Intercohort competition in stream salmonids: effects on behaviour, habitat use and correlates of fitness

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Abstract

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Émilie Housego

The underlying mechanisms driving population dynamics, such as density-dependence, are not fully understood, but are important for conservationists and fisheries managers. Intercohort competition can play an important role in regulating population size. To investigate the role of intercohort competition, I completed a field experiment and a meta-analysis. In the field experiment, I examined age-class interactions and how they affected the individual growth and survival of brook trout (*Salvelinus fontinalis)*. I manipulated the density of brook trout with three different density treatments in a Newfoundland stream: age 0+ fish only at a density of 4 fish/m2; fish aged 1 year or older (age 1+) only, at a density of 1 fish/m2; and, age 0+ fish at a density of 4 fish/m2 combined with age 1+ at a density of 1 fish/m2. The average daily growth rates and survival for age 0+ fish were lower, but not significantly so, in the presence of age 1+ fish, compared to when alone, likely due to a small sample size and a lack of statistical power. The meta-analysis showed that age 1+ fish had a significantly negative effect on the behaviour, habitat use and fitness correlates of age 0+ fish, but age 0+ fish had no significant effect on age 1+ fish. Differences in the stream habitats used by different cohorts of stream salmonids appear to be the result of intercohort competition, rather than representing different fundamental niches. The findings of the meta-analysis have implications for guiding the management of salmonid populations and their habitats.

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Introduction

Intraspecific competition plays a crucial role in diversifying niche breadth (Svanbäck & Bolnick 2006), modifying habitat use (Fretwell and Lucas 1970), and regulating population size (Begon et al. 1996; Keddy 1989). In species with indeterminate growth, such as most fishes, individuals continue to grow throughout life. Hence, large size differences can occur within populations, particularly between different age-classes. In strongly seasonal breeders, distinct cohorts of fish emerge of differing age and body size. The size structuring of populations has important implications for the dynamics of fish populations, where a strong cohort often has negative competitive effects on the subsequent cohorts (Kaspersson et al. 2012; Louhi et al.2014; Nordwall et al. 2001).

Intraspecific competition is typically divided into two forms: interference, where individuals interact directly via threat or aggression; and, exploitation, where individuals interact indirectly by depleting the availability of resources (Keddy 1989). The outcome of interference competition is typically settled by resource holding potential (Parker 1974), which is strongly correlated with body size (Huntingford 2013). Larger animals almost always win dyadic encounters for important resources (Miller & Frey 1972; Huntingford 2013). However, predicting winners in exploitation competition is more complicated. Small individuals may be more nimble when competing for resources (Blanckenhorn 2000), or could have the advantage during prolonged bouts of competition because they require fewer resources (i.e. food) to survive (Hamrin & Persson 1986). Alternatively, larger fishes swim faster (Webb 1975) and have greater visual acuity (e.g. Dunbrack and Dill 1983), which can be advantageous when competing for prey.

Stream salmonids are a good model system to investigate the importance of intercohort competition. Salmonids form age-structured populations in streams, most with only a few different cohorts that can be distinguished by size (Hutchings and Jones 1998; Nislow et al. 2010). Younger, smaller salmonids often occupy different ecological niches than their older, larger, conspecifics (Keeley and Grant 1997). Differences include their choice of habitat (Bohlin 1977; Heggenes 1988; Maki-Petäys 1997), foraging sites (Jenkins 1969; Bachman 1984), and of prey (Fahy 1980; Rose 1986). For example, age 0+ brown trout (*Salmo trutta*) tend to be found in shallow, smooth-bottom riffles, whereas older trout tend to be found in deeper pools with

rocky substrates (Bohlin 1977). As for foraging sites, dominant fish typically choose the best foraging position, with subordinates being relegated to downstream positions (Jenkins 1969; Bachman 1984). Dominance hierarchies in salmonids are typically based on size (Bachman 1984; Elliott 1994), with larger fish eating larger prey (Fahy 1980; Rose 1986). There is no consensus however, about whether these differences between age 0+ and older fish are due to different fundamental niches (Reece et al. 2014) or to intercohort competition (Nislow et al. 2010). If the former, then any observed differences are not the result of competition, but are due to different sized fishes occupying slightly different ecological niches.

While intracohort competition is well documented in the salmonid literature (Grant & Kramer 1990; Elliott 1994; Keeley 2001; Imre et al. 2005), intercohort competition has received less attention (Nislow et al. 2010). Additionally, most studies on the subject have failed to detect effects of intercohort competition on growth or survival (Elliott 1985). Body size is thought to play an even more important role in competition between cohorts than within cohorts, but this will depend on which type of intercohort competition is prevailing within a population. For example, if the foraging niches of several cohorts overlap strongly, then the abundance of any given cohort may exert a large negative pressure on food availability and slow the growth rate of individuals of both cohorts (Kaspersson et al. 2012; Kvingedal & Einum 2010). In this scenario, exploitation would be the main form of competition. In contrast, if different cohorts eat the same food resources, individuals from the older cohort may interfere directly with smaller individuals, thus limiting their access to food. Interference competition of this sort would likely differentially affect the individual growth rate of the smaller individuals.

Population regulation and dynamics may be influenced differently depending on the prevailing mode of competition (Kaspersson, et al. 2013). For example, in a field study, Kaspersson et al. (2013) manipulated the density of brown trout above natural levels by adding large individuals, which resulted in a negative growth response in smaller individuals. However, adding small individuals had no effect on the growth rate of large individuals. Hence, their findings suggested that interference competition was the primary mode of competition in juvenile brown trout. They concluded that this interference competition can have negative effects on fish fecundity and their ability to withstand harsh winters. Conversely, young-of-the-year (YOY) vendace (*Coregonus albula*) lowered the food supply available to older cohorts by exploitation, resulting in reduced fecundity and cyclic population dynamics (Hamrin & Persson,

1986). These results illustrate how the type of intercohort competition has implications for understanding population dynamics.

To my knowledge, few experimental studies have investigated intercohort competition in salmonids and how it varies across populations. Even fewer of these studies have been performed in the field (e.g. Einum & Kvingedal, 2011; Hamrin & Persson 1986; Kaspersson et al., 2012, 2013; Nordwall et al., 2001). Most knowledge concerning density-dependent regulation in stream-living salmonids has been obtained through monitoring wild populations over time (Ward et al. 2007). However, such observational studies cannot control for environmental variables (Matte et al. in press), or for the high mobility of fish. Furthermore, there is still no consensus in the literature about the underlying mechanisms of density-dependence (Forrester & Steele, 2000; Imre et al., 2005). For these reasons, I conducted a field experiment to investigate the effects of intercohort competition on growth and survival in a wild brook trout (*Salvelinus fontinalis*) population and a meta-analysis to synthesize the available information in the literature. When alone, age 0+ salmonids prefer deeper habitats, such as pools, to shallow riffles. In the presence of older cohorts, it is predicted that they will shift their behaviour and habitat use and diet (Jenkins 1969; Bachman 1984), resulting in reduced growth and survival rates (Hill and Grossman 1993) and increased exposure to predators (Lonzarich and Quinn 1995). In the presence of older, larger fish, age 0+ salmonids are also predicted to decrease their rate of aggression and foraging (Stringer & Hoar 1955; Newman 1956; Jenkins 1969). Because of the higher predation risk in shallow habitats, age 0+ are predicted to hide more and reduce their activity levels (Bohlin 1977). If competition is primarily via interference, then age 1+ fish will not experience any significant negative effects on their behaviour, habitat use or fitness, when in the presence of age 0+ fish. However, if the presence of age 0+ decreases the total food available or increases the energetic costs of older fish, then age 0+ fish will have a negative effect on older fish.

Methods

Field experiment

Study sites

3

My study sites were in Bob's Cove stream, near Cape Race, Newfoundland, on the southeastern tip of the Avalon Peninsula. Cape Race is home to populations of brook trout, which inhabit many of the small streams in the area (Wood et al. 2014). These streams are ideal for experimental studies for a number of reasons: (1) their small size facilitates sampling; (2) the populations are isolated from each other, which allows for interpopulation comparisons; (3) long-term studies of these streams provides an abundance of background information about the populations (Belmar-Lucero et al. 2012; Ferguson et al. 1991; Hutchings 1993, 1994).

