

1 **Interactions between local population density and limited**  
2 **habitat resources determine movements of juvenile**  
3 **Atlantic salmon**

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41

42 **Abstract**

43 Competition for limited resources and the resulting density-dependent processes are key  
44 factors in driving stream salmonid population dynamics. Here we test for the combined  
45 effects of density and shelter availability on the movement of juvenile Atlantic salmon in a  
46 Norwegian river. Individually marked, hatchery reared salmon juveniles were released at 26  
47 sites along a 2.5 km long stretch and recaptured after 12 months. The spatial variation in  
48 shelter availability and density of salmonids was quantified prior to the release. We found no  
49 effect of released fish number on the number of marked salmon moving more than 12.5 –  
50 112.5 m away from their release site. However, the ratio of pre-experiment fish density per  
51 shelter was positively related to the number of movers. Thus, fish that were released at sites  
52 where the amount of shelter was low relative to the density of the pre-experiment population  
53 were more likely to move. These results support the prediction from smaller scale  
54 experimental studies that shelter availability may act to determine local carrying capacity in  
55 stream living salmonid populations.

56

57 **Introduction**

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

68  
69 Of the few available empirical studies, Finstad et al. (2009) also highlight the heterogeneous  
70 spatial distribution of habitat quality, which in turn is strongly affected by the availability of  
71 limiting resources. In such cases, spatial variation in performance caused by competition for  
72 limited resources, and hence corresponding competition-driven movements, is predicted to  
73 depend not on local population density *per se*, but rather on density relative to the local  
74 abundance of limiting resources (Berryman 2004). Recent attempts at elucidating the  
75 mechanisms behind density dependence have successfully incorporated such information  
76 (Shima and Osenberg 2003; Forrester and Steele 2004; Einum 2005; Einum and Nislow 2005;  
77 Finstad et al. 2009). However, because of the lack of individual level data, previous field  
78 studies have been unable to distinguish between mortality and movement responses to varying  
79 amounts of limiting resources.

80

81 One habitat characteristic which has been widely identified as a limiting resource is the  
82 availability of structural refuge (e.g. Harwood et al. 2002; Griffiths et al. 2004; Davey et al.  
83 2009). Such shelters provide protection from predators until the available shelter space is  
84 saturated (Begon et al. 1996; Hossie and Murray 2010). Limited shelter opportunities may  
85 therefore result in intense intra- (Beck 1997; Shima and Osenberg 2003; Moksnes 2004;  
86 Davey et al. 2009) and interspecific competition (Söderbäck 1994; McDonald et al. 2001;  
87 Harwood et al. 2002; Griffiths et al. 2004; Wieters et al. 2009). For example, juvenile  
88 Dungeness crabs (*Cancer magister*) compete with juvenile shore crabs (*Carcinus maenas* L.)  
89 for shelter in mollusk shells. The dominant shore crab often physically evicts the less  
90 aggressive Dungeness crab from shelter, thus exposing it to an increased risk of predation  
91 (McDonald et al. 2001). Therefore, competition for shelters may influence population  
92 carrying capacity (Harwood et al. 2002).

93  
94 Shelter use in stream dwelling salmonids has been the focus of numerous studies (e.g.  
95 Valdimarsson and Metcalfe 1998; Orpwood et al. 2003; Millidine et al. 2006; Finstad et al.  
96 2007; Teichert et al. 2010). Salmonids may seek shelter in interstitial spaces in the stream  
97 substrate both to avoid predators and to protect themselves against harsh physical conditions  
98 (Valdimarsson and Metcalfe 1998; Millidine et al. 2006). Apart from the obvious benefits of  
99 reduced mortality and energy expenditure, the presence of shelter also reduces standard  
100 metabolic costs (Millidine et al. 2006). Density-dependent regulation at the population level is  
101 well understood in salmonids (reviewed in Elliott 1994; Einum and Nislow 2011). Recent  
102 studies have highlighted the importance of spatial structure of population density during  
103 breeding and early juvenile stages in shaping levels of density-dependence and the subsequent  
104 influence on population dynamics (Einum et al. 2006; Einum et al. 2008b; Finstad et al. 2010;  
105 Teichert et al. 2011). With respect to spatial distribution of shelters, Finstad et al. (2009)

