry. However, the proportion of the variance explained by the preference models in this study was seen to be relatively small, never exceeding $30 \%$. This is not surprising given that only one habitat property was considered: other habitat variables including proximity to spawning sites (Klemetsen et al., 2003), velocity and depth (Gries and Juanes, 1998), predation (Dionne and Dodson, 2002), temperature and light intensity (Heggenes and Dokk, 2001) will have affected juvenile densities, and caused some of the unexplained variance in the preference models.

The main limitations of the previous application of preference models are that: (i) they are not presented with any statistic describing their explanatory power and (ii) the means by which the habitat range is partitioned into distinct classes is arbitrary. Showing the explanatory power alongside the model's description of the shape of the relationship is important because it allows the quantification of how much confidence can be placed in the relationship, and aids comparison between relationships established for different species or lifestages, for different habitat properties or for the same property sampled at different scales. For example, in this study it was seen that the relationship between parr and D50 was stronger than that between fry and D50. Partitioning in preference models is usually determined in an arbitrary fashion, with no rationale given for how the width and position of the partitions are determined-this width and position will affect both the shape and strength of the established relationship. In this study, by using the binary recursive approach of regression trees to achieve optimal partitioning, it was possible to remove this subjectivity in fitting the models, and by doing so, increase their explanatory power. It is therefore suggested that this approach be considered for the construction of preference models in the future.

The key-finding of this research is that synoptic habitat data from remote sensing (that is, habitat data collected over the entire river cross-section for an along-stream distance of approximately 50 m surrounding the fishing station) were more effective for modelling juvenile salmon sub-
strate use than habitat data from a ground survey (collected over the smaller $5 \mathrm{~m} \times 20 \mathrm{~m}$ dimensions of the station). Most previous studies have relied upon in situ habitat samples. This has often limited habitat analysis to the determination of micro-scale relationships, a scale where there may be low explanatory power given that fish are motile and may use multiple habitats. In this study, preference models based on mean image D50 explained a greater proportion of the variance in juvenile salmon density than those based on parcel D50. This is particularly interesting given that the remotely sensed imagery was acquired in only one of the years in which salmon were sampled, whereas a parcel D50 was acquired for every measurement of juvenile salmon density-any temporal variation in substrate size across the 8year period in which juvenile salmon density was determined would have adversely affected the relationship between density and mean image D50. It is proposed here that the relative lack of explanatory power of the parcel D50 was because it only provided information on the substrate where the juvenile salmon were found, and not on the surrounding habitat that may have affected their density. For example, an area of cobbles, which would be optimal habitat for fry may not support a high fry density if it is surrounded by a sub-optimal habitat of substrates that are much smaller or larger.

We suggest that the parameters of the remote sensing mission used in this study have a temporal and spatial applicability that will produce similar results in other river systems. That is, it is necessary to: (i) ensure a very high spatial resolution because the minimum detectable substrate size is dependent on the pixel size (such a resolution is currently only obtainable from an airborne platform), (ii) use a sensor that can discriminate different wavelength regions of the electro-magnetic spectrum (i.e. true-colour or multispectral) because this can help in determining channel or riverbed properties, such as substrate size or depth, or help in identifying features that it is necessary to mask, such as vegetation or shadow and (iii) acquire the imagery as near to mid-day as possible to ensure a high sun elevation and minimise the effect of shadows from riparian vegetation.

## REFERENCES

Bardonet, A., Baglinière, J.-L., 2000. Freshwater habitat of Atlantic salmon (Salmo salar). Can. J. Fish. Aquat. Sci. 57, 497-506.
Carbonneau, P.E., Lane, S.N., Bergeron, N.E., 2004.
Catchment-scale of mapping of surface grain size in gravel bed rivers using airborne digital imagery. Water Resour. Res. 40 (7) (Art. No. W07202).
Dionne, M., Dodson, J.J., 2002. Impact of exposure to a simulated predator (Mergus merganser) on the activity of juvenile salmon (Salmo salar) in a natural environment. Can. J. Zoo. 80, 2006-2013.

Dunham, J.B., Cade, B.S., Terrell, J.W., 2002. Influences of spatial and temporal variation on fish-habitat relationships defined by regression quantiles. Tran. Am. Fish. Soc. 131, 86-98.
Gibson, R.J., Hillier, K.G., Whalen, R.R., 1998. A comparison of three methods for estimating substrate coarseness in rivers. Fish. Manage. Ecol. 5, 323-330.