Experimental design

I manipulated the density and age-structure of small groups of brook trout in 5-m^2 sections of the stream (width about 1 m) to quantify the strength of intercohort interactions. The experimental design consisted of three treatments (see below), each with four replicates at one time within the stream. I planned to run the experiment twice over the summer for a total of 24 trials (3 treatments x 4 replicates x 2 times per year), each of 23 days. Each stream section had an area of 5 m^2. The three treatments were: age 0+ fish only at a density of 4 fish/m^2 (approximate biomass of 2g/m^2); fish aged 1 year or older (hereafter, age 1+) only, at a density of 1 fish/m^2 (approximate biomass of 4g/m^2); and, age 0+ fish at a density of 4 fish/m^2 (approximate biomass of 2g/m^2) combined with 1+ at a density of 1 fish/m^2 (approximate biomass of 4g/m^2), for a total density of 5 fish/m^2. The different stream sections were blocked off using net barriers (3 m long by 1.3 m high, mesh size of 6 mm), which kept the fish from moving between sections without obstructing the flow of water, particles and invertebrates. The three treatments were randomly arranged along the stream (see Fig. 2 from Wood et al, 2014). The treatments sections were never abutting, with an estimated mean distance of 20 m between sections (range = 5-100 m).

Because my study investigated the effects of competition between individuals differing in body size, I used an additive design (Fausch 1998). The additive design allows one to test for the effects of adding fish from different cohorts together, compared to being alone. A substitutive design keeps the total density constant across treatments. However, such a design is less practical when considering the effects of two age classes that differ drastically in body size (Fausch 1998). Hence, I compared the growth and survival and age 0+ fish when alone versus when combined with age1+ fish and age 1+ fish when alone versus when combined with age 0+ fish.

On June 15th 2018, the fish were removed from all the sections of the stream, using a backpack electrofisher (Smith-Root LR-24), and released in sections of the stream that were not used for the experiment - at least a few hundred metres away from experimental sections. On June 16th 2018, the fish required for the experiment were collected, also using the backpack electrofisher. These fish were collected downstream of the experimental area, at least several hundred metres away. The fork length of each fish was measured to the nearest mm, and they were sorted into age 0+ and older; the cut-off length for age 0+ fish was 50 mm. The fish were then placed into the different stream sections in accordance with the three experimental treatments. All 12 trials began on June 16th 2018. After three weeks, on July 9th 2018, I removed the fish from each section using the backpack electrofisher, counted the survivors and measured body size. The electrofishing was performed starting from the downstream end, using several passes until no fish were caught on two consecutive passes (see Matte et al. 2019). On average, I completed 3 passes per section (range = 3-4). Unfortunately, my second round of trials ended prematurely due to flooding. Hence, I will report the data from round one only. When the experiment was over, the nets were removed and the fish were released into the stream.

Statistical analysis

The response variables in this study were growth and survival rates. Growth rate was quantified as the relative growth rate (Lugert et al. 2016) based on the average difference in length of fish between the beginning and end of the experiment:

$$\frac{\left(\frac{Average\ final\ length-\ Average\ initial\ length}{Average\ initial\ length}\right)*100}{\#\ Days\ of\ the\ experiment}$$

Survival rate was calculated as:

$$\frac{Final\ \#\ of\ recovered\ fish}{Initial\ \#\ of\ fish\ stocked}*100$$

I compared the growth and survival of individuals between treatments using a one-way ANOVA.

Meta-analysis

I used a meta-analysis to determine the effects of intercohort competition on the behaviour, ecology and fitness correlates (hereafter, fitness) of age 0+ and 1+ stream salmonids. The studies included in the meta-analysis were obtained through a search of the primary literature using the online database Web of Science. The following combination of words was used for the initial search: "Salmo*", "Trout*", "Intercohort*", "Age*Class*", "Age*Structure", "Compet*". The term "Salmonella*" was excluded from the search, as it produced thousands of irrelevant studies. The initial search produced 239 results. The first round of article selection was based on the relevance of the title. Each article was accorded a score of 0 or 1, depending on whether the title seemed irrelevant or relevant, respectively. After this first round of selection, 69 articles were retained. The second round of selection was based on the relevance of the abstract. Again, a score of 0 or 1 was attributed to each article, depending on whether the abstract seemed irrelevant or relevant, respectively. After this second round of selection, 35 articles were retained. The third and final round of selection was based on the results in each study. The article was included if it provided all of the following: (1) the means of at least one response variable (see below) for control and experimental groups; (2) the standard deviations, standard errors or variances of the means, or the raw data for their calculation; (3) the sample sizes for the control and experimental groups. Only 11 articles remained after this final round of selection. To complete the search, all references cited by these 11 articles were examined and evaluated based on the criteria mentioned above; eight more articles were included in the meta-analysis, for a total of 19 articles. The data were extracted from the text, figures or tables and included the following variables: (1) individual growth rate; (2) survival rate; (3) activity level (number of movements/minute) (4) aggression rate; (5) foraging rate; (6) diet composition; (7) dispersal (% downstream-moving and distance moved from release point) and a variety of habitat use variables including (8) use of cover; (9) use of deep habitats; (10) water velocity; and, (11) instream position (distance from shore and distance from a riffle). I also noted variables that could affect the results: (1) experimental versus observational study; (2) experimental setting (natural, semi-natural or artificial); (3) fish density; (4) duration of experiment in days; (5) geographic location; (6) season(s) in which the experiment was performed; and, (7) statistical tests used.

Meta-analysis

      Meta-analysis is a technique that statistically quantifies the effect of an independent variable on a dependent variable (i.e., the effect size) by combining data from multiple published studies. It also measures the level of heterogeneity across studies and attempts to explain this variability using moderator variables (Harrison 2011). Hence, it provides a formal statistical framework for combining and comparing the results of different experiments, and is preferred over other methods, such as "vote counting" (Hedges & Olkin 1980; Nakagawa, 2007). Null-hypothesis-significance-testing does not measure the magnitude of the effect of independent variables on dependent variables, but only notes the statistical significance. Only significant results are considered in vote counting, which makes it a very conservative approach. Furthermore, vote counting lacks statistical power since p-values are heavily influenced by sample size. Therefore, non-significant, but small effects may be overlooked because of small sample size. Meta-analysis overcomes this problem by calculating standardized effect sizes, which are corrected for sample size and weighted by within-study variance. It has long been recognized in other fields, such as medicine and social sciences, that methods such as "vote counting" are not adequate for synthesizing research (Hedges & Olkin 1985). However, meta-analyses have only more recently been introduced to the field of ecology (Järvinen 1991; Gurevitch et al. 1992).

      I used Hedge's g (Hedges 1981) as the effect size in my study, because it uses the pooled weighted standard deviation in its calculation, as opposed to just the pooled standard deviation, which is used in calculating Cohen's d (Cohen 1969). Therefore, it corrects for small sample sizes (Lakens 2013). Hedge's g is interpreted in a similar way as Cohen's d. An effect size of 0.2 is considered a small effect, which cannot be discerned by the naked eye; 0.5 is a medium effect; 0.8 is a large effect, which can be discerned by the naked eye (Cohen 1988). The value of Cohen's d was calculated for each variable in each study and then transformed into Hedge's g. The following calculations were used to calculate Cohen's d, and then Hedge's g (Cohen 1988; Hedges 1981):

$$s = \sqrt{\frac{SD_1^2 + SD_2^2}{2}}$$

$$d = \frac{\bar{x}_1 - \bar{x}_2}{s}$$

$$g = d * \left(1 - \frac{3}{(4(df) - 1)}\right)$$

where s is the pooled standard deviation, SD_1 and SD_2 are the standard deviations for the control and experimental treatments of a particular study, $\bar{x}_1$ and $\bar{x}_2$ are the mean values for the control and experimental treatments, and *df* are the degrees of freedom. When a correlation coefficient r value was extracted from a study, it was first transformed into a Cohen's d value, and then into Hedge's g, using the following calculation:

$$d = \frac{2r}{\sqrt{1 - r^2}}$$

The meta-analysis was then conducted using the "metafor" package (Viechtbauer 2010) in R (R Core Team 2013), using the previously calculated Hedge's g values. The results were presented in the form of forest plots. The convention was that variables were presented as having a negative value if they had a detrimental effect on the individual, due to the intercohort competition. To verify if there was any variance in effect size between studies, the significance of the Q statistic was verified for each variable, and the I_2 statistic was calculated; I_2 values of 25%, 50% and 75% are indicative of low, medium and high levels of heterogeneity, respectively (Del Re, 2015). Funnel plots for each variable were also created, using the metafor package (Viechtbauer 2010) in R. The funnel plots compare the distribution of effect sizes across different study sample sizes, in order to reveal publication bias (Egger et al. 1997; Light & Pillemer 1994). If there is a bias, for example, due to studies with smaller sample sizes and no significant effects remaining unpublished, the plot will have an asymmetrical appearance. The relationships between sample sizes and effect sizes were quantified using Spearman's correlation coefficient. The relationships between effect sizes and the Percent Habitat Saturation index (PHS), an allometrically corrected measure of abundance, were also quantified using Spearman's correlation coefficient. PHS was calculated as:

$$PHS = 100 * \sum_{i=0}^{n} * D_i / D_i max$$

$$= 100 * \sum_{i=0}^{n} * D_i * T_i * 1.19$$

where D_i is the density (per m_2) of size class i, 1.19 is a factor that corrects for the bias introduced when the data were $\log_{10}$ transformed (Sprugel 1983), and T_i is the territory size (m_2) for size-class i predicted from the territory size-body regression (Grant & Kramer 1990):

$$log_{10}area = 2.61 * log_{10}length - 2.83$$

where area is the territory size (m_2) and length is the body length (cm). Unlike PHS, combining densities or biomass of different age class of fish is not allometrically correct.

Results

Field experiment

The average daily growth rates for age 0+ fish were lower, but not significantly, in the presence of older fish compared to when alone in the control sections (0.338% and 0.552%, respectively; ANOVA, $F_{(1,6)}=2.853$, $p=0.142$) (Fig. 1). The mean effect size (Hedge's g) of growth for age 0+ fish calculated from these results was -1.199. Of the 160 age 0+ fish used in this experiment, 54 survived until the end of the experiment. The average survival rates for age 0+ fish were lower, but not significantly, in the presence of older fish compared to when alone in the control sections (33.8% and 36.3%, respectively; ANOVA, $F_{(1,6)}=0.147$, $p=0.714$) (Fig. 2). The mean effect size (Hedge's g) of survival for age 0+ fish calculated from these results was -0.296. Of the 40 age 1+ fish used in this experiment, only 11 survived until the end of the trials with only three of eight sections containing age 1+ fish at the end of the trials. Hence, my sample size for age 1+ fish was 8 (4+4) for survival and 3 (1+2) for growth. The average daily growth rates for age 1+ fish were higher, but not significantly, in the presence of younger fish compared to when alone in the control sections (0.344% and 0.106%, respectively; ANOVA, $F_{(1,1)}=0.193$, $p=0.737$) (Fig. 3). The average survival rates for age 1+ fish were lower, but not significantly, in the presence of younger fish compared to when alone in the control sections (15% and 40%, respectively; ANOVA, $F_{(1,6)}=1.471$, $p=0.271$) (Fig. 4).

Meta-analysis

The literature survey yielded 19 studies that reported sufficient information to calculate the means and standard deviations for at least one of the variables of interest. Of the three salmonid species included in this meta-analysis, 58% of the data used to calculate effect sizes were based on studies conducted on brown trout, 31% on Atlantic salmon and 11% on rainbow trout. The meta-analysis included 55 effect sizes for 12 dependent variables, for three species of salmonids. Of the 55 effective sizes, 37 and 18 quantified the effect of age 1+ fish on age 0+ and vice versa, respectively.

Effects of age 1+ on age 0+ salmonids

Overall, age 1+ fish had a significantly negative effect on the behaviour, habitat use and fitness of age 0+ fish (Random effects model, $p< 0.0001$; Fig. 5). Of the 37 effect sizes, 34 were negative and 14 were significantly negative, based on the 95% CIs (Fig. 5).

Behaviour: activity, aggression, foraging, diet and dispersal

Overall, older fish had a negative effect on the behaviour of age 0+ fish (Random effects model, $p= 0.022$; Fig. 6). The mean effect size of -0.905 was significantly negative (CI (95%): [-1.676; -0.133]). However, there was significant heterogeneity among studies in the magnitude of the effect sizes ($I_2=77.9\%$, $Q=36.16$, $df=8$, $p< 0.0001$). In general, activity levels decreased, aggression increased, diet was different, and fish dispersed farther in the presence of older fish. Part of the heterogeneity may be explained by the countries in which each study took place (Random effects model, $p=0.035$). For some unknown reason, the effect sizes were more negative in France, than in Finland, Sweden and Scotland. The funnel plot did not reveal any obvious bias (Spearman's, $rho=0.353$, $p=0.492$).

Habitat use: instream position, depth and velocity

Older fish had a negative effect on all habitat-use variables (Random effects model, $p= 0.033$; Fig. 6). The mean effect size of -0.402 was significantly negative (CI (95%): [-0.772; -0.032]). In general, age 0+ fish shifted their habitat use to shallower, faster water in the presence of older fish. A moderate degree of heterogeneity was found among studies in the magnitude of

the effect sizes (I_2=68.1%, Q=43.85, df=14, p< 0.0001). This heterogeneity may be due to the fact that the effect size of habitat use for age 0+ fish increased with the total density of fish used in each study (Spearman's rho=0.628, n=14, p=0.016). The funnel plot did not reveal any obvious bias (Spearman's, rho=0.502, p= 0.067).

Fitness: survival and growth rates

Older fish had a negative effect on both survival and growth rates for 0+ fish (Random effects model, p=0.0015; Figure 6). The mean effect size of -0.929 was significantly negative (CI (95%): [-1.502; -0.357]). However, there was significant heterogeneity among studies in the magnitude of the effect sizes (I_2=70.2%, Q=47.02, df=14, p< 0.0001), partly due to differences in effect size values for growth and survival. While there was no heterogeneity in the effect sizes for survival (I_2=0.0%, Q=3.69, df=6, p=0.718), there was still high heterogeneity for the growth variable (I_2=82.5%, Q=40.07, df=7, p< 0.0001). The growth rate heterogeneity was partly due to differences in the total fish density used in each study (Random effects model, p= 0.032) (see below). The funnel plot did not reveal any bias with respect to effect size and sample size (Spearman's, rho=0.302, p=0.274).

Effect of age 0+ on age 1+ salmonids

Overall, age 0+ fish had a negative, but not significant, effect on the behaviour, habitat use and fitness of age 1+ fish (Random effects model, p= 0.266; Fig. 7). Of the 18 effect sizes, seven were negative and one was significantly negative, based on the 95% CIs; Fig. 5).

Effect of density on effect size

The effect size of growth rate for age 0+ fish was positively correlated to PHS in each study (Spearman's rho=0.707, n=8, p=0.05). In addition, a meta-regression, using a mixed-effects model, revealed that the effect size of growth for age 0+ fish increased with the total density of fish used in each treatment (Spearman's rho=0.659, n=8, p=0.05). However, there was no significant relation between PHS and the effect sizes of survival (Spearman's rho=-0.406, n=6, p=0.425), fitness overall (Spearman's rho=0.313, n=14 , p=0.276), behaviour (Spearman's rho=0.055, n=7, p=0.908), or habitat use (Spearman's rho=0.017, n=13 , p=0.957) for age 0+ fish. However, a meta-regression, using a mixed-effects model, revealed that the effect size of

habitat use for age 0+ fish increased with the total density of fish used in each treatment (Spearman's rho=0.628, n=14, p=0.016). Furthermore, there was no significant relation between PHS and the effect sizes of fitness (Spearman's rho=0.8, n=4, p=0.333), behaviour (Spearman's rho=0.256, n=7, p=0.505), or habitat use (Spearman's rho=0.738, n=4 , p=0.262) for age 1+ fish. The same was true for the relation between above-mentioned variables and density.

