

**Revisiting the restricted movement paradigm: the dispersal of Atlantic salmon fry from
artificial redds**

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Abstract

Revisiting the restricted movement paradigm: the dispersal of Atlantic salmon fry from artificial redds

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According to the restricted movement paradigm (RMP), salmonid fry should typically disperse less than 50 m upstream and 500 m downstream from nests or stocking locations. However, recent evidence of juveniles dispersing up to 1600 m suggests that the RMP may be oversimplified for juvenile Atlantic salmon. To test the RMP, we implanted 679 997 eyed Atlantic salmon eggs (*Salmo salar* L.) into 19 artificial redds over six years in seven tributaries of a large river and then recovered fry via electrofishing to characterize their dispersal over their first summer of life. As expected, most fry dispersed downstream, but an average of 35% of fry moved upstream. Surprisingly, fry moved just as far upstream as downstream (medians = 403 and 404 m, respectively), with average maximum distances of 1.23 km and 2.14 km, respectively. Fry were larger at lower densities and farther from redd sites, consistent with density-dependent growth. After controlling for density, however, fry were larger upstream than downstream, suggesting that larger fry move upstream compared to downstream. While there was variation among streams and years, kurtosis values were largely consistent with a normal distribution around the redd site, with only two of the 19 distributions being leptokurtic. Tributaries had even mixtures of mobile and stationary individuals, indicating a largely homogeneous movement strategy. Our data suggests that salmon fry were more mobile than previously thought, which should facilitate their stocking or reintroduction to new habitats.

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Several years ago, I was involved in a salmon recolonization project as a Biological Technician for the US Fish and Wildlife Service in Lake Champlain, situated between the Adirondack mountains in New York and the Green Mountains in Vermont. In the fall of the year, I met James Grant while walking down a dirt road next to a steep gorge on a tributary to the Winooski River. We were about to test new egg implanting equipment developed by a researcher working with the Maine Department of Marine Resources, his name was Paul Christman. There, Jim and I got to talking about the future of the Atlantic salmon restoration program in the Champlain Valley. Shortly into the discussion, the topic of grad school came up. The rest is history.

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Introduction

The movement of individuals between habitats has important implications for meta-population dynamics, gene flow, colonization of novel habitats, and recolonization of historic habitats (Vøllestad et al. 2012; Foldvik et al. 2017). More specifically, how an individual moves through its environment provides valuable information about what habitat types are important or its survival (Yeakel et al. 2018), and what cues prompt individuals to settle or disperse (Roy et al. 2013). From a management perspective, animal movement can confirm the success of habitat restoration projects, aid in determining the carrying capacity of a particular stream, and help to monitor and control the spread of invasive species (Šlapanský et al. 2020). Consequently, interest in the characterization of animal movements has increased in the past decade (Ronce 2007; De Bie et al. 2012; Clobert et al. 2012; Rasmussen and Belk 2017).

Traditionally, dispersal of animals has been modelled with simple geometric or exponential distributions (Porter and Dooley 1993; Turchin 1998). However, these models may over-simplify movement behaviour (Foldvik et al. 2017), given the differences and interactions between individuals (Ewers and Didham 2006; Drakou et al. 2009; Rasmussen and Belk 2017), and the temporal and spatial variability in the abiotic environment (Queller and Goodnight 1989; Vøllestad et al. 2012).

Stream fishes provide an ideal system for examining movement behaviour, as this movement can be quantified in a single dimension (e.g. upstream/downstream), which reduces model complexity and simplifies parameter estimations (Rodríguez 2002). It is widely accepted that stream fish are relatively sedentary, often living within in a single pool or a small stream reach – the restricted movement paradigm (RMP; Gerking 1959; Rodriguez 2002; Teichert et al. 2011; but see Gowan et al. 1994). When applied to stream salmonids (Gowan et al. 1994;

Rodriguez 2002), the RMP suggests that stream salmonids spend most of their lives within short (20-50m) stream reaches during non-migratory periods, such as the summer (e.g. Gowan et al. 1994). Even the movement of fry from redds, which should be an active dispersal phase to find suitable habitat in which to settle (Einum and Nislow 2005), is typically only at most 50 m upstream and 500 m downstream (Egglshaw and Shackley 1973; Egglshaw and Shackley 1980; Marty and Beall 1989; Beall et al. 1994; Crisp 1995; Einum et al. 2011). However, recent work has challenged the restricted fry dispersal paradigm by showing that some fry disperse downstream up to 1600 m from redds or stocking sites (Brodeur 2006; Webb et al. 2001; Radinger and Wolter 2014; Brunson et al. 2017). Furthermore, most studies quantifying salmonid fry dispersal draw conclusions from single redds or implant locations, from multiple locations but without temporal replication, or from spatial and temporal replication with censored data (Egglshaw and Shackley 1973; Marty and Beall 1989; Beall et al. 1994; Crisp 1995; Jokikokko 1999; Webb et al. 2001; Hudy et al. 2010; Einum et al. 2012; Vøllestad et al. 2012). For example, including more sampling effort downstream than upstream, or releasing fry below dams, waterfalls, or velocity barriers, could severely underestimate upstream dispersal and bias our understanding of the dispersal process.

To add an additional layer of complexity, populations may comprise varying mixtures of stationary and mobile individuals (Paradis et al. 1998; Gomez and Zamora 1999; Rodriguez 2002). These heterogeneous populations typically generate a leptokurtic frequency distribution of displacement distances, characterized by a higher central peak for stationary individuals and a larger tail with more frequent outliers than a normal distribution for mobile animals (Paradis et al. 1998; Gomez and Zamora 1999; Fraser et al. 2001; Radinger and Wolter 2014). Conversely, populations with homogeneous dispersal behaviour should have fewer and less extreme outliers,

characterized as platykurtic (Skalski and Gilliam 2000). In stream salmonids, these stationary and mobile components have been modelled by the pattern of decline in the number of recaptured fry with the distance from their home section (Gowan et al. 1994). In a partial reconciliation of the RMP with the recently (see above) observed mobility of salmonid fishes, Rodriguez (2002) showed that high rates of dispersal from the home site are compatible with low total displacement. However, Rodriguez (2002) relied on data that included some adult life-stages and only included individuals moving a maximum of 400 m. Due to the spatial ordering of mark-recapture studies, simple statistics are not sensitive to bimodalities (i.e. multiple life-strategies), necessitating a more effective way for modelling dispersal (Rodríguez 2002).

Another challenge in characterizing fry dispersal is capturing the spatial and temporal variance among populations or regions. For instance, environmental factors such as gradient, water velocity, geographical location, and stochastic events can have a profound influence on dispersal due to varying swimming capacities amongst fry (Ottaway and Clarke, 1981; Elliott, 1994; Gowan et al. 1994). More specifically, higher gradients and water velocities could cause the passive dispersal of fry farther in the downstream direction (Heggenes and Dokk 2001; Yeakel et al. 2018). Such passive dispersal is often thought to be density independent (Einum and Nislow 2005; Foldvik et al. 2017).

Beyond environmental variation, regulatory processes such as density-dependence may also differ among populations (e.g. Matte et al, 2020). For example, fry may disperse to avoid the costs of density-dependent growth and mortality (Grant and Imre 2005; Grossman et al. 2012). Larger, dominant, or early emerging individuals may be more successful at establishing and defending territories near the redd, forcing less competitive individuals to disperse farther away (Elliott 1994). In this scenario, those closer to the redd would have higher fitness.

Alternatively, individuals that disperse farther from the redd may reap the benefits of higher growth rates under lower densities (Einum et al. 2012).

To date, no study of stream salmonid dispersal has tested the predictions of the RMP while accounting for environmental factors or the spatial and temporal variation within and among streams, with respect to their dispersal curves. Hence, we conducted a field experiment across multiple tributaries, in which we implanted eyed eggs in historical spawning areas to characterize the full distribution of dispersing fry with spatial and temporal replication. We buried eyed eggs of Atlantic salmon across the Sandy River watershed in Maine, USA, and quantified the distribution of 0+ juveniles upstream and downstream of 19 artificial redds. We tested the following predictions: [1] more fry will disperse downstream than upstream, and the percentage moving downstream will be higher in streams with higher flow or gradient; [2] fry will move farther downstream than upstream; [3] the distance moved downstream and upstream will increase and decrease, respectively, with increases in stream velocity and gradient; [4] fry body size will increase with dispersal distance in both directions, consistent with density-dependent growth; [5] after controlling for density, fry will be larger upstream than downstream, consistent with larger fry being able to move upstream against the flow; and [6] fry will exhibit heterogeneous dispersal behaviour within populations, resulting in leptokurtic distributions in relation to the redd site, and bimodal downstream dispersal distributions, following Rodriguez (2002).

Methods

Fish origin and study sites

The study area encompassed most of the Sandy River and its six major tributaries in Maine, U.S.A., an area of 1 536 km² (Maine Department of Marine Resources 2014; hereafter MDMR; Fig. 1). The Sandy River descends 471 m to its confluence with the Kennebec River and comprises an excess of 2 300 000 m² of Atlantic salmon rearing habitat (MDMR 2014). The local gradients (see below) ranged from 0.65-0.71% in the mainstem of the Sandy River, and 1.09-8.88% in the adjacent tributaries (Ries et al 2017).

A total of 679 997 eyed Atlantic salmon eggs were planted in seven streams from 2010-2018 (see below, Table 1; Table S1), and the subsequent post emergence distributions were characterized. All the field work was completed by the Maine Department of Marine Resources before the onset of my thesis. Eggs were from the Penobscot River stock at the Green Lake National Fish Hatchery. The adults that produced our F2 eggs had one full generation in captivity. Sea-run adults were captured in the Penobscot River and held at Craig Brook National Fish Hatchery until spawning. Eyed eggs were moved to Green Lake National Fish Hatchery, where they were reared to adulthood (Fig. S1). Each year Green Lake spawns 500 or more families in waves as adult salmon mature, resulting in the spawning of as many as 297 females at one time (Mean = 110, SD = 78; Table S2). For more information on spawning, see Supplementary Methods.

The equipment used to bury the eggs was developed by the MDMR for large-scale Atlantic salmon restoration. For this project, we planted eggs 30 cm below the surface of the stream bed, within the normal range for Atlantic salmon (Bley 1987). When the depth was

reached, the standpipe was removed, leaving the funnel in the gravel. Three to five hundred eggs were then poured underwater into the funnel (Fig. S2).

On average, 35 789 eggs (range = 5 350 - 104 130; Table 2) were buried in a single artificial redd at densities ranging from 3 200 - 8 608 eggs/m²; the number of eggs was estimated from photos taken prior to planting. The location of each redd site was measured from its closest landmark and was identified by the distance measured in km from the confluence of the next downstream river following the drainage; e.g. Sandy River 73.73 km was 73.73 km upstream of the confluence of the Kennebec River. We chose sites that were ideal spawning habitat for Atlantic salmon, typically large shallow gravel shoals (Loui et al. 2008), easily accessible by road, and surrounded by continuous reaches of high-quality rearing habitat (sensu Armstrong et al. 2003; Girard et al. 2003).