Gilvear, D.J., Davids, C., Tyler, A.N., 2004. The use of remotely sensed data to detect channel hydromorphology; River Tummel, Scotland. River Res. Appl. 20, 795-811.
Gries, G., Juanes, F., 1998. Microhabitat use by juvenile Atlantic salmon (Salmo salar) sheltering during the day. Can. J. Zoo. 76, 1441-1449.
Hedger, R.D., Dodson, J.J., Bergeron, N.E., Caron, F., 2005. Habitat selection by juvenile Atlantic salmon: the interaction between physical habitat and abundance. J. Fish Biol. 67, 1054-1071.
Heggenes, J., Dokk, J.G., 2001. Contrasting temperatures, waterflows, and light: seasonal habitat selection by young Atlantic salmon and brown trout in a boreonemoral river. Regul. Rivers 17, 623-635.
Heggenes, J., Bagliniere, J.L., Cunjak, R.A., 1999. Spatial niche variability for young Atlantic salmon (Salmo salar) and brown trout (S-trutta) in heterogeneous streams. Ecol. Freshwater Fish. 8, 1-21.
Jacobs, J., 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. Oecologia 14, 413-417.
Jones, M.L., Stockwell, J.D., 1995. A rapid assessment procedure for the enumeration of salmonide population in streams. N. Am. J. Fish. Man. 15, 551-562.
Junge, Ch. O., Libosvàrsky, J., 1965. Effects of size selectivity on population estimates based on successive removals with electrofishing gears. Zool. Listy 14, 171-178.
Klemetsen, A., Amundsen, P.-A, Dempson, J.A., Jonsson, B., Jonnson, N., O'Connell, M.F., Mortensen, E., 2003. Atlantic salmon Salmo sala L., brown trout Salmo trutta L. and Salvelinus alpinus (L.): a review of aspects of their life histories. Ecol. Freshwater Fish 12, 1-59.
Lane, S.N., Westaway, R.M., Hicks, D.M., 2003. Estimation of erosion and deposition volumes in a large, gravel-bed, braided river using synoptic remote sensing. Earth Surf. Proc. Land. 28, 249-271.
Legleiter, C.J., Roberts, D.A., Marcus, W.A., Fonstad, M.A., 2004. Passive optical remote sensing of river channel morphology
and in-stream habitat: physical basis and feasibility. Remote Sens. Environ. 93, 493-510.
May, J.T., Brown, L.R., 2002. Fish communities of the Sacramento River Basin: implications for conservation of native fishes in the Central Valley, California. Env. Biol. Fishes 63, 373-388.
Martin-Smith, K.M., Armstrong, J.D., Johnsson, J.I., Bjornsson, B.T., 2004. Growth hormone increases growth and dominance of wild juvenile Atlantic salmon without affecting space use. J. Fish Biol. 65 (Suppl. A), 156-172.
Meador, R.M., 2003. Assessing the efficacy of single-pass backpack electrofishing to characterize fish community structure. Tran. Am. Fish. Soc. 132, 39-46.
Mertes, L.A.K., 2002. Remote sensing of riverine landscapes. Freshwater Biol. 47, 799-816.
Paller, M.H., 2002. Temporal variability in fish assemblages from disturbed and undisturbed streams. J. Aquat. Ecosyst. Stress Recov. 9, 149-158.
Rahel, F.J., Nibbelink, N.P., 1999. Spatial patterns in relations among brown trout (Salmo trutta) distribution, summer air temperature, and stream size in rocky mountain streams. Can. J. Fish. Aquat. Sci. 56 (Suppl. 1), 43-51.
Reyjol, Y., Lim, P., Belaud, A., Lek, S., 2001. Modelling of microhabitat used by fish in natural and regulated flows in the river Garonne (France). Ecol. Model. 146, 131-142.
Talbot, T., Lapointe, M., 2002. Numerical modeling of gravel bed river response to meander straightening: the coupling between the evolution of bed pavement and long profile. Water Resour. Res. 38 (6) (Art No. 1074).
Terrell, J.W., Cade, B.S., Carpenter, J., Thompson, J.M., 1996. Modeling stream fish habitat limitations from wedge-shaped patterns of variation in standing stock. Tran. Am. Fish. Soc. 125, 104-117.
Whited, D., Stanford, J.A., Kimnall, J.S., 2002. Application of airborne multispectral digital imagery to quantify riverine habitats at different base flows. River Res. Appl. 18, 583-594.


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