Size-dependent habitat use in juvenile Atlantic salmon (Salmo salar L.)

Frøydis Bolme Hamnes
Preface

This thesis is a part of the Environmental impacts of hydroppeaking (EnviPEAK) project at the Centre for Environmental Design of Renewable Energy (CEDREN). The main objective of the EnviPEAK project is to develop knowledge and tools to analyse, predict and mitigate environmental impacts from rapid and frequent changes in hydropower production regimes. I wish to thank my supervisors Sigurd Einum and Ole Kristian Berg, both from NTNU, for useful help and guidance during fieldwork and the writing process.

The thesis is written and formatted as a manuscript, following the manuscript guidelines for the journal *Oecologia*.

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Table of contents

Abstract.................................................................................................................................1
Introduction............................................................................................................................2
Material and Methods.........................................................................................................5
  Study site and experimental design..................................................................................5
  Pilot experiment...............................................................................................................5
  Experimental procedures..............................................................................................6
  Statistics.........................................................................................................................7
Results...............................................................................................................................8
  Preferred habitat............................................................................................................8
  Summer experiment.......................................................................................................8
  Autumn experiment.......................................................................................................8
Discussion...........................................................................................................................10
Acknowledgements...........................................................................................................13
References..........................................................................................................................14
Tables................................................................................................................................20
Figure legends....................................................................................................................23
Figures...............................................................................................................................24
Abstract

Size-dependent habitat use is a well-known phenomenon for many animal species. Thus, many studies have been conducted in this field, using different approaches. In the present study it was tested if size-dependent habitat distribution of YOY Atlantic salmon is according to the ideal free distribution (IFD) or the ideal despotic distribution (IDD). This was tested by manipulating density on a small spatial scale, using artificial stream-channels which were divided into deep and shallow habitats. Both during summer and autumn, habitat use of YOY was size-dependent, with larger individuals more often being found in the deep habitat than smaller individuals. YOY habitat use was affected by the presence of larger salmon and time of day, with more individuals being found in the shallow habitat in the presence of the older cohort and at night-time. Due to marginal effects of density on YOY habitat use, YOY appeared to be distributed according to IFD. However, the effect of the presence of older fish suggested that these had a more despotic-type effect on YOY. Thus, for salmonid populations, both IFD and IDD may occur simultaneously, with their relative importance depending on the range of body sizes present.

Keywords: YOY, density, IFD, IDD, spatial scale.
Introduction

According to the ideal free distribution (IFD) (Fretwell and Lucas 1970), individuals in a population distribute among all available habitats according to suitability, and how many conspecifics are already settled in each habitat. Such a distribution results in equal fitness for all individuals in the population, and a local population density that is equivalent to the amount of resources in each habitat. The IFD theory assumes that all individuals in a population are able to disperse, have perfect knowledge and are free to enter any habitat. The distribution of individuals among habitats therefore remains constant with a change in density. These assumptions do not always hold in nature. If a species is territorial, dominant individuals may gain access to high-quality habitats (Hughes 1992; Wauters et al. 2001), with subordinate individuals being restricted to low-quality habitats (Bachman 1984; Armstrong et al. 2002), obtaining lower fitness than those in the high quality habitat. With an increased population density we will then find a proportional increase in utilization of less preferred, low-quality habitats. This phenomenon is known as the ideal despotic distribution (IDD) (Fretwell and Lucas 1970).

Size-dependent habitat use, where distinct body sizes lead to individuals utilizing distinct habitats is well known in the animal kingdom (Hacker and Steneck 1990; Harvey and Stewart 1991; Sweitzer and Berger 1992), and can be due to ontogenetic shifts as individuals grow (Werner and Gilliam 1984). Such distinct habitat use can be used as anti-predator strategies, to decrease intra- and inter-cohort competition, or to enhance feeding (Garcia-Berthou 2001; Bystrom et al. 2003; Davey et al. 2005). One potential explanation for such observations is that individuals within a population distribute according to IFD, and that individuals with different sizes have distinct intrinsic habitat preferences. Alternatively, populations may be distributed according to IDD, with large individuals monopolizing the preferred habitats. Thus, pure observational studies of size distributions across habitats will not be able to distinguish between IFD and IDD.

