NTNU
Norwegian University of
Science and Technology

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

Frøydis Bolme Hamnes

Biology
Submission date: May 2011
Supervisor: Sigurd Einum, IBI
Co-supervisor: Ole Kristian Berg, IBI

Norwegian University of Science and Technology
Department of Biology

Preface

This thesis is a part of the Environmental impacts of hydropeaking (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*.

Frøydis Bolme Hamnes

Trondheim

May 2011

Table of contents

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). These 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 m^2 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 m^2 was used as low density and three YOY per m^2 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:

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

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

, 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. α and β are the fixed parameters, a_j and a_k are the random intercepts for section and replicate respectively, and ε_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

I thank my supervisors Sigurd Einum and Ole Kristian Berg for valuable comments on the manuscript and guidance with the statistical analyses. I also thank Michael Puffer, Vidar Bentsen and the staff at NINA research station, Ims, for great collaboration during the experimental work. The experiments were funded by the EnviPEAK project at CEDREN. The study was conducted according to national regulations for the treatment and welfare of experimental animals.

References

Armstrong JD, Holm CF, Gilvear DJ (2002) Holding station against the flow: a reply to Ibbotson & Dunbar. Journal of Fish Biology 61:308-312

Baayen RH (2006) Practical Data Analysis for the Language Sciences with R. University of Nijmegen http://magnuson.psy.uconn.edu/mirman/R/Baayen.pdf

Bachman RA (1984) Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113:1-32

Bates D, Maechler M (2010) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-37 http://lme4.r-forge.r-project.org/

Begon M, Townsend CR, Harper JL (2006) Ecology. From individuals to ecosystems, 4 edn. Blackwell Publishing

Breau C, Weir LK, Grant JWA (2007) Individual variability in activity patterns of juvenile Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick. Canadian Journal of Fisheries and Aquatic Sciences 64:486-494

Bremset G, Berg OK (1999) Three-dimensional microhabitat use by young pool-dwelling Atlantic salmon and brown trout. Animal Behaviour 58:1047-1059

Bult TP, Riley SC, Haedrich RL, Gibson RJ, Heggenes J (1999) Density-dependent habitat selection by juvenile Atlantic salmon (*Salmo salar*) in experimental riverine habitats. Canadian Journal of Fisheries and Aquatic Sciences 56:1298-1306

Bystrom P, Andersson J, Persson L, De Roos AM (2004) Size-dependent resource limitation and foraging-predation risk trade-offs: growth and habitat use in young Arctic char. Oikos 104:109-121

Bystrom P, Persson L, Wahlstrom E, Westman E (2003) Size- and density-dependent habitat use in predators: consequences for habitat shifts in young fish. Journal of Animal Ecology 72:156-168

Cutts CJ, Brembs B, Metcalfe NB, Taylor AC (1999) Prior residence, territory quality and life-history strategies in juvenile Atlantic salmon (*Salmo salar* L.). Journal of Fish Biology 55:784-794

Davey AJH, Hawkins SJ, Turner GF, Doncaster CP (2005) Size-dependent microhabitat use and intraspecific competition in *Cottus gobio*. Journal of Fish Biology 67:428-443

Einum S, Kvingedal E (2011) Relative importance of size-based competitive ability and degree of niche overlap in inter-cohort competition of Atlantic salmon (*Salmo salar*) juveniles. Canadian Journal of Fisheries and Aquatic Sciences 68:1-8

Einum S, Nislow KH (2005) Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. Oecologia 143:203-210

Einum S, Robertsen G, Nislow KH, McKelvey S, Armstrong JD (2011) The spatial scale of density-dependent growth and implications for dispersal from nests in juvenile Atlantic salmon. Oecologia 165:959-969

Einum S, Sundt-Hansen L, Nislow KH (2006) The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. Oikos 113:489-496

Elliott JM (2002) Shadow competition in wild juvenile sea-trout. Journal of Fish Biology 61:1268-1281

Finstad AG, Armstrong JD, Nislow KH (2011) Freshwater habitat requirements of Atlantic salmon. In: Aas Ø, Einum S, Klemetsen A, Skurdal J (eds) Atlantic salmon ecology, chapter 3. 1 edn. Wiley-Blackwell

Finstad AG, Einum S, Saettem LM, Hellen BA (2010) Spatial distribution of Atlantic salmon (*Salmo salar*) breeders: among- and within-river variation and predicted consequences for offspring habitat availability. Canadian Journal of Fisheries and Aquatic Sciences 67:1993-2001

Fraser NHC, Metcalfe NB (1997) The costs of becoming nocturnal: Feeding efficiency in relation to light intensity in juvenile Atlantic Salmon. Functional Ecology 11:385-391

Fretwell SD, Lucas HL (1970) On territorial behaviour and other factors influencing distribution in birds. Acta Biotheoretica 19:16-36

Frey DF, Miller RJ (1972) Establishment of dominance relationships in blue gourami, *Trichogaster trichopterus* (pallas). Behaviour 42:8-62

Garcia-Berthou E (2001) Size- and depth-dependent variation in habitat and diet of the common carp (*Cyprinus carpio*). Aquatic Sciences 63:466-476

Giannico GR, Healey MC (1999) Ideal free distribution theory as a tool to examine juvenile coho salmon (*Oncorhynchus kisutch*) habitat choice under different conditions of food abundance and cover. Canadian Journal of Fisheries and Aquatic Sciences 56:2362-2373

Gibson AJF, Bowby HD, Amiro PG (2008) Are wild populations ideally distributed? Variations in density-dependent habitat use by age class in juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 65:1667-1680

Girard IL, Grant JWA, Steingrímsson SÓ (2004) Foraging, growth, and loss rate of young-of-the year Atlantic salmon (*Salmo salar*) in relation to habitat use in Catamaran Brook, New Brunswick. Can. J. Fish. Aquat. Sci. 61:2339–2349

Gotceitas V, Godin JGJ (1992) Effects of location of food delivery and social-status on foraging-site selection by juvenile Atlantic salmon. Environmental Biology of Fishes 35:291-300

Gowan C (2007) Short-term cues used by foraging trout in a California stream. Environmental Biology of Fishes 78:317-331

Grant JWA, Imre I (2005) Patterns of density-dependent growth in juvenile stream-dwelling salmonids. Journal of Fish Biology 67:100-110

Grant JWA, Kramer DL (1990) Territory size as a predictor of the upper limit to population-density of juvenile salmonids in streams. Canadian Journal of Fisheries and Aquatic Sciences 47:1724-1737

Gustafsson P, Bergman E, Greenberg LA (2010) Functional response and size-dependent foraging on aquatic and terrestrial prey by brown trout (*Salmo trutta* L.). Ecology of Freshwater Fish 19:170-177

Hacker SD, Steneck RS (1990) Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal-amphipod. Ecology 71:2269-2285

Harrel Jr F, E. (2009) Design: Design package. R package version 2.3-0 http://biostat.mc.vanderbilt.edu/s/Design

Harvey BC, Stewart AJ (1991) Fish size and habitat depth relationships in headwater streams. Oecologia 87:336-342

Harwood AJ, Metcalfe NB, Armstrong JD, Griffiths SW (2001) Spatial and temporal effects of interspecific competition between Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in winter. Canadian Journal of Fisheries and Aquatic Sciences 58:1133-1140

Hedger RD, Dodson JJ, Bergeron NE, Caron F (2005) Habitat selection by juvenile Atlantic salmon: the interaction between physical habitat and abundance. Journal of Fish Biology 67:1054-1071

Heggenes J, Bagliniere JL, Cunjak RA (1999) Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in heterogeneous streams. Ecology of Freshwater Fish 8:1-21

Hughes NF (1992) Ranking of feeding positions by drift-feeding arctic grayling (*Thymallus arcticus*) in dominance hierarchies. Canadian Journal of Fisheries and Aquatic Sciences 49:1994-1998

Huss M, Bystrom P, Persson L (2008) Resource heterogeneity, diet shifts and intra-cohort competition: effects on size divergence in YOY fish. Oecologia 158:249-257

Imre I, Grant JWA, Cunjak RA (2005) Density-dependent growth of young-of-the-year atlantic salmon *Salmo salar* in Catamaran Brook, New Brunswick. Journal of Animal Ecology 74:508-516

Keenleyside MHA (1962) Skin-diving observations of Atlantic salmon and brook trout in the Miramichi river, New-Brunswick. Journal of the Fisheries Research Board of Canada 19:625-634

Kvingedal E, Einum S (2011) Intracohort and intercohort spatial density dependence in juvenile brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 68:115-121

