Spatial diffusion modelling of juvenile Atlantic salmon (Salmo salar) shows ontogenetic increase in movement rates

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<tr>
<th>Journal:</th>
<th>Canadian Journal of Fisheries and Aquatic Sciences</th>
</tr>
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<tbody>
<tr>
<td>Manuscript ID</td>
<td>cjfas-2015-0315.R2</td>
</tr>
<tr>
<td>Manuscript Type:</td>
<td>Article</td>
</tr>
<tr>
<td>Date Submitted by the Author:</td>
<td>18-Apr-2016</td>
</tr>
<tr>
<td>Complete List of Authors:</td>
<td>Foldvik, Anders; Norwegian Institute for Nature Research Einum, Sigurd; Norwegian University of Science and Technology Finstad, Anders; NTNU, Department of Natural History</td>
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<tr>
<td>Keyword:</td>
<td>SPATIAL ANALYSIS &lt; General, RIVERS &lt; Environment/Habitat, FRESHWATER FISHES &lt; General, SALMON &lt; Organisms, MOVEMENT &lt; General</td>
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Spatial diffusion modelling of juvenile Atlantic salmon (Salmo salar) shows ontogenetic increase in movement rates

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Abstract

For organisms with extensive ontogenetic changes in phenotypes, knowledge of how movement of individuals changes throughout life is pivotal to understanding ecological processes. Here, we study the spatial distribution of a cohort of Atlantic salmon (*Salmo salar*) from hatching to their third summer of juvenile life, during which they go through a fourfold change in body size. The fish originated from three distinct breeding sites and their distribution was mapped using electrofishing throughout the river at 10 sampling periods. The spatial distribution throughout ontogeny was analysed using diffusion models. The distribution changed from three distinct non-overlapping distributions centred on the individual breeding sites at the early first summer stage, to a single continuous distribution at the end of the study. The diffusion coefficient increased throughout ontogeny, and spatial distributions were well-described using diffusion models, explaining 46-89 % of the variation. This highlights the utility of diffusion models when considering spatial habitat structure both in conservation and research.
Introduction

Movement of individuals, whether it involves dispersal from a natal site to a new reproductive site, or movement between different habitat patches (Hawkes 2009), plays a key role in population ecology. The rates of such movement influence both demographic processes, community structure and metapopulation dynamics (Warren 1996; Tilman, Lehman & Kareiva 1997; Hanski & Gilpin 1997), and the quantitative understanding of these processes has increasingly been shown to be of importance in ecological applications, spanning from the management of biological invasions to habitat fragmentation and population responses to climate change (Zheng, Pennanen & Ovaskainen 2009).

The extent of movement varies among species, partly due to variation in phenotypic traits such as body mass (Whitmee & Orme 2013). Furthermore, individual variation in these may arise within species due to phenotypic differences, or due to phenotype-specific responses to environmental variation (Skalski & Gilliam 2000; Zabel 2002; Snider & Gilliam 2008). In particular, for organisms with extensive ontogenetic changes in phenotypes, knowledge about how movement patterns may change throughout life is of vital importance. For example, local density-dependent mortality during life stages with low mobility may have pronounced effects in spatially explicit models of population dynamics (Einum et al. 2008a).

Ontogenetic changes in terms of spatial distribution can be expected to be of particular importance for spatially structured populations where mobility increases and habitat requirements change rapidly with size. For such species, the spatial arrangement of propagules relative to habitats used at different life history stages can affect local levels of competition and population dynamics. Adequate description of changes in mobility and spatial distribution is then of pivotal importance in order to study and understand such processes.
Here, we use a diffusion-based modelling framework to follow the spatial distribution of a single cohort of juvenile Atlantic salmon (*Salmo salar* L.) over a three year period which involves considerable changes in the individuals’ body mass. Diffusion models are especially useful when data on individual movements of animals is unavailable (Turchin 1998). As an analogy to particles in inorganic diffusion, the combined movement of a large number of individuals may be approximated using diffusion models (Turchin 1998). Diffusion models have previously been successfully used to describe individual movement and population distribution in a range of organisms (e.g. Turchin 1998; Sibert *et al.* 1999; Ovaskainen 2004; Coombs & Rodríguez 2007; Morales *et al.* 2010). Both movement rates and diffusive spread have received considerable theoretical and empirical interest. However, there is to our knowledge no empirical example that tests the ability of diffusion-type models to describe the changes in spatial distribution of entire cohorts in natural populations over time scales that incorporate ontogenetic shifts in movement rates.

Populations of stream-living fishes such as juvenile Atlantic salmon constitute excellent systems for studies of spatial distributions due to several empirical and analytical advantages. The clearly defined and confined habitat enables extensive sampling throughout the range of the population, and emigration and immigration is in some cases, such as the present study, known to be close to zero. Also, small rivers and streams can be conceptualized as one-dimensional habitats making mathematical inference less complex than in 2D or 3D environments. Atlantic salmon reproduce and spend their first years as juveniles in rivers. During breeding, 100s to 1000s of eggs are deposited in discrete, often patchily distributed nests (Geist & Dauble 1998; Moir *et al.* 2004; Isaak & Thurow 2006). This creates local aggregations of juveniles near nest sites following emergence. Nest distribution has been shown to influence early juvenile survival (Einum & Nislow 2005; Einum *et al.* 2008b) due to local density-dependent processes (Gee, Milner & Hemsworth 1978; Dumas & Prouzet 2003;
Einum, Sundt-Hansen & Nislow 2006). Previous studies of spatial distributions of Atlantic salmon juveniles generally suggest restricted movement during early life (e.g. Saunders & Gee 1964; Webb et al. 2001; Foldvik, Finstad & Einum 2010), but formal quantification of spatial spread throughout the juvenile stage in a natural environment has been lacking.

In the present study we utilize a unique dataset on initial colonization of a cohort of juvenile Atlantic salmon. The cohort originated from reproduction by radio-tagged adults, allowing us to locate and assign sites of reproduction confidently to individual females. Sampling of resulting juveniles, with a high spatial resolution over the subsequent three years, enabled us to test for ontogenetic changes in rates of movement using diffusion models.

**Material and methods**

The study was conducted in the River Ingdalselva central Norway (63°27′38″ N; 9°54′23″ E) (Fig. 1). The river is a gravel-bed type with a substrate consisting of gravel and cobble. The channel morphology is dominated by alternating riffle and run segments, and the few pools (N < 10) are shallow and short. Annual mean discharge is approximately 5 m$^3$ s$^{-1}$. The catchment has insignificant human influence from agriculture and urban infrastructure and is dominated by spruce and pine forest. Historically, the river has only contained a population of resident brown trout (*Salmo trutta* L.) due to an impassable waterfall located just upstream from the outlet into the fjord (Fig. 1). In 1994 three female (lengths 80, 85, and 98 cm) and four male (lengths 58, 65, 67, and 70 cm) Atlantic salmon, caught in the nearby River Orkla, were released and later spawned in River Ingdalselva. All fish were radio-tagged, enabling accurate location of breeding sites of individual females (Johnsen & Hvidsten 2002). The distribution of juveniles in the following three consecutive years after breeding was monitored by electrofishing. Electrofishing locations were distributed along the study reach every 50 - 60 m, but in some areas every 25 and even 12.5 m (Fig. 1). Electrofishing was carried out by sampling an approximately 2.5 meter wide area across the width of the river, and then moving
2.5 meters up before sampling in the same way back to the bank the fishing started from. All fish were measured to the nearest mm before being released at the sampling site. All locations were permanently marked using spray paint. The electrofishing was carried out ten times during 1995-97 and a total of 1937 fish were caught at transects (Table 1). Not all transects were fished during every sampling, and during the study the distribution of fish was not restricted by any upstream barriers.

Due to a lack of previous breeding, assigning fish to year class was straightforward in 1995 and 1996. Since adult fish were also released and spawned in the river in 1995, distinguishing one year olds (1+) from two year olds (2+) in 1997 was done by plotting fish length against location in the river. Age-length relationships varied within the study area, but were clearly stratified. When establishing the age-length relationships, supplementary data from three-pass electrofishing stations within the study area, sampled on the same dates for other purposes, were also included ($N = 203$).

The combined distribution of three diffusion equations (Turchin 1998) was used to model the abundance (individuals $m^{-1}$) of the cohort of juvenile Atlantic salmon originating from the three breeding sites $i$ at location $x$ along the river measured from the migration barrier above the outlet:

$$f(x, D, N, t, w) = \sum_{i=1}^{3} \frac{N w_i}{\sqrt{4\pi Dt}} e^{-\frac{(x-x_{0i})^2}{4Dt}}$$  \hspace{1cm} (Eq. 1)

were $D$ is the diffusion coefficient ($m^2 t^{-1}$) quantifying the rate of spread from the point of origin $x_{0i}$, $N$ is the total number of fish, $t$ is time in days after swim up and $w_i$ is the fraction of $N$ originating from breeding location $x_{0i}$. The fraction ($w_i$) of $N$ originating from deposition at $x_{0i}$ was estimated by first converting female length to weight assuming a K-factor of 1 for all females, then assuming a linear weight/fecundity relationship making $w_i$ equal to the weight of the female that spawned at $x_i$ divided by total weight of females. Models were fitted for all sampling events and parameter estimates represent the period $t_0$ to $t_i$. Swim-up date ($t_0$) was
set to 1 July 1995 based on breeding time (Jensen, Johnsen & Heggberget 1991) and observed
swim up date in 1996. Direct observations of redds were not conducted, and values of \( x_i \) were
based on the centres of three distinct non-overlapping distributions found in the initial
sampling. Some downstream movement is expected to have occurred between swim-up and
first sampling (Foldvik et al. 2010). Models assume hatching and swim-up date to be the same
for all fish. Further, no between or within family differences were assumed in movement
behaviour.

For individual timelags the diffusion coefficient was found using:

\[
D_{(t_{i-1}, t_i)} = \frac{D_{(t_0, t_i)}}{t_i - t_{i-1}} \quad \text{(Eq. 2)}
\]

Were \( D_{(t_{i-1}, t_i)} \) respresents the diffusion coefficient in the period \( t_{i-1} \) to \( t_i \) (Table 1). Samplings
within years were conducted within a short period, meaning that estimates of \( D_{(t_{i-1}, t_i)} \)
within years will strongly affected by the accuracy of the previous estimate of \( D \). To reduce
such effects we also used \( \bar{D} \) of samplings the previous year as starting points for
calculations of \( D \) over individual timelags (\( D_{(t_{i-j}, t_i)} \)), were \( j \) is the time from \( \bar{D} \) of previous
year to \( t_i \).

In the present analyses we used number of fish captured per meter along the river
instead of estimated density as the dependent variable. This was done since, due to changes in
water discharge (and hence transect widths), density of fish at a transect can change
dramatically between samplings, even if the actual number of fish stays constant. Due to
increased catchability with increasing size of the fish, especially in the first pass (Dolan &
Miranda 2003; Sandlund et al. 2011; Saunders, Fausch & White 2011), the overall number of
fish appears to increase \textit{ex nihil} with age. Underestimation of \( N \) during the early stages does
not, however, influence estimates of the diffusion parameter (\( D \)).
Results

A total of 2140 fish were caught during electrofishing (1937 at transects), 725 as young-of-the-year, 1122 as one year olds and 293 as two year olds (Table 1). Average transect width ranged from 4.0 to 30.2 m (median 16.9, mean 16.8 ± 5.4). The distribution of juveniles changed from three distinct non-overlapping distributions early in the first year, to a more or less continuous distribution as spatial spread continued throughout the second (1+ stage) and third summer (2+ stage) after hatching (Fig. 2).

Estimated diffusion coefficient calculated from \( t_0 \) to \( t_i (D_{(t_0,t_i)}) \) increased from 13.72 m\(^2\) t\(^{-1}\) at 10 days after swimup to 876.23 m\(^2\) t\(^{-1}\) at the end of the study period (Fig. 3). And the change in \( D_{(t_0,t_i)} \) was best described as a quadratic function of time (Fig. 3). Also individual timelags from \( t_{i-1} \) to \( t_i (D_{(t_{i-1},t_i)}) \), Tab. 1 showed a general increase with time. However, these estimates were highly variable and some even gave negative estimates. This variability was reduced when \( \bar{t} \) and \( \bar{D} \) of samplings the previous year were used as starting points for calculations of \( D \) for timelags \( (D_{(t_{i-j},t_i)}) \), Fig. 4), with all timelags showing an increase with time and body length (Fig. 5). Estimates of the number of fish \( (N, \text{Tab. 1}) \) ranged from 798 to 3522.

Discussion

The high spatial and temporal resolution of the present data gives a unique picture of a cohort spreading throughout its juvenile stages in a natural environment, and of how the rate of spread changes through ontogeny. The spatial distribution of juveniles from eggs to their third year of life was well-described as a diffusion process, capturing the change from three distinct non-overlapping distributions, reflecting the three areas of origin, to a single continuous distribution. The shape of the distributions also changed with ontogeny, from being narrow during the first year of life to broad in the second and third. The narrow distribution observed
in the first year of life strongly suggest that movement is not density-dependent, since repulsion between individuals should quickly level off the sharp peak seen in narrow distributions (Turchin 1998).

The diffusion coefficient increased throughout the study, showing a marked ontogenetic increase in movement rates accompanying the increase in body size. The estimated diffusion coefficient \( D(t_0, t_i) \) spanning the time from \( t_0 \) to \( t_i \), does not take into account lower estimates of \( D \) at earlier samplings. This implies that the actual increase in movement is indeed higher, which becomes clear when looking at diffusion coefficients calculated for timelags \( D(t_{i-1}, t_i) \) and \( D(t_{i-j}, t_j) \). For short timelags \( D(t_{i-1}, t_i) \) in some cases were negative, likely reflecting either overestimation of \( D(t_{i-2}, t_{i-1}) \) or underestimation of \( D(t_{i-1}, t_i) \) rather than a contraction of the distribution.

Both the increased diffusion coefficient and the change in distributions are coherent with an increase in mobility with size. In addition, it is possible that increased energy demands with increasing size require larger feeding areas and territories. This may further encourage movement. Also, stream-living salmonids shift environmental requirements as they grow (Finstad et al. 2010), which may lead to active movement in search of new habitats. The increase in spread could also be expected due to allometric increases in both metabolism and territory size (Steingrimsson & Grant 1999; Nislow, Armstrong & Grant 2010), leading to a reduction in how many territories an area can support. Variation in environmental variables among transects will clearly affect numbers of fish, and much of the unexplained variation is likely to be due to this.

Although the diffusion models in this study adequately describe the distribution of a cohort through ontogeny, no organisms meet all the underlying assumptions of diffusion models (Turchin 1998). This obviously lays such simple diffusion models open to reproach. However, whether or not organisms spread randomly or move directed (based on interactions
with other individuals or environment), if the combined sum of movement mimics the
distribution created from random movement, diffusion models still are a powerful and useful
tool for understanding and predicting population spread. Adequate descriptions of population
level spatial distribution throughout ontogeny are especially important for species such as
Atlantic salmon where breeding often has a patchy spatial distribution. This spatial structure,
coupled with strong density dependent effects on both growth and survival during juvenile
stages, has the potential to strongly influence the population dynamics (Kocik & Ferreri 1998;
Einum et al. 2008a). This makes movements through ontogeny extremely important for both
conservation and management, since both the effect of density dependence and the proportion
of river area accessible to juveniles are dependent on the characteristics of these movement
patterns.

Overall the results support previous findings, with both spatial distribution and
distances being similar to previous studies of juvenile Atlantic salmon dispersal from nests
(Eglishaw & Shackley 1980; Einum & Nislow 2005; Foldvik et al. 2010) and point stocking
of fry (Heggenes & Borgstrom 1991; Crisp 1995). There was no support for density-
dependent movement during early juvenile stages, but results do concur with previous
findings of density-dependent dispersal of older juveniles (Einum et al. 2006). The findings of
increased diffusion coefficient throughout later ontogeny, are however, in contrast with other
reports of high site fidelity of older juvenile salmon (Hesthagen 1988, Garcia de Leaniz 1989,
Armstrong 1997), and demonstrate that the spatial extent of the river that can be utilized by
juvenile salmon originating from one breeding location vastly increases with age.

The models used here are quite simple, and could be extended, for example by
including both density-dependent dispersal and survival. However, adding more complex
terms would vastly increase the number of parameters and potentially obscure the impact and
interpretation of the variables of interest. As the spatial distribution of individuals almost
certainly plays a key role in population dynamics of most species, knowledge of how
parameters related to movement change through time, ontogeny or seasons, may be crucial to
better understanding and predicting population level responses to changes in spatial
distributions of habitat or breeding patterns.

Acknowledgements

We sincerely thank B. O. Johnsen and N. A. Hvidsten for letting us analyse data they
spent years on acquiring. They both planned the sampling design and conducted most of the
fieldwork. Not many scientist would be so generous. We also thank G. Østborg and J. G.
Jensås for assisting them during the fieldwork. The critical review of Agnes Bardonnet of an
erlier version of this manuscript, and two anonymous reviewers have contributed greatly to
its present form.

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Coombs, M.F. & Rodríguez, M.A. (2007) A field test of simple dispersal models as predictors

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stocking together with some information from scatter-stockbing. Ecology of Freshwater Fish,
4, 1–8.


**Tables**

**Table 1:** Days after swim up \((t)\) and number \((N)\) and length of juvenile Atlantic salmon caught at transects in River Ingdalselva at the ten sampling times. Estimated total number of fish in the river from models \((\text{Est. } N)\), model fit \((R^2)\), estimated diffusion coefficients \((m^2 \text{ } t^{-1})\) over timelags \(t_0 \text{ to } t_i (D_{(t_0 \text{, } t_i)})\) and \(t_{i-1} \text{ to } t_i (D_{(t_{i-1} \text{, } t_i)})\).

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<tr>
<th>Date</th>
<th>N</th>
<th>(SD)</th>
<th>t</th>
<th>Est.N</th>
<th>R^2</th>
<th>(D_{(t_0 \text{, } t_i)})</th>
<th>(D_{(t_{i-1} \text{, } t_i)})</th>
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<td>121</td>
<td>(1.18)</td>
<td>10</td>
<td>798</td>
<td>0.89</td>
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<tr>
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<td>30</td>
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<td>0.84</td>
<td>50.16</td>
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<tr>
<td>18-22 August 1995</td>
<td>212</td>
<td>(4.13)</td>
<td>48</td>
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<td>0.65</td>
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<tr>
<td>21-22 September 1995</td>
<td>207</td>
<td>(5.15)</td>
<td>82</td>
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<tr>
<td>12-13 June 1996</td>
<td>222</td>
<td>(5.61)</td>
<td>347</td>
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<td>0.51</td>
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<td>2664</td>
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<td>2749</td>
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1Average length and SD include additional data sampled at three-pass electrofishing stations: 19-21 August 1996 (N = 51) and 30 June 1997 (N = 152).
Figures

Fig. 1: (a) Location of the River Ingdalselva. (b) Map of the entire study area, arrow indicates location of waterfall, black rectangle represents extent of (c) a portion of the study area showing the three breeding sites (circles) and electrofishing transects (black lines).
Fig. 2: Distribution of Atlantic salmon juveniles caught by electrofishing (grey lines) per meter river along the River Ingdalselva during the period 1995 – 1997. Fish were sampled in bank-to-bank transects. Black lines represent fitted values using Eq. 1. Panel numbers indicate days after swim up (see Table 1 for dates, and parameter estimates). Y-axes shows number of fish (N) caught per meter along the river, x-axes show the distance in meters from migration barrier located above the outlet. Small black bars on x-axes indicate the locations of the three breeding events (1205, 1365 and 1650 m upstream from outlet).
Estimated diffusion coefficient \(D_{(t_0, t_i)} \text{m}^2 \text{days}^{-1}\) plotted against days after swimup. (see Table 1 for dates). Solid line is a fitted quadratic model \((41.83 -0.1538 \cdot t +0.001789 \cdot t^2\), adjusted \(R^2: 0.94\)) and stippled line represents fit of a linear model \((-52.36 +0.99 \cdot t\), adjusted \(R^2: 0.78\)).

Fig. 4: Estimated diffusion coefficient between yearly samplings \(D_{(t_{i-j}, t_i)} \text{m}^2 \text{days}^{-1}\) plotted against days after swimup. Starting point of dashed lines connected to dots indicate \(\ddot{t}\)
and \( \bar{D} \) of previous year, \( j \) is the time from \( \bar{t} \) of previous year to \( t_i \). For the first year calculated as for \( D(t_0, t_i) \).

**Fig. 5**: Estimated diffusion coefficient between yearly samplings \( D(t_{i-j}, t_i), \text{m}^2 \text{days}^{-1} \), plotted against mean body length (mm) of juvenile Atlantic salmon. Bars indicate ± SD.