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Adaptive maternal investment in the wild? Links between maternal growth trajectory and offspring size, growth and survival in contrasting environments

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Abstract

Life history theory predicts that investment per offspring should correlate negatively with the quality of environment offspring are anticipated to encounter; parents may use their own experience as juveniles to predict this environment and may modulate offspring traits such as growth capacity as well as initial size. We manipulated nutrient levels in the juvenile habitat of wild Atlantic salmon *Salmo salar* to investigate the hypothesis that the egg size maximising juvenile growth and survival depends on environmental quality. We also tested whether offspring traits were related to parental growth trajectory. Mothers that grew fast when young produced more, smaller offspring than mothers that had grown slowly to reach the same size. Despite their size disadvantage, offspring of faster-growing mothers grew faster than those of slow-growing mothers in all environments, counter to the expectation that they would be competitively disadvantaged. However, they had lower relative survival in environments where the density of older predatory/competitor fish was relatively high. These links between maternal (but not paternal) growth trajectory and offspring survival rate were independent of egg size, underscoring that mothers may be adjusting egg traits other than size to suit the anticipated environment faced by their offspring.

Introduction

A major goal in evolutionary ecology is to understand the sources and significance of individual variation in juvenile life histories (Rollinson and Rowe 2016; Vindenes and Langangen 2015), since it is evident that phenotypic variation in early life can have profound effects on lifetime reproductive success (Cam et al. 2016; Plaistow et al. 2015). At a basic level, survival in early life is positively related to body size (Rollinson and Rowe 2015) with individual size largely determined by parental provisioning (Sinervo et al. 1992). Parents can therefore enhance offspring survival by increasing investment per offspring (Smith and

Fretwell 1974). However, the resources available for allocation in offspring are finite, and so parents must trade the number of offspring they produce versus their size (Lack 1947).

Accordingly, the fitness cost of decreased fecundity must be balanced against the gains in fitness accrued from greater investment per offspring, with the optimal balance between size and number of offspring generally occurring at some intermediate size (Smith and Fretwell 1974). Theory suggests that optimal offspring size will vary across environments, with low-quality juvenile environments favouring a relatively large optimal offspring size since larger offspring experience greater survival under conditions of e.g., high predation or starvation (Einum and Fleming 2004; Hendry and Day 2003; McGinley et al. 1987; Schultz 1991).

These classic tenets of offspring-size theory have been well supported (with the effect of offspring size often being negligible in higher quality environments. Einum and Fleming 1999; Hutchings 1991; Rollinson and Hutchings 2013; Sinervo et al. 1992), and recent work has therefore focussed on understanding variation in parental provisioning and its interaction with environmental quality, as a source of variation in juvenile life histories and fitness (Burton et al. 2013a; Dantzer et al. 2013; Plaistow et al. 2015).

Variation in parental provisioning may affect fitness in two ways. First, if variation in provisioning is manifested purely in terms of offspring size, then it is expected that mothers should invest more in each offspring if offspring are likely to encounter a poor environment (Fischer et al. 2011; McGinley et al. 1987). Evidence across a range of taxa supports this prediction: females produce larger young as both a genetic and plastic response to harsh environments (Allen et al. 2008; Fox et al. 1997; Leips et al. 2009; Mashiko 1992). Second, other important offspring traits, such as growth capacity, might be influenced by phenotypic plasticity (Dantzer et al. 2013) and/or genetic variation (Choh et al. 2011; Johnson et al. 2011). Recent evidence suggests that mothers might simultaneously influence both the size and capacity for growth of their offspring (Burton et al. 2013a): offspring from faster-

growing mothers were smaller initially but capable of faster growth than offspring from slower-growing mothers. Thus, a major goal of the present work is to explore the links between environmental conditions and maternal influences on both growth- and offspring-size variation in the wild.

The impetus for our study arises from the observation that, across a range of fish species, individuals that grow slowly as juveniles subsequently produce relatively larger eggs at adulthood (Jonsson et al. 1996; Morita et al. 1999; Taborsky 2006; Vrtílek and Reichard 2015). This relationship between maternal growth trajectory (MGT) and offspring size is perhaps most widely documented in migratory salmonid fishes (Burton et al. 2013b; Jonsson et al. 1996; Thorpe et al. 1984), a group in which females exhibit high reproductive fidelity to their natal stream, but where provisioning of eggs occurs while the females are still at sea, in an environment far removed from the one that their offspring will first experience. Jonsson et al. (1996) provide evidence to suggest that, rather than base resource allocations on their current marine environment, pre-spawning migratory salmonids may actually use their own growth experience as a juvenile (or another proxy such as juvenile density, since this negatively impacts growth rate) to plastically adjust the size of their offspring to match the environment they are anticipated to face. Despite the widespread association between MGT and egg size, especially in fishes (Morita et al. 1999; Taborsky 2006; Thorpe et al. 1984; Vrtílek and Reichard 2015), the evidence in favour of such plastic provisioning remains correlative. In particular, no study has demonstrated experimentally that mothers that grew slowly as juveniles produce offspring that actually perform relatively better in low-quality environments than the offspring of mothers that had faster juvenile growth. Further, while there is evidence that MGT is related to offspring growth over-and-above effects of egg size, the fitness consequences remain enigmatic (Burton et al. 2013a; Burton and Metcalfe 2014). Finally, to our knowledge, all manipulative studies that explore variation in offspring size in

response to MGT have been performed in the laboratory (e.g. cladocerans, Perrin 1989; cichlid fish, Taborsky 2006). Exploring the consequences of MGT in the wild would lead to a better understanding of the linkage between environmental conditions, MGT, offspring initial size and growth rate, ultimately broadening our knowledge of how the early-life environment interacts with parental influences to shape development.

The present study focuses on Atlantic salmon (*Salmo salar*), a species where mothers generally home with great accuracy to their natal stream for spawning, such that environmental conditions experienced by juveniles are expected to broadly correlate with those experienced by their mothers when young (Fleming 1996). Juveniles are highly territorial, defending food-based territories from conspecifics, and they live in fresh water until smolting (the physiological and morphological preparation for marine life). The seaward smolt migration occurs only during spring; fish that fail to smolt in a given spring remain in fresh water for at least another year. Smolting is subject to a developmental threshold, occurring only above a minimum body size (Dodson et al. 2013; Metcalfe 1998). Local adaption in this threshold is likely, as part of the variation in the size at which smolting occurs is heritable (Dodson et al. 2013). However, the time taken to reach that threshold will nonetheless be influenced by spatial and temporal variation in growth opportunity, meaning that the fastest growing individuals smolt and migrate to sea a year or more ahead of those that grow at a slower rate; as a result, smolt age varies both within- and among- river systems (Metcalfe and Thorpe 1990). The duration of the freshwater stage of the life cycle influences subsequent egg size: females within a population that grew relatively slowly as juveniles (i.e., smolted at older ages) produce larger eggs, even when controlling for differences in body size at the time of spawning (Burton et al. 2013b; Jonsson et al. 1996; Thorpe et al. 1984). Further, many adults can die after spawning, leaving behind marine-derived nutrients that enrich the freshwater stream environment and potentially improve conditions for their

offspring (Auer et al. 2018; Bardonnet and Bagliniere 2000; Nislow et al. 2004; Williams et al. 2010; Williams et al. 2009). These aspects of the salmon life cycle allow for a biologically-relevant manipulation of the quality of the juvenile environment, where more adult carcasses correspond to a more productive juvenile environment (Williams et al. 2009). They also suggest that (a) growth conditions for juveniles might differ spatially and temporally, especially if there is annual variation in the number of adults that die on or around the spawning grounds, and (b) both genetic variation and the developmental environment could shape the optimal phenotype of offspring. In this study we capitalize upon naturally occurring variation in MGT to first confirm that mothers that grew slowly as juveniles produced fewer, larger eggs at adulthood than fast-growing mothers. We then test the following predictions of the plastic provisioning hypothesis (Jonsson et al. 1996): (1) selection on egg size will be stronger in low-quality vs high-quality environments; (2) larger offspring produced by slower-growing mothers will have relatively (2A) faster growth and (2B) greater survival in low-quality environments than will the smaller offspring produced by faster-growing mothers. Finally, we also explore the possibility that (3) the effect of MGT on juvenile survival is not restricted to variation in egg size alone, so that in low-quality environments offspring produced by slower-growing mothers will have higher survival, even when controlling for initial differences in offspring size, than the offspring produced by faster-growing mothers. In contrast, we expect that the influence of MGT on offspring growth and survival will be negligible when environmental quality is relatively high. Given that the current study draws on natural variation in MGT, we are unable to categorically distinguish between a plastic or genetic mode of inheritance for this trait. However, the alternative possibility that variation in MGT is the result of genetic divergence would receive support if the offspring of faster-growing mothers have faster growth and/or greater survival across environments.

Materials and methods

Selection and spawning of parental stock

The protocol for the selection and spawning of parental fish followed that of (Burton et al. 2013a), but with some minor modifications. Atlantic salmon undertaking their spawning migration were captured at the Loch na Croic fish trap on the River Blackwater, Ross Shire, northern Scotland. At the trap site, males and females were distributed among ten dark circular tanks (4 m diameter, 1.5 m deep), supplied with water from the River Blackwater, until the salmon reached spawning condition. We determined spawning condition of the salmon by netting and lightly squeezing the sides of each fish to detect the presence of loose eggs within the body cavity. One sea-winter (1SW) fish were distinguished from multi-sea winter (MSW) fish on the basis of body size distributions. We randomly selected 103 spawning-ready, 1SW females between 4th – 6th Dec 2011, which was within 20 days of their capture. A sample of scales from each fish was collected for confirmation of sea-age and age at smolting (both determined by inspection of scale annuli, e.g. Friedland and Haas 1996); we also measured fork length (LF, to 0.5 cm) and body mass (to 0.1 g) prior to stripping eggs. Each female's entire clutch was drained of ovarian fluid and then weighed to the nearest 0.1 g.

A sub-sample of approximately 10 g of eggs from each clutch was weighed (to 0.01 g) and preserved with 5% buffered formalin (Fleming and Ng 1987). Eggs from each sub-sample were later counted to estimate the mean mass of individual eggs (hereafter 'egg size') per female. The remaining eggs from each female were fertilised *in vitro* with sperm from a wild anadromous 1SW male (confirmed from scale samples, one different male per egg batch) to create full sibling families. Adipose fin clips were removed from the parental fish to enable offspring parentage assignment (see supplementary material). The fertilised eggs were

transferred to the Scottish and Southern Electricity hatchery at Contin, where they were reared as separate clutches under ambient water temperatures until the eyed stage.

From the initial group of 103 clutches, a subset of 48 clutches was chosen to provide eggs for the field experiment, based on the mothers' time spent as juveniles in fresh water prior to seaward migration. Scale readings confirmed that all the selected female spawners were virgin fish that had spent one year at sea (1SW), but varied in their early growth rate. Those that had grown faster (fast early growth mothers, MFEG, $n = 24$) had reached the size threshold necessary for seaward migration earlier (Metcalf and Thorpe 1990), and had become smolts at two years of age, whereas slower growing females had taken three years to reach the smolt stage (slow early growth mothers, MSEG, $n = 24$). These females were chosen such that there was no significant difference in body size, body condition or relative reproductive investment (i.e. relative clutch mass) among the two smolt classes of mother, since these traits can correlate with offspring growth and/or survival (Burton et al. 2013a) (see Appendix & Table S1 for full details). Whilst the focus of the current study was on the relationship between maternal growth trajectory and the growth/survival of offspring, we couldn't exclude the possibility of a similar influence on offspring from the fathers (i.e. of early paternal growth trajectory, hereafter PGT). Scale readings confirmed that the male spawners used to fertilise each batch of eggs had also spent a single year at sea, having smolted at the same two ages as the maternal fish (fast early growth fathers, PFEG, $n = 26$, slow early growth fathers, PSEG, $n = 22$). Further details regarding the selected paternal fish are provided in Table S2. Ideally a factorial mating design, for example where one male was crossed with both a FEG and a SEG female, would have helped to disentangle any maternal from paternal influence on offspring. However, this was impractical due to constraints imposed by field conditions at the fish trap and issues relating to animal welfare. Thus, of the 24 families with FEG mothers, 14 were sired by FEG fathers and 10 by SEG fathers (giving

14 MFEG-PFEG and 10 MFEG-PSEG families). Likewise, of the 24 families with SEG mothers, 12 were sired by SEG fathers and 12 by FEG fathers (giving 12 MSEG-PSEG and 12 MSEG-PFEG families). Egg mortality was recorded for each selected clutch until egg stocking (see next section).

Field experiment

The growth and survival of offspring was estimated in 6 tributary streams of the River Conon, all of which had suitable habitat for salmon juveniles but had no natural spawning due to barriers to upstream adult migration. Between the 5th and 10th of March 2012, six streams were seeded with eyed-stage eggs from each of the 48 selected females ($n = 1000$ eggs per family, $n = 48,000$ total). All eggs were first pooled, mixed thoroughly, then divided volumetrically among 48 Whitlock-Vibert nest boxes (Federation of Fly Fishers, Montana, USA); this created nests of 1000 eggs, approximating natural numbers for this species (Fleming 1996). In each of the six streams 8 nest boxes were sited in suitable spawning habitat: 4 nests spaced approximately 25 m apart were placed 100 - 250 m upstream from the remaining 4 similarly spaced nests, thereby creating two “sections” of stream, each with 4 nests. Previous work in this catchment has found that juvenile dispersal from artificial nests is typically less than 100 m downstream (Einum et al. 2011a), and our minimum separation distance of 100 m (mean \pm sd = 174 ± 49.6 m, range = 100 – 250 m, Table S3) between the lowermost control nest box and uppermost treatment nest box therefore minimised the chance that juveniles originally stocked in upstream control sites moved downstream into the treatment sites. No other salmon eggs were stocked in these streams in this year.

At the same time as stocking with eggs, the four most downstream nests were given a nutrient treatment (referred to hereafter as ‘high’ nutrient sites) by the addition of 6 salmon carcasses per nest (total carcass mass per out-planted nest, 7.2 – 11.0 kg). These carcasses were 1SW

males that had died naturally during routine hatchery spawning and were then frozen. The carcasses were encased within coarse galvanised steel mesh (diameter approx. 20 mm), to prevent removal by scavengers, and anchored to the streambed immediately upstream of the nest. This technique has previously been shown to increase juvenile salmon productivity in this river catchment (Williams et al. 2009). The four most upstream nests did not receive this addition of salmon carcasses; we therefore refer to these upstream control nests as 'low' nutrient sites given that they did not receive any additional nutrient input and the streams are all oligotrophic. Thus, our design ensured that offspring from the selected females were approximately evenly represented in the initial hatching of juveniles, in terms of both their number and their distribution, over both the 'high' and 'low' nutrient sites of each stream. Survival and growth was estimated when the surviving juveniles were approximately 3.5 - 4 months old, by electrofishing one stream per day between 17th - 25th July 2012. Nest boxes were excavated prior to electrofishing to check for egg mortality. Electrofishing was conducted in discrete blocks of each stream (hereafter termed 'sites') downstream of two of the nests (with the uppermost boundary of each site within 18 m of the nest) in each of the enriched and control sections. To reduce any bias in the proportion of juveniles from each family group that could be captured, the electrofishing sites were chosen so that (a) they were located below nests with zero egg mortality (nests were excavated and checked in advance of electrofishing) and (b) the enriched and control sites within a stream covered a similar range of microhabitats (see below). A schematic illustration showing the general position of the high and low nutrient electrofishing sites relative to the location of the nests is given in the supplemental material (Fig A1). Two electrofishing teams worked simultaneously during the surveying, with one in the lowest enriched site and the other in the lowest control site. Each site was fished with 3 electrofishing passes in an upstream direction from the downstream boundary of the site, and allowed to 'rest' for 30 minutes between each pass. After

completing the first site within a section, the teams swapped, so that they then sampled a site in the opposing treatment section. Rapidly rising water levels forced us to abandon electrofishing in a low nutrient site (see Table S3 for further details). Measurements of site length (range: 8 – 18 m, variation due to presence of pool habitats not suitable for 0+ juvenile salmon) and wet widths (range: 1.8 – 5.0 m) were used to compute the area of each site (range: 27.75 – 82.5 m²), where width was estimated with five evenly-spaced measurements made along the longitudinal axis of each site. Captured fish consisted of experimental juvenile salmon as well as brown trout and non-experimental salmon from older age classes (which had been stocked in previous years). No other species of fish were encountered during the electrofishing surveys. Experimental fish were given a lethal dose of MS222 before being preserved in 100% ethanol for subsequent morphological measurement and genetic analysis. Based on a previous calibration, body mass measurements of experimental juveniles preserved in ethanol were converted to estimates of fresh mass by the equation, $M_{B1} = 1.49M_{B2} + 68.34$, where M_{B1} and M_{B2} are fresh and preserved mass values, respectively. See Appendix for full description of body mass conversion and parentage assignment.

Proportional coverage of water depths and substratum size classes at each site were measured according to the Scottish Fisheries Coordination Centre (SFCC) electrofishing guidelines for stream habitat measurement (Anonymous 2007). Water depth coverage was originally estimated in intervals of 10 cm from zero to ≥ 50 cm depth. However, depths ranging from 21 to > 50 cm were combined into a single category (≥ 21 cm) due to the low number of data points in these classes. The substrate structure at each site was measured by estimating the proportional coverage of the following substratum size classes, class 1: ‘gravel’ (2 - 16 mm diameter), class 2: ‘pebble’ (16 – 64 mm), class 3: ‘cobble’ (64–256 mm) and class 4: ‘boulder’ (> 256 mm). The enriched and control sites did not differ in the proportional coverage of any of the substratum or water depth classes (see Tables S3 and S4 for full

details on electrofishing sites).

Data analysis

To confirm that slower-growing mothers produce fewer, larger offspring than faster-growing mothers, we fitted general linear models to compare the size and number (fecundity) of eggs from the two maternal groups (i.e. MFEG vs MSEG). Maternal body size (fork length, L_F) was fitted as a covariate, to account for any size related variation in per offspring investment.

To test Prediction 1, that selection on egg size will be stronger in low-quality vs high-quality environments, we estimated linear (s) and quadratic (C) selection on egg size for each stream-treatment combination; s was estimated as the linear slope of the regression of mean-standardized survival over variance-standardized egg size (Lande and Arnold 1983), and C as the quadratic coefficient from a regression of mean-standardized survival over variance-standardized egg size squared. All estimates of C and their SE's were doubled (Stinchcombe et al. 2008).

For the remainder of our predictions, we employed an information theoretic approach, using the corrected Akaike Information Criterion (AIC_C) for small sample sizes, and multi-model averaging (Burnham and Anderson 2002). We adopted such an approach because there are multiple combinations of explanatory variables (i.e. alternative hypotheses) to compare when evaluating Predictions 2A, 2B and 3, and we inferred support for our predictions by examining the relevant model-averaged term and its confidence intervals. We employed linear mixed-effect modelling (described below), fit by maximum likelihood, to relate offspring growth and survival to MGT and PGT (plus their interaction) as well as nutrient enrichment, and the density of salmonid fishes in each stream reach.

Previous studies in this catchment have shown that enrichment, MGT and also local densities of salmonids (which can act as competitors and/or predators; (Henderson and Letcher 2003)

can all strongly affect the survival and growth of juveniles (Burton et al. 2013a; Einum et al. 2011b; Williams et al. 2009). Thus, to test for interactions between growth or survival and environmental quality, we formulated three subsets of candidate models, one set for offspring growth (Prediction 2A), and two for offspring survival (Prediction 2B and 3). Specific growth was estimated for each juvenile according to Ostrovsky (1995):

$$\Omega = \frac{M_t^b - M_0^b}{b \cdot t} 100,$$

Where M_0 is the mean family egg size (in g), M_t is the weight (in g) of a captured juvenile, b is the allometric weight exponent for the relationship between specific growth rate and body weight (0.31 for juvenile Atlantic salmon, Elliott and Hurley 1997) and t is the number of days between fertilisation and recapture. Given that electrofishing was restricted to sites where zero egg mortality was recorded, we assume that the initial number of individuals from each family and thus MGT grouping was the same overall. As such, offspring survival was estimated as the sum of the captured juveniles per family group, per site within each stream (i.e. as a count, $n = 1104$ estimates of survival in total).

For Predictions 2A and 2B, each model subset comprised the same 40 models featuring specific combinations of the fixed explanatory variables; nutrient enrichment (high or low nutrients), maternal growth trajectory (MGT; MFEG or MSEG), paternal growth trajectory (PGT; PFEG or PSEG), site specific density of salmonid fishes (combined density of 0+ experimental juveniles plus older 1+ non-experimental juveniles stocked in previous years plus resident brown trout of all ages, see Supplemental Material for full details) and two-way interactions between these variables that represented ecologically plausible hypotheses (summarised in Tables S5 and S6). The base model in each of these subsets shared a common random effect structure; family group was specified as a random intercept term to control for the non-independence of measurements made on siblings. To account for spatial and

temporal correlations specific to each electrofishing site, an additional random intercept term of site nested within stream was specified. The base survival model was fitted with a Poisson error distribution and additionally, an offset term (area of each electrofishing site, in m^2), to account for variation in capture rates caused by differences in the extent of the sites that were electrofished. For the survival models, site specific density estimates excluded the 0+ experimental juveniles due to the strongly collinear relationship with the response variable (i.e. counts of sibling 0+ salmon per site).

For Prediction 3 we adopted the same model formulation approach as above, while also statistically controlling for the effects of variation in mean egg size among mothers. This resulted in a set of 63 models (summarised in Table S7), 40 of which had the same fixed effect structure as the model subset formulated to test prediction 2B (summarised in Table S6). However, in this set, candidate models could also include the fixed effect of mean egg size per family and optionally, two-way interactions between this variable and the other fixed terms, meaning that 23 additional models were also tested. We did not explore how growth relates to egg size, because mean family egg size was used to estimate growth and would thus be collinear with the response variable.

We evaluated the relative support for our hypotheses using AICc-based Akaike weights (w_i), and used model averaging to incorporate model uncertainty into parameter estimation (Burnham and Anderson 2002). Conditional model-averaged parameter estimates (i.e., considering only the models in which a given term appears) were calculated from models fitted with the *lme4* package (Bates et al. 2015) using the *AICcmodavg* package (Mazerolle 2019). Continuous explanatory variables were centered (i.e., the mean was subtracted) then divided by two standard deviations (Gelman 2008), so that effect sizes of explanatory variables could be meaningfully compared (Schielzeth 2010). All statistical analyses were conducted in R version 3.5.1 (R Development Core Team 2018). Model diagnostics for

heteroscedasticity and normality were inspected from residual plots produced from the most complex models fitted during each of the three iterations of model-averaging. For both the survival analyses (poisson glmm's), dispersion was assessed by comparing the summed squared pearson residuals to the residual degrees of freedom (Bolker 2019) from the most complex model fitted. In both cases, these parameters were less than 1. Data are deposited in the Dryad Digital Repository (Burton et al. 2019).

Results

Egg size and number were positively associated with maternal body size but for a given body size, slow-early growth (MSEG) females invested in eggs that on average were 12.6 % larger but 9.0 % fewer in number (Table 1, Fig 1a,b) than fast-early growth (MFEG) females. This confirmed that a relatively slow maternal growth trajectory (MGT) is associated with greater investment per offspring at adulthood.

A total of 947 experimental juvenile salmon were captured during the electrofishing surveys and of these, 904 could unambiguously be assigned to a family and 896 of these could be considered for statistical analysis (individuals captured in the abandoned low nutrient electrofishing site were omitted, see Methods). The relative survival of experimental juveniles varied widely among families (MFEG: $n = 412$ captured juveniles, MSEG: $n = 484$, $n = 3 - 41$ captured individuals per family), despite each female contributing approximately equal numbers of eggs to each of the experimental nests. Directional selection on egg size was positive in 11 of the 12 sites (6 streams x 2 treatments), and significantly positive in 5 of these cases (Table 2). Significant stabilizing selection on egg size was observed in only one stream-treatment combination (Table 2). Contrary to Prediction 1, linear selection on egg size did not differ between the high nutrient sites (mean \pm SD; 0.226 ± 0.194 , $n = 6$ streams) and low nutrient sites (mean \pm SD, 0.271 ± 0.164 , $n = 6$ streams, paired t-test, $t = 0.596$, $P = 0.59$,

n = 6 pairs.

Our manipulation of nutrient levels had no effect on juvenile growth rates, but growth was lower when the density of salmonids was relatively high (Fig. 2a, c). Growth rate was nearly 5% lower for MSEG juveniles overall (Fig. 2a,b), and contrary to Prediction 2A, there was no evidence that they had a growth rate advantage over the offspring of MFEG mothers in poor environments, since there were no significant MGT x environment interactions (Fig. 2a).

Prediction 2B received mixed support. Although (contrary to our prediction) survival was not influenced by an interaction between MGT and nutrients, MSEG offspring survived better than MFEG offspring when the density of older, larger 1+ salmon and trout was high (i.e., an MGT x density interaction; Fig. 3b). Since these other fish are competitors and/or predators, this matches the prediction that MFEG offspring survive less well than MSEG offspring in low-quality environments (Fig. 3a,c). As would be expected, survival rates were enhanced by nutrient enrichment (22 % higher on average) but reduced at increasing densities (Fig. 3). However, the effect of nutrients depended on the density of 1+ salmonids, ameliorating the negative effect of high 1+ densities (Fig. 3c); this apparent difference in survival is unlikely to be attributable to emigration of experimental juveniles from low (upstream) to high nutrient sites (downstream) within each stream, since the overall recovery rates of experimental juveniles were similar among the two site types (average number of captured experimental juveniles \pm SE: high nutrient sites, 1.01 ± 0.14 individuals m^{-2} ; low nutrient sites, 0.84 ± 0.17 , parameter estimate for high nutrient sites relative to low nutrient sites from linear mixed effect model with stream fitted as a random intercept, 0.18 ± 0.19 , t-value = 0.99, $p = 0.34$).

When considering egg size as a covariate in the survival analysis, we found that juveniles hatching from larger eggs had greater survival overall (Fig 4a, b), and this survival advantage increased with the density of 1+ salmonids (i.e., egg size x density interaction; Fig. 4a,c).

Most importantly however, Prediction 3 was upheld: when densities were high, MSEG offspring had higher survival rates than MFEG offspring even after controlling for the difference in their egg size (Fig. 4a), suggesting that mothers with contrasting growth trajectories are producing offspring that differ in more than just their initial size. In fact, all main effects and interactions were essentially of the same magnitude and in the same direction whether or not egg size was accounted for in our analyses (Figs 3a, 4a). Neither paternal growth trajectory (PGT), nor its interaction with MGT was observed to have any bearing on the relative support for predictions 2A, 2B or 3 (see Fig. 2a, 3a and 4a).

Discussion

The present study provides novel insight into the hypothesis that the production of relatively large offspring by mothers who themselves grew slowly early in life is a plastic response to low-quality juvenile environments (Jonsson et al. 1996). Having manipulated the quality of the natural environment of juvenile Atlantic salmon, we predicted that the growth capacity and survival of offspring from mothers with a relatively slow early life growth trajectory would be superior in low-quality environments. We found mixed support for this hypothesis. On the one hand, the growth and survival of offspring did not respond as predicted to the addition of nutrients (salmon carcasses) to the stream. While the addition of carcasses can have an effect on juvenile salmon growth rates in this catchment (Auer et al. 2018), the response depends on the extent of the input (Williams et al. 2009) and the number of carcasses placed in each stream in the present experiment could have been insufficient to reveal the predicted FEG \times nutrient treatment effect on offspring. Nevertheless, the relative survival of offspring from fast- and slow-growing mothers did depend on the density of competitors and fish predators (density of 0+ and 1+ salmonids), which can also reflect environmental quality (Leips et al. 2009). Specifically, offspring survival was related to an interaction between the local density of older salmonids and maternal growth trajectory

(MGT), where at high densities, offspring from mothers with fast early growth (MFEG) survived less well than those from mothers with slow early growth (MSEG), in line with our prediction.

Offspring growth was not associated with an interaction between MGT and either of our measures of environmental quality (nutrient enrichment or density); instead, growth was simply lower overall when juvenile density was high and was faster for MFEG offspring. Our work thus suggests that MFEG offspring grow relatively faster than MSEG offspring regardless of their smaller initial size, corroborating findings from several other fish species (Eldridge et al. 1982; Leblanc 2011; Segers et al. 2011). Given that this pattern was observed to persist irrespective of either metric of environmental quality it suggests that the correlation between MGT and offspring growth capacity (and potentially the subsequent pattern of investment in reproduction as well) likely arises from genetic adaptation, not plasticity. The results therefore provide significant insight into an otherwise enigmatic pattern of phenotypic variation that has long been described in the literature (Morita et al. 1999; Perrin 1989; Taborsky 2006; Thorpe et al. 1984; Vrtílek and Reichard 2015).

Moreover, our experiment suggests that the link between maternal early growth and offspring traits is not mediated through egg size alone, since MGT was a predictor of offspring growth rate and survival even after controlling for egg size. How might genetic differentiation in growth capacity arise in this species? Atlantic salmon are capable of fine spatial homing to their natal watersheds (Fleming 1996), such that FEG and SEG females are likely to spawn in the same tributary streams of a catchment in which they developed themselves. Thus, FEG/SEG phenotypes might result from local adaptation to streams that differ in productivity (e.g. warm, eutrophic lowland vs cold, oligotrophic upland, as suggested by Bacon et al. 2012). However, due to the presence of overlapping year classes within a given stream, variation in the size and age structure of juvenile salmon could conceivably favour alternative

FEG/SEG life histories that reflect contrasting positions along a slow-fast continuum of life-history variation (Dammhahn et al. 2018; Ricklefs and Wikelski 2002). Juvenile salmonids are territorial, and securing a high-quality territory helps ensure survival through the first growing season (Elliott 1989; Elliott 1990). MFEG juveniles have been shown to be more aggressive when competing for territories than MSEG juveniles (Burton et al. 2016). The greater aggression shown by MFEG juveniles might aid them in acquiring feeding territories upon emergence from the nest, especially in competition with older, larger individuals since dominance is not related to size at this age (Huntingford et al. 1990). The apparent capacity of MFEG juveniles for more rapid growth may also be critical to their chances of overcoming size-selective mortality during their first winter (Quinn and Peterson 1996). The rapid early growth of FEG individuals presumably carries a cost that might be deferred until later in life (e.g. molecular or cellular damage reducing lifespan, Lee et al. 2013) or perhaps manifest in certain conditions. For example, MFEG juveniles in our study had reduced survival when the density of other fishes (including older, larger predators) was high. This suggests that MFEG offspring might be less vigilant against predation, due to their higher levels of aggression or a higher feeding motivation and requirement to spend time feeding that results from their higher growth capacity (Brick 1998; Gotthard 2000). Mothers producing many poorly-provisioned but fast-growing offspring may therefore have relatively high fitness when the environment contains few predators and is sufficiently productive (e.g. in warm summers or when in-stream nutrient levels are high following the deposition of a large numbers of adult carcasses around the spawning grounds) to support their relatively small fry during the critical transition to exogenous food. On the other hand, SEG offspring could represent a relatively conservative phenotype, as their larger egg size (and hence greater nutritional reserves and initial body size) provides an early survival advantage in lower quality environments, e.g. in particularly cold summers or when densities of 1+ salmon and trout,

which can both compete with and predate upon 0+ juveniles, are relatively high (Fig 3b), and this survival advantage could be maintained by exhibiting a conservative growth strategy.

The present study also confirms some central tenets of offspring size evolution. Theory predicts that the minimum viable offspring size and optimal egg size will be relatively large in low-quality environments (Brockelman 1975). Similarly, a stronger covariance of offspring size and fitness is expected in low-quality environments, owing to size-related differences in nutritional reserves that are more important when resources are scarce (Brockelman 1975; Eium and Fleming 1999; Hutchings 1991). We observed that directional selection on egg size was typically strong and positive (Table 1), although selection on egg size was not stronger in lower nutrient sites. In the present case, however, egg size is itself strongly associated with different offspring growth strategies, and the survival consequences of these strategies depend on the environment. The selection differentials we measured are therefore confounded with growth strategy, and this was difficult to model since many families had few surviving representatives with which to estimate survival rate on a per-site basis. Nevertheless, estimates of offspring survival were positively related to egg size (Fig 4b), a relationship that was particularly evident when the density of competitors/predators was relatively high (Fig 4c). This link between environmental quality and the fitness consequences of egg size variation corroborates previous work on Atlantic salmon (Rollinson and Hutchings 2013) and is a central assumption of most models of egg size evolution (Eium and Fleming 2004; McGinley et al. 1987; Schultz 1991).

In this study we investigated the hypothesis that the relatively large offspring produced by slower-growing mothers is a plastic response to a low-quality developmental environment. However, our data indicate that mothers who grew relatively quickly themselves produce juveniles that also grow quickly, irrespective of environmental quality, indicating genetic, rather than plastic inheritance of early growth rate and possibly the subsequent life history.

Whilst this capacity for faster growth was associated with poorer survival in certain conditions, it nonetheless contradicts the general expectation that, in natural populations, larger young should have a competitive advantage over smaller young and hence grow faster (e.g. Einum and Fleming 1999). Clearly, early life growth trajectory is associated with per-capita investment in offspring at maturity, but in the case of Atlantic salmon, growth phenotypes are markedly different even after accounting for differences in initial size, underscoring that it may not always be possible to generalise upon the fitness consequences of initial offspring size.

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Appendix from T. Burton et al., “Adaptive maternal investment in the wild? Links between maternal growth trajectory and offspring size, growth and survival in contrasting environments”

Selection of broodstock

From the initial sample of 103 wild adult females, we defined body condition as somatic mass (i.e. total body mass minus clutch mass) relative to body length, calculated as the residuals of a linear regression (both variables log-transformed) of somatic mass against fork length. Similarly, reproductive investment was defined as the residuals of clutch mass regressed on fork length (both variables log-transformed). Thus, the subset of 48 females used to provide eggs for the field experiment did not differ significantly in body size, relative investment in reproduction or body condition with respect to smolt age (t-test's for all three comparisons, $p > 0.6$, see Table S1)

Correcting juvenile body mass measurements after shrinkage in ethanol

To account for shrinkage in body mass of experimental juveniles caused by preservation in ethanol during electrofishing, we weighed a sub-sample ($n = 78$) of juveniles obtained from 4 of the 6 experimental streams (captured below the experimental sites) immediately after terminal anaesthesia and again after 4 days of storage in 100 % ethanol. Shrinkage in body mass was analysed using a regression ($p < 0.0001$, $r^2 = 0.99$) between fresh (M_{B1} range, 265 – 1578 mg) and preserved body mass values (M_{B2} range, 146 – 1051 mg). The relationship between M_{B1} and M_{B2} is described by the equation, $M_{B1} = 1.49M_{B2} + 68.34$, which was used to convert measurements of juveniles preserved in ethanol to estimates of fresh mass prior to statistical analysis.

Electrofishing

Natural populations of resident brown trout (all ages) were present in all six streams, which were also open to mammalian and avian predators of juvenile salmon. Trout were divided into two age groups, 0+ (fry) and 1+ (parr and adults) based on a bi-modal fork length distribution (age 0+, $n = 77$; fork length (L_F) range, 34 – 68 mm, age 1+, $n = 128$; (L_F) range, 73 – 210 mm). Older juvenile salmon that had been stocked as eggs in previous years were present in one of the streams (Gleann Meinich). In this stream, a bi-modal distribution of lengths was used to separate experimental 0+ salmon fry ($n = 123$; fork length (L_F) range 34 – 50 mm) from non-experimental conspecifics belonging to older age classes, 1+ ‘parr’ ($n = 85$; L_F range 76 – 108 mm). Conspecifics from older age classes and brown trout were allowed to recover from anaesthesia in enclosures placed within the stream before being released.

Genotyping

DNA was extracted from caudal fin clips using the PureLink Pro 96 Genomic DNA Kit (Invitrogen, Paisley, UK) following the manufacturer’s protocol. Genotyping was performed using a Single Nucleotide Polymorphism panel of 93 informative markers scattered across the genome. This panel of markers for European Atlantic Salmon has been customized for internal use by Landcatch Natural Selection using a Sequenom SNP genotyping platform (California, USA). This technology required the generation of allele specific products with distinct masses by primer-extension, and the detection by MALDI-TOF (Matrix-Assisted Laser Desorption/Ionization Time-of-flight) mass spectrometry. Analysis for parentage assignment by exclusion was carried out with the software Vitassign 8.3 (Vandeputte et al., 2006) allowing a maximum of five allele mismatches. 904 0+ salmon (>95%) were uniquely assigned to a single set of parents, and only forty three not assigned, mostly due to a failure of PCR amplification. These individuals were included in estimates of 0+ salmon densities for

data analysis. Twenty eight individuals could not be assigned to any combination of parents because they had unusual microsatellite fingerprints. These individuals were most probably juvenile brown trout that had been wrongly identified as 0+ salmon during field work and were re-classified as such for the calculation of 0+ salmonids density for our data analysis.

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Tables

Table 1. Summary of general linear models comparing variation in the fecundity and size of eggs produced by female salmon with different early life growth trajectories: MFEG, fast early growth mothers; MSEG, slow early growth mothers. Each analysis controlled for the influence of maternal body size (fork length, L_F). Parameter estimates are presented relative to the MFEG maternal grouping.

	estimate	se	t-value	p-value
egg size				
intercept (MFEG)	-52.80	37.96	-1.40	0.17
maternal body size	0.22	0.07	3.25	< 0.01
MSEG	11.75	3.15	3.73	< 0.001
fecundity				
intercept (MFEG)	-5630.60	1433.20	-3.93	< 0.001
maternal body size	16.75	2.51	6.67	< 0.0001
MSEG	-329.48	119.05	-2.77	< 0.01

Table 2: Estimates of linear (i.e. directional, s) and quadratic (i.e. stabilizing, C) selection on egg size for all stream-nutrient treatment combinations, and for all sites pooled by treatment ($\pm 1SE$). * $p \leq 0.10$, † $p < 0.05$.

Stream	Treatment	s	SE	C	SE
RB	high nutrient	0.18	0.15	-0.084	0.27
	low nutrient	0.36*	0.19	-0.113	0.35
GM	high nutrient	0.59†	0.17	-0.16	0.30
	low nutrient	0.39†	0.14	0.16	0.25
CM	high nutrient	0.048	0.13	-0.13	0.24
	low nutrient	0.17	0.12	-0.083	0.22
AFB	high nutrient	0.28†	0.11	-0.12	0.202
	low nutrient	0.31†	0.12	-0.0083	0.22
AGS	high nutrient	0.12	0.12	-0.26	0.21
	low nutrient	-0.015	0.13	-0.49†	0.23†
AG	high nutrient	0.14	0.13	-0.11	0.24
	low nutrient	0.41†	0.18	-0.064	0.32
Pooled	high nutrient	0.20†	0.072	-0.15	0.13
	low nutrient	0.26†	0.072	-0.10	0.13

Figure Legends

Figure 1. Prediction 1. (a) Average size of eggs produced by female Atlantic salmon in relation to their early life growth trajectory: MFEG, fast early growth mothers; MSEG, slow early growth mothers. Error bars give ± 1 SE. (b) Average fecundity of female Atlantic salmon in relation to their early life growth trajectory: MFEG, fast early growth mothers; MSEG, slow early growth mothers. Error bars give ± 1 SE.

Figure 2. Prediction 2A. (a) Model-averaged coefficients ($\pm 95\%$ confidence intervals) for linear mixed effect models describing variation in the growth rate ($\Omega \% d^{-1}$) of juvenile Atlantic salmon in relation to the density of 0+ salmonids present in a given electrofishing site, maternal and paternal growth trajectories and nutrient treatment. Note: model-averaged coefficients are presented for MSEG (maternal slow early growth) juveniles relative to MFEG (maternal fast early growth) juveniles, PSEG (paternal slow early growth) juveniles relative to PFEG (paternal fast early growth) juveniles and for low nutrients relative to high nutrients respectively. Confidence intervals that do not overlap zero are assumed to indicate statistical significance. (b) Juvenile growth in relation to maternal growth trajectory (MGT). (c) Juvenile growth in relation to density of 0+ salmonids in each electrofishing site.

Figure 3. Prediction 2B. (a) Model-averaged coefficients ($\pm 95\%$ confidence intervals) for generalised linear mixed effect models describing variation in the survival of juvenile Atlantic salmon in relation to the density of 1+ salmonids present in a given electrofishing site, maternal and paternal growth trajectories and nutrient treatment. Note: model-averaged coefficients are presented for MSEG (maternal slow early growth) juveniles relative to MFEG (maternal fast early growth) juveniles, PSEG (paternal slow early growth) juveniles relative to PFEG (paternal fast early growth) juveniles and for low nutrients relative to high nutrients respectively. Confidence intervals that do not overlap zero are assumed to indicate

statistical significance. (b) Juvenile survival in relation to the density of 1+ salmonids and maternal growth trajectory (MGT): open symbols = fast early growth mothers (MFEG); filled symbols = slow early growth mothers (MSEG). Solid and dashed lines are model estimates for the respective survival of MSEG and MFEG fish. (c) Juvenile survival in relation to the density of 1+ salmonids and nutrient treatment. High nutrient sites = filled symbols, low nutrient control sites = open symbols. Solid and dashed lines are model estimates for the respective survival of juveniles in high and low nutrient sites. Note that in (b) and (c) data are plotted on original scale and survival is shown as the average density of resampled juveniles per family in each electrofishing site. Model estimates in these plots were produced by fitting a poisson glmm to the uncentered, unstandardized survival data (same random effect and offset structure as the model averaging), with the predictor variables being only those whose model-averaged coefficients differed significantly from zero (i.e. enrichment \times density and MGT \times density interactions, lower order terms included).

Figure 4. Prediction 3 (a) Model-averaged coefficients (\pm 95% confidence intervals) for generalised linear mixed effect models describing variation in the survival of juvenile Atlantic salmon in relation to the density of 1+ salmonids present in a given electrofishing site, maternal and paternal growth trajectories, nutrient treatment and the average size of eggs from which they hatched. Note: model-averaged coefficients are presented for MSEG (maternal slow early growth) juveniles relative to MFEG (maternal fast early growth) juveniles, PSEG (paternal slow early growth) juveniles relative to PFEG (paternal fast early growth) juveniles and for low nutrients relative to high nutrients respectively. Confidence intervals that do not overlap zero are assumed to indicate statistical significance. (b) Total juvenile survival in relation to mean family egg size. (c) Estimated change in the effect of egg size (i.e. increase in model coefficient for the effect of egg size) on juvenile survival in

relation to the density of 1+ salmonids present in each electrofishing site. Shaded region indicates 95% confidence intervals. Change in egg size coefficient and confidence intervals were produced with the interplot package (Hu 2018). Data showing MGT \times density and enrichment \times density interactions are not re-plotted here as the model-averaged coefficients for these terms were quantitatively very similar to those displayed in Figure 3a.

Figure A1. Schematic illustration of study design as implemented within a given stream.

Circles = nests, rectangles = electrofishing sites and the arrow shows the direction of water flow. Two high and two low nutrient electrofishing sites were sampled in each stream. A buffer zone of minimum distance 100 m was established between the lowermost low nutrients nest and uppermost high nutrients nest to minimise the chance that juveniles originally stocked in upstream control sites moved downstream into the treatment sites.

Illustration is not to scale.