It was unlikely that wild fry affected our data. In annual redd surveys from 2010-18, a total of 85 wild redds were found in the Kennebec watershed (Table S3). Only one wild redd was ever found within 11 km of an implant site; it was 0.4 km upstream of the implant site on Perham stream in 2014 (Table S3). However, no fry were captured at that location during surveying, indicating the redd was likely unsuccessful or abandoned before fertilization.

Sampling

Electrofishing (Smith-Root LR-24) for 0+ fry focused on representative sites that were upstream and downstream from the implant sites. Sampling was conducted between the first week of August and the first week of September by a crew of 2 to 3 people. On average, there were 8.6 sampling sites (mean length = 15.4 m, SD = 6.67 m, range = 3.7-33.2 m) surrounding each redd, with 5.2 sites downstream (SD = 1.96, range = 2-9; Table S1) and 3.4 sites upstream

(SD = 1.98, range = 1-8) for a total sampling area of 998.4 m² (SD= 392.62 m², range = 437 - 1607.64 m²; see Table S1). The mean distance between sampling sites was 394.1 m (SD = 257.8 m, range = 50 – 1 620 m), spread over a mean length of stream of 1 145.3m upstream (SD = 1 236.16 m, range = 60 – 4 770 m) and 2 063.68 m downstream (SD = 1 233.13 m, range = 780- 4 790 m). Each site was sampled with a single pass, without blocking nets, totalling 300 s of electrofishing. Sampling continued in an outward direction in both directions from the planting site until fewer than three 0+ parr were captured at a site. All fish captured were counted, measured and weighed (Fig. S3). Age class was assigned by fork length, with mean size of 0+ fry of 55.4 mm, (SD = 7.40 mm). Less than 1% of all parr were thought to be age 1+, so any misclassification was unlikely to affect our analyses.

To estimate the number of fry that survived from each redd, the total number of fry captured per site was first divided by 0.64, the average catchability for fry (P. Christman, unpublished data), somewhat higher than what is found in other studies (Niemelä et al. 2000), but is not uncommon (Hedger 2018). The density per site (i.e. m⁻²) was used to estimate the density and number of 0+ fry for the area of the stream halfway to the next sampling site in both directions (Fig. S1). Percent egg to 0+ fry survival was calculated by dividing the estimated number of fry around (see Fig. S1) each implant site by the number of eggs planted.

We used two measures of the gradient of the stream (percent rise · run⁻¹): (i) local gradient, for the length of stream in which fry were found; and (ii), stream gradient, for the entire stream from the headwaters to its confluence. Stream gradient was included to incorporate watershed effects on fry dispersal, such as how high mountain peaks might affect snow-pack runoff, water temperature, and current velocities. Local gradient was determined using ArcGIS

(version 10.7.0.10450), whereas stream gradient was determined using regression equations generated in USGS StreamStats GIS database (version 4.3.8).

Statistical Analysis

We used paired *t*-tests to compare the proportion and median dispersal distance of fish moving upstream and downstream from redd implant locations. Then, generalized least square regressions (GLS) were used to quantify the impact of demographic and environmental variables on the proportion of fish moving upstream, median dispersal distance, and fish body length. GLS models were used to account for important heterogeneity of variance across streams. The most parsimonious models were selected using backwards model selection with AICc (Burnham and Anderson 2004; Zuur et al. 2010). Collinearity was assessed with the variance inflation factor (VIF) before model selection. Kurtosis was also used to describe the shape of the complete (i.e. upstream and downstream) dispersal distributions: values near 0 were considered mesokurtic, whereas values larger than 3 and smaller than -3 were considered leptokurtic and platykurtic, respectively. These threshold values (-3, 3) were used given our relatively large sample size (George and Mallery 2010). The methodology described by Rodriguez (2002) was used to investigate whether each stream's dispersal distribution in the downstream direction only could be best explained by single or two parameter non-linear equations. For homogeneous dispersal, the single parameter equation is defined as:

$$f(x) = \lambda e^{-\lambda x}$$

where $f(x)$ is a dispersal function relating the decline in density with distance, x is the distance (m), and λ (m^{-1}) is the inverse of mean displacement distance. However, with heterogeneous dispersal behaviour within a population, dispersal is best described by a two parameter equation:

$$f(x) = p\lambda_s e^{-\lambda_s x} + (1 - p)\lambda_m e^{-\lambda_m x}$$

where λ_s and λ_m represent the stationary and mobile components, respectively, p represents the proportion of stationary individuals and $1-p$ represents the proportion of mobile individuals.

Both single and two parameter models were fit to each distribution, after which their respective performance were compared using AICc.

Results

A mean density of 22.7 fry · 100 m⁻² (SD = 42.57, range = 0-333.8) were captured at the 173 electrofishing sites. When these densities were prorated to the entire stream reaches, we estimated a total of 125 650 fish survived until sampling, or 18.5% of the 679 997 eggs that were planted (mean = 22.0%, SD = 18.3, range = 2.5-78.0). While the patterns of dispersal varied widely among streams, there appeared to be some consistent patterns within streams over years (Fig. 2, see below).

Prediction 1: More fry disperse downstream than upstream

As expected, significantly more fish moved downstream than upstream (Table 2; paired t-test: $t_{18} = 3.75$, $p = 0.00146$). However, the percentage of fry moving upstream varied considerably from a low of 0% in Orbeton Stream to a high of 68.5% in Cottle Brook (mean = 34.5, SD = 18.06; Table 2; Fig. 2). In contrast with expectations, the percentage of fish moving upstream was not correlated with any of the predicted environmental parameters (all P -values > 0.2; Table 3A); these results were supported by the null model having the lowest AICc value during model selection (Δ AICc = 4.71; Table 3A).

Prediction 2: Dispersal is farther downstream than upstream

In contrast to the prediction, median fry dispersal distance was not farther downstream than upstream (paired t-test: $t_{18} = -0.004$, $df = 18$, $p = 0.997$); the average median dispersal distance downstream (mean = 403.7 m, SD = 286.7 m, range = 60-1280 m; Table 2) was similar to upstream (mean = 403.2 m, SD = 476.3 m, range = 0-1600 m). The mean maximum distance dispersed upstream and downstream was 1.23 and 2.14 km, respectively, farther than a maximum of 500 m downstream ($t_{18} = 5.60$, $p = 0.00002$) or 50 m upstream ($t_{18} = 4.01$, $p = 0.0007$) predicted by the RMP.

Prediction 3a: Downstream dispersal distance increases with increasing velocity or gradient

Opposite to the predictions, median downstream dispersal distance decreased with increasing velocity ($t_{16} = 8.49$, $p < 0.0001$) and stream gradient ($t_{16} = 7.46$, $p < 0.0001$; Table 3B). As predicted, however, maximum downstream dispersal distance increased with increasing velocity ($t_{16} = 5.90$, $p < 0.0001$) and with body length ($t_{16} = 17.58$, $p < 0.0001$). Contrary to predictions, gradient had no significant effect on maximum upstream or downstream dispersal distance (Table 3C).

Prediction 3b: Upstream dispersal distance decreases with increases in velocity and gradient

Median upstream dispersal distance was not affected by gradient or velocity but did increase with body size ($t_{17} = 31.46$, $p < 0.0001$; Table 3D). However, maximum upstream dispersal distance decreased with increasing stream velocity ($t_{16} = 19.16$, $p < 0.0001$; Table 3E), increased with body size ($t_{16} = 27.81$, $p < 0.0001$; Table 3E), but was not affected by stream gradient (Table 3E).

Prediction 4: Body size decreases with density

Model selection indicated that water velocity, egg mortality, distance from the redd, direction, and population density (Table 3F) had independent effects on mean body length. As predicted, mean body length (mean = 57.5 mm, SD = 4.8 mm) decreased with increasing density ($t_{16} = 4.43, p < 0.0001$; Fig. 3a), consistent with density-dependent growth. However, there was also an independent effect of distance from the implant location, consistent with the prediction that larger fish moved farther ($t_{16} = 6.19, p < 0.0001$; Fig 3b).

Prediction 5: Fry will be larger upstream than downstream

Independent from the density effect, fish were significantly larger upstream than downstream ($t_{16} = 5.04, p < 0.0001$), consistent with the prediction that larger fish are able to move upstream more easily than smaller fish. While controlling for stream, model selection indicated that median upstream dispersal distance increased with body length ($t_{16} = 31.46, p < 0.0001$). Body size also increased with percent egg mortality ($t_{16} = 8.30, p < 0.0001$), suggesting a higher mortality rate for smaller fish. Unexpectedly, body size also increased with water velocity ($t_{16} = 3.15, p = 0.002$), perhaps an indication of more food (i.e. drifting invertebrates) available in faster rivers.

Prediction 6: Heterogeneous vs homogeneous dispersal

Values of kurtosis varied among streams (range = -1.27 to 4.76; Table 4): of the 19 distributions, 17 were not significantly different from a normal distribution (i.e. mesokurtic; kurtosis values between -3 and 3), 2 were leptokurtic (high-peaked, long tails; value >3) and none were platykurtic (low-peaked, short tails; value < -3 ; see Fig. S4). Contrary to predictions,

no streams were consistently leptokurtotic over years, evidence against heterogeneity in dispersal behaviour within streams.

Sixteen distributions had sufficient data to test for a one- versus two-parameter downstream dispersal curve; three distributions were excluded because they had fewer than four observations. Despite the paucity of leptokurtic distributions, only eight downstream distributions were best described by a single-parameter model (i.e. only a stationary component, Table 4), whereas eight were best described by a two-parameter model (i.e. both mobile and stationary components, Table 4). Two-parameter models were characterized by lower densities around the implant site, with a second peak of density farther from the implant site (Fig. 4). Alternatively, one-parameter models were characterized by high densities around the implant site and the absence of a second peak in density.

Whether a stream was best described by a one- versus two-parameter model was somewhat consistent across years (Chi-square: $\chi^2_{16} = 5.025$, $p = 0.087$). More specifically, two-parameters were selected in four of five years in Mt. Blue and three of four years in Temple, whereas Sandy River was best explained by a single-parameter model in all 3 years (Table 4, Fig. 4).

Discussion

Collectively, our results for Atlantic salmon fry do not support the Restricted Movement Paradigm as applied to the dispersal of salmonid fry from a nest or stocking site. We observed fry moving large distances in both the upstream and downstream directions, in multiple streams. Fry were larger at the lower densities farther from redds, and upstream than downstream, consistent with density-dependent growth and with larger fish being better able to disperse

upstream, respectively. However, downstream dispersal was inversely related with velocity and stream gradient, contrary to the passive dispersal hypothesis (Elliott 1966; Marty and Beall 1989; Hesthagen 1988; but see Ottaway and Clarke 1981). Only two of 19 dispersal distributions were leptokurtic, suggesting that most streams comprised a homogenous population of somewhat mobile individuals. When we considered downstream dispersal only, there was evidence of a bimodal population of dispersers in half of the streams.

