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Desnity dependent habitat use of Atlantic salmon, Salmo salar L.- stranding in hydropower rivers

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Density dependent habitat use of Atlantic salmon, *Salmo salar* L. - stranding in hydropower rivers

Master's thesis

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Abstract

An experiment was performed in four artificial stream channels during summer and autumn to investigate the effects of biotic and abiotic factors on habitat choice of juvenile Atlantic salmon (*Salmo salar*). To investigate factors determining habitat choice, the stream channels had sloped river beds creating two distinct habitats (shallow and deep). The main factor, *large Atlantic salmon present* (large present), was the most important factor affecting juvenile habitat choice during summer experiments. During autumn experiments, the two main factors *large Atlantic salmon present* and *time of day* (exclusive for autumn experiments), were important factors affecting habitat choice. The highly significant effect on juvenile habitat choice of having a large Atlantic salmon present identifies inter-cohort competition and/or risk of predation as important factors affecting habitat choice in juveniles. This, in turn, could have direct or indirect effects on juvenile survival and growth. The differences between proportions of fish in the deep between night and day highlights a diel change in habitat use by juveniles.

Introduction

Many organisms of different species have to compete for limited resources at one, or several, stages during their life cycle. Individuals will thus have to compete with other individuals of the same, and of different, species for that given resource. The strength of the intra-specific (within species) competition will depend on population density, habitat availability and the given competitive interactions within the population (Campbell & Reece, 2005). Individuals incapable of acquiring such limited resources, like shelters/territories, will have reduced fitness compared to individuals inhabiting suitable territories (Andreo *et al.,* 2009; Hasegawa & Yamamoto, 2010)

A suitable territory/habitat is a defendable, limited resource. Because of the limitations in regards to resources like habitat availability, many organisms have developed territoriality (Stamps & Tollesrud, 1983). A territorial individual typically inhabits a preferred area and defends it against conspecifics and/or other species. When competing for territories, individuals physically interact with one another and a more dominant individual will usually chase a less dominant individual away (Mathis, 1990). The size of a given individual often plays an important role when considering competitive ability, where larger size leads to competitive dominance (Schwinning & Weiner, 1998; Schmitt & Holbrook, 1999; Serrano-Meneses *et al.,* 2007). Inter-cohort competition, in such cases, will favour older cohorts since they have a larger body size than younger age-classes (Maki-Petays *et al.*, 2004). Increased density will in turn lead to increased intensity of the competition for habitat. The amount and/or quality of the habitat can thus contribute to setting the boundaries for the population-size (carrying capacity), and the population density will have strong influence on the intensity of the competition for a suitable patch within the habitat. Habitat quality, together with high

population density, can in this way act as a limiting factor on the population (Clark & Hare, 2002).

A well documented example of such territorial individuals, where inter-cohort competition for limited habitat plays an important role in regulating populations, are Atlantic salmon (*Salmo salar)* juveniles (Finstad *et al.,* 2008; Gibson *et al.,* 2008; Steingrimsson & Grant, 2008). A juvenile Atlantic salmon typically defends a specific area in the river, foraging on drifting prey that enters the territory (Keeley & Grant, 1995). Territory size is positively correlated to body size (Steingrimsson & Grant, 2008). After attacking a prey-item, the fish typically returns to its previous position (Steingrimsson & Grant, 2008). If another individual enters the territory, the fish already inhabiting it will try to defend it by chasing the intruder away. Hungry fish tend to be more aggressive than satiated fish, hence the strength of the territoriality and territory size increases when food becomes scarce (Symons, 1968, Imre *et al.,* 2005). Territoriality in Atlantic salmon is not only a mechanism for protecting a good area for foraging, but also important for protecting shelters (predator avoidance). Densities of YOY (young-of-year) after emergence can be very high locally, since Atlantic salmon does not disperse very well during this early life-stage (Einum & Nislow, 2005; Teichert *et al.*, 2010). Shelter is therefore crucial for the survival of newly emerged fish. The lack of dispersal ability is believed to be caused by high predation risk and high energetic costs related to the actual dispersal. This leads to strong density-dependent survival during the first 2 months after emergence (Einum & Nislow, 2005). Older fish swim better and are usually less exposed to predation as a direct effect of their larger size. The quality of the habitat, both in regards to foraging and finding shelter from predators, therefore plays an important role in regulating Atlantic salmon populations.

Salmonid fish use a wide variety of habitats and are flexible when adjusting to habitat variation (Maki-Petays *et al*., 1997). Habitat use in Atlantic salmon is affected by many variables, and several of the given factors may affect habitat choice simultaneously: Habitat availability, substrate-size, fluctuations in water flow, depth and water-current, time of day/night, season, temperature, food availability, risk of predation, fish size, mode of activity and rate of inter-/intra-specific competition (Maki-Petays *et al*., 1997). Activity levels are often linked to feeding behaviour; an important factor when considering habitat use of Atlantic salmon. Atlantic salmon are visual predators (Ali, 1961), leading to reduced drift feeding efficiency when light levels decrease (Fraser & Metcalfe, 1997). Even though drifting invertebrates are numerous at night (Brittain & Eikeland 1988), juveniles most likely respond to this reduced foraging-efficiency by switching to benthic feeding behaviour when it gets dark (Amundsen *et al.,* 2000). In autumn, as nights get longer and darker, an increase in nocturnal activity can be observed in juveniles as a response to increased night activity in invertebrate prey (Amundsen *et al.,* 1999; Amundsen *et al.,* 2000). Habitat choice thus varies between day and night and also between seasons.