Discussion

The results obtained from the field experiment suggested that age 0+ salmonids were negatively affected by competition from older fish in terms of growth as well as survival. The lack of a significant effect of older fish on the growth and survival of age 0+ fish may have been the result of the low replication (n=4) and power of our field experiment. Given the variance depicted in Figure 1, 11 replicates would have been required to make the observed difference significant at an alpha of 0.05. Given the variance depicted in Figure 2, 31 replicates would have been required to make the observed difference significant at an alpha of 0.05.

In the meta-analysis, age 0+ fish experienced reduced growth and survival rates in the presence of age 1+ fish, supporting the trends observed in the field experiment. The mean effect sizes (Hedge's g) of growth for age 0+ fish obtained from the field study and from the meta-analysis were -1.199 and -1.301, respectively. The mean effect sizes of survival for age 0+ fish obtained from the field study and from the meta-analysis were -0.296 and -0.254, respectively. Thus, the meta-analysis confirmed the validity of the results obtained in the field experiment, despite the small sample sizes. These results indicate that larger individuals mostly affect smaller individuals' growth rates, rather than their survival rates. This finding is consistent with many experimental field studies on the subject (Bohlin et al. 2002; Kaspersson et al. 2013; Sundström et al. 2004).

The meta-analysis showed that intercohort competition had differential effects on the two age-classes. Overall, age 1+ fish had a negative effect on the behaviour, habitat use and fitness of age 0+ fish. Furthermore, it appeared that the habitat occupied by age 0+ fish was not a result of their own choice, but the result of competition with larger competitors. These results were consistent with the hypothesis that interference is the dominant mode of competition within salmonid populations (Kaspersson et al. 2012). As for the effects of intercohort competition on

1+ fish, overall, age 0+ fish had a negative, but not significant, effect on their behaviour, habitat use and fitness.

The behaviour of age 0+ fish responded in the predicted ways to intercohort competition by age 1+ fish. In the presence of older conspecifics, the activity rates of age 0+ fish were lower, likely due to the younger fish minimizing their movement to avoid attracting the attention of their larger conspecifics (Vehanen et al. 1999). Therefore, age 0+ fish also made fewer foraging attempts, which likely reduced prey intake, and contributed to their lower growth rate. When alone, age 0+ fish preferred deep pool habitats compared to shallow habitats, such as riffles, likely to avoid predation from terrestrial and avian predators (Heggenes & Borgstrøm 1988). In sympatry, however, age 0+ fish were excluded to suboptimal habitats, such as shallow riffles, with less cover. Our analysis suggests that age 0+ salmonids are not limited to certain habitats (i.e. shallow areas) because of their swimming abilities, but because of intercohort competitive exclusion.

This habitat partitioning is likely due to the despotic behaviour of the larger, dominant fish excluding others from the best feeding sites (Fausch 1984). Such shifts in habitat use are also accompanied by diet shifts from chironomids and larval blackflies in equal proportions to mostly larval blackflies, which were more abundant in shallow, fast habitats (Louhi et al. 2013). Age 0+ growth rates were negatively affected in the presence of age 1+ fish, likely due to the higher swimming costs in the riffle habitats and the shift to less preferred prey. In fact, chironomids are known to be an important part of the diet of 0+ salmonids (Keeley & Grant 1997). Similar results were observed in habitat-choice experiments with cutthroat trout (Rosenfeld & Boss 2001). In allopatry, age 0+ cutthroat trout preferred deep pools, and had higher growth rates in pools than in riffles (Rosenfeld & Boss 2001). In contrast, field surveys demonstrated that age 0+ cutthroat trout were most often found in shallow habitats (Glova 1984, Rosenfeld et al. 2000). These data support the idea that age 0+fish are forced into these suboptimal habitats when in the presence of older conspecifics due to intercohort competition. Similarly, competition and predation from older fish influences the habitat use by juvenile minnows and sunfish (Gilliam & Fraser 1987, Werner & Hall 1988). However, the idea of intercohort competitive exclusion has rarely been investigated in the salmonid literature thus far (Bohlin 1977, Rosenfeld & Boss 2001).

The effect size for growth for age 0+ fish was positively correlated to the total density used in each study from the meta-analysis. This result supports the idea that age 0+ salmonid growth is density-dependent, which is widely accepted in the literature (Grant & Imre 2005, Amundsen et al. 2007, Vincenzi et al. 2008). The effect size for habitat use for age 0+ fish was also positively correlated to the total density used in each study from the meta-analysis. However, the effect sizes for survival and all other behaviour variables were not density dependent.

As predicted, age 0+ fish did not have any significantly negative effects on the behaviour, habitat use, or fitness variables for 1+ fish. This result is consistent with the idea that interference is the main type of competition prevailing within salmonids. Age 1+ fish are larger and dominant to age 0+ fish, (Johnsson et al. 1999), with free access to their preferred habitats, and types of prey.

There were some notable exceptions to the trends noted in our meta-analysis. As previously mentioned, Hamrin & Persson (1986) found that young-of-the-year (YOY) vendace (*Coregonus albula*) lowered the food supply available to older cohorts by exploitation, resulting in reduced fecundity and cyclic population dynamics. Furthermore, a field experiment by Kvingedal & Einum (2010) found that age 0+ brown trout had a negative effect on the growth performance of yearlings. These studies may have been able to detect this negative effect of age 0+ fish on older fish because they were conducted over the course of several years (in the case of Hamrin & Persson 1986); large fluctuations overtime in the relative abundance of the two cohorts may have increased the power to detect intercohort interactions. Furthermore, Kvingedal & Einum used energy or lipid levels as a measure of growth, instead of body size, which may have led to more precise results and hence, different conclusions.

The results obtained from this study, particularly those concerning the habitat preferences of 0+ salmonids, can help guide conservation and riparian management practices. The fact that there was lower growth in riffles for 0+ fish emphasizes the importance of pools at a population level. Therefore, it would be important to prioritize practices that create a maximum amount of pool habitat in streams, such as increasing large woody debris inputs (Murphy & Koski 1989).

In conclusion, this study provides clarity on the effects of intercohort competition in stream salmonids, which were unclear in the literature. The findings from this study provide evidence for reduced growth rates, as well as for habitat exclusion for 0+ salmonids in sympatry with