More fry disperse downstream than upstream

Compared with past studies (e.g. Egglisshaw and Shackley 1973; Egglisshaw and Shackley 1980; Beall et al. 1994; Crisp 1995; Marty and Beall 1989; Einum et al. 2011), a much higher proportion of fry (35%), moved upstream in our study. In contrast, the mean percentage moving upstream in the other studies (Fig. 5) was only 12.4% (SD = 16.25%, range = 0 to 51.4%). Egglisshaw and Shackley (1973) may have had a higher percentage of fry moving upstream due to the placement of fry between a deep gorge (downstream) and a waterfall (upstream).

While none of our environmental variables could explain differences among streams in this tendency for upstream dispersal, there was some consistency in streams over years. For example, Perham stream had the highest consistent upstream dispersal with 44, 44.1, and 51.6% over years. In contrast, Sandy River had 18.7, 21.9, and 36.1% moving upstream over the years sampled. We can only surmise that our stocked fry were responding to some un-measured variable to produce such consistent behaviour over years.

We suspect that the low percentage of upstream dispersal detected in previous studies may have been due to an unconscious or deliberate censoring of upstream movement. For

instance, the first study to show that fry dispersal is primarily downstream was likely Elliott (1966), followed by Egglisshaw and Shackley (1973), and then Mary and Beall (1989). All of these studies had inherent downstream biases. After these studies, it became common practice to stock or implant fry at the upstream end of a section of fast-flowing water or immediately downstream of waterfalls or dams (e.g. Beall et al. 1994; Crisp 1995; Brunsdon et al. 2017).

Fry dispersed great distances both downstream and upstream

Our results demonstrate large-scale median dispersal distances both upstream (403 m) and downstream (404 m) (Fig. 3a, 5), far greater than the predictions of RMP for this life stage (10 and 50 m, respectively). Surviving fry that disperse far from the redd could have major implications for gene flow and colonization of new or historic habitat (Crisp 1995; Fraser et al. 2001; Yeakel et al. 2018). More specifically, dispersal away from the redd contributes to genetic rescue, species resilience and stability, and other connections within meta-populations, in which salmonid populations thrive (Gilbert 2016; Yeakel et al. 2018).

It is possible the large dispersal distances in our study were due to the stock used for implanting, which were not locally adapted to the region. Fitness and survival of Atlantic salmon is greatly reduced when they are reared in a hatchery (Araki et al. 2008; Milot et al. 2013; Dittman et al. 2015), and the rate of stray is increased (Jonsson et al. 2003, Dittman et al. 2015). However, other studies suggesting restricted movement also used hatchery fish (Egglisshaw and Shackley 1973; Gustafson-Greenwood and Moring 1990; Beall et al. 1994; Crisp 1995; Einum and Nislow 2005; Einum et al. 2012), or implanted wild stock from another river (Marty and Beall 1989). A difference in river size could also have influenced the distance dispersed, but we

included a wide range of river sizes (6.7-64.9 m in width; Table 1), all of which had tremendous dispersal distances (Table 2).

Dispersal behaviour observed in this study might be partially due to habitat quality in the watershed or at the sites where eggs were initially deposited. Habitat can have a major influence on the movement and behaviour of Atlantic salmon (Heggenes 1990), and quality is on the decline in many areas (Jelks et al. 2008). Habitat that was suitable in the fall after being selected and excavated by the female parent could be unsuitable for rearing at the time of emergence, necessitating a higher-than-average upstream (and/or downstream) dispersal (Heggenes 1990). Similarly, the sites selected for implanting may have appeared ideal, but were suboptimal for emerging fry. We think poor habitat quality is an unlikely explanation for our results for two reasons. First, implant sites were selected based on historical spawning areas (P. Christman, unpublished data). Second, the estimated average survival rates of 22% compared favourably to previous studies showing restricted movement (Crisp 1995).

Previous study designs have made it difficult to characterize the spatial extent and probability of upstream movement and have likely increased the potential for unnatural behaviour, such as forced dispersal events by implanting fish immediately downstream of barriers or unsuitable habitat (Fig. 5). Nevertheless, the variability in dispersal distance observed between studies (Fig. 5) suggests that other factors are at play, such as the effects of local environmental conditions or local adaptation of populations. For example, intense predation on dispersing fry combined with a prior resident advantage to early emerging fry could lead to the restricted movement of fry (Einum et al. 2012).

Passive versus active dispersal

At first glance, downstream dispersal distance seemed to be active rather than passive - median downstream dispersal decreased in streams with higher velocities and gradients, suggesting that fish were choosing to settle sooner in adverse conditions. However, maximum downstream dispersal increased with gradient/velocity and body size, consistent with the passive-dispersal and active-swimming hypotheses, respectively. In summary, no clear picture of what drives downstream dispersal distance emerged, but something other than just swimming capacity was likely important (Ottaway and Clarke 1981).

In contrast to downstream dispersal, upstream dispersal distance was consistent with the active dispersal hypothesis. Both median and maximum distance increased with body size and maximum distance decreased with increasing stream velocity. Furthermore, fish were larger upstream than downstream, suggesting that larger fish were better able to swim upstream against the current.

Density-dependent body size

Consistent with density-dependent growth (Grant and Imre 2005), fry were larger at lower densities. However, the independent effect of distance from the implant site suggests that larger fish disperse farther (see above). The larger size of fry in streams with faster flows suggests a higher abundance of drifting invertebrates in larger, faster streams. These results highlight the possible advantage afforded to the individuals capable of moving away from the redd or implant location, especially if it is in the upstream direction.

Homogeneous dispersal

Persistent leptokurtosis and bimodal dispersal curves suggest population heterogeneity in movement behaviour (Paradis et al. 1998; Gomez and Samora 1999; Skalski and Gilliam 2000; Fraser et al. 2001; Radinger and Wolter 2014). In contrast to previous studies, our results suggested relatively homogeneous behaviour: few dispersal curves were leptokurtic and only half of downstream distributions were bimodal. If heterogeneity is a response to divergent selection pressures in the wild (Skalski and Gilliam 2000; Fraser et al. 2001), then it is possible that the selective regime acting in the hatchery is responsible for the homogeneous behaviour observed in our study. Other stocked populations, however, have also exhibited heterogeneous behaviour, consisting of both mobile and stationary individuals (Rodriguez 2002)

While heterogeneity in dispersal is thought to contribute to gene flow, a mixture of mobile and stationary individuals can still follow the RMP (Rodriguez 2002). At the time, the maximum spatial extent for Atlantic salmon was only 346 m, much less than the 4770 m in our study or in Brunsdon et al. (2017). Our results suggest less heterogeneity within populations, but greater overall mobility that should promote gene flow and the colonization of empty habitats. Taken together with past studies, our results highlight the potential for greater variability in movement behaviour between Atlantic salmon populations than previously thought, which has implications for the management of this important species.

Caveats and recommendations

We deposited more eggs in each artificial redd than would normally be found in natural redds (see Table 2). However, we think these higher densities cannot explain the large dispersal distances observed here. First, the lower range of eggs in our study were similar to what would

be found in a natural redd (Reid and Chaput 2012). Second, there was no effect of egg density on median dispersal distance. Third, the growth rate and estimated survival rate in our study were high compared to other studies (e.g. Brunsdon et al. 2018), suggesting no adverse effects of the high initial densities.

Many studies that have previously quantified salmonid fry dispersal placed artificial redds or released stocked fish downstream of a barrier, such as a waterfall, dam, or zone of fast water (Egglshaw and Shackley 1973; Crisp 1995). Hence, such studies could not effectively describe the magnitude of upstream movement at this early life stage (Marty and Beall 1989, Beall et al. 1994). The downstream dispersal observed in these early, influential studies may have unconsciously biased later studies to focus most of their sampling efforts downstream rather than upstream (e.g. Jokikokko 1999; Einum et al. 2011; Brunsdon et al. 2017).

Quantifying the complexity of Atlantic salmon fry dispersal can help us understand the correlates of fitness, habitat use, the mechanisms driving movement, and can help to identify patterns connecting source and sink populations. Researchers and managers should not necessarily assume that restricted movement always applies to the fry life stage. Rather, patterns of dispersal may vary on a per stream basis. A formal synthetic analysis may be required to explore the variability among studies and the degree to which potential biases influence our understanding of this important phase of the life history of stream salmonids.

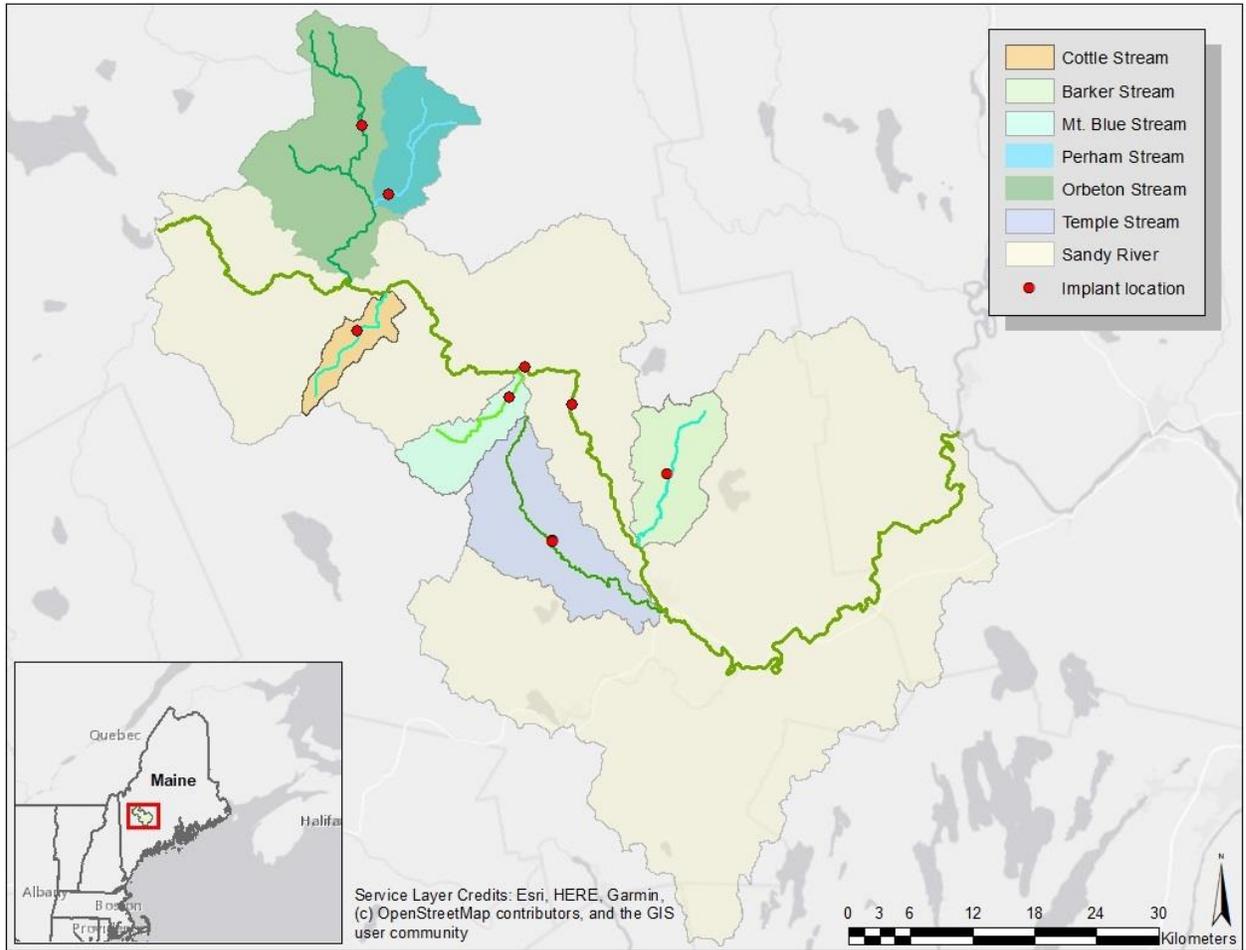


Figure 1. Map of six tributaries and Sandy River (confluence: 44.7643, -69.8895) in southwest Maine, USA.

