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Natal movement in juvenile Atlantic salmon: a body size-dependent strategy?

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Abstract If competitive ability depends on body size, then the optimal natal movement from areas of high local population density can also be predicted to be size-dependent. Specifically, small, competitively-inferior individuals would be expected to benefit most from moving to areas of lower local density. Here we evaluate whether individual variation in natal movement following emergence from nests is consistent with such a size-dependent strategy in Atlantic salmon, and whether such a strategy is evident across a range of environmental conditions (principally predator presence and conspecific density). In stream channel experiments, those juveniles that stayed close to nests were larger than those that emigrated. This result was not sensitive to predator presence or conspecific density. These observations were mirrored in natural streams in which salmon eggs were planted in nests and the resulting offspring were sampled at high spatial resolution. A negative relationship was found between juvenile body size and distance from nests early in development whereas in those streams sampled later in ontogeny, individuals that had moved furthest were largest. Thus, movement away from nests appeared to result in a reduced competitive intensity and increased growth rate. The fact that there is ultimately a growth advantage associated with moving suggests that there is also a cost that selects against movement by the larger individuals. Thus, natal movement in juvenile Atlantic salmon appears to represent a body size-dependent strategy.

Keywords Conditional strategy · Density dependence · Dispersal · *Salmo salar* · Spatial distribution

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Introduction

A wide range of organisms move away from natal sites. A large body of work has focussed on understanding the forces that shape such behaviour and the resulting distribution of individuals (reviewed by Clobert et al. 2001, 2009). Most such studies have examined the factors that affect natal dispersal senso stricto. Natal dispersal has been defined as an "active or passive attempt to move from a natal/breeding site to another breeding site" (Clobert et al. 2009) and is thus concerned with the trans-generational timescales. However, it can be predicted that many of the same factors will also influence movement of juveniles away from natal sites motivated by access to food resources. This applies particularly to organisms that produce

spatial clusters of propagules. Movements may have benefits, but also costs in terms of reduced growth and increased risk of mortality (reviewed by Belichon et al. 1996; Yoder et al. 2004). Thus, many of the evolutionary pressures that shape natal dispersal (senso stricto) should also act on shaping natal movement when the benefit of moving is improved growth rather than improved reproduction.

The distances moved during natal dispersal can vary extensively within populations in association with other phenotypic characteristics. In particular, a sex-bias in dispersal is commonly found, which may be explained by inbreeding avoidance, kin selection or cooperation (reviewed by Handley and Perrin 2007). However, for natal movement that occurs well before the onset of maturation this factor may be less likely to influence dispersal (but see Nagata and Irvine 1997). An important trait that may be correlated with natal movement under such circumstances is body condition, and particularly body size. Body size usually influences competitive ability (e.g., Buston 2003; Bel-Venner and Venner 2006; Calsbeek and Smith 2007). Intense competition at high local density close to the natal site should therefore have more pronounced negative effects on smaller, competitively inferior individuals. As a consequence, it is reasonable to hypothesise the evolution of a size-dependent adaptive strategy, such that smaller individuals exhibit a higher degree of natal movement to reach areas of lower competitive intensities. Smaller individuals that successfully reach more distant sites with lower density would then be expected to benefit from relatively high growth which, over time, may cause them to exceed the size of those staying closer to natal sites, which initially were largest. However, this scenario remains conjecture because in general, the well studied effects of sex and age on movement is mirrored by a lack of detailed studies on effects of other phenotypic traits, including body size (Clobert et al. 2009).

Atlantic salmon (Salmo salar L.) is one species for which fitness pressures on natal movement are likely to be particularly important. This species reproduces primarily in streams, creating nests within the gravel bed where eggs are deposited in large numbers. This behaviour results in high local densities of propagules near the nest sites following emergence (reviewed by Fleming and Einum 2011). The spatial extent of competition among recently emerged salmon fry is over distances of ca. 10 m (Einum et al. 2011) which leads to intense competition in the vicinity of nests. Hence, it can be sensibly predicted that natal movement away from nests will increase growth prospects for those individual fry that are competitively inferior (Einum et al. 2011). Since large body size provides a competitive advantage in direct interactions (e.g., Cutts et al. 1999), the growth benefit of moving away from nest

sites to less densely populated areas would be expected to be more pronounced in smaller individuals. The alternative to emigration would be occupation of poor quality micro-habitats (Nislow et al. 1999, 2000) close to the nest possibly ultimately resulting in death by starvation (cf. Kennedy et al. 2008). However, emigration movements may increase vulnerability to predation, which in this species occurs from older salmonid fishes on the early life stages (Henderson and Letcher 2003; reviewed by Ward and Hvidsten 2011). Thus, natal movements of juveniles are likely to entail a trade-off between costs of movement and benefits of reduced competition (Einum et al. 2011), and body size dependent benefits are expected to select for a size-dependent strategy.