In fish, size-dependent habitat use has been well described in many species. Larger and older individuals mostly utilize deep water habitats, whereas smaller and younger fish are found in shallower habitats (Schlosser 1987; Harvey and Stewart 1991; Garcia-Berthou 2001). Larger individuals also utilize the upper part of the water column more frequently than smaller individuals (Gustafsson et al. 2010). In addition, different sizes utilize distinct substratum sizes, with larger individuals inhabiting coarser substrata than smaller individuals (Davey et
al. 2005). As mentioned above, size-dependent habitat use in animal populations can be present both under IFD and IDD. Many studies have found that size-dependent habitat use of fish is caused by ontogenetic shifts in habitat preferences. In a stream environment, Harvey and Stewart (1991) found that larger individuals vacate shallow habitats to avoid visual terrestrial predators, whereas smaller individuals utilize shallow habitats to decrease predation by piscivorous fishes. Such a size-dependent distribution can thus be present under IFD. In freshwater lakes, size-dependent habitat use may also be caused by distinct habitat preferences, this to decrease predation risk or to find a trade-off between predation risk and profitable feeding (Werner et al. 1983; Werner and Hall 1988; Bystrom et al. 2004). In addition to anti-predator strategies, a change in mouth structure as the fish grows can lead to size-dependent habitat use. Mouth structures can delimit the fish, so that distinct sizes prefer distinct food sources, and therefore also different habitats (Garcia-Berthou 2001). Despite the apparent common occurrence of ontogenetic shifts in preferred habitats, there are also examples showing that a size-dependent habitat distribution can be present under IDD. For example, in stream living bullhead (*Cottus gobio* L.), both juvenile and adult individuals used the same type of habitat at low densities. However, with increased density, juveniles had an increased use of less preferred habitat implying that the juveniles were excluded from their preferred habitat by the adults (Davey et al. 2005).

Habitat use in the freshwater phase for Atlantic salmon (*Salmo salar* L.) is well described (Finstad et al. 2011). Size-dependent habitat use, with inter-cohort habitat segregation between YOY (young-of-the-year) and older juveniles is especially well described. Observational studies have shown that YOY use low-velocity, shallow habitats close to the shoreline and bottom substrate (Bremset and Berg 1999; Girard et al. 2004; Mäki-Petäys et al. 2004), while parr (juvenile salmon after the fry stage), use habitats that are deeper, have higher velocity, coarser substratum size and are further from the river bank (Mäki-Petäys et al. 2004; Hedger et al. 2005; Linnansaari et al. 2010). Size-dependent habitat use can also occur within one year class, because of intra-cohort size differences (Huss et al. 2008).

Whether salmonids distribute between habitats according to IFD or IDD has been debated. Pure observational studies performed in natural river systems have suggested that juvenile Atlantic salmon habitat use is following an ideal free distribution rather than an ideal despotic distribution. (Girard et al. 2004; Hedger et al. 2005). In contrast, observational studies in artificial stream environments have found evidence for both IFD (Giannico and Healey 1999; Maclean et al. 2005) and IDD (Gotceitas and Godin 1992; Giannico and Healey 1999).
latter studies used fish of equal size, preventing size-dependent habitat use from occurring. By manipulating density in experimental riverine enclosures, Bult et al. (1999) got results indicating the presence of density-dependent habitat use, and thereby also IDD. However, these experiments were done on a coarse mesohabitat scale, without the possibility to detect interactions occurring on microhabitat scale. The different approaches of the studies mentioned above can explain the different outcomes, with some studies suggesting IFD as the most probable outcome of intra-specific interactions, whereas other studies suggesting IDD.

One issue that has received little attention in this debate is the effect of spatial scale with regards to usage of habitat types and how this is studied. Because of the spatial scale of a typical Atlantic salmon river the juveniles are not able to detect all profitable habitats (Gowan 2007). This is both due to dispersal limitations (Einum and Nislow 2005; Einum et al. 2006) and dispersal costs (Ruxton et al. 1999; Einum and Nislow 2005; Einum et al. 2006). Especially YOY have very restricted mobility (Webb et al. 2001; Einum and Nislow 2005), reflected by higher density of YOY close to nest sites (Teichert et al. 2011), which are often patchily distributed (Moir and Soulsby 1998; Finstad et al. 2010). Limited mobility confines the spatial scale over which individuals can be expected to behave according to IFD or IDD, and large scale studies become difficult to interpret. A mesohabitat scale with pool, riffle and run habitats (Bult et al. 1999; Hedger et al. 2005; Gibson et al. 2008), may then be too coarse, and a microhabitat scale should be more relevant.

