

Genetic and maternal effects on juvenile survival and fitness-related traits in three populations of Atlantic salmon

Aimee Lee S. Houde, Craig A. Black, Chris C. Wilson, Trevor E. Pitcher, and Bryan D. Neff

Abstract: Although studies addressing natural selection have primarily focused on additive genetic effects because of their direct relationship with responses to selection, nonadditive genetic and maternal effects can also significantly influence phenotypes. We partitioned the phenotypic variance of survival and fitness-related traits in juvenile Atlantic salmon (*Salmo salar*) from three allopatric populations (LaHave, Sebago, and Saint-Jean) into additive genetic, nonadditive genetic, and maternal environmental effects using a full-factorial breeding design. We also modelled the potential increase in offspring performance if nonrandom mating (e.g., mate choice) is considered instead of random mating. The three populations exhibited significant differences in trait values as well as the genetic architecture of the traits. Nevertheless, nonadditive genetic and maternal environmental effects tended to be larger than the additive genetic effects. There was also a shift from maternal environmental to genetic effects during development in two of the populations. That is, maternal environmental effects were larger at early (egg and alevin) life stages, whereas nonadditive effects were larger at the later (fry) life stage. The amount of additive genetic effects was small, suggesting the traits will respond slowly to selection. We discuss how different maternal environmental effects across years may influence the genetic architecture of offspring traits.

Résumé : Si les études sur la sélection naturelle se sont principalement intéressées aux effets génétiques additifs en raison de leur lien direct avec les réactions à la sélection, les effets génétiques non additifs et les effets maternels peuvent également exercer une influence significative sur les phénotypes. Nous avons subdivisé la variance phénotypique de caractères associés à la survie et à l'aptitude chez des saumons atlantiques (*Salmo salar*) juvéniles de trois populations allopatriques (LaHave, Sebago et Saint-Jean) en des effets génétiques additifs, génétiques non additifs et reliés à l'environnement maternel, en utilisant un plan factoriel complet de l'accouplement. Nous avons également modélisé l'augmentation potentielle de la performance de la progéniture pour un scénario d'accouplement non aléatoire (p. ex. choix du partenaire) plutôt que d'accouplement aléatoire. Les trois populations présentaient des différences significatives en ce qui concerne la valeur et l'architecture génétique des caractères. Cela dit, les effets génétiques non additifs et les effets de l'environnement maternel avaient tendance à être plus grands que les effets génétiques additifs. En outre, dans deux des populations, les effets initiaux de l'environnement maternel cédaient le pas à des effets génétiques au cours du développement. Autrement dit, les effets de l'environnement maternel étaient plus forts aux premières étapes du cycle de vie (œufs et alevins vésiculés), alors que les effets non additifs étaient plus importants à l'étape plus tardive (fretin). La quantité des effets génétiques additifs était faible, donnant à penser que les caractères réagissent lentement à la sélection. Nous discutons de l'influence possible de différents effets de l'environnement maternel sur l'architecture génétique des caractères de la progéniture. [Traduit par la Rédaction]

Introduction

Quantitative genetic studies addressing responses to selection have primarily focused on additive genetic effects (Falconer and Mackay 1996). By contrast, the importance of nonadditive genetic effects on phenotypic variation and responses to natural selection has received comparatively little attention, potentially because of the difficulties associated with linking nonadditive genetic influences to selection outcomes (Lynch 1994; Neff and Pitcher 2005). Similarly, although substantial literature exists on maternal influences on life-history traits (e.g., Bernardo 1996; Green 2008), their role in population responses to selection has received less attention (Mousseau and Fox 1998; Wilson et al. 2005; Räsänen and Kruuk 2007). For example, nonadditive genetic variance can be converted to additive genetic variance, the material that can be

used by selection, during a bottleneck (Carson 1990; Neff and Pitcher 2008). Also, maternal effects (maternal additive genetic and maternal environmental) can modify the rate and direction of a change in response to selection (Mousseau and Fox 1998; Wilson et al. 2005; Räsänen and Kruuk 2007). Moreover, additive and nonadditive genetic effects can also be used to understand mating systems (reviewed by Neff and Pitcher 2005). Traits that are mainly influenced by additive genetic effects indicate the importance of beneficial alleles present in only certain parents, whereas traits that are mainly influenced by nonadditive genetic effects indicate the importance of the compatibility of alleles between parents. Such differences can govern mating patterns and affect the effective population size (e.g., Saccheri et al. 1998; also see Neff et al. 2011); for example, mate choice for compatible gene

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combinations can be an important mechanism for maintaining genetic diversity (Neff and Pitcher 2005) as well as offspring fitness (Pitcher and Neff 2006, 2007). Therefore, additive genetic, nonadditive genetic, and maternal effects, as well as mating systems, should all be considered when examining evolutionary potential.

The contributions of genetic and maternal environmental effects to phenotype can also shift during development. Maternal environmental components tend to be larger at early life stages because of the influence of maternal investment, such as egg quality, whereas genetic components tend to be larger at later life stages because greater organismal complexity and independence (Lindholm et al. 2006; Kruuk et al. 2008; Evans et al. 2010). For example, in mammals, maternal environmental effects typically decline from birth to adulthood, whereas additive genetic effects remain constant over this period (e.g., Wilson and Réale 2006) or increase during development (e.g., Cheverud et al. 1983).

We examined the phenotypic variance of survival and fitness-related traits at early life-history developmental stages (egg, alevin, and fry) in three populations of Atlantic salmon (*Salmo salar*). These populations are being considered for reintroduction into Lake Ontario (Dimond and Smitka 2005). Atlantic salmon were extirpated from Lake Ontario over 100 years ago (Crawford 2001), and decades of reintroduction attempts have yet to succeed in establishing a self-sustaining population (COSEWIC 2006, 2010). Three source populations were chosen for the reintroduction effort based on contrasting ecology and life-history traits (Dimond and Smitka 2005). We used a full-factorial quantitative genetic breeding design to partition phenotypic variance in survival and fitness-related traits at the early life stages to maternal environmental, additive, and nonadditive genetic effects. In a previous study, we examined the genetic architecture of survival and fitness-related traits for the LaHave and Sebago populations only (Houde et al. 2013). In that study, maternal environmental and genetic effects explained a mean of 52% of the phenotypic variance in the traits. The present study is novel because we are (i) assessing the repeatability of genetic architecture estimations for survival and fitness-related traits in the same environment, (ii) including the third candidate population (Lac Saint-Jean) for the first time, and (iii) modelling the potential increase in offspring performance under contrasting reproductive scenarios of nonrandom mating (e.g., mate choice) versus random mating. This latter analysis is valuable for directing conservation breeding programs, where random mating is most commonly used.

Materials and methods

Families

Adult broodstock fish from each source population were provided by the Ontario Ministry of Natural Resources and Forestry (OMNRF). Fertilized eggs from single-pair matings of wild Atlantic salmon from the LaHave River (hereafter referred to as LaHave), Nova Scotia (44°14'N, 64°20'W) were received in 1995, and subsequent generations were produced in captivity. Fertilized eggs from single-pair matings of wild Atlantic salmon from tributaries of Sebago Lake (Sebago), Maine (Panther River; 43°53'N, 70°27'W), and Lac Saint-Jean (Saint-Jean), Quebec (Rivière-aux-Saumons; 48°41'N, 72°30'W), were received in 2006 and 2007, respectively. For this study, 75 families each for the LaHave, Sebago, and Saint-Jean populations were produced in early November 2011 at the OMNRF Harwood Fish Culture Station (Harwood, Ontario) following the methods outlined in Pitcher and Neff (2006, 2007). Three groups of five females and five males from each population were mated in all possible combinations to produce a three-block 5 × 5 full-factorial breeding design (Lynch and Walsh 1998, p. 598). Subsamples of eggs ($n = 20$) from each female from only one family were measured for diameter (nearest 0.01 mm) using digital callipers and mass (nearest 0.0001 g) using a digital scale. The remain-

ing eggs of each family were randomly placed into two sections (replicates) of vertical incubation trays (tray $n = 29$ and section $n = 16$ per tray) at the OMNRF Codrington Research Facility (Codrington, Ontario), trying to keep within-family egg densities equal between sections. Digital photographs of the single layer of eggs in each section were taken and the number of eggs was calculated using ImageJ version 1.38 (NIH, Bethesda, Maryland, available at <http://rsb.info.nih.gov/ij/index.html>).

After hatching, the number of offspring within sections was counted. Owing to rearing space limitations, each family from one 5 × 5 block per population was moved to two separate tanks (replicates) after hatching (tank $n = 75$ and section $n = 2$ per tank). Offspring from the remaining two 5 × 5 blocks per population were pooled for release into the wild. Details of the rearing of the families are provided in Houde et al. (2013).

Survival and fitness-related traits

We measured four survival metrics, as direct measures of early life fitness: egg survival (fertilized egg to hatch, Day 0–74), alevin survival (posthatch until yolk sac absorption, Day 75–121), fry survival (yolk sac absorption until released into the wild, Day 122–186), and overall survival (fertilized egg until released into the wild). We also measured six traits that are known to be related to fitness in salmonids (Metcalfe and Thorpe 1992; Berg et al. 2001; Pakkasmaa et al. 2001; Koskinen et al. 2002): egg diameter and mass, body length and mass at hatch, body length and mass at yolk sac absorption. Details on the methodology to estimate these parameters are provided in Houde et al. (2013).

Statistical analysis of parental and population effects

All four survival and all six fitness-related traits were examined for population differences. Traits were also examined for individual parental effects (dam and (or) sire effects), position effects (tray and tank effects), and density effects using Akaike information criteria (AIC) forward step-wise model selection in R 3.0.1 (available at <http://www.r-project.org/>). Main effects were examined only, i.e., no interactions among effects. Linear models were used for fitness-related traits and binomial models were used for survival (i.e., 1 for alive and 0 for dead). Effects that did not change the AIC by more than 10 were considered to be poorly supported and were removed to produce the final model (Burnham and Anderson 2002). Remaining effects were tested for significance using an analysis of variance (ANOVA) for linear models and analysis of deviance (ANODEV) for binomial models. Statistical significance was set at $\alpha = 0.05$. Nonsignificant effects were removed from the final model.

If individual parental effects or position effects were retained by the model selection, the model was rebuilt using mixed effects that treated individual parental effects and position effects as random intercepts and examined population as a fixed effect. Density was also treated as a fixed effect when retained. Restricted Maximum Likelihood (REML) linear mixed-effects models were used for fitness-related traits and Laplace approximation binomial generalized linear mixed-effects models were used for survival using the lme4 package of R. The mixed-effects model output in the lme4 package does not produce significance values for fixed effects; therefore, significance of the population effect was determined using a likelihood ratio test between the full model and a reduced model without population.

Statistical analysis of genetic architecture

We also examined the genetic architecture of seven of the ten survival and fitness-related traits. The three traits that were not examined were overall survival, because we could not control for position effects, and the two egg traits (i.e., diameter and mass), because data were collected from fertilized eggs from only one family for each female, so there was missing information for the fertilized eggs of the remaining four families of each female.

Table 1. Summary of survival and fitness-related traits from three populations of Atlantic salmon (*Salmo salar*).

Trait	n	LaHave	n	Sebago	n	Saint-Jean
Egg traits						
Diameter (mm)	300	5.42±0.31	300	5.59±0.33	300	5.63±0.49
Mass (g)	300	0.0911±0.0171	300	0.1002±0.0182	300	0.1025±0.0273
Survival (%)						
Egg, Day 0–74	150	53.3±26.7	150	47.2±20.2	150	22.9±19.5
Alevin, Day 75–121	50	91.0±10.2	50	93.1±5.0	50	83.8±11.6
Fry, Day 122–186	50	28.1±17.7	50	55.6±23.9	—	—
Overall	25	13.8±9.9	25	29.1±17.6	—	—
Size traits						
Body length at hatch (mm)	250	24.8±1.3	250	27.3±1.5	200	27.1±1.4
Body mass at hatch (g)	250	0.108±0.017	250	0.154±0.028	200	0.139±0.023
Body length at yolk sac absorption (mm)	750	30.0±2.5	750	33.8±2.3	—	—
Body mass at yolk sac absorption (g)	750	0.262±0.073	750	0.407±0.088	—	—

Note: Displayed are the means ± 1 SD from 75 families (5 females × 5 males × 3 blocks) per population. Egg traits were based on 20 eggs per female. Egg survival numbers (n) represent the number of families per population by the total number of replicates: two per family. Alevin and fry survival numbers (n) represent one block of families per population (25 families) by the total number of replicates: two per family. Size traits at hatch were represented by five individuals per family replicate and at yolk sac absorption were represented by 15 individuals per family replicate (two replicates per family for one block per population).

A mixed-effects model was used to partition phenotypic variance using random effects for dam ID (V_D), maternal additive genetic and maternal environmental variance), sire ID (V_S , paternal additive genetic variance), and dam ID × sire ID ($V_{D \times S}$, nonadditive genetic variance). Position effects were always included as a random effect so as to not overestimate nonadditive genetic effects. Although position effects were treated as fixed effects for determining their influence on traits using model selection, in the present analyses, they were treated as random effects because they are a source of stochastic variation. Density effects were not included in the analysis because they came after individual parental effects for only two traits using model selection, suggesting that maternal environmental and genetic effects had larger influences on phenotypic variance than did density effects (see Results). Block effects were included as a random effect for egg survival. Individual estimates were used for all traits because within-family variation using family replicates can overestimate genetic effects (see Puurtinen et al. 2009; Neff et al. 2011). Significance of the variance components was determined by likelihood ratio tests as detailed above. The additive, nonadditive, and maternal environmental variance components were calculated based on Lynch and Walsh (1998, p. 509): $V_D = (1/4) V_A + V_M$; $V_S = (1/4) V_A$; and $V_{D \times S} = (1/4) V_N$. Negative variance components were set to a value of zero.

Variance component 95% confidence intervals (CI) were produced using a bootstrap method outlined in Houde et al. (2013). First, individuals were resampled with replacement within each family replicate until the original size was reproduced. Individuals were resampled to account for within-family variation, as resampling family replicates could overestimate genetic effects (Puurtinen et al. 2009). Second, additive, nonadditive, and maternal environmental variance components were calculated as a percentage of the phenotypic variance for the resampled data set (Lynch and Walsh 1998). The process was repeated 1000 times to produce a 95% CI for each trait. In addition, pairs of populations were compared by calculating for one population the proportion of comparisons that were either larger or smaller than the other population. The proportions served as one-tailed *p* values testing for pair-wise differences between populations.

Model of nonrandom mating

We constructed two models to examine the potential benefits of nonrandom mating (e.g., mate choice) on offspring traits: (i) random mating and (ii) optimal mating using the best male of a given number of males method outlined in Pitcher and Neff

(2007). The random model repeatedly selected a random female and “mated” her with a randomly selected male within each 5 × 5 block. The random model thus represents the average trait value of all the families. The optimal mating model repeatedly selected a random female and then chose the best mate from randomly sampled sets of two to five males within each 5 × 5 block. In each case, the female is assumed to “mate” with the male that would maximize the offspring fitness traits. For example, the female would mate with the male that would produce the highest offspring survival. The process was repeated 10 000 times for each sampled set of males for each trait, and the distribution of values was used to calculate a mean and standard error.

Results

Summary statistics of survival and the fitness-related traits are presented in Table 1 and supplementary Tables S1–S4¹. There was nearly 100% mortality for Saint-Jean offspring beyond the alevin stage. Thus, Saint-Jean offspring were not used in analyses beyond the alevin stage. Individual parental effects and position effects in the incubation trays and tanks had significant influences on survival and fitness-related traits for model selection (Table 2). These effects were subsequently treated as random effects in the mixed-effects models as detailed above. Density effects were also detected for body length and mass at hatch, but came after individual parental effects in their influence on these traits (Table 2).

On average, maternal environmental and genetic effects collectively explained 40% of the phenotypic variance of the traits (Fig. 1; Table S5¹). On average, nonadditive effects were larger than additive genetic effects for survival and the fitness-related traits. Specifically, nonadditive genetic effects explained a mean of 18%, additive genetic effects explained a mean of 6%, and maternal environmental effects explained a mean of 17% of the phenotypic variance across the traits. For traits related to egg quality (egg and alevin), maternal environmental effects explained a mean of 19% of the phenotypic variance, whereas genetic effects explained 11% of the variance. In contrast, for traits related to the fry stage, genetic effects, largely influenced by nonadditive effects, explained a mean of 12%, and maternal environmental effects explained 13%.

Survival

The populations differed in life-stage specific survival, although Sebago and LaHave did not differ in overall survival (Table 1).

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0472>.

Table 2. Model selection and population effect results for survival and fitness-related traits in three populations of Atlantic salmon (*Salmo salar*).

Trait	Model selection	Mixed-effects model: population effect, <i>p</i> value
Egg traits		
Diameter	dam ID	0.048
Mass	dam ID	0.048
Survival		
Egg, Day 0–74	dam ID + sire ID + tray ID	<0.001
Alevin, Day 75–121	dam ID + tank ID + sire ID	0.016
Fry, Day 122–186	tank ID + dam ID + sire ID	0.027
Overall	dam ID + sire ID	0.078
Size traits		
Body length at hatch	dam ID + sire ID + density	<0.001
Body mass at hatch	dam ID + sire ID + density	<0.001
Body length at yolk sac absorption	dam ID + tank ID + sire ID	<0.001
Body mass at yolk sac absorption	dam ID + tank ID + sire ID	<0.001

Note: All mixed-effects models contained a fixed effect for population. Mixed-effects models also contained a fixed effect for density and random effects for dam ID, sire ID, tray ID, and tank ID, if these effects were identified during model selection.

Sebago had larger egg and alevin survival than Saint-Jean, but not LaHave (Table 1). However, Sebago had larger fry survival than LaHave. Overall survival could not be compared for Saint-Jean versus the other populations due to insufficient fry survival (Table 1).

In all three populations, dam effects were significant for egg survival but not for alevin survival (except LaHave) and fry survival (Table S5¹). Sire effects were not significant for any population, with the exception of Sebago egg survival; similarly, dam × sire effects were only significant for egg and fry survival in the Sebago population. For the Saint-Jean population, maternal environmental effects were larger than genetic effects in their contribution to egg survival, but maternal environmental effects decreased during the alevin stage (Fig. 1). For the LaHave and Sebago populations, nonadditive genetic effects were larger than maternal environmental effects in their contribution to egg survival, and maternal environmental effects similarly decreased during the alevin and fry stages. These patterns resulted in differences between populations in the genetic architecture of offspring survival for additive and nonadditive genetic effects. Sebago had significantly higher additive genetic effects for egg survival than LaHave, followed by Saint-Jean (randomization routine one-tailed $p = 0.001$). LaHave had significantly higher nonadditive genetic effects for egg survival than Sebago and Saint-Jean, but lower nonadditive genetic effects for fry survival than Sebago (randomization routine one-tailed $p < 0.010$). Differences were also observed among the populations for maternal environmental effects. Saint-Jean had significantly higher maternal environmental effects for egg survival than LaHave, followed by Sebago, but lower maternal environmental effects for alevin survival than LaHave (randomization routine one-tailed $p = 0.001$).

Fitness-related traits

The populations differed at all of the six fitness-related traits that we measured (Table 2). Sebago had larger body mass at hatch than both LaHave and Saint-Jean (0.031 g, 22.8% of the mean) and larger body mass at yolk sac absorption than LaHave (0.145 g, 43.3%) (Table 1). Among populations, the differences for egg diameter, egg mass, body length at hatch, and body length at yolk sac absorption were generally small. Saint-Jean had larger egg diameter (0.21 mm, 3.8%) and mass (0.0114 g, 11.6%) than LaHave, but not Sebago. Sebago had a larger body length at hatch than both LaHave and Saint-Jean (1.4 mm, 5.1%) and a larger body length at yolk sac absorption than LaHave (3.8 mm, 11.9%).

Dam effects were significant for all three populations for body length and mass at hatch and for LaHave and Sebago for body length and mass at yolk sac absorption (Table S5¹). Sire effects on

the fitness-related traits were not significant in any population, whereas dam × sire effects were significant for LaHave body length at hatch only. Nonadditive effects explained more of the phenotypic variance than maternal environmental effects for body mass at hatch (except Saint-Jean), whereas the opposite was observed for body length at hatch (except LaHave) (Fig. 1). Also, nonadditive effects explained more of the phenotypic variance than maternal environmental effects for Sebago body length and mass at yolk absorption, whereas the opposite was observed for LaHave. There were significant differences among the populations for all the genetic architecture values for the fitness-related traits. Sebago had higher additive genetic effects for all four fitness-related traits than LaHave (randomization routine one-tailed $p < 0.018$ for all) but not Saint-Jean (randomization routine one-tailed $p > 0.102$ for all). Differences were also observed among the populations for maternal environmental effects. LaHave had higher maternal environmental effects for all four fitness-related traits than Sebago (randomization routine one-tailed $p < 0.040$ for all) but not Saint-Jean (randomization routine one-tailed $p > 0.098$ for all).

Nonrandom mating

The model of optimal nonrandom mating indicates that offspring survival and size can be increased through appropriate pairings, as compared with random mating (Fig. 2). Egg survival (average across populations: 4.9% to 8.1%), alevin survival (4.7% to 5.8%), and fry survival (6.1% to 11.7%) all increase substantially when optimally mating females with a choice of two to five males. Alevin mass (7.5% to 11.2%, 0.010 to 0.015 g), alevin length (1.3% to 2.4%, 0.35 to 0.63 mm), fry mass (3.3% to 6.9%, 0.011 to 0.023 g), and fry length (1.0% to 2.2%, 0.31 to 0.70 mm) also increase when optimally mating males and females. Over the entire developmental period examined (egg to fry), offspring survival and body size can be increased by an average of 8.5% and 5.7%, respectively, if females are mated with the best of the available males.

Discussion

This study provides evidence for shifts in the genetic architecture of survival and fitness-related traits during early life-history stages of three populations of Atlantic salmon reared under shared conditions. Maternal environmental and genetic effects collectively explained about half of the phenotypic variance of the traits, and nonadditive genetic effects tended to be larger than additive genetic effects. Our results, therefore, suggest that additive genetic effects may not be as important as maternal environmental and

Fig. 1. The maternal environmental, additive, and nonadditive effects underlying phenotypic variance of survival and fitness-related traits in three populations of Atlantic salmon (*Salmo salar*): (a) LaHave, (b) Sebago, and (c) Saint-Jean. Displayed are the median and 95% confidence intervals for maternal environmental, additive genetic, and nonadditive genetic effects (see text for details).

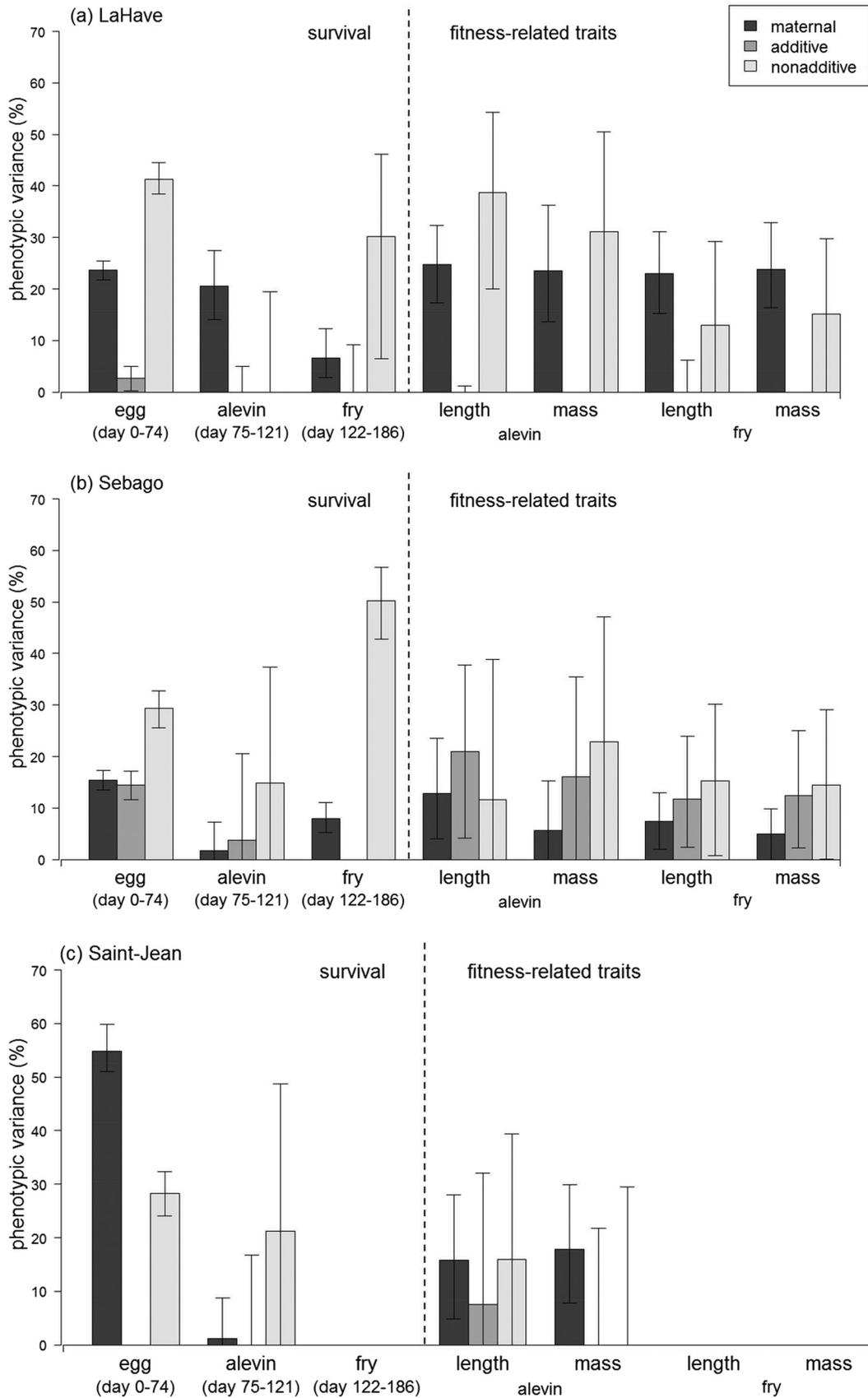
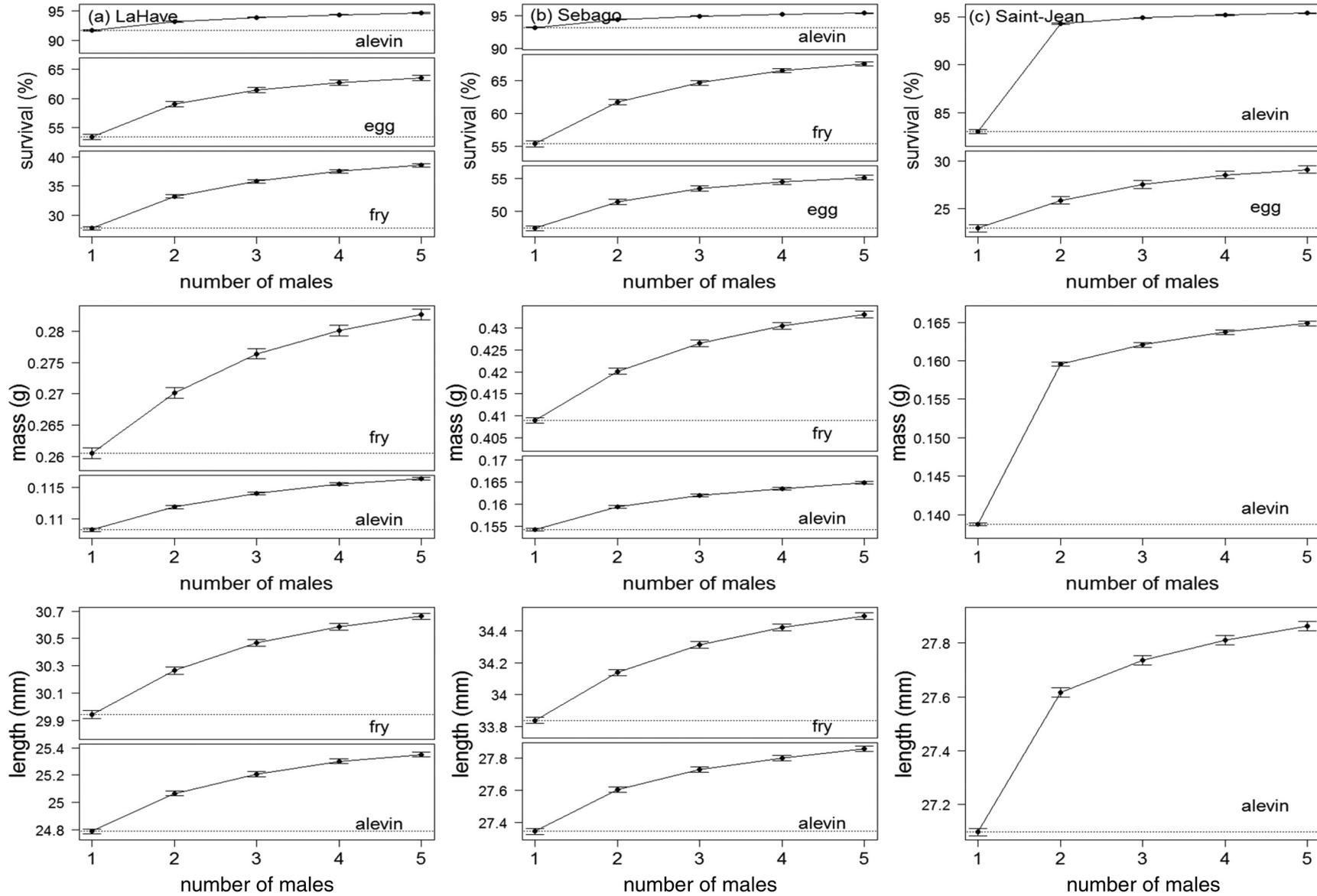


Fig. 2. Model results demonstrating the potential increase in survival, body mass, and body length given nonrandom mating for Atlantic salmon (*Salmo salar*) in the three populations: (a) LaHave, (b) Sebago, and (c) Saint-Jean. Displayed are the means \pm 2SE for traits. The dotted lines represent the random model (average of the trait for females randomly mated to a single male); in other words the random model represents the average trait value of all the families. The solid lines represent the optimal model (potential benefit of selecting from up to five males based on maximizing trait values).



nonadditive genetic effects for survival and fitness-related traits at these early life stages (also see Crnokrak and Roff 1995; Falconer and Mackay 1996; Roff and Emerson 2006). In particular, maternal environmental effects were larger at early (egg and alevin) life stages, whereas nonadditive effects were larger at the later (fry) life stage. The results suggest an ontogenetic shift in their relative influences, with genetic effects, both nonadditive and additive, becoming increasingly important with advancing life stage. Moreover, although maternal environmental effects and nonadditive genetic effects can influence the responses to selection of traits under certain circumstances (Carson 1990; Räsänen and Kruuk 2007), the small amounts of additive genetic effects we found in survival and fitness-related traits suggest that they are unlikely to respond rapidly to selective pressures (Falconer and Mackay 1996).

Assessing variation in the genetic architecture of survival and fitness-related traits is important for drawing conclusions, and rarely has a full factorial design been examined more than once in the same species and populations (e.g., Wedekind et al. 2001, 2008). Part of the objectives of the current study was to examine the repeatability of the results from our previous study (Houde et al. 2013) by producing new families using new parents. The LaHave and Sebago populations were not significantly different in trait values and the genetic architecture of the traits in the previous study (Houde et al. 2013), but all three populations differed in the values for survival and fitness-related traits as well as the genetic architecture of those traits in the present study. Because the rearing environments across the two studies were nearly identical, the population differences in trait values may be associated with differences in the genetic architecture underlying the traits. Indeed, in the present study, we found that the three populations differed in the genetic architecture, mainly nonadditive genetic effects, of all seven traits that could be examined. Other studies have also found that populations can differ in the amount of nonadditive genetic effects that explain traits (e.g., Waldmann 2001; Evans and Neff 2009). Given that the LaHave population has been in captive breeding longer than the Sebago and the Saint-Jean populations, the results might also reflect genetic changes caused by selection in a captive environment, at least for that population. Because nonadditive genetic effects result from specific pairings of gametes (e.g., genotype effects), large quantitative breeding designs are needed to fully detail their effects (see Lynch and Walsh 1998; Neff et al. 2011). Some caution is otherwise warranted when interpreting results, including those of our studies, because of the susceptibility to sampling error. The three Atlantic salmon populations also differed in the maternal environmental effects for six out of the seven traits. One important maternal environmental effect is dam age: older salmonid females generally produce larger offspring with higher survival relative to younger salmonids (Green 2008). In Houde et al. (2013), the LaHave dams were a year older than the Sebago dams, whereas in the present study the dams were the same age in all populations. Differences in maternal environmental effects and nonadditive genetic effects might thus explain the variation in population comparisons of trait values across studies. Moreover, they highlight the need for repeatability in studies of genetic architecture to make robust conclusions.

The large nonadditive genetic effects in both the present and previous study (Houde et al. 2013) indicate the importance of the compatibility of alleles between parents for offspring fitness. Such compatibility has been of recent interest in the field of behavioural ecology in the context of mate choice (reviewed in Neff and Pitcher 2005). Our optimal mating model suggests that allowing nonrandom mating can increase offspring survival by up to 6% relative to random mating. Observational mate choice studies comparing the offspring produced by natural matings with those produced by random matings have also found similar increases in survival and fitness-related traits for the offspring produced by natural matings in Atlantic salmon (e.g., Consuegra and Garcia de

Leaniz 2008; also see Agbali et al. 2010). This concurrence indicates that females do assess genetic compatibility. Moreover, breeding programs should consider nonadditive genetic effects in their mating designs as a way to increase offspring fitness.

Interestingly, we found that the Saint-Jean population had low survival during the early life stage. Although we did not examine the Saint-Jean population in the previous study (Houde et al. 2013), a similarly high mortality for this population has been observed at the Ontario Ministry of Natural Resources and Forestry fish culture facilities. The Saint-Jean broodstock we used are first-generation descendants from the source (natural) population, so the offspring may be subject to a strong “domestication” selection event. The first generation in captivity can cause a large decline in fitness with lesser declines in fitness in subsequent generations in captivity (e.g., Araki et al. 2007, reviewed by Fraser 2008). The other two populations we used have been exposed to captive rearing over the early part of the life cycle (Sebago) and entire life cycle (LaHave). Another potential explanation is population differences in thermal tolerance. The Saint-Jean population experiences the coldest spring and summer temperatures (mean, 18.0 °C) relative to the other two populations (LaHave: 20.0 °C; Sebago: 21.5 °C), which have values closer to those of southern Ontario streams, such as the source stream for the rearing facility used in our study (Kayla Gradil, University of Western Ontario, unpublished data). However, a study indicates that Atlantic salmon have a high degree of cardiac plasticity for thermal tolerance (Anttila et al. 2014), so this explanation seems less likely to explain the low survivorship of the Saint-Jean population. If the low survivorship is in fact a result of a selection event in the move to captivity, then subsequent generations should show an increase in performance.

In conclusion, our results have described the components explaining the phenotypic variance of survival and fitness-related traits during the early life stages of three Atlantic salmon populations. Our results here and those of Houde et al. (2013) support a shift from maternal environmental effects to genetic effects during development and highlight the importance of nonadditive genetic effects in explaining the phenotypic variance of traits. The variability in the both trait values and the genetic architecture of the traits across our two studies may reflect effects of dam age (a maternal environmental effect) and nonadditive genetic effects. This variability suggests some level of caution when interpreting results from one study. Finally, the amount of additive genetic effects was small, suggesting a weak response to any kind of direction selection on the traits.

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