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Size-dependent habitat use of juvenile brown trout (*Salmo trutta* L.) in an artificial river

Øystein Nordeide Kielland

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"Hvorfra jeg får lyst til at skrive?
– Ja de kan ikke tro, hvor det i
grunnen morer mig. Når jeg
begynder et kapittel, som jeg har
riktig varmt i hovedet, er det så
morsomt – ja jeg vil ikke påstå at
det er fullt så morsomt som at
have en laks på stangen, men i
alle fall som en stor ørret."

Alexander Kielland

Abstract

Hydropeaking increases the variation in water levels with possible deleterious effects on organisms living in rivers. Fishes occurring in shallow areas will be vulnerable to stranding and thus increased mortality. The effect of density on deep/shallow habitat use of young-of-the-year (YoY) brown trout (*Salmo trutta* L.) was investigated in experimental small-scale ($10m^2$) outdoor streams. YoY were modeled by individual body size and as relative size of larger conspecifics. Density did not affect habitat use during summer, but in autumn a weak difference was observed between treatments where larger conspecifics (age-1) were present and absent. This interaction disappeared when the absolute size measurement was converted to a better size variable that took each individual's competitive ability into consideration. Intercohort competition by larger conspecifics (2-5x larger than YoY) affected strongly the habitat use of YoY, making them use shallower habitat. Within the YoY cohort, trout with larger body size used deeper habitat. Seasonal variation occurred in size-dependent habitat use when larger conspecifics were present. Previous work with identical setup with Atlantic salmon (*Salmo salar* L.) showed same trends as for brown trout, although salmon YoY displayed a higher preference for the deeper habitat and a density-dependent habitat use in autumn. These results suggest that fish mortality in the shallow caused by hydropeaking will result in vacant territories, which are re-occupied by individuals from the deeper parts of the river in a sink-source dynamic. This will give additive mortality for populations subjected to hydropeaking mortality.

Sammendrag

Effektkjøring i vannkraftverk gir økt variasjon i vannstand med mulige skadelige effekter på organismer som lever i elver. Fisker, som forekommer i de grunne habitatene av elva, kan være sårbare for stranding og dermed ha økt dødelighet. Effekten av tetthet påvirkning på dypt eller grunt habitatbruk for årsyngel av ørret (*Salmo trutta* L.) ble undersøkt i eksperimentelle bekker liten skala ($10m^2$). Tetthet påvirket ikke habitatbruk om sommeren, hvor yngel før ble modellert etter individuell kroppsstørrelse og som relative størrelse av større ørret (1-åringer). Om høsten ble en forskjell observert mellom behandlingene der større ørret var tilstede og der disse var fraværende. Mellom-kohort-konkurransen fra eldre, og dermed større, fisk (2-5 ganger større enn yngelen) påvirket kraftig yngelens habitatbruk ved at grunnere habitat ble brukt. Innad yngel-årsklassen viste kroppstørrelse en positiv korrelasjon med sannsynligheten for å bruke det dype habitatet. Sesongvariasjon ble observert hvor større fisk var tilstede, i form av at om sommeren var det en negativ korrelasjon mellom kroppstørrelse og sannsynlighet for å velge det dype habitatet, mens om høsten var denne korrelasjonen positiv. Tidligere arbeid med identisk oppsett for laks (*Salmo salar* L.) viste samme resultat som hos ørret, selv om lakseyngel viste en høyere preferanse for dypt habitat og hadde tetthetsavhengig habitatbruk om høsten. Resultatene fra dette studiet tyder på at eventuell dødelighet fra effektkjøring i den grunne delen av elva vil resultere i ledige territorier som vil bli gjenintatt av individer fra de dypere delene av elva i en sink-source dynamikk og dermed gi grunnlag for additiv dødelighet i respektive populasjoner.

Introduction

Territory size and function is related to food availability for territorial animals (Marschall and Crowder 1995, Grant et al. 1998, Toobaie and Grant 2013). Competition of defended resources is referred to as *interference competition*, and occurs when the competitors interact with one another in order to reduce the other individual's ability to exploit the resource (Krebs and Davies 1993). This is opposed to *exploitative competition,* where fitness decreases due to resource exploitation of other nearby individuals. Territoriality, defense of a limited resource, pays off if the surplus energy gained by defending the profitable space exceeds the expenses connected to the defense (i.e. energy spent chasing off competitors) (Brown 1964, Grant 1993).

The sudden and varying need for electricity leads hydropower producers to produce and sell electricity, on a frequently changing, daily scale basis (Morrison and Smokorowski 2000). With a new international market, this type of production has increased during the latest years and is predicted to increase in the future even further. When river discharge changes rapidly and frequently due to hydropower production, it is referred to as *hydropeaking*. Due to the possible deleterious effects on the stocks and well-being of stream-living organisms, a hydropeaking knowledge base is necessary to make the effects of hydropower as environmentally friendly as possible. In order to dismantle the possible direct deleterious effects from hydro peaking, the effects on habitat use from the other remaining variables need to be known.

Populations of salmonids are strongly density regulated during their fresh water phase, due to territoriality and food availability (Bohlin 1977, Jenkins et al. 1999, Einum 2005, Grant and Imre 2005). The habitat use of each individual in an ecosystem is thus the result of territorial competition with other individuals in its vicinity. The density effects on the habitat use of Atlantic salmon in their first year, also referred to as *young-of-the-year* (YoY), have been covered in earlier experiments, and shown to have no density-dependent effect in summer and weak effect in autumn (Bentsen 2011, Hamnes 2011). The differences in habitat use of brown trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) have been covered extensively, especially the meso- and macrohabitat use (Heggenes et al. 1995, Heggenes et al. 2002) and in field studies in sympatric sites. Atlantic salmon selects the sites in the river with the higher water velocity and depth and brown trout use the shallower sites with lower water velocity (see Jonsson and Jonsson (2011) for a detailed comparative review). Brown trout is known to

increase its range of habitat use when living allopatrically, compared to sites where it has to compete with other fish species, such as Arctic charr (*Salvelinus alpinus*) and whitefish (*Coregonus lavaretus)* (Klemetsen et al. 2003).

Deducted from Brown (1964), theory predicts that when a rich habitat has no more available territories, the poorer habitats are being utilized. Experiments indicate that the habitat use by brown trout correspond with this theory (Bohlin 1977). For brown trout the only density related studies provide information about the YoY brown trout's mesohabitat (run/riffle/pool) use as the density of YoY increases (Bohlin 1977, Greenberg 1994). Bohlin (1977) discovered that young trout preferred the deeper pools (in this experiment only 15cm deep), but started to use the shallower riffles (7cm deep) as density increased. Only the age was reported, the size of the different fish was not reported. Greenberg (1994) also investigated the influence of density (1.5 and 3 fish m^{-2}) on habitat use, but found the exact opposite result: an increase in pool use when density increased. If mesohabitat use truly follows the density-dependent habitat distribution hypothesis Greenberg proposed, then possible deleterious hydropeaking effects would only tend to increase as populations of YoY decreased.

Body size and age are two variables of high importance when competing for positions within the brown trout population hierarchy in streams (Symons 1968, Bachman 1984). Body size seems to be the most important factor when competing for a territory, where larger fish occupy the deepest parts, evicting the smaller ones (Bohlin 1977, Greenberg 1994, Vehanen et al. 1999, Kaspersson et al. 2012). Body size and age correlate and it has been shown for Atlantic salmon, that when the cohorts (age classes) overlap closely in size, more competition occurs (Einum and Kvingedal 2011). This was considered to be of importance for similar species that experience *ontogenetic niche shifts* (here: change in diet and habitat use with increasing size and age). As the difference in body size increased, the competition decreased between the cohorts and resulted in increased growth for the individuals most affected by inter-cohort competition. Brown trout undergo an ontogenetic habitat shift and it happens earlier when a population experiences fast growth (Klemetsen et al. 2003).

The *asset protection principle* states that if an individual already is of large size, and this results in increased fitness, it should take fewer risks than an individual of smaller size (Clark 1994). Being active during day-time increases the risk to encounter predation due to the increased chances of being visually spotted by e.g. avian predators (Fraser et al. 1993). For Atlantic salmon shows this activity pattern for parr vs. YoY (Imre and Boisclair 2004). The

asset protection principle might explain the size-hierarchy in regards to depth as seen in many streams (Schlosser 1987, Heggenes et al. 1999), and this hierarchy might be stronger in rivers known to inhabit size-selective predators (Greenberg 1994, Greenberg et al. 1997, Magoulick 2004).

In winter, smaller trout (<25cm) usually seek shelter during daytime and start feeding at night-time (Heggenes et al. 1993, Bremset 2000). This phenomenon is probably caused by a combination of water temperature and light conditions. In a study on Atlantic salmon, fish switched from diurnal to nocturnal feeding (Fraser et al. 1993) when temperatures dropped below 10° C. For brown trout this nocturnal shift can be seen as early as August/September in Sweden with temperatures ranging from 10-12°C as a threshold value (Greenberg et al. 1996). As for depth, changes in preferences can be seen already from June to July, the YoY selecting deeper waters in July (Harris et al. 1992). Light conditions might be one important factor, but differences between populations and geographic areas might complicate the picture. In a river in Finland, the youngest YoY preferred shallow areas with large amounts of aquatic cover during summer and autumn (Mäki-Petäys et al. 1997), whereas in winter they preferred shallower areas with less aquatic cover. Considering the current knowledge base on the different complex interactions between seasons and habitat use, it's important to account for this in an experimental setting in order not to draw false conclusions. Furthermore, a seasonal change observed in i.e. Harris et al. (1992) might be the result of a spurious relationship, an artifact, due to YoY size change and thus higher preference for larger substrate and deeper water.