In the present experimental study, the presence of IFD vs. IDD in juvenile Atlantic salmon was tested for on a small spatial scale. Density was manipulated, and how the use of shallow vs. deep habitats depends on juvenile body size was modelled, in addition to whether this interacts with density (as predicted from IDD) or not (as predicted from IFD). Habitat use is expected to vary under distinct environmental conditions. Thus to increase the generality of the results, the study was conducted at different times of the day, year, and in the presence/absence of potential predators/larger conspecifics.
Material and methods

Study site and experimental design

Experiments were performed during 2010, at the NINA Research Station at Ims (58° 54'N, 5° 57'E), South-western Norway. Four outdoor circular arenas were used in the experiments, and water for these was drawn from a nearby freshwater lake. To simulate a natural river system, a natural streambed substrate was used. Each arena had a water inlet and outlet, which were screened off with mesh, providing stream-channels in between them. Each of the stream-channels were divided into three sections, separated by screens, each with an area of about 10 m² and constant water flow through them (Fig. 1). About 50 % of each section was covered with white plastic above the water surface to provide overhead covers (Fig. 1). Differences in the water depth between the outer and inner walls of the stream-channels were created by a sloped riverbed, creating a shallow habitat on one side and a deeper habitat on the other (Table 1). Chosen water depths and velocity was in the preferred range of Atlantic salmon juveniles (Heggenes et al. 1999), though these variables did slightly vary between sections. Section effects were taken into account in the statistical analyses. To observe habitat use at the end of a trial, the shallow and deep parts of the sections were separated by lowering escape proof screens that were installed longitudinally along the stream. The screens were held in place above the water surface with two bolts during a trial, which could be removed by pulling two strings without disturbing the fish. This caused the screen to drop rapidly, and hence preventing further movement of fish between the two habitat types.

Pilot experiment

A summer experiment was conducted during 14 June - 29 June, and an autumn experiment during 31 August - 17 September. A pilot experiment was conducted prior to the summer experiment to determine the time required for each trial to obtain a stable habitat use distribution. After sampling at different trial durations, a time of approximately 20 hours was chosen due to no further change in habitat use distribution after this amount of time. Observational studies also confirmed that the fish behaved normally after this time period. In these studies a random focal fish was observed 10 minutes every hour, and feeding attempts were recorded. Fish started feeding consistently after five hours in seven out of seven
observations. Four out of seven observational studies showed that fish was feeding consistently after three hours.

Experimental procedures

Because of few dark hours in the summer experiment, only day time trials were performed in these, whereas both day- and night-time trials were performed in the autumn experiment. When performing night trials, the arenas were stocked at about 02:00 am, and closed and fished again at 00:00 the next night, when it already had been completely dark for about three hours. The same procedures used for daytime were used at night-time, except for use of additional light during sampling.

Both YOY and 1+ (one year old) hatchery reared Atlantic salmon, originating from the local stock in river Imsa, were used in both experiments, with body length ranging from 33 to 235 mm. The YOY were start fed at two different dates in May, creating a desirable intra-cohort size variation. Mean body length of the YOY was 47 mm (range 38 – 58 mm) and 82 mm (range 64 – 103 mm) in summer and autumn respectively. Mean body length of the 1+ was 169 mm (range 161 - 178 mm) and 206 mm (range 201 – 212 mm) in summer and autumn respectively.

Stocking of arenas depended on the type of treatment (Table 2), with one section being one replicate. Each treatment was performed equally many times in each arena to neutralize section differences. For different treatments, two distinct densities and the presence/absence of large fish (1+) were used, both at day and night-time. One YOY per m² was used as low density and three YOY per m² was used as high density. The chosen densities were within the range of densities found in wild populations of juvenile salmonids (Wankowski and Thorpe 1979; Grant and Imre 2005; Imre et al. 2005). In treatments with large fish present, two individuals were used, both at high and low densities.

Recapture of fish was done by lowering the screens followed by electrofishing. Habitat choice was determined by counting the number of salmon in shallow versus deep habitat in each section. Body length (fork length, ±1mm) was measured immediately after fishing when the fish were still slightly stunned.
Statistics

The influence of density, body length, day or night (only for autumn experiments), and the presence of large fish on the habitat choice (deep/shallow), of individual YOY Atlantic salmon was modelled using a generalized linear mixed model (GLMM), with section and replicate (nested within section) as random factors. The function `lmer` with a binomial error distribution from the `lme4` package was used (Bates and Maechler 2010). Separate models were run for the summer and autumn experiments. Thus, the full models can be written as:

$$PS_{ijk} = \alpha + \beta_1 D_k + \beta_2 L_k + \beta_3 B_i + \beta_4 D_k L_k + \beta_5 B_i D_k + \beta_6 B_i L_k + a_j + a_k + \epsilon_i$$

$$PA_{ijk} = \alpha + \beta_1 T_k + \beta_2 D_k + \beta_3 L_k + \beta_4 B_i + \beta_5 T_k D_k + \beta_6 T_k L_k + \beta_7 T_k B_i + \beta_8 D_k L_k + \beta_9 B_i D_k + \beta_{10} B_i L_k + a_j + a_k + \epsilon_i$$

where $PS$ and $PA$ is the probability of an individual being in the deep habitat in summer and autumn, respectively. $D$ is the density, $L$ is large fish present, $B$ is the body length and $T$ is the time of day. Indices $i$, $j$ and $k$ represent individuals, sections and replicates, respectively. $\alpha$ and $\beta$ are the fixed parameters, $a_j$ and $a_k$ are the random intercepts for section and replicate respectively, and $\epsilon_i$ is the random error structure.

After fitting the two full models shown above, the residuals were plotted using the function `plot.logistic.fit.fnc` from the `languageR` package (Baayen 2006) and the function `cut2` from the `Design` package (Harrel Jr 2009). The residuals showed no evidence of heteroscedasticity. Evaluation of the fixed effects and removal of two-way interactions and main terms was done by sequentially backward removal of terms, according to (Zuur et al. 2009). The final full model was then refitted with restricted maximum likelihood estimation (REML) and validated. The statistical analyses were done using R, v. 2.11.1. (R Development Core Team 2010).
Results

Preferred habitat

In general, YOY preferred the deep habitat, with on average 85.3% of the YOY being in the deep habitat in summer, and 82.3% in autumn. The 1+ were seldomly using the shallow habitat, with only three out of 272 fish being found in the shallow habitat in summer, 14 of 188 fish in autumn, nine of them at night-time.

Summer experiment

During summer, habitat use of YOY was influenced by their body length and the presence of larger 1+ salmon. Both the main term density (p = 0.58) and the interaction density x body length (p = 0.074) were removed from the model without causing a significant decrease in log-likelihood, implying that density did not have any effect on size-dependent habitat use. The interaction between body length and 1+ present was the only one remaining in the model after the sequential backward removal procedure (Table 3). These results imply that in the absence of 1+, the YOY had a higher probability for being in the deep habitat the larger they were. With the presence of 1+, there was a trend (p < 0.001) showing that the larger the YOY, the less likely it was that they would be found in the deep habitat (Fig. 2).

Autumn experiment

From the autumn experiment, both the two-way interactions time x density and time x 1+ present, and the main term body length proved significant (Table 3). This implies that both time of day, density, body length and the presence of 1+ affected the habitat use of the YOY. Also in the autumn model the interaction density x body length was removed (p = 0.229). At daytime there was a lower probability for finding a YOY in the deep habitat when there were 1+ present, than if they were absent, although this probability increased with increasing body length (Fig. 3). Independent of the presence/absence of 1+, low density decreased the probability for a YOY being in the deep habitat, in comparison to high density (Fig. 3).