Habitat choice in juvenile Atlantic salmon also differ among different age classes, where YOY have a tendency of positioning themselves closer to the river bank and also closer to the substrate than individuals of larger size (Bremset & Berg, 1999). The behavioral tendency in juvenile salmonids to choose habitats close to the river bank/substrate is a combination of many factors like finding shelter from strong currents, inter-cohort competition and risk of predation. This leads to a size-dependent segregation where different size-classes of fish inhabit different depths (Vehanen & Hamari, 2004; Maki-Petays *et al.*, 2004). As an example, preferred depth during summer and autumn for small (4-6cm), medium (7-10cm) and large (11-17cm) Atlantic salmon has been reported to be 5-20 cm, 5-35 cm and 25-60 cm,

respectively (Maki-Petays *et al.*, 2004). This segregation is believed to be caused mainly by risk of predation and/or inter-cohort competition where larger and more dominant individuals are capable of restricting smaller individuals to less favorable habitats. When taking into account that competition for good, or less good, shelters/habitats in Atlantic salmon is density-dependent (Armstrong & Griffiths, 2001), it becomes clear that inter-cohort competition and population density are important when considering habitat choice. In winter and spring the segregation between the different size classes is less obvious due to similar habitat preferences between all cohorts (Maki-Petays *et al.*, 2004). These seasonal differences in habitat choice indicate a well documented shift in behavior in Atlantic salmon between winter and summer (Fraser *et al.,* 1993; Maki-Petays *et al*., 1997; Valdimarsson & Metcalfe, 1997; Whalen *et al.,* 1999; Vehanen & Hamari, 2004; Huusko *et al.,* 2007). Choosing a habitat close to the river bank in shallow water, could have effects on survival when water flow/discharge varies. Human activity, like hydropower production, is known to affect these physical features (Ugedal *et al.,* 2006; Hansen *et al.,* 2008; Irvine *et al.,* 2009).

Much effort has been done to investigate natural habitat choice of Atlantic salmon. However, few experiments have been conducted to investigate the actual factors affecting the habitat selection. The present study was conducted to test the effects of density, large Atlantic salmon present and time of day on habitat choice in juvenile Atlantic salmon. This was achieved by using an artificial river-channel under controlled conditions.

Based on the literature outlined above it is hypothesized that;

(i) habitat choice of Atlantic salmon is density-dependent. Altering the densities will thus have an effect on habitat choice,

(ii) large Atlantic salmon (dominant) will have an effect on habitat choice of juveniles and

(iii) shifts in foraging behaviour and varying risk of predation will lead to diel differences in habitat choice.

Materials and methods

Study site and experimental design

A 2x2x2 factorial design (density high/low, large fish present/absent, and time day/night) was used to investigate factors affecting habitat choice in Atlantic salmon juveniles. All experiments, both summer and autumn trials, were performed from May to September 2010, at the NINA Research Station at Ims (58° 54'N, 5° 57'E), in southwestern Norway.

Experimental facilities

The four circular arenas (Fig. 1a) used as stream channels in the experiments were located outdoors in a fenced area preventing people from disturbing the fish. Diel differences (day/night) in habitat choice could thus be investigated by conducting natural night time/day time experiments. To simulate a natural river system within the arenas, a natural streambed substrate consisting of stones/cobbles of different sizes was used. Water was drawn from a nearby lake. A sloped river bed within the stream channels created a shallow habitat in the inner parts of the arenas, and a deep habitat in the outer parts (Fig. 1b). The four arenas were constructed similarly and thus had similar appearance. Each arena was divided into three sections of 10 m^2, with escape proof mesh separating both the sections and water inlets/outlets. Physical features (water depth, current at bottom and current at 60% deep) were measured using a Schiltknecht water velocity meter (Table I). Eight transects stretching from shallow to deep, with each transect containing 5 measuring-points, were used to measure physical features in each section. Each section thus contained 80 measuring-points, 40 in the shallow habitat and 40 in the deep. 40 spots thus created a mean value for the shallow or deep habitat in a single section. Depths and currents varied slightly between arenas and sections, and this was controlled for in the statistical analysis by using section number as a random

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factor (see statistics). Water temperature during summer experiments ranged from 13.3-20.8°C (mean 17.1 ± 1.7 SD) and from 10.7-17.3°C (mean 15.7 ± 0.8 SD) during autumn. White plastic tarp was used to simulate overhead cover along the river bank, with each tarp covering half of the total area of each section (Fig. 1c). This created overhead shelter and shadow from the sun. No food was added during the experiments, restricting fish to forage on food items on the substrate or entering through the water inlet.

Table I. Mean values for physical features (depth, current velocity at bottom and current velocity at 60% depth) for all sections, as well as standard deviation between the sections. Anemometer details: Schiltknecht Messtechnik; Gossau, Switzerland; MiniAir 20 Multiprobe anemometer with water probe; precision ± 1 cm·sec^{-1}; 3 seconds measurement time.

	Mean ± SD
Deep Habitats:	
Depth (cm)	31.20 (3.39)
Current bottom (m·s^{-1})	0.06 (0.03)
Current 60% (m·s^{-1})	0.10 (0.03)
Shallow Habitats:	
Depth (cm)	18.00 (3.16)
Current bottom (m·s^{-1})	0.03 (0.01)
Current 60% (m·s^{-1})	0.05 (0.01)

a)

Water inlet
Water outlet
Outer/inner walls
Frames for attaching "curtain"
Escape proof mesh
1-3   Sections
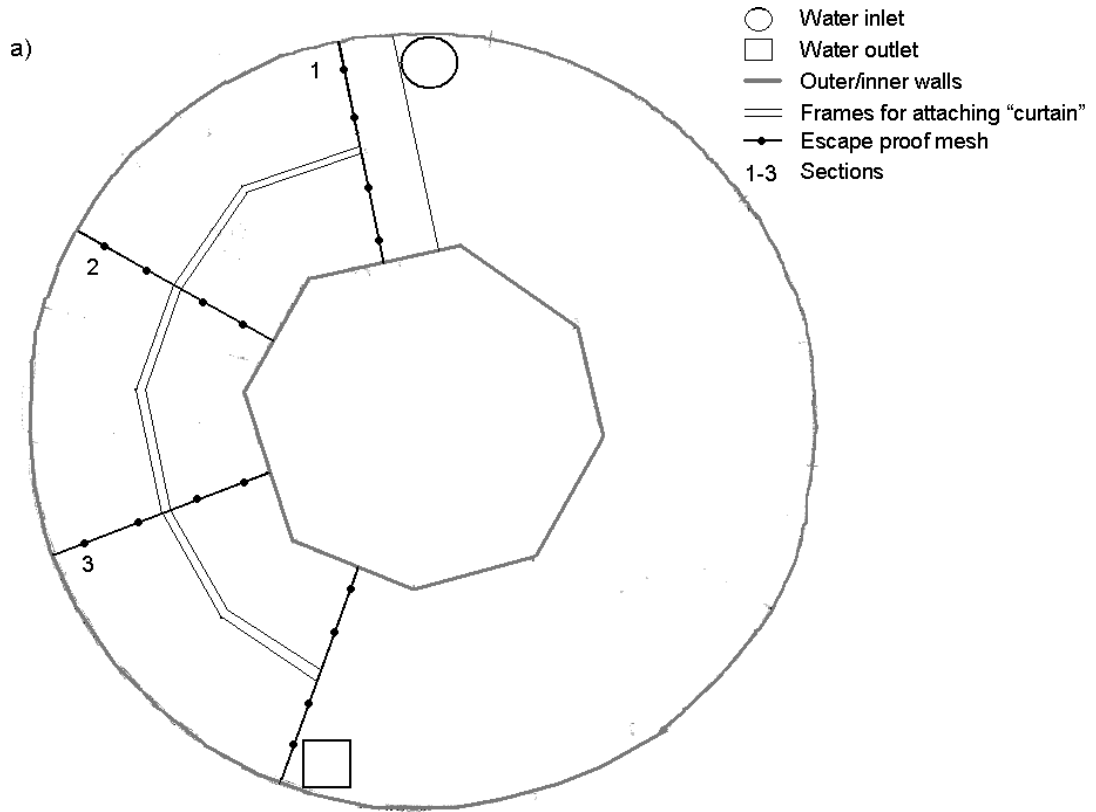
1