Linnansaari T, Keskinen A, Romakkaniemi A, Erkinaro J, Orell P (2010) Deep habitats are important for juvenile Atlantic salmon *Salmo salar* L. in large rivers. Ecology of Freshwater Fish 19:618-626

Lubin Y, Henschel JR, Baker MB (2001) Costs of aggregation: shadow competition in a sit-and-wait predator. Oikos 95:59-68

Maclean A, Huntingford FA, Ruxton GD, Morgan IJ, Hamilton J, Armstrong JD (2005) Testing the assumptions of the ideal despotic distribution with an unpredictable food supply: experiments in juvenile salmon. Journal of Animal Ecology 74:214-225

Mäki-Petäys A, Erkinaro J, Niemela E, Huusko A, Muotka T (2004) Spatial distribution of juvenile Atlantic salmon (*Salmo salar*) in a subarctic river: size-specific changes in a strongly seasonal environment. Canadian Journal of Fisheries and Aquatic Sciences 61:2329-2338

Metcalfe NB, Fraser NHC, Burns MD (1999) Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. Journal of Animal Ecology 68:371-381

Metcalfe NB, Valdimarsson SK, Fraser NHC (1997) Habitat profitability and choice in a sit-and-wait predator: juvenile salmon prefer slower currents on darker nights. Journal of Animal Ecology 66:866-875

Moir HJ, Soulsby C (1998) Hydraulics and sedimentary characteristics of habitat utilized by Atlantic salmon for spawning in the Girnock Burn, Scotland. Fisheries Management and Ecology 5:241-254

Railsback SF, Harvey BC, Hayse JW, LaGory KE (2005) Tests of theory for diel variation in salmonid feeding activity and habitat use. Ecology 86:947-959

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria http://www.R-project.org

Ruxton GD, Armstrong JD, Humphries S (1999) Modelling territorial behaviour of animals in variable environments. Animal Behaviour 58:113-120

Schlosser IJ (1987) The role of predation in age-related and size-related habitat use by stream fishes. Ecology 68:651-659

Sweitzer RA, Berger J (1992) Size-related effects of predation on habitat use and behavior of porcupines (*Erethizon dorsatum*). Ecology 73:867-875

Teichert MAK, Foldvik A, Forseth T, Ugedal O, Einum S, Finstad AG, Hedger RD, Bellier E (2011) Effects of spawning distribution on juvenile Atlantic salmon (*Salmo salar*) density and growth. Canadian Journal of Fisheries and Aquatic Sciences 68:43-50

Valdimarsson SK, Metcalfe NB (1998) Shelter selection in juvenile Atlantic salmon or why do salmon seek shelter in winter? Journal of Fish Biology 52:42-49

Valdimarsson SK, Metcalfe NB (2001) Is the level of aggression and dispersion in territorial fish dependent on light intensity? Animal Behaviour 61:1143-1149

Vehanen T, Hamari S (2004) Predation threat affects behaviour and habitat use by hatchery brown trout (*Salmo trutta* L.) juveniles. Hydrobiologia 525:229-237

Wankowski JWJ, Thorpe JE (1979) Spatial-distribution and feeding in Atlantic salmon, *Salmo salar* L. juveniles. Journal of Fish Biology 14:239-247

Wauters LA, Gurnell J, Preatoni D, Tosi G (2001) Effects of spatial variation in food availability on spacing behaviour and demography of Eurasian red squirrels. Ecography 24:525-538

Webb JH, Fryer RJ, Taggart JB, Thompson CE, Youngson AF (2001) Dispersion of Atlantic salmon (*Salmo salar*) fry from competing families as revealed by DNA profiling. Canadian Journal of Fisheries and Aquatic Sciences 58:2386-2395

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics 15:393-425

Werner EE, Gilliam JF, Hall DJ, Mittelbach GG (1983) An experimental test of the effects of predation risk on habitat use in fish Ecology 64:1540-1548

Werner EE, Hall DJ (1988) Ontogenetic habitat shifts in bluegill - the foraging rate predation risk trade-off. Ecology 69:1352-1366

Wilson DS (1974) Prey capture and competition in the ant lion. Biotropica 6:187-193

Wilzbach MA, Cummins KW, Hall JD (1986) Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology 67:898-911

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

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.

	Mean ± SD
Deep habitat	
Depth (cm)	31.20 (3.39)
Current bottom (m/sec)	0.06 (0.03)
Current 60% (m/sec)	0.10 (0.03)
Shallow habitat	
Depth (cm)	18.00 (3.16)
Current bottom (m/sec)	0.03 (0.01)
Current 60% (m/sec)	0.05 (0.01)

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.

Season	**Density**	**1+**	**Time of day**	**# of replicates**
Summer	Low	Absent	Day	21
Summer	High	Absent	Day	21
Summer	Low	Present	Day	61
Summer	High	Present	Day	63
Autumn	Low	Absent	Day	20
Autumn	High	Absent	Day	21
Autumn	Low	Present	Day	24
Autumn	High	Present	Day	24
Autumn	Low	Absent	Night	24
Autumn	High	Absent	Night	24
Autumn	Low	Present	Night	24
Autumn	High	Present	Night	24

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.

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

[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

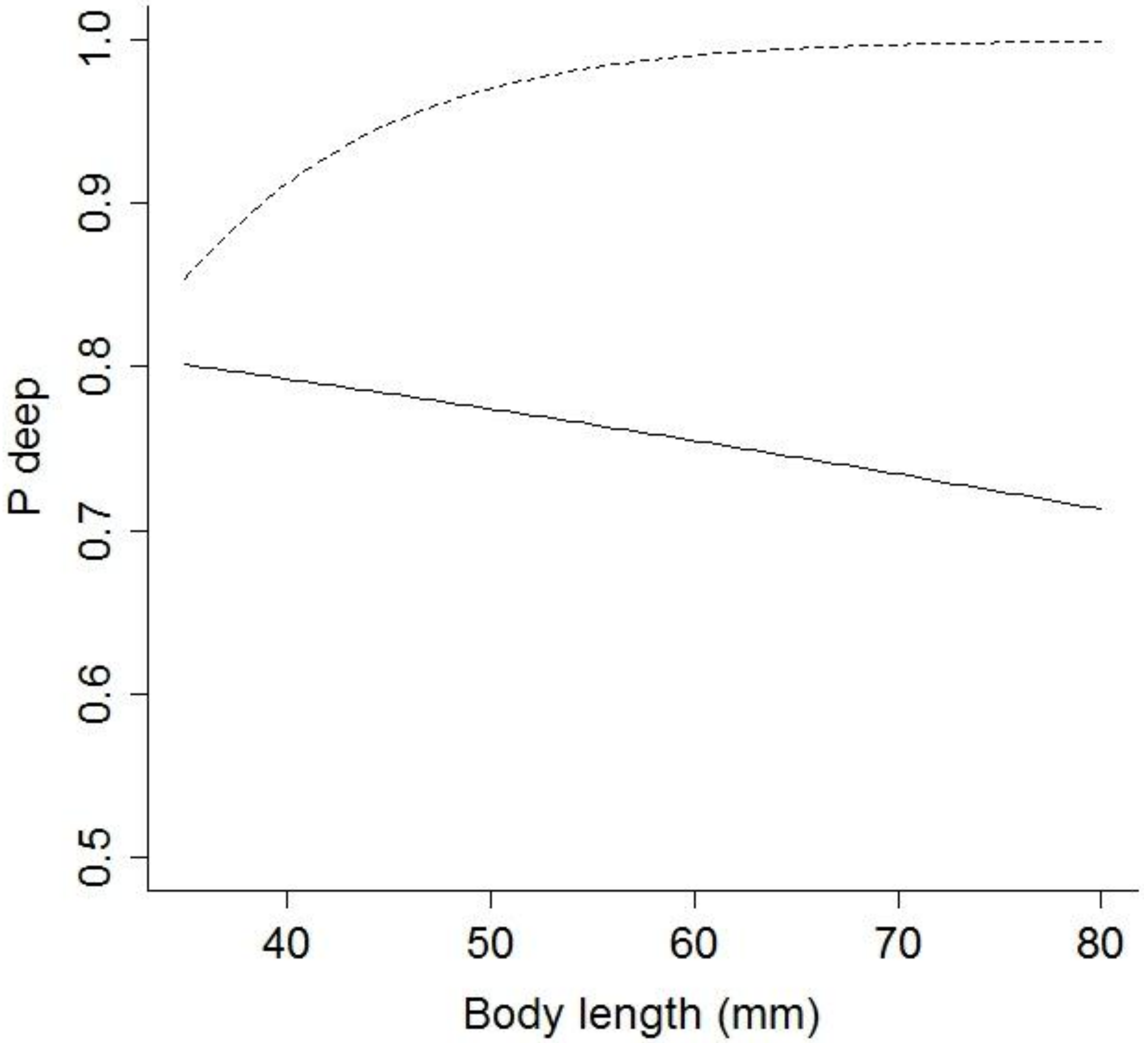

Fig. 3

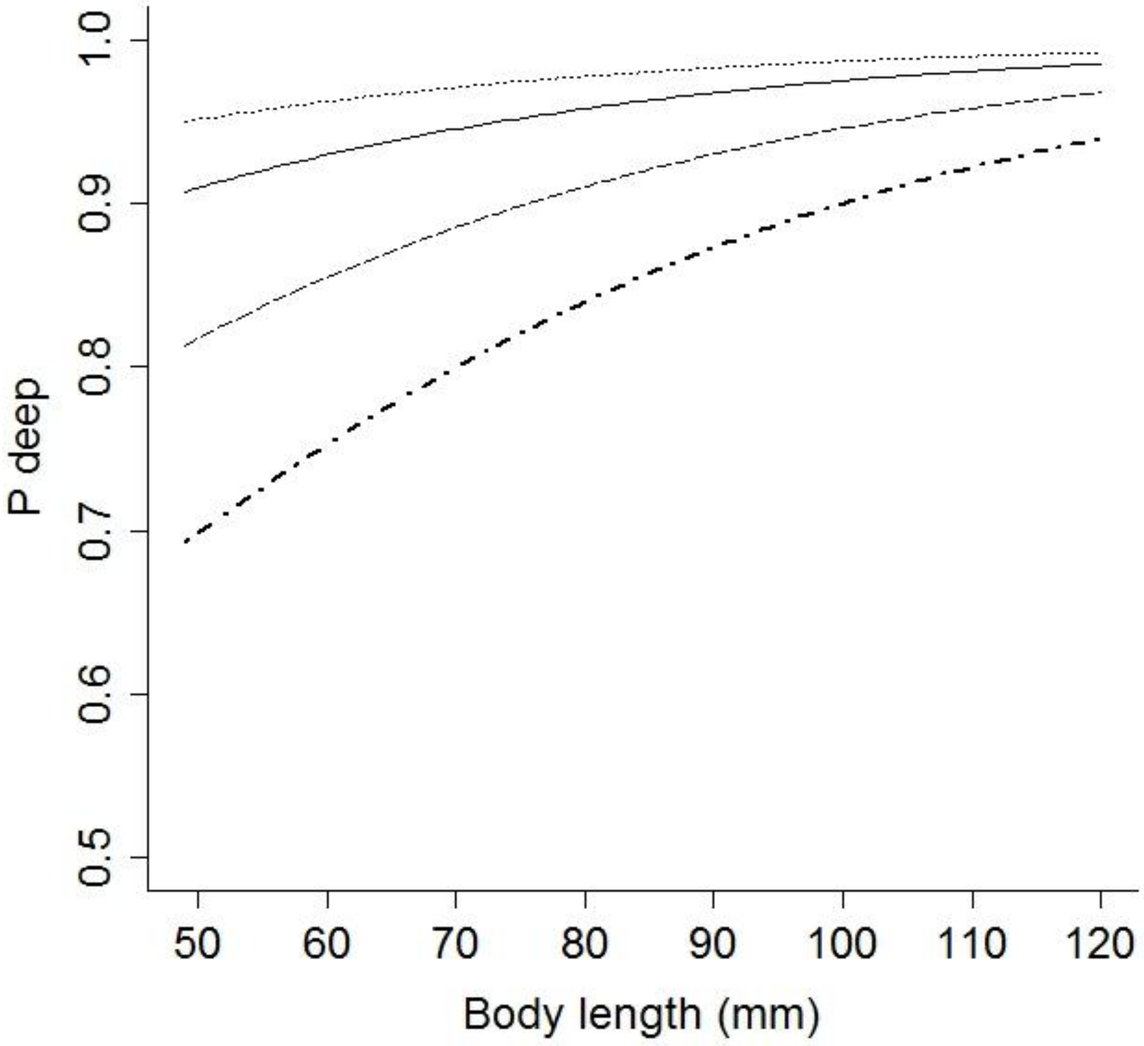

Fig. 4