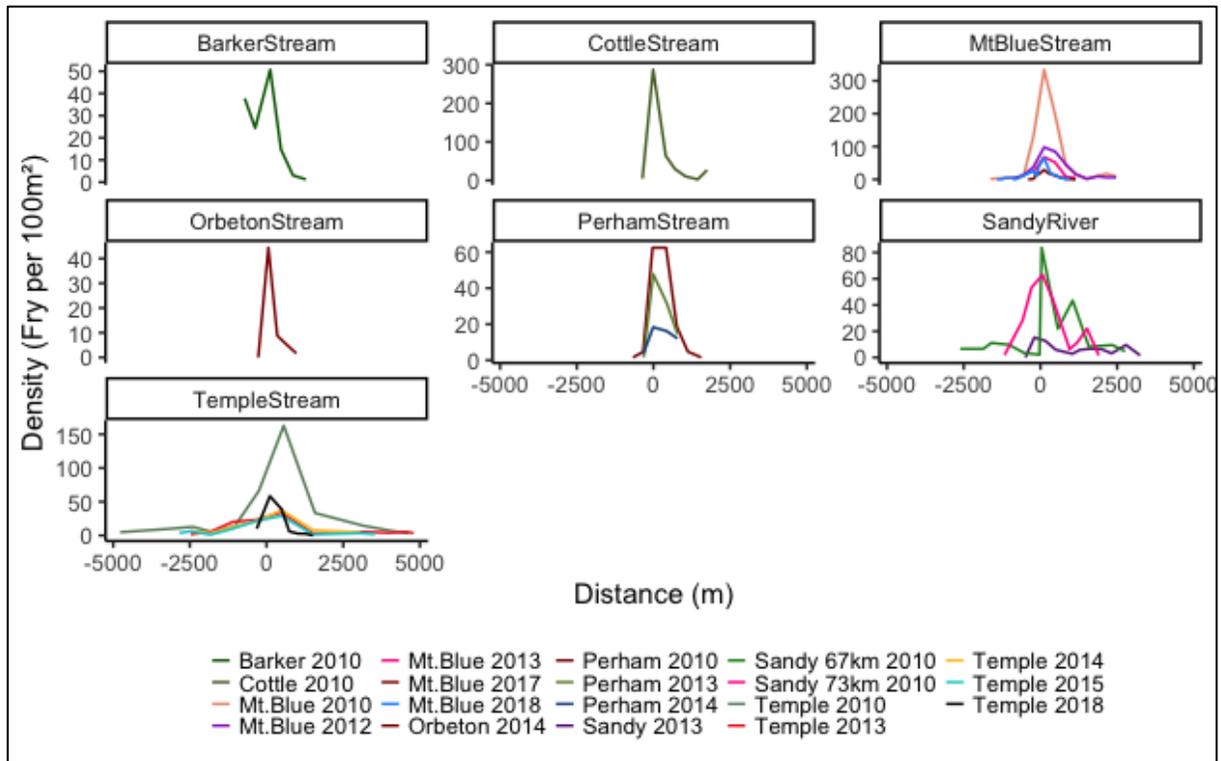


Figure 2. Density distributions of Atlantic salmon fry upstream and downstream (negative and positive, respectively) of each implant site (denoted by 0) in the Sandy River drainage. Note the y-axes have different scales.

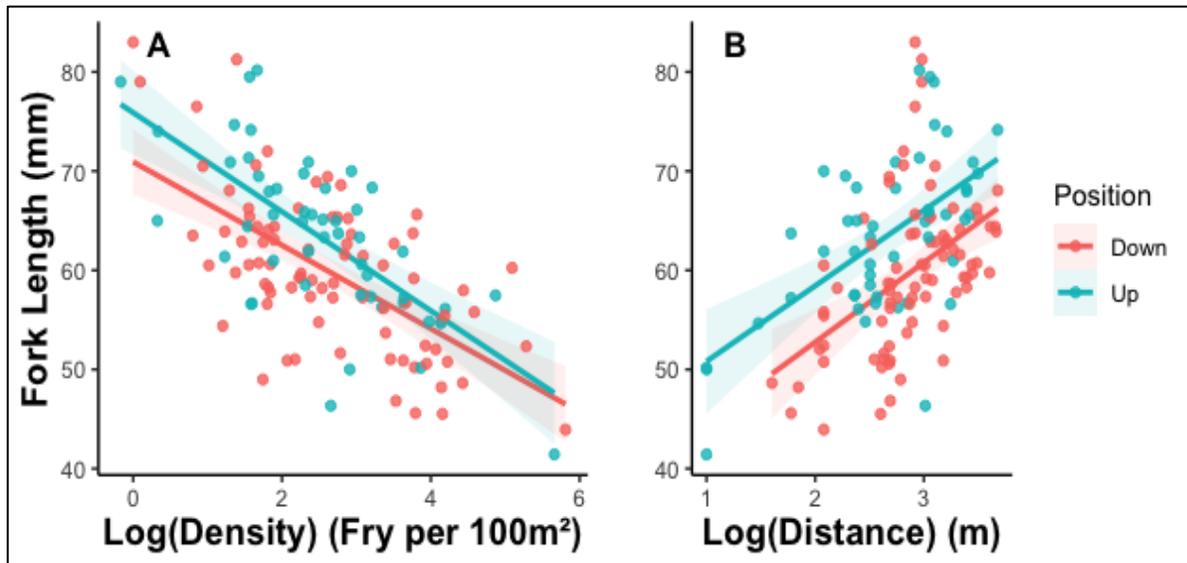


Figure 3. Linear regression (with 95% confidence interval) of fork length (mm) of Atlantic salmon fry in relation to log₁₀ of (A) density at each sampling site; and (B) distance from the redd site in the Sandy River drainage, separated by upstream (blue) and downstream (red) directions.

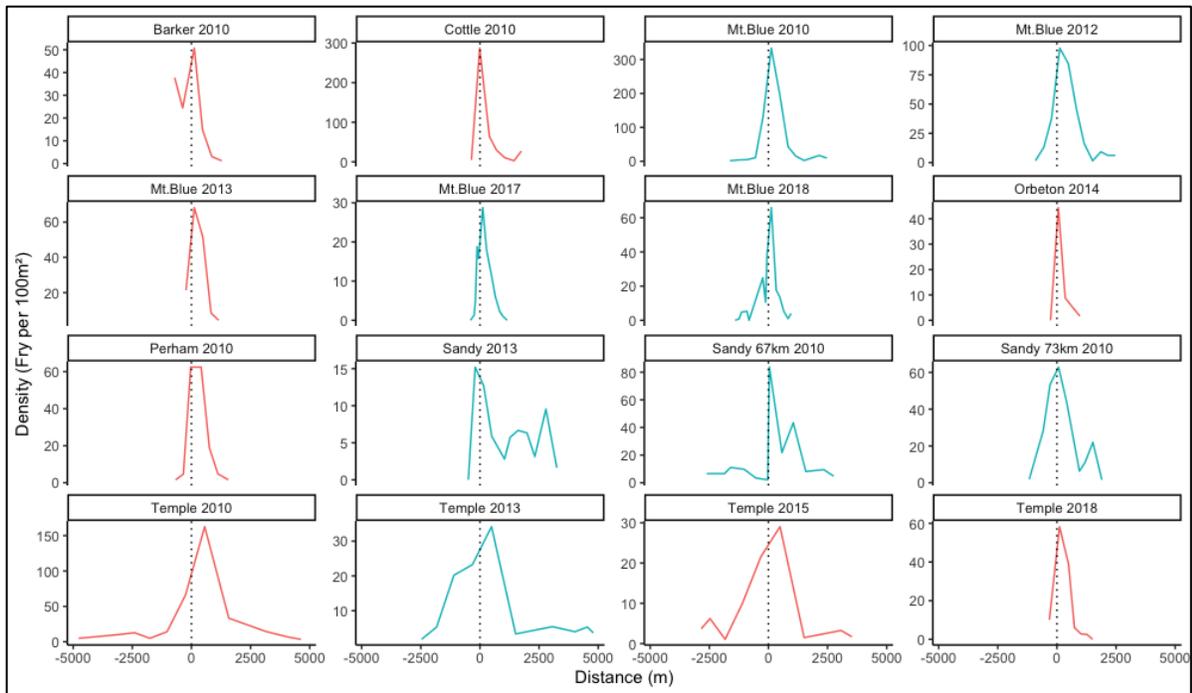


Figure 4. Streams coloured by whether a one-parameter (red) or two-parameter (blue) model was selected using a theoretical equation described by Rodriguez (2002). Note the y-axes have different scales.