2

3

b)

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Fig. 1. Illustrations/photos of experimental stream channels showing (a) schematic drawing where water from the water inlet flows counter-clockwise towards the water outlet. All sections (1-3) have the same total area (10 m^2), (b) sloped river bed creating deep/shallow habitat. A "curtain" for separating the two habitats is held in place by metal pins attached to ropes. The curtain is let down by pulling the ropes. (c) three sections of a single arena, where half of the total area of each section is covered by a white plastic tarp, creating overhead shelter and shadow from the sun. Ropes attached to curtains for separating the habitats can be seen attached to the centre of the stream channel.

To determine juvenile habitat choice (deep/shallow), it was possible to separate the shallow/deep habitats using an escape proof wooden "curtain" (Fig. 1b). A curtain was closed by pulling 2 ropes attached to it, thus sliding it into a frame extending well above the water line. This made it impossible for fish to cross between the two habitats.

Experimental fish

In total, 3404 fish were tested during summer experiments, and 3771 during autumn. Two cohorts, YOY and 1+ were used in all experiments, with fork lengths ranging from 35 to 235

mm. Two timing groups of YOY (hatched at different time periods) were used to create experimental size-variation (body length early timing group: 35-48 mm, body length late timing group: 41-47 mm). YOY were termed "juveniles" and the 1+ smolt cohort was termed "large". Large fish was always twice the size of medium/small fish, making them potential predators for the smaller size classes (L`Abèe-Lund *et al.*, 1992; Sandlund & Næsje, 1992; Henderson & Letcher, 2003; Finstad *et al.,* 2006). Stomach content was investigated during summer experiments, but no predation on juveniles was observed. Experimental fish was never re-used. All treatments of fish and experimental procedures were conducted according to national and international rules for animal welfare.

All size classes had a rapid growth from early summer to autumn, causing a considerable size-difference between seasons (mean body length summer = 47 ± 1 mm, mean body length autumn = 82 ± 1 mm). Since there was no overlap in body length between large and medium/small, it was possible to do experiments where large fish still had an effect on juveniles during autumn.

Experimental procedures

Fish sizes used (fish composition) and densities varied between different experiments. Experiments were completed by separating the deep and shallow habitat (closing of curtains), and electro-fishing all sections thereafter. Habitat choice was determined by counting the number of juvenile salmon in the shallow habitat versus the number in the deep habitat for each section, yielding a "proportion of fish in the deep". The fork length of each fish was measured immediately after recapture (precision 1 mm) as the fish was easy to handle while still stunned. Fork lengths were measured to control for effects of size-difference on habitat

choice. By investigating whether proportions of fish in the deep varied between different treatments, factors affecting habitat choice could be identified.

The same fish composition/density was always used in an entire arena (3 sections) for a single experiment, making stocking and fishing easier. Treatments with "large Atlantic salmon present" were never done in the same arena simultaneously to treatments where large was absent. This was done to avoid changes in behavior in juveniles caused by possible "predator detection" between neighboring sections (Mirza & Chivers, 2001; Kelley & Magurran, 2003). 10 juveniles per section (1 fish per m^2) were stocked for low-density treatments, and 30 juveniles per section (3 fish per m^2) were stocked for high-density treatments (Grant & Imre, 2005; Imre *et al.*, 2005; Imre *et al.*, 2010). For experiments including large Atlantic salmon present, 10 juveniles and 2 large were stocked for low-density treatments, and 28 juveniles and 2 large were stocked for high-density treatments. Different treatments for density and fish composition could thus be stocked in a controlled way. In total, 12 different treatments were performed in the final summer and autumn experiments (Table II). Four treatments were performed during summer, and 8 during autumn.

Table II. Overview of all treatments performed during summer and autumn, as well as the amount of experiments (trials) conducted for each treatment (n).

Season	Density	Large present	Day/Night	n (trials)
Summer	Low	No	Day	21
Summer	Low	Yes	Day	61
Summer	High	No	Day	21
Summer	High	Yes	Day	63
Autumn	Low	No	Day	20
Autumn	Low	Yes	Day	24
Autumn	High	No	Day	21
Autumn	High	Yes	Day	24
Autumn	Low	No	Night	24
Autumn	Low	Yes	Night	21
Autumn	High	No	Night	24
Autumn	High	Yes	Night	24
Total	-	-	-	348

The summer experiments were performed from 25 May - 29 June, and the autumn experiments from 31 August - 17 September. When performing night time experiments, the arenas were stocked at about 02:00 at night, and curtains were closed and fished at 00:00 the following night. At closing (00:00), it had thus been completely dark for about three hours. Curtains were closed without using artificial light. The same procedures were used for day time and night time fishing. Since night in Norway during summer is very short, night time experiments were only conducted during autumn. Day time experiments, however, were conducted during both seasons.

Acclimation

Pre-experiments and observational studies were necessary to establish acclimation time, which was set to twenty hours. Observational studies recording feeding/feeding attempts during 10 minutes of every hour showed that fish started feeding consistently after 5 hours in 7 out of 7 studies. Based on this, an acclimation time of 20 hours seemed to be more than enough.

