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**Size-related habitat use in juvenile Atlantic salmon: the importance
of inter-cohort competition**

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Abstract:

In stream-living salmonids, an underlying mechanism for the critical period after emergence has generally been assumed to be size-dependent swimming capacity constraining fry (age-0) to low-velocity habitats with reduced food availability and intense competition. A further plausible mechanism is that inter-cohort habitat exclusion confines fry to marginal habitats. This possibility was tested using a semi-natural stream with 16 test arenas each comprising one high-velocity, deep, habitat and one low-velocity, shallow, habitat. We observed groups of newly emerged Atlantic salmon *Salmo salar* fry, either alone or in sympatry with one or two age-1 salmon. Salmon fry used high-velocity areas ($42.2 \pm 0.4 \text{ cm s}^{-1}$) most extensively in the absence of inter-cohort competition, where they obtained more food than in low-velocity areas ($3.3 \pm 0.3 \text{ cm s}^{-1}$), even though foraging efficiency was lower (though not significantly so). In sympatry with older cohorts, fry increased their use of the low-velocity habitat, with a reduced foraging activity, suggesting that strong older cohorts in natural populations may have the potential to influence the strength of the recruiting cohort by negative density-dependence due to interference competition for habitat.

Keywords: Inter-cohort, Competition, Atlantic salmon, Habitat, Performance

Introduction

In an environment with limited food supply, growth of organisms may be associated with increased *per capita* demands, resulting in a progressive reduction in their total number. Such progressive density-dependent self-thinning has been observed in organisms as diverse as plants competing for light, barnacles competing for space on rocks and young salmonid fishes competing for space and food in streams (Grant & Kramer 1990; Begon et al. 1996).

However, populations of salmonid fishes have been shown to experience substantial mortality at a critical period soon after emergence from the gravel bed (Elliott 1989) after which a cohort may never approach the saturated levels associated with self-thinning (although later periods may also be critical in some populations (e.g., Bohlin et al. 2002; Lobon-Cervia 2005)). This early critical phase, most thoroughly investigated in the classic studies by Elliott (1989) on brown trout *Salmo trutta* L, is associated with the depletion of yolk sac nutrients and onset of exogenous feeding in newly emerged fry (age-0). The duration of population losses may extend to several weeks after the actual point of emergence but the underlying mechanisms are not thoroughly understood.

Juvenile salmonids are sit-and-wait foragers that mainly feed on a continuous supply of drifting invertebrates (Keeley & Grant 1997). Flux of drift may tend to increase with current velocity (Hill & Grossman 1993), and a plausible explanation for the early critical period is that size-dependent swimming capacity constrains young fish to only a fraction of the stream (Armstrong 1997) where the velocity and availability of food are low. This ontogenetic limitation of foraging space at emergence may not only result in a reduced *per capita* food intake rate but can also reinforce intra-cohort competition for favourable feeding territories, thus increasing the variance in performance among individuals in the new cohort. As swimming capacity and food capture efficiency increase with body size (Beamish 1978; Nislow et al.

1999), those fish that survive and continue to grow may experience an increased availability of stream habitats with a wider range of water velocities. Hence, older and larger fish may therefore have relaxed constraints on survival, suggesting that carrying capacity is not fixed but increases with size, at least to a certain point.

Empirical evidence in support of this foraging space limitation theory is provided through laboratory tests of foraging-based models that incorporate food availability, spatial distribution and performance (foraging, growth or survival) from a number of drift-feeding fishes (Faush 1984; Nislow et al. 1999, reviewed by Piccolo et al. 2014). For example, Nislow et al. (1999) used a simple laboratory derivation of optimum velocity, where only a narrow range of low water velocities ($0.08 - 0.18 \text{ m s}^{-1}$) enabled newly emerged Atlantic salmon (*Salmo salar* L.) (20 - 25 mm) to maximize their feeding rates, while the corresponding velocity range for late season juveniles (45 - 65 mm) was more than double ($0.21 - 0.57 \text{ m s}^{-1}$). The theory seems to hold also in the field where performance of age-0 salmonids correlates with velocities that are predicted to maximize food consumption (e.g. Hill & Grossman 1993; Nislow et al. 1999). Additional support is also based on indirect evidence through correlations of distribution and local velocities (see Armstrong et al. 2003 for a review), although such data provide no insight into mechanisms underlying ontogenetic shifts in habitat use.