In the present study we use a novel approach to evaluate the possibility of a relationship between body size and probability of natal movement in Atlantic salmon (Salmo salar) following their emergence from nests. We first test whether downstream movement rates following emergence from nests depends on body size across a range of environmental conditions (variation in density and presence of potential predators) in standardised experimental stream-channels. Next, we compare the relationship between distance moved from nest sites and body size across a range of natural streams. The streams were sampled at different stages of the summer. The ontogenetic development stage at each sampling point was predicted using stream-specific temperature profiles combined with laboratory-derived models for emergence from nests and subsequent growth. Size-dependent movement from nest sites would be expected to produce a negative relationship between body size and distance moved away from nests early in the season. Furthermore, in a previous analysis of the same data we showed that local fish density decreased with distance from nests (Fig. 4 in Einum et al. 2011). Thus, we predict that the relationship between distance moved away from the nest and body size changes from being negative at early ontogenetic stages to becoming positive at later ones.

Methods

Ims stream channel study

Fertilised eggs from ten full-sib Atlantic salmon families from the River Imsa population were mixed into one batch during the fall of 2005 and incubated at the Norwegian Institute for Nature Research (NINA) Research Station, Ims, Norway. On April 5, 2006, alevins that had hatched from these eggs were planted out into artificial nests in eight semi-natural stream channels (2.1 × 10.3 m). The upstream half of each channel was shallow (mean depth 15 cm), whereas the lower part was deeper (mean 40 cm).

Each channel received a water flow of 260 l min^{-1}. Substrate comprised natural river gravel, and water was run in the channels for several months prior to the experiment to allow a natural invertebrate fauna to colonise. No additional food was provided. To test for consistency of dispersal patterns across environmental conditions, two levels of density (100 or 700 alevins per channel) and two levels of interactions with potentially predatory larger brown trout (*Salmo trutta* L.) were applied (absent or four individuals present), giving two replicates of each of the four treatment. The nests were constructed using 3 l plastic containers that were filled with coarse gravel, and received water through a pipe at the bottom of the bucket, while overflow allowed emerging juveniles to enter the channel. The containers were placed in the upstream part of each channel. To equalize nest sizes between density treatments, one and seven nests were used in the low and high density treatment, respectively. The brown trout used as potential predators were hatchery-reared 1-year-old from the River Figgjo population (mean ± SD body length of 254 ± 15 mm). A metal mesh screen (10 mm) at the outlet of each channel retained predators but was permeable to salmon fry thus allowing them to leave. Salmon leaving the channels were collected in traps which were checked and emptied daily after the onset of emergence. Trapped juveniles were frozen for later measurements of dry mass following a treatment of 48 h at 70°C. Dry mass was used in this experiment due to the small size of the fish (particularly from the traps), which was considered to make measurements of length or wet mass more susceptible to measurement noise. Based on observed temporal distribution of movements out of channels, the experiment was terminated on May 24, when fish remaining were removed by repeated draining of the channels and filtering the water, and killed and dried before measurements of dry weight. Water temperatures during the period the fish were caught in the traps ranged from 3.6 to 14.2°C. Temperature experienced by the eggs in the hatchery combined with temperatures in the stream channels were used to estimate the median date of emergence of YOY from the nests (Crisp 1981, 1988).

Conon field study

Fish origin and study sites

Atlantic salmon caught in a fish trap in the River Blackwater, a tributary to the River Conon, Ross-shire, Northern Scotland, during October 2007, were used to produce ten unique full-sib family groups. The fertilized eggs were incubated in a hatchery at Contin where the family groups were kept separate in hatchery trays. Eyed eggs were planted in ten small tributaries of the River Conon, during

17–26th February, 2008. All these streams are located above barriers to salmon upstream migration and hence were devoid of naturally spawned salmon. Natural brown trout populations were present in all but one of the streams, and older salmon (≥1+ age) resulting from stockings in previous years were present in seven of the streams (see Einum et al. 2011 for details).

Each stream received a single nest containing equal numbers of eggs from all the 10 family groups. The eggs from the different family groups were held in separate Vibert boxes (Federation of Fly Fishermen, Bozeman, MT, USA) which were placed within a depression in the gravel bed of the stream and covered with gravel and larger stones. Two stocking densities were used, one low (1000 eggs per nest, with 100 from each family), and one high (3000 eggs per nest, with 300 from each family), and these were assigned randomly to the different streams. The rationale for the two stocking treatments was to increase the potential for overall variation in environmental conditions among streams beyond that provided by other biotic and abiotic sources. In combination with genotyping of captured juveniles this allowed for quantification of consistency in relative family performance among environments in other analyses. However, due to the relatively low number of replicate streams and the presence of other sources of environmental variation among them, these data are not suitable in the present study for testing for effects of initial population-level density on overall juvenile growth. Thus, although we include the possibility for an effect of egg stocking density in the full statistical model (see below), the present study should not be viewed as a powerful test of such effects. For more appropriate analyses relating to this issue see e.g., Jenkins et al. (1999), Keeley (2001), Imre et al. (2005), Einum et al. (2006, 2011).

Sampling

During 15–24th July 2008 the streams were sampled to obtain information on the spatial distribution and body size of the resulting salmon YOY. Each stream was electrofished in a section stretching from 150 m below the nest-site to 50 m up-stream, or until a clear barrier to salmon migration was reached within those 50 m. In two streams, substantial numbers of YOY were recaptured approaching 150 m downstream of the nest sites. In these cases, additional sampling was performed down to 200 and 210 m below the nest-site. From one to three complete electro-fishing passes were performed depending on logistic constraints. For further details see Einum et al. (2011). The linear stream distance from nests that each YOY was captured was recorded (±1 m). Each captured fish was killed and put in an individual tube filled with ethanol. YOY body lengths (±1 mm) were measured within

2 weeks (i.e., during the sampling period). At the same time, the fish were cut in half to provide genetics samples (for a different study), and field scales available during sampling gave unreliable measurements. Thus, statistical analyses from this experiment are based on body lengths.

Predicted maximum body mass

Water temperature loggers (Levelogger, Solinst Canada Ltd.®, 35 Todd Road, Georgetown, Ontario, Canada L7G 4R8) were deployed in each stream at the time of stocking. As for the stream-channel experiments, median dates of emergence of YOY from the nests were estimated based on temperatures experienced by the eggs in the hatchery combined with recorded stream temperatures (Crisp 1981, 1988). Daily mean temperatures experienced following predicted emergence time were then used to calculate the predicted maximum body mass at the time of sampling (assuming a common starting mass value of 0.15 g), based on the model of fast growing salmon (Forseth et al. 2001):

$$M_t = (M_0^b + (b(td(T - T_L)(1 - e^{g(T-T_U)}))/100))^{1/b}$$

where M_0 is the initial fish mass, and M_t is the mass of the fish growing at its maximum potential for t days at T°C. The constants b, d, g and c are given as 0.31, 0.530, 0.208 and 4.72, respectively, whereas the lower (T_L) and upper (T_U) temperatures for growth are given as 6.0 and 24.5°C (Forseth et al. 2001). Using this model, values for M_t were iterated in a stepwise fashion for each population and for each day t of the growth period.

Statistical analyses

Ims stream channel study

All statistical analyses were conducted using the statistical software R, v. 2.9.2. (R Development Core Team 2009). We first tested for effects of relative date (T, first day of observed movement out was given a value of 1), density treatment (D) and presence/absence of predators (P) on the mean daily dry mass of fish caught in the traps, with stream channel (k) as a random effect. We also included interactions between relative date and density, and between relative date and presence/absence of predators in the initial model. To satisfy assumptions of normality and homogeneity of residuals, dry mass was log-transformed. Thus, the full model can be represented as:

$$Y_{j,k} = \alpha + \beta_1 T_j + \beta_2 D_j + \beta_3 P_j + \beta_4 T_j D_j + \beta_5 T_j P_j + b_k + \varepsilon_j$$

where j is an individual index, and where $\varepsilon_j \sim N(0, \sigma^2)$. To test for stream channel effects, we first compared two models with and without channel as a random effect. To

allow for such a comparison the models were implemented using the linear mixed-effects model function *lme* and the generalized least squares function *gls* in the linear and nonlinear mixed effects models package *nlme* (Pinheiro et al. 2009). Comparison of these models used likelihood ratio tests (calculated based on REML and compared with ANOVA, Zuur et al. 2009). This contrast showed no indication of a stream channel effect ($P = 0.999$). We therefore proceeded with the *gls* model to compare different fixed effects structures. This was done using a backwards selection procedure where fixed effects were removed sequentially, starting with the interactions, until no further model simplification could be made without causing a significant ($P < 0.05$) decrease in log-likelihoods (calculated based on ML and compared with ANOVAs, Zuur et al. 2009). As a complementary approach for this and subsequent analyses, we also calculated the AIC value (Burnham and Anderson 1998) for all the alternative models to check whether this gave results consistent with the model selection. A model was deemed superior to another if ΔAIC >2 (Burnham and Anderson 1998).

We also examined whether salmon density in nests and presence/absence of predators influenced final body mass of individuals staying in the stream channels until the end of the experiment. This was done using the same approach as described above. Again, no stream channel effects were detected, allowing the use of *gls*.

Due to a lack of a significant effect of relative date on body mass (see results), we could directly compare the dry mass of individuals that moved out of the stream channels with those that stayed. The initial model for this comparison contained movement and the presence of predators, as well as the interaction between these parameters, as fixed effects. Again, we found no random effect of stream channel (log-likelihood contrast, $P = 0.717$), and we thus proceeded with model selection based on a *gls* model as described above.

Conon field study

We used the linear mixed-effects model function *lmer* from the linear mixed-effects models package *lme4* (Bates et al. 2010) to model individual YOY final body length (Y_j) of individuals caught at or downstream of nest sites as a function of distance from nest at recapture (L, in meters), stream-specific predicted maximum body mass (i.e., maximum body mass predicted from the growth model, M, in grams), as well as the interaction between these variables. We modelled only downstream movement because the majority of early movement is downstream (e.g., Garcia de Leaniz et al. 2000; Foldvik et al. 2010), and because individual variation in such movement is not expected to be constrained by swimming capabilities (in contrast to

upstream movement against the water current). We used *lmer* rather than *lme* in this analysis to allow for using the *arm* package (Gelman et al. 2011) to obtain 95% confidence intervals for the parameter estimates. In addition, we tested for the main effect of egg stocking density (*D*, high or low) as well as for an interaction between stocking density and distance from nest. To account for variation in mean final size among streams in addition to that of predicted maximum body mass (*M*), stream (*k*) was included as a random variable. Thus, the full model can be represented as:

$$Y_{j,k} = \alpha + \beta_1 L_j + \beta_2 M_j + \beta_3 L_j M_j + \beta_4 D_j + \beta_5 L_j D_j + b_k + \varepsilon_j$$

where *j* is an individual index, and where $\varepsilon_j \sim N(0, \sigma^2)$. YOY body length was log-transformed to satisfy assumptions of normality and homogeneity of residuals. Using this full model we applied model selection as described above. *P* values for parameter estimates of the final model were obtained using the function *pvals.fnc* within the *languageR* package (Baayen 2010).

Results

Ims stream channel study

The first observation of juveniles in the trap occurred on April 6. The daily counts were low over the following 30 days, and the majority of movement out of the channels occurred between day 30 and day 40 (Fig. 1). Median predicted date of emergence was on day 33, and varied little among the channels (range 31–35). The experiment
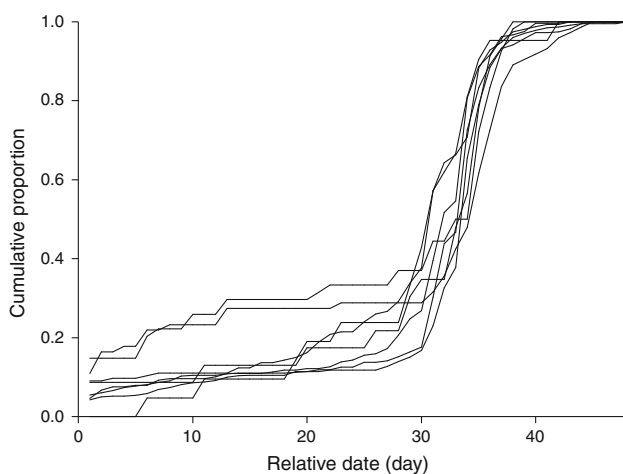

Fig. 1 Temporal pattern of the cumulative proportions of YOY Atlantic salmon caught in traps at the outlet of eight stream-channels during and following the period of emergence from nests. Day 1 = April 6

was terminated on day 49. The average total number (trap + channel) of recaptures from the four treatments were: low density, predators absent = 85; low density, predators present = 25; high density, predators absent = 610; high density, predators present = 205. Thus, the presence of predators reduced the mean recapture rates by 70% at low density and 66% at high density.

For our analyses of variation in dry body mass among the movers, both interaction terms could be removed (*P* > 0.802 for both), as could the main effect of density (*P* = 0.316) and relative date (*P* = 0.060). Thus, the only term that could not be removed from the initial model was the main effect of predator presence (*P* < 0.001). Predator presence had a positive effect on body mass [log mean dry weight (mg) = 2.50 (±0.03) + 0.18 (±0.04) × predator presence]. This was confirmed in the comparison of AIC values for models, where all models containing the predator presence term had substantially lower AIC values than models without this term (all ΔAIC ≥12.5). The model with the lowest AIC contained the main effects of predator presence and relative date. However, this model was not substantially better than the simpler model containing only predator presence (ΔAIC = 1.6). The relative date effect, although non-significant based on the model selection procedure, was negative, with size decreasing with date in most stream channels (Fig. 2, estimated effect (±SE) of relative date when retaining this term in the model was −0.003 ± 0.002). For our analyses of variation in dry body mass among the fish caught in the channels, all model terms could be removed (*P* > 0.522 for all). Thus, neither the presence of predators nor initial density influenced the final body size of these.

In the comparison between dry mass of juveniles caught in the trap and those staying in the channels, the final model shows a clear effect of behavioural type, with those in the channels being larger than those caught in traps (Table 1; Fig. 3). Furthermore, the interaction between predator presence and behavioural type could not be removed (*P* = 0.022). This interaction reflects the facts that although movers caught in the traps were smaller when predators were absent than when they were present, the size of the juveniles staying in the channels until the end of the experiment was not influenced by the presence of predators (Fig. 3). This result was consistent with AIC comparisons, where the full model was substantially better than the next best one which only included the main effects of behavioural type and predator presence (ΔAIC = 3.2).

Conon field study

A total of 2291 YOY were captured within the relevant spatial extent of the sampling (i.e., from 0 to 210 m downstream of nest sites), and were included in the
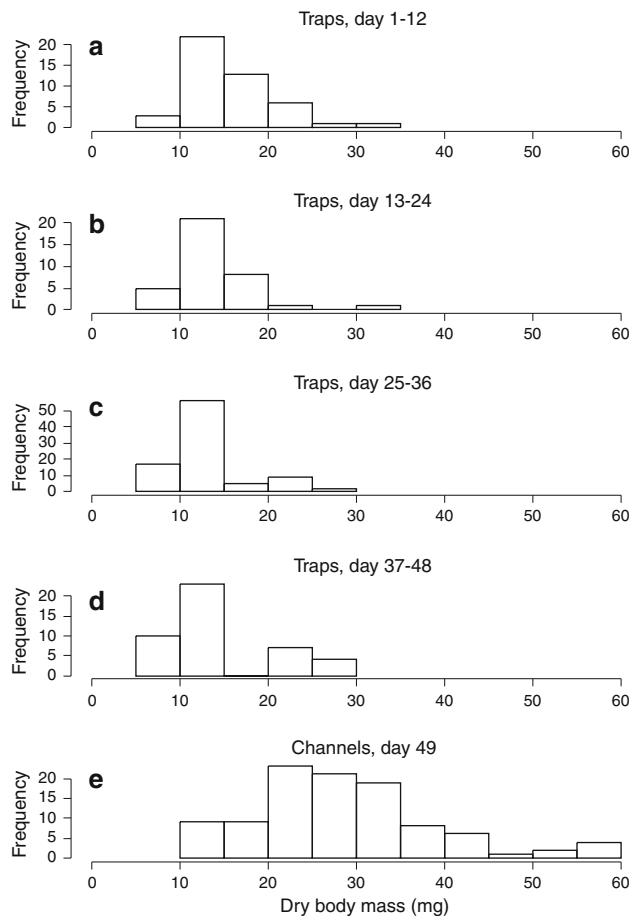
Fig. 2 Histograms showing the body size distributions of YOY Atlantic salmon from stream-channels being **a–d** caught in traps in different periods during and following the time of emergence (day 1 = April 6), and **e** staying until the end of the experiment (day 49). Data from eight stream-channels are pooled. Note differences among panels in scale of y-axis

Fig. 3 Body size of YOY Atlantic salmon staying (*grey bars*) and moving out of eight stream-channels (*white bars*) in the presence and absence of predatory trout. *Error bars* represent 1 SE

Table 1 Summary of a linear model describing variation in dry mass (log, mg) of YOY Atlantic salmon in stream channels as a function of movement behaviour (remaining in channels vs. being caught in traps) and presence of predatory trout

	Parameter (95% CI)	t	P
Intercept (channel)	3.30 (3.22 to 3.38)	90.73	<0.001
Traps[a]	−0.80 (−0.90 to −0.70)	−16.90	<0.001
Predator present	−0.02 (−0.18 to −0.14)	−0.26	0.794
Traps[a] × predator present	0.20 (0.02 to 0.38)	2.28	0.023

[a] Parameters given are for individuals moving out of stream channels and being caught in traps relative to those staying in them throughout the experiment

statistical analyses. Predicted median dates of emergence ranged from 12 May to 1 June among streams. Based on predicted date of emergence and temperature regimes experienced up to the sampling, the growth model
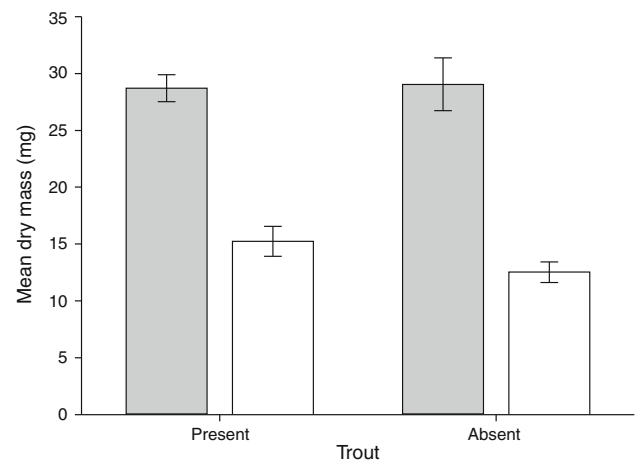
predicted body mass to range from 0.58 to 2.08 g among streams. These predictions correlated well with the mean body lengths observed among streams ($n = 10$, $r = 0.75$, $P = 0.013$). Thus, the range of temperature regimes experienced during and after incubation produced a wide among-stream range in predicted ontogenetic stages reached at the time of sampling.

The stream-specific relationships between YOY body length and distance moved away from nests varied from being negative to positive (Fig. 4). The interaction between distance from nest and stocking density was not included in the model that best explained variation in YOY body length, since this term could be removed without a significant reduction in the log-likelihood ($P = 0.351$), as could the main effect of stocking density ($P = 0.078$). In contrast, the interaction between distance from nest and predicted maximum body mass was highly significant and could not be removed ($P < 0.001$). A comparison of AIC values among all candidate models was consistent with the results from the model selection, with the model including the main effects of distance from nest, predicted maximum body mass, and the interaction between these parameters being considerably better than all other models (all ΔAIC $\geq$ 3.6). Whereas the main effect of distance from nest was negative, the positive interaction term (Table 2) shows that the relationship between distance from nest and YOY body length was more positive in streams where the predicted maximum body mass was larger at the time of sampling (Fig. 5).

Discussion

Our results strongly support the hypothesis that natal movement represents a body size-dependent strategy in

Fig. 4 Relationship between distance from nests and body length of YOY Atlantic salmon captured in 10 tributaries to the River Conon, ordered by mean body length (increasing from **a** to **j**). Note differences among *panels* in scale of *x*-axis
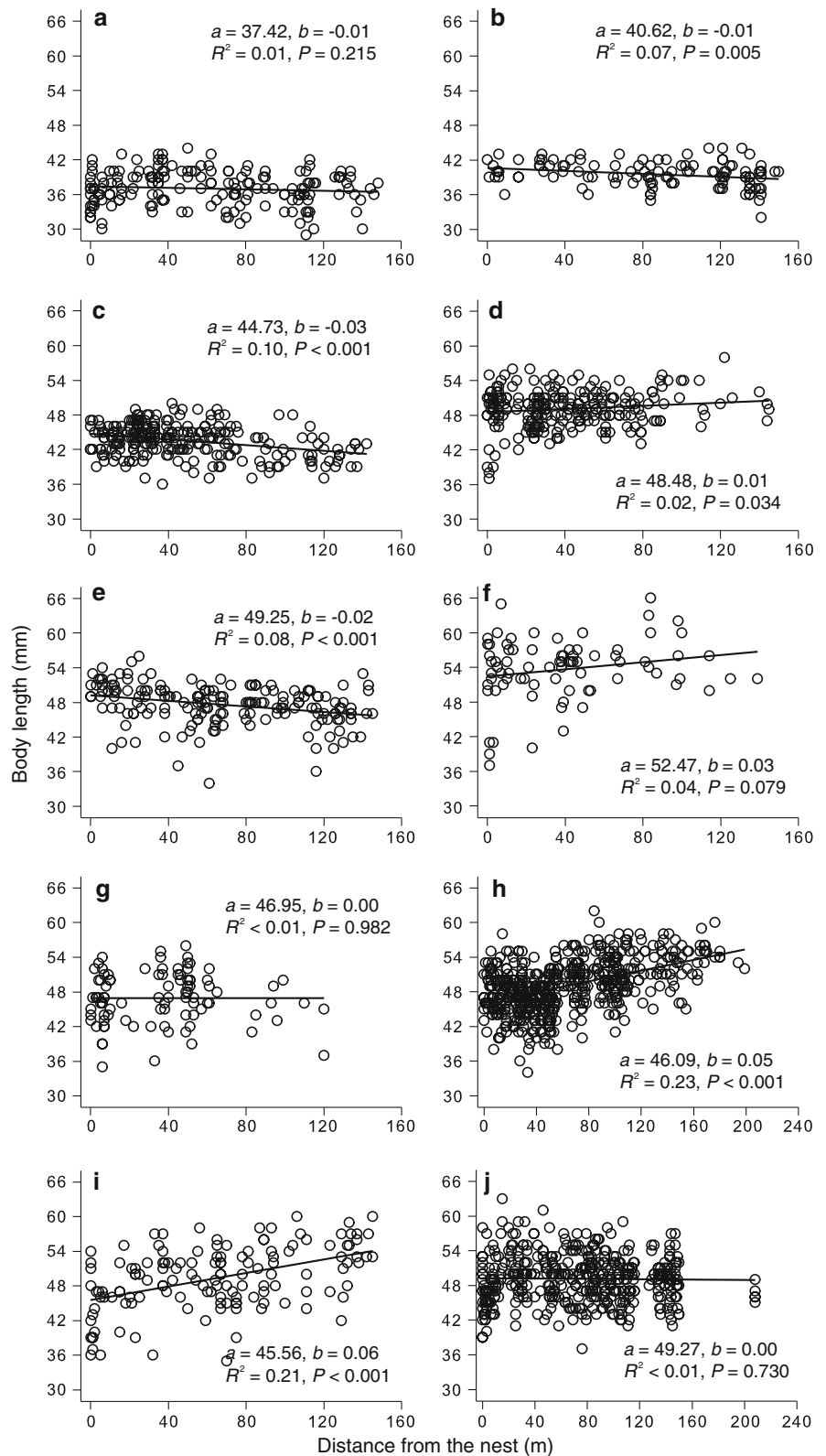
juvenile Atlantic salmon. Relatively small individuals, which were predicted to have the most to gain energetically by dispersing to areas of low density, were the most likely to leave experimental stream channels, and early in ontogeny juvenile body size was negatively correlated with distance from nests in natural streams. Later in ontogeny

Table 2 Summary of a linear mixed effects model describing variation in body length (log, mm) of YOY Atlantic salmon in 10 tributaries to the River Conon as a function of distance from nest sites (distance, m), and predicted maximum body mass based on a growth model (MaxMass)

	Parameter (95% CI)	t	P
Random	0.070 (0.083)		
Intercept	3.6000 (3.5256 to 3.6744)	48.37	<0.001
Distance	−0.0004 (−0.0005 to −0.0003)	−2.85	0.005
MaxMass	0.1604 (0.1085 to 0.2123)	3.09	0.002
Distance × MaxMass	0.0004 (0.0003 to 0.0005)	4.84	<0.001

Estimated parameters for random are the SD of the random intercept, with SD of residual variation given in brackets. *P* values are based on MCMC, and *n* is 2291 individuals
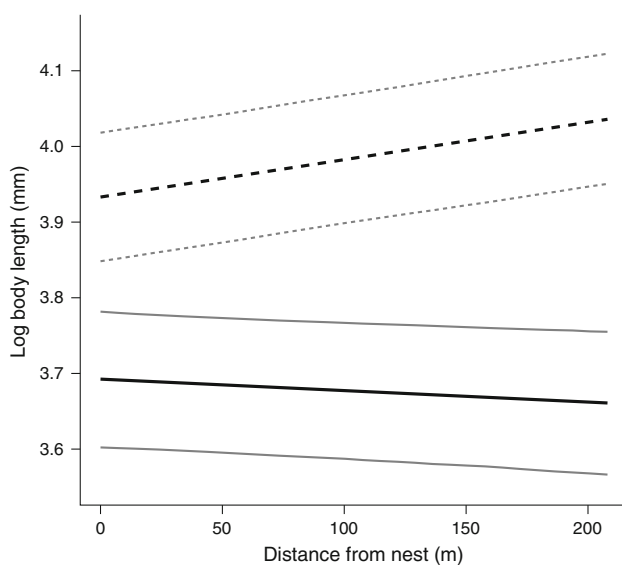

Fig. 5 Estimated relationship between body length of Atlantic salmon YOY and distance from nests when sampled at the smallest (*solid line*) and largest (*dotted line*) predicted maximum body mass (from growth models, see text) observed among the 10 tributaries to the River Conon used in this study. *Gray lines* indicate 95% confidence intervals (based on posterior simulations of the parameter estimates)

(i.e., for streams with a larger predicted maximum body mass), this pattern was reversed. These results suggest a mechanistic explanation for variation in movement behaviour during early life history, and help reveal the relative strength of the different factors determining the costs and benefits of natal movements.

Considering the local scale of competition in Atlantic salmon juveniles, an energy benefit of natal movement away from the nest area was predicted (Einum et al. 2011). This prediction is confirmed in the present study by the reversal of the relationship between distance from nest and body size over developmental time; that is fish that were

initially relatively small moved away and as the summer progressed ended up to be relatively large. This begs the question: why don't we see more pronounced movements and a larger degree of spatial homogenization of juvenile densities within salmon rivers (cf. Foldvik et al. 2010; Teichert et al. 2011)? Clearly, the limited movement cannot be caused by limitations in movement abilities, because if that had been the case we would expect to see more movement by larger and more mobile individuals. Furthermore, downstream movement would not be expected to be limited even in the absence of movement abilities since the fish could move passively with the water flow. An alternative explanation could be that individuals that move have to compete with individuals already present when settling in a new location and that the latter ones would have the advantage of prior residence (Kvingedal and Einum 2011). However, given the typical patchy distribution of Atlantic salmon spawners and the resulting patchiness of juveniles during the first summer (Finstad et al. 2010), it seems reasonable to assume that in many cases movers should manage to locate vacant positions. Thus, the most likely explanation for the restricted movement appears to be that movement poses increased mortality risks for the early stage juveniles. This explanation is consistent with predation by piscivorous fish being high during the first period after emergence (Henderson and Letcher 2003; Ward et al. 2008). Older salmonids dominate the fish fauna of the majority of Atlantic salmon streams and are known predators of emerging juveniles. However, the per capita consumption of emerging juveniles by these predators appears to be relatively modest compared to their exploitation of other prey items (Henderson and Letcher 2003). It has therefore been suggested that these are opportunistic rather than specialist predators of emerging juveniles (Henderson and Letcher 2003). Thus, rather than actively moving to locations of high juvenile densities it may be more likely that they stay at their regular feeding locations and intercept moving juveniles.

Given this understanding of costs and benefits of movement away from nest sites among juvenile Atlantic salmon, we suggest that the observed variation in natal movement may represent a body size-dependent strategy. Juvenile fish have previously been shown to adaptively choose habitats which minimize the ratio between mortality rate and foraging rate (Gilliam and Fraser 1987; Werner and Hall 1988). However, more complex habitat choice rules based on current and expected future energy states may be expected in populations that vary phenotypically. In such cases, the expected probability of reaching maturity (EM) may be more appropriate to explain habitat choice (Railsback and Harvey 2002). This measure includes the size of the fish relative to its requirement for maturation and the probability of surviving

starvation and other risks. For large juvenile Atlantic salmon, the fitness benefit of increased foraging when moving to less dense areas may be modest compared to the cost in terms of increased predation risk, causing the EM to decrease. This is because large juveniles are more likely to win during direct competitive interactions (Cutts et al. 1999), and would therefore be less affected by high local density near the nest site. In support of this view, a study of brown trout, which in many ways are ecologically similar to Atlantic salmon, found that juveniles that are large when emerging from the nest have an energy advantage under high, but not low, levels of competition (Einum and Fleming 1999). In contrast to this situation for large fish, the foraging benefit of moving to less dense areas for small juveniles can be expected to be pronounced. Thus, for the smaller juveniles, movement may result in a substantial increase in net energy gain that overrides risk of reduced survival due to predation when moving, and increases the EM. There is, however, one caveat in this adaptive explanation in that we lack a quantification of size-selective predation during movement. If such selection is sufficiently strong, with smaller movers running a much higher risk of being eaten than larger ones, then this may outweigh the size-dependent energy benefit of moving. If this is the case, then variation in movement patterns can no longer be thought of as representing a size-dependent adaptive strategy. Although direct observations regarding this aspect are lacking, the difference in size of movers in absence and presence of predators was relatively small in our stream-channel experiments, suggesting that such size-selective predation may not be particularly pronounced.

Most previous studies that have evaluated the relationship between body size and natal movement in salmonids have also found that smaller juveniles are more likely to move away from nest sites than larger ones (Johnston 1997; Bujold et al. 2004; Landergren 2004). However, the opposite pattern has also been shown (Bradford and Taylor 1997). This inconsistency may be associated with the methodological challenges in these types of studies. For experimental studies in semi-natural stream-channels, one approach has been to release post-emergence juveniles (i.e., juveniles that have started exogenous feeding) of different sizes and make direct observations of movement rates (Bradford and Taylor 1997). However, it is not clear whether body size effects found in such experiments reflect those under natural emergence of juveniles from nests. A more realistic scenario may be obtained by releasing pre-emergent juveniles that stay on/in the substrate until the onset of exogenous feeding (Landergren 2004). However, previous experiments that have used pre-emergent juveniles have been conducted in the absence of predators. If juveniles can detect the risk of predation from older salmonids, the lack of predators in an experiment may remove the perceived cost of movement and may thereby make small and vulnerable individuals more likely to move. In the present study we included the possibility for juveniles to respond to the risk of predation, but the results (i.e., that individuals leaving the channels were smaller than the ones staying) were qualitatively similar across treatments. Furthermore, the results were similar for high and low density treatments. Thus, our results suggest that the size-dependent natal movement is not, at least qualitatively, sensitive to the environmental conditions tested. This conclusion was supported by the results from our field experiment. In previous studies that have been conducted in natural populations, the body size of juveniles caught by drift samplers have been compared with those caught using electro-fishing during/following periods of emergence (Johnston 1997; Bujold et al. 2004). However, this methodology assumes that fish caught by electro-fishing are indeed not among those that are in the process of moving. Furthermore, it assumes that body size does not influence catchability in drift samplers, an assumption that may not always be satisfied (Johnston 1997). Finally, since there is pronounced variation in breeding time, and hence timing of emergence in natural populations (Fleming and Einum 2011), it is possible that drift sampling may catch mainly recently emerged juveniles, whereas larger proportions of older fish would be caught by electro-fishing. Our design, where individuals that originated from a known nest site were sampled a relatively long period after the timing of emergence, should avoid these kinds of problems.

In conclusion, our results provide support for the hypothesis that variation in natal movement results from a size-dependent strategy in Atlantic salmon, with large individuals staying close to nest sites and small ones moving downstream to obtain more favourable feeding locations. Although further studies should clarify to what extent the risk of being eaten by predators during movement depends on body size, our experiments suggest that such size-selective predation is not particularly pronounced. Thus, the main driving force behind the evolution of this size-dependent strategy appears to be the body size dependence in effects of local competition on energy intake.

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