



Early-life fitness trait variation among divergent European and North American farmed and Newfoundland wild Atlantic salmon populations

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ABSTRACT: It has long been clear that interbreeding between domesticated and wild Atlantic salmon can lead to negative fitness consequences for native populations. Few studies, however, have examined these consequences at critical early life stages, particularly in the context of distinct geographical and ancestral relationships among populations as well domestication selection. In Newfoundland (NF), Canada, while the majority of aquaculture sites use the North American (NA) Saint John River strain, site-specific permission has been granted to farm a strain of European origin (EO). We designed a common-garden experiment to compare fitness-related traits (e.g. development time, survival, size and growth) at different early-life stages (eye development, hatch and yolk absorption) among EO and NA farmed, 2 NF wild and F₁ hybrid groups. Significant differences ($p < 0.001$) were observed in development time, survival, growth and energy conversion among farmed, F₁ hybrid and wild populations. While pure populations (farmed and wild) differed amongst one another, we found few differences in fitness-related traits between F₁ hybrids and their maternal wild/farmed strains. This suggests that the early-life fitness consequences of F₁ hybridization will be largely manifested through the action of maternal effects. Additionally, significant associations between the maternal effects of egg size and alevin development time, size, survival, growth, condition and energy conversion efficiency were found. These findings suggest that early-life fitness-related trait differences among farmed, wild and their related F₁ hybrids are generated by the geographic and ancestral relationship and maternal effects of egg size and less so by domestication selection.

KEY WORDS: Early-life development · Fitness-related traits · Hybridization · *Salmo salar* · Farmed–wild salmon interaction · Maternal effect · Egg size

1. INTRODUCTION

It is increasingly clear that interactions between domesticated and wild organisms have the potential to lead to negative effects on wild populations, and as such, are of concern (Rhymer & Simberloff 1996,

Fleming & Petersson 2001, Ellstrand 2003, Laikre et al. 2010, Frankham et al. 2011, Glover et al. 2017). Successful interbreeding between domestic and wild conspecifics may result in the loss of adaptive genetic variation with maladaptive fitness consequences for wild populations. These fitness effects may become

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lasting within the wild population should the hybrids themselves successfully reproduce, leading to introgression (Edmands 2002, 2007, Garcia de Leaniz et al. 2007, Reed et al. 2015). The Atlantic salmon *Salmo salar* is one of the species for which there are concerns that successful breeding of escaped domesticated individuals and the resultant hybridization with native individuals will cause ecological and genetic impacts on wild populations and threaten local adaptation (McGinnity et al. 1997, 2003, Fleming et al. 2000, Fraser et al. 2011, Skaala et al. 2012, 2019, Bradbury et al. 2020).

Farmed salmon are often genetically distinct from wild counterparts because of geographical origin (Gjedrem 2010), founder effects (Skaala et al. 2006), genetic drift (Glover et al. 2012, 2013) and, especially, domestication selection in captivity (Solberg et al. 2013, Harvey et al. 2016). Directed selection for economically important traits (e.g. faster growth, delayed maturation, disease resistance) in combination with unintentional and relaxed selection on non-target traits (e.g. aggression, risk aversion, feeding behaviour) can lead to rapid genetic changes in farm strains (Einum & Fleming 1997, Fleming & Einum 1997, Huntingford & Adams 2005, Houde et al. 2010a,b, Debes & Hutchings 2014, Perry et al. 2019, Solberg et al. 2020). This has, for example, resulted in farmed salmon displaying a growth rate that is over 2- to 3-fold higher than that of wild conspecifics reared under identical culture environments (Glover et al. 2018). In contrast to farm strains, wild salmon populations are genetically structured, with substantial genetic differences among populations at multiple spatial scales (Verspoor et al. 2005, Garcia de Leaniz et al. 2007, Bourret et al. 2013). Gene flow from escaped farmed to wild salmon could rapidly reduce the genetic diversity and local adaptation inherent in wild populations (Taylor 1991, Hindar et al. 2006, Fraser et al. 2011). Introgressive hybridization between escaped farmed and wild salmon may then lead to reduced fitness in the wild (Sylvester et al. 2019). Cultured salmon have lower fitness in the wild, and empirical evidence has mounted that farmed-wild hybrids may also have reduced survival (McGinnity et al. 2003, Tymchuk et al. 2007, Skaala et al. 2012, 2019). Likewise, offspring of escaped farmed and hybrid fish may compete with wild salmon for food, habitat and other resources, thereby potentially altering the genetics and depressing the numbers and productivity of wild salmon (Fleming et al. 2000, McGinnity et al. 2003, Sundt-Hansen et al. 2015, Robertsen et al. 2019, Bradbury et al. 2020).