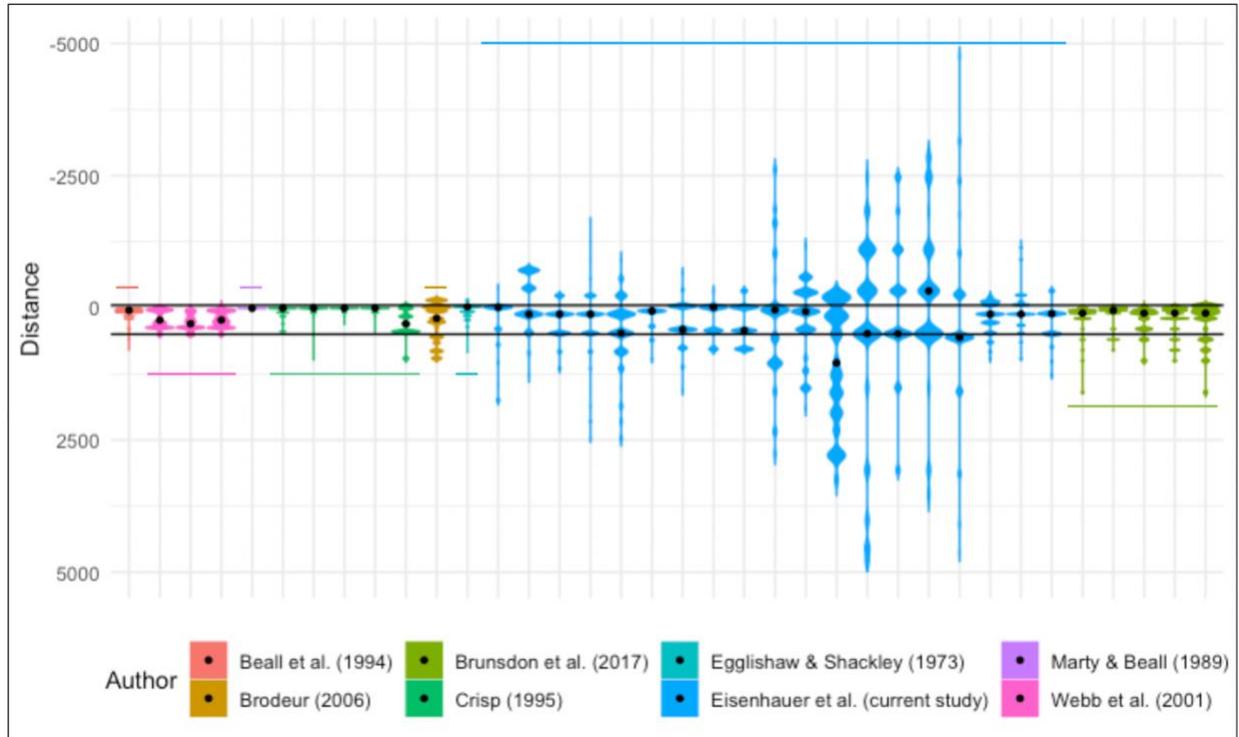


Figure 5. Violin graph illustrating the median (black dot) and maximum dispersal distance and the frequency of Atlantic salmon fry versus distance (m) from implant or redd location (zero distance) in upstream (negative numbers) and downstream directions. The upper and lower lines indicate 0 and 500 m downstream, respectively, the putative limits of dispersal in the literature. The thickness of the lines or bars represent higher densities. Bars above and below distributions represent different studies.

Table 1. Description of seven streams used in the study of 0+ Atlantic salmon fry dispersal in the Sandy River, ME, USA. All measurements calculated using USGS regression equations provided by the StreamStats Web-based Geographic Information Systems (GIS) application (Version: 4.3.8).

Name	Drainage Area (km ²)	Average Width (m)	Mean Basin Slope (%)	Basin Elevation Mean; Max (m)	Years Sampled	Coordinates [†]
Mt Blue Stream	31.1	8.5	17.0	431.8; 973.0	5	44.8036, -70.2715
Temple Stream	87.0	14.5	15.4	989.7; 792.4	5	44.6541, -70.1472
Perham Stream	40.7	9.8	16.2	651.5; 1234.7	3	44.9049, -70.3967
Orbeton Stream	153.8	19.5	17.0	594.1; 1259.2	1	44.8559, -70.4176
Sandy River	1541	64.9	11.8	286.5; 1259.2	3	44.7643, -69.8895
Cottle Brook	19.7	6.7	13.5	386.9; 768.7	1	44.8510, -70.3872
Barker Stream	50.0	10.9	12.4	232.8; 612.9	1	44.6954, -70.1662

[†]Latitude and longitude at mouth of the stream.

Table 2. Summary of Atlantic salmon fry movements (m) upstream (U) and downstream (D) from artificial redds in the Sandy River, Maine, USA and six tributaries from 2010-2018.

Stream	Year	Eggs Implanted	Percent* Recovered	Mean distance		Median distance		Maximum distance		Percent Upstream
				U	D	U	D	U	D	
Baker Stream	2010	5825	18.54	576.5	247.1	710	120	710	1280	47.1
Cottle Brook	2010	42500	9.87	15.9	811.9	10	700	360	1750	68.5
Mt. Blue Stream	2010	51457	45.87	313.2	431.2	230	120	1630	2470	19.4
Mt. Blue Stream	2012	28780	30.24	330.9	586.3	230	480	910	2470	16.4
Mt. Blue Stream	2013	28442	14.93	230	338.6	230	120	230	1150	13.9
Mt. Blue Stream	2017	4968	25.09	110.3	309.8	120	280	240	960	37.8
Mt. Blue Stream	2018	5350	77.98	246.9	263.9	120	120	1240	960	44.0
Orbeton Stream	2014	41760	6.13	0†	179.1	0	60	-60	970	0.0
Perham Stream	2010	46160	11.65	65.5	544.2	30	410	670	1560	44.0
Perham Stream	2013	23736	13.19	20	540.5	10	430	320	780	51.6

Perham Stream	2014	31710	4.78	64.9	579.7	10	430	320	780	44.1
Sandy River (67km)	2010	47940	13.84	1494.6	639.3	1600	570	2610	2760	18.7
Sandy River (73km)	2010	104130	16.26	407.8	527.7	290	410	1170	1900	36.1
Sandy River (73km)	2013	58232	11.94	200	1429.3	200	1280	200	3250	21.9
Temple Stream	2010	47940	29.31	1107.1	1054.4	250	560	4770	4630	33.8
Temple Stream	2013	49553	14.86	866.2	1717.6	1100	490	2470	4790	47.5
Temple Stream	2014	41760	2.45	1003.6	892	1100	490	2470	3070	46.9
Temple Stream	2015	14404	25.44	1073.1	914	1100	490	2840	3530	54.5
Temple Stream	2018	5350	46.39	320	331.9	320	110	320	1510	8.5
Averages	-	35789	22.0	444.6	649.4	403.2	403.7	1232.6	2135.3	34.46

*Percent recovered determined by dividing the population estimate by the total eggs implanted.

†No upstream dispersal reported for Orbeton 2014.

Table 3. Multiple GLS regression results relating fry dispersal variable to *a priori* predictors.

Variables	Value	SE	t-value	P-value
(A) % Upstream (n= 19, df= 18, ΔAICc= 4.71)				
Intercept	2.51	0.170	14.794	<0.00001
(B) Median downstream distance (n= 19, df= 16 ΔAICc= 2.84)				
Intercept	4495.814	378.349	11.883	<0.00001
Stream velocity	-356.345	41.9481	-8.495	<0.00001
Stream gradient	-209.143	28.021	-7.464	<0.00001
(C) Maximum downstream distance (n= 19, df= 16, ΔAICc= -1.27)				
Intercept	-5242.46	367.272	-14.274	<0.00001
Stream velocity	703.747	119.250	5.901	<0.00001
Body length	90.021	5.121	17.577	<0.00001
(D) Median upstream distance (n= 19, df= 17, ΔAICc= 3.85)				
Intercept	-119.028	3.784	-31.457	<0.00001
Body length	2.468	0.079	31.457	<0.00001
(E) Maximum upstream distance (n= 19, df= 16, ΔAICc= 1.11)				
Intercept	-1142.423	77.741	-14.695	<0.00001
Stream velocity	-379.106	19.791	-19.155	<0.00001
Body length	42.013	1.511	27.811	<0.00001
(F) Body Length (n= 19, df= 16, ΔAICc= 0.51)				
Intercept	32.755	4.183	7.830	<0.00001
Stream velocity	0.006	0.002	3.151	0.002

Egg mortality	0.220	0.026	8.305	<0.00001
Log (Distance from redd)	5.241	0.847	6.187	<0.00001
Position: Upstream	3.986	0.791	5.042	<0.00001
Density	-0.051	0.012	-4.431	<0.00001

Table 4. Comparison between a single- (stationary) or two- (mobile and stationary) parameter nonlinear equations (sensu Rodriguez 2002) to downstream dispersal distributions in seven Atlantic salmon populations. Kurtosis values are for each complete distribution (i.e. upstream and downstream).

Population	Year	AICc* (Single)	AICc (Two)	Best fit	Kurtosis	Distribution
Barker	2010	†	-16.870	Two	-0.581	Mesokurtic
Cottle	2010	68.216	-14.596	Two	3.450	Leptokurtic
Mt. Blue	2010	83.272	110.583	Single	4.761	Leptokurtic
	2012	71.395	99.396	Single	1.960	Mesokurtic
	2013	†	8.132	Two	0.344	Mesokurtic
	2017	35.230	†	Single	0.078	Mesokurtic
Mt. Blue	2018	46.822	†	Single	2.882	Mesokurtic
	Orbeton	2014	†	-14.898	Two	2.835
Perham	2010	†	-17.279	Two	0.778	Mesokurtic
	2013	*	*	*	-1.105	Mesokurtic
	2014	*	*	*	-1.241	Mesokurtic
Sandy	2013	55.293	76.040	Single	-1.266	Mesokurtic
	2010	64.808	†	Single	0.594	Mesokurtic
	2010	59.743	†	Single	0.021	Mesokurtic
Temple	2010	61.827	-34.671	Two	2.454	Mesokurtic
	2013	50.940	†	Single	0.369	Mesokurtic

2014	*	*	*	0.589	Mesokurtic
2015	†	-3.825	Two	0.948	Mesokurtic
2018	64.376	-15.624	Two	0.914	Mesokurtic

* Denotes distributions that were excluded due to small sample size (< 3)

† Denotes overfitted models.

Bold denotes selected model.

Supplementary Methods

Egg take:

Sea run adult Atlantic salmon were captured in the Penobscot River and held at Craig Brook National Fish Hatchery until spawning. They were moved to Green Lake National Fish Hatchery as eyed eggs and reared to adulthood. Each year Green Lake spawns 500 or more families of adults. Given that the salmon don't all spawn at the same time, the hatchery personnel spawn the broodstock in waves, as they mature. In a given season, they will spawn anywhere from 2-6 waves (i.e. takes). Each take is made up of a different number of families, that are fertilized at different times and, hence, vary in developmental stage. In the winter as each take reaches the eyed stage, the offspring are divided into samples destined for planting in multiple sites. Each sample of eggs will comprise a different number of potential families. For example, in 2017, Mt Blue eggs were composed of 230 families from a single take. In most cases, the sex ratio for spawning was a 1:1. For the age 4 females, the number of family groups are similar to the number of females as the hatchery personnel cross age 4 females with age 3 males. For age 3 females, the number of family groups may be reduced if the hatchery is short of age 4 males and therefore spawns some males twice. Any differences in the number of eggs transferred to the Kennebec Drainage and the Eyed Egg Take (Table S2) indicate that eggs were distributed to other programs and or mortality incurred after the initial enumeration.

All eyed eggs were counted and transferred from the hatchery in insulated shipping containers the afternoon prior to planting (Fig. S1). Each styrofoam shipping container (49cm x 42cm x 39cm high) had six trays with four compartments. Each compartment was fitted with wetted cheese cloth, and eggs were placed on top. No eggs were placed in the bottom or the top tray. The bottom tray acts as a spacer to keep the eggs out of the water caused by melting ice

which is located in the top tray. As trays were loaded, they were stacked in the container. When the container was full, the last tray on top was filled with ice and dampened with a small amount of water. Containers were held overnight at room temperature. Upon arrival the following day at the river, the eggs were removed from the shipping containers and placed in jugs of water to reduce the chance of freezing prior to burial.

