**Spatial variation in the relationship between performance and metabolic rate in wild juvenile Atlantic salmon**

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**Summary**

**1.** Maintenance metabolic rate (*MR*, the energy cost of self-maintenance) is linked to behavioural traits and fitness and varies substantially within populations. Despite having received much attention, the causes and consequences of this variation remain obscure.

**2**. Theoretically, such within-population variation in fitness-related traits can be maintained by environmental heterogeneity in selection patterns, but for *MR* this has rarely been tested in nature.

**3.** Here, we experimentally test if the relationship between *MR* and performance can vary spatially by assessing survival, growth rate and movement of Atlantic salmon (*Salmo salar* L.) juveniles from 10 family groups differing in *MR* (measured as egg metabolism) that were stocked in parallel across 10 tributaries of a single watershed.

**4.** The relationship between *MR* and relative survival and growth rate varied significantly among tributaries. Specifically, the effect of *MR* ranged from negative to positive for relative survival, whereas it was negative for growth rate. The association between *MR* and movement was positive and did not vary significantly among tributaries.

**5.** These results are consistent with a fitness cost of traits associated with behavioural dominance that varies across relatively small spatial scales (within a single watershed). More generally our results support the hypothesis that spatial heterogeneity in environmental conditions contributes to maintain within-population variation in fitness-related traits, such as *MR*.

**Key-words:** dispersal, energetics, intraspecific variation, natural selection, standard metabolic rate

## Introduction

Maintenance metabolic rate (*MR*, the minimum energy required to support basic life functions) is increasingly recognised as being linked to behavioural traits (Bryant & Newton 1994; Mathot *et al*. 2009; Biro & Stamps 2010; Huntingford *et al*. 2010; Killen, Marras & McKenzie 2011) and ultimately fitness (Jackson, Trayhurn & Speakman 2001; Artacho & Nespolo 2009; Boratyński & Koteja 2009; Larivée *et al*. 2010; Boratyński *et al*. 2010). Furthermore, *MR* commonly varies extensively among individuals within populations (McNab 1988; Metcalfe, Taylor & Thorpe 1995; Burness, Ydenberg & Hochachka 1998; Nespolo, Lardies & Bozinovic 2003a) as well as among populations (Lahti *et al*. 2002; Lardies & Bozinovic 2006, 2008), and some of the variation seems to be genetically based (Nespolo, Bacigalupe & Bozinovic 2003b; Sadowska *et al*. 2005; Nilsson, Akesson & Nilsson 2009; Tieleman *et al*. 2009; Kaseloo *et al.* 2012; Zub *et al*. 2012; Boratyński *et al*. 2013, but see Bacigalupe, Nespolo & Bustamante 2004). Several hypotheses explaining maintenance of within-population variation in *MR* have been proposed (reviewed in Burton *et al*. 2011) but the underlying mechanisms remain largely unknown. Among the suggested hypotheses is environmental heterogeneity in selection patterns (Burton *et al*. 2011). This hypothesis is circumstantially supported by laboratory studies suggesting that selection on *MR* can vary depending on food availability (e.g. Bochdansky *et al*. 2005). The demonstration that selection on *MR* can vary temporally in bank voles in the wild (*Myodes glareolus*, Boratyński & Koteja 2010) provides further support. Temporal environmental variation is, however, likely to be less powerful than spatial variation in maintaining genetic variation (Bulmer 1971; Ellner & Hairston 1994). Thus, studies that examine whether the performance consequences of different levels of *MR* can vary spatially under natural conditions are needed.

It is also of interest that foregoing studies on consequences of environmental conditions for effects of *MR* on performance have all treated *MR* at the individual level (e.g. Reid, Armstrong & Metcalfe, 2011, 2012). However, *MR* also varies at the family level (Pakkasmaa, Penttinen & Piironen 2006). Hence, the relative performance of juveniles from families with different mean *MR* could be expected to vary depending on environmental conditions, and thus vary in time and/or space.

Atlantic salmon (*Salmo salar* L.) juveniles are well suited for studies of spatial variation of costs and benefits (in terms of e.g. survival) associated with different *MR* levels. First, both abiotic and biotic environmental conditions in nursery streams vary considerably across space within populations (e.g. Arnekleiv, Finstad & Rønning 2006; Finstad *et al*. 2009; Einum *et al*. 2011). Second, natural selection during the juvenile stage can be both strong and spatially variable, as illustrated by studies of selection on egg size and timing of emergence from nests (Einum & Fleming 2000; Skoglund, Einum & Robertsen 2011; Robertsen, Skoglund & Einum 2013). Third, salmonids commonly inhabit small streams which are relatively easy to sample accurately, and produce relatively large eggs that can be artificially fertilised and planted in the wild. Fourth, their within-population variation in *MR* is pronounced and likely associated with both genetic variation (Pakkaksmaa *et al*. 2006) and maternal effects (Pakkasmaa *et al*. 2006; Régnier *et al*. 2010; Rossignol *et al*. 2010; Sloman 2010). Finally, the link between behaviour and *MR* in salmonid juveniles has been the subject of numerous studies. According to these studies, individuals with high *MR* have higher dominance ranks and exhibit more aggressive behaviour compared to those with low *MR* (e.g. Metcalfe *et al*. 1989, 1995; Cutts, Adams & Campbell 2001; McCarthy 2001; Lahti *et al*. 2002).

To test for the occurrence and nature of variation in the relationship between families in *MR* and performance across a range of environmental conditions, we conducted a large-scale field experiment with juvenile Atlantic salmon from 10 families across 10 streams located within a single watershed. Specifically, we tested whether mean family egg *MR* influenced performance of the resulting offspring in terms of survival, growth rate and movement, and whether such effects varied spatially.

## Methods

### EXPERIMENTAL FISH AND STUDY SITES

Twenty adult Atlantic salmon caught during October 2007 in a fish trap in the River Blackwater, a tributary of the River Conon, Ross-shire, Scotland, were used to produce 10 full-sib families. All fertilizations were done on the same day and samples of the parents' adipose fins were taken and stored in ethanol for later genetic analyses. The fertilized family groups of eggs were incubated separately in a hatchery at Contin. From each family, 20 eyed eggs were fixed in a 4% formalin buffer and weighed (± 0.1 mg). The mean egg mass differed significantly among the families (range: 0.095 – 0.180 g, ANOVA: $F_{9,190} = 460$, $P < 0.001$). To quantify timing of emergence from nests, 10 eggs were randomly sampled from each family and planted in an artificial nest in the hatchery. Subsequently, the timing of emergence was recorded and genetic samples (fin clips) of the juveniles taken. Median date of emergence did not differ by more than 2.5 days among families whereas the median maximum difference within families was 5.5. Accordingly, the within-family variation in emergence timing was much larger than the among-family variation. Emergence timing was therefore not included as a variable when analysing the data. During 17-26 February 2008, eyed eggs were stocked in 10 tributaries of the River Conon (Table 1). Eggs from the different family groups were placed in separate Vibert boxes (Federation of Fly Fishermen, Bozeman, MT, USA) which were placed in a depression in the stream bed gravel and covered with gravel and larger stones. To ensure sufficient variation in environmental conditions tributaries were chosen from across a wide range of altitudes (65 - 484 m.a.s.l., see Table 1). In addition, two release number treatments were allocated randomly to the 10 tributaries (five with 1000 eggs, and five with 3000 eggs). Each tributary received an equal number of eggs from each family (i.e. 100 or 300). All of these tributaries are located above barriers to migration of naturally occurring Atlantic salmon. However, older salmon (≥ 1years age, resulting from previous stockings) were present in seven of the tributaries, and all the tributaries except one had naturally occurring brown trout populations (see Table 1, Einum *et al*. 2011 for details). Thus, differences in stocking treatments combined with variation in biotic and abiotic factors among tributaries ensured substantial variation in the environmental conditions experienced by the juvenile salmon.

MEASUREMENT OF METABOLIC RATE

Since it was logistically impractical to measure *MR* of juveniles in sufficient numbers to perform a valid field experiment, this was measured in eyed eggs. The families had their *MR* measured simultaneously in the hatchery (21-27 February 2008). Values of mean family egg *MR* were obtained by putting groups of eggs in sealed plastic bottles (0.5 L) that were filled with water. Two trials were conducted using 30 and 50 eggs from each family and lasted for ~78 and 62 h, respectively. Two bottles containing water but no eggs served as controls in each trial. At regular time intervals (ca. every 14 h) all bottles were gently turned upside down to prevent formation of oxygen gradients. Temperatures stayed between 5-6˚C during both trials. Total oxygen consumption in each bottle was measured with a micro cathode oxygen electrode (model 1320) connected to an oxygen meter (model 781, Strathkelvin Instruments Ltd, Glasgow, Scotland). Oxygen consumption in the bottles containing eggs was calculated relative to controls. Mean family-specific $O_2$ consumption (mg egg$^{-1}$ hour$^{-1}$) in the 1st and 2nd trial were significantly correlated ($r^2$ = 0.73, $F_{1,8}$ = 22.1, $P$ = 0.002) and family-specific oxygen consumption from the two trials ranged from 0.54 to 0.66 µg egg$^{-1}$ hour$^{-1}$. To obtain family specific estimates of metabolic rates while controlling for variation in egg mass, the mean amount of $O_2$ consumed per egg per hour by each family in the two trials was regressed against mean family egg mass. Because of the allometric relationship between *MR* and body size, oxygen consumption and egg mass were ln-transformed prior to the regression to linearize the relationship ($r^2$ = 0.63, $F_{1,8}$ = 13.7, $P$ = 0.006). The family-specific residuals from this regression were not significantly correlated with egg mass ($r_s$ = 0.59, $P$ = 0.075), and were used when testing for effects of mass-specific metabolic rates on juvenile performance.

SAMPLING

Following fry emergence the Vibert boxes were retrieved from the nest sites and the number of dead eggs counted to quantify the number of juveniles hatched from each family. During 15–24th July 2008 all the tributaries were electrofished from 150 m below the nest site to 50 m above it, or until a migration barrier was reached within those 50 m. In one tributary, where initial sampling suggested extensive movement, stretches further downstream than 150 m from the nest site were sampled. Depending on logistic constraints, 1-3 passes were conducted in each tributary. When caught, young of the year salmon were killed by a blow to the head before being put in plastic tubes containing ethanol for later processing, including fork length measurements and clipping of fins for genetic analyses to identify their family origin. The location where individuals were caught was recorded to the nearest 1 m relative to the nest site.

GENOTYPING AND PARENTAL ALLOCATION

To assign individual juveniles to their respective family groups, fin clips of the recaptured juveniles and of the parental fish were genotyped by Matís-Prokaria (Reykjavik, Iceland) using eight microsatellite markers. DNA was extracted using Chelex (Biorad 10%) (Walsh, Metzger & Higuchi 1991). The PCR reactions were performed in 15 µl volumes, and consisted of 5 µl DNA template (1/10 dilution), 1U of Teg DNA polymerase (3 U/µl) (Matís-Prokaria, Iceland) (comparable with Taq DNA polymerase), 1.5 µl of 10 x buffer, 1.5 µl of dNTP (10 mM), and the following amount of reverse and forward primers (100 µM) were amplified in a single PCR: *SSsp*3016 (0.075 µl), *SSsp*2210 (0.075 µl), *SSsp*G7 (0.075 µl), *Ssa*197 (0.050 µl), *Ssa*171 (0.100 µl), *Ssa*202 (0.100 µl), *SSsp*2201 (0.125 µl), *Ssa*D157 (0.150 µl) (O'Reilly *et al*. 1996; Gibley *et al*. 2004; Paterson *et al*. 2004; King, Eackles & Letcher 2005; Withler, Supernault & Miller 2005). The forward primers were fluorescently labelled with FAM (*SSsp*2210, *Ssa*202), VIC (*Ssa*197, *Ssa*D157), PET (*SSsp*G7, *SSsp*2201) and NED (*Ssa*171, *SSsp*3016), and all reverse primers were fitted with a GTTTCTT PIG-tail (Brownstein, Carpten & Smith 1996). PCR was performed in a MJ Research PTC-225 and conducted as follows: 4 min denaturation at 94 °C followed by 30 cycles of 94 °C for 50 s, 56 °C for 50 s and 72 °C for 90 s. Final extension was conducted for 7 min at 72 °C. PCR products were run on an ABI 3730 DNA Analyser (Applied Biosystem) and were size-called according to the 500LIZ™ standard. Alleles were automatically called and manually checked in GeneMapper V4.0. PAPA V2.0 (Duchesne, Godbout & Bernatchez 2002) was used to assign individual offspring to parents.

FAMILY-SPECIFIC PERFORMANCE

Movement (*M*) was measured as the absolute distance between where an individual was captured and the nest site. Growth (*G*) was calculated for each individual as daily growth ([final length – mean family length at emergence]/number of days) between median date of emergence in each tributary (predicted based on tributary temperatures recorded using loggers and the development model of Crisp [1981, 1988]), and sampling. To standardise data among tributaries, only fish captured between 50 m upstream and 150 m downstream of the nest site were included for *M* and *G*. Family-specific apparent survival (*S*) was measured as the ratio between total number of recaptured individuals from each family in each tributary and the corresponding number of eggs hatched (i.e. controlling for egg mortality). Even though this is not an accurate measure of absolute survival, as not all salmon juveniles in the tributaries were recaptured, it represents an appropriate measure of relative survival among families within tributaries. Furthermore, the spatial distribution of recaptured individuals (decrease in numbers at the upper and lower limits of the sampling sites) suggested that the reaches over which samples were obtained included the majority of juveniles (Fig. 1).

## STATISTICAL ANALYSES

All statistical analyses were conducted in R, v. 2.15.1 (2012). Statistical models that include interaction terms between *MR* and tributary identity (*T*) were used to test whether the relationship between relative performance (*M*, *G* and *S*) and family-specific mean *MR* (for absolute *MR*, see Supporting information). To control for the effect of egg mass, mean family egg mass (*E*) and its interactions with tributary identity were added in the models. When testing whether movement away from the nest site or growth was related to family level *MR* or *E* and whether any such effect varied among tributaries, linear mixed models (LMM) with Gaussian distributions and family (*k*) as random factors (intercept, *b*) were used. Thus, the initial model for movement for individual *i* belonging to family *k* in tributary *j* can be represented as:

$$M_i = \alpha T_j + \beta_1 MR_k + \beta_2 E_k + \beta_3 MR_k T_j + \beta_4 E_k T_j + b_k + \varepsilon_i$$

and for growth (*G*):

$$G_i = \alpha T_j + \beta_1 MR_k + \beta_2 E_k + \beta_3 MR_k T_j + \beta_4 E_k T_j + b_k + \varepsilon_i$$

where $\varepsilon$ is the residual error and $\alpha$ and $\beta$ are fixed factors. To test for relationships between survival and *MR* (and egg mass), and whether these relationships varied among tributaries (*T*), we applied a generalized linear mixed model (GLMM) with a binomial error structure. Because survival (*S*) was a family (*k*) specific measure per tributary (*j*), the initial model can be described as:

$$S_{jk} = \alpha T_j + \beta_1 MR_k + \beta_2 E_k + \beta_3 MR_k T_j + \beta_4 E_k T_j + b_k + \varepsilon_{jk}$$

For LMM and GLMM we used the function *lmer* from the *lme4* package (Bates & Maechler 2010). Evaluation of fixed effects was done according to the protocol recommended in Zuur *et al*. (2009), and was thus based on sequential removal of fixed effects with subsequent comparisons until log-likelihoods decreased significantly ($P < 0.05$). For main fixed effects *P* -values from the final linear mixed models (with Gaussian error distribution) were obtained using the function *pvals.fnc* from the *languageR* package (Baayen 2010).

## Results

### GENOTYPING

Out of a total of 2720 genotyped juveniles, seven samples did not give DNA of sufficient quality to do genetic analyses. These seven were removed from the data set. A total of 2663 samples were assigned to parents, including individuals retrieved further down than 150 m below nest sites.

## MOVEMENT

When testing for effects of *MR* and egg mass on the relative movement of individuals within tributaries, the interaction between *MR* and tributary identity could be removed, whereas the interaction between egg mass and tributary as well as the main effect of *MR* was left in the final model (Table 2). Thus, the relationship between *MR* and relative movement did not vary significantly among tributaries, whereas the relationship between egg mass and relative movement did. According to this model, distance moved away from the nest site was positively related to *MR* (slope estimate ± *SE*: 169.90 ± 79.77, $t = 2.13$, $P = 0.03$) and overall negatively related to egg mass (all tributary-specific estimates of egg mass effects on movement were negative, see Fig. 3a and Fig. S1, Supporting information). In this model the random intercept for family accounted for 4.5 % of the variation (value for variance of random intercept and residual variance: 71.32 and 1511.11).

## GROWTH

The model selection dealing with effects of *MR* and egg mass on growth rate showed stream-specific relationships between growth rate and both *MR* and egg mass (Table 2). In this model the random intercept for family gave 3.4% of the variation (value for variance of random intercept and residual variance: 0.0001 and 0.0037). According to this model, individuals belonging to a family with a high mean egg *MR* had a lower daily growth rate than individuals from families with lower egg *MR*, but the strength of this relationship varied among tributaries (Fig. 2a and Fig. S2a, Supporting information). The relationship between mean family egg mass and daily growth was not consistent among tributaries and ranged from positive in some tributaries, to negative in others (Fig. 3b and Fig. S2b, Supporting information).

APPARENT SURVIVAL

All main factors and interaction terms were retained in the final model when testing for effects of *MR* and egg mass on apparent survival (Table 2). Accordingly, the relationships between and egg *MR* and survival, and egg mass and survival, were tributary-specific. The slope of the relationship between egg *MR* and apparent survival ranged from negative to positive across streams (Fig. 2b and Fig. S3a, Supporting information). The slopes of the relationships between egg mass and apparent survival were either positive or close to zero (Fig. 3c and Fig. S3b, Supporting information).

## Discussion

By planting out eggs from the same 10 families across 10 tributaries we revealed that the relative performance of juveniles from families with different mass-specific egg *MR* varied within a single watershed. Moreover, this study demonstrates that the variation in performance consequences of different *MR* previously revealed at the individual level under laboratory conditions (e.g. Reid *et al*. 2012) hold at the family level and under natural conditions.

The role of environmental variation on *MR* selection patterns should depend on the way in which specific traits are associated with different levels of *MR*. Individuals with high *MR* have been found to have higher dominance ranks and exhibit more aggressive behaviour compared to those with low *MR* (Metcalfe *et al*. 1989, 1995; Cutts *et al*. 2001; McCarthy 2001; Lahti *et al*. 2002). Evidence from previous studies suggests that the costs and benefits and therefore fitness consequences of high metabolic rate and associated high dominance are influenced by resource availability and variability (Harshman, Hoffmann & Clark 1999; Mueller & Diamond 2001; Millidine, Armstrong & Metcalfe 2009; Armstrong, Millidine & Metcalfe 2011) and habitat complexity (Höjesjö, Johnsson & Bohlin 2004; Reid *et al*. 2012). As these and other factors inevitably vary across sites in the natural environment, we would expect corresponding variation in the relationship between *MR* and performance. This expectation is supported by our results as both the sign and the magnitude of the relationship between egg *MR* and apparent survival differed among tributaries (Fig. 2c and Fig. S3b, Supporting information). Although we cannot identify the specific environmental factors responsible, to our knowledge this is the first time the effect of *MR* on a survival proxy has been shown to vary in sign. Thus, the potential for facilitation of maintained within-population variation in *MR* has now been demonstrated through temporal variation in individual reproductive success (Boratyński & Koteja 2010) and through spatial variation in relative family survival (present study). Additionally, this points to the possibility that results from previous studies showing a negative, or no, effect of *MR* on survival in the wild (i.e. brown trout, Alvarez & Nicieza 2005; garden snail, Artacho & Nespolo 2009; red squirrels, Larivée *et al*. 2010) must be regarded as potentially context dependent (Burton *et al*. 2011), and that other results may have been obtained under different environmental conditions.

In accordance with other studies of salmonids showing a negative relationship between dominance or *MR* and growth rate in complex environments (Höjesjö *et al*. 2004; Alvarez & Nicieza 2005; Reid *et al*. 2011, 2012), we found a general negative effect of *MR* on growth (see Fig. 2b and Fig. S2a, Supporting information). Higher *MR* was also associated with longer distances moved away from nest sites (see Fig. 2a). This may be linked to juveniles with high *MR* showing a greater willingness to take risks and explore new areas (Huntingford *et al*. 2010; Killen *et al*. 2011). It is also possible that individuals with high *MR* have higher energy requirements and hence are more prone to leave areas with high conspecific densities (e.g. close to the nest site) to search for areas with growth conditions that can sustain their high metabolic demands. This is consistent with the finding that brown trout juveniles with high *MR* were more likely to migrate out of their stream than low *MR* juveniles (Lans *et al*. 2011). In contrast to the positive relationship between *MR* and distance moved, there was a negative relationship between egg mass and distance moved (see Fig. 2a and Fig. S1, Supporting information). A similar mechanism may explain this finding; high resource levels of offspring from large eggs enable them to stay longer in the high density area close to the nest site, even if this leads to poorer growth conditions (Vøllestad & Lillehammer 2000; Einum *et al*. 2011; Teichert *et al*. 2011). Einum *et al.* (2012) provide support for this interpretation as they found that small Atlantic salmon juveniles are more likely to move away from areas of high density than larger ones are. Furthermore, juveniles that moved away from nest sites outgrew individuals residing close to the nest site, suggesting that there must be some survival costs (i.e. predation) that selects against such movement for initially larger individuals (Einum *et al.* 2012). Combined with our finding that individuals with high *MR* and thereby higher energy expenditure were more likely to disperse from nest sites, this suggests that natal movement in Atlantic salmon is conditioned by energy state and requirements.

An assumption for the interpretation of the results of this study is that the relative *MR* in eggs is related to that in juveniles. This assumption is backed up by findings in a range of studies. First, differences in *MR* among individuals early in the egg stage have been shown to be predictive of *MR* in later egg and larval stages of salmonids (Régnier *et al*. 2010). These differences even increase throughout the development so that they are more pronounced among larvae close to timing of emergence than during the egg stage (Régnier *et al*. 2010). In addition, relative *MR* is temporally repeatable over time in a range of organisms (reviewed in Nespolo & Franco, 2007), including juvenile salmonids (Cutts *et al*. 2001; McCarthy 2000, but see Seppänen, Piironen & Huuskonen 2010). This is true even for individuals that have increased in body mass by a factor of 20 (McCarthy 2000). Finally, differences in *MR* among individuals are consistent over a range of environmental conditions (Cutts *et al*. 2001).

In conclusion, the finding that the survival effects of high family *MR* varied among tributaries indicates that spatial heterogeneity in environmental conditions may lead to variable selection pressures, and may thereby contribute to maintain within-population genetic and phenotypic variation in this fitness-related trait. A better understanding of the specific factors involved (e.g. prey availability, con- and interspecific competition, habitat quality and heterogeneity, water flow and temperature regimes) will be necessary for predicting potential changes in the distribution of this key phenotypic trait and to understand the potential consequences of these changes for fitness and population dynamics.

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The following Supporting Information is available for this article online: The estimated relationships between *MR* and the performance proxies plotted on top of the raw data (Appendix S1, Figs. S1-S3), and the results of selection of models using absolute *MR* instead of mass specific *MR* (Figs. S4-S6).

Data available from the Dryad Digital Repository doi:10.5061/dryad.f260s Data files: Movement and Growth, Apparent survival.

Table 1. Number of Atlantic salmon egg stocked, hatched and the total number of juveniles retrieved by electro-fishing in 10 study sites of the River Conon. Location of the tributaries in meters above sea level (m.a.s.l.), recapture rates (%, *S*) are also given, as well as mean distance moved (m, *M*) and growth rate (mm $day^{-1}$, *G*) based on juveniles recaptured between 50 m upstream of to 150 m downstream of the nest site. Asterisks indicate presence of older salmon juveniles (≥ 1 year).

| tributary (*T*) | m.a.s.l. | no. eggs (hatched) | no. retrieved | *S* | *M* ± *SD* | *G* ± *SD* |
|---|---|---|---|---|---|---|
| 1. Allt Aradaidh | 256 | 1000 (1000) | 95 | 9.5 | 33.7 ± 29 | 0.30 ± 0.07 |
| 2. Distillery Burn* | 65 | 1000 (884) | 99 | 11.2 | 35.2 ± 32 | 0.40 ± 0.08 |
| 3. Gleann Chorainn* | 244 | 1000 (988) | 275 | 27.8 | 37.7 ± 32 | 0.37 ± 0.06 |
| 4. Tuill Bhain* | 318 | 1000 (992) | 278 | 28 | 43.7 ± 36 | 0.27 ± 0.04 |
| 5. Coire a Bhuic | 191 | 1000 (963) | 167 | 17.3 | 54.1 ± 44 | 0.32 ± 0.09 |
| 6. Am-fuar Alltan | 484 | 3000 (2922) | 200 | 6.8 | 52.5 ± 45 | 0.20 ± 0.06 |
| 7. Upper Meig* | 311 | 3000 (2996) | 138 | 4.6 | 74.2 ± 46 | 0.20 ± 0.04 |
| 8. Chaisecain* | 128 | 3000 (2994) | 491 | 16.4 | 67.8 ± 47 | 0.31 ± 0.06 |
| 9. Scardroy Burn* | 160 | 3000 (2989) | 621 | 20.8 | 54.1 ± 38 | 0.34 ± 0.07 |
| 10. Glen Meinich* | 231 | 3000 (2933) | 205 | 7.0 | 60 ± 43 | 0.32 ± 0.06 |

Table 2. Model selection results in the three different analyses (dependent variables: movement away from the nest sites [LMM], daily growth rate [LMM] and apparent survival [GLMM] in Atlantic salmon). Independent variables are mean family egg metabolic rate (*MR*), mean family egg mass (*E*), and tributary identity (*T*). The initial models for all response variables: *MR***T* + *E***T* (an interaction [*] always includes both main effects). *P*-values given refer to the decrease in log-likelihood when excluding a term from the model (based on the model selection procedure recommended in Zuur et al. 2009). Model terms given in bold are those that when removed caused a significant ($P < 0.05$) decrease in log-likelihood of the model, and hence are retained in the final model.

| | $\chi^2$ | *DF* | *P* |
|---|---|---|---|
| Movement | | | |
| *MR***T* | 14.16 | 9 | 0.12 |
| ***E**T**[1] | **17.36** | **9** | **0.04** |
| ***MR***[1] | **5.01** | **1** | **0.03** |
| Growth | | | |
| ***MR**T**[1] | **32.69** | **9** | **< 0.001** |
| ***E**T**[1] | **30.78** | **9** | **< 0.001** |
| Survival | | | |
| ***MR**T**[1] | **42.81** | **9** | **< 0.001** |
| ***E**T**[1] | **33.56** | **9** | **< 0.001** |

[1]Estimated slope - values ± *SE* for each tributary are given in Figs. 2 and 3. The fit of the parameter estimates from these models to data is presented in Figs. S1, S2 and S3, Supplementary material.

**Figure legends**

Fig. 1. Number of Atlantic salmon juveniles caught at each meter sampled relative to the location of the nest site in 10 tributaries (*T*1-*T*10, cf. Table 1) of the River Conon. Negative and positive values at the x-axis represent upstream and downstream directions from nest sites, respectively. Vertical grey lines indicate outer boundaries of the section sampled in each stream. Note differences in scale on the y-axes among panels.

Fig. 2. Estimated slopes ± *SE* of the relationship between mean family egg metabolic rate (residuals) and the (a) daily growth rate (from the best LMM), and (b) apparent survival rates (from the best GLMM) of Atlantic salmon juveniles in 10 tributaries of the River Conon. For daily growth: $n$ = 2536 individuals from 10 families; for apparent survival rates: $n$ = 100 (10 families in 10 tributaries). The fit of the estimates to data is presented in Figs. S1, S2 and S3, Supplementary material. The slope estimate ± *SE* for distance moved away from nest sites (169.90 ± 79.77, $t$ = 2.13, $P$ = 0.03) is not presented here since it did not vary significantly among tributaries.

Fig. 3. Estimated slopes ± *SE* of the relationship between mean family egg size (g) and the (a) absolute distance moved away from nest sites (from the best LMM), (b) daily growth rate (from the best LMM), and (c) apparent survival rates (from the best GLMM) of Atlantic salmon juveniles in 10 tributaries of the River Conon. For the distance moved from nest sites and daily growth: $n$ = 2536 individuals from 10 families; for apparent survival rates: $n$ = 100 (10 families in 10 tributaries). The fit of the estimates to data is presented in Figs. S1, S2 and S3, Supplementary material.

**Figures**

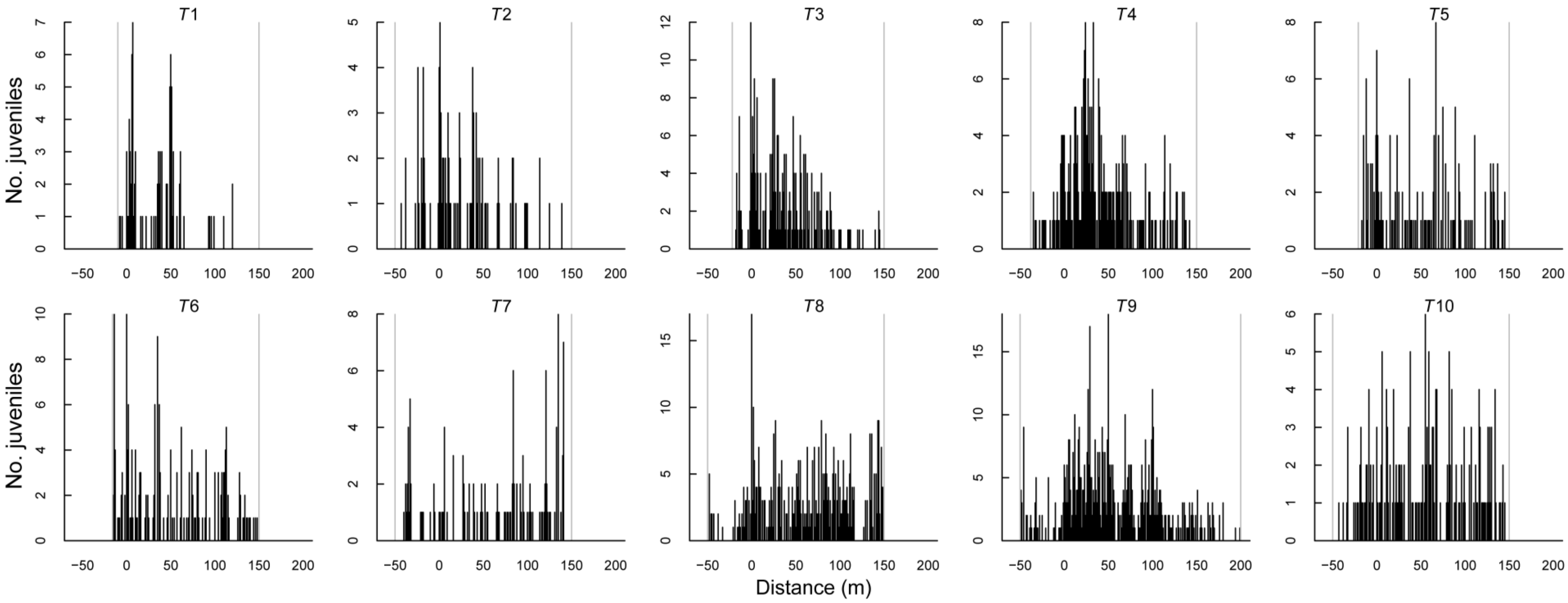



Fig. 1.

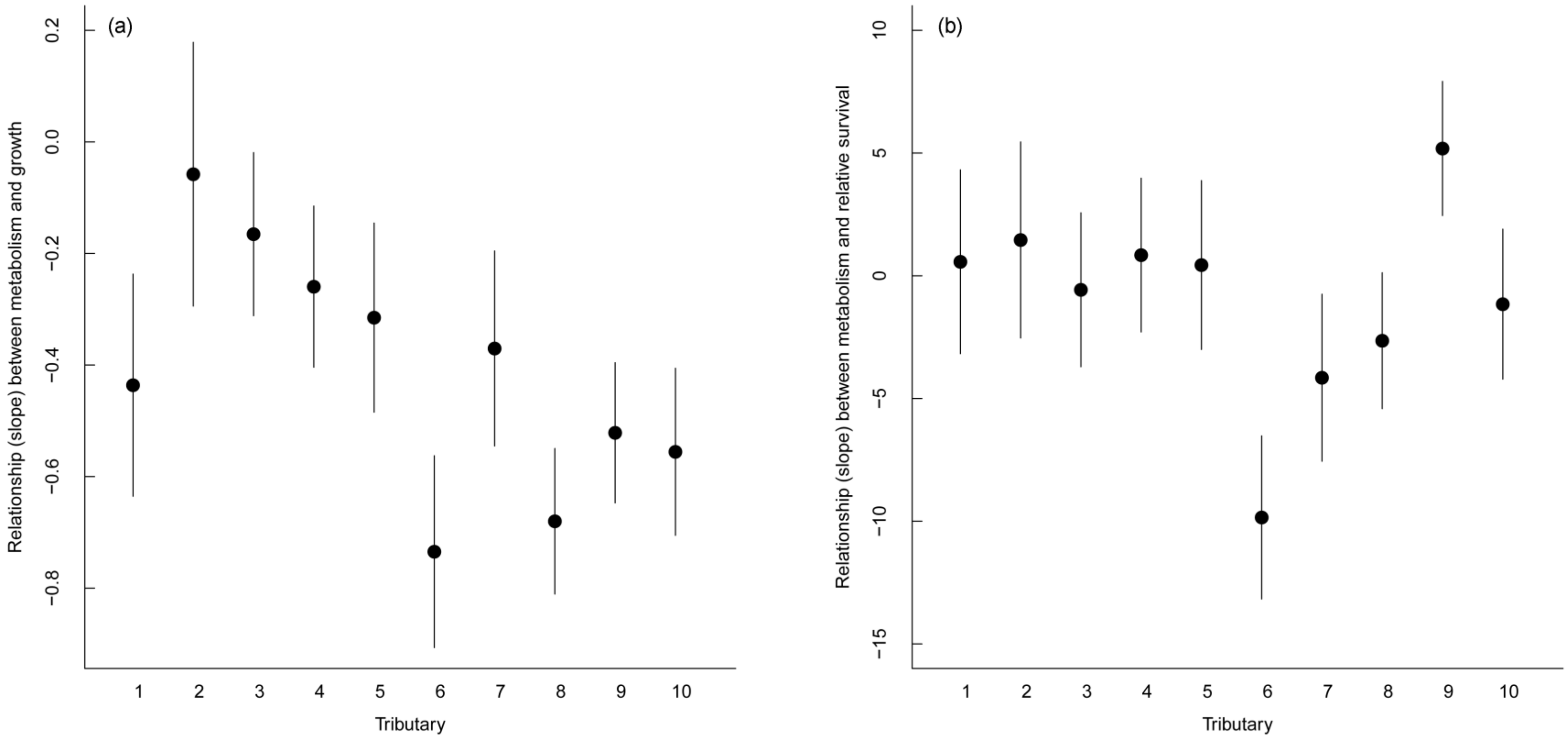
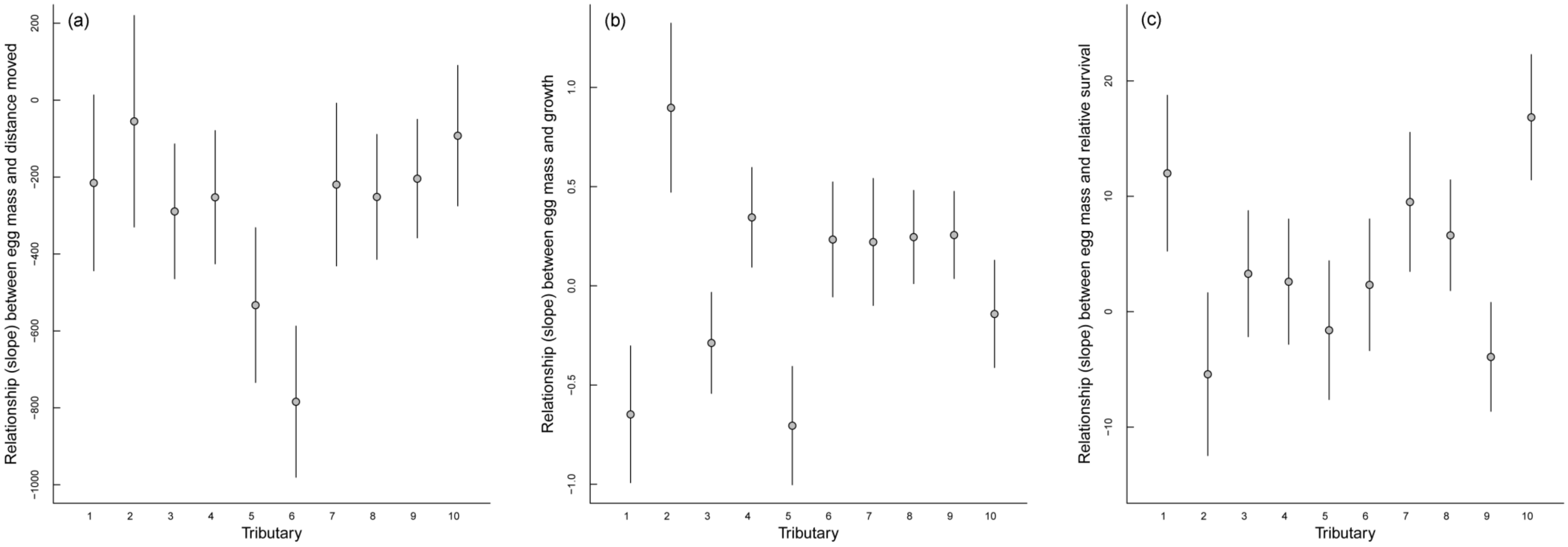

(a)
Relationship (slope) between metabolism and growth
0.2
0.0
−0.2
−0.4
−0.6
−0.8
1
2
3
4
5
6
7
8
9
10
Tributary
(b)
Relationship (slope) between metabolism and relative survival
10
5
0
−5
−10
−15
1
2
3
4
5
6
7
8
9
10
Tributary

Fig. 2.



(a)
Relationship (slope) between egg mass and distance moved
200
0
-200
-400
-600
-800
-1000
1
2
3
4
5
6
7
8
9
10
Tributary
(b)
Relationship (slope) between egg mass and growth
1.0
0.5
0.0
-0.5
-1.0
Tributary
(c)
Relationship (slope) between egg mass and relative survival
20
10
0
-10
Tributary


Fig. 3.