Thus, most previous studies considering the critical period tend to think of regulation as occurring within the age-0 cohort because of age-specific swim performance limitations driving preferences for specific habitats (see Armstrong et al. 2003 for a review). However, this simple model applies only if spatial segregation of cohorts is not itself a result of competition with larger fish, including older cohorts of their same species (Armstrong and Nislow 2006). Natural populations of stream-living salmonids often comprise several coexisting cohorts within a relatively restricted stream area and, as in most organisms with indeterminate growth, the

difference in body size can be substantial (e.g. Elliott 1994). Body size and prior residency are two key variables for predicting social rank and resource defence in juvenile salmonids (Kalleberg 1958; Johnsson et al. 1999). In accordance, field and laboratory studies show that large individuals have priority to both favourable winter shelters (Orpwood et al. 2003) and upstream feeding territories (Hughes 1998) from which they may reduce the food availability in downstream habitats through filtering interference (Nilsson et al. 2004). Previous empirical evidence provides support for inter-cohort competition in populations of brown trout (*Salmo trutta* L.), with improved age-0 performance (i.e. growth and survival) in experimental stream sections in which density within older cohorts was reduced (Kaspersson & Höjesjö 2009; Kaspersson et al. 2012; Nordwall et al. 2001). However, the nature of the competition (e.g. exploitation via filtering of food vs. interference through spatial exclusion) was not determined.

Inferring mechanisms of competition in complex natural streams may be difficult, while observations from overly simple laboratory experiments may have limited relevance to natural habitats. To help overcome this problem, we used an indoor semi-natural stream environment that included realistic habitat complexity and fish social structure while allowing direct observation and a capacity to replicate standardised treatment types. The experiment was conducted during the critical weeks after emergence in spring and early summer. Focussing on the age-0 cohort, we investigated whether Atlantic salmon are constrained to slow-flowing marginal habitats due to habitat choice and physical limitations in their foraging performance or excluded from faster flowing areas by an older (age-1) cohort. In the wild, age-0 salmon has been recorded within a velocity range (mean water column velocities) of up to 40 cm.s^{-1} during their first summer (Armstrong et al 2003), with velocity use increasing with the size of the fry (Heggenes 1990). The test arenas in this experiment ($n = 16$) included two distinctly different habitat types; one deep high-velocity ($42.2 \pm 0.4 \text{ cm s}^{-1}$) habitat and one shallow low-velocity

($3.3 \pm 0.3 \text{ cm s}^{-1}$) habitat, with food provided to each habitat in proportion to the current velocity regime. Hence, the high velocity habitat in our experiments was near the limit of observed velocities used by large fry in the wild.

Atlantic salmon juveniles have large pectoral fins that act as hydrofoils enabling them to hold position in high-velocity habitats at very low energy costs. This adaptation can allow position-holding up to about 60 cm s^{-1} with no active swimming (Arnold *et al.* 1991). Hence, since fry may inhabit an area even if they cannot use it for feeding, profitability of habitat use was assessed throughout the experiment by observing activity and feeding behaviour (food intake).

We predicted that fast-flowing areas would be preferred feeding habitat for age-1 salmon due to associated higher food availability. Furthermore, we predicted that this habitat would be used by age-0 salmon only if they could manage to forage efficiently and, if so, that they would be displaced in the presence of an older cohort through interference competition. Although salmon juveniles are territorial and despotic at a local level, it has been suggested that they may follow an Ideal Free Distribution (IFD) in which local density is proportional to food supply (e.g. Hedger *et al.* 1991; Girard *et al.* 2004), and this might particularly be the case when they are settling into habitats at an early life stage. Therefore, we also tested the prediction that the distribution of salmon approximates an IFD in the absence of an older cohort, but becomes more skewed towards the low food low velocity habitat under inter-cohort competition. In addition to habitat use we observed overall activity (changes in position), foraging activity and efficiency, capture success, proportion of fish observed and interactions within and between cohorts.