At night-time there was also a lower probability for a YOY individual being in the deep habitat when there were 1+ present, and as during daytime this probability increased with
increasing body length (Table 3, Fig. 4). Independent of the presence/absence of 1+, high density slightly decreased the probability for a YOY being in the deep habitat, in comparison to low density. Night-time habitat use also differed from the daytime habitat use in the overall probability for being in the deep habitat. Independent of treatment, YOY were less likely to be in the deep habitat at night-time compared to daytime (Table 3). Nevertheless, the most evident result in autumn was that independent of treatment, there was an increasing probability for a YOY salmon being found in the deep habitat with increasing body length.
Discussion

By conducting seasonal day and night experiments in stream-channels where both density and the presence/absence of an older cohort were manipulated, there was found significant evidence for size-dependent habitat use among YOY Atlantic salmon. For both juvenile cohorts, the deep habitat was the preferred habitat, while the shallow habitat was mostly avoided. However, juvenile habitat use differed between seasons and between day and night. Amongst YOY there was an increasing use of deep habitat with increasing body length. For all treatments, there was significantly less YOY utilizing deep habitat if the older cohort was present. The proportional utilization of deep habitat remained nearly constant with a change in density.

The interaction between density and body length did not have a significant effect on YOY habitat use, neither in summer nor in autumn. In addition, there was no and weak effects of density in summer and autumn, respectively. This suggests that size-dependent habitat use among YOY was not caused by direct interactions. Under IDD, one would predict a decreased proportional utilization of the preferred habitat, and a stronger effect of body size on habitat use with increasing density, which was not the case.

Even though juvenile Atlantic salmon show territorial behaviour (Grant and Kramer 1990; Cutts et al. 1999; Valdimarsson and Metcalfe 2001) and thereby carry out interference competition (Begon et al. 2006), exploitative competition over food can occur among juveniles in a stream system (Imre et al. 2005; Einum et al. 2011; Kvingedal and Einum 2011). One type of exploitative competition, where food abundance for individuals in one part of a habitat is depressed by individuals located in another part of the habitat (Begon et al. 2006), is shadow competition. Foragers closest to the food source reduce the abundance of food for individuals located further away. Shadow competition is mostly demonstrated in invertebrate species (Wilson 1974; Lubin et al. 2001), though also in some vertebrate species like sea trout (Salmo trutta L.) (Elliott 2002). Since juvenile Atlantic salmon are mainly feeding on drifting invertebrates (Keenleyside 1962) they could also be a subject to this type of exploitative competition (Imre et al. 2005; Einum et al. 2011; Kvingedal and Einum 2011), possibly on a small spatial scale (Einum et al. 2011). The results from the present experiments, showing that size-dependent habitat use among YOY was in accordance with IFD despite a body size advantage during direct interactions, can be explained by the presence of exploitative competition. Under this scenario, an individual may choose to move to the less
preferred, shallow habitat with increasing density, even if it is large and able to defend a preferred territory. This is because such a defence does not prevent negative effects of upstream individuals on its prey encounter rate.

In the summer experiment, there was found clear evidence for size-dependent habitat use among the YOY, both with and without 1+ present. Without potential predators/larger conspecifics present there was a higher chance for a YOY being in the deep habitat the larger it was, as expected. Contrary, with 1+ present, there was a higher chance for a YOY being in the deep habitat the smaller it was. This reverse pattern can be due to a higher intensity of competitive interactions with the 1+ for larger YOY (Einum and Kvingedal in press). Thus, large YOY were forced to utilize the less preferred shallow habitat, where no 1+ competitors were present.

Both at day and night in autumn there was a clear presence of size-dependent habitat use, with larger YOY more often utilizing deep habitat than smaller individuals. Furthermore, the overall decrease of YOY utilizing deep habitat at night in autumn was according to previous studies on juvenile habitat use (Harwood et al. 2001; Railsback et al. 2005; Linnansaari et al. 2010). Such a shift in habitat use is thought to enhance visual foraging (Metcalfe et al. 1997), since juvenile Atlantic salmon are visual foragers (Wilzbach et al. 1986) that attempt to improve their night-time vision in shallow water with less riffles (Metcalfe et al. 1997). A shift to more usage of shallow habitat can also be due to higher abundance of drifting invertebrates at night (Fraser and Metcalfe 1997; Metcalfe et al. 1999), or because of decreased predation by visual predators (Valdimarsson and Metcalfe 1998; Breau et al. 2007). Like in summer, YOY individuals had a lower probability for being in the deep habitat if there were 1+ present. Contrary to the summer experiments with 1+ present, there was an expected size-dependent distribution in autumn, with the largest YOY utilizing deep habitat, also if 1+ were present. This could be caused by small YOY vacating deep habitat due to perceived predation risk from larger 1+. Density had a slight effect on juvenile habitat choice. However, at daytime, there was a higher chance for a YOY being in the preferred deep habitat at high densities than at low densities. In contrast, at night-time there was a slight effect in the opposite direction. Thus, due to the weak and inconsistent effect of density these particular results appear inconclusive.
The proportional utilization of deep habitat remained nearly constant with a change in YOY density. Thus, without larger salmon present, YOY were distributed according to IFD, and not IDD, with different sized individuals choosing different habitat according to environmental factors like season and time of day. In contrast, the effect of 1+ on the distribution of YOY suggests that interactions between age-classes may more appropriately be described as leading to IDD. Whereas 1+ stayed predominantly in the deep habitat, they caused a decreased use of this habitat by YOY. The large body size of the 1+ may have scared the YOY out of the deep habitat, especially the smallest ones, because of a higher fighting ability with increasing body size (Frey and Miller 1972). YOY may even have viewed 1+ as potential predators, or at least the 1+ would have the ability to inflict serious bite injuries. This could be a probable explanation since avoidance of habitats because of threats from piscivorous fishes is well known, also among other fish species (Harvey and Stewart 1991; Vehanen and Hamari 2004). The findings in this study suggest that in natural salmonid populations, both IFD and IDD may occur simultaneously, with their relative importance depending on the range of body sizes present.
Acknowledgments

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Tables

Table 1 Physical features of experimental arenas, with mean of mean and SD values for the different sections, N = 80 measurements equidistantly spaced across transects and SD is standard deviation for mean values among sections. “Depth” is total water depth, “Current bottom” is water velocity two cm above bottom substrate and “Current 60%” is water velocity 60% above bottom substrate.

<table>
<thead>
<tr>
<th></th>
<th>Mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Deep habitat</strong></td>
<td></td>
</tr>
<tr>
<td>Depth (cm)</td>
<td>31.20 (3.39)</td>
</tr>
<tr>
<td>Current bottom (m/sec)</td>
<td>0.06 (0.03)</td>
</tr>
<tr>
<td>Current 60% (m/sec)</td>
<td>0.10 (0.03)</td>
</tr>
<tr>
<td><strong>Shallow habitat</strong></td>
<td></td>
</tr>
<tr>
<td>Depth (cm)</td>
<td>18.00 (3.16)</td>
</tr>
<tr>
<td>Current bottom (m/sec)</td>
<td>0.03 (0.01)</td>
</tr>
<tr>
<td>Current 60% (m/sec)</td>
<td>0.05 (0.01)</td>
</tr>
</tbody>
</table>
Table 2 Summer and autumn experiments with treatments and amount of replicates of each treatment. Treatments were low/high density of YOY, presence/absence of large fish and time of day.

<table>
<thead>
<tr>
<th>Season</th>
<th>Density</th>
<th>1+</th>
<th>Time of day</th>
<th># of replicates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer</td>
<td>Low</td>
<td>Absent</td>
<td>Day</td>
<td>21</td>
</tr>
<tr>
<td>Summer</td>
<td>High</td>
<td>Absent</td>
<td>Day</td>
<td>21</td>
</tr>
<tr>
<td>Summer</td>
<td>Low</td>
<td>Present</td>
<td>Day</td>
<td>61</td>
</tr>
<tr>
<td>Summer</td>
<td>High</td>
<td>Present</td>
<td>Day</td>
<td>63</td>
</tr>
<tr>
<td>Autumn</td>
<td>Low</td>
<td>Absent</td>
<td>Day</td>
<td>20</td>
</tr>
<tr>
<td>Autumn</td>
<td>High</td>
<td>Absent</td>
<td>Day</td>
<td>21</td>
</tr>
<tr>
<td>Autumn</td>
<td>Low</td>
<td>Present</td>
<td>Day</td>
<td>24</td>
</tr>
<tr>
<td>Autumn</td>
<td>High</td>
<td>Present</td>
<td>Day</td>
<td>24</td>
</tr>
<tr>
<td>Autumn</td>
<td>Low</td>
<td>Absent</td>
<td>Night</td>
<td>24</td>
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<td>Autumn</td>
<td>High</td>
<td>Absent</td>
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<td>Autumn</td>
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<td>Present</td>
<td>Night</td>
<td>24</td>
</tr>
<tr>
<td>Autumn</td>
<td>High</td>
<td>Present</td>
<td>Night</td>
<td>24</td>
</tr>
</tbody>
</table>
Table 3 Summary of best general linear mixed models, for summer and autumn experiments, describing the probability of a YOY Atlantic salmon using the deep habitat. n = 3133 individuals from 166 experiments and n = 3581 individuals from 185 experiments in summer and autumn, respectively.

<table>
<thead>
<tr>
<th></th>
<th>Estimate ± SE</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Summer model</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Random effects</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Serial number</td>
<td>0.15 (0.39)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Section number</td>
<td>0.19 (0.44)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Fixed effects</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-2.23 ± 0.95</td>
<td>-2.36</td>
<td>0.02</td>
</tr>
<tr>
<td>Body length</td>
<td>0.11 ± 0.02</td>
<td>5.11</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1+ present</td>
<td>4.00 ± 1.00</td>
<td>3.99</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Body length x 1+ present</td>
<td>-0.12 ± 0.02</td>
<td>-5.31</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><strong>Autumn model</strong></td>
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<td></td>
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<tr>
<td><strong>Random effects</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Serial number</td>
<td>0.51 (0.71)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Section number</td>
<td>0.10 (0.32)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Fixed effects</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Intercept</td>
<td>0.95 ± 0.45</td>
<td>2.11</td>
<td>0.03</td>
</tr>
<tr>
<td>Time$^1$</td>
<td>-1.55 ± 0.34</td>
<td>-4.61</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Density$^2$</td>
<td>0.66 ± 0.26</td>
<td>2.57</td>
<td>0.01</td>
</tr>
<tr>
<td>1+ present</td>
<td>-1.47 ± 0.28</td>
<td>-5.33</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Body length</td>
<td>0.03 ± 4.4e-03</td>
<td>6.19</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Time$^1$ x Density$^2$</td>
<td>-0.76 ± 0.32</td>
<td>-2.35</td>
<td>0.02</td>
</tr>
<tr>
<td>Time$^1$ x 1+ present</td>
<td>0.74 ± 0.34</td>
<td>2.20</td>
<td>0.03</td>
</tr>
</tbody>
</table>

$^1$ Estimated parameter is for night

$^2$ Estimated parameter is for high density
Figure legends

**Fig. 1** One of four arenas used for the experiments. Each stream-channel had three sections (see 1, 2, 3), screens separating deep and shallow habitat within each of these, plastic covers, and constant water flow.

**Fig. 2** The probability for a YOY Atlantic salmon being in the deep part of a section in summer, in relation to its body length in millimetre. Dashed and solid line represent without and with 1+ present, respectively.

**Fig. 3** The probability for a YOY Atlantic salmon being in the deep part of a section in autumn at daytime, in relation to its body length in millimetre. Dotted line represents high density without 1+ present, solid line represents low density without 1+ present, long-dashed line represents high density with 1+ present and dot-dashed thick line represents low density with 1+ present.

**Fig. 4** The probability for a YOY Atlantic salmon being in the deep part of a section in autumn at night, in relation to its body length in millimetre. Solid line represents low density without 1+ present, dotted line represents high density without 1+ present, dot-dashed thick line represents low density with 1+ present and long-dashed line represents high density with 1+ present.
Figures

Fig. 1
Fig. 2

![Graph showing the relationship between depth (P) and body length (mm). The graph depicts two lines: one that rises and one that falls.](image)
Fig. 3
Fig. 4

A graph showing the relationship between body length (mm) and $P_{\text{deep}}$. The graph includes multiple curves that illustrate different scenarios or conditions. The $y$-axis represents $P_{\text{deep}}$ values ranging from 0.5 to 1.0, while the $x$-axis represents body length in millimeters, ranging from 50 to 120.