In-stream incubation system:

The equipment used to bury the eggs was developed by the Maine Department of Marine Resources (MDMR) for large scale Atlantic salmon restoration (Fig. S2). The new In-Stream Incubation System has three components. A backpack carried a Honda WX15 four stroke 49cc water pump with a capacity of 272.5L/min attached to a 3.1cm diameter standpipe with a flexible hose. A funnel was made of a 152mm X 460mm pipe attached to a reducer that brings the diameter down to a 360mm long pipe, just large enough in diameter for the standpipe to fit inside. The standpipe was fitted with a hose clamp and rubber stopper to keep the pipe from protruding out of the bottom of the funnel. The funnel and standpipe, with the pump running, were inserted into the gravel to the desired depth. For this project we planted eggs 30cm below the surface of the stream bed, within the normal range for Atlantic salmon (Bley 1987). When the depth was reached, the standpipe was removed from the funnel leaving it in the gravel. Three to five hundred eggs were then poured underwater into the funnel. When sufficient time has passed for the eggs to reach the lower end of the funnel, it was lifted several cm, so that more eggs could be poured in. Two groups of eggs were deposited each time the funnel was inserted. The density of eggs ranged from 3,200-8,608 eggs/m². Most of the eggs were planted by a single

crew of 3-5 people. On several occasions each year, two crews were deployed due to the number of eggs that were ready for planting.

Wild reproduction:

Wild, naturally reared, adult Atlantic salmon captured in Waterville, Maine on the mainstem Kennebec River, were transported to the uppermost portion of the Sandy River (96.86km) almost 30km upstream of our study sites on the Sandy River. Annual redd surveys were conducted to map the subsequent distribution of natural Atlantic salmon nests. Other than a few instances of wild reproduction, eyed eggs are the only other Atlantic salmon life stage released into the drainage.

Studies used in Fig. 4:

The data used to model frequency distributions of Atlantic salmon fry in Fig. 4 were extracted from figures and tables using the 'digitize' function in the package CRAN (RStudio version 1.2.0.5033) and text from each specific study, then modeled using a violin plot built in ggplot2 (RStudio version 1.2.0.5033).

Egglshaw and Shackley (1973) implanted Atlantic salmon eggs into the Fender Burn in Perthshire, Scotland, a steep stream with multiple waterfalls and gorges. The number of fry were estimated using electroshocking units and blocking seines. The lower distribution was not used as fry were sprinkle stocked over a long distance, 20 m below a waterfall. Upper distribution distances were conservatively assigned so as to not inflate dispersal distances. Fry were recorded 120 m upstream and 810 m downstream. Eggs were planted below a gorge.

Marty and Beall (1989) observed over 50% of surviving fry (75% of planted eggs) settling within 50m downstream from redds in Lapitxuri Experimental Stream, Saint-Pée-sur-Nivelle, France. Their results showed two waves of downstream dispersal. The first occurred before the onset of aggressive territorial behavior, soon after emergence, to fill useable space. The second, denoted as late emerging fry, were displaced by territoriality. They used box traps and electroshocking to determine dispersal distance and timing. Upstream dispersal was blocked by a net.

Beall et al. (1994) captured 1 270 fry in 8 traps, each trap occupying 5% of the total flow (7785 fry) in Lapitxuri Brook, a tributary to River Nivelle, Basque Country, France. 15 000 eyed eggs were implanted, so the survival rate would be about 51%. An estimated 6 491 fry settled between traps and 32 fry settled past the last trap (800m). No upstream dispersal was measured but estimated to be 57 fry. The highest density of fry was 90-150m below the redd in a stretch of very similar habitat.

Crisp (1995) assessed dispersal of stocked Atlantic salmon fry in Bollihope Burn, Co. Durham, England. The author reported some fish dispersing up to 50m upstream or 500m downstream of the stocking point, but the majority remained close to the point of release (see Crisp 1995, Tables 1, 2, 3 and Fig. 1). Fry had to negotiate a concrete slab at a 14% grade to access upstream habitat.

Webb et al. (2004) assessed natural emergence of Atlantic salmon fry, using microsatellite DNA profiling (see Webb et al. Table 2, Fig. 2). The author reported densities of families in each sector of the main study reach. Three redds were planted on the same location, one was a short distance downstream. No fry were caught more than 940m downstream or 90m upstream of its stocking point. Only families F5,6, and 7 were used (Table 2, Fig. 2)

Brodeur (2006) quantified the dispersal of Atlantic salmon fry via snorkel surveys. Microsatellite markers were used (78% estimated correctness probability) to assess the local-scale distribution patterns of 81 juvenile Atlantic salmon in Catamaran Brook, a tributary to the Little Southwest Miramichi River, New Brunswick. Fry distributions ranged from 9-154m upstream and 50-955m downstream, with a median dispersal distance of 154m upstream and 542m downstream (Fig. 2.4.).

Brunsdon et al. (2017) manipulated densities of Atlantic salmon fry in the Boquet River, NY, to evaluate the effects of clumped- (releasing all the fish at one location) and dispersed-stocking (releasing the fish evenly over a complete reach) treatments on habitat use, dispersal, growth, and survival across 14 rivers. They documented “greater than expected” mobility of fish in clumped-stocking reaches; fry dispersed up to 1600 m, with 41% moving over 200 m downstream. Upstream sampling terminated at 50m due to sampling design.



Fig S1. Insulated Styrofoam shipping container (right) used to transport eyed Atlantic salmon eggs from the Green Lake National Fish Hatchery to implant sites. One of six four-compartment trays (top left), used to stack eggs in the shipping container. One wetted cheese cloth (bottom left), used to cover each tray.



Fig. S2. Maine Department of Marine Resources (MDMR) In-Stream Incubation System. Honda WX15 four stroke 49cc water pump (middle top), 3.1cm diameter standpipe with a flexible hose (left), intake hose for pump with debris guard (middle bottom), and metal funnel for receiving standpipe and implanting eggs (right).

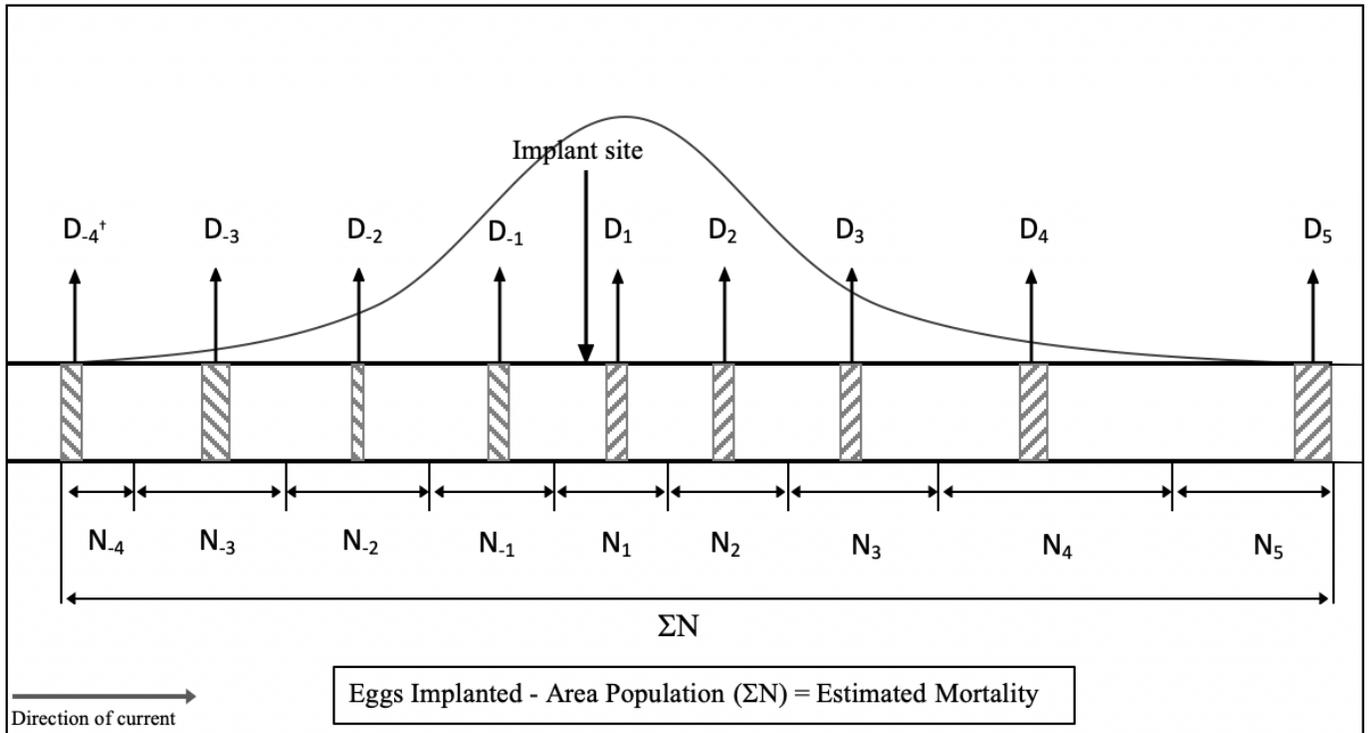


Fig. S3. Schematic of the typical sampling plan. $D_{\#}$ = density estimate from CPUE electroshocking event. $N_{\#}$ = Population estimate for shocking reach and distance between reaches. †Negative subscript denotes upstream position.

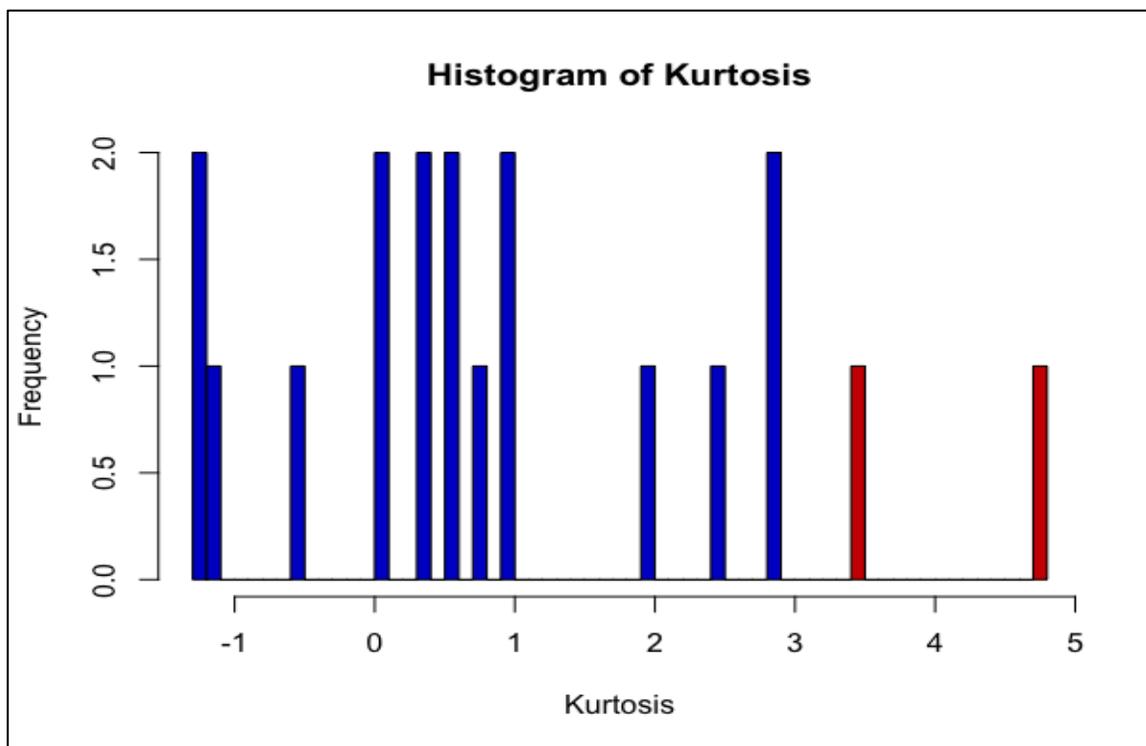


Fig. S4. Histogram of Kurtosis values. Blue indicates the frequency of normal distributions; red indicates the frequency of leptokurtic distributions.