The purpose of this investigation was to discover which factors and combinations affect habitat use in brown trout. Are there any densities or conditions where the populations will not be affected by possible deleterious effects from hydropeaking? Density dependence was investigated in an experimental artificial river divided in a deep and shallow section. This was investigated by the variation of density in two seasons that currently lack comparative examples: summer (June) and autumn (October). Although extensive theory exists on the size-hierarchy, and thus inter-cohort competition in rivers, it is unclear when competition based upon size starts to occur. This was done by testing inter-cohort competition with age-1 fish, using an individual size-based model to compare with existing theory.

## Materials and methods

Experimental design and procedures

The experiments were conducted in two rounds: between 9th-18th of June and between 30th of September-10th of October 2012, at the NINA Research Station at Ims, near Sandnes, southwest in Norway (58° N). Water temperatures ranged from 13.6°C- 16.0°C, with a mean of 15.1°C (SD 0.8°C) in June and 10.2°C-11.0°C in September/October, with a mean of 10.8°C (SD 0.4°C). The experimental methods and design followed the protocol similar to the Atlantic salmon experiments conducted the year before the present study (Bentsen 2011, Hamnes 2011).

An outdoor artificial stream was built to contain two habitat types, a deep and a shallow part (see Fig.1 a,b from (Bentsen 2011)). This arena was used to test habitat use of YoY brown trout in four different treatments. These treatments followed a 2x2 factorial design, with high/low density of YoY and presence/absence of age-1 trout as the two major explanatory variables. A total of four experimental arenas were used each day. This allowed for a balanced design, where each arena switched treatment each day.

The arenas were each $30m^2$ and divided into $3 \times 10m^2$ sections. The sections were separated by a mesh, penetrable to water without any notable effect on water velocity. Physical properties of the sections (Tab. 1) had not been altered significantly since the similar experiments the year before, and therefore assumed to have approximately the same values (see Bentsen (2011) for more details of the measurement method). A summary of these values was reproduced from Bentsen (2011) . Substrate consisted of homogenously distributed pebble and gravel of various sizes.

Table 1. Physical parameters for the artificial streams. Values taken from measurements by Bentsen (2011).

	Mean (SD)
Deep Habitats:	
Depth (cm)	31 (3.4)
Current bottom ($cm \cdot s^{-1}$)	6 (3)
Current 60% ($cm \cdot s^{-1}$)	10 (3)
Shallow Habitats:	
Depth (cm)	18.0 (3.2)
Current bottom ($cm \cdot s^{-1}$)	3 (1)
Current 60% ($cm \cdot s^{-1}$)	5 (1)
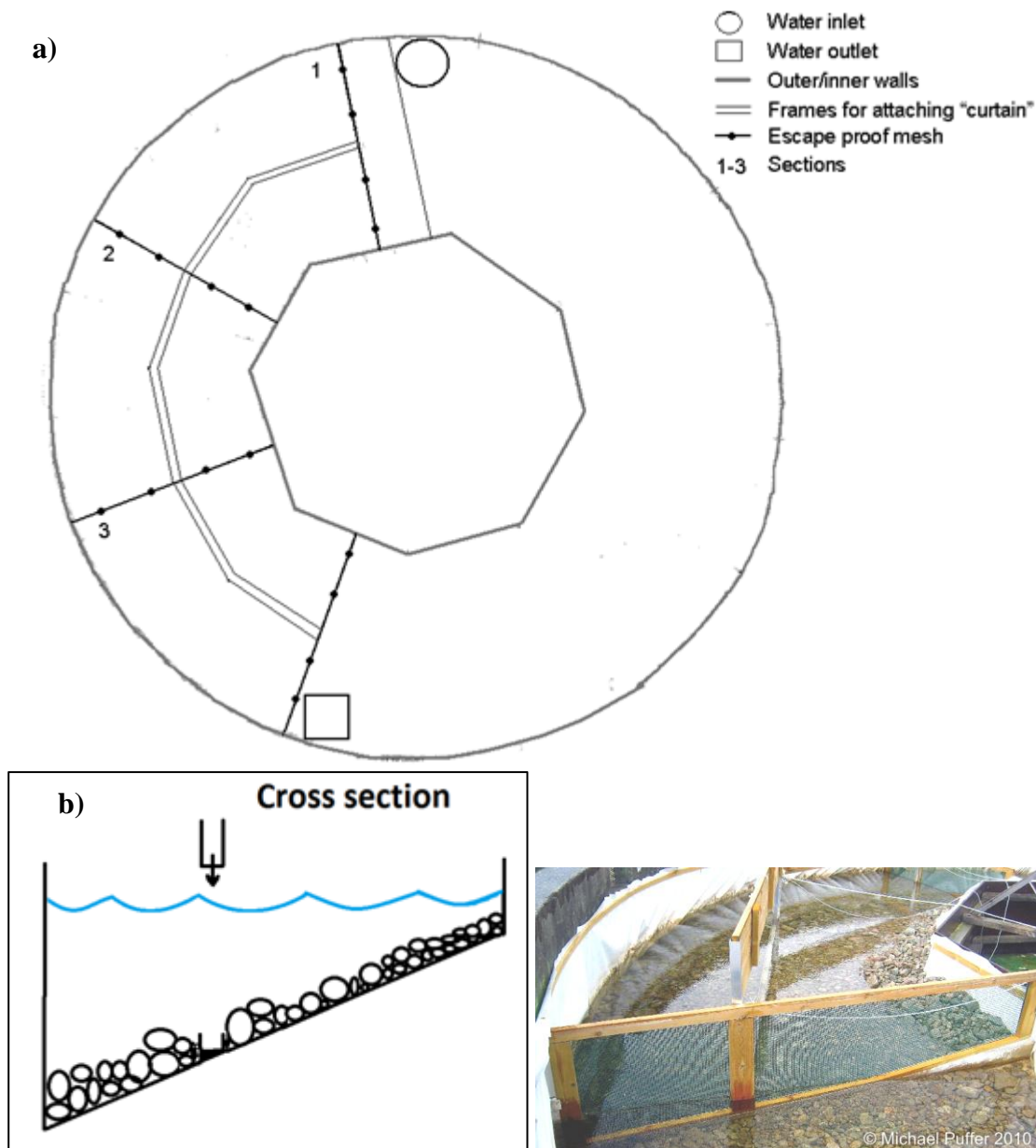
Figure 1 Schematic overview over the experimental arena, showing the arena from above a) and the stream's cross section b). The deep and shallow habitat parts of each section are at the end of the experiment divided by an impenetrable curtain. This curtain is dropped remotely by pulling ropes with metal bolts that held the curtain suspended above the water line. The middle, octangular, part of the arena is considerably lower than the artificial stream, giving the staff partial camouflage whilst operating the curtains.

A low density treatment included 10 YoY, while a high density treatment had 30 YoY, the density of a low and high density treatment was thus one and three fish m^{-2}, respectively. If the treatment included presence of larger fish, two age-1 fish were added in each section. The three sections of each arena had the same treatment the same day, to avoid possible vicinity effects from other treatments. Fish used in the experiment were hatchery reared. Both cohorts of brown trout belonged to the same local strain. This was a strain from the local stream *Fossbekk* which is known to have anadromous variants of brown trout. The same individual

Table 2. Number of trout (YoY and age-1) used in the experiment and their respective sizes (fork length).

	Number of fish	Mean size mm (SD)
YoY		
Summer	2276	46 (5)
Autumn	2377	79 (12)
Total	4553	
Age-1		
Summer	120	155 (14)
Autumn	96	207 (19)
Total	216	

was not used twice in an experiment, according to Norwegian laws and standards for animal research and welfare. Details about the subjects can be seen in Tab. 2. It should be noted that the YoY grew in average 5 mm during the 10 day experimental period during summer; in autumn the fish grew in average 11 mm during the 10 day period. The hatchery reared age-1 fish were larger than they would have been after one year living *in situ*. Any competition observed in this experiment should thus be regarded as competition from a fish of size *x,* rather than a fish of age *y*.

The fish were stocked daily in the arenas and had access to both the deep and shallow section of the artificial stream. Earlier experiments have shown that fish behave normally after 5 hours and showed no change in habitat distribution after approx. 20 hours, making the experimental period reliable (Bentsen 2011, Hamnes 2011). YoY were always stocked ahead of the addition of larger age-1 fish. Age-1 fish were gutted after the first day of the experiment and no YoY was found in the stomach content. One experiment lasted for 18-24 hours, mostly for keeping a practical daily schedule, which allowed fishing during day time (10.00-18.00). An overhead white tarp was covering about 50% of each section in order to prevent unwanted schooling effects and to prevent additional stress for the fish during the summer. After the experimental period was over the habitat distribution was *fixed* by dropping down the curtains in the middle of the stream, separating the shallow from the deep habitat type. The fish were then recaptured with portable electro-fishing gear at 250V. The curtain between the two habitats allowed fishing one habitat type without stressing the fish in the other one. After fishing the section once, about 60-70% of all fish had been recaptured. Several rounds of careful fishing, with recovery time for the fish in between the recapturing, were thus necessary in order to catch all individuals. Once captured, each fish was measured and gathered in a small fish tank.