Statistics

The effect of density, mean size, presence of large Atlantic salmon, time of day (day time or night time) and their interactions on proportions of fish in the deep were tested using linear mixed effect models. Section numbers 1-12 were used as random effect allowing mean differences between sections. Visual inspection of the residuals from the summer experiments indicated no violations of the assumptions.

Inspection of the residuals from autumn experiments indicated residual differences between treatments with/without large present. Variance was stabilized by allowing different residual spreads for this variable (*varIdent* function). This model performed better than the initial model which did not allow for different residual spreads.

Habitat use was modelled using data from the summer experiments, with the following initial full model:

$$PS_{ij} = \alpha + \beta_1 D_j + \beta_2 L_j + \beta_3 M_j + \beta_4 D_j L_j + \beta_5 D_j M_j + \beta_6 L_j M_j + a_i + \varepsilon_j \tag{1}$$

PS is the proportion of fish inhabiting the deep part in section i, for replicate j, where α and β's are the fixed parameters, the random intercept $a_i \sim N(0, d^2)$, and the residual $\varepsilon_{ij} \sim N(0, \sigma^2)$. D is density, L is large fish present, M is mean size and DL, DM and LM are the interaction terms.

For the autumn experiments, where observations were done during both day and night, we also included a term for time of day in the initial full model:

$$PA_{ij} = \alpha + \beta_1 D + \beta_2 L_j + \beta_3 M_j + \beta_4 T_j + \beta_5 D_j L_j + \beta_6 D_j M_j + \beta_7 L_j M_j + \beta_8 D_j T_j + \tag{2}$$
$$\beta_9 L_j T_j + \beta_{10} M_j T_j + a_i + \varepsilon_j$$

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PA is the proportion of fish inhabiting the deep part of the arena, for replicate j at section i,

Where α and β´s are the fixed parameters. D is density, L is large fish present, M is mean size,

T is time of day and DL, DM, LM, DT, LT and MT are the interaction terms. The random

intercept $a_i \sim N(0, d^2)$, the residual $\varepsilon_{ij} \sim N(0, \sigma^2)$, where the model allows for different spreads

for large present/absent.

The "protocol" for model selection from Zuur *et al.* (2009) was used for evaluating fixed

effects using sequential backward removal of terms tested by ML. The *lme* command from the

nlme package (Pinheiro *et al.*, 2008) in R v2.11.1 was used for the analyses.

Results

Summer

For the summer experiments, all interactions could be removed (p-values > 0.3310). Also, the main effects mean size and density could be removed (p-values > 0.1145). The last effect, large present, was highly significant (p-value < 0.001). The optimal model for explaining the proportions of fish in the deep during summer was therefore a linear mixed effect model with section number as random factor and the main term large present (Fig. 2).

Autumn

When evaluating the optimal model for the autumn experiments, all interactions could be removed (p-values > 0.1302). Also, the main effects mean size and density could be removed (p-values > 0.7390). The remaining main effects, large present and night time, were highly significant with both p-values < 0.001. A linear mixed effect model with section number as random factor and the main effects large present and night time was therefore the best performing model for explaining the proportions of fish in the deep during autumn (Fig. 2).
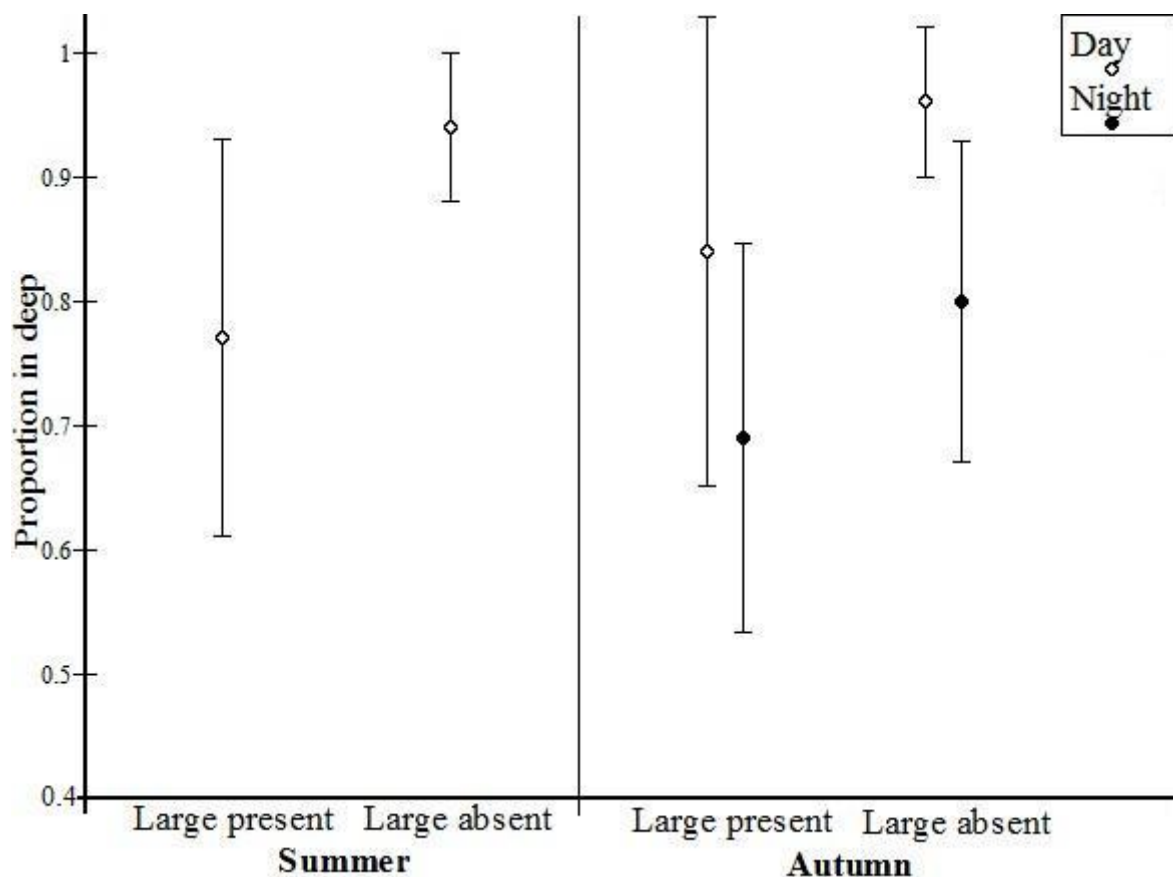
Fig. 2. Mean proportions of fish in the deep and standard deviations for experiments including significant factors for both summer and autumn (large present and time of day). Large Atlantic salmon present and night time led to more fish inhabiting the shallow areas.