Table S1. Number and size of sampling sites in each stream.

^αArea reported in meters squared, width reported in meters

Stream	Year	Width (m)	Total area	
			(m ²)	# of sites
Temple	2010	7.12	1235.67	11
Sandy 73	2010	22.8	1356.51	9
Sandy 67	2010	18.62	1514.61	12
Cottle	2010	4.58	634.96	7
Mt. Blue	2010	7.42	1607.64	13
Perham	2010	7.28	847.02	7
Barker	2010	4.48	556.14	6
Mt. Blue	2012	6.85	1005	9
Perham	2013	9.28	520	6
Mt. Blue	2013	8.22	642	7
Sandy 73	2013	27.74	1249	11
Temple	2013	10.31	1075	11
Orbeton	2014	10.66	568	6
Perham	2014	8.09	467	6
Temple	2014	8.79	633	7
Temple	2015	9.63	1181	11
Mt. Blue	2017	7.08	1465.95	12

Temple	2018	6.78	860.68	7
Mt. Blue	2018	7.86	1550.87	15

Table S2. Details about egg sampling in each year.

Stock Year	Spawn Year	Take Date	Take	Females	Age- Class	Date of Stripping	No. Transferred to Kennebec	No.Eyed Eggs After Sorting
2010	2009	11/4/09	1	59	4	12/18/09		83,660
2010	2009	11/9/09	2	147	4	1/5/10	535,500	259,931
2010	2009	11/17/09	3	106	4	1/28/10		234,495
2012	2011	11/15/11	1	54	4	1/16/12	137,540	144,100
2012	2011	11/21-22/2012	2	297	4	2/2-3/2012	773,349	789,202
2013	2012	11/19/12	1	13	4	2/12/13	15,758	19,758
2013	2012	11/27/12	2	129	4	2/25/13	334,015	339,891
2013	2012	12/3/12	3a+b	210	4	3/8/13	304,309	462,096
2014	2013	11/13/13	1	35	4	2/4/14	75,432	90,272
2014	2013	11/19/13	2a	151	4	2/18-19/2014	415,773	493,197
2014	2013	11/20/13	2b	126	3	2/20/14	213,293	214,871
2014	2013	11/26/13	3	205	4	3/3-4/2014	446,832	546,592
2015	2014	11/19/14	1b	16	3	2/12/15	23,696	27,696
2015	2014	11/26/14	2b	121	3	2/24/15	181,507	181,707
2015	2014	12/1/14	3b	66	3	3/3/15	69,384	95,844
2017	2016	11/15/16	1	4	4	1/24/17	938	8,251
2017	2016	11/16/16	1b	20	3	1/24/17	17,608	23,408

2017	2016	11/22/16	2b	230	3	2/8/17	328,592	328,992
2017	2016	11/30/16	3b	93	3	2/24/17	99,968	127,616
2018	2017	11/21/17	1	61	4	2/9/18	108,900	173,700
2018	2017	11/27/17	1b	30	3	2/20/18	39,321	39,321
2018	2017	11/28/17	2.1	148	4	2/21/18	318,273	436,729
2018	2017	11/29/17	2.2	163	4	2/22/18	237,300	443,414
2018	2017	12/5/17	2b	164	3	3/2/18	239,232	239,632

Table S3. Summary of wild Atlantic salmon activity in headwaters of Kennebec River

Year	Number of adults moved	# redds	Distance to implant (km)
2010	5	0	N/A
2011	64	27	N/A*
2012	5	2	N/A*
2013	8	0	N/A
2014	18	5	0.4
2015	31	21	11.95
2016	39	24	N/A**
2017	36	3	N/A*
2018	11	3	N/A*

*No redds in river with implanting sites

**No implant sites this year

Table S4. Predictions about how environmental variables will affect Atlantic salmon fry dispersal. ^aSC = Swimming capacity; DD = Density dependence

Variable	Predictions	Rationale*	Results
% Moving	Downstream > upstream	SC	True
% Moving upstream	Velocity: -	SC	True‡
	Gradient: -	SC	True‡
	Stream Width: -	DD	True‡
	Discharge: -	SC	True‡
	Body size: +	DD, SC	False‡
	Number of eggs: +	DD	False‡
	Egg mortality: -	DD	False‡
Distance downstream	Velocity: +	SC	True
	Gradient: +	SC	False
	Stream Width: -	DD	False
	Discharge: +	SC	True‡
	Body size: +	DD	True‡
	Number of eggs: +	DD	True‡
	Egg mortality: -	DD	True‡
Distance Upstream	Velocity: -	SC	False‡

Gradient: -	SC	True
Stream Width: -	DD	False‡
Discharge: -	SC	True‡
Body size: +	DD, SC	True‡
Number of eggs: +	DD	True‡
Egg mortality: -	DD	True‡

References

- Araki, H., Berejikian, B. A., Ford, M. J., and Blouin, M. S. 2008. Fitness of hatchery-reared salmonids in the wild. *Evol Appl.* **1**(2): 342–355. doi:10.1111/j.1752-4571.2008.00026.x.
- Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M., and Milner, N. J. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fish. Res.* **62**(2): 143-170. doi:10.1016/S0165-7836(02)00160-1.
- Beall, E., Dumas, J., Claireaux, D., Barriere, L., and Marty, C. 1994. Dispersal patterns and survival of Atlantic salmon (*Salmo salar* L.) juveniles in a nursery stream. *ICES J. Mar. Sci.* **51**(1):1–9. doi:10.1006/jmsc.1994.1001.
- Bley, P. W. 1987. Age, growth, mortality of juvenile Atlantic salmon in streams: a review. U. S. Fish and Wildlife Service. Department of the Interior. Biological Report, **87**(4).
- Brodeur, N. N. 2006. Dispersion Patterns of kin in young-of-year Atlantic salmon (*Salmo salar* L.) in Catamaran Brook, New Brunswick. M.Sc. thesis, Department of Biology, Concordia University, Montreal.
- Brunsdon E. B., Fraser D. J., Ardren W. R., and Grant J. W. A. 2017. Dispersal and density-dependent growth of Atlantic salmon (*Salmo salar*) juveniles: clumped versus dispersed stocking. *Can. J. Fish. Aquat. Sci.* **74**(9):1337-1347. doi:10.1139/cjfas-2015-0488.
- Burnham, K. P., and Anderson, D. R. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Fort Collins, CO: Colorado Cooperative Fish and Wildlife Research Unit (USGS-BRD).
- Clobert, J., Baguette, M., Benton, T. G., and Bullock, J. M. 2012. Dispersal Ecology and Evolution. Oxford: Oxford University Press.
- Crisp, D.T. 1995. Dispersal and growth rate of 0-group salmon (*Salmo salar* L.) from point-

- stocking together with some information from scatter-stocking. *Ecol. Freshw. Fish.* **4**(1):1–8. doi:10.1111/j.1600-0633.1995.tb00021.x.
- De Bie, T., Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., and Gucht, K. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecol. Lett.* **15**(7):740–747. doi:10.1111/j.1461-0248.2012.01794.x.
- Dittman, A. H., Pearsons, T. N., May, D., Couture, R. B., and Noakes, D. L. G. 2015. Imprinting of Hatchery-Reared Salmon to Targeted Spawning Locations: A New Embryonic Imprinting Paradigm for Hatchery Programs. *Fish.* **40**(3):114-123. doi:10.1080/03632415.2015.1007206.
- Drakou, E. G., Bobori, D. C., Kallimanis, A. S., Mazaris, A. D., Sgardelis, S. P., and Pantis. J. D. 2009. Freshwater fish community structured more by dispersal limitation than by environmental heterogeneity. *Ecol. Freshwat. Fish*, **18**: 369–379. doi: 10.1111/j.1600-0633.2009.00354.x.
- Egglishaw, H. J., and Shackley, P. E. 1973. An experiment on faster growth of salmon (*Salmo salar* L.) in a Scottish stream. *J. Fish Biol.* **5**(2):197-204. doi:10.1111/j.1095-8649.1973.tb04448.x.
- Egglishaw, H. J., and Shackley, P. E. 1980. Survival and growth of salmon (*Salmo salar* L.) planted in a Scottish stream. *J. Fish Biol.* **16**(5):565-584. doi:10.1111/j.1095-8649.1980.tb03734.x.
- Einum, S., and Nislow, K. H. 2005. Local-scale density-dependent survival of mobile organisms in continuous habitats: An experimental test using Atlantic salmon. *Oecologia*, **143**(2):203-210. doi:10.1007/s00442-004-1793-y.