106 showed that the variation in the change in Atlantic salmon cohort abundance from age-0 to  
107 age-1 among locations in a natural population was best explained by modeling the local  
108 carrying capacity as a function of shelter availability. On a smaller spatial scale they  
109 experimentally demonstrated that the number of individuals moving out of artificial streams  
110 was negatively correlated to the amount of unoccupied shelter. Further, the spatial distribution  
111 of shelters was found to vary substantially across rivers, and increased heterogeneity in shelter  
112 abundance was linked to reduced salmon production on the population scale (Finstad et al.  
113 2009; Teichert et al. 2013). This latter finding suggests a limitation in the ability of fish to  
114 distribute according to, and hence efficiently utilize heterogeneously distributed resources.  
115 Nevertheless, the ability of individuals to make movement decisions based on the availability  
116 of limiting resources has not been sufficiently assessed.

117

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

125

## 126 **Methods**

### 127 *Study area*

128 The study was conducted in the River Dalåa, central Norway (63°25'N, 11°74'E). The river is  
129 regulated with mean discharge of  $\sim 2 \text{ m}^3 \text{ s}^{-1}$  and has an average wetted width of 16.9 m within  
130 the study section. Anadromous salmonids do not naturally occur in this river, due to a barrier

131 preventing upwards migration from the River Stjørdalselva (63°27'N, 10°54'E). However,  
132 mitigation agreements with the local waterpower operator include releasing hatchery reared  
133 Atlantic salmon juveniles and eggs into the river which migrate to sea via the River  
134 Stjørdalselva. Salmon juveniles are released as 0+ during October each year and the majority  
135 of these introduced fish smoltify at the age of 2+ - 3+ (Arnekleiv et al. 2001, in Norwegian).  
136 Brown trout *Salmo trutta* are also present, but their abundance has declined since the  
137 introduction of Atlantic salmon, which now is the dominant species in the river (Arnekleiv et  
138 al. 2001, in Norwegian). The study stretch was about 2500 m long and contained by a  
139 migration barrier at the upstream end. Migration barriers were present at approximately 1600  
140 m, 1700 m and 2000 m, measured from the downstream end of the study stretch. All  
141 migration barriers could be passed by the fish in a downstream direction. The morphology of  
142 the river in the study stretch changes after the first ~1.2 km from a fairly narrow and steep  
143 valley, where the river is dominated by large rocks and boulders to a more open landscape,  
144 where the river substrate consists mainly of gravel and sand. Subsequently, habitat type also  
145 changes from riffle dominated to glide dominated, respectively.

146

#### 147 *Electrofishing and habitat survey*

148 Fish present in the river prior to the experiment are termed “resident”. To establish how their  
149 density varied spatially, densities of resident juvenile salmon and trout were surveyed during  
150 20. - 22. August 2008 by single-pass electrofishing. Approximately 1.5 m wide transects were  
151 fished across the width of the river at regular 25 m longitudinal intervals throughout the study  
152 area, resulting in a total number of 109 transects. The 25 m intervals were measured with a  
153 tape measure and the position of each transect spatially referenced by GPS. Each 25 m  
154 interval is termed section and used as the main unit to describe movement within the study  
155 stretch (Fig. 1). Within-stream spatial variation in abundance is generally much larger than

156 variation due to habitat-specific catch efficiency in electrofishing surveys (Hankin, 1984;  
157 Bohlin et al., 1989). Single pass approaches therefore provide cost effective estimates of  
158 spatial variation in abundance which highly correlate with those obtained from traditional,  
159 more accurate but also more time-consuming multi-pass censuses (Prevost and Nihouarn  
160 1999; Bateman et al. 2005; Reid 2008). In areas of rapidly flowing water (i.e. riffles) a banner  
161 net of approximately 1 m<sup>2</sup> was used to catch any stunned fish drifting downstream, else two  
162 dip nets were used. Juveniles observed escaping the area being fished were noted and added  
163 to the capture count. For each section, the mean of the total summed number of juvenile  
164 salmon and trout (observed and caught) of the two bordering transects was divided by its  
165 width (m) to provide relative density indices. Juvenile Atlantic salmon and brown trout have a  
166 high niche overlap and potentially high interspecific competition (Nislow et al. 2010). To  
167 adequately represent locally experienced densities, the numbers of the two species were  
168 pooled in the analysis, of which ~90 % consisted of salmon.