Significant results from both model selections (autumn and summer) are summarized in Table III. The highly significance of having a large fish present during both summer and autumn experiments shows that fish is more likely to choose the shallow habitat if a larger fish is inhabiting the deep habitat. During summer experiments, only 3 out of 272 large fish were caught in the shallow habitat. For autumn experiments, 14 out of 188 large fish were caught in the shallow habitat. Night time was also highly significant, indicating that fish more often choose the shallow habitat at night compared to day time (Fig. 2).

Table III. Summary of the best linear mixed effects models for summer and autumn experiments. The summary shows which factors affected the proportions of fish in the deep. Estimated parameters for random effects are the standard error of random intercept in models with standard error of residual variation given in brackets.

	Estimate ± SE	T	P
Summer model			
Random effects			
Section.nr	0.09 (0.19)		
Fixed effects			
Intercept	1.39 (0.04)	34.92	<0.001
Large present	-0.29 (0.03)	-8.76	<0.001
Autumn model			
Random effects			
Section.nr	0.05 (0.24)		
Fixed effects			
Intercept	1.44 (0.03)	49.30	<0.001
Large present	-0.18 (0.03)	-5.88	<0.001
Time[1]	-0.27 (0.03)	-9.05	<0.001

[1] Estimated parameter is for night time.

Discussion

Habitat use and experimental fish

All the fish used in the experiments were hatchery reared Atlantic salmon, with parents originating from the local stock (River Imsa). The behavior of hatchery reared salmonids has been shown to vary from that of wild fish (Deverill *et al.,* 1999; Sundstrøm & Johnsson, 2001; Griffiths & Armstrong, 2002). The present experiment must thus be treated conservatively when investigating factors affecting habitat choice in wild Atlantic salmon.

Fish used in the experiments were not starved, hence the fish was satiated for some time into the experiments (fish that was cut open after an experiment still had pellets in the stomach). A starved individual may have to take more risks than a satiated individual to fulfil energy demands. In our case, assuming that foraging during the day is more risky than foraging during the night (Orpwood *et al.,* 2006), satiated fish should be less diurnal compared to hungry fish (hungry fish are more risk prone). In the present study, this could have caused an increased sheltering behaviour during the day. No experiments were conducted at dusk or dawn, which are considered to be the two time periods when drift feeding is most intense (Brittain & Ekeland, 1988; Thorpe *et al.,* 1988; Angradi & Griffith, 1990), and replicates from these time-periods may have yielded different results than the night/day time experiments.

For experiments during summer and autumn, investigating habitat choice for juveniles when competition was low (low density) and large fish was absent, most of the fish preferred the deep habitat (mean proportion summer = 0.95, mean proportion autumn = 0.96). For low density treatments, with 1 fish per m^2, space should not be a limiting factor (Grant & Kramer, 1990). As large fish was found predominantly in the deep (460 out of 477 large fish

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recaptured were found in the deep), it is reasonable to assume that all size classes used in the experiments preferred the deepest part of the river channel, thus competing for the same habitat during the day. Greater depth (providing shelter during the day) together with increased current velocity (increasing drift forage efficiency) could have been factors making the deep habitat more preferable during day time compared to the shallows (Abrahams & Kattenfield, 1997; Armstrong, 2010; Aas *et al.,* 2011).

The stream channels used were created to mimic natural habitats. Current velocity, substrate composition and overhead cover were all factors taken into account when creating the river channels. Plastic tarp was used to create overhead cover, as trees do in a natural system. In nature, trees would also increase the availability of food for salmon juveniles, perhaps making shallow areas in nature more preferable compared to the shallows in the present experiment (Orpwood *et al.*, 2010).

Large Atlantic salmon present

Atlantic salmon juveniles more often occupied the shallow habitat when a large Atlantic salmon was present. This is consistent with the hypothesis that a large Atlantic salmon has an effect on habitat choice of smaller size classes. The highly significant effect of having a large Atlantic salmon present during both summer and autumn indicates that inter-cohort competition and/or risk of predation has significant impact on the habitat choice of juveniles. Large Atlantic salmon used in the experiments were always large enough to be a potential predator for the smaller fish (Finstad *et al.,* 2006). Younger cohorts experience the presence of a potential predator visually, by chemical cues or by direct interactions with the larger fish (Mirza & Chivers, 2001; Kelley & Magurran, 2003). A large and dominant individual will control its preferred habitat and also restricts smaller individuals with similar habitat choice to

less preferred habitats. The fact that smaller size classes appeared to have similar habitat preferences compared to the larger size class (deep), further supports that juveniles loose when competing for habitat with larger fish. This, in turn, led to increased juvenile density in the shallow habitats (less preferred habitat) and was probably caused by a combination of fish physically interfering with each other, and the visual risk of predation smaller fish experienced when large fish was present (Kelley & Magurran, 2003).

The increased variation in proportions of juveniles in the deep when a large fish was present, as indicated by the higher standard deviations for these experiments (Fig. 2), can be explained by individual differences between the large fish used. It is reasonable to assume that an active and aggressive large fish would have a more negative effect on juvenile proportions in the deep compared to a large individual which was less active. This study highlights that large Atlantic salmon are dominating smaller conspecifics when competing for suitable habitat, and that juvenile Atlantic salmon choose a wide range of water depths (habitats) as competitive interactions and, possibly, risk of predation vary within the habitat.