- Einum, S., Robertsen, G., Nislow, K. H., McKelvey, S., and Armstrong, J. D. 2011. The spatial scale of density-dependent growth and implications for dispersal from nests in juvenile Atlantic salmon. *Oecologia (Berl.)*, **165**(4):959–969. doi:10.1007/s00442-010-1794-y.
- Einum, S., Finstad, A.G., Robertsen, G., Nislow, K. H., McKelvey, S., and Armstrong, J. D. 2012. Natal movement in juvenile Atlantic salmon: a body size-dependent strategy? *Popul. Ecol.* **54**(2):285–294. doi: 10.1007/s10144-011-0296-z.
- Elliott, J. M. 1966. Downstream movements of trout fry (*Salmo trutta*) in a Dartmoor stream. *J. Fish. Res. Board Can.* **23**(1):157-159. doi:10.1139/f66-014.
- Elliott, J. M. 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford.
- Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.*, **81**:117–142.
doi:10.1017/S1464793105006949
- Foldvik, A., Einum, S., and Finstad, A. G. 2017. Spatial diffusion modelling of juvenile Atlantic salmon (*Salmo salar*) shows ontogenetic increase in movement rates. *Can. J. Fish. Aquat. Sci.* **74**(2):202-207. doi:10.1139/cjfas-2015-0315.
- Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N. and Skalski, G. T. 2001. Explaining leptokurtic movement distributions: Intra-population variation in boldness and exploration. *Am. Nat.* **158**(2):124–135. doi:10.1086/321307.
- George, D., and Mallery, P. 2010. SPSS for Windows Step by Step: A Simple Guide and Reference 18.0 Update.
- Gerking, S. D. 1959. The restricted movement of fish populations. *Biol. Rev.* **34**(2):221-242. doi:10.1111/j.1469-185X.1959.tb01289.x
- Gibert, J. P. 2016. The effect of phenotypic variation on metapopulation persistence. *Popul. Ecol.*

- 58**:345-355. doi:10.1007/s10144-016-0548-z.
- Girard, I. L., Grant, J. W. A., and Steingrímsson, S. O. 2004. Foraging, growth, and loss rate of young-of-the-year Atlantic salmon (*Salmo salar*) in relation to habitat use in Catamaran Brook, New Brunswick. *Can. J. Fish. Aquat. Sci.* **61**(12): 2339-2349.
- Gomez, J. M., and Zamora, R. 1999. Generalization vs. specialization in the pollination systems of *Hormathophylla spinosa* (*Cruciferae*). *Ecology*, **80**(3):796-805. doi:10.1890/0012-9658(1999)080[0796:GVSITP]2.0.CO;2.
- Gowan, C., Young, M. K., Fausch, K. D., and Riley, S. C. 1994. Restricted movement in resident stream salmonids: A paradigm lost. *Can. J. Fish. Aquat. Sci.*, **51**(11):2626-2637. doi:10.1139/f94-262.
- Grant, J. W. A., and Imre, I. 2005. Patterns of density-dependent growth in juvenile stream-dwelling salmonids. *J. Fish Biol.* **67**(SB):100-110. doi:10.1111/j.1095-8649.2005.00916.x.
- Grossman, G. D., Nuhfer, A., Zorn, T., Sundin, G., and Alexander, G. 2012. Population regulation of brook trout (*Salvelinus fontinalis*) in hunt creek, Michigan: A 50-year study. *Freshw. Biol.* **57**(7):1434-1448. Doi:10.1111/j.1365-2427.2012.02806.x.
- Gustafson-Greenwood, K.I., and Moring, J.R. 1990. Territory size and distribution of newly-emerged Atlantic salmon (*Salmo salar*). *Hydrobiologia*, **206**:125-131. doi:10.1007/BF00018638.
- Hedger, R. D., Diserud, O. H., Sandlund, O. T., Saksgård, L., Ugedal, O., and Bremset, G. 2018. Bias in estimates of electrofishing capture probability of juvenile Atlantic salmon. *Fish. Res.* **208**:286-295. doi:10.1016/j.fishres.2018.08.005.
- Heggenes, J. 1990. Habitat utilization and preferences in juvenile Atlantic salmon (*Salmo salar*)

- In streams. *Regul. Rivers Res. Manage.* **5**(4): 341-354. doi:10.1111/j.1365-2427.2012.02806.x.
- Heggenes, J. and 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 Res. Manage.* **17**(6):623-635. doi:10.1002/rrr.620.
- Hesthagen, T. 1988. Movements of brown trout (*Salmo trutta*) and juvenile Atlantic salmon (*Salmo salar*) in a coastal stream in northern Norway. *J. Fish. Biol.* **32**(5): 639-653. doi:10.1111/j.1095-8649.1988.tb05404.x
- Hudy, M., Coombs, J. A., Nislow, K. H., and Letcher, B. H. 2010. Dispersal and within-stream spatial population structure of brook trout revealed by pedigree reconstruction. *Trans. Am. Fish. Soc.* **139**(5):1276–1287. doi:10.1577/T10-027.1.
- Jelks, H. L., Walsh, S. J., Burkhead, N. M., Contreras-Balderas, S., Diaz-Pardo, E., Hendrickson, D. A., Lyons, J., Mandrak, N. E., McCormick, F., Nelson, J. S., Platania, S. P., Porter, B. A., Renaud, C. B., Schmitter-Soto, J. J., Taylor, E. B., and Warren, M. L. J. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, **33**(8):372-407. doi:10.1577/1548-8446-33.8.372.
- Jokikokko, E. 1999. Density of brown trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) parr after point and scatter stocking of fry. *Fish. Manag. Ecol.* **6**(6):475-486. doi:10.1046/j.1365-2400.1999.00163.x.
- Jonsson, B., Jonsson, N. and Hansen, L. P. 2003. Atlantic salmon straying from the River Imsa. *J. Fish Biol* **62**:641-657. doi:10.1046/j.1095-8649.2003.00053.x.

- Louhi, P., Mäki-Petäys, A., and Erkinaro, J. 2008. Spawning habitat of Atlantic salmon and brown trout: general criteria and intragravel factors. *River Res. Appl.* **24**(3):330–339. doi:10.1002/rra.1072.
- Maine Department of Marine Resources (MDMR). 2014. Kennebec River Atlantic Salmon Interim Management Plan 2015-2020. Augusta, ME: Maine Department of Marine Resources.
- Marty, C., and Beall, E. 1989. Modalites spatio-temporelles de la dispersion d’alevins de saumon Atlantique (*Salmo salar* L.) a l’emergence. *Revue des Sciences de l’eau*, **2**(4):831-846. doi:10.1002/iroh.19860710308.
- Matte, J-M, Fraser, D. J., and Grant, J. W. A. 2020. Population variation in density-dependent growth, mortality and their trade-off in a stream fish. *J. Anim. Ecol.* **89**(2):541-552. doi:10.1111/1365-2656.13124.
- Milot, E., Perrier, C., Papillon, L., Dodson, J. J., and Bernatchez, L. 2013. Reduced fitness of Atlantic salmon released in the wild after one generation of captive breeding. *Evol Appl.* **6**(3):472–485. doi:10.1111/eva.12028.
- Niemelä, E., Julkunen, M., and Erkinaro, J. 2000. Quantitative electrofishing for juvenile salmon densities: assessment of the catchability during a long-term monitoring programme. *Fish. Res.* **48**(1):15-22. doi:10.1016/S0165-7836(00)00113-2.
- Ottaway, E. M., and Clarke, A. 1981. A preliminary investigation into the vulnerability of young trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) to downstream displacement by high water velocities. *J. Fish Biol.* **19**(2):135-145. doi:10.1111/j.1095-8649.1981.tb05818.x.
- Paradis, E., Baillie, S. R., Sutherland, W. L., and Gregory, R. D. 1998. Patterns of natal and

- breeding dispersal in birds. *J. Anim. Ecol.* **67**(4):518–536. doi:10.1046/j.1365-2656.1998.00215.x.
- Porter, J. H., and Dooley, J. L. Jr. 1993. Animal dispersal patterns: a reassessment of simple mathematical models. *Ecology*, **74**(8):2436-2443. doi:10.2307/1939594.
- Radinger, J., and Wolter, C. 2014. Patterns and predictors of fish dispersal in rivers. *Fish. Fish.* **15**(3): 456–473. doi:10.1111/faf.12028.
- Rasmussen, J. E., and Belk, M. C. 2017. Individual movement of stream fishes: Linking ecological drivers with evolutionary processes. *Rev. Fish. Sci. and Aquac.* **25**(1):70–83. doi:10.1080/23308249.2016.1232697.
- Reid, J. E., and Chaput, G. 2012. Spawning history influence on fecundity, egg size, and egg survival of Atlantic salmon (*Salmo salar*) from the Miramichi River, New Brunswick, Canada. *ICES J. Mar. Sci.* **69**(9):1678-1685. doi:10.1093/icesjms/fss091.
- Ries, K. G., III, Newson J. K., Smith, M. J., Guthrie, J. D., Steeves, P. A., Haluska, T. L., Kolb, K. R., Thompson, R. F., Santoro, R. D., and Vraga, H. W., 2017, StreamStats, version 4: U.S. Geological Survey Fact 2017–3046, 4 p. doi:10.3133/fs20173046.
- Rodriguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. *Ecology*, **83**(1):1-13. doi:10.2307/2680115.
- Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Evol. Syst.* **38**(1):231–253. doi:10.1146/annurev.ecolsys.38.091206.095611.
- Roy, M. L., Roy, A. G., Grant, J. W. A, and Bergeron, N. E. 2013. Individual variability in the movement behaviour of juvenile Atlantic salmon. *Can. J. Fish. Aquat. Sci.* **70**(2):339-347. doi:10.1139/cjfas-2012-0234.

- Skalski, G. T. and Gilliam, J. F. 2000. Modelling diffusive spread in a heterogeneous population: a movement study with stream fish. *Ecology*, **81**(6):1685–1700. doi:10.1890/0012-9658(2000)081[1685:MDSIAH]2.0.CO;2.
- Šlapanský, L., Janáč, M., Roche, K., and Jurajda, P. 2020. Round goby movement patterns in a non-navigable river. *Can. J. Fish. Aquat. Sci.* **77**(3):475-483. doi:10.1139/cjfas-2018-0488.
- Teichert, M. A. K., Foldvik, A., Forseth, T., Ugedal, O., Einum, S., Finstad, A. G., Hedger, R. D., and Bellier, E. 2011. Effects of spawning distribution on juvenile Atlantic salmon (*Salmo salar*) density and growth. *Can. J. Fish. Aquat. Sci.* **68**(1):43-50. doi: 10.1139/F10-141.
- Turchin, P. 1998. *Quantitative Analysis of Movement: Measuring and Modelling Population Redistribution of Plants and Animals*. Sinauer Associates, Sunderland, MA.
- Queller, D. C., and Goodnight, K. F. 1989. Estimating relatedness using genetic markers. *Evolution*, **43**(2):258–275. doi:10.2307/2409206.
- Vøllestad, L. A., Serbezov, D., Bass, A., Bernatchez, L., Olsen, E. M., and Taugbøl, A. 2012. Small-scale dispersal and population structure in stream-living brown trout (*Salmo trutta*) inferred by mark–recapture, pedigree reconstruction, and population genetics. *Can. J. Fish. Aquat. Sci.* **69**(9):1513-1524. doi:10.1139/f2012-073.
- Webb, J. H., Fryer, R. J., Taggart, J. B., Thompson, C. E., and Youngson, A. F. 2001. Dispersion of Atlantic salmon (*Salmo salar*) fry from competing families as revealed by DNA profiling. *Can. J. Fish. Aquat. Sci.* **58**(12):2386-2395. doi:10.1139/cjfas-58-12-2386.
- Yeakel, J. D., Gibert, J. P., Gross, T., Westley, P. A. H., and Moore, J. W. 2018. Eco-

evolutionary dynamics, density-dependent dispersal and collective behaviour:
implications for salmon metapopulation robustness. *Phil. Trans. R. Soc. B.* **373**(1746).
doi:10.1098/rstb.2017.0018.

Zuur, A. F., Leno, E. N., and Elphick, C. S. 2010. A protocol for data exploration to avoid
common statistical problems. *Methods Ecol. Evol.* **1**(1):3–14. doi: 10.1111/j.2041-
210X.2009.00001.x.