Interactions between local population density and limited habitat resources determine movements of juvenile Atlantic salmon

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Abstract

Competition for limited resources and the resulting density-dependent processes are key factors in driving stream salmonid population dynamics. Here we test for the combined effects of density and shelter availability on the movement of juvenile Atlantic salmon in a Norwegian river. Individually marked, hatchery reared salmon juveniles were released at 26 sites along a 2.5 km long stretch and recaptured after 12 months. The spatial variation in shelter availability and density of salmonids was quantified prior to the release. We found no effect of released fish number on the number of marked salmon moving more than 12.5 – 112.5 m away from their release site. However, the ratio of pre-experiment fish density per shelter was positively related to the number of movers. Thus, fish that were released at sites where the amount of shelter was low relative to the density of the pre-experiment population were more likely to move. These results support the prediction from smaller scale experimental studies that shelter availability may act to determine local carrying capacity in stream living salmonid populations.
Introduction

Usually, research on density-dependent processes has focused on effects on growth, survivorship and fecundity. However, parallel with an increasingly recognized role for spatial scale amongst ecologists, there has been a growing interest in density-dependent movement rates (Matthysen 2005 and references therein). Density-dependent movement, i.e. net movement out of high density areas, will in general reduce spatial variation in competitive intensities (Enfjäll and Leimar 2009), thereby stabilizing population fluctuations in heterogenous environments (Matthysen 2005). Particularly for vertebrates, however, both positive and negative density-dependent movement relationships have been reported (Travis et al. 1999; Matthysen 2005; Kim et al. 2009) and empirical evidence is largely inconsistent (see reviews in Matthysen 2005; Bowler and Benton 2005).

Of the few available empirical studies, Finstad et al. (2009) also highlight the heterogeneous spatial distribution of habitat quality, which in turn is strongly affected by the availability of limiting resources. In such cases, spatial variation in performance caused by competition for limited resources, and hence corresponding competition-driven movements, is predicted to depend not on local population density *per se*, but rather on density relative to the local abundance of limiting resources (Berryman 2004). Recent attempts at elucidating the mechanisms behind density dependence have successfully incorporated such information (Shima and Osenberg 2003; Forrester and Steele 2004; Einum 2005; Einum and Nislow 2005; Finstad et al. 2009). However, because of the lack of individual level data, previous field studies have been unable to distinguish between mortality and movement responses to varying amounts of limiting resources.
One habitat characteristic which has been widely identified as a limiting resource is the availability of structural refuge (e.g. Harwood et al. 2002; Griffiths et al. 2004; Davey et al. 2009). Such shelters provide protection from predators until the available shelter space is saturated (Begon et al. 1996; Hossie and Murray 2010). Limited shelter opportunities may therefore result in intense intra- (Beck 1997; Shima and Osenberg 2003; Moksnes 2004; Davey et al. 2009) and interspecific competition (Söderbäck 1994; McDonald et al. 2001; Harwood et al. 2002; Griffiths et al. 2004; Wieters et al. 2009). For example, juvenile Dungeness crabs (*Cancer magister*) compete with juvenile shore crabs (*Carcinus maenas* L.) for shelter in mollusk shells. The dominant shore crab often physically evicts the less aggressive Dungeness crab from shelter, thus exposing it to an increased risk of predation (McDonald et al. 2001). Therefore, competition for shelters may influence population carrying capacity (Harwood et al. 2002).

Shelter use in stream dwelling salmonids has been the focus of numerous studies (e.g. Valdimarsson and Metcalfe 1998; Orpwood et al. 2003; Millidine et al. 2006; Finstad et al. 2007; Teichert et al. 2010). Salmonids may seek shelter in interstitial spaces in the stream substrate both to avoid predators and to protect themselves against harsh physical conditions (Valdimarsson and Metcalfe 1998; Millidine et al. 2006). Apart from the obvious benefits of reduced mortality and energy expenditure, the presence of shelter also reduces standard metabolic costs (Millidine et al. 2006). Density-dependent regulation at the population level is well understood in salmonids (reviewed in Elliott 1994; Einum and Nislow 2011). Recent studies have highlighted the importance of spatial structure of population density during breeding and early juvenile stages in shaping levels of density-dependence and the subsequent influence on population dynamics (Einum et al. 2006; Einum et al. 2008b; Finstad et al. 2010; Teichert et al. 2011). With respect to spatial distribution of shelters, Finstad et al. (2009)
showed that the variation in the change in Atlantic salmon cohort abundance from age-0 to age-1 among locations in a natural population was best explained by modeling the local carrying capacity as a function of shelter availability. On a smaller spatial scale they experimentally demonstrated that the number of individuals moving out of artificial streams was negatively correlated to the amount of unoccupied shelter. Further, the spatial distribution of shelters was found to vary substantially across rivers, and increased heterogeneity in shelter abundance was linked to reduced salmon production on the population scale (Finstad et al. 2009; Teichert et al. 2013). This latter finding suggests a limitation in the ability of fish to distribute according to, and hence efficiently utilize heterogeneously distributed resources. Nevertheless, the ability of individuals to make movement decisions based on the availability of limiting resources has not been sufficiently assessed.

Here we study movement decisions in relation to local population density and the availability of shelter, using Atlantic salmon juveniles. In a field experiment, batch and individually tagged fish were released into a small Norwegian river in two different density treatments. We expected movement from areas where the available shelter was low in relation to fish density. Further, growth differences were predicted between dominant individuals able to establish territory at their respective release sites and less competitive fish having to move in search of suitable habitat.

Methods

Study area

The study was conducted in the River Dalåa, central Norway (63°25’N, 11°74’E). The river is regulated with mean discharge of ~2 m³ s⁻¹ and has an average wetted width of 16.9 m within the study section. Anadromous salmonids do not naturally occur in this river, due to a barrier...
preventing upwards migration from the River Stjørdalselva (63°27’N, 10°54’E). However, mitigation agreements with the local waterpower operator include releasing hatchery reared Atlantic salmon juveniles and eggs into the river which migrate to sea via the River Stjørdalselva. Salmon juveniles are released as 0+ during October each year and the majority of these introduced fish smoltify at the age of 2+ - 3+ (Arnekleiv et al. 2001, in Norwegian). Brown trout *Salmo trutta* are also present, but their abundance has declined since the introduction of Atlantic salmon, which now is the dominant species in the river (Arnekleiv et al. 2001, in Norwegian). The study stretch was about 2500 m long and contained by a migration barrier at the upstream end. Migration barriers were present at approximately 1600 m, 1700 m and 2000 m, measured from the downstream end of the study stretch. All migration barriers could be passed by the fish in a downstream direction. The morphology of the river in the study stretch changes after the first ~1.2 km from a fairly narrow and steep valley, where the river is dominated by large rocks and boulders to a more open landscape, where the river substrate consists mainly of gravel and sand. Subsequently, habitat type also changes from riffle dominated to glide dominated, respectively.

**Electrofishing and habitat survey**

Fish present in the river prior to the experiment are termed “resident”. To establish how their density varied spatially, densities of resident juvenile salmon and trout were surveyed during 20. - 22. August 2008 by single-pass electrofishing. Approximately 1.5 m wide transects were fished across the width of the river at regular 25 m longitudinal intervals throughout the study area, resulting in a total number of 109 transects. The 25 m intervals were measured with a tape measure and the position of each transect spatially referenced by GPS. Each 25 m interval is termed section and used as the main unit to describe movement within the study stretch (Fig. 1). Within-stream spatial variation in abundance is generally much larger than
variation due to habitat-specific catch efficiency in electrofishing surveys (Hankin, 1984; Bohlin et al., 1989). Single pass approaches therefore provide cost effective estimates of spatial variation in abundance which highly correlate with those obtained from traditional, more accurate but also more time-consuming multi-pass censuses (Prevost and Nihouarn 1999; Bateman et al. 2005; Reid 2008). In areas of rapidly flowing water (i.e. riffles) a banner net of approximately 1 m$^2$ was used to catch any stunned fish drifting downstream, else two dip nets were used. Juveniles observed escaping the area being fished were noted and added to the capture count. For each section, the mean of the total summed number of juvenile salmon and trout (observed and caught) of the two bordering transects was divided by its width (m) to provide relative density indices. Juvenile Atlantic salmon and brown trout have a high niche overlap and potentially high interspecific competition (Nislow et al. 2010). To adequately represent locally experienced densities, the numbers of the two species were pooled in the analysis, of which ~90 % consisted of salmon.

Shelter availability (i.e. number of interstitial spaces in the river bed > 3cm deep) was measured according to Finstad et al. (2007), using a 13 mm rubber tube in three 0.25 m$^2$ sampling quadrates, which were equally spaced along each transect (i.e. one in the middle and two half way left and right of it). The 13 mm tube was previously found to best explain variation in fish sheltering, compared to other tube diameters between 5 and 22 mm (Finstad et al. 2007). In the same way as for the density indices, measured shelter from the surrounding two transects was averaged to provide a single value for each section. Further, wetted area was calculated in ArcGIS based on aerial photographs (www.norgebilder.no). All photographs were taken at the same date and at standard discharge (0.5 m$^3$ s$^{-1}$).

**Study fish**
Study fish were offspring of wild adult Atlantic salmon returning to the River Stjørdalselva, from which eggs were hatched and reared at the nearby Stjørdalsvassdraget hatchery. Before the experiment, the fish were reared for one summer in standard fibreglass 4 m$^2$ tanks. These were filled ca 0.5 m deep with water and contained fish densities between 7000 and 14000 individuals per tank, depending on fish size, which were fed pelleted food (Skretting Nutra 0.5-1.0, Skretting). Average smolting age is 2+ in the River Dalåa. Fish were anaesthetized using Tricaine methanesulfonate (MS-222) immediately prior to tagging and length measurements (± 1 mm, fork length) during 3.-5. September 2008. Individual size ranged between 57 and 114 mm (mean ± SD = 81 ± 10 mm). Twelve mm half duplex PIT tags were used to individually tag one third of the experimental fish (n = 5868) and tags were surgically inserted in accordance with Gries and Letcher (2002) by two experienced field scientists. The remaining fish (n = 11589) were fin-clipped (adipose fin) to be able to differentiate them from PIT tagged or other fish released during previous seasons. All individuals were returned to their tanks to recover from tagging for at least one night prior to release.

Release design

Fish were released at 26 sites, each separated by 100 m (Fig. 1). The wetted area surrounding each site 50 m up- and downstream was calculated (i.e. 100 m x average wetted width), so that the number of fish introduced at each release site could be standardized according to its wetted area. Fish were released on 8. Sep. 2008 in two alternating densities (high and low, 0.68 and 0.14 fish m$^{-2}$, respectively), where the low density treatment consisted only of PIT tagged fish and the high density treatment consisted of both PIT tagged and adipose-clipped fish. These densities were chosen to create a contrast within the natural range of 0.002 – 0.722
fish m$^{-2}$ observed within Norway (Johansen et al. 2005). Fish were placed in mesh cages at the release sites and left for an hour before being released.

Recapture

PIT tagged fish were recaptured one year later between 25.-28. August 2009 by continuously single-pass electrofishing the entire stretch of the study river. Five small areas could not be fished, due to large water depth. However, none of these areas comprised an entire section, so that data for all sections could be gathered. All captured salmon were checked for adipose fin clips and PIT tags, and their recapture section and size recorded. Recaptured PIT-tagged individuals were matched with data on their initial size and release site, so that growth (length at recapture – length at release), distance moved and habitat and shelter conditions could be compared.

Statistical analysis

For analyses of magnitude of fish movement away from release sites, our main interest was the effects of density treatment (low or high) and the ratio of resident density (i.e. density of fish present prior to the release) to shelter availability (resident density/shelter). We term this latter measure Density Shelter Ratio (DSR). However, movement rates may also vary among release site due to the presence of migration barriers (i.e. movement upstream from a release site located just below a barrier is not possible). Furthermore, it is possible that fish moved downstream out of the sampled study stretch. Thereby, movement rates may be underestimated for release sites from which fish had moved but could not be recaptured within the sampled area. This effect may be of an increasing magnitude for release sites being more closely located to the lower end of the stretch, where there was no barrier present to prevent downstream movement. Because the shape of such effects of release location were
unknown *a priori*, but could be assumed to be spatially correlated (e.g. the bias in estimates due to downstream migration would be expected to gradually decline when going from the lowermost release site and upstream), it was modeled as a smoothed term in a Generalized Additive Model (GAM). GAMs are semi-parametric extensions of generalized linear models (GLMs), where the linear predictor has been exchanged for a smoothed, additive predictor. These models have been described as being data- rather than model-driven, as the relationship between response and predictor variables is determined by the data instead of an *a priori* assumed parametric function. Thus, the use of GAMs avoids making untested assumptions about the relationship between response and predictor variables (Hastie and Tibshirani 1990; Guisan et al. 2002). GAMs were constructed using a backward stepwise procedure. Starting with the following global model, containing all relevant predictors, the most insignificant terms were sequentially removed until all remaining terms were significant:

\[
\text{Number of fish moved} \sim \text{smooth(release section)} + \text{DSR} + \text{shelter} + \text{density treatment} * \text{resident density}
\]

The asterisk (*) indicates that the terms left and right of it are treated both as main effects and interactions in the model. For each release site, the number of fish moving a certain minimum distance (see below) was used as the poisson distributed response variable and the natural logarithm of the total number of PIT-tagged fish recaptured was entered as an offset to account for varying catches per section (Webb et al. 2001). This approach was conducted at different spatial scales to evaluate whether results were scale dependent. In other words, different spatial extents of the “home” range surrounding the release site (i.e. areas within which the fish was defined to not have moved) was applied in separate models. This was done by incrementally increasing the home range by four 25 m sections up- and downstream of the release site (i.e. number of fish moved > 12.5 m, > 37.5 m, > 62.5 m, > 87.5 m or > 112.5 m) (Fig. 1). DSR values were averaged for each of these home ranges, resulting in five separate
models. Density treatment and resident density are treated independently in the models, as the competitive strength of residents can be expected to be higher than that of the released fish, due to prior residency effects. Such effects have been demonstrated in field experiments with a prior residency advantage of as little as four days (Kvingedal and Einum 2011), highlighting the importance of testing for the effects of the two types of fish separately.

Relationships between salmon growth and the above predictor variables as well as relationships between individual movement and initial length were analyzed using linear mixed effects models (LMM), with release site or recapture section being used as a random factor for movement and growth models, respectively. For the movement model, heterogeneity in model residuals was accounted for, using the appropriate covariance structure. Insignificant fixed effects variables were sequentially excluded from the global model based on log-likelihood tests of maximum likelihood (ML) estimation according to the procedures recommended in Zuur et al. (2009). Linear regression was used to analyze the relationship between resident density and shelter. Finally, to compare mean characteristics of individuals staying close to the release site with those of individuals moving away we grouped these into two categories which were compared using ordinary t-tests. Previous shorter term studies (months) suggest movements over more than 100 m for these sizes of juvenile Atlantic salmon in streams of this size to be rare both for released hatchery reared (Einum et al. 2006) and wild fish (Einum et al. 2011a). Thus, in these latter analyses, fish that had moved more than 112.5 m from their release sites were classified as movers and the remainder as stayers.

All analyses were completed using the statistical software package R 2.6.0 for Windows (The R Foundation for Statistical Computing 2007). GAMs were from the mgcv library (Wood...
The degree of smoothness of model terms in GAMs from this library is estimated as part of the fitting. Smooth terms in the GAMs were penalized regression splines. Linear mixed effect models were computed using the *lme* function from the *nlme* library (Pinheiro et al. 2009).

**Results**

The 2008 transect survey of resident fish density and shelter availability showed fish densities to vary between 0 and 1.08 (mean = 0.24) fish m\(^{-1}\), while shelter counts ranged between 0 and 17 (mean = 3.33). Continuous electrofishing of the study reach in 2009 yielded a total of 317 trout and 2158 salmon, of which 286 were PIT tagged, thus giving a recapture of ~5% of the released tagged salmon juveniles. Captured fin-clipped salmon could not be reliably differentiated from fish released in previous years, as these fish were also clipped and size overlap was too large to separate these groups by length only. Average size of recaptured tagged fish was slightly smaller than that of the original tagged release group (77 and 81 mm, respectively), indicating that the largest individuals were not recaptured. The following results, therefore, apply to the 286 recaptured tagged salmon, which are not necessarily representative of the entire tagged release group. There was a positive relationship between shelter availability and resident density (linear regression: \(F_{1,99} = 63.21, r^2 = 0.39, p < 0.001\), no correction for spatial correlation necessary) (Fig. 2). The number of sections moved by individuals ranged between 30 sections down- and 58 sections upstream (median = 0, mode = 0) and the majority (48%) moved upstream, rather than downstream (30%). However, 65% of the fish remained within four sections (112.5 m) above or below their release sites (Fig. 3). Distance moved was strongly reduced for individuals above ~85 mm (size at release) and the
corresponding model predicted a decrease in movement distance with increasing body size (LMM: $\beta = -0.21 \pm 0.07$, $t = -3.03$, $p = 0.003$, Fig. 4).

The number of fish moving from their release site was not significantly related to either resident density or shelter availability independently and could be removed from the model without causing significant decrease in log-likelihoods at all spatial scales (all $p > 0.86$). However, their ratio (DSR) did significantly affect the number of fish moving at all spatial scales except for the smallest one, i.e. the section containing the release site (Table 1, Fig. 5). This positive relationship became stronger as the area included increased (Table 1, Fig. 5). Thus, as the proportion of unoccupied shelter decreased more fish moved away from these areas. Density treatment did not significantly affect movement at any scale (GAM: all $z > -0.58$, all $p(z) > 0.56$). Further, mean DSR significantly differed between release and recapture site for the movers ($t = -2.62$, df = 171.88, $p = 0.010$). Here, mean DSR was lower at the recapture sites, i.e. movers were recaptured in areas with more available shelter relative to their release sites (mean ± SD, 0.66 ± 0.48 and 0.51 ± 0.33 for recapture and release areas, respectively).

Length at release and DSR at the recapture site had a significant negative effect on growth (LMM: $\beta = -0.19 \pm 0.04$, $t = -4.27$, $p < 0.001$ and $\beta = -3.49 \pm 1.67$, $t = -2.10$, $p = 0.039$, respectively). Removing either term caused a significant reduction in log-likelihoods ($p < 0.040$ for both) and were therefore retained in the model. Growth was not significantly different between movers and stayers ($t = 1.10$, df = 207.10, $p = 0.27$, 19 ± SD 7 mm and 20 ± 7 mm for movers and stayers, respectively).

Discussion
In the present study we show that density-dependent movement of juvenile Atlantic salmon was positively linked to the availability of shelter as a limiting resource. When local density was high relative to available shelters, excess individuals moved to find areas of habitat with unoccupied shelter. Whilst smaller sized individuals were more likely to move, average growth was not different between movers and stayers. Further, mean DSR differed between release and recapture sites for the movers, where fish moved from areas of higher DSR (less available shelter) to areas of lower DSR (more available shelter). Similarly, Lin et al. (2006) found that prairie voles (*Microtus ochrogaster*) only moved to similar or higher quality patches, characterized by high-quality food and more vegetative cover. Thus, it appears that fish were able to assess the joint effect of resident fish density and shelter availability on habitat quality and make movement decisions accordingly. It may be argued that other habitat variables important for stream dwelling salmonids, e.g. water velocity and depth may alternatively account for the detected movements. This cannot be entirely discounted, as such variables were not measured. However, the hatchery reared and therefore comparatively large 0+ fish used in this study can likely utilize a broader range of velocities and habitats than the smaller wild 0+ salmon. The latter tend to be limited by habitats with low water velocity, which facilitate successful feeding (Nislow et al. 1998; Nislow et al. 1999; Kennedy et al. 2008). Therefore, shelter availability may be the more important resource for these large bodied 0+ salmon.

The low recapture rate may have been due to high mortality of released fish, but low catchability due to difficult electrofishing conditions may be equally likely.

As a complement to the small-scale experimental results on movements from Finstad et al. (2009) we are able to show that juvenile Atlantic salmon are likely able to track larger scale natural variation in resource gradients, i.e. the ratio of fish density to the available shelter. The observed movements towards areas with unoccupied shelter provide further evidence that
shelter may be a limiting resource and that individuals distribute according to a given carrying
capacity defined by shelter availability (Finstad et al. 2009). Moreover, our results
demonstrate movement responses to shelter at an individual level. Growth was negatively
related to DSR, indicating a cost associated with insufficient shelter opportunity. This may be
the result of increased metabolic costs from harsh environmental conditions and an increased
standard metabolic rate associated with the lack of shelter (Valdimarsson and Metcalfe 1998;
Millidine et al. 2006). Further, energetic costs may arise from increased competitive
interactions for limited shelter opportunities (Finstad et al. 2007).

Our finding that movement behavior depended on body size (i.e. large individuals moved
less) may be best explained by the relationship between body size and competitive ability. In
organisms that establish and defend territories, body size is often linked with dominance
status, such that larger individuals are more likely to be successful competitors (Grand and
Dill 1997; Hakoyama and Iguchi 2001; Gibson et al. 2008), reducing the necessity to move.
However, in contrast, in many organisms, bioenergetic costs of movement are initially large,
but will decrease with increasing size. Thus large body size should favor increased movement
rates (Einum et al. 2006; Einum et al. 2008a). Size-related differences in movement are well
studied in salmonid juveniles in the early stage following emergence from nests, where
smaller individuals are displaced by territorial intraspecific competition and may be forced to
relocate downstream (Beall et al. 1994; Johnston 1997; Kahler et al. 2001; Bujold et al. 2004;
Anderson et al. 2008). The subsequent growth rates that mobile fish experience will depend
on the intrinsic quality of habitat they encounter (Kahler et al. 2001) as well as the local
density (Einum et al. 2011b), although it is commonly presumed that they are forced to accept
marginal habitat associated with slow growth (e.g. Elliott 1984; Johnston 1997; Bujold et al.
2004). However, the picture is less clear for older life history stages, due to the paucity of
studies quantifying size specific movements in these fish. Kahler et al. (2001) found no
difference in initial sizes between movers and stayers of young-of-the-year and parr of three
salmonid species (coho salmon, cutthroat trout and steelhead trout), but higher growth rates
for the movers. However, in that study the habitat the fish left actually had lower density than
that in which they remained, suggesting that movement was more a matter of habitat selection
than competitive displacement. In contrast, our results show that the smaller parr appear to
move most, making it more likely that their movements were a result of territorial
competition. Further, movers were able to achieve the same growth rates as stayers, which
suggests that these individuals were able to relocate to habitat of similar quality.

Averaging total population abundance over the entire available area may underestimate the
ture intensity of competitive interactions experienced by most individuals, due to
heterogeneity in local densities. Spatial patchiness may therefore influence carrying capacity
and recruitment within populations (Foldvik et al. 2010). The spatial aggregation of resources
further affects the strength of competitive interactions (Finstad et al. 2009). For example,
locally limited availability of structural refuge results in intense competition in both reef fish
(Shima and Osenberg 2003; Forrester and Steele 2004) and intertidal crabs (Moksnes 2004;
Wieters et al. 2009). It is the combined effect of these two spatial patterns that shapes the
spatial variation in individual performance, in the same way as it does for temporally
fluctuating resources (Shima and Osenberg 2003; Berryman 2004; Forrester and Steele 2004;
Einum 2005; Finstad et al. 2009). For Atlantic salmon, the present study suggests that high
local loss rates in areas with a high population density relative to limiting resources, as
observed during the transition from young-of-the-year to 1-year old (Finstad et al. 2009), at
least in part can be caused by effects on movement rates. Yet, the observation that population
productivity is relatively lower in rivers with higher heterogeneity in shelter abundance
(Finstad et al. 2009) suggests that effects of such heterogeneity extends beyond effects on movements, and that it can reduce the ability of populations to efficiently utilize the total amount of available resources on larger spatial scales over which movements may be less likely to homogenize competitive intensities.

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References


Table 1. GAM results of best fit models, predicting the number of fish moving away from their release sites. Models differ in the spatial scale of how movement is defined, i.e. fish are only considered to have moved if they were recaptured more than 12.5, 37.5, 62.5, 87.5 or 112.5 m away from their release site. $\beta$ indicates regression slopes and $s()$ indicates smoothed terms. $z$ values refer to the parametric term (DSR) and $\chi^2$ values refer to the smoothed term (release site).

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<th>$\beta$</th>
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**Figure captions**

**Figure 1.** Schematic overview of the release design, showing locations of electrofishing transects (dashed lines) and a release site (black dot). The 25 m distance between electrofishing transects is termed section. Numbers relate to different spatial scales used in the analysis, ranging from only the release site to four sections up- and downstream of it.

**Figure 2.** Linear regression giving the relationship between shelter availability and resident density of fish prior to the experiment.

**Figure 3.** Histogram of number of sections moved (i.e. distance between release site and recapture section) for the 286 recaptured PIT-tagged juvenile salmon from River Dalåa. Negative values indicate downstream movement.

**Figure 4.** Initial length of the 286 recaptured PIT-tagged juvenile salmon at release against the number of sections moved (i.e. distance between release site and recapture section).

**Figure 5.** Relationship between Density Shelter Ratio (DSR) and number of fish moving away from their release site. Y-axis values represent partial residuals for DSR from the respective Generalized Additive Model for five different home range sizes (a) > 12.5 m, (b) > 37.5 m, (c) > 62.5 m, (d) > 87.5 m and (e) > 112.5 m sections.
Figure 1.

Figure 2.
Figure 3.

Figure 4.
Figure 5.