Materials and methods

Experimental design

The experiment was performed in a large indoor semi-natural stream at the Marine Scotland Science field station at Almondbank, Perthshire, UK. To detect any effect of ontogenetic development as well as to make sure that the crucial early phase of emergence was covered, the experiment was repeated over two periods: 20 April – 5 May 2009 (Period 1) and 17 June – 11 July 2008 (Period 2). The stream was continuously supplied with water from the nearby river Almond and was equipped with a glass-sided outer wall to enable behavioural observations from a darkened hide (Figure 1 and 2). Each of the 16 test arenas was landscaped into two markedly different habitats, one shallow ($12.2 \text{ cm} \pm 1.3\text{SD}$) and one deep ($23.9 \text{ cm} \pm 1.0 \text{ SD}$). The overall water velocity of the indoor stream was adjusted at the water inlet and the velocity of the habitats was primarily facilitated by the difference in water depth, but water flow was also directed to the deep areas by division of the water using a solid plastic screen placed at the upper end of each shallow area (Fig. 2). Hence, water flow was centrally adjusted for all test arenas, and any upstream-downstream gradient in velocity was accounted for by randomizing the distribution of treatments. Water depth and velocity were measured at three positions using Geopacks Advanced Flowmeter 1 (Devon, UK) along a longitudinal transect of each test arena (upstream, middle and downstream). In the shallow habitat, water velocity was measured once per longitudinal position (middle of water column), while three measurements per position were taken in the deep habitat (bottom, middle and surface of the water column). The average velocity was $42.2 \text{ cm s}^{-1} (\pm 0.4)$ and $3.3 \text{ cm s}^{-1} (\pm 0.3)$ in the deep habitat and shallow habitat respectively ($\pm \text{SE}$).

In each habitat of the test arenas, an under-gravel feeding tube ($\varnothing$ 4 mm), had its outlet 15 cm downstream from the upper screen equidistant from each side of the habitat and 5 cm above the gravel bed (Fig. 2). Field studies have shown that juvenile salmon early in the season mainly feed on drifting prey items (Keeley and Grant 1997). Hence, in our system, fish were provided dead, 5-10 mm long, thawed Chironomid larvae that drifted downstream from the outlet of the feeding tube. We provided larvae to each habitat in an approximate proportion to the water velocity to further resemble the expected differences in prey availability at different velocities under natural conditions. Food was provided through an automatic fish feeder (ASU 2000) (MacLean et al. 2003). The feeder system comprised 16 aerated (to avoid clumping of food items) buckets placed above the experimental stream, each filled with 8500 ml of stream water and approximately 260 Chironomids (two cubes) at the start of each observation day. The rate of delivery was set through 32 solenoid valves (one per tube and habitat), activated via a computer program every 30 s in the high-velocity (deep) habitat (delivery rate was 0.21 ± 0.009 chironomids min^{-1}) and every 600 s in the low-velocity (shallow) habitat (0.02 ± 0.002 chironomids min^{-1}) (i.e. the high-velocity habitat had approximately 10 times greater food availability) ($\pm$ SE). The downstream screens prevented chironomids from drifting into neighbouring test arenas and these were cleaned to remove uneaten food items and sediment at the end of each observation day. Although most natural drift from the river Almond was removed through an upstream drum filter (mesh size 0.5 mm), some background food was available to the fish. This supply was however negligible in relation to the abundance and energy value of the chironomids provided. The provided ration was intended to generate a pronounced difference in quality between habitats, and was intentionally held at relatively low levels in comparison to natural conditions (Brittain and Eikeland 1988) for several reasons. First, trials with a higher food density resulted in a higher amount of items being collected at the

downstream mesh, necessitating a more frequent cleaning program, and hence increasing the risk of stressing the fish. Second, trials with higher food delivery rate (and thus higher density of chironomids in the food delivery buckets) resulted in clumping due to the aeration system being unable to mix the content successfully, and hence less of a natural food delivery. Third, and in association with the latter, a higher food delivery rate made it more difficult to determine fish behaviour in association with foraging. In this experiment, probably all food items could be seen by all fish in all treatments.

Each habitat of the test arenas was equipped with one shelter (two per test arena, each a sheet of opaque grey PVC, supported by four stainless steel legs). Stream-living salmonids often seek shelter in the wild as a way of avoiding predation (Fraser & Metcalfe 1997) and water current (Gries & Juanes 1998) and in semi-natural stream environments, shelters have been shown to reduce metabolic rate (Milidine et al 2006). The shelters measured 5×12 cm (W $\times$ L) and were positioned 50 cm from the upper screen equidistant from each side of the habitat with the sheet placed horizontally 5 cm above the gravel bed (Fig. 2). Natural photo period was simulated using an electronic timer and the test arenas were illuminated using eight 400-W Philips SON Agro bulbs, suspended at between 126 and 148 cm above the water surface. Water temperature in the indoor stream corresponded to that in the natural stream environment and was recorded by an automatic logger (Period 1: 11.2 ± 1.3 °C, range 8.3 to 15 °C; Period 2: 14.1 ± 1.3 °C, range 10.5 to 17.5 °C) ($\pm$ SD).

Study fish

The age-0 Atlantic salmon used at Period 1 were hatched and reared at the laboratory because wild fish of this age cannot be reliably caught and identified to species. The hatchery reared fry were the progeny of two females and two males, wild-caught from the river Almond and held in

flow-through tanks with water from their natal river. The adults were stripped in November 2008, the eggs hatched 20 – 24 February 2009 and first feeding of fry was observed on 3 April 2009. We started trials on the April 20 when all families were large enough to be observed in the stream.