169

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

179

180 *Study fish*

181 Study fish were offspring of wild adult Atlantic salmon returning to the River Stjørdalselva,  
182 from which eggs were hatched and reared at the nearby Stjørdalsvassdraget hatchery. Before  
183 the experiment, the fish were reared for one summer in standard fibreglass 4 m<sup>2</sup> tanks. These  
184 were filled ca 0.5 m deep with water and contained fish densities between 7000 and 14000  
185 individuals per tank, depending on fish size, which were fed pelleted food (Skretting Nutra  
186 0.5-1.0, Skretting). Average smolting age is 2+ in the River Dalåa. Fish were anaesthetized  
187 using Tricaine methanesulfonate (MS-222) immediately prior to tagging and length  
188 measurements ( $\pm 1$  mm, fork length) during 3.-5. September 2008. Individual size ranged  
189 between 57 and 114 mm (mean  $\pm$  SD = 81  $\pm$  10 mm). Twelve mm half duplex PIT tags were  
190 used to individually tag one third of the experimental fish (n = 5868) and tags were surgically  
191 inserted in accordance with Gries and Letcher (2002) by two experienced field scientists. The  
192 remaining fish (n = 11589) were fin-clipped (adipose fin) to be able to differentiate them from  
193 PIT tagged or other fish released during previous seasons. All individuals were returned to  
194 their tanks to recover from tagging for at least one night prior to release.

195

196

### 197 *Release design*

198 Fish were released at 26 sites, each separated by 100 m (Fig. 1). The wetted area surrounding  
199 each site 50 m up- and downstream was calculated (i.e. 100 m x average wetted width), so  
200 that the number of fish introduced at each release site could be standardized according to its  
201 wetted area. Fish were released on 8. Sep. 2008 in two alternating densities (high and low,  
202 0.68 and 0.14 fish m<sup>-2</sup>, respectively), where the low density treatment consisted only of PIT  
203 tagged fish and the high density treatment consisted of both PIT tagged and adipose-clipped  
204 fish. These densities were chosen to create a contrast within the natural range of 0.002 – 0.722



205 fish m<sup>-2</sup> observed within Norway (Johansen et al. 2005). Fish were placed in mesh cages at the  
206 release sites and left for an hour before being released.

207

### 208 *Recapture*

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

217

### 218 *Statistical analysis*

219 For analyses of magnitude of fish movement away from release sites, our main interest was  
220 the effects of density treatment (low or high) and the ratio of resident density (i.e. density of  
221 fish present prior to the release) to shelter availability (resident density/shelter). We term this  
222 latter measure Density Shelter Ratio (DSR). However, movement rates may also vary among  
223 release site due to the presence of migration barriers (i.e. movement upstream from a release  
224 site located just below a barrier is not possible). Furthermore, it is possible that fish moved  
225 downstream out of the sampled study stretch. Thereby, movement rates may be  
226 underestimated for release sites from which fish had moved but could not be recaptured  
227 within the sampled area. This effect may be of an increasing magnitude for release sites being  
228 more closely located to the lower end of the stretch, where there was no barrier present to  
229 prevent downstream movement. Because the shape of such effects of release location were

230 unknown *a priori*, but could be assumed to be spatially correlated (e.g. the bias in estimates  
 231 due to downstream migration would be expected to gradually decline when going from the  
 232 lowermost release site and upstream), it was modeled as a smoothed term in a Generalized  
 233 Additive Model (GAM). GAMs are semi-parametric extensions of generalized linear models  
 234 (GLMs), where the linear predictor has been exchanged for a smoothed, additive predictor.  
 235 These models have been described as being data- rather than model-driven, as the relationship  
 236 between response and predictor variables is determined by the data instead of an *a priori*  
 237 assumed parametric function. Thus, the use of GAMs avoids making untested assumptions  
 238 about the relationship between response and predictor variables (Hastie and Tibshirani 1990;  
 239 Guisan et al. 2002). GAMs were constructed using a backward stepwise procedure. Starting  
 240 with the following global model, containing all relevant predictors, the most insignificant  
 241 terms were sequentially removed until all remaining terms were significant:

242 Number of fish moved  $\sim$  smooth(release section) + DSR + shelter + density treatment \*  
 243 resident density

244 The asterisk (\*) indicates that the terms left and right of it are treated both as main effects and  
 245 interactions in the model. For each release site, the number of fish moving a certain minimum  
 246 distance (see below) was used as the poisson distributed response variable and the natural  
 247 logarithm of the total number of PIT-tagged fish recaptured was entered as an offset to  
 248 account for varying catches per section (Webb et al. 2001). This approach was conducted at  
 249 different spatial scales to evaluate whether results were scale dependent. In other words,  
 250 different spatial extents of the “home” range surrounding the release site (i.e. areas within  
 251 which the fish was defined to not have moved) was applied in separate models. This was done  
 252 by incrementally increasing the home range by four 25 m sections up- and downstream of the  
 253 release site (i.e. number of fish moved > 12.5 m, > 37.5 m, > 62.5 m, > 87.5 m or > 112.5 m)  
 254 (Fig. 1). DSR values were averaged for each of these home ranges, resulting in five separate

255 models. Density treatment and resident density are treated independently in the models, as the  
256 competitive strength of residents can be expected to be higher than that of the released fish,  
257 due to prior residency effects. Such effects have been demonstrated in field experiments with  
258 a prior residency advantage of as little as four days (Kvingedal and Einum 2011), highlighting  
259 the importance of testing for the effects of the two types of fish separately.

260

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

277

278 All analyses were completed using the statistical software package R 2.6.0 for Windows (The  
279 R Foundation for Statistical Computing 2007). GAMs were from the mgcv library (Wood

280 2001). The degree of smoothness of model terms in GAMs from this library is estimated as  
281 part of the fitting. Smooth terms in the GAMs were penalized regression splines. Linear  
282 mixed effect models were computed using the *lme* function from the *nlme* library (Pinheiro et  
283 al. 2009).

284

## 285 **Results**

286

287 The 2008 transect survey of resident fish density and shelter availability showed fish densities  
288 to vary between 0 and 1.08 (mean = 0.24) fish m<sup>-1</sup>, while shelter counts ranged between 0 and  
289 17 (mean = 3.33). Continuous electrofishing of the study reach in 2009 yielded a total of 317  
290 trout and 2158 salmon, of which 286 were PIT tagged, thus giving a recapture of ~5 % of the  
291 released tagged salmon juveniles. Captured fin-clipped salmon could not be reliably  
292 differentiated from fish released in previous years, as these fish were also clipped and size  
293 overlap was too large to separate these groups by length only. Average size of recaptured  
294 tagged fish was slightly smaller than that of the original tagged release group (77 and 81 mm,  
295 respectively), indicating that the largest individuals were not recaptured. The following  
296 results, therefore, apply to the 286 recaptured tagged salmon, which are not necessarily  
297 representative of the entire tagged release group. There was a positive relationship between  
298 shelter availability and resident density (linear regression:  $F_{1,99} = 63.21$ ,  $r^2 = 0.39$ ,  $p < 0.001$ ,  
299 no correction for spatial correlation necessary) (Fig. 2). The number of sections moved by  
300 individuals ranged between 30 sections down- and 58 sections upstream (median = 0, mode =  
301 0) and the majority (48 %) moved upstream, rather than downstream (30 %). However, 65 %  
302 of the fish remained within four sections (112.5 m) above or below their release sites (Fig. 3).  
303 Distance moved was strongly reduced for individuals above ~85 mm (size at release) and the

304 corresponding model predicted a decrease in movement distance with increasing body size  
305 (LMM:  $\beta = -0.21 \pm 0.07$ ,  $t = -3.03$ ,  $p = 0.003$ , Fig. 4).

306

307 The number of fish moving from their release site was not significantly related to either  
308 resident density or shelter availability independently and could be removed from the model  
309 without causing significant decrease in log-likelihoods at all spatial scales (all  $p > 0.86$ ).

310 However, their ratio (DSR) did significantly affect the number of fish moving at all spatial  
311 scales except for the smallest one, i.e. the section containing the release site (Table 1, Fig. 5).

312 This positive relationship became stronger as the area included increased (Table 1, Fig. 5).

313 Thus, as the proportion of unoccupied shelter decreased more fish moved away from these  
314 areas. Density treatment did not significantly affect movement at any scale (GAM: all  $z > -$   
315  $0.58$ , all  $p(z) > 0.56$ ). Further, mean DSR significantly differed between release and recapture  
316 site for the movers ( $t = -2.62$ ,  $df = 171.88$ ,  $p = 0.010$ ). Here, mean DSR was lower at the  
317 recapture sites, i.e. movers were recaptured in areas with more available shelter relative to  
318 their release sites (mean  $\pm$  SD,  $0.66 \pm 0.48$  and  $0.51 \pm 0.33$  for recapture and release areas,  
319 respectively).

320

321 Length at release and DSR at the recapture site had a significant negative effect on growth  
322 (LMM:  $\beta = -0.19 \pm 0.04$ ,  $t = -4.27$ ,  $p < 0.001$  and  $\beta = -3.49 \pm 1.67$ ,  $t = -2.10$ ,  $p = 0.039$ ,  
323 respectively). Removing either term caused a significant reduction in log-likelihoods  
324 ( $p < 0.040$  for both) and were therefore retained in the model. Growth was not significantly  
325 different between movers and stayers ( $t = 1.10$ ,  $df = 207.10$ ,  $p = 0.27$ ,  $19 \pm$  SD  $7$  mm and  $20 \pm$   
326  $7$  mm for movers and stayers, respectively).

327

328 **Discussion**

329 In the present study we show that density-dependent movement of juvenile Atlantic salmon  
330 was positively linked to the availability of shelter as a limiting resource. When local density  
331 was high relative to available shelters, excess individuals moved to find areas of habitat with  
332 unoccupied shelter. Whilst smaller sized individuals were more likely to move, average  
333 growth was not different between movers and stayers. Further, mean DSR differed between  
334 release and recapture sites for the movers, where fish moved from areas of higher DSR (less  
335 available shelter) to areas of lower DSR (more available shelter). Similarly, Lin et al. (2006)  
336 found that prairie voles (*Microtus ochrogaster*) only moved to similar or higher quality  
337 patches, characterized by high-quality food and more vegetative cover. Thus, it appears that  
338 fish were able to assess the joint effect of resident fish density and shelter availability on  
339 habitat quality and make movement decisions accordingly. It may be argued that other habitat  
340 variables important for stream dwelling salmonids, e.g. water velocity and depth may  
341 alternatively account for the detected movements. This cannot be entirely discounted, as such  
342 variables were not measured. However, the hatchery reared and therefore comparatively large  
343 0+ fish used in this study can likely utilize a broader range of velocities and habitats than the  
344 smaller wild 0+ salmon. The latter tend to be limited by habitats with low water velocity,  
345 which facilitate successful feeding (Nislow et al. 1998; Nislow et al. 1999; Kennedy et al.  
346 2008). Therefore, shelter availability may be the more important resource for these large  
347 bodied 0+ salmon.

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

350 As a complement to the small-scale experimental results on movements from Finstad et al.  
351 (2009) we are able to show that juvenile Atlantic salmon are likely able to track larger scale  
352 natural variation in resource gradients, i.e. the ratio of fish density to the available shelter. The  
353 observed movements towards areas with unoccupied shelter provide further evidence that

354 shelter may be a limiting resource and that individuals distribute according to a given carrying  
355 capacity defined by shelter availability (Finstad et al. 2009). Moreover, our results  
356 demonstrate movement responses to shelter at an individual level. Growth was negatively  
357 related to DSR, indicating a cost associated with insufficient shelter opportunity. This may be  
358 the result of increased metabolic costs from harsh environmental conditions and an increased  
359 standard metabolic rate associated with the lack of shelter (Valdimarsson and Metcalfe 1998;  
360 Millidine et al. 2006). Further, energetic costs may arise from increased competitive  
361 interactions for limited shelter opportunities (Finstad et al. 2007).

362

363 Our finding that movement behavior depended on body size (i.e. large individuals moved  
364 less) may be best explained by the relationship between body size and competitive ability. In  
365 organisms that establish and defend territories, body size is often linked with dominance  
366 status, such that larger individuals are more likely to be successful competitors (Grand and  
367 Dill 1997; Hakoyama and Iguchi 2001; Gibson et al. 2008), reducing the necessity to move.  
368 However, in contrast, in many organisms, bioenergetic costs of movement are initially large,  
369 but will decrease with increasing size. Thus large body size should favor increased movement  
370 rates (Einum et al. 2006; Einum et al. 2008a). Size-related differences in movement are well  
371 studied in salmonid juveniles in the early stage following emergence from nests, where  
372 smaller individuals are displaced by territorial intraspecific competition and may be forced to  
373 relocate downstream (Beall et al. 1994; Johnston 1997; Kahler et al. 2001; Bujold et al. 2004;  
374 Anderson et al. 2008). The subsequent growth rates that mobile fish experience will depend  
375 on the intrinsic quality of habitat they encounter (Kahler et al. 2001) as well as the local  
376 density (Einum et al. 2011b), although it is commonly presumed that they are forced to accept  
377 marginal habitat associated with slow growth (e.g. Elliott 1984; Johnston 1997; Bujold et al.  
378 2004). However, the picture is less clear for older life history stages, due to the paucity of

379 studies quantifying size specific movements in these fish. Kahler et al. (2001) found no  
380 difference in initial sizes between movers and stayers of young-of-the-year and parr of three  
381 salmonid species (coho salmon, cutthroat trout and steelhead trout), but higher growth rates  
382 for the movers. However, in that study the habitat the fish left actually had lower density than  
383 that in which they remained, suggesting that movement was more a matter of habitat selection  
384 than competitive displacement. In contrast, our results show that the smaller parr appear to  
385 move most, making it more likely that their movements were a result of territorial  
386 competition. Further, movers were able to achieve the same growth rates as stayers, which  
387 suggests that these individuals were able to relocate to habitat of similar quality.

388

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



404 (Finstad et al. 2009) suggests that effects of such heterogeneity extends beyond effects on  
405 movements, and that it can reduce the ability of populations to efficiently utilize the total  
406 amount of available resources on larger spatial scales over which movements may be less  
407 likely to homogenize competitive intensities.

408

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**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).

Spatial scale	Best fit model	$\beta$	df	$z/\chi^2$	$p/p(z)$
> 12.5 m	DSR	0.28	-	1.02	0.309
	$s(\text{release site})$	-	1	3.413	0.065
> 37.5 m	DSR	0.83	-	1.95	0.051
	$s(\text{release site})$	-	1	8.504	0.004
> 62.5 m	DSR	2.11	-	3.13	0.002
	$s(\text{release site})$	-	1	16.08	< 0.001
> 87.5 m	DSR	4.08	-	2.61	0.009
	$s(\text{release site})$	-	4.054	21.66	< 0.001
> 112.5 m	DSR	7.17	-	2.53	0.012
	$s(\text{release site})$	-	4.293	24.28	< 0.001

566



567 **Figure captions**

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

572

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

575

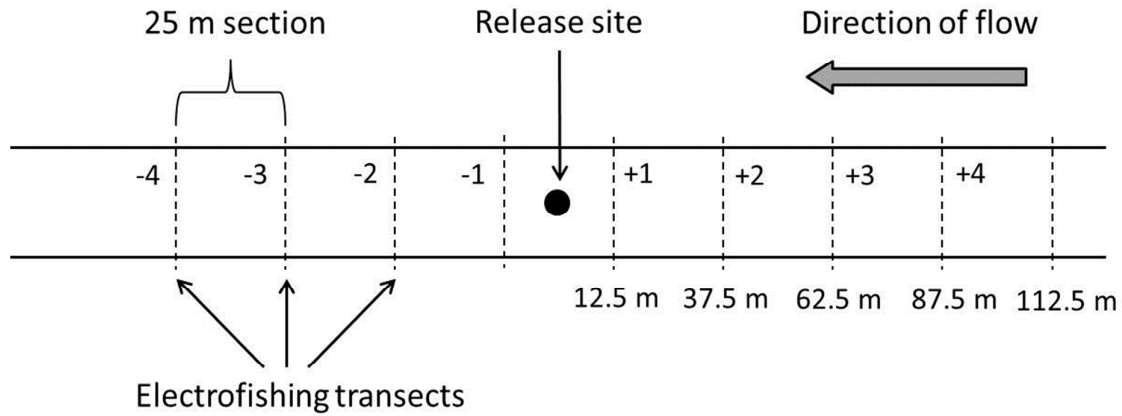
576 **Figure 3.** Histogram of number of sections moved (i.e. distance between release site and  
577 recapture section) for the 286 recaptured PIT-tagged juvenile salmon from River Dalåa.  
578 Negative values indicate downstream movement.

579

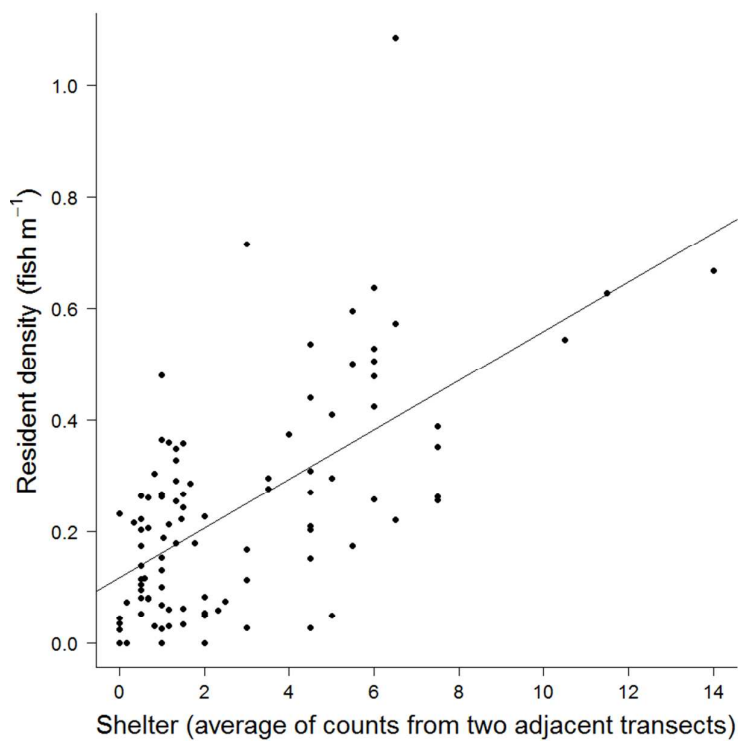
580 **Figure 4.** Initial length of the 286 recaptured PIT-tagged juvenile salmon at release against  
581 the number of sections moved (i.e. distance between release site and recapture section).

582

583 **Figure 5.** Relationship between Density Shelter Ratio (DSR) and number of fish moving  
584 away from their release site. Y-axis values represent partial residuals for DSR from the  
585 respective Generalized Additive Model for five different home range sizes (a) > 12.5 , (b) >  
586 37.5 m, (c) > 62.5 m, (d) > 87.5 m and (e) > 112.5 m sections.



**Figure 1.**



**Figure 2.**

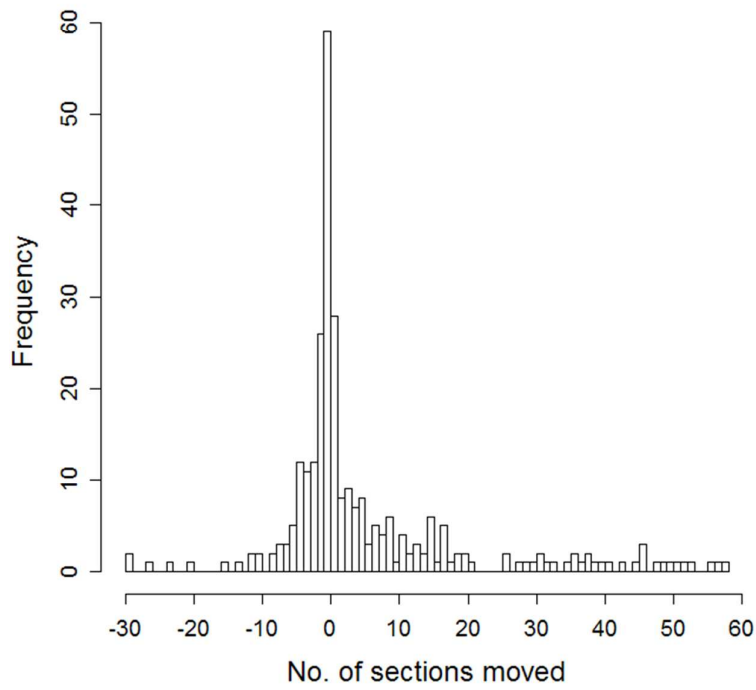


Figure 3.

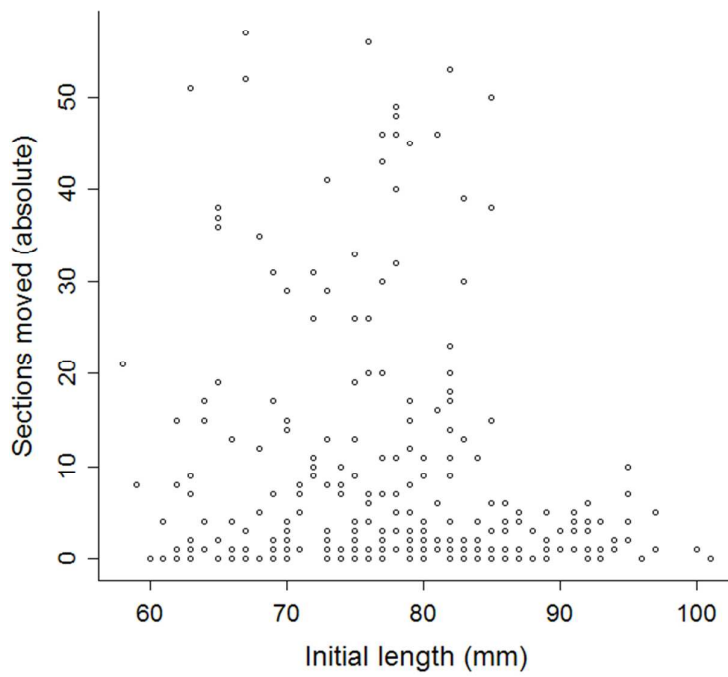


Figure 4.

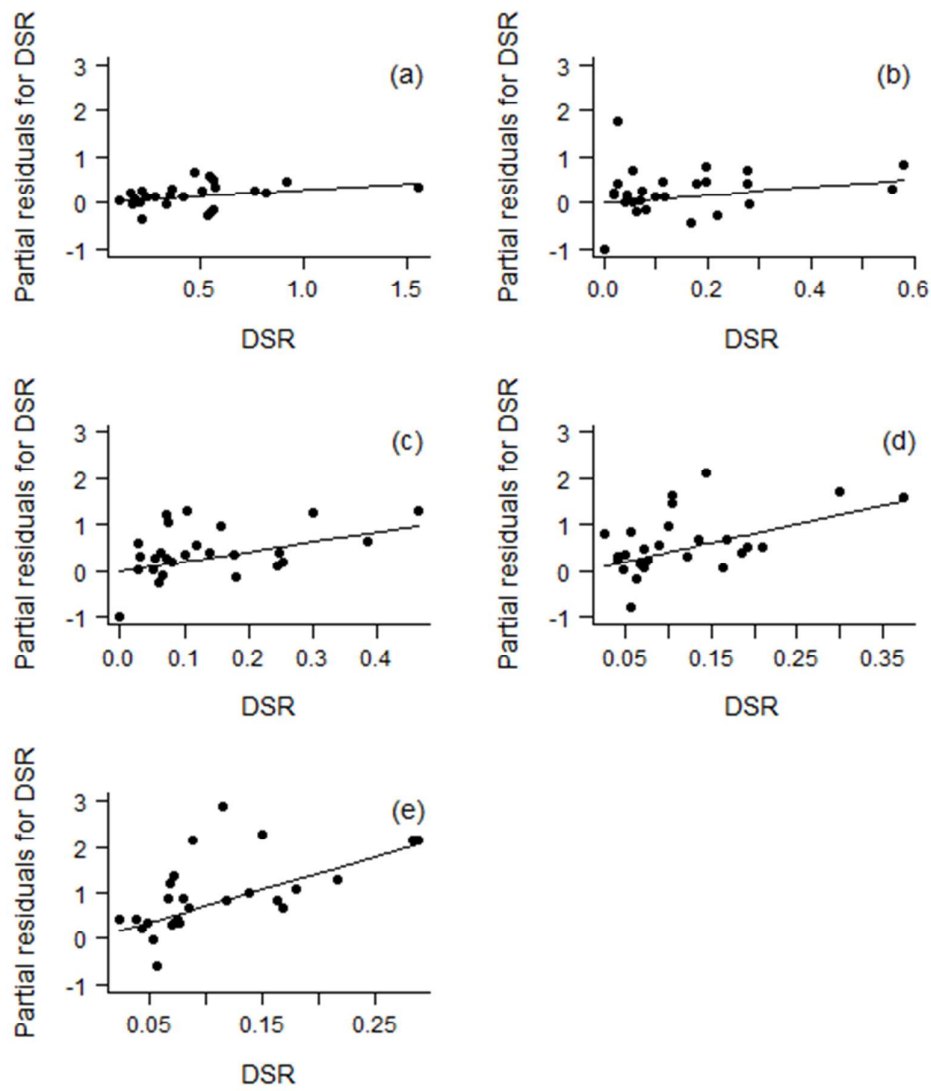


Figure 5.