Time of day

By conducting autumn experiments which included the main effect time of day, it was shown that fish during night time tend to choose the shallow habitat more often than during day time. This is consistent with the hypothesis that there are diel differences in habitat choice of Atlantic salmon juveniles. The cause of the increased proportions of fish in the deep during night time could be that large fish was more active at night, thus chasing more juveniles away from the deep habitat, or that the shallows simply become more preferable at night due to altered behaviour. The "asset protection principle" (Clark, 1994), claims that individuals with larger body size, where a large body equals accumulated fitness, should be more risk averse

compared to smaller individuals. Thus "protecting" the energy already gained from earlier growth. According to this, larger Atlantic salmon should be less active during day time than smaller individuals, as fish foraging during the day is more exposed to visual predators as compared to those foraging at dusk, dawn or during the night (Orpwood *et al.,* 2006). Imre & Biosclair (2004) found that Atlantic salmon parr were more nocturnal and less day-active compared to YOY, thus supporting the asset protection principle. However, no significant interaction between night time and large fish present was found in the present study. That is, there were no significant differences on proportions of juveniles in the deep between having a large Atlantic salmon present during night time compared to day time. This suggests that large fish is not more active, when it comes to chasing juveniles away from the deep, at night time as compared to day time. Drift feeding efficiency in visual predators like Atlantic salmon decreases with decreasing light (Fraser & Metcalfe, 1997; Mazur & Beauchamp, 2003; Turesson & Bronmark, 2007). Juveniles most likely switch to benthic feeding behaviour as a response to this (Bergersen, 1989; Amundsen *et al.,* 1999; Amundsen *et al.,* 2000). In the dark, fish is less exposed to visual predators, and when foraging success is not correlated to water current as it is during day time, it is reasonable to assume that the shallow habitat simply becomes more preferable at night as feeding behaviour change and risk of predation decrease.

Density

No significant effects of density on proportion of juveniles in the deep was found (p-value density during summer = 0.11, p-value density during autumn = 0.74). Given that available shelters seem to be an important limited resource for juveniles (Finstad *et al.,* 2007; Breau *et al.,* 2007) and that juveniles compete for shelters (Armstrong & Griffiths, 2001), the lack of

importance of this factor in the present study is surprising. No significant interaction between density and any other factor was found (large present/density, density/time of day). That is, proportional distribution of fish was similar for low/high density experiments. Shallow habitats were more often preferred during night time and when a large fish was present. For experiments with large fish present, these controlled a rather large area of the deep, and juveniles distributed themselves at equal proportions between the remaining available habitats in the deep/shallows for both high- and low density experiments, yielding no effect of density on proportions of fish in the deep. The same distribution was found between high/low density treatments during night time. This result could indicate that competition for habitat in Atlantic salmon juveniles in the present experiment not simply occur between shallow/deep (large scale), where deep is always better, but that competition for habitat happens on a much smaller scale (microhabitats). Some of the microhabitats in the shallows may therefore be more preferable compared to some of the microhabitats in the deep (Bremset, 2000). Fish thus distribute themselves by occupying the "best" available habitat, or by out-competing an individual already inhabiting a territory. As deep is not always the best, the distribution will be very similar for high/low density experiments. This, of course, means that the same proportion of fish can be found in the shallows irrespective of population density.

It may be argued that the use of starved fish could have been a better approach when investigating effects of density. Starved fish are more aggressive than satiated fish, as food abundance affects territory size (Symons, 1968; Imre *et al.*, 2005). Higher aggression, in our case, could have led to higher competition, especially for experiments with high density. Density manipulations yielding similar results when using starved fish would further support that juveniles distribute themselves at similar proportions for high/low density populations.

Ecological impacts and management implications

Identifying and understanding factors affecting habitat selection is crucial for understanding biological requirements of animals. Knowledge about how species interact with their habitat to fulfil biological needs will in turn be essential when considering habitat management, and thereby, management of the species living there.

The present study identifies time of day, inter-cohort competition and/or risk of predation as significant factors affecting habitat choice in Atlantic salmon juveniles. These results show how habitat choice in juveniles varies when competitive interactions change within the habitat. They also highlight a diel change in habitat choice, where shallow habitats are occupied more often at night compared to day time, probably caused by changes in foraging activity and/or reduced risk of predation by visual predators.

The preference to shallow habitats could have severe impacts on the risk of stranding, especially in rivers regulated for hydropower production. Hydropower plants running to fulfil exact energy demands may cause rapid changes in water levels, referred to as "hydro-peaking". In these hydropower rivers, stored water from a reservoir is released according to energy demands, where increased energy demands leads to more water being released from the reservoir. Together with extreme drops in water levels when energy demand is low, hydro-peaking may cause dewatering of the shallow areas along the river bank several times during a single day. In Norway, 25% of all rivers are regulated for hydropower production, and 1/3 of these catchments contain wild Atlantic salmon (Helleraker *et al.,* 2007). Hydro-peaking occurs in many rivers in Norway and is expected to increase in near future (Saltveit *et al.,* 2001). In regulated rivers, the differences in habitat choice between different age/size classes of Atlantic salmon could have impact on the risk of stranding. YOY "hiding" in the

substrate close to the river bank are less willing/capable of moving away from their shelters than larger fish in the deep and are, during such dewatering events, therefore more vulnerable to stranding. Hvidsten (1985) showed that YOY Atlantic salmon were more vulnerable to stranding than older individuals as a consequence of their preferred habitat (Bremset, 2000).

The results from the present study suggest that dewatering/ramping down should be avoided during night time, as shallow areas close to the river bank appear to be more preferable during night time as compared to day time. There was no effect of density on proportion of fish in the shallows. That is, the same proportion of the population is at risk of stranding in shallow areas whether the density is high or low. This, of course, has important management implications for small populations. Further studies, investigating if/how mortality caused by stranding may be compensated for by increased growth in the remaining population, together with studies investigating direct effects of habitat choice on the risk of stranding is therefore necessary in order to evaluate population effects of eventual stranding.

Understanding the effects of varying water flow/discharge on Atlantic salmon populations are crucial for future improvements of the way hydropower plants operate. At times, large proportions of the juveniles in an Atlantic salmon population occupy shallow areas exposed to stranding (Fig. 2). Improvements in the way hydropower plants operate will not only strengthen Atlantic salmon populations, but it will also strengthen the general view of hydropower as an environmentally friendly source of energy.

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Acknowledgments

References

Aas, Ø., Einum, S., Klementsen, A., Skurdal, J. (2011). *Atlantic Salmon Ecology.* 1th edition. Wiley Blackwell, 97-98.

Abrahams, M. & Kattenfield, M. (1997). The role of turbidity as constraint on predatory-prey interactions in aquatic environments. *Behavioral Ecology and Sociobiology* **40**, 169-174.

Ali, M. A. (1961). Histophysiological studies on the juvenile Atlantic salmon (*Salmo salar)* retina: II. Responses to light intensities, wavelengths, temperatures and continuous light or   dark. *Canadian Journal of Zoology* **39***,* 511-526.