older conspecifics. It would appear that the habitat choices of 0+ salmonids observed in the wild are likely the result of intercohort competition, and not of ontogenetic preference. These findings have implications for understanding the mechanisms behind density dependent population regulation as well as for guiding the management of salmonid populations and their habitats.
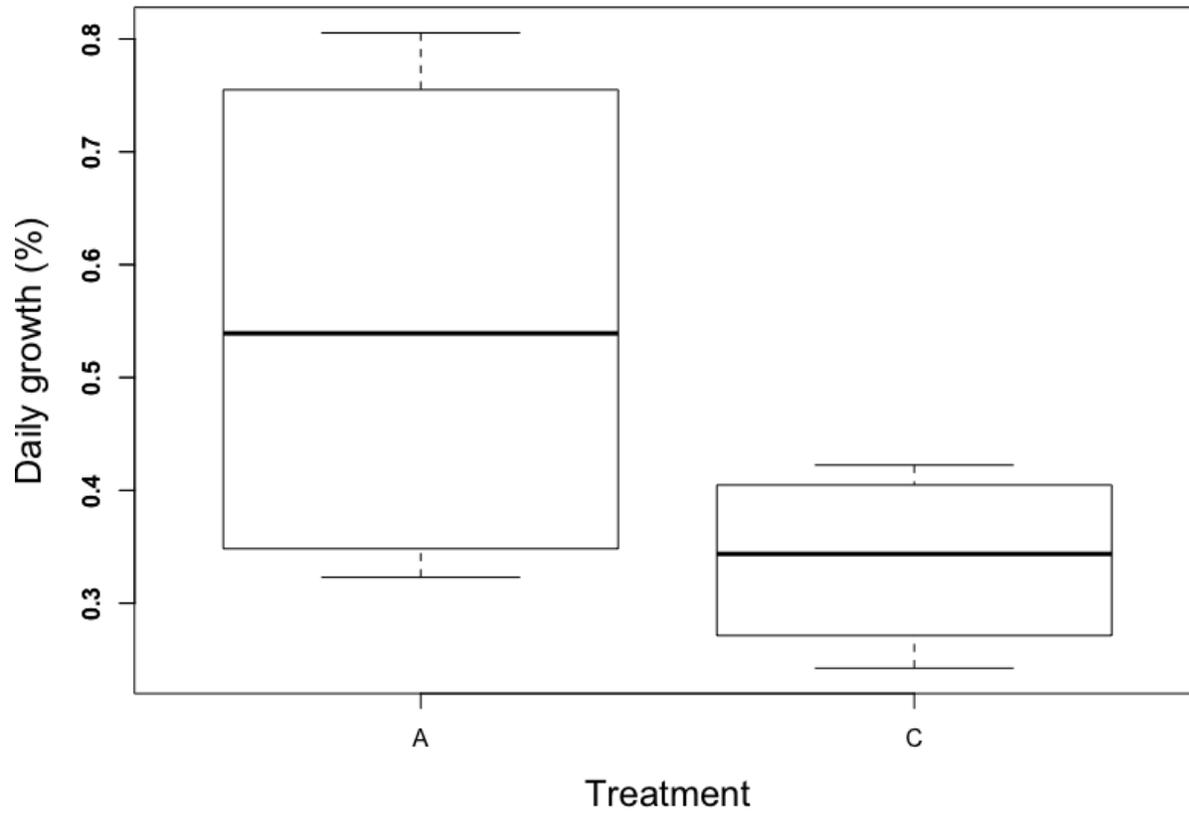
Figure 1: Daily growth rates (%) of age 0+ brook trout when alone (A) and in the presence of age 1+ brook trout (C).
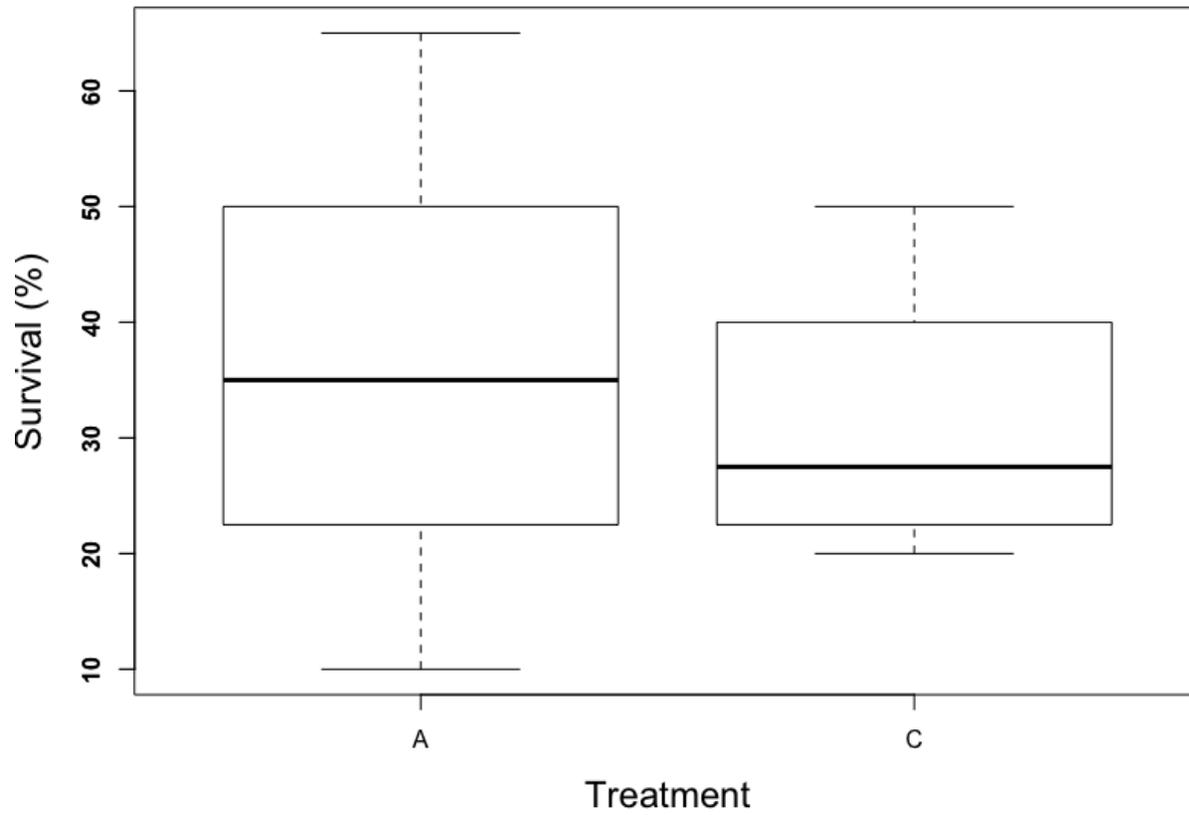
Figure 2: Survival rates (%) of age 0+ brook trout when alone (A) and in the presence of age 1+ brook trout (C).
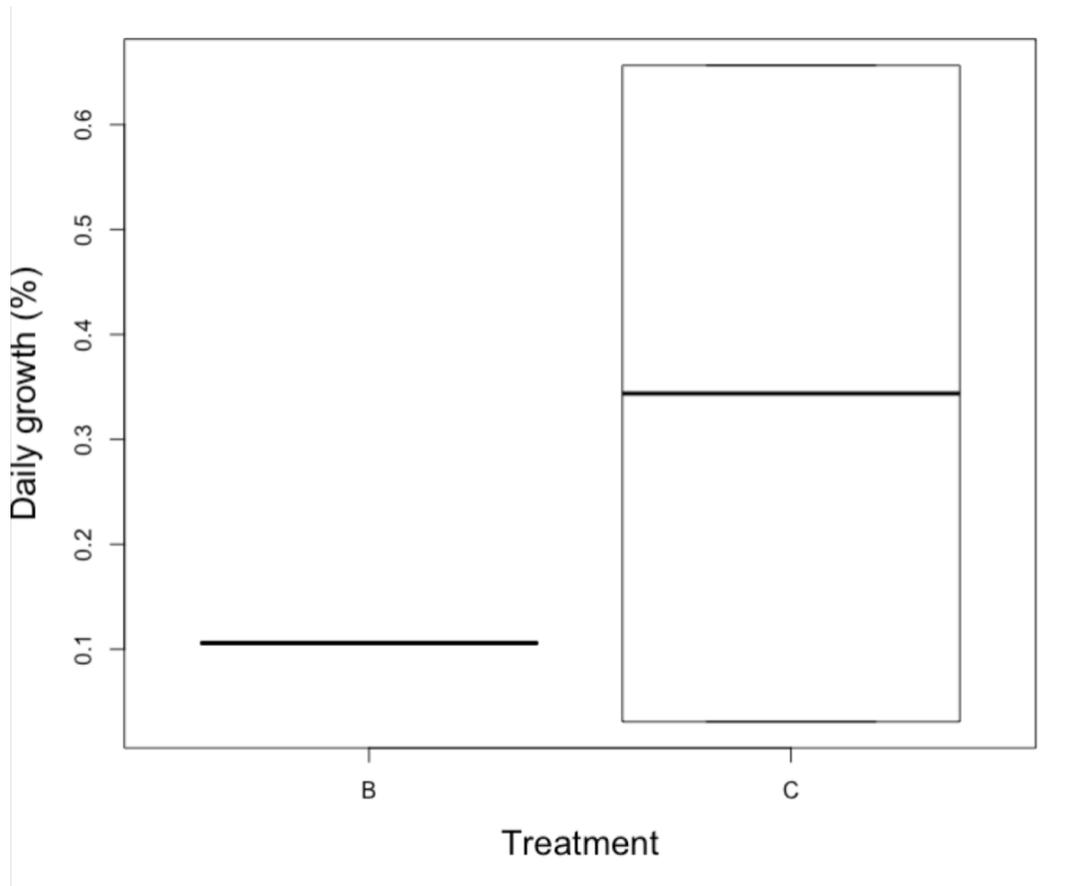
Figure 3: Daily growth rates (%) of age 1+ brook trout when alone (B) and in the presence of age 0+ brook trout (C).
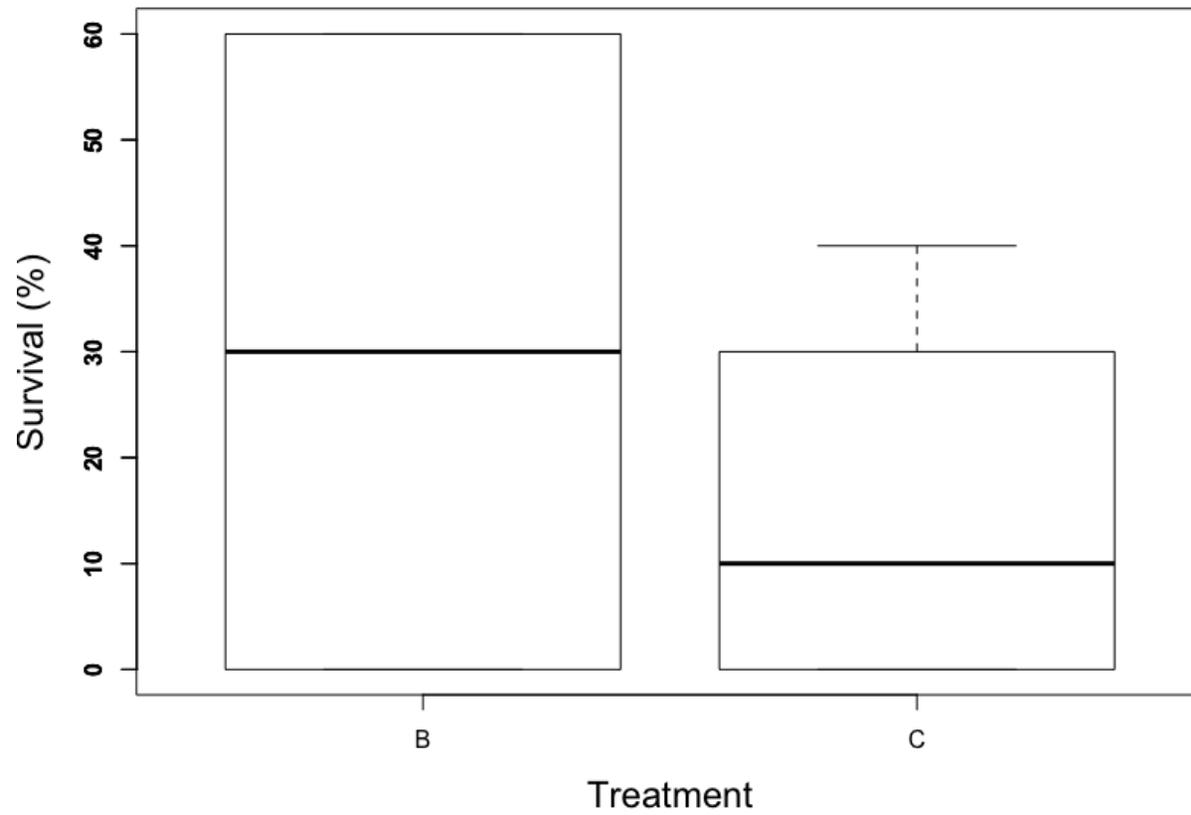
Figure 4: Survival rates (%) of age 1+ brook trout when alone (B) and in the presence of age 0+ brook trout (C).

Figure 5: The effect of age 1+ salmonids on the mean effect size (± 95% C.I.) of behavioural variables (foraging rate, activity, aggression rate, dispersal), habitat use variables (depth, instream position) and correlates of fitness (growth, survival), ordered by effect size (note: the x-axis was trimmed to -10 to +10 for visual purposes) for age 0+ salmonids.
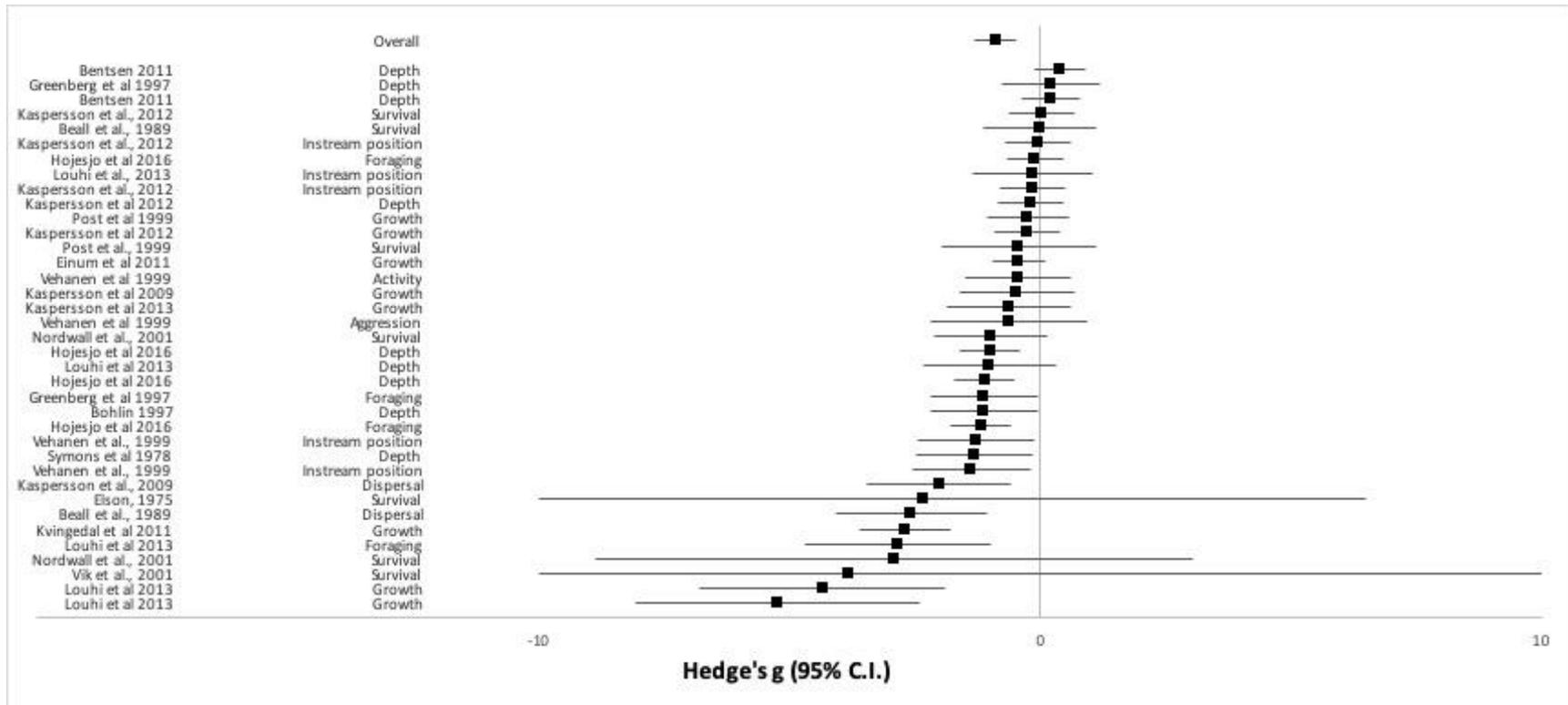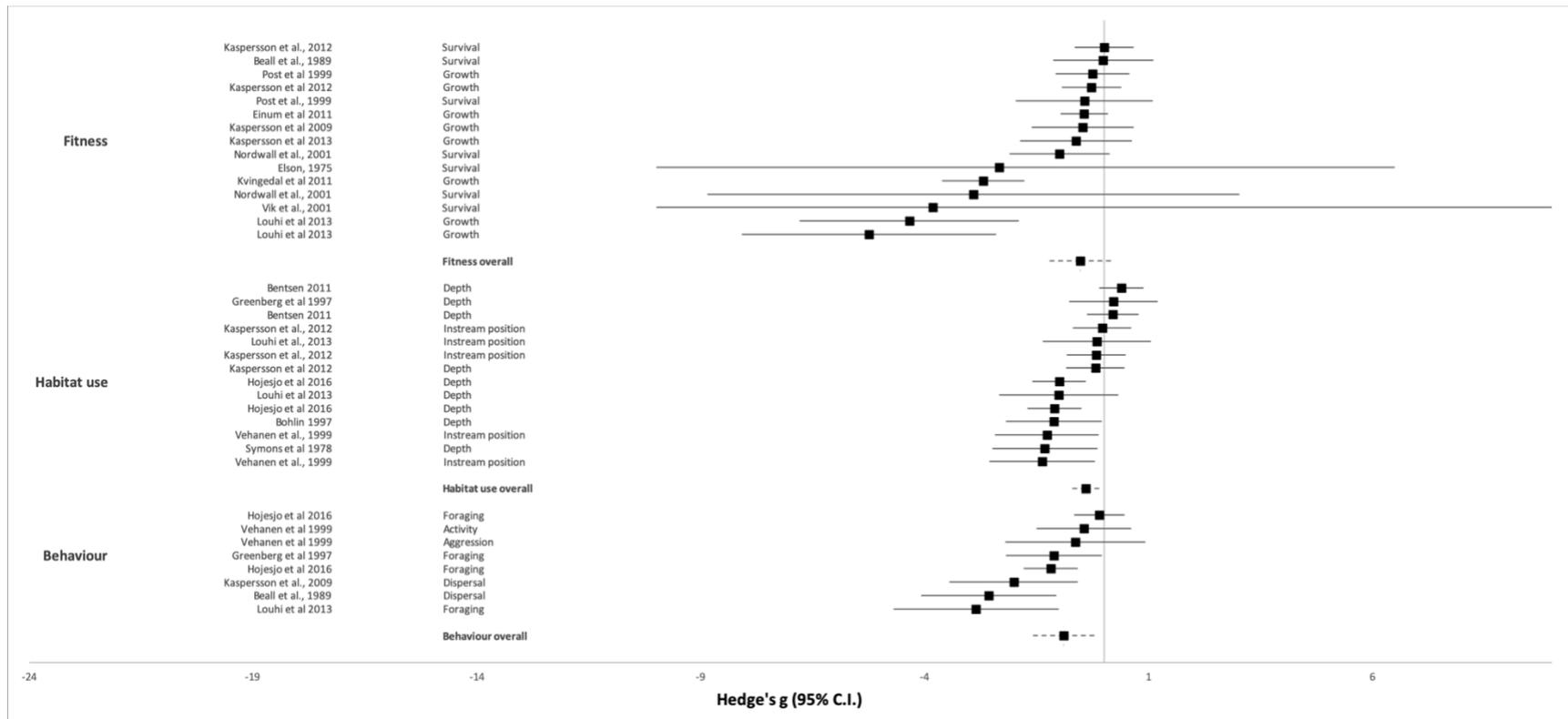
Figure 6: The effect of age 1+ salmonids on the mean effect size (± 95% C.I.) of behavioural variables (foraging rate, activity, aggression rate, dispersal), habitat use variables (depth, instream position) and correlates of fitness (growth, survival) for 0+ salmonids (x-axis range of -10 to +10).

Figure 7: The overall effect of competition by age 0+ salmonids on the mean effect size (± 95% C.I.) of behavioural variables (foraging rate, activity, aggression rate), habitat use variables (depth, instream position) and correlates of fitness (growth) of age 1+ salmonids, ordered by effect size.

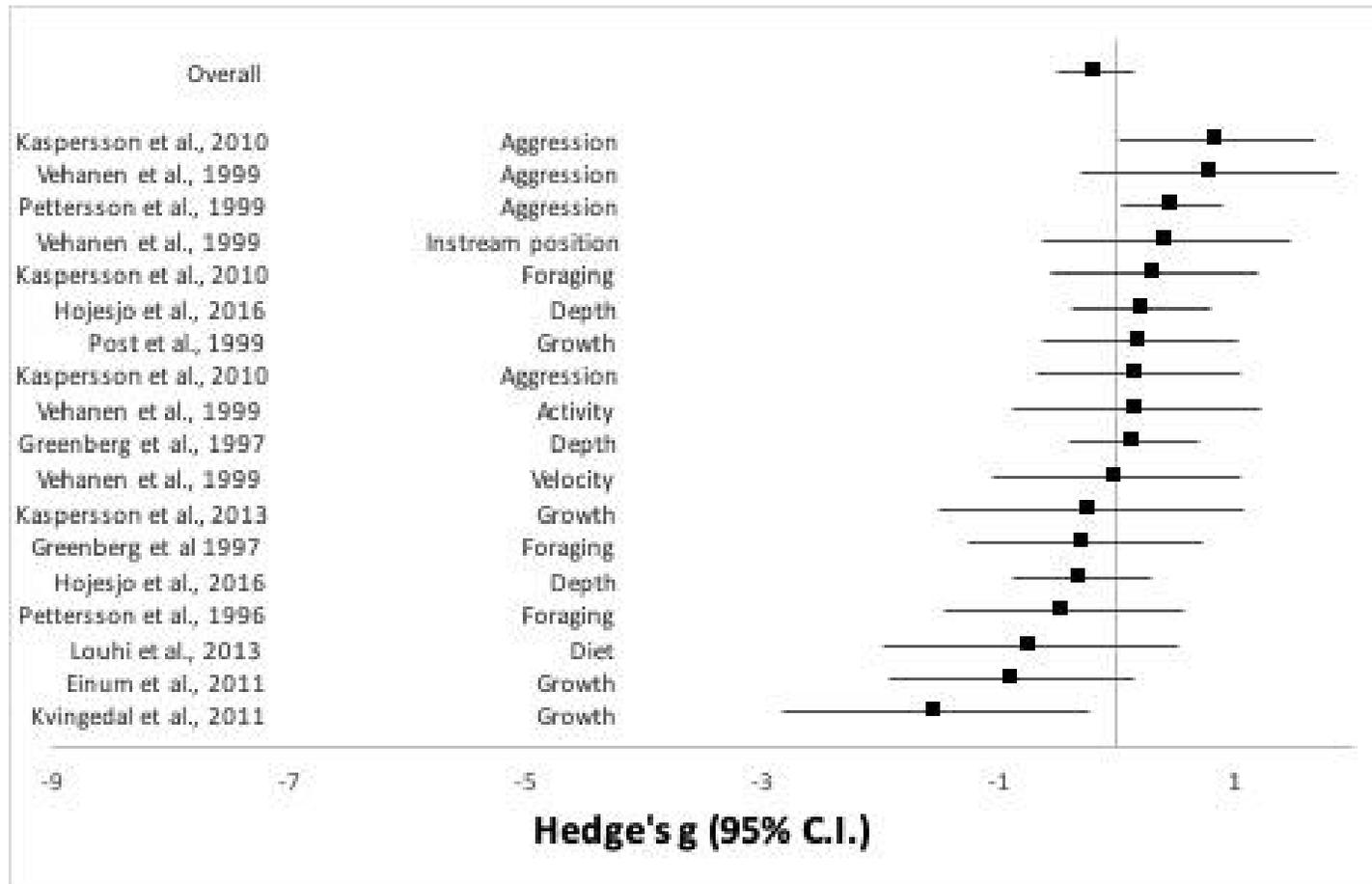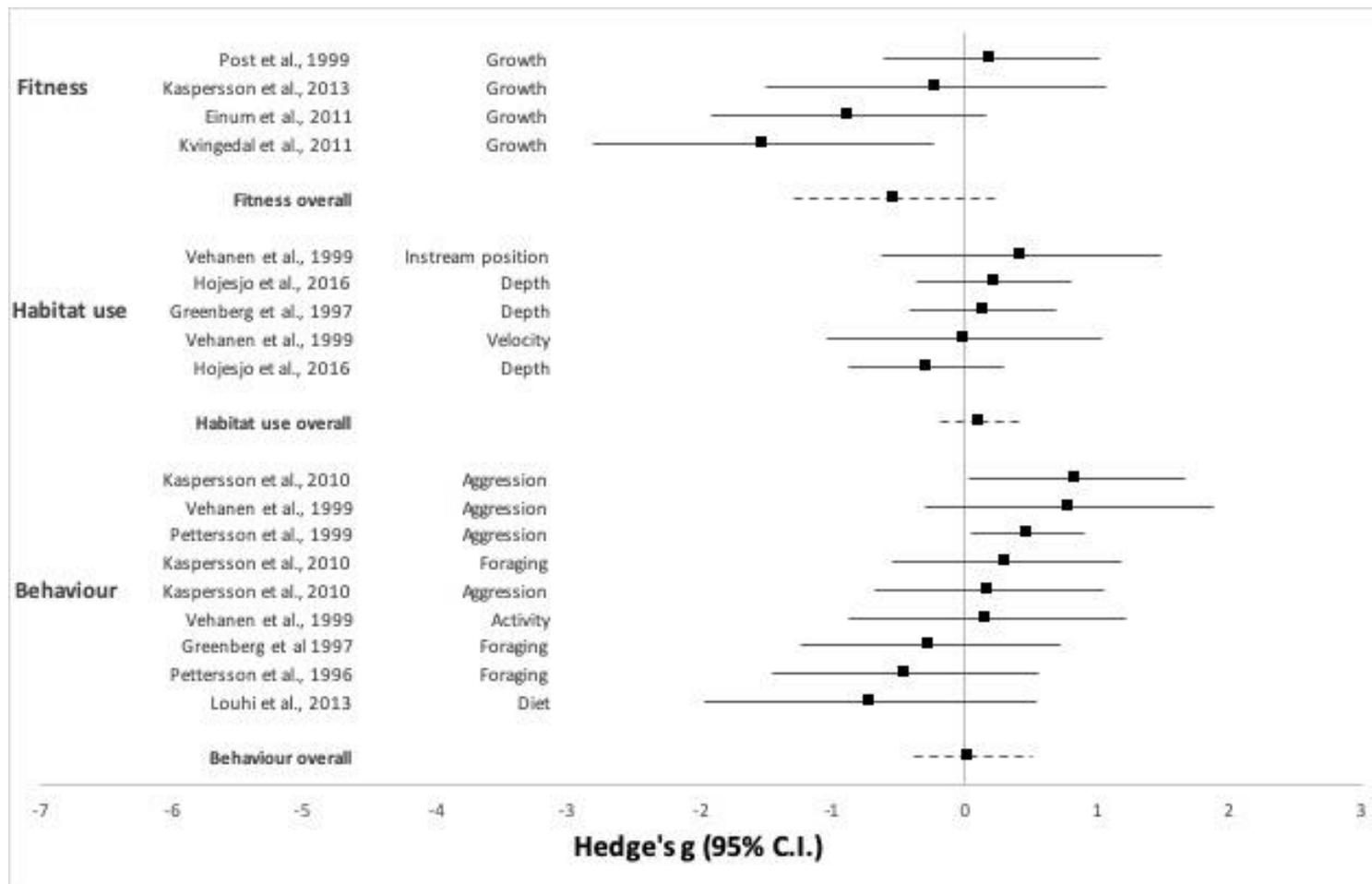**Figure 8:** The overall effect of competition by 0+ salmonids on the mean effect size (± 95% C.I.) of behavioural variables (foraging rate, activity, aggression rate), habitat use variables (depth, instream position) and correlates of fitness (growth) for 1+ salmonids.
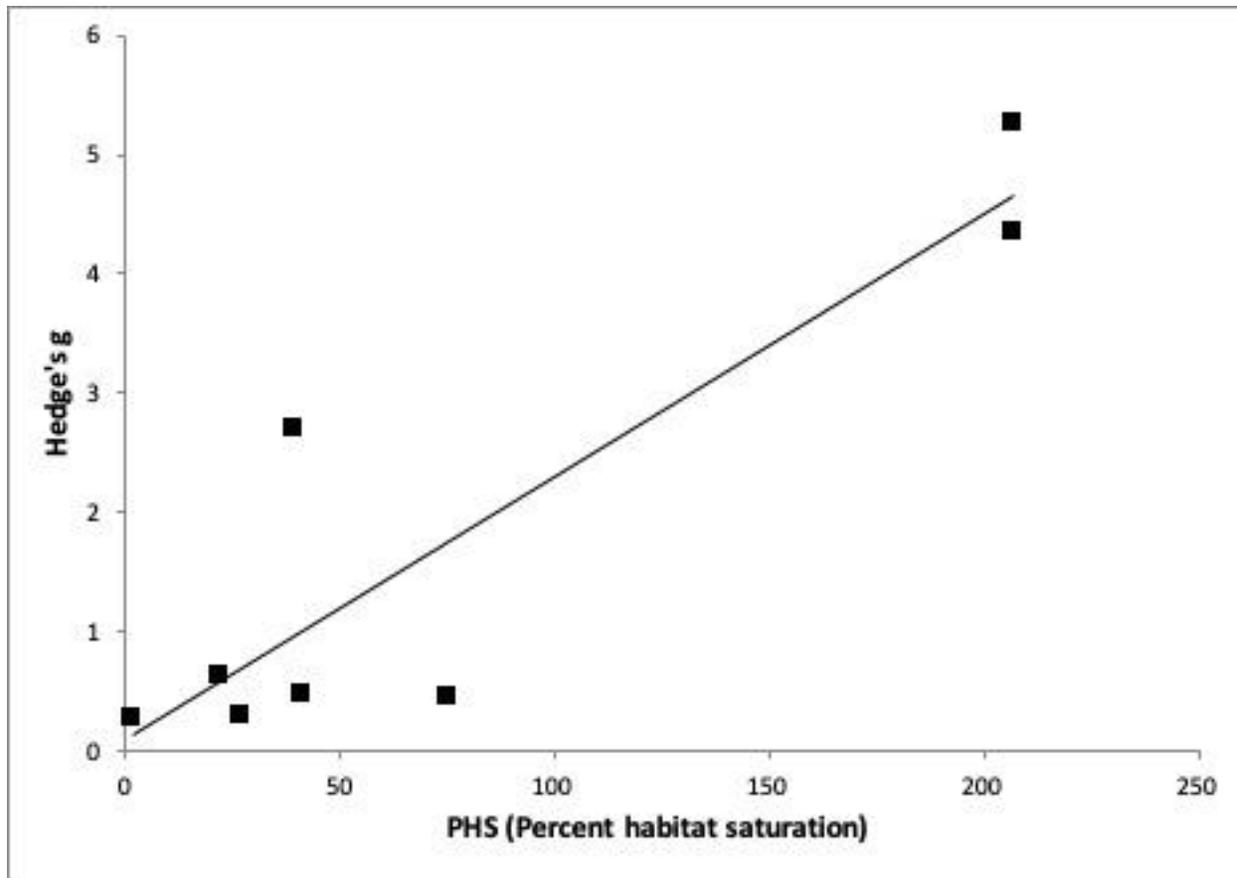
Figure 9: The relation between the absolute value of effect size for growth of 0+ salmonids and percent habitat saturation

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Note: References used in the meta-analysis are marked with an *.

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