Wild age-0 (Period 2) and age-1 salmon (Period 1 and 2) were collected from the river Almond using electro-fishing. Fish were collected as needed during the experimental periods to reduce the time in captivity prior to experiments. Immediately after capture, the fish were transported to the laboratory in a container with oxygenated stream water. At the laboratory, fish were held in 1m diameter circular holding tanks awaiting the start of the experiment, with a continuous supply of water from river Almond, opaque plastic tubes for shelter and fed *ad libitum* with thawed Chironomids. Fish in holding tanks were exposed to the same temperature and light conditions as in the experimental stream (see above).

At the start of each observation run (day 1), fish were anaesthetised (Benzocaine, 20 mg L⁻¹), measured (to nearest mm), weighed (to nearest 0.1 gram) (see Table 1 for body-sizes) and assigned to one of the following five treatments:

- (i) Age-0 salmon absent, one age-1 salmon (n=20)
- (ii) Age-0 salmon absent, two age-1 salmon (n=20)
- (iii) Eight age-0 salmon, age-1 salmon absent (n=24)
- (iv) Eight age-0 salmon, one age-1 salmon (n=25)
- (v) Eight age-0 salmon, two age-1 salmon (n=22)

giving an age-0 density of 15 fish m⁻² in treatments iii-v,. These densities are similar both to those recorded in a long-term study of a Perthshire stream (Egglishaw and Shackley 1977) and in small coastal streams in Sweden (Kaspersson & Höjesjö 2009; Kaspersson et al. 2012; Höjesjö et al. 2014). After recuperating from the procedure, each group of fish was released into a randomly assigned test arena. The fish were left to acclimatize in the stream for two days while being exposed to the same food and light regime as during the observations. At day four to eight, each section was observed two times (one observation in the morning and one in the afternoon) in a random pattern, each observation lasting 10 minutes.

Experimental protocol

We noted the position of age-0 and age-1 salmon every 30 s according to (i) number of individuals that used the high-velocity (deep) and the low-velocity (shallow) habitat and (ii) the distribution of fish within each habitat on a scale from one (upstream third of test arena) to three (downstream third of the test arena). Aggressive interactions within the age-0 cohort as well as from age-1 against age-0 salmon were noted continuously throughout the observation and were characterized as display (lateral or frontal, erected fins), chase (one fish pursues an escaping fish), bite and charge (attack), according to the classification of Keenleyside and Yamamoto (1962). We also noted encounter rate (number of available chironomids per age-0 salmon per minute drifting through the test arena at each observation) to verify the number of food items presented in the different treatments, number of food items consumed, as well as number of unsuccessful attempts (attempt to catch the prey but with no succeeding intake) by the age-0 fish.

Data analyses

The response variables were: habitat use (percentage of age-0 and age-1 salmon in the high-velocity (deep) habitat), aggressive interactions (total number of aggressive interactions within the age-0 cohort as well as total number of interactions initiated by age-1 salmon against age-0 fish, per observed age-0 salmon and minute), foraging activity (sum of both successful and unsuccessful strikes per observed age-0 salmon per minute), foraging efficiency (proportion of the foraging activity that resulted in food intake), activity index (number of times age-0 salmon changed position in the test arena, per observed age-0 salmon per minute) and “proportion of fish observed” (percentage of the age-0 salmon that was observed during the trial)

Each treatment was replicated between eight and 14 times during seven weeks, arenas where age-0 salmon were undetectable or showed no foraging activity during an entire observation were excluded from the analysis, since it was assumed to indicate elevated stress levels and less natural behaviour (see supplementary material for detailed information). Averages per day and per observation period (week) were used in the analyses. Habitat use, observation rate, activity, foraging activity, foraging efficiency and interactions were analysed using a General Linear Model (Dependent Variable = Treatment + Period + Treatment x Period). The overall distribution of the fish was also tested against the Ideal Free Distribution (IFD) using a one way t-test where salmon was predicted to use the deep high velocity at a ratio 10:1 relative to the shallow low velocity area due to differences in food encounter rate. The difference in activity and foraging between habitats were analysed using a paired t-test. All interaction terms were excluded if not significant. SYSTAT 13 was used for all statistical analyses. The experiment was performed under UK Home Office licence.

Results

Significantly more age-0 salmon used the high-velocity (deep) habitat rather than shallow habitat in the absence of age-1 salmon ($p < 0.001$, $t = 9.41$, $df = 23$) (Fig. 3a). A stronger preference for the deep habitat was detected during Period 1 than Period 2 ($F_{1,66} = 6.7$, $p = 0.012$). An IFD would be expected if food supply alone is the driving force of habitat use, where fish will be distributed according to food delivery rate. Here, distribution differed significantly in relation to the expected (IFD) for all treatments ($p < 0.001$), with fish tending to use shallow habitat more than expected at a population level. Nevertheless, on average 73 % of 0+ salmon used the high food/high velocity habitat, a deviation of only 17 % from the IFD. Salmon decreased their time spent in the high-velocity (deep) habitat in the presence of age-1 salmon, regardless of the density of the latter ($F_{2,66} = 12.55$, $p < 0.001$, Fig. 3a). In this case the deviation from the IFD increased to 45 % when two 1+ salmon were present, a significantly higher deviation than for 0+ salmon in allopatry ($p < 0.0001$, $F_{2,66} = 38.18$).

Overall, solitary age-1 salmon tended to use the high-velocity (deep) habitat but there was a substantial increase in the use of the low-velocity (shallow) habitat when pairs of age-1 fish coexisted within the same test arena ($F_{3,79} = 6.014$, $p = 0.001$; Fig. 3b). This effect was more pronounced in period 2 when fish were larger, as reflected in the interaction between treatment and period ($F_{3,79} = 3.56$, $p = 0.018$) and age-1 salmon in period 1 used the two habitats at a more equal frequency. In addition, the preference for deep high velocity area was higher in period 2 ($F_{1,79} = 6.39$, $p = 0.013$, Fig. 3b).

The proportion of age-0 salmon observed was generally relatively high in the absence of older cohorts but decreased to approximately 50 % in presence of two age-1 salmon ($F_{2,67} = 13.26$, $p = 0.006$, Fig. 3c). Age-0 activity also decreased in the presence of older cohorts

($F_{2,64}=5.47$, $p=0.006$, Fig. 3d), an effect that was more pronounced in period 2 as indicated by the interaction between treatment and period ($F_{2,64}=3.45$, $p=0.038$). This might be explained by an overall lower activity (number of times age-0 salmon changed position) at Period 1 ($F_{1,64}=26.74$, $p<0.001$).

Overall foraging activity of age-0 salmon was very low (<0.012 chironomids .fish⁻¹.min⁻¹) but more than twice as high in the high-velocity (deep) as in the low-velocity (shallow) habitat ($p<0.001$, $t=-4.53$, $df=69$); Fig. 4b). Foraging activity decreased in the presence of age-1 salmon (independent of their density) ($F_{2,64}=6.78$, $p=0.002$) and was most pronounced in Period 1 (Interaction effect: $F_{2,64}=5.47$, $p=0.006$, Fig. 5a). More specifically, foraging activity decreased with the number of age-1 salmon ($F_{2,64}=8.64$, $p=0.001$) in the deep (high-velocity) habitat whereas no such difference could be detected in the shallow (low velocity) habitat ($p>0.1$) (Fig. 5c). Although foraging efficiency was lower in the high velocity habitat, it was not significantly so (Fig. 4c) nor was there any effect due to number of age-1 salmon ($p>0.1$ both cases).

Aggressive interactions within the age-0 cohort occurred more frequently at Period 2 (30 % of the observations) than at Period 1 (12 % of the observations) ($F_{1,66}=7.61$, $p=0.008$), with charge being the most common type (81 % of all interactions), followed by nip (13 %), chase (3 %) and display (3 %). In addition, aggression within the age 0+ cohort was more frequent in the shallow low velocity habitat during period 2 ($p=0.006$, $t=3.58$, $df=13$). We found no effect of age-1 density on the frequency of aggressive interactions within the age-0 cohort ($p>0.1$).

While age-1 salmon were observed to initiate aggressive interactions against age-0 fish on only one occasion during Period 1, aggression was more common during Period 2 ($F_{1,66}=5.09$, $p=0.027$) and occurred in 11 % of the observations categorized as charge (70 %), display (22 %) and nip (8 %). In this period, the frequency of aggression was also higher in the low-velocity (shallow) than in the high-velocity (deep) habitats ($p=0.008$, $t=2.87$, $df=24$).

316

317 **Discussion**

318 Presence of an older cohort caused age-0 salmon to shift from using deeper, faster habitats to
319 shallow, slower flowing, areas where they acquired less food than in allopatry. In the absence of
320 an older cohort, age-0 salmon were able to maintain position and forage effectively in the
321 relatively deep, fast-flowing, areas that tend to be occupied by age-1 salmon in the wild
322 (Armstrong et al. 2003). Hence, this study extends the velocity-limitation model (Nislow et al.
323 1999; Hill & Grossman 1993), by showing that, offspring body-size, and hence swimming
324 ability, does not constrain Atlantic salmon fry to marginal areas during the critical period after
325 emergence, at least within the velocity range used in this experiment. Our results suggest that
326 size and dominance act as hierarchical constraints on the distribution of salmonids. First, size-
327 related swimming performance of fish will exert a primary control on the area of available
328 habitat for each cohort. This primary constraint, or filter, defines the fundamental niche.
329 Secondary constraints include a broad range of local biological factors, including social
330 interactions, predation risk and energy value of a patch, which collectively will define the
331 realized niche. Competition from age-1 fish acted as the secondary filter in our experiment;
332 altering the patch quality and causing more age-0 individuals to avoid the deep habitat.

333 In our study we found a small deviation from the Ideal Free Distribution for 0+ fish alone
334 suggesting that although foraging opportunity is higher in the deeper areas there is also a cost
335 associated with this habitat such that some individuals therefore chose the shallow less
336 profitable habitat. Although it is not possible to evaluate the nature of such costs in the current
337 experiment, they may relate to elevated costs of foraging and/or perceived risks of predation due
338 to reduced maneuverability in a fast flowing environment. The costs may also be social since it

is well established that Atlantic salmon are highly despotic with dominant fish excluding others from the best feeding sites (Fausch 1984) as suggested by the greater use of shallow habitat by age-1 salmon at high density.

Hill and Grossman (1993) and Nislow et al. (1999), suggested that optimum foraging locations for drift feeders can be identified by considering the concurrent effects of an increase in food availability but decrease in foraging efficiency with current velocity. In our experiments, there was a ten-fold differential in food availability with current speed, but no significant difference in foraging efficiency, so that the rate of food intake was much higher in the deep fast flowing area. It is possible that relative differences in foraging efficiency and energy gain between velocity patches would be more pronounced if smaller food items were involved. However, the chironomid larvae used are known to be important in the diets of 0+ salmon (eg Keeley & Grant 1997).

Although we were not able to detect a significant difference in foraging efficiency of age-0 salmon between velocity areas, foraging activity (total number of attempts and intakes) was higher in the deep high-flow habitat, which not only provided more drifting food items but also a larger search area (Hughes and Dill 1990). In consequence, when age-0 salmon at Period 1 were displaced to low-flow areas in sympatry with age-1 salmon, both their foraging activity and detectability (% observed fish) decreased markedly. Use by age-0 salmon of high-velocity deep habitats suggests that the additional food availability outweighs any extra costs of foraging, resulting in higher net energy gain compared to low-flow habitats in our experimental set up (Hill and Grossman 1993, Piccolo et al. 2008), despite the overall low prey encounter rate (0.2 chironomids.min⁻¹ in the high velocity area) relative to a natural system of 1-2 drift forays min⁻¹ (Nislow et al. 1997) where smaller food items may predominate (Brittain & Eikeland 1988).

Age-1 salmon selected high-flow deep habitats during Period 2, while being indiscriminate to water-flow and depth in Period 1. A possible explanation for this pattern is that age-1 salmon were foraging most intensively during night at the lower water temperature of Period 1 (e.g., Taylor 1988; Heggenes et al. 1993; Breau et al. 2007). In contrast, age-0 salmon showed a greater consistency across periods in using high-velocity habitats in the absence of inter-cohort competition, suggesting that their lower energy reserves and higher energy demands (Schultz and Conover 1997) necessitated day-time foraging activity, despite low temperatures. Moreover, increased energy reserves as the fish grow may also provide an explanation for the lower age-0 foraging activity and the lack of treatment effect on foraging activity at Period 2.

That age-0 salmon used low-flow areas irrespective of age-1 density also suggests that the mere presence of older fish was sufficient to induce habitat avoidance behaviour (Griffiths and Armstrong 2002). Moreover, the frequency of inter-cohort aggression in this study was low, providing further evidence of more subtle mechanisms underlying inter-cohort habitat exclusion. Presence of an older cohort may reduce the number of patches used within the central placed territory of age-0 fish (Steingrimsson and Grant 2008), suggesting that general activity was reduced to avoid reception of aggression. Presence of potential aggressors may also influence the energy balance of salmon not just by reducing food intake but by elevating resting metabolic rate (Millidine et al. 2009).

The exclusion of age-0 salmon to less profitable stream areas suggests that older cohorts in natural populations may have the potential to influence the strength of the recruiting cohort through negative density-dependence. Indeed, experimental field-studies (Nordwall et al. 2001; Kaspersson and Höjesjö 2009; Kaspersson et al. 2012) provide evidence of population-level effects of inter-cohort competition among stream-living salmonids and similar findings have been reported for lake dwelling rainbow trout where young of the year fish were confined to

marginal habitats in the presence of older cohorts (Post et al 1999; Walters & Juanes 1993). Hence, the behavioural mechanisms we observed are consistent with field observations at a population level and suggest that habitat use by young-of-the-year fish during the early critical period are strongly influenced by older cohorts which may shape their cohort strength and/or development rate. As a consequence, this result suggests that the distribution of micro-habitats and inter-cohort competition within a stream may have a large influence on population structure of stream salmonids. Examining brown trout habitat selection patterns in three Iberian rivers, Ayllon et al. (2013) similarly demonstrated that habitat selection by all age classes varied among years depending on the densities of older but not younger age groups.

The results provided here suggest that the age-0 cohort has a potential to occupy much of the habitat used by older fish if the competitive strength from the older cohorts decreases. It is relevant, therefore, to consider what determines the fundamental niche in Atlantic salmon. Unfortunately, current understanding of ontogenetic changes in swimming abilities of Atlantic salmon is not sufficient to clearly define how capacity for capturing food changes with body size. Although size-related swimming performance is well-defined in other salmonids (e.g., Brett & Glass 1973), these relationships are not relevant to position holding in Atlantic salmon which use their pectoral fins as hydrofoils, and make forays from a home rock to intercept prey. Hence, it may be the speed of short bursts that is of most relevance to defining the fundamental niche, but these remain poorly defined, and complicated by the effects of turbulent flow (Enders et al. 2003). Despite these uncertainties, burst swimming is about $10 \text{ body lengths} \cdot \text{s}^{-1}$ on average among a range of fish species (Videler & Wardle 1991), which for our age-0 salmon would equal about $24\text{--}31 \text{ cm} \cdot \text{s}^{-1}$ in Period 1 and $25\text{--}47 \text{ cm} \cdot \text{s}^{-1}$ in Period 2. With this rough approximation, most individual age-0 salmon in our experiments would be unable to hold station by swimming against the flow at average water column velocity in the fast flowing treatment.

However, they may nevertheless feed successfully because Atlantic salmon can catch prey by launching into the current and intercepting items downstream of their starting point (Stradmeyer & Thorpe 1987), returning to their holding station near the stream bed where velocities are much lower. Better understanding of key factors that determine capture efficiency (eg. visual acuity and precision of attacks as functions of local current velocity and turbulence) is at least as important as swimming performance for defining the fundamental niche of Atlantic salmon. Further empirical observations are required to define the fundamental niche of juvenile Atlantic salmon as a function of fish size, roughness of the substratum, and type of food.

Modelling the effects of habitat structure on the potential of a stream to produce salmon smolts as part of fisheries management requires an understanding of habitat needs of different life stages. It is established that age-0 salmon can affect older cohorts through filtering competition (Einum et al. 2011), and it would be expected that such an effect would be reciprocal, with the older cohort affecting the younger one. The present study emphasises the likely importance of an additional mechanism of competitive exclusion of age-0 salmon from relatively fast-flowing areas. This process would be expected to facilitate population resilience by increasing habitat availability and densities in an 0+ cohort that follows a particularly weak cohort. Empirical data from a long-term monitoring study (Bacon et al. 2015) suggest that such mechanisms do indeed have a profound effect at the population level.

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Table 1. Initial length and mass of age-0 and age-1 salmon at Period 1 (20 April – 5 May 2009) and Period 2 (17 June – 11 July 2008). Sd represents standard deviation.

Measured variables		Period 1		Period 2	
		Age-0	Age-1	Age-0	Age-1
Length (mm)	mean	28.14	62.35	34.46	76.86
	range:	24-31	50-71	25-47	65-92
	sd:	1.12	5.67	4.56	5.74
Mass (gram)	mean	0.16	2.45	0.37	4.56
	range:	0.09-0.29	1.20-3.90	0.12-1.00	2.70-7.90
	sd:	0.03	0.73	0.16	1.07

Draft

Fig. 1. A schematic drawing of the indoor flumed used in the experiment. The 16 test arenas ($W \times L$: 0.60×0.90 m) were divided by stainless-steel wire screens (mesh size 3 mm) and observations were made through a plastic hide.

Fig 2. A figure showing one of the 16 subsections; A shallow (12.2 ± 0.2 cm), slow-flowing habitat (3.3 ± 0.003 cm s⁻¹; range: 0 - 14 cm s⁻¹) was created by placing concrete blocks covered with a layer of gravel ($\varnothing$ 1 cm) longitudinally in the inner half of each arena (30 cm from the inner wall). In the outer half (30 cm from the glass-sided outer wall) no concrete blocks were placed and this area had twice the depth (23.9 ± 0.1 cm) and on average 12 times greater water velocity (42.2 ± 0.004 cm s⁻¹; range: 23 - 62 cm s⁻¹) (mean $\pm$ SE).

Fig. 3. The effect of density treatment on (a) % age-0 salmon in the high-velocity (deep) habitat, (b) % age-1 salmon in the high-velocity habitat, (c) % observed age-0 salmon (observation rate), (d) activity index (number of times age-0 salmon changed position, per age-0 salmon and minute) at Period 1 (20 April – 5 May 2009) and Period 2 (17 June – 11 July 2008). Bars represent mean + SE. * denotes significant relationships ($P < 0.05$).

Fig. 4. Mean + SE difference in (a) encounter rate (number of available Chironomids per age-0 salmon and minute), (b) foraging activity (foraging attempts and intakes), (c) foraging efficiency (proportion of the foraging activity that resulted in intake), between age-0 fish in low-velocity habitats (black bars) and high-velocity habitats (grey bars) and between periods (Period 1: 20 April – 5 May 2009 and Period 2: 17 June – 11 July 2008). * denotes significant relationships ($P < 0.05$).

598 **Fig 5.** The effect of density treatment on (a) overall foraging activity (attempts and intakes, per
599 age-0 salmon and minute), (b) foraging activity in the deep (high-velocity) habitat and (c)
600 foraging activity in the shallow (low-velocity) habitat, between periods (Period 1: 20 April – 5
601 May 2009; Period 2: 17 June – 11 July 2008). Note the scales on the y-axes. Bars represent
602 mean + SE. * denotes significant relationships between xxxx ($P < 0.05$).

Draft

Fig. 1. A schematic drawing of the indoor flumed used in the experiment. The 16 test arenas (W × L: 0.60 × 0.90 m) were divided by stainless-steel wire screens (mesh size 3 mm) and observations were made through a plastic hide.
305x88mm (150 x 150 DPI)

Fig 2. A figure showing one of the 16 subsections; A shallow (12.2 ± 0.2 cm), slow-flowing habitat (3.3 ± 0.003 cm s⁻¹; range: 0 - 14 cm s⁻¹) was created by placing concrete blocks covered with a layer of gravel ($\varnothing$ 1 cm) longitudinally in the inner half of each arena (30 cm from the inner wall). In the outer half (30 cm from the glass-sided outer wall) no concrete blocks were placed and this area had twice the depth (23.9 ± 0.1 cm) and on average 12 times greater water velocity (42.2 ± 0.004 cm s⁻¹; range: 23 - 62 cm s⁻¹) (mean $\pm$ SE).

118x157mm (150 x 150 DPI)

Fig. 3. The effect of density treatment on (a) % age-0 salmon in the high-velocity (deep) habitat, (b) % age-1 salmon in the high-velocity habitat, (c) % observed age-0 salmon (observation rate), (d) activity index (number of times age-0 salmon changed position, per age-0 salmon and minute) at Period 1 (20 April – 5 May 2009) and Period 2 (17 June – 11 July 2008). Bars represent mean + SE. * denotes significant relationships ($P < 0.05$).
139x113mm (150 x 150 DPI)

Fig. 4. Mean + SE difference in (a) encounter rate (number of available Chironomids per age-0 salmon and minute), (b) foraging activity (foraging attempts and intakes), (c) foraging efficiency (proportion of the foraging activity that resulted in intake), between age-0 fish in low-velocity habitats (black bars) and high-velocity habitats (grey bars) and between periods (Period 1: 20 April – 5 May 2009 and Period 2: 17 June – 11 July 2008). * denotes significant relationships ($P < 0.05$).

70x152mm (150 x 150 DPI)

Figure S1

Fig 5. The effect of density treatment on (a) overall foraging activity (attempts and intakes, per age-0 salmon and minute), (b) foraging activity in the deep (high-velocity) habitat and (c) foraging activity in the shallow (low-velocity) habitat, between periods (Period 1: 20 April – 5 May 2009; Period 2: 17 June – 11 July 2008). Note the scales on the y-axes. Bars represent mean + SE. * denotes significant relationships ($P < 0.05$).