Understanding the ultimate impact of interbreeding between wild and escaped farm salmon requires measures of reproductive and post-reproductive success following interaction. For instance, the timing of (i.e. phenology) and size at early life stages can have important fitness consequences for juvenile salmonids. Juveniles that emerge relatively sooner or are larger at emergence can have a competitive advantage over smaller conspecifics in the establishment of a feeding territory, which in turn increases their growth opportunities and survival probability (Metcalfe & Thorpe 1992, Einum & Fleming 2000a). Hence, spawning and development time in wild populations is believed to be adapted to seasonal resource availability in order to secure optimal time of hatch and alevin emergence (Brannon 1987, Webb & McLay 1996, Einum & Fleming 2000a). In the domestic environment, on the other hand, the reduction in natural selective pressure may allow for both early and late onset of spawning and/or prolonged spawning time, which may increase development time variance (Solberg et al. 2014). How the patterns of domestication selection may impact early-life development time in salmon originating from differing strains and geographic regions remains unknown.

Empirical evidence suggests that traits expressed during early life tend to be strongly influenced by maternal effects (Sargent et al. 1987, Einum & Fleming 1999, 2004, Houde et al. 2011, 2015, Thorn & Morbey 2018). However, maternal influences on early life-history traits are driven by trade-offs faced by mothers and shaped by environmental conditions (Smith & Fretwell 1974, Einum & Fleming 2000b). Furthermore, the trade-off between egg size and fecundity can vary by female size (Hendry et al. 2001, Hendry & Day 2003). These relationships among female size, egg size and offspring fitness can be scaled up to generate hypotheses describing influences of selection on female and egg size at the population level. Taken together, a potentially complex set of interacting selective pressures act to maximize female reproductive fitness in terms of optimum number and size of eggs produced that in turn influences offspring fitness through alevin and fry development, growth and survival and energy utilization patterns.

Hybridization is expected to lead to a reduction in fitness during early life stages, with increasing genetic divergence between parental populations, their origin and patterns of domestication (Edmands 1999, Barton 2001, Frankham et al. 2002, Neff 2004, Baskett & Waples 2013, Huisman & Tufto 2013). At present, salmon aquaculture practices in Atlantic Canada are using farmed strains that originate from

the Saint John River, New Brunswick (NB). A recent approval has also been granted to allow culture, as triploids, of a farm strain from Europe (hereafter 'EO') which was domesticated from wild Norwegian populations, to be farmed in Newfoundland (NF), Canada. Evidence indicates that the North American farmed strain (Saint John River strain; hereafter 'NA') and EO farmed strain (Norwegian) are highly divergent genetically ($F_{st} > 0.40$; Jeffery et al. 2018, S. J. Lehnert pers. comm.). Although phenotypic and genetic differences exist among wild salmon populations within NF (e.g. $F_{st} = 0.12$ between Northeast Placentia and Garnish River populations; S. J. Lehnert pers. comm.), the divergence between NF wild and NA farmed salmon populations is larger ($F_{st} = 0.14\text{--}0.20$; see Bradbury et al. 2018). It has already been documented that if a portion of non-triploid EO farmed salmon escape and breed successfully, they will interact genetically and ecologically with wild populations (O'Reilly et al. 2006). The outcome of genetic and ecological interactions of the EO farmed strain (compared to NA farmed strain) with local NF wild populations is still unknown and may depend on the genetic differences between these farm strains and local wild populations.

Here, we designed a common-garden experiment (i.e. examining cross types under common environmental conditions) to compare early-life development time, size, growth and survival of EO and NA farm strains with NF wild fish and conspecific hybrids.

We hypothesized that (1) both EO and NA farm fish will exhibit similar patterns of fitness trait differences (development time, size, growth and survival) relative to wild fish; (2) the early-life fitness trait differences will be reflected by their geographic and ancestral relationships; (3) hybrids will display altered fitness traits relative to wild and farm fish; and (4) the association between maternal effects of egg size and early-life fitness traits will differ among EO and NA farmed, NF wild salmon and F_1 hybrids.

2. MATERIALS AND METHODS

2.1. Parental populations and crosses

The experiments were conducted across 2 years with 2 cohorts of fish. Crosses were created using salmon gametes collected from 4 base populations (see Fig. 1 for the geographical origin of study populations; modified from Islam et al. 2020). Farm (EO) was a Norwegian farm strain, produced in an Icelandic facility (StofnFiskur), that had been recently approved for aquaculture as triploids in southern NF. Diploid gametes were transported by air from Iceland to St John's, NF, and crosses were generated within 24 h of stripping under the authority of an experimental permit. Farm (NA), a major aquaculture strain in Atlantic Canada, originated from the Saint John River, NB. Farm (NA) gametes were pro-

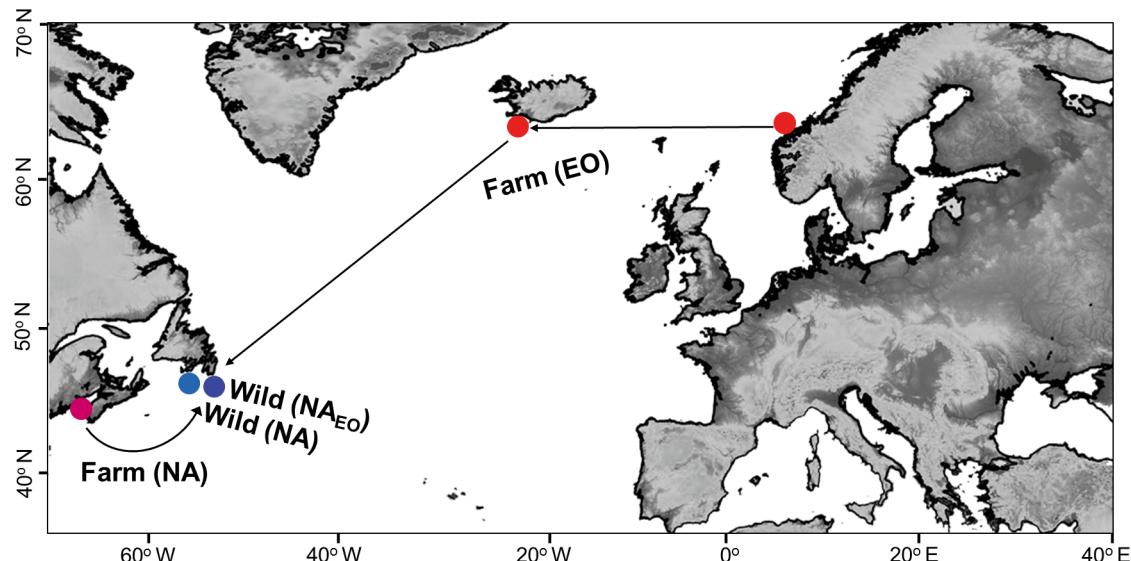


Fig. 1. Approximate geographical origin of wild (Wild [NA] and Wild [NA_{EO}]) populations and farmed (Farm [NA] and Farm [EO]) strains of Atlantic salmon. The Farm (EO) strain (StofnFiskur) derives from Norwegian strains that is produced in an Icelandic facility (adapted from Islam et al. 2020)

vided by Northern Harvest, a local aquaculture company with operations on the south coast of NF. The wild population for the 2015 cohort, which derived from the Northeast Placentia River, NF (47.2408° N, 53.9566° W), has a signal of EO ancestry (hereafter 'Wild [NA_{EO}]'). These fish were captured at a fishway facility and transported on 27 July 2015 to the Ocean Science Centre (OSC; Memorial University of Newfoundland), where they were held in broodstock tanks until performing the crosses. This population shows evidence of EO introgression because of historical trans-Atlantic straying and colonization in southeastern NF, Canada (~10 000 yr before present; see Bradbury et al. 2015). The wild population for the 2016 cohort (hereafter 'Wild [NA]'), which derived from the Garnish River, NF (47.2348° N; 55.3615° W), were collected at a salmon fence facility and transported to the OSC on 9 August 2016, where they were held in broodstock tanks until crossing. The 2015 cohort of crosses was generated between 20 November and 5 December 2015. Six cross types were generated to produce a total of 76 families: (1) 20 Farm (NA); (2) 11 Wild (NA_{EO}); (3) 13 F₁ Farm (NA)(♀)-x-Wild (NA_{EO})(♂) hybrid (referred to as 'Hyb [NA_{f_o}]'); (4) 10 Farm15 (EO); (5) 12 F₁ Farm (EO)(♂)-x-Wild (NA_{EO})(♀) hybrid (referred to as 'Hyb15 [EO_{w_o}]'); and (6) 10 F₁ Farm (EO)(♀)-x-Wild (NA_{EO})(♂) hybrid (referred to as 'Hyb15 [EO_{f_o}]'). The 2016 cohort was generated on 27 November 2016. Four cross types were generated to produce a total of 40 families: (1) 10 Farm16 (EO) (again gametes were collected from the Icelandic facility; the same strain which was used for the 2015 cohort); (2) 10 Wild (NA); (3) 10 F₁ Farm (EO)(♂)-x-Wild (NA)(♀) hybrid (referred to as 'Hyb16 [EO_{w_o}]'); and (4) 10 F₁ Farm (EO)(♀)-x-Wild (NA)(♂) hybrid (referred to as 'Hyb16 [EO_{f_o}]') (see Fig. 2 for schematic crossing design). Crosses for the 2015 and 2016 cohorts were conducted and reared in Heath-tray incubation facilities at the OSC. Biological information about the parental salmon used in the crosses is provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/q013p323_supp.pdf.

2.2. Experimental protocol

Experimental conditions and protocols were the same between years.

Following fertilization, the eggs were water-hardened and disinfected with 0.5% Ovadine (Syndel) for 30 min, which is not expected to affect egg survival (Fowler & Banks 1991). Fertilized eggs were then incubated in Heath trays, with each family placed within an individual basket, and raised under common environmental conditions (ambient water temperature: $3.1\text{--}7.9^{\circ}\text{C}$; pH: 5.7–6.2; dissolved oxygen: 8.0–8.5 mg l⁻¹). To minimize density effects, each family consisted of ca. 500 eggs. Dead and unfertilized eggs were counted and removed every 2–3 d. As the eggs hatched, the number of alevins were counted daily, and at 50% hatch, 10 alevins family⁻¹ were weighed and photographed digitally to determine yolk sac dimensions and total length (using ImageJ; Rasband 2014). Similarly, at yolk sac absorption, 10 randomly chosen fry from each family were photographed for total length and weighed. All animals were treated following the guidelines provided by the Canadian Council on Animal Care during holding and experimentation, and approval was granted by the Memorial University Animal Care Committee (15-21-IF).

2.3. Fitness-related trait differentiation

We first compared maternal body length and egg size and then quantified a series of traits that are known to be linked to early-life fitness in salmonids:

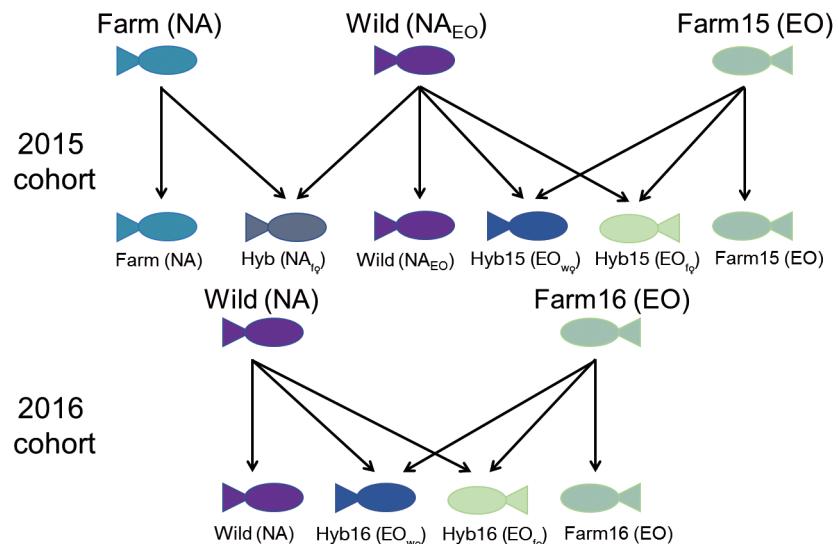


Fig. 2. Schematic of crossing design among wild (Wild [NA] and Wild [NA_{EO}]) populations and farmed (Farm [NA] and Farm [EO]) strains of Atlantic salmon. For the 2015 cohort, the number of generated families was 20 Farm (NA); 13 Hyb (NA_{f_o}); 11 Wild (NA_{EO}); 12 Hyb15 (EO_{w_o}); 10 Hyb15 (EO_{f_o}); and 10 Farm15 (EO). For the 2016 cohort, 10 families of each cross type were generated

development time, survival, size, specific growth rate (SGR), condition factor, yolk sac volume and yolk sac conversion efficiency (YCE) (Metcalfe & Thorpe 1992, Koskinen et al. 2002, Fraser et al. 2010a, Houde et al. 2013). Development time was measured in cumulative degree-days ($DDs = \sum^{\circ}C d^{-1}$) from fertilization to the eyed stage (i.e. when black dots representing the eyes first appear), eyed to hatch and hatch to yolk absorption. SGR of length (SGR_{length}) and mass (SGR_{mass}) were calculated as $100 \times [\ln(\text{body length or mass at yolk sac absorption}) - \ln(\text{body length or mass at hatch})] / \sum^{\circ}C d^{-1}$ (Koskinen et al. 2002, Houde et al. 2013). Fulton's body condition factors ($K = 100 \times (\text{mass} / \text{length}^3)$) were calculated separately at hatch and at yolk absorption (Robinson et al. 2008). Yolk sac volume was calculated as yolk sac length \times yolk sac width² $\times \pi / 6$ (Koskinen et al. 2002, Houde et al. 2013), and YCE was calculated as $(\text{body length at yolk sac absorption} - \text{body length at hatch}) / \text{yolk sac volume}$ (Fraser et al. 2010a, Houde et al. 2013).

2.4. Statistical analyses

All statistical analyses were performed in R version 4.0.5 (R Core Team 2021). Statistical significance was inferred if $p < 0.05$ after sequential Bonferroni adjustment (Rice 1989). All data were checked visually (using Q-Q plots and histograms), and a Shapiro-Wilks test was also applied to examine normality (Crawley 2005). A Bartlett test was performed to check the constancy of variance, and homoscedasticity was checked visually (using residuals vs. fitted values) (Crawley 2005).

Overall development time, length and mass at yolk absorption, SGR_{length} and SGR_{mass} , condition factor at yolk absorption, yolk sac volume and YCE were analysed using linear mixed-effects (LME) models with the 'lme4' package (Bates et al. 2015). Cross type was included as a categorical fixed effect and egg size as a continuous fixed covariate. Maternal identity (dam), paternal identity (sire) and Heath tray unit (for position effect) were included as random intercepts. Mass data were \log_{10} transformed. The fitted final model was selected from the full model with the 'lmerTest' package, using the 'step' function, which allowed for automatic model selection (Kuznetsova et al. 2017). This function performed backwards selection; non-significant random covariates were eliminated first followed by the removal of non-significant fixed covariates. Non-significant interaction terms were removed before the fixed covariates, and if significant interaction terms were found, all fixed co-

variates were included in the final model, regardless of their significance level. While significance values for the fixed effects were obtained using an *F*-test based on Satterthwaite's approximation, the p-values for random effects were estimated using likelihood ratio tests (LRTs). The fitted final model was confirmed by using plots of the model residuals, and the normality of the fitted model residuals was confirmed visually using histograms.

Overall survival was analysed using a generalized linear mixed-effects model (GLMM) with a binomial distribution (logit-link function), again with the 'lme4' package (Bates et al. 2015) using Laplace approximation. Cross type was included as a categorical fixed effect and egg size as a continuous fixed covariate. Again, dam, sire and Heath tