

Adaptive Maternal Investment in the Wild? Links between Maternal Growth Trajectory and Offspring Size, Growth, and Survival in Contrasting Environments

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Submitted March 13, 2019; Accepted September 11, 2019; Electronically published March 3, 2020

Online enhancements: appendix, supplemental PDF. Dryad data: <https://doi.org/10.5061/dryad.pr9543d>.

ABSTRACT: Life-history theory predicts that investment per offspring should correlate negatively with the quality of the environment that 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 and initial size. We manipulated nutrient levels in the juvenile habitat of wild Atlantic salmon (*Salmo salar*) to investigate the hypothesis that the egg size that maximizes 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 offspring and smaller offspring than mothers that grew slowly to reach the same size. Despite their size disadvantage, offspring of faster-growing mothers grew faster than those of slower-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 environment their offspring are anticipated to face.

Keywords: maternal effects, early life, reaction norm, egg size, environmental quality.

Introduction

A major goal in evolutionary ecology is to understand the sources and significance of individual variation in juvenile life histories (Vindenes and Langangen 2015; Rollinson and Rowe 2016), since it is evident that phenotypic variation in early life can have profound effects on lifetime reproductive success (Plaistow et al. 2015; Cam et al. 2016). 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, so parents must trade the number of offspring they produce with offspring 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 favoring a relatively large optimal offspring size, since larger offspring experience greater survival under conditions of high predation or starvation, for example (McGinley et al. 1987; Schultz 1991; Hendry and Day 2003; Einum and Fleming 2004). These classic tenets of offspring size theory have been well supported (with the effect of offspring size often being negligible in higher-quality environments; Hutchings 1991; Sinervo et al. 1992; Einum and Fleming 1999; Rollinson and Hutchings 2013), and

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Am. Nat. 2020. Vol. 195, pp. 678–690. © 2020 by The University of Chicago. 0003-0147/2020/19504-5911\$15.00. All rights reserved.
DOI: 10.1086/707518

recent work has therefore focused 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 (McGinley et al. 1987; Fischer et al. 2011). Evidence across a range of taxa supports this prediction: females produce larger young as both a genetic and a plastic response to harsh environments (Mashiko 1992; Fox et al. 1997; Allen et al. 2008; Leips et al. 2009). 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 the 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 in adulthood (Jonsson et al. 1996; Morita et al. 1999; Taborsky 2006; Vrtilík and Reichard 2015). This relationship between maternal growth trajectory (MGT) and offspring size is perhaps most widely documented in migratory salmonid fishes (Thorpe et al. 1984; Jonsson et al. 1996; Burton et al. 2013b), a group in which females exhibit high reproductive fidelity to their natal stream but 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 prespawning 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), rather than basing resource allocations on their current marine environment, 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 (Thorpe et al. 1984; Morita et al. 1999; Taborsky 2006; Vrtilík and Reichard 2015), the evidence in favor 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. Furthermore, 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 (Metcalfe 1998; Dodson et al. 2013). Local adaptation to 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 (Thorpe et al. 1984; Jonsson et al. 1996; Burton et al. 2013b). Furthermore, many adults can die after spawning, leaving behind marine-derived nutrients that enrich the freshwater stream environment and potentially improve conditions for their offspring (Bardonnet and Bagliniere 2000; Nislow et al. 2004; Williams et al. 2009, 2010; Auer et al. 2018). 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 on naturally occurring variation in MGT to first confirm that mothers that grew slowly as juveniles produced fewer and larger eggs at adulthood than did 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 versus high-quality environments and (2) larger offspring produced by slower-growing mothers will have relatively (2A) faster growth and (2B) greater survival in low-quality environments than 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 than offspring produced by faster-growing mothers even when controlling for initial differences in offspring size. 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 the natural variation in MGT, we are unable to categorically distinguish between a plastic and a 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.

Material 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 10 dark circular tanks (4 m in diameter, 1.5 m deep) supplied with water from the River Blackwater and kept there until the salmon reached spawning condition. We determined the 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 December 4 and December 6, 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 (L_F ; to 0.5 cm) and body mass (to 0.1 g) before stripping eggs. Each female's entire clutch was drained of ovarian fluid and then weighed to the nearest 0.1 g.

A subsample 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 subsample were later counted to estimate the mean mass of individual eggs (hereafter, "egg size") per female. The remaining eggs from each female were fertilized 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 the supplemental PDF, available online). The fertilized 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 on the basis of the mothers' time spent as juveniles in fresh water before seaward migration. Scale readings confirmed that all the selected female spawners were virgin fish that had spent 1 year at sea (1SW) but varied in their early growth rate. Those that had grown faster (mothers with fast early growth [FEG], $n = 24$) had reached the size threshold necessary for seaward migration earlier (Metcalf and Thorpe 1990) and had become smolts at 2 years of age, whereas slower-growing females (mothers with slow early growth [SEG], $n = 24$) had taken 3 years to reach the smolt stage. 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) between the two smolt classes, since these traits can correlate with offspring growth and/or survival (Burton et al. 2013a; see the appendix and table S1 for full details; the appendix and tables S1–S7 are available online). While the focus of the current study was on the relationship between MGT and the growth/survival of offspring, we could not exclude the possibility of a similar influence on offspring from the fathers (i.e., of early paternal growth trajectory [PGT]). Scale readings confirmed that the male spawners used to fertilize each batch of eggs had also spent 1 year at sea, having smolted at the same two ages as the maternal fish (fathers with FEG, $n = 26$; fathers with SEG, $n = 22$). 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 an

FEG and an SEG female—would have helped to disentangle any maternal influence from paternal influence on offspring. However, this was impractical because of 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 were sired by SEG fathers (giving 14 maternal FEG–paternal FEG and 10 maternal FEG–paternal SEG families). Likewise, of the 24 families with SEG mothers, 12 were sired by SEG fathers and 12 were sired by FEG fathers (giving 12 maternal SEG–paternal SEG and 12 maternal SEG–paternal FEG families). Egg mortality was recorded for each selected clutch until egg stocking (see next section).

Field Experiment

The growth and survival of offspring were estimated in six tributary streams of the River Conon, all of which had a suitable habitat for salmon juveniles but had no natural spawning because of barriers to upstream adult migration. Between March 5 and March 10, 2012, six streams were seeded with eyed-stage eggs from each of the 48 selected females ($n = 1,000$ eggs per family, $n = 48,000$ total). All eggs were first pooled, mixed thoroughly, and then divided volumetrically among 48 Whitlock-Vibert nest boxes (Federation of Fly Fishers, Livingston, MT); this created nests of 1,000 eggs, approximating natural numbers for this species (Fleming 1996). In each of the six streams, eight nest boxes were sited in suitable spawning habitats: four nests spaced approximately 25 m apart were placed 100–250 m upstream from the remaining four similarly spaced nests, thereby creating two “sections” of stream, each with four 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 the uppermost treatment nest box therefore minimized the chance that juveniles originally stocked in the 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 that eggs were stocked, the four most downstream nests were given a nutrient treatment (referred to hereafter as “high-nutrient sites”) by the addition of six salmon carcasses per nest (total carcass mass per outplanted 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 in coarse galvanized steel mesh (diameter: ~ 20 mm) to prevent removal by scavengers and anchored to the streambed immediately upstream of the nest. This tech-

nique 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 an 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-nutrient and the low-nutrient sites of each stream.

Survival and growth were estimated when the surviving juveniles were approximately 3.5–4 months old by electrofishing one stream per day between July 17 and July 25, 2012. Nest boxes were excavated before 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 appendix (fig. A1, available online). 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 three electrofishing passes in an upstream direction from the downstream boundary of the site and allowed to “rest” for 30 min 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 nonexperimental 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. Using a previous

calibration, we converted body mass measurements of experimental juveniles preserved in ethanol 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 the appendix for a 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 Co-ordination Centre electrofishing guidelines for stream habitat measurement (SFCC 2007). Water depth coverage was originally estimated in intervals of 10 cm from 0 to ≥ 50 cm. However, depths ranging from 21 to >50 cm were combined into a single category (≥ 21 cm) because of 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 (diameter: 2–16 mm); 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, S4 for full details on electrofishing sites).

Data Analysis

To confirm that slower-growing mothers produce fewer and 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., FEG vs. SEG mothers). Maternal body size (fork length, L_F) was fitted as a covariate to account for any size-related variation in investment per offspring.

To test prediction 1, that selection on egg size will be stronger in low-quality versus 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 was estimated as the quadratic coefficient from a regression of mean-standardized survival over variance-standardized egg size squared. All estimates of C and their standard errors were doubled (Stinchcombe et al. 2008).

For the remainder of our predictions, we employed an information-theoretic approach using the Akaike information criterion corrected for small sample sizes (AIC_C) and multimodel 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 effects modeling (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 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 (Williams et al. 2009; Einum et al. 2011b; Burton et al. 2013a). 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 (predictions 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 (g), M_t is the weight (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 fertilization 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 from each 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; $n = 1,104$ 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), MGT (FEG or SEG mothers), PGT (FEG or SEG fathers), site-specific density of salmonid fishes (combined density of 0+ experimental juveniles plus older 1+ nonexperimental juveniles stocked in previous years plus resident brown trout of all ages; see the supplemental PDF for full details), and two-way interactions between these variables that represented ecologically plausible hypotheses (summarized in tables S5, S6). The base model in each of these subsets shared a common random effects structure; family group was specified as a random intercept term to control for the nonindependence 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 an offset term (area

of each electrofishing site [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 because of 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 (summarized in table S7), 40 of which had the same fixed effects structure as the model subset formulated to test prediction 2B (summarized in table S6). However, in this set, candidate models could also include the fixed effect of mean egg size per family and 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 AIC_c-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), and then divided by 2 SDs (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 survival analyses (Poisson generalized linear mixed models), dispersion was assessed by comparing the summed squared Pearson residuals with the residual degrees of freedom (Bolker 2019) from the most complex model fitted. In both cases, these parameters were less than 1. Data have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.pr9543d>; Burton et al. 2019).

Results

Egg size and number were positively associated with maternal body size, but for a given body size, SEG mothers invested in eggs that were on average 12.6% larger but 9.0% fewer in number (table 1; fig. 1) than eggs from FEG

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

	Estimate	SE	<i>t</i>	<i>P</i>
Egg size:				
Intercept (FEG mothers)	−52.80	37.96	−1.40	.17
Maternal body size	.22	.07	3.25	<.01
SEG mothers	11.75	3.15	3.73	<.001
Fecundity:				
Intercept (FEG mothers)	−5,630.60	1,433.20	−3.93	<.001
Maternal body size	16.75	2.51	6.67	<.0001
SEG mothers	−329.48	119.05	−2.77	<.01

Note: Each analysis controlled for the influence of maternal body size (fork length). Parameter estimates are presented relative to the FEG maternal grouping. FEG = fast early growth; SEG = slow early growth.

mothers. This confirmed that a relatively slow MGT is associated with greater investment per offspring at adulthood.

A total of 947 experimental juvenile salmon were captured during the electrofishing surveys; 904 could be unambiguously 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 “Material and Methods”). The relative survival of experimental juveniles varied widely among maternal groupings (maternal fast early growth [MFEG]: $n = 412$ captured juveniles; maternal slow early growth [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 (six streams \times two treatments) and significantly positive in five 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 the low-nutrient sites (mean \pm SD: 0.271 ± 0.164 , $n = 6$ streams; paired t -test: $t = 0.596$, $P = .59$, $n = 6$ 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, 2C). Growth rate was nearly 5% lower for MSEG juveniles overall (fig. 2A, 2B), and contrary to prediction 2A, there was no evidence that they had a growth rate advantage over MFEG offspring in poor environments, since there were no significant MGT \times 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

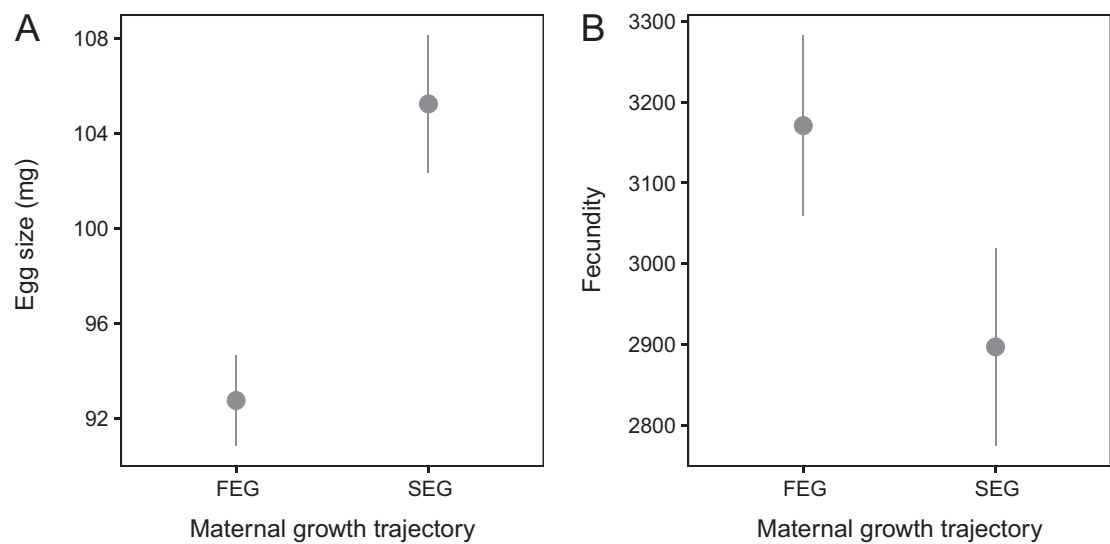


Figure 1: Prediction 1. *A*, Average size of eggs produced by female Atlantic salmon in relation to their early-life growth trajectory. *B*, Average fecundity of female Atlantic salmon in relation to their early-life growth trajectory. Error bars show ± 1 SE. FEG = fast early growth; SEG = slow early growth.

survived better than MFEG offspring when the density of older, larger 1+ salmon and trout was high (i.e., an MGT \times density interaction; fig. 3*B*). 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. 3*A*, 3*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, which ameliorated the negative effect of high 1+ densities (fig. 3*C*); this apparent difference in survival is unlikely to be attributable to emigration of experimental juveniles from low-nutrient (upstream) to high-nutrient (downstream) sites within each stream, since the overall recovery rates of experimental juveniles were similar between 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 effects model with stream fitted as a random intercept: 0.18 ± 0.19 ; $t = 0.99$, $P = .34$).

When considering egg size as a covariate in the survival analysis, we found that juveniles hatching from larger eggs had greater survival overall (fig. 4*A*, 4*B*), and this survival advantage increased with the density of 1+ salmonids (i.e., egg size \times density interaction; fig. 4*A*, 4*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. 4*A*), suggesting that moth-

ers 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 regardless

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 (± 1 SE)

Stream, treatment	<i>s</i>	SE	<i>C</i>	SE
Rogie Burn:				
High nutrient	.18	.15	-.084	.27
Low nutrient	.36 ⁺	.19	-.113	.35
Gleann Meinich:				
High nutrient	.59	.17	-.16	.30
Low nutrient	.39 [*]	.14	.16	.25
Corriemoillie:				
High nutrient	.048	.13	-.13	.24
Low nutrient	.17	.12	-.083	.22
Allt na Feithe Baine:				
High nutrient	.28 [*]	.11	-.12	.202
Low nutrient	.31 [*]	.12	-.0083	.22
Allt Gleann Sgathaich:				
High nutrient	.12	.12	-.26	.21
Low nutrient	-.015	.13	-.49 [*]	.23 [*]
Allt a Ghlinne:				
High nutrient	.14	.13	-.11	.24
Low nutrient	.41 [*]	.18	-.064	.32
Pooled:				
High nutrient	.20 [*]	.072	-.15	.13
Low nutrient	.26 [*]	.072	-.10	.13

⁺ $P \leq .10$.

^{*} $P < .05$.

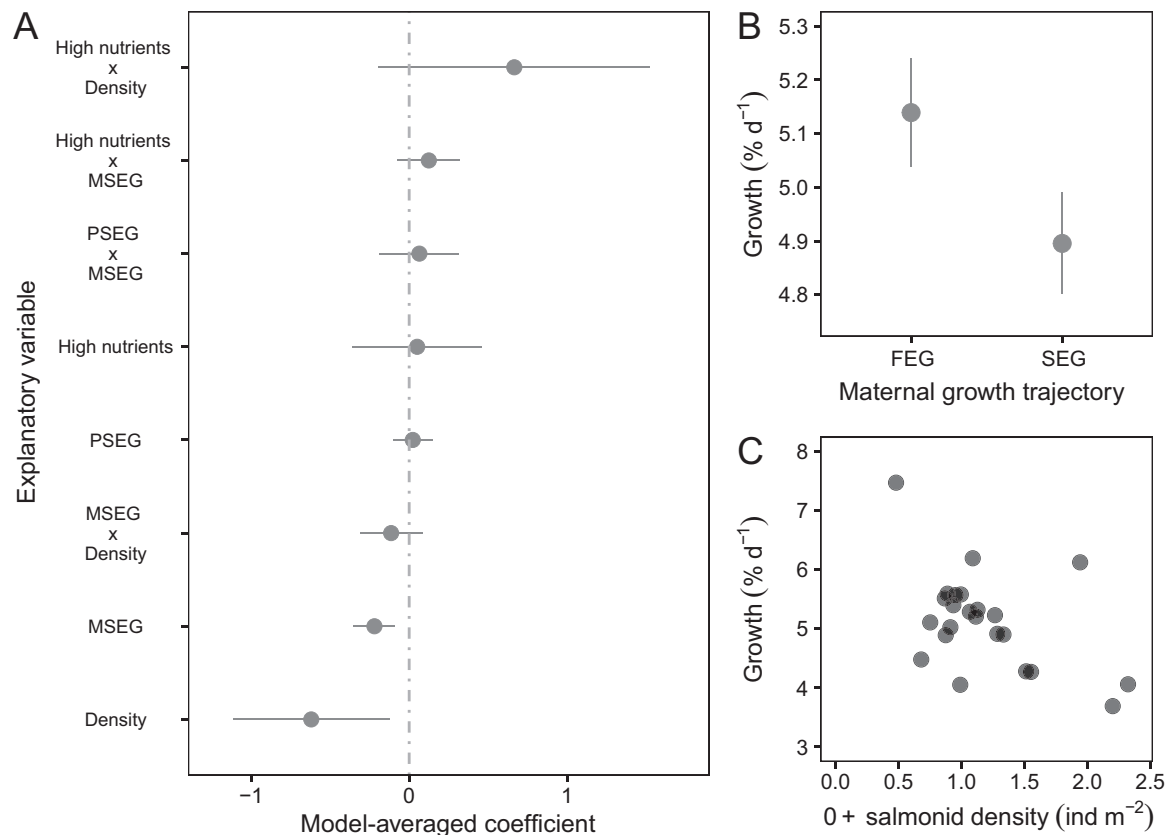


Figure 2: Prediction 2A. A, Model-averaged coefficients ($\pm 95\%$ confidence intervals) for linear mixed effects models describing variation in the growth rate (Ω % day $^{-1}$) of juvenile Atlantic salmon in relation to the density of 0+ salmonids present in a given electrofishing site, maternal and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

of whether egg size was accounted for in our analyses (figs. 3A, 4A). Neither PGT nor its interaction with MGT was observed to have any bearing on the relative support for predictions 2A, 2B, or 3 (see figs. 2A, 3A, 4A).

Discussion

The present study provides novel insight into the hypothesis that the production of relatively large offspring by mothers who 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 one hand, the growth and survival of offspring did not respond as predicted to the ad-

dition 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 MGT, with MFEG offspring surviving less well than MSEG offspring where salmonid densities are high, which is in line with our prediction.

Offspring growth was not associated with an interaction between MGT and either of our measures of environmental

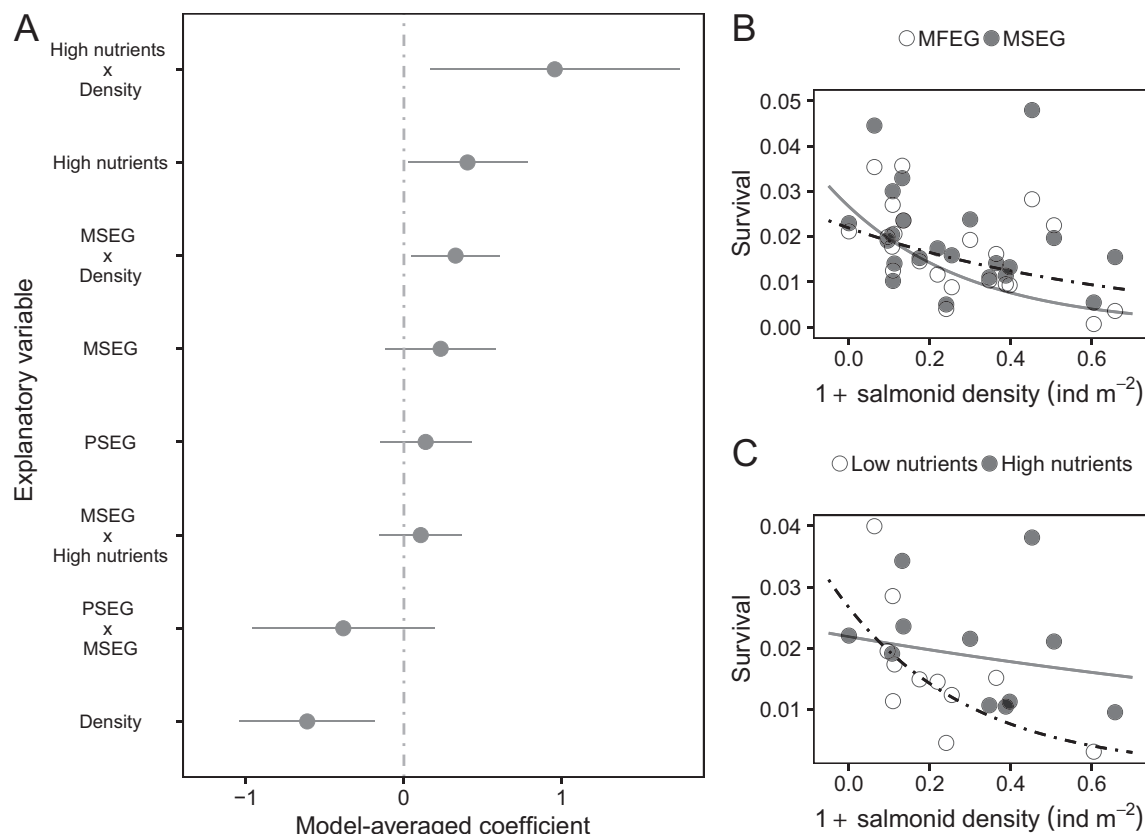


Figure 3: Prediction 2B. *A*, Model-averaged coefficients ($\pm 95\%$ confidence intervals) for generalized linear mixed effects models describing variation in the survival of juvenile Atlantic salmon in relation to the density of 1 + salmonids present in a given electrofishing site, maternal and paternal growth trajectories, and nutrient treatment. Note that model-averaged coefficients are presented for maternal slow-early-growth (MSEG) juveniles relative to maternal fast-early-growth (MFEG) juveniles, paternal slow-early-growth (PSEG) juveniles relative to paternal fast-early-growth (PFEG) juveniles, and low nutrients relative to high nutrients. 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). 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. 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 the 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 generalized linear mixed model 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). A color version of this figure is available online.

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, the correlation between MGT and offspring growth capacity (and potentially the subsequent pattern of investment in reproduction) likely arises from genetic adaptation, not plasticity. The results therefore provide significant insight into an otherwise enigmatic pat-

tern of phenotypic variation that has long been described in the literature (Thorpe et al. 1984; Perrin 1989; Morita et al. 1999; Taborsky 2006; 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. Thus, FEG/SEG phenotypes might result from

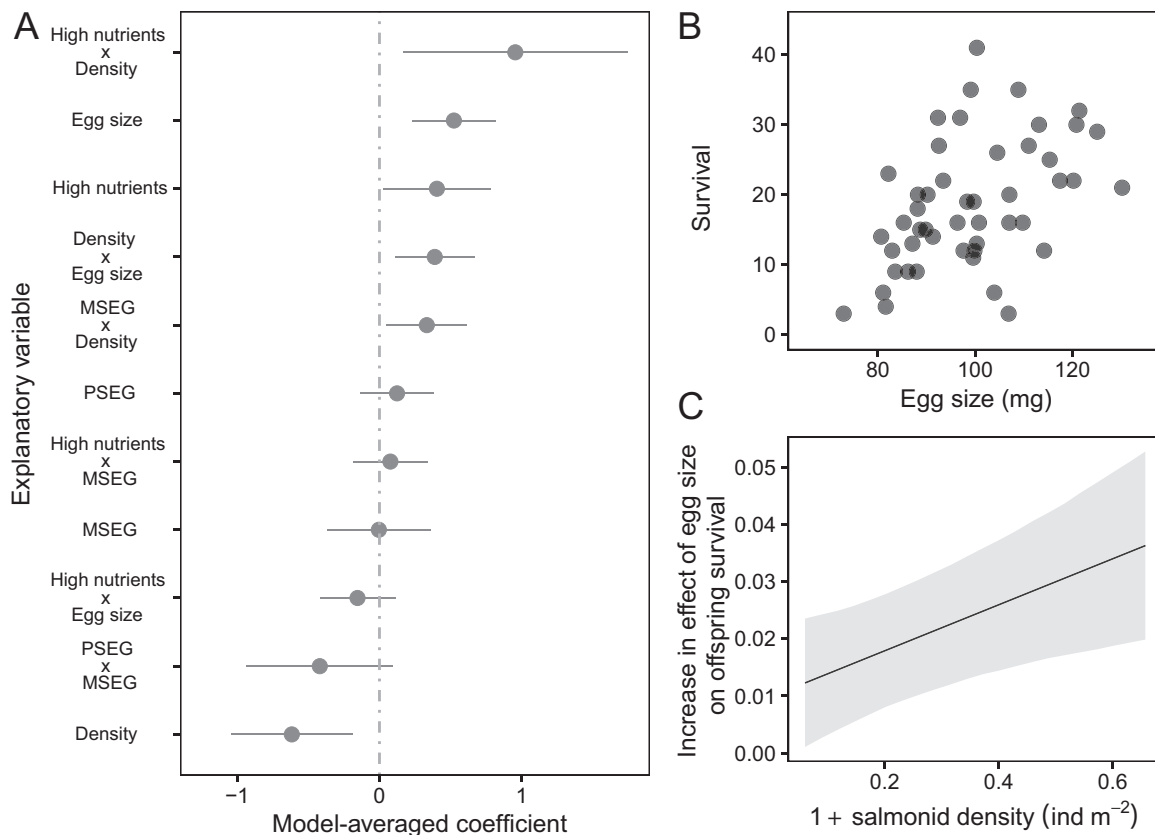


Figure 4: Prediction 3. A, Model-averaged coefficients ($\pm 95\%$ confidence intervals) for generalized linear mixed effects models describing variation in the survival of juvenile Atlantic salmon in relation to the density of 1+ salmonids present in a given electrofishing site, maternal and paternal growth trajectories, nutrient treatment, and average size of eggs from which they hatched. Note that model-averaged coefficients are presented for maternal slow-early-growth (MSEG) juveniles relative to maternal fast-early-growth (MFEG) juveniles, paternal slow-early-growth (PSEG) juveniles relative to paternal fast-early-growth (PFEG) juveniles, and low nutrients relative to high nutrients. 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 was produced with the interplot package (Hu 2018). Data showing MGT \times density and enrichment \times density interactions are not replotted here, as the model-averaged coefficients for these terms were quantitatively very similar to those displayed in figure 3A. A color version of this figure is available online.

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, because of the presence of overlapping year classes within a given stream, variation in the size and age structure of juvenile salmon could conceivably favor alternative FEG/SEG life histories that reflect contrasting positions along a slow-fast continuum of life-history variation (Ricklefs and Wikelski 2002; Dammhahn et al. 2018). Juvenile salmonids are territorial, and securing a high-quality territory helps ensure survival through the first growing season (Elliott 1989, 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 on

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 life span; 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 owing to their higher levels of aggression or to 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 number of adult carcasses around the spawning grounds) to support their relatively small fry during the critical transition to exogenous food. On the other hand, MSEG 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 on 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; Hutchings 1991; Einum and Fleming 1999). 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 (McGinley et al. 1987; Schultz 1991; Einum and Fleming 2004).

In this study, we investigated the hypothesis that the production of relatively large offspring by slower-growing mothers is a plastic response to a low-quality developmental environment. However, our data indicate that mothers that grew relatively quickly produce juveniles that also grow quickly irrespective of environmental quality, indi-

cating genetic rather than plastic inheritance of early growth rate and possibly the subsequent life history. While 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 generalize the fitness consequences of initial offspring size.

Acknowledgments

We thank J. Henry, the late M. Wyndham, and L. McKelvey for assistance with fieldwork and J. Mota-Velasco from Landcatch Natural Selection for performing the genotyping. We are also very appreciative of the detailed and constructive reviews provided by two reviewers and Associate Editor Jeff Leips. We dedicate this work to the memory of S. McKelvey, who passed away during the completion of this article. This work was supported by the Natural Environment Research Council (grant NE/I025182/1) and latterly by a European Research Council Advanced Grant (322784 to N.B.M.), a Marie Skłodowska-Curie Fellowship (MSCA-IF 658530 to T.B.), and the Norwegian Research Council Klimaforsk program (grant 244046 to T.B.). The work presented here was authorized by licenses from the United Kingdom home office and Scottish Natural Heritage.

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