Statistical approach

The probability for a YoY to be in the deep habitat was modeled as response variable using fish size, presence of larger fish (age-1) and density as explanatory factors. A generalized linear mixed effect model (GLMM) was used in the analysis of the data, with the lme4 package (Bates et al. 2013) in the statistical software *R* (R Core Team 2013) with a binomial error distribution. The random effects were included in the model due to known differences in the variation between the sections in regards to habitat structure. Variance also differed a great deal from replicate to replicate, making it impossible to ignore as a random effect. For both experimental periods, the variance of the response variable also differed significantly from day to day (summer: p<0.004, autumn: p<0.001).

For selecting the final model, an approach more closely described by Zuur et al. (2009) was followed. If the residuals of the models show any form for heterogeneity, the appropriate variance covariate was selected by the varIdent and ANOVA function, which is the variance structure used for binomial data. This procedure yielded the following model used later in the backwards model selection for both seasons:

$$\pi_{ijkl} = \alpha + \beta_1 D_j + \beta_2 L_j + \beta_3 S_i + \beta_4 S_i D_j + \beta_5 S_i L_j + \beta_6 D_j L_j \qquad \text{(Eq. 1)}$$

$$+\beta_7 S_i D_j L_j + \alpha_j + \alpha_k + \alpha_l + \varepsilon_i$$

Where $p = \frac{e^\pi}{1+e^\pi}$ $\qquad$ (Eq. 2)

$$i = 1, \dots n \quad j = 1, \dots 120 \quad k = 1, \dots 10 \quad l = 1, \dots 12$$

In Eq. 1 π gives logit of the probability, *p* (Eq. 2), for a YoY fish to be in the deep habitat for individual *i* in replicate *j* on day *k* in section *l*. This response variable depends on the intercept, α, the estimated parameters from the model, β_{1-7}, the size of each individual, *S*, presence or absence of larger fish, *L*, and high or low density, *D*. The terms that include β_{4-7} are the estimates for the interactions between the main terms, *S*, *L*, and *D*. The last two parts of the equation give the random intercept, α_{j-l}, and the residuals, ε_i.

The selection of the correct model was later made using backwards selection from the full model listed in eq.1 and validated with ANOVA. Using lmer4, models were fitted and estimates were approximated with Laplace approximation through the selection process.

Results

Summer (June)

Density showed a non significant effect in summer on habitat distribution of the YoY from increasing the density of the YoY (see appendix for details of the full model). The density main term, being the effect from density *per se*, was barely significant (p< 0.041). But when the three-way interaction with body size and presence of age-1 brown trout (p<0.092) was removed from the model, the significance of both the interactions and the main term dropped to an even lower significance level (p= 0.22). After several rounds of backwards selection, neither of the terms that included any effect from density were left in the final model. In the final model only body size, presence of larger age-1 fish, and the interaction between these two variables were significant (all of these p<0.001, see Tab. 3 for details). Selection of models using ANOVA, which is testing for a significant change in log-likelihood between each model, provided the same final model.

Mean probability for the YoY of being in the deep section was 0.45, regardless of treatment. The same probability for the age-1 fish was 0.85. Without larger fish present the probability was 0.61 and when present the probability was 0.29 There was a strong significant negative correlation between depth preferences and body size within the YoY cohort (see Fig. 2), in treatments that included the larger age-1 conspecifics. When the age-1 is not present, however, YoY body size is positively correlated with the probability of being in the deep habitat. Due to the back-transformation of the data from logit form, the graph could not include the respective confidence intervals. Details regarding this statistical part are included in the appendix.

Table 3. GLMM results for the summer experiment, fitted with Laplace approximation. Section, day and replicate number were used as random effects. The response variable is the probability of being in the deep habitat for the YoY fish. n=2276 individuals, replicates= 119.

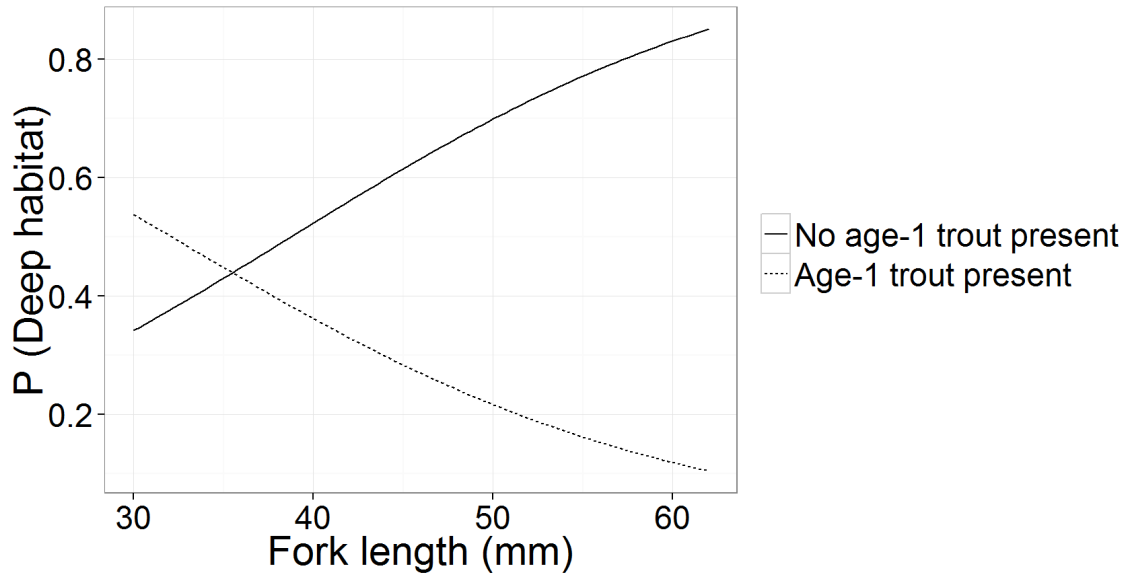| Term	Estimate	Z	P
Intercept	-3.002	-4.012	<0.001
Body size	0.077	4.899	<0.001
Presence of age-1	4.485	4.723	<0.001
Body size: presence of age-1 interaction	-0.139	-6.332	<0.001

Figure 2. The summer experiment showed opposing results for size dependent habitat use between treatments where age-1 conspecific individuals were present or absent.

Autumn (October)

Density affected the habitat distribution of the YoY significantly, but only in the interaction with a larger conspecific present (p<0.015, see Tab. 4). The main term, the effect solely from density, remained insignificant (p<0.17), but was included in the full final model due to the significant interaction. Body size and presence of large conspecific age-1 were, as in the summer, significant variables affecting habitat distribution (both p<0.001). Contrary to the results from the summer experiment, the interaction between body size and presence of large conspecifics was missing. In both treatments, with and without large conspecifics, body size was positively correlated with the probability of being in the deepest section (see Fig. 3). Only predicted graphs are shown, without the confidence intervals. (For confidence interval and full model, see appendix)

Table 4. GLMM results for the autumn experiment, fitted with Laplace approximation. Section, day and replicate number were used as random effects. The response variable is the probability of being in the deep habitat for the YoY. n= 2377 individuals, replicates= 120.

Term	Estimate	Z	P
Intercept	-1.24	-3.05	0.003
Body size	0.033	6.83	<0.001
Presence of age-1	-1.153	-5.7	<0.001
Low density	0.293	1.32	0.186
Age-1 present: low density interaction	-0.814	-2.47	0.014
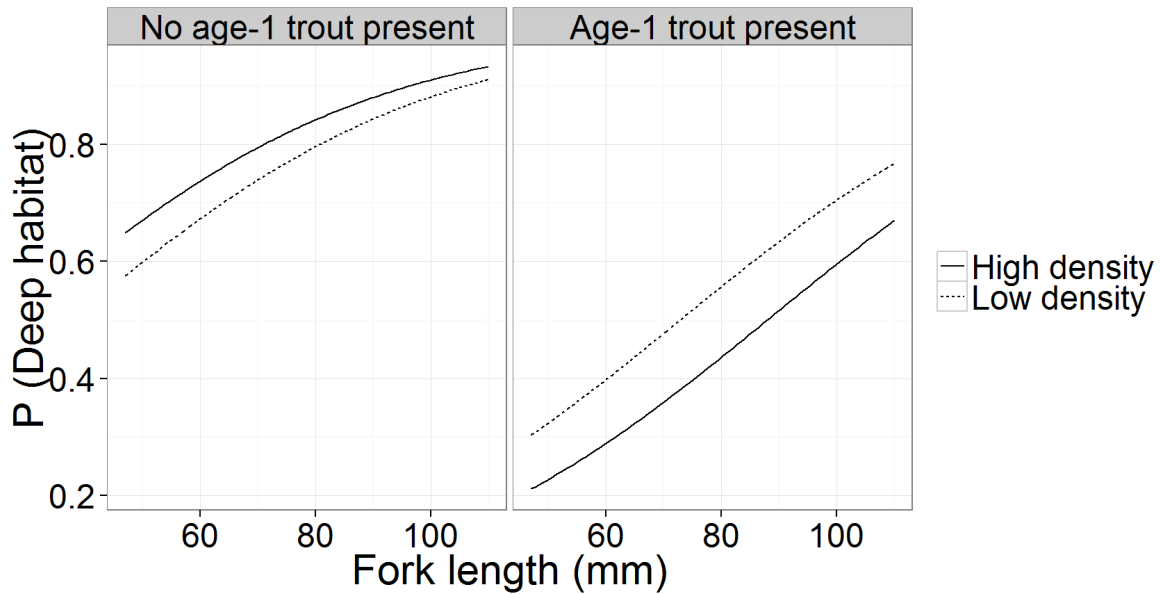
Figure 3. The autumn experiment showed an overall increase in mean depth preference. A positive correlation between body size and the probability of being in the deep habitat was observed for all treatments.

Overall, the YoY showed an increase from the summer experiments (probability 0.45) in mean preference for the deeper section in the autumn, to 0.67, regardless of treatment. Mean probability for the YoY of being in the deeper habitat, without larger age-1 conspecific present, was 0.79. When the larger age-1 conspecifics were present, however, the mean probability dropped to 0.50. Mean probability to be in the deep habitat for the age-1 fish had increased from the summer experiments (0.85) to 0.94 and they had also grown by 5cm in average body size. Considering the effect of density, the means for the treatments *without* large conspecifics were not significantly different ($p=0.177$). But the different density treatments with large conspecifics *present* had significantly different means ($p<0.025$), where high densities of YoY increased the chance for the YoY of being in the deep habitat.
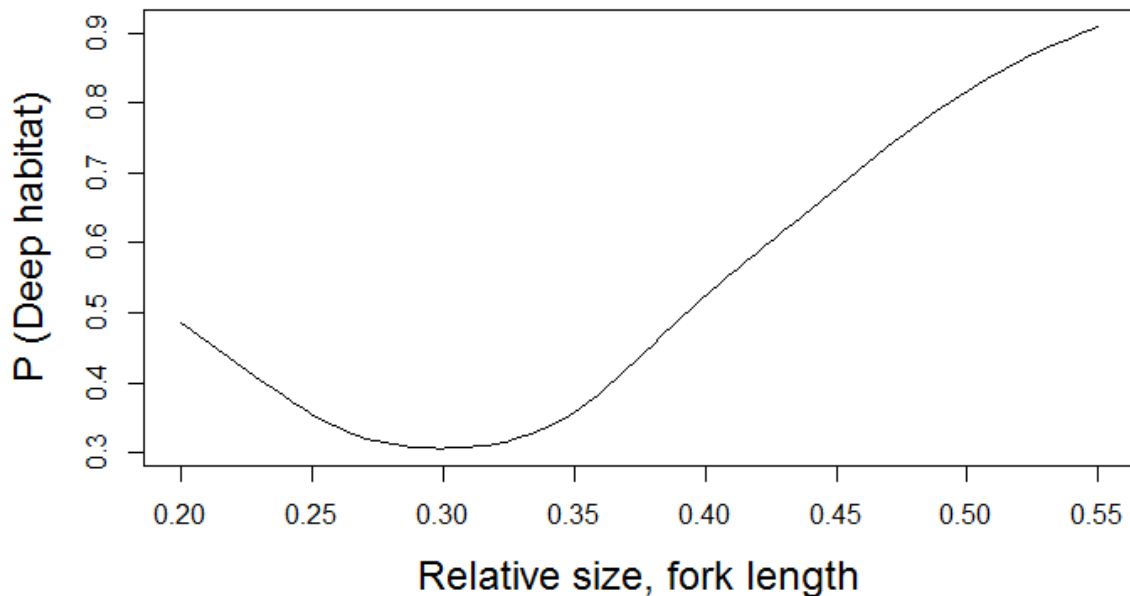
Treatments with age-1 fish present

Using data from both seasons, the Gamm4 package was used (Wood 2012) in *R* to create a GAMM based upon the full GLMM model. This model included only fish size, primarily, and sequence number as a random factor. Using the *predict* function, a hypothetic graph combined the two seasons in Fig. 4. The good thing about having a large number of observations is that the standard errors for body sizes are quite small. But as a wary reader may notice: where the

two seasons overlapped few data existed due to being in the extreme sizes for the respective seasons.

The lack of confidence overlap of the fish sizes between seasons (Fig. 4) craved for a different type of analysis. A decision was made to convert from the original absolute fish size to the more season-overlapping and biologically relevant variable, relative size (Size of each YoY divided by the size of the biggest age-1 in their experimental trial). Using relative size instead of absolute size immediately improved the AIC of the GLMM model by 5. If a smoother term in a GAMM model is i.e. squared or cubic with relatively more than one degree of freedom, then a linear mixed effect model (GLMM) would be inappropriate (Zuur et al. 2009). This new model had a significant smoother term (p<0.001) and nearly 3.5 degrees of freedom, which indicates that the smoother curve is non-linear. A GAMM model for the merged dataset of both seasons would thus be better, and the result using relative size as the only explanatory variable can be seen in Fig. 5.
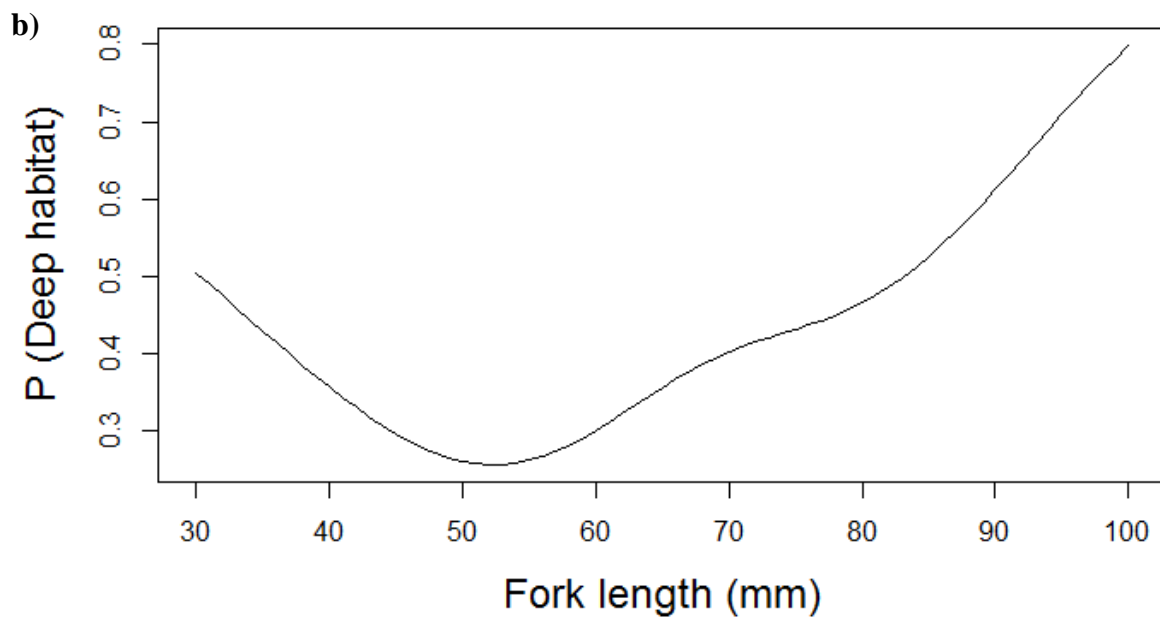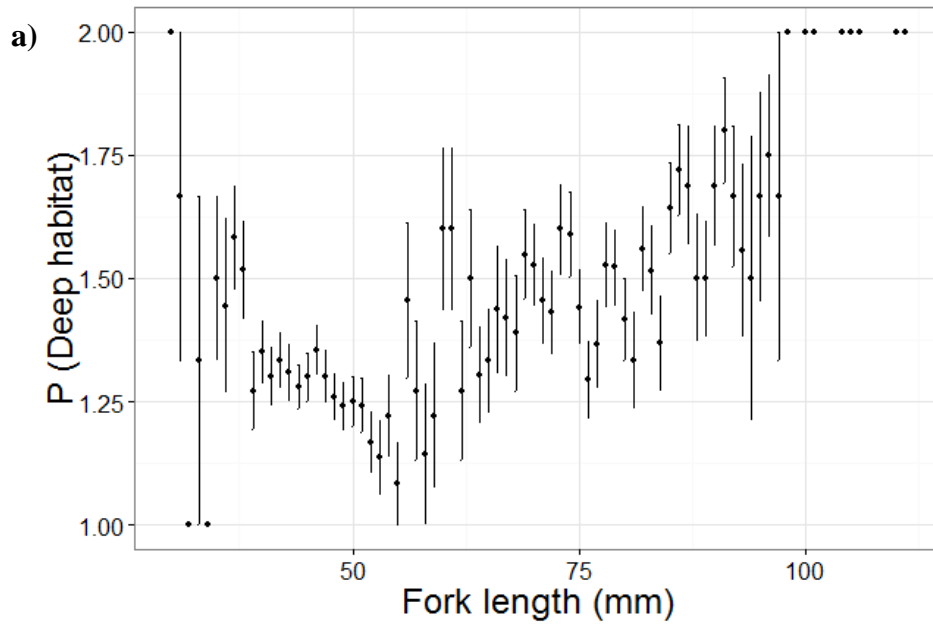
Figure 4 Habitat distribution of the YoY when larger fish is present, pooled for both types of densities. a) Body size as a factor, with standard error bars of the means of each mm of size. b) GAMM model used to predict the plot using absolute size as the only explanatory variable .

Figure 5. For trials with age-1 fish present, relative size is plotted as explanatory variable$\left(\frac{S_{YoY}}{S_{age-1}}\right)$. A GAMM model was used with merged data from both seasons.

Having seen an obvious and logical trend in the merged data, it is yet to analyze whether or not there is a seasonal difference. Inspecting the GAMM model, both season and its interaction with relative size were highly significant factors ($p<0.001$). Plotting $\hat{p}$ for relative size (x-axis interval= 0.01) and differing between the seasons, two different plots of "residuals" was extracted (Fig. 6). Although autumn showed a dip-shaped curve (n=92 individuals for relative sizes 0.24-0.29, n=5 ind. for relative sizes 0.21 and 0.23), summer showed a consistent negative correlation (n=274 ind. for relative sizes 0.31-0.35, n=14 ind. for relative sizes 0.36-0.39). Further analysis (ANOVA) for the autumn data showed that a GLMM with a squared relative size (relative size^2) as explanatory variable was significantly different than the original values for relative size ($p<0.05$). Since summer data showed no such significance ($p<0.4$), a GLMM for both seasons was used, including a squared relative size term in the autumn model. Thus, two different models were the frame for the last graph in this part, which illustrates the relative size- and seasonal-dependent difference in habitat use (Fig. 7). The new model with relative size no longer showed a significant effect from density ($p=0.062$).
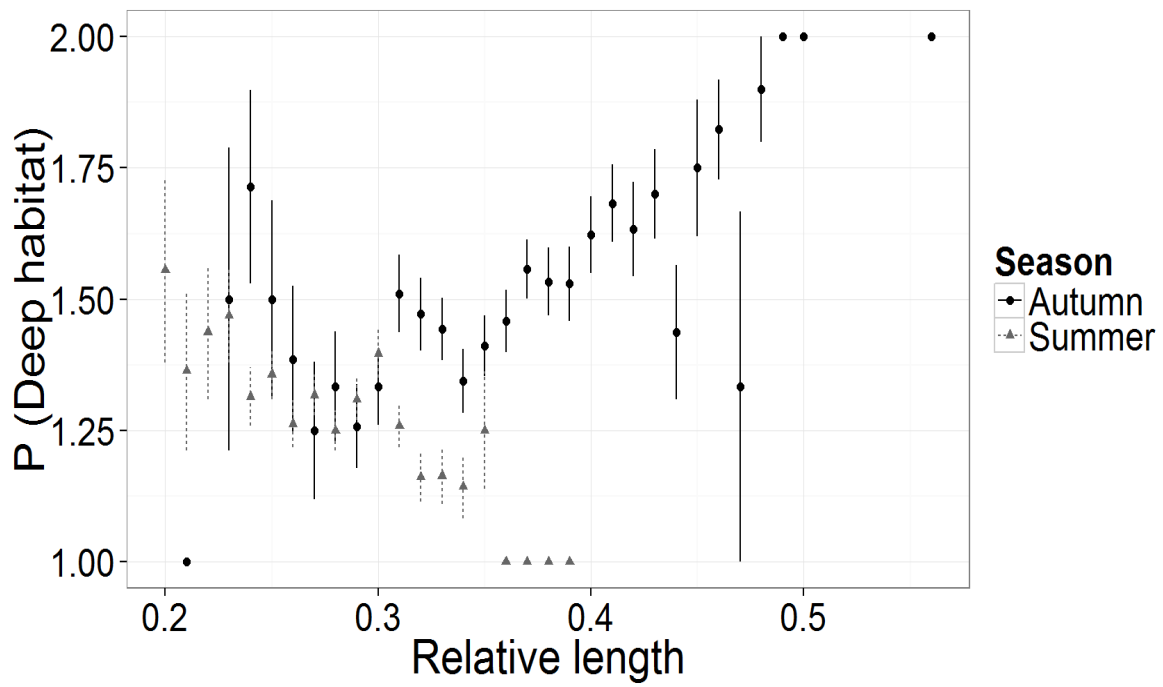
Figure 6. $\hat{p}$ with respective SE for relative body sizes, divided by season. Relative size interval: 0.01.
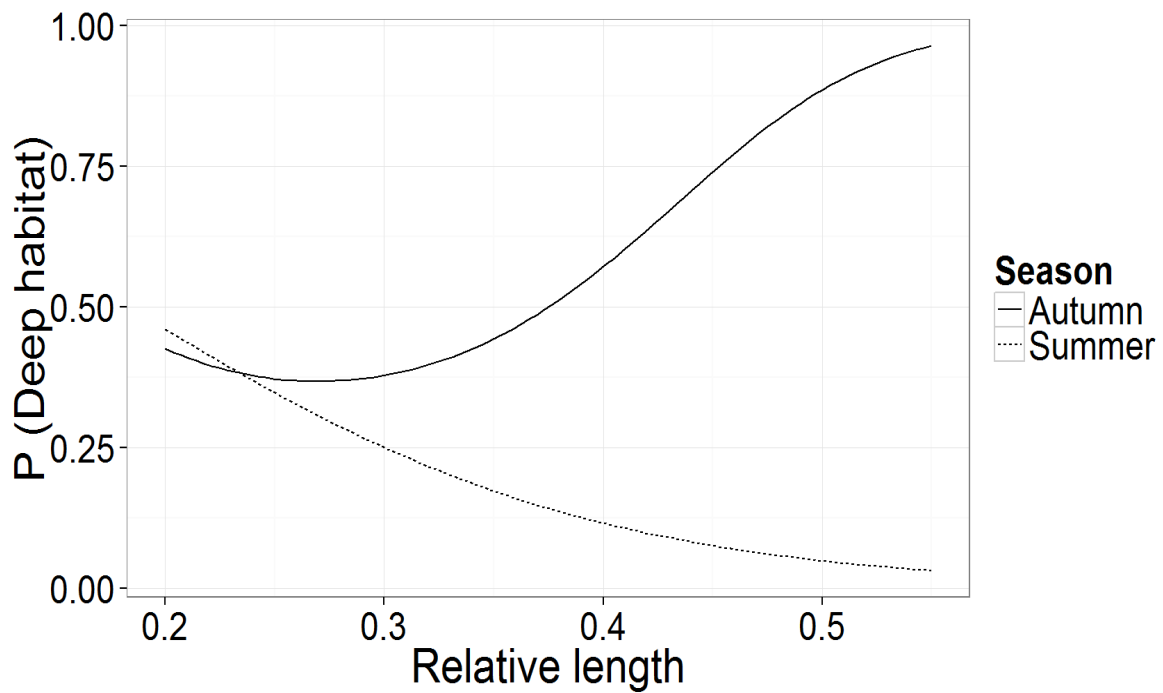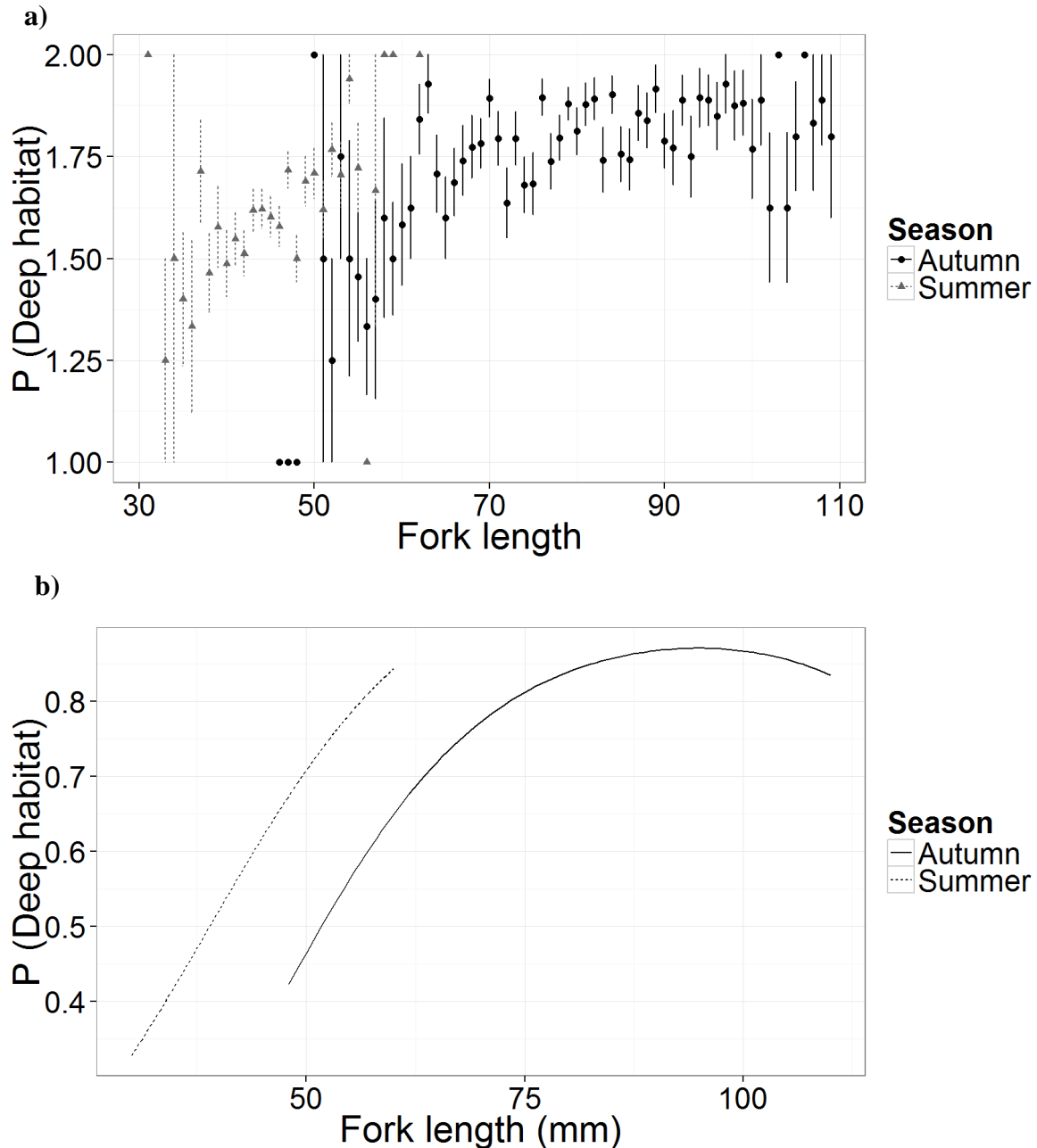

Figure 7. Seasonal differences modeled by a GLMM, using relative size as explanatory variable to the response variable YoY habitat use. For autumn data, relative size was squared and added in addition to using a non-squared term.

Treatments without age-1 present

Treatments where only YoY were present were analyzed in the same manner and showed a significant difference in intercept values for each season (p<0.05, Fig. 8). The initial model also showed a seasonal slope difference (interaction between body size and season: p<0.01). Further analysis, however, showed that a cubic term (body size^3) was most appropriate, and this new included term made the seasons' slopes equal.

a)

b)

Figure 8 Seasonal differences for treatments where only YoY were present. a) $\hat{p}$ with respective SE for each mm of absolute body sizes, divided by season. b) GLMM models using absolute sizes as explanatory variables. For autumn values cubic values of absolute size are included.

The correlation between the probability of being in the deeper habitat and body size was positive in both seasons. If this positive correlation was based upon a size-dominance

hierarchy, a hierarchy-based size variable should provide a better model than absolute size. Standardized size ($\left(\frac{s_i - s_{\bar{j}}}{SD(s_j)}\right)$ where s = size, i = YoY individual, j = replicate) takes into account large size differences within a replicate, and reflects asymmetric size differences based upon the standard deviation of the sizes in each trial. However, this worsened the AIC of the model by 4 where both seasons were included. Another choice for a size-dominated hierarchy variable could be normalized size ($\left(\frac{s_i - s_{\bar{j}}}{s_{\bar{j}}}\right)$ where s = size, i = YoY individual, j = replicate), which does not take the standard deviation into account. This variable did improve the model by 2 AIC for the treatments without a larger fish present. As for the model with a cubic absolute size, the normalized size variable showed no interaction with season. Furthermore, when normalized size was squared, it improved the model by another 2 in AIC. A graphical representation of this improved model (Fig. 9) needs to be seen in light of Fig. 8.

When concluding at the end of this analysis, it is certain that each individual needs to be seen as a competitor and influenced by nearby competitors. The probability of a fish to use the preferred habitat was best explained by variables that accounted for its *relative* competitive ability compared to other competing individuals in the river.
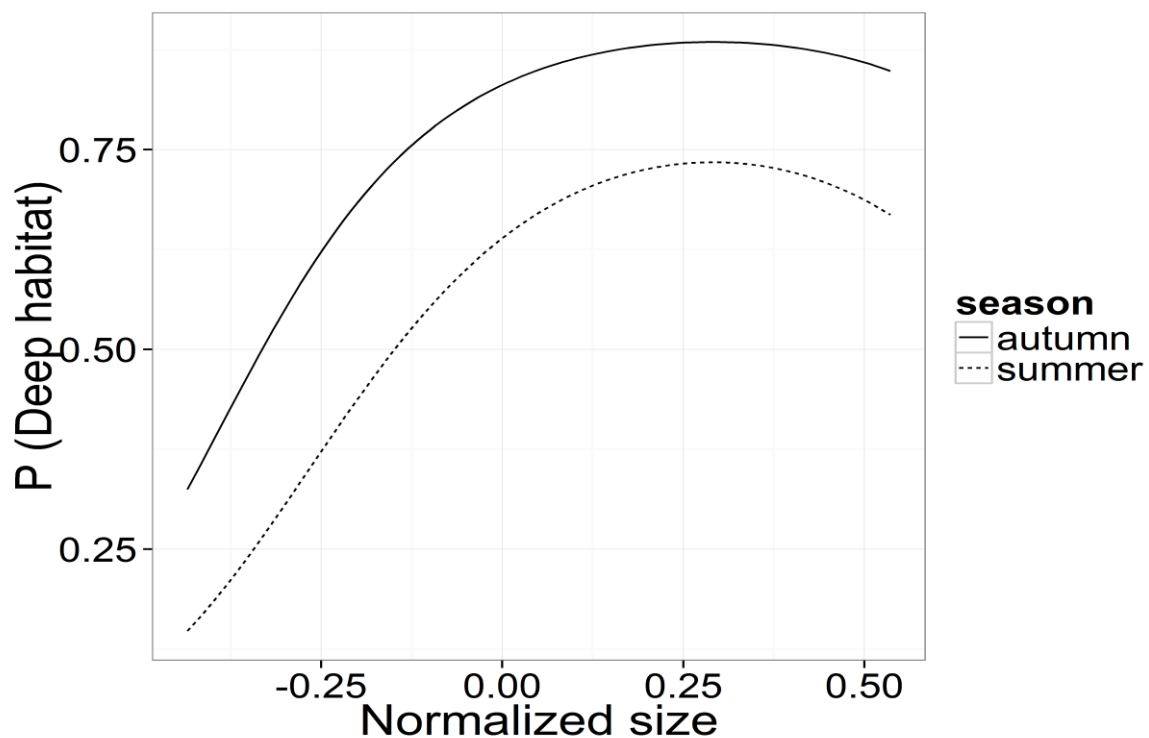
Figure 9. Probability of a YoY to be in the deep habitat, based upon normalized size $\left(\frac{s_i - s_{\bar{j}}}{s_{\bar{j}}}\right)$, plotted for the two seasons. This size variable is closely linked to absolute size, but takes into account big differences in absolute size, and thus each individual's competitive ability related to the other individuals in its replicate.

Discussion

Density effects

Due to the improved models with normalized and relative size, the significant density interaction between treatments with age-1 present and absent becomes obsolete since there is no comparable variable. The effect of density is probably strongest when a large territorial conspecific is present. As the number of conspecifics increases, the energy spent fencing off competitors starts to increase, and at one point the costs exceed the benefits of having a large territory- making it likely to observe decreased territory sizes (Krebs 1971). It has been shown in brown trout that territories of age-1fish were not lost despite increased densities of YoY (Kaspersson et al. 2010) , although the number of unsuccessful foraging attempts by the dominating larger fish increased. In contrast to the expectations, brown trout was shown to compensate by increasing stress levels and aggression as density increased (Kaspersson et al. 2010). This means that there is a great advantage in big asymmetric differences in size when it comes to spatial dominance, and that territories are worth to keep fighting for.

Seasonal changes

If any seasonal difference was to occur on the habitat distribution of the YoY, the only experimental design would require comparing exactly the same size ranges of YoY compared to exactly the same size range of age-1 fish. This was not possible as the fish grew considerably in size during the four months between the experimental rounds. By using absolute size it's not possible to say that there is seasonal difference *per se*. It could just as well be a size-dependent preference of habitat. Using relative and normalized sizes, it becomes easier to compare the data for seasonal differences. That being said, using relative or normalized fish size involves looking at fish of comparable rank within the dominance hierarchy, yet the respective fishes can have quite different physical abilities or from absolute size, i.e. keep their position with increasing water velocity and available burst speed or energy that may affect preference or habitat use (Finstad et al. 2007).