Amundsen, P. A., Bergersen, R., Huru, H., Heggberget, T. G. (1999). Diel feeding rhythms and daily food consumption of juvenile Atlantic salmon in the river Alta, northern Norway. *Journal of Fish Biology* **54***,* 58-71.

Amundsen, P. A., Gabler, H. M., Herfindal, T., Riise, L. S. (2000)*.* Feeding chronology of Atlantic salmon parr in subarctic rivers: consistency of nocturnal feeding. *Journal of Fish Biology* **56***,* 676-686.

Andreo, V., Lima, M., Provensal, C., Priotto, J., Polop, J. (2009). Population dynamics of two rodent species in agro-ecosystems of central Argentina: intra-specific competition, land-use, and climate effects. *Population ecology* **51***,* 297-306.

Angradi, T. R. & Griffith, J. S. (1990). Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho*. Canadian Journal of Fisheries and Aquatic Sciences* **47***,* 199–209.

Armstrong, J. D. & Griffiths, S. W. (2001). Density-dependent refuge use among over-wintering wild Atlantic salmon juveniles. *Journal of Fish Biology* **58***,* 1524-1530.

Armstrong, J. D. (2010). Variation in habitat quality for drift-feeding Atlantic salmon and brown trout in relation to local water velocities and river discharge. In: *Salmonid Fisheries: Freshwater Habitat Management.* Blackwell Publishing Ltd.

Bergersen, R. (1989). Zoobenthos and food of Atlantic salmon (*Salmo salar L.)* fry in Alta river, northern Norway – and notes on the measurement of faunal resemblence. *Nordic Journal of Freshwater Research* **65***,* 99-115.

Breau, C., Weir, L. K., Grant, J. W. A. (2007). Individual variability in activity patterns of juvenile Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick. *Canadian Journal of Fisheries & Aquatic Sciences* **64***,* 486-494.

Bremset, G. (2000). Seasonal and diel changes in behaviour, microhabitat use and preferences by young pool-dwelling Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta. Environmental Biology of Fishes* **59***,* 163-179.

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

Brittain, J. E. & Eikeland, T. J. (1988). Invertebrate drift – A review. *Hydrobiologica* **166***,* 77-93.

Campbell, N. A. & Reece, J. B. (2005). *Biology*. 7th edition. Pearson Education, 1140-1150.

Clark, C. W. (1994). Antipredator behaviour and the asset-protection principle. *Behavioural Ecology* **5**, 159–170.

Clark, W. G. & Hare, S. R. (2002). Effects of climate and stock size on recruitment and growth of Pacific halibut. *North American Journal of Fisheries Management* **22**, 852-862.

Deverill, J. I., Adams, C. E., Bean, C. W. (1999). Prior residence, aggression and territory acquisition in hatchery-reared and wild brown trout. *Journal of Fish Biology* **55**, 868–875*.*

Einum, S. & Nislow, K. H. (2005). Local-scale density-dependent survival of mobile

organisms in continuous habitats: an experimental test using Atlantic salmon.

Oecologia **143**, 203–210.

Finstad, A. G., Ugedal, O., Berg, O. K. (2006). Growing large in a low gradient environment:

size dependent foraging gain and niche shifts to cannibalism in Atctic char. *Oikos* **112***,*

73-82.

Finstad, A. G., Einum, S., Forseth, T., Ugedal, O. (2007). Shelter availability effects bahviour,

size-dependent and mean growth of juvenile Atlantic salmon. *Freshwater Biology* **52***,*

1710-1718.

Finstad, A. G., Einum, S., Ugedal, O., Forseth, T. (2008). Spatial distribution of limited

resources and local density regulation of juvenile Atlantic salmon. *Journal of Animal

Ecology* **78**, 226-235.

Fraser, N. H. C., & Metcalfe, N. B. (1997). The costs of becoming nocturnal: feeding

efficiency in relation to light intensity in juvenile Atlantic salmon. *Functional Ecology*

11*,* 385-398.

Fraser, N. H. C., Metcalfe, N. B., Thorpe, J. E. (1993). Temperature-dependent switch

between diurnal and nocturnal foraging in salmon. *Proceedings: Biological Sciences B*

252*,* 135-139.

Gibson, A. J. F., Bowlby, H. D., Amiro, P. G. (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.

Griffiths, S. W. & Armstrong, J. D. (2002). Rearing conditions influence refuge use among

over-wintering Atlantic salmon juveniles. *Journal of Fish Biology* **60***,* 363-369.

Grant, J. W. A. & Kramer, D. L. (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.

Grant, J. W. A. & Imre, I (2005). Patterns of density-dependent growth in juvenile
   stream-dwelling salmonids. *Journal of Fish Biology* **67**, 100-110.

Hansen, L. P., Fiske, P., Holm, M., Jensen, A. J., Sægrov, H. (2008). Bestandsstatus for laks i
   Norge. Prognoser for 2008. Rapport fra arbeidsgruppe. *Utredning for DN 2008* **5**, 1-66
   [in Norwegian].

Hasegawa, K. & Yamamoto, S. (2010). The effect of flow regime on the occurrence of
   interference and exploitative competition in a salmonid species, white-spotted char
   (Salvelinus leucomaenis). *Canadian Journal of Fisheries and Aquatic Science* **67**,
   1776-1781.

Helleraker, J. H., Sundt, H., Alfredsen, K. T., Dangelmaier, G. (2007). Application of
   multiscale environmental flow methodologies as tools for optimized management of
   Norwegian regulated national salmon watercourse. *River Research and Applications*
   23, 493-510.

Henderson, J. N. & Letcher, B. H. (2003). Predation on stocked Atlantic salmon (*Salmo salar*)
   fry. *Canadian Journal of Fisheries & Aquatic Sciences* **60**, 32-42.

Huusko, A., Greenberg, L., Stickler, M., Linnansari, T., Nykanen, M., Vehanen, T., Koljonen,
   S., Louhi, P., Alfredsen, K. (2007). Life in the ice lane: The winter ecology of stream
   salmonids. *River Research and Applications* **23**, 469-491.

Hvidsten, N. A. (1985). Mortality of pre-smolt. Atlantic salmon, *Salmo salar* L., and brown
   trout, *Salmo trutta* L., caused by rapidly fluctuating water levels in the regulated River
   Nidelva, central Norway. *Journal of Fish Biology* **27**, 711-718.

Imre, I. & Boisclair, D. (2004). Age effects on diel activity patterns of juvenile Atlantic

    salmon: parr are more nocturnal than young-of-the-year. *Journal of Fish Biology* **64**,

    1731-1736.

Imre, I., Grant, J. W. A., Cunjak, R. A. (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.

Imre, I., Grant, J. W. A., Cunjak, R. A.. (2010). Density-dependent growth of young-of-the-

    year Atlantic salmon (*Salmo salar*) revisited. *Ecology of Freshwater Fish* **19**, 1-6.

Irvine, R. L., Ousseren, T., Baxter, J. S., Schmidt, D. C. (2009). The effects of flow reduction

    rates on fish stranding in British Colombia, Canada. *River Research and Applications*

    25, 406-415.

Keeley, E. R. & Grant, J. W. A. (1995). Allometric and environmental correlates

    of territory size in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal*

    of Fisheries and Aquatic Sciences **52**, 186–196.

Kelley, J. & Magurran, A. E. (2003). Learning predator recognition and antipredator

    responses in fishes. *Fish and Fisheries* **4**, 216-226.

L`Abèe-Lund, J. H., Langeland, A., Sægrov, H. (1992). Piscivory by brown trout *Salmo trutta*

    L. and Arctic charr *Salvelinus alpinus* (L.) in Norwegian lakes. *Journal of Fish*

    Biology **41**, 91-101.

Maki-Petays, A., Muotka, T., Huusko, A., Tikkanen, P., Kreivi, P. (1997). Seasonal changes

    in habitat use and preference by juvenile brown trout, *Salmo trutta*, in a northern

    boreal river. *Canadian Journal of Fisheries and Aquatic Science* **54**, 520-530.

Maki-Petays, 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 Science* **61***,* 2329-2338.

Mathis, A. (1990). Territoriality in a terrestrial salamander: the influence of resource quality and body size. *Behaviour* **112***,* 162-175.

Mazur, M. & M., Beauchamp, D. A. (2003). A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. *Environmental Biology of Fishes* **67**, 397-405.

Mirza, R. S. & Chivers, D. P. (2001). Are chemical alarm cues conserved within salmonid fishes? *Journal of Chemical Ecology* **27***,* 1641-1655.

Orpwood, J. E., Griffiths, S. W., Armstrong, J. D. (2006). Effects of food availability on temporal activity patterns and growth of Atlantic salmon. *Journal of Animal Ecology* **75***,* 677-685.

Orpwood, J. E., Armstrong, J. D., Griffiths, S. W. (2010). Interactions between riparian shading and food supply: a seasonal comparison of effects on time budgets, space use and growth in Atlantic salmon Salmo salar. *Journal of Fish Biology* **77***,* 1835-1849.

Pinheiro. J., Bates, D., Debroy. S., Sarkar. D & the R Core Team. (2008). nlme: Linear and nonlinear mixed effects models. R package version 3.1-88.

Saltveit, S. J., Halleraker, J. H., Arnekleiv, J. V., Harby, A. (2001). Field experiments on stranding in juvenile Atlantic salmon (*Salmo salar)* and brown trout (*Salmo trutta*) during rapid flow decrease caused by hydropeaking. *Regulated Rivers: Research & Management* **17***,* 609-622.

Sandlund, O. T. & Næsje, T. F., (1992). Storørretens betydning i økosystemet. Nordisk seminar om forvaltning av storørret. *Direktoratet for naturforvaltning, rapport* **4***,* 6-17. [in Norwegian].

Schmitt, R. J. & Holbrook, S. J., (1999). Mortality of juvenile damselfish: Implications for
assessing processes that determine abundance. *Ecology* **80,** 35-50.

Schwinning, S. & Weiner, J. (1998). Mechanisms determining the degree of size asymmetry
in competition among plants. *Oecologia* **113**, 447-455.

Serrano-Meneses, M. A., Cordoba-Aguilar, A., Mendez, V., Layen, S. J., Szekely, T. (2007).
Sexual size dimorphism in the American rubyspot: male body size predicts male
competition and mating success. *Animal Behaviour* **73**, 987-997.

Stamps, J, A. & Tollesrud, K. (1983). Prospective resource defense in a territorial species. *The
American Naturalist* **123**, 99-114.

Steingrimsson, S. O. & Grant, J. W. A. (2008). Multiple central-place territories in wild
young-of-the-year Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* **77**, 448-
457.

Sundstrøm, L. F. & Johnsson, J. I. (2001). Experience and social environment influence the
ability of young brown trout to forage on live novel prey. *Animal Behaviour* **61**, 249–
255.

Symons, P. E. K. (1968). Increase in aggression and in strength of the social hierarchy among
juvenile Atlantic salmon deprived of food. *Journal of Fisheries Research Board of
Canada* **25**, 2387-2401.

Teichert, M. A. K., Kvingedal, E., Forseth, T., Ugedal, O., Finstad, A. G. (2010). Effects of
discharge and local density on the growth of juvenile Atlantic salmon (*Salmo salar).
Journal of Fish Biology* **76**, 1751-1769.

Thorpe, J. E., Morgan, R. I. G., Pretswell, D., Higgins, P. J. (1988). Movement rhythms in
juvenile Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology* **33**, 931–940.

Turesson, H. & Bronmark, C. (2007). Predator-prey encounter rates in freshwater piscivores:
effects of prey density and water transparency. *Oecologia* **153**, 281-290.

Ugedal, O., Næsje, T. F., Thorsdad, E. B., Forseth, T., Saksgård, L. M., Heggeberg, T. G. (2006). Twenty years of hydropower regulation in the River Alta: long-term changes in abundance of juvenile and adult Atlantic salmon. *Hydrtobiologia* **609***,* 9-23.

Valdimarsson, S. K. & Metcalfe, N. B. (1997). Shelter selection in juvenile Atlantic salmon, or why do salmon seek shelter in winter? *Journal of Fish Biology* **52***,* 42-49.

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

Whalen, K. G., Parrish, D. L., Mather, M. E. (1999). Nocturnal habitat use in Atlantic salmon parr in winter. *Canadian Journal of Fisheries and Aquatic Sciences* **56***,* 1543-1550.

Zuur. A. F., Ieno. E. N., Walker. N. J., Saveliev. A. A., Smith. G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer.