**Historical abundance and spatial distributions of spawners determine juvenile habitat accessibility in salmon: implications for population dynamics and management targets**

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**Abstract:** Spatial distribution of spawning may have important ramifications for population dynamics in species where early life stages suffer from low mobility and high density-dependent mortality. Here, we use time series of spatial spawning distribution in Atlantic salmon (*Salmo salar* L.) to test for density-dependent behavioural effects on the spatial utilisation of spawning sites and resulting juvenile habitat availability. The probability of utilizing spawning sites in a given year increased both with increasing spawner abundance and proximity to sites used the previous year. The accessible area for juveniles increased asymptotically with both current and time-lagged spawner abundance. Several non-exclusive mechanisms may be responsible for the observed direct and lagged density dependence of spawner distributions, including social aggregation, asymmetric competition for space, local homing and habitat modification by the previous year’s spawners. Time-lagged density-dependent spawner distributions can be predicted to reduce the realized population growth rate. If such effects are not accounted for, this may lead to a downward bias in estimates of spawning targets or other associated conservation or management measures derived from population abundance time series.

**Introduction**

Although individual variation in behaviour may be a key factor when assessing and predicting population dynamics (DeAngelis and Gross 1992; Sutherland 1996; Sutherland and Norris 2002), it is rarely included explicitly in studies of population regulation. In particular, individual behavioural decisions that influence within-population spatial heterogeneity in density likely affect competition intensity, and may have a fundamental role in shaping population dynamics and carrying capacity (Flather and Bevers 2002). Such behavioural decisions may be particularly relevant for stage-structured organisms where habitat and food utilisation change throughout ontogeny. When mobility is restricted, the spatial distribution at one stage will be shaped by preferences or events at previous stages (Einum et al. 2008). Mobility usually varies considerably among ontogenetic stages. Mobile larval stages and sessile adults are commonly found in animals such as barnacles and mussels, where dispersal of larvae is important for the resulting adult distribution (Connolly et al. 2001; Underwood and Keough 2000). Conversely, many fishes with highly mobile adult stages spawn in specific habitats and have less mobile juvenile stages. Here, the maternal choice of spawning site becomes important in shaping both the spatial distribution and population structure of juveniles ([Einum et al. 2008](#_ENREF_1), [Foldvik et al. 2010](#_ENREF_2)).

A number of mechanisms may shape spatial spawning distributions. Physical requirements for spawning habitat accompanied by a non-random distribution of suitable habitat types represent an obvious mechanism (e.g. Isaak and Thurow 2006). However, it is usually less clear to what extent such distributions are shaped by social intra- and inter-specific interactions. For certain fishes, sexually selected reproductive behaviour such as social aggregation (Bietz 1981, Warner 1988, Windle and Rose 2007) and anti-predator related behaviour such as schooling during reproduction (Axelsenet al*.* 2000) may produce distinct spatial patterns in the distribution of spawning. If such interactions among individuals are influenced by population density, density-dependent behavioural decisions may also influence the spatial distribution of spawners (Warner 1988). An even more intriguing situation may arise if there also is a temporal dependency in the spatial distribution, such that suitable spawning sites used in one year tends to be closely located to those used in the previous year. Local homing (Warner, 1988, 1990, Fleming 1998, Nevilleet al. 2006) or the increase in the suitability of spawning habitats by previous use (Essington et al. 1998, Montgomeryet al. 1996; Macdonald et al. 2010, Youngson et al. 2011) may represent two potential mechanisms for why such temporal dependencies in spawner distributions may exist. For example, stream spawning salmonids commonly deposit their eggs in nests in the gravel substrate. The digging of nests imposes modification of the riverbed substrate that overrides year to year variation in bed load movement caused by hydrological impact (MacDonald et al. 2010), and likely increases offspring survival due to removal of fine sediments (Louhi et al. 2011). Such temporal dependencies can cause a “system memory” where spawner density at time *t* influences their spatial distribution, which in turn influences the distribution of spawners at time *t*+1. Given limited juvenile movement abilities, this also means that the area accessible for the offspring of spawners at time *t*+1 will depend on the spawner density at time *t*. If juvenile habitat is a limiting resource, this mechanism may have interesting consequences for population dynamics.

Despite of the potential consequences a combined density-dependent and temporally-dependent spatial distribution of spawning may have on population dynamics, we are not aware of any explicit studies of such effects in natural systems. In the present study, we use time series of spatial spawner distributions in four populations of Atlantic salmon (*Salmo salar* L.) to estimate the effect of density on the spatial utilisation of spawning sites, and to model the resulting dynamics in offspring habitat accessibility. Atlantic salmon spawn in rivers, where juveniles spend one to eight years before migrating to the sea. When returning from sea, adult salmon females build discrete nests in which they deposit anywhere from hundreds to thousands of eggs. Usually, between 4 and 9 nests are constructed sequentially at the same location to form what is called a redd (Fleming 1996; de Gaudemar et al. 2000). One female can construct two or more redds that are commonly clumped in a particular area of the river (Heggberget et al. 1988). Females have specific spawning habitat preferences, and the number of available spawning sites is therefore usually restricted (Armstronget al. 2003). Due to restricted mobility of juveniles (Einum and Nislow 2005), heterogeneity in the egg distribution influences the subsequent spatial distribution of juveniles during their first summer. Aggregation of spawning will result in pronounced spatial heterogeneity in the distribution of eggs within a population. This transfers into effects on juvenile growth and survival over relatively small spatial scales both in natural and experimental settings (Einum and Nislow 2005; Einumet al. 2008; Foldvik et al. 2010; Teichertet al. 2011). In a previous paper (Finstadet al. 2010), we analysed time series of spawning distributions from Norwegian rivers in order to describe within- and among-river variation in spawning distributions. The study demonstrated extensive variation in spawning distributions both among rivers and temporal variation within rivers. However, it remains unknown to what extent this variation is driven by density-dependent processes and temporally-dependent spatial distribution of spawning. In the present study we address these issues using a subset of the data utilized in Finstad et al. (2010) that fulfil the requirements for such analyses (i.e. sampled with a consistent spatial resolution). We here first test if the probability of utilizing a given spawning location in a given year depends on the spawner density and/or the proximity to locations used in the previous year. Thereafter, we model the proportion of the total habitat within the river accessible to juveniles as a function of the spawner density to evaluate the potential effects on carrying capacity. We show that spawner distributions can be both density-dependent and dependent on historical distributions. Further, we examined how this may reduce the realized population growth rate and lead to a downward bias in estimates of spawning targets or other associated conservation or management measures derived from population abundance time series.

**Material and methods**

**Breeding distribution time series**

The four rivers included in the study are gravel-bed rivers with substrate consisting mainly of gravel and cobble, and hydrologic habitat shifting between adjacent riffles and pools. The gradients are relatively steep (Table 1), but without any migration barriers within the anadromous stretch. For river Aurland, the upper-most part of the anadromous stretch above the lake Vassbygdvatn was excluded, as spawning areas upstream from there are only found within a small stream supporting a minor part of the population. The spawner distribution data (Table 1) were collected by direct observations from the river bank (Sættem 1995; Finstadet al. 2010). All observations were done at the time close to or at the start of the spawning period. After the initial up stream migration, Atlantic salmon display a “holding phase” prior to spawning, during which there is little in-stream movement (Økland et al. 2004). Radio-tagging studies following Atlantic salmon throughout the last part of the spawning migration and the spawning period confirms that most females spawn in close proximity to their holding position (Webb and Hawkins 1989, Økland et al. 2004, Finstad et al. 2005). Although the spawning period of Atlantic salmon may last for several weeks, the observed distribution of spawners immediately prior to or at the start of the spawning period is therefore likely to closely coincide with the distribution of actual spawning. Some individuals do however migrate significant distances also during the spawning period. Although this will add noise to the data it is not expected that this minority of the population will introduce a significant bias with respect to the conclusions of this study.

The rivers were divided into equally sized sections (50 m long) and the number of observed spawners in each section was recorded. This method provides a minimum estimate on the number of breeders, but due to the high visibility in these rivers (drainage is mainly from sparsely vegetated high alpine areas, causing low input of DOC to the watershed; Larsen et al. 2011) observations are likely to be independent of local habitat conditions, and the spatial patterns accordingly unbiased.

**Statistical modeling**

We first tested for effects of density and the previous year’s distribution of spawners on the probability of utilizing individual spawning sites. The probability of observing a spawning Atlantic salmon in a section of the river was modelled as a function of distance to spawning sites utilised the previous year and spawner abundance. The latter was estimated as the average number of fish observed per section (N section-1) in each river in each year as a density index. Due to differences in age and size maturation among male and female Atlantic salmon, sex ratios are usually uneven and may vary among rivers depending on regional location and size and age at maturation. All the study rivers are closely spatially located (Table 1) and share spawning stock characteristics in terms of adult size. We therefore assumed sex-ratio to be similar among the rivers included in the present study, and added no correction for unequal sex ratios. The models where fitted using the lmer-procedure in the nlm4 library (Bates and Maechler 2010) in R 2.11.1. Here, year was entered as a random factor nested within river and the response variable was presence or absence of spawners in a given section, modelled using the logit link function. The full model consisted of river as a fixed factor, and abundance of spawners and distance to spawning sites utilised the previous year as covariates, as well as all two- and three-way interactions among these. The inclusion of the random year effect was supported by a comparison with a model without it (comparison of log-likelihoods, P < 0.001, calculated using REML). Comparisons of different fixed effects structures were done using a backwards selection procedure where different fixed effects were removed sequentially until no further model improvement in terms of AIC (based on ML) could be attained (Zuuret al. 2009).

We then modelled the area accessible to juveniles as a function of standardized spawner abundance (N section-1). Under a random distribution of spawners among available suitable locations (see below) and limited mobility among the resulting offspring, the proportion of the total area accessible for offspring (A) can be expected to increase with increasing spawner abundance as more sites are taken into use. Since there is an upper limit to the number of available spawning locations, this relationship can be expressed by an asymptotic function of abundance (N section-1) in a given year t (Nt) as:

 $A∝ α(1-e^{-βN\_{t}})$ (1)

where the parameter *α* is the maximum area accessible to offspring and *β* is the rate at which the asymptote is reached. However, distribution of spawning individuals may, for behavioural reasons outlined in the introduction, not be random, but rather density-dependent. In the present study we use this theoretical framework to assess how the abundance of spawners influences the area accessible for the resulting offspring. This was done in two steps.

First we calculated for each river-year the proportion (*A*) of the total habitat within the river accessible to juveniles during the first few weeks after swim-up, when competition is expected to be severe and survival highly density-dependent (Einum and Nislow 2005). The starting point for this was presence or absence of spawners within each 50 m section in a given river for a given year. We then assumed that if spawners were present within a 50 m section, these included at least one female, and that spawning occurred at the center of the section. Since juvenile movement constraints are unknown and likely to vary between rivers, we calculated accessible habitat under different maximum downstream movement distance scenarios. Although some upstream movement from nests may occur, this is expected to be limited both with respect to frequency and distance during this initial stage. Downstream movement has been observed to occur up to 1km downstream of nests throughout the first summer (Crisp 1995; Webbet al. 2001), but movement over such long distances appears to be rare, and utilization can therefore be expected to be low for the majority of habitat within such a long distance. Furthermore, long-distance movement is likely even less common during the first few weeks after emergence from nests, and Einum and Nislow (2005) reported a median absolute movement distance of 41m (range 0 – 884 m) one month after emergence. We therefore chose three maximum downstream movement distance scenarios: 150, 250 and 500m. Variation in movement distance among rivers is unknown, but these limits should at least be applicable to a range of Atlantic salmon populations. Because we implicitly assume in our model that all habitat within a given maximum movement distance is equally accessible, our predictions in terms of the proportion of the total river habitat that cannot be used are likely conservative.

In the second step we used these calculated values for *A* and modeled the effect of observed adult Atlantic salmon abundance using eq. 1. The model was fitted using the nls function in R. To test for non-randomness in spawner distributions, we additionally also compared how observed relations between adult population abundance and *A* differed from those observed when simulating a random allocation of spawners to the 50-m sections assumed suitable for breeding. In this latter analysis we defined sections that had adult observations at least once during the time period as being suitable.

**Results**

The probability of using a specific spawning site was best described by a model including river, abundance of spawners, distance to spawning sites used the previous year, the river by abundance and river by distance interactions, and year nested within river as a random factor (Table 2; Δ AIC between selected model and models without the three-way interaction and interaction between abundance and distance to spawner site used the previous year > 29.9; Δ AIC to further simplified models > 37.7). As evident from the main effects, the probability of utilizing individual spawning areas increased with increasing abundance and decreased with increasing distance to spawning areas used the previous year (Table 2, Fig. 1). Also, the effect of distance and abundance differed among rivers. Specifically, compared to the other three rivers, River Lærdal had a considerable steeper increase in probability of spawning area use with decreasing distance to spawning the previous year, and a less pronounced increase with increasing abundance (Fig. 1).

The proportion of the river habitat accessible to juveniles increased asymptotically with abundance in all rivers (Fig. 2, Table 3). The spawning abundance required for approaching the asymptotic proportion of habitat accessible decreased with increasing modeled maximum movement distance of juveniles. This occurs because of an increasing degree of spatial overlap in accessible habitat for juveniles from more than one spawning location as the number of spawners increase. There was also among-river differences in the asymptotic proportion of the river accessible to juveniles for a given modeled movement distance. This likely reflects variation in distribution of suitable spawning areas. It is also notable that even for the largest maximum dispersal distance modeled (500 m), significant proportions of rivers were always inaccessible for juveniles.

The accessible area for juveniles was also generally less than expected from a random distribution of spawners, even at high spawner abundances (Fig. 2). Maximum accessible area was significantly lower than predicted from a random distribution, except for the river Flåm, where the difference approached significance. However, this is also the shortest time-series in the analyses and low test power was to be expected.

**Discussion**

In the present study we show that the probability of utilizing individual sections of rivers for spawning by Atlantic salmon decreases with increasing distance to spawning sites used the previous year, and increases with density in the current year. In species with offspring of low mobility and which experience local density-dependent mortality in early life stages, the carrying capacity will be a function of the area accessible to the offspring. This area depends both on the number of spawning locations and their distribution, as well as the offspring’s scope for movement. As we show here for Atlantic salmon, a species with low juvenile mobility and local density-dependent mortality (Einum and Nislow 2005; Einumet al. 2008; Foldvik et al. 2010; Teichert et al. 2011), the number and quality of spawning locations used increases with increasing number of spawners and also depends on the spawning distribution the previous year. Spawning distributions in a given year will then be affected by density in preceding years through the effects this has on historical spatial distributions. Accordingly, the increase in area accessible to juveniles with increasing spawner abundance should not only depend on density the current year, but also historical densities. Assuming again that there is an upper limit to the number of spawning sites, and accordingly that the relationship between spawner abundance and area accessible to juveniles (*A*) can be described by an asymptotic function, the rate at which the population reaches the asymptotic value should depend upon time-lagged population abundance. This can be expressed as an additive effect of previous years` spawner abundances on the *β* parameter in eq. 1, which describes the increase in accessible juvenile habitat (*A*) with increasing density:

 $A∝ α(1-e^{(-β+β\_{1}N\_{t-1}+β\_{2}N\_{t-2}…. +β\_{n}N\_{t-n})N\_{t}})$ (2)

where *Nt-n*is population size at time *t-n*. An obvious question arising from this observation is then how to best model the effect of this on the population dynamics. Such a model should reflect the fact that the density in previous years can be thought of as positively influencing the carrying capacity through effects on availability of juvenile habitat.

Related models have previously been developed for describing the irruptive behaviour of introduced large herbivore populations, which typically reaches a peak before crashing and finally stabilizing at a level lower than the initial peak (e.g. Caughley 1970). For that situation, there is a negative lagged effect of population size due to a gradual depletion of resources (food), and the resulting population dynamics can be modelled (at least for some populations) as a logistic growth function where the carrying capacity is a function of time after introduction (Forsyth and Caley 2006). In our case, the carrying capacity (*K*) is likely determined by the area accessible to juveniles and should be modelled as a function of population size the previous year, yielding the following model for the realized per capita growth rate *r*:

  (3)

, where *rm* is the maximum per capita growth rate and *K(Nt-1)* is an asymptotically increasing function. For a given value of *rm*, such a model will show a reduced realized growth rate compared to the standard logistic growth model. This may be particularly important for harvested populations, which may then more easily be kept at low population sizes. Furthermore, for heavily harvested populations (i.e. populations being kept substantially below the maximum attainable *K*), a single year of low harvest levels yielding spawner abundances that would cause recruitment to reach its maximum value under a standard logistic growth model or within a stock-recruitment modeling framework, would not do so for the current model. Rather, multiple years of low harvest would be required, allowing the population to gradually rebuild and use all available areas. This also points towards the risk of using stock-recruitment models based on data from heavily harvested populations to establish spawning targets (as done for a wide range of fish species, including Atlantic salmon, Hindaret al. 2011), because greater recruitment could be attained for a larger spawner abundance if the population was left unharvested over longer time periods.

The observed increased probability for utilization of spawning locations with increasing abundance and proximity to locations used the previous year may be caused by several non-exclusive mechanisms. Breeding habitats may be made increasingly beneficial by being used by previous cohorts. In stream living salmonids, females modify the substrate when digging nests. This disturbance of the substrate causes decreased fine sediment load and increased water flow through the substrate which is vital for egg respiration and survival (Montgomeryet al*.* 1996; Macdonald et al. 2010). It is therefore likely that spawning grounds recently used may be preferred by females (Essington et al. 1998; Youngsonet al*.* 2011). Previous studies have also suggested that distribution of spawning salmonids should follow an ideal despotic distribution type of pattern (Purchase and Hutchings 2008). Competition for spawning space among individuals (Fleming and Gross 1989; Purchase and Hutchings 2008) may then cause movement away from the initially selected location. Nearby suitable spawning habitats are then likely to be used first. Furthermore, aggregations caused by local homing of spawners (Wagner 1969; Stewart et al. 2004) can contribute to such a temporal dependency in spawning distributions. However, for species like Atlantic salmon, with considerable time-lag induced by long generation time (in the present populations usually from 5 to 8 years), considerably longer time-series would be needed to test for effects of local homing. Nor do we have data to infer temporal variation in spawning habitat. Thus, the present data do not allow us to conclude about the underlying mechanisms causing this pattern.

In our approach we treat spawning habitat quality as a dichotomous variable (suitable vs. not suitable) based on direct observations of the spatial distribution of spawners throughout the study period (used at least once vs. never used). It can be expected that spawning areas of particular high quality or larger spawning areas attract more fish. However, obtaining such detailed habitat quality data on a sufficiently large spatial scale to allow for studies of whole populations in the way that we do here seems at best to be difficult. In particular, obtaining objective, quantitative measures of spawning habitat quality would appear to be challenging for most organisms. Our simplified habitat classification could potentially affect the parameter estimates related to the effect of density or distance to previously used spawning sites. However, it allowed us to develop a powerful approach to obtain a qualitative assessment of the effects of population abundance and historical spawning distributions on juvenile habitat availability, and this approach may relatively easily be applied to other organisms for which time-series of spatial spawner distributions exist. Another simplifying component to our approach relates to the predicted effect of spawner distributions on population carrying capacities. The prediction that the carrying capacity increases with increasing number of used spawning sites assumes that habitats in the vicinity of spawning sites that are used only at high abundance are suitable for juvenile rearing. Although this seems like a reasonable assumption, we lack the necessary data to quantify such spatial configurations.

Spawning site distributions may potentially have large impacts on population dynamics and inference of such. Many marine species with large commercial and conservation focus show the same general patterns as stream spawning salmonids when it comes to spawning site aggregations. For example, cod (*Gadus morhua* L.) show homing to local breeding locations (Bradburyet al*.* 2008; Skjaeraasenet al. 2011), lekking behaviour (Windle and Rose 2007), limited dispersal as juveniles, and density-dependent survival and growth in early life history (Juanes 2007). Aggregation behavior such as observed in the present study may result in the loss of sites during periods with low population abundance. As discussed above, estimated sustainable yield, spawning targets or other associated conservation limits may be biased downwards when based on data from harvested populations. Behavioral mechanisms in spawning site choice may therefore have large applied consequences in species with limited juvenile dispersal and density-dependent regulation during early life history.

**Acknowledgements**

We thank two anonymous referees for comments improving the manuscript. Financial support was provided by the Norwegian Research Council through the Wild Salmon Program and the Norwegian Institute for Nature Research. We thank Torkjeld Grimelid and Olav Tokvam for assistance with registration in the Rivers Lærdal and Aurland, respectively.

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**Table 1** Study rivers, position of river outlet, length of river accessible to anadromous fish (km), annual mean discharge (m3/s), altitude of migration barrier for anadromous salmon, and years with observations of breeder distribution and mean number of spawners counted each year (± S.D.). Length and altitude for river Aurland refers to the studied part of the river.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| River | River outlet | Length  | Discharge | Altitude | Years  | Mean counts |
| Aurland |

|  |
| --- |
| 60º54’N 7º11’E |

 | 9.8 | 37.56 | 50 | 1966-1993 | 65 (±43) |
| Flåm | 60º52’N 7º08’E | 4.7 | 15.93 | 188 | 1988-1994,1998 | 54 (±40) |
| Lærdal | 61º06’N 7º28’E | 24.8 | 36.34 | 174 | 1979-1982,1984-1994 | 603 (±281) |
| Nærøydal | 60º53’N 6º51’E | 11.1 | 15.56 | 180 | 1989, 91, 92, 94,1998-2005 | 70 (±43) |

**Table 2** Summary of best mixed effect model explaining the probability of using an individual spawning area as a function of distance to nearest spawning location used the previous year (Distance, m) and density of spawners in the current year (N section-1). Year (Yr) nested within river was included as a random factor. Estimated parameters for random effects are the SD of random intercepts in the models, with SD of residual variation given in brackets

|  |  |  |  |
| --- | --- | --- | --- |
|  | Parameter ± SE | z-value | P-value |
| Random effects |  |  |  |  |
| Yr (intercept) (Nærøydal) | 0.129 | (0.359) |  |  |
| Yr within Flåm | 0.117 | (0.343) |  |  |
| Yr within Aurland | 0.115 | (0.340) |  |  |
| Yr within Lærdal | 0.173 | (0.414) |  |  |
| Fixed effects |  |  |  |  |
| Intercept (Nærøydal) | -1.300 | ± 0.271 | -4.80 | <0.000 |
| Flåm | -0.030 | ± 0.579 | -0.05 | 0.958 |
| Aurland | -1.047 | ± 0.295 | -3.54 | <0.001 |
| Lærdal | 1.657 | ± 0.325 | 5.09 | <0.001 |
| Distance (Nærøydal) | -0.001 | ± 0.001 | -3.23 | 0.001 |
| Density (Nærøydal) | 1.045 | ± 0.682 | 2.13 | 0.033 |
| Flåm x Density | 1.039 | ± 1.277 | 0.814 | 0.415 |
| Aurland x Density | 1.500 | ± 0.725 | 2.07 | 0.038 |
| Lærdal x Density | -1.019 | ± 0.697 | -1.46 | 0.014 |
| Flåm x Distance | -0.001 | ± 0.001 | -1.26 | 0.208 |
| Aurland x Distance | -0.001 | ± 0.001 | -0.647 | 0.500 |
| Lærdal x Density | -0.008 | ± 0.001 | -11.19 | <0.001 |

**Table 3** Summary of least square non-linear regressions for proportion of river habitat accessible to juvenile Atlantic salmon (*A*) against abundance (spawners section-1) at each year (*Nt*) ($A=α\left(1-e^{-β\_{1}N\_{t}}\right)$. Parameter estimates ± SE, *t*-values and *p*-values (10, 6, 16 and 13 d.f. for Nærøydal, Flåm, Aurland and Lærdal, respectively) are given for each river and for assumed 150, 250, and 500 m dispersal distance.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | **α** |  |  |  | **β** |  |
|  | **Parameter** | ***t*** | ***p*** |  | **Parameter** | ***t*** | ***p*** |
|  **150 m** |  |  |  |  |  |  |  |
| Nærøydal | 0.29 (±0.04) | 6.93 | <0.001 |  | 6.71 (±0.04) | 2.27 | 0.046 |
| Flåm | 0.40 (±0.10) | 4.06 |  0.006 |  | 3.16 (±1.17) | 1.85 | 0.113 |
| Aurland | 0.56 (±0.02) | 20.20 | <0.001 |  | 3.06 (±0.31) | 9.86 | <0.001 |
| Lærdal | 0.50 (±0.01) | 36.70 | <0.001 |  | 3.57 (±0.62) | 5.74 | <0.001 |
|  |  |  |  |  |  |  |  |
| **250 m**  |  |  |  |  |  |  |  |
| Nærøydal | 0.43 (±0.05) | 8.36 | <0.001 |  | 7.60 (±3.03) | 2.51 | 0.031 |
| Flåm | 0.47 (±0.08) | 5.99 | <0.001 |  | 5.06 (±2.73) | 1.85 | 0.113 |
| Aurland | 0.66 (±0.03) | 26.06 | <0.001 |  | 4.35 (±0.41) | 10.53 | <0.001 |
| Lærdal | 0.69 (±0.01) | 52.02 | <0.001 |  | 4.28 (±0.71) | 6.05 | <0.001 |
|  |  |  |  |  |  |  |  |
| **500 m** |  |  |  |  |  |  |  |
| Nærøydal | 0.65 (±0.05) | 12.09 | <0.001 |  | 10.14 (±3.47) | 2.91 | 0.015 |
| Flåm | 0.59 (±0.05) | 13.17 | <0.001 |  | 10.71 (±5.83) | 1.83 | 0.116 |
| Aurland | 0.80 (±0.02) | 36.82 | <0.001 |  | 7.21 (±0.63) | 11.33 | <0.001 |
| Lærdal | 0.89 (±0.01) | 117.20 | <0.001 |  | 5.83 (±0.76) | 7.71 | <0.001 |

**Figure legends**

**Fig. 1** Relationship between the probability of Atlantic salmon utilizing a section defined as suitable for spawners (Probability of utilization) as a function of density (N section-1) and distance to sections used the previous year (m) for rivers a) Nærøydal, b) Flåm, c) Auland and d) Lærdal. Sections were defined as suitable if spawners were observed there once or more during the study period.

**Fig. 2** Proportion of the river habitat accessible to juvenile Atlantic salmon plotted against density (N section-1), given a 150 m (a-d), 250 m (f-i) and 500 m (j-k) downstream dispersal distance for the observed spawning distributions from the rivers Nærøydal (a, f, j), Flåm (b, g, k), Aurland (c, h, l) and Lærdal (d, j, m). Parameter estimates are given in Table 3. Solid lines illustrate proportions of rivers accessible (*A*) modeled as an exponential function of abundance (*Nt*); $A=α(1-e^{-βN\_{t}}) $. Stippled lines give 95% confidence intervals from 1000 simulations where the probability of using each suitable spawning area was equal (random distribution).