A seasonal difference occurred in treatments where age-1 individuals were absent (Fig. 8). Season seemed to have a size-independent effect on the depth preference of trout, lowering the probability to be in the deep habitat for fish of comparable sizes. The probability decrease for the biggest body sizes (absolute size: Fig. 8 and normalized size Fig. 9) in this

investigation, which gives a dome-shaped function, should be disregarded, as there is no biological reason why there should be one. Considering the mean probability of the ~16-21cm age-1 was 0.85-0.95 of being in the deep, there is reason to believe the probability function should slowly increase up to this value as body size increases. The decrease in probability at big body sizes is probably a result of statistical noise of the extremes. A question could be raised about the size-distribution we observe in nature of similar-sized trout: Is the distribution a result of size-dependent competition or of size-dependent habitat preferences? On one hand, it could be a seasonal effect, which lowered P(deep) for the comparable sizes by 0.3. On the other hand, this could be the result of the absolute size change in the size-hierarchy. Research on this matter was conducted on two size classes of relatively big YoY trout (10 and 12cm) (Greenberg et al. 1997). The only effect of intracohort competition was the difference in foraging rate. The treatments included having the size-classes together (sympatry) and alone (allopatry). There was no intracohort competition effect on the distribution, when occurring in sympatric populations as opposed to living alone (Greenberg et al. 1997). Vehanen *et al.* (1999), on the other hand, showed a significant change in distribution for the YoY when competing with the 3 cm larger one year old fish, also referred to *age-1* fish. Previous discussion considered substrate difference in the experimental arenas to be the causal part of the difference. Both studies used water velocity as the main variable for habitat description. Although water velocity is highly correlated with water depth, water depth has been shown to be the regulating factor controlling the habitat preferences for young of year trout (Bardonnet et al. 2006). Furthermore, it has been shown for the closely related Atlantic salmon that prior residence (Kvingedal and Einum 2011) and standard metabolic rate (Cutts et al. 1999) are better variables when determining intracohort dominance for YoY.

Intracohort competition

Normalized size was considered as a good variable to use when modeling habitat use for YoY in the present study. This is an indication of a size-dominated hierarchy (Symons 1968, Abbott et al. 1985). The fact that Greenberg et al. (1997) failed to find a spatial change in the size-class experiments might be the result of comparing population means, and not individual data. There might be a relative size threshold when significant changes in habitat distribution start to occur. This threshold might be closely linked to aggression, territory size and the size-assessment theory model. Thus, if the individuals are closely related in size, there will be

more competition for the best territories, and less likelihood of observing a change in size dependent habitat distribution on a population based model. The habitat dominance, in these situations, could be further complicated by individual differences in standard metabolic rate, but not prior residence, as we introduced all the fish at once in this study (Cutts et al. 1999). The relationship between normalized size and probability of being in the deep habitat (Fig. 9) is an example of this argumentation. All positive values of normalized size indicate that the fish is either equal to the mean or bigger than the mean size within its replicate. If normalized size >0, the function is flat, in other words the function shows *no change in habitat distribution*. On the other hand, if normalized size <0, these individuals are in an increasing rate located in the shallow habitat. This might suggest that the spatial competition threshold starts at negative normalized size values within a size-dominated hierarchy.

Intercohort competition

The bigger fish-deeper habitat correlation found in this investigation matches other existing theories for intercohort competition in brown trout (i.e. Bohlin 1977, Bachman 1984, Mäki-Petäys et al. 1997, Vehanen et al. 1999, Kaspersson et al. 2012). The mechanisms behind exclusion of smaller fish from their preferred habitats may be two-folded. Firstly, the YoY may be directed to the shallower stream bank due to interference competition from the larger, dominant, individuals. It clearly falls into the definition of interference competition, since the YoY suffer decreased growth in these habitat types (Kaspersson et al. 2012). Secondly, the smaller fish may perceive the larger fish as a predator, and thus avoid the predator's habitat. The decreased growth seen in the shallows might just as well be the result of reduced time to forage and more time spent being vigilant (Metcalfe et al. 1987). It should be repeated that cannibalism was not observed during the experiment. That being said, the effect of interference competition on a spatial scale can be hard to disentangle from anti-predation behavior if both effects provide same patterns of habitat use.

Cannibalism is traditionally not considered to be an important factor for stream-dwelling trout populations. However, cannibalism can be present and it is considered by some researchers to be important for the mortality of YoY in certain rivers, especially if the rivers are regulated (Vik et al. 2001). In brown trout, the proportion of the population that is piscivorous can be as high as 20%, as reported by Vik et al. (2001), but has a great variation and averages at around 5% (L'abée-Lund et al. 1992). When cannibalism occurs it's probable that the potential

victims adjust their behavior in the vicinity of their potential consumers, regardless how rarely it occurs. L'abée-Lund et al. (1992) concluded that brown trout cannibalism is rare and probably limited to populations where brown trout occur allopatrically, since the species catches other fish species more easily. However, if the species has been cannibalistic at some point during evolution, the effect on fitness and adapting behavior against cannibalism would be strong.

The *size-assessment theory* (Enquist and Leimar 1983) provides a model that mathematically predicts the outcomes of contests between two individuals of unequal size/fighting capability. One of the conclusions from the model is that a weaker animal will assess the fighting capability of the stronger contestant through many steps/interactions. The larger size difference between the individuals, the quicker the weakest individual should realize this and give up. This pattern has been confirmed for brown trout, where the smallest individuals were less aggressive than the largest, dominant individuals (Vehanen et al. 1999, Kaspersson et al. 2010). Given a very large size difference between two competing trout size classes, the weakest individual could assess the potential result of the conflict, before it even occurs, and never even try to establish a territory at the most preferable site (Abbott et al. 1985). In the present and similar studies it is therefore vital to account for large size asymmetric differences, and put emphasis on the *relative size* of the fish and not the *age*. The intercohort correlation between body size and preference for the deeper part (dotted curve, Fig. 2) is hard to explain, but is not unique as it is similar for Atlantic salmon (Hamnes 2011). Following the size-assessment principle, more competitive interactions are likely to occur between two individuals of similar size, than two of dissimilar size (Enquist and Leimar 1983, Beeching 1992, Boscolo et al. 2011) and matches perfectly with data for brown trout (Kaspersson et al. 2010). A larger territory intruder might also be easier spotted than a small one (Valdimarsson and Metcalfe 2001). The biggest fish of the younger cohort might therefore be more prone to aggressive encounters from the larger cohorts than the smaller ones. Symons (1968) noticed smaller individuals in the vicinity of larger fish in natural streams (cited in Lahti and Lower 2000), who might have shared habitats because their niches overlapped less than if they would have been more similar in size. Relative size is therefore of vital importance as it probably tells the superior individual the loss in feeding rate it will receive, and thus the importance of keeping its competitor away from its dinner plate. The ability to fend off competitors is likely

to decrease as the competitor starts to match the individual in size, and thus the discussion around normalized size that was brought up earlier becomes increasingly important!

Seasonal changes in intercohort competition

The negative size-dependent probability to be in the deep occurs only during summer, so the main concern is therefore why it shows a seasonal difference. One explanation could involve increased movement (Vehanen et al. 1999) and thus higher encounter rates between individuals, which in turn lead to more interactions. Another explanation returns to the earlier discussion as L'abée-Lund et al. (1992) showed in their extensive study of over 13 Norwegian lakes that large conspecific trout can eat prey size up to 40% of their body length, but averaged at about 33%. Some fish even started being cannibalistic at 10cm length (L'abée-Lund et al. 1992), considerably less than the sizes of age-1 fish used in this experiment. In the present study, the YoY grew a lot from summer to autumn in relative length of the age-1, its average value increasing from 29% to 39%. This makes a majority of the YoY too big for the larger trout to theoretically be consumed in the autumn, but almost the entire size range in summer falls within the preferred prey size category.

The reasons behind habitat use, based upon absolute size results for both seasons (Fig. 4), can thus be caused both by differences in relative size and seasonal differences. In addition to the study of L'abée-Lund et al. (1992), there has been an extensive amount of aquatic studies with size-dependent, *dome-shaped*, predation relationship between large predators and its prey (i.e. Cowan et al. 1996, Lundvall et al. 1999, Taylor 2003, Staudinger and Juanes 2010).While larger prey becomes too large for the predator (gape limitation) (Elner and Hughes 1978), or enjoys better swimming capacity (Ojanguren and Brana 2003, Taylor 2003), the smallest prey is also expected to have an increased survival-rate from predation. Although smaller fish suffers a fairly large risk of being caught by a large predator (Christensen 1996), the smallest individuals might be spared due to energy-maximizing predators choosing larger prey (Elner and Hughes 1978, Christensen 1996, Scharf et al. 2002), and might also have a decreased chance of being spotted (Breck and Gitter 1983, Howick and O'brien 1983). If the size-dependent predation relationship between a predator and its prey is dome shaped (i.e. Fig. 1a in Lundvall et al. 1999), then the individuals at most risk should avoid the hazardous zones with a predator present. A size-dependent habitat use, according to this theory, should be dip shaped. Without seasonal differences, relative size results (Fig. 5) would have implied that anti-predation might have been the reason behind the YoY habitat choice.

As the fish increase in size from summer to autumn experiment, it is also likely that shelter availability differed (Finstad et al. 2007). The confidence intervals (appendix) indicated a high reliability for the predictions obtained in the overlapping relative sizes (Fig. 5), but this was probably due to skewed observations in this particular range. However, there was a seasonal difference (Fig. 6) and it exemplified how it is possible to violate a dataset by merging data on a continuous variable (Fig.5). If relative size had not been introduced, results from absolute size (Fig. 4) would have given false conclusions. Since both season and its interaction with relative size were significant in the GAMM model, it means that it is safe to assume a seasonal effect. Using a squared relative size term for autumn was safe, since there were a fairly large number of observations for the majority of the $\hat{p}$. This means that anti-predation behavior cannot be ruled out in autumn, but for summer it seems highly unlikely that this is the driving factor behind habitat choice, since the fish should be fairly safe from predation risk above 0.4 in relative size. The conclusion is that from the present results there is only room for speculations why the patterns in habitat use are the way they are, with larger conspecifics present. Due to the differences in absolute sizes used during the different seasons, it still remains unclear whether or not this truly is a seasonal effect. Further studies need to be conducted in order to disentangle the mechanism behind this seasonal size-dependent change in habitat use.

Conclusions and implications

Although brown trout showed a lower preference for the deep than Atlantic salmon, the results were strikingly similar for all comparable treatments (Bentsen 2011, Hamnes 2011). Both species showed no density-dependent habitat distribution during summer, but in autumn Atlantic salmon showed, although weak, density dependent habitat distribution and brown trout showed a density dependent interaction with presence of larger fish. Due to the similarity of the species, these results could be universal for other territorial stream dwelling salmonids. Of these two species, brown trout YoY seem to be most exposed to stranding incidences and thus more likely to experience deleterious effects from hydropeaking, especially in the summer when 55% of the YoY used shallow habitats with mean depth of 18cm. The effect from larger conspecifics strongly influences the habitat use of both Atlantic salmon and brown trout, even though the mechanism behind the seasonal difference remains unclear. Since there is reason to believe that most regulated rivers will have larger

conspecifics present and predators (Greenberg 1994, Greenberg et al. 1997, Vik et al. 2001), this will certainly further cause natural populations of YoY to use even shallower habitats and show the size-dominated hierarchy observed in nature (Mäki-Petäys et al. 1997). However, different relative sizes of YoY will be affected in a varying degree. The present results show that there is always a proportion of the population inhabiting the shallow part, even at low densities. For Atlantic salmon, there is even more fish in the shallow part of the river at low densities than at high densities in the autumn, using an individual model (Hamnes 2011). In the case of Atlantic salmon, hydropeaking mortality in the shallows could cause an additional increase in the mortality rate at low densities, than they would at high densities. This means that regardless of density, YoY habitat distribution will provide a sink-source dynamic from the deep part to the shallow part of the river if hydropeaking causes extra mortality in the shallow section.

The present investigation indicates that brown trout are more susceptible than Atlantic salmon to hydropeaking, since they are more often located in shallower habitats. In contrast to the results (and expectations) from the empirical work in this study, the stranding rate of brown trout has been shown to be equal to that of Atlantic salmon in summer/autumn (Saltveit et al. 2001). Since salmonid populations generally self-thin during their first summer and autumn (Armstrong 1997), any loss of individuals observed during this period might result in compensated growth by the remaining individuals in their first growth season. However, stranding does not equal mortality (Saltveit et al. 2001) and salmonids do generally not show self-thinning after their first critical period (Armstrong 1997). This means that the effects, mortality or not, on a population level or smolt production would be interesting to investigate in a long term study. The results from this investigation can thus have severe implications for river management of fish populations, if hydropeaking studies show deleterious effects for organisms or their food sources in the shallow zone of the river.

Acknowledgements

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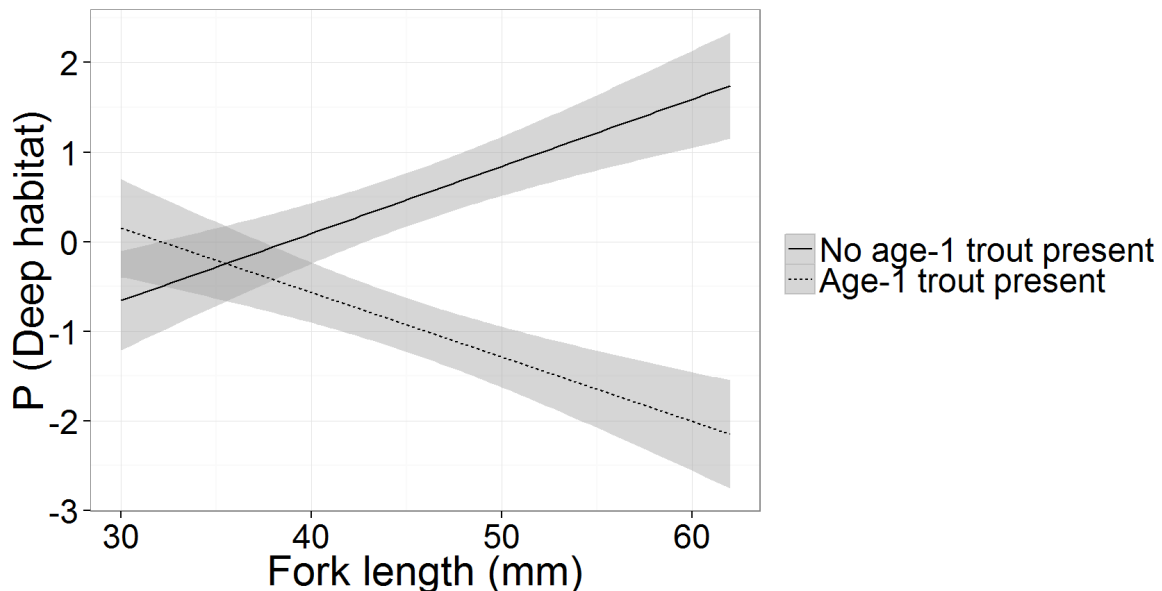
Appendix

Appendix 1. Full initial model of summer results, used for backwards selection. Colons indicate an interaction between two or more terms. n=2276, replicates=119

Term	Estimate	Z	P
Intercept	-3.887	-4.459	<0.001
Body size	0.096	5.174	<0.001
Density	3.108	2.046	<0.05
Presence of Age-1	5.883	4.976	<0.001
Body size : low density	-0.066	-1.986	<0.05
Body size : presence age-1	-0.162	-6.359	<0.001
Low density : presence age-1	-3.618	-1.650	0.099
Body size : low density : presence age-1	0.081	1.685	0.092

Appendix 2. Full initial model of autumn results, used for backwards selection. Colons indicate an interaction between two or more terms. n=2364, replicates=120

Term	Estimate	Z	P
Intercept	-1.470	-1.521	0.12
Body size	0.034	3.193	<0.002
Density	0.724	0.647	0.517
Presence of Age-1	-1.919	-1.221	0.222
Body size : low density	-0.013	-0.935	0.350
Body size : presence age-1	<0.001	-0.006	0.995
Low density : presence age-1	0.096	0.053	0.958
Body size : low density : presence age-1	0.009	0.387	0.699

Appendix 3. Fig. 2 before logit transforming the response variable with its respective confidence intervals. Grey zones show confidence intervals around the slope and the dark grey zones indicate an overlap in the confidence levels between the two different factor levels: with and without larger conspecifics present.

Appendix 4. Fig. 3 before logit transforming response variable with its respective confidence intervals. Grey zones show confidence intervals around the slope and the dark grey zones indicate an overlap in the confidence levels between the two different factor levels: high and low density.
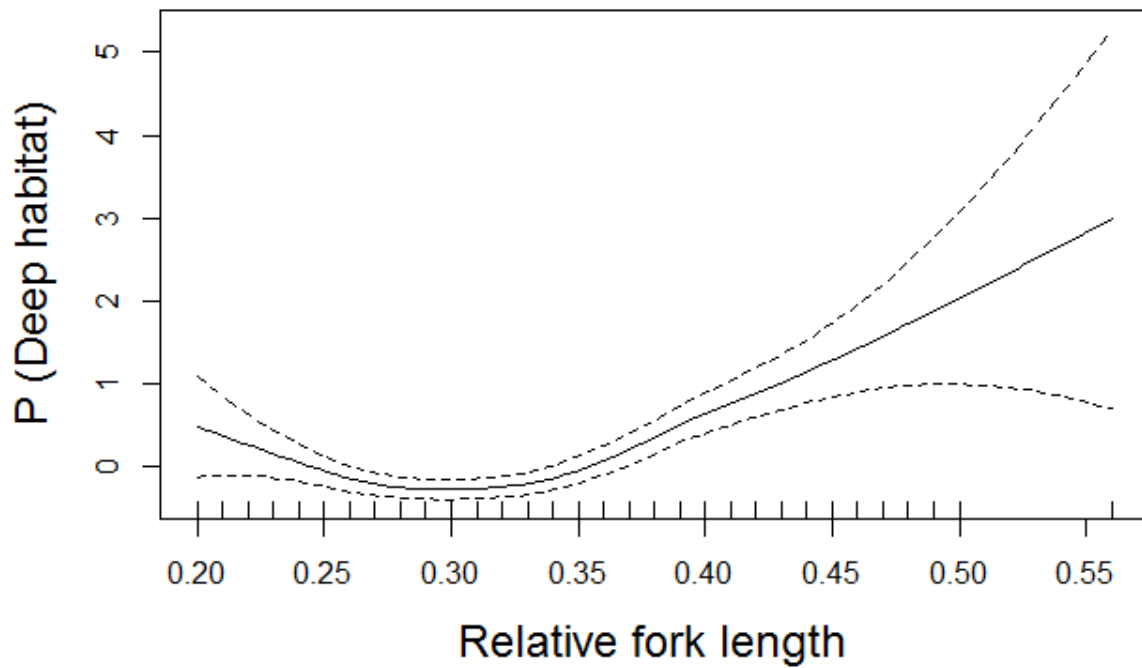
Appendix 5. GAMM model, yet to be logit transformed pooled for both seasons, with the 95% confidence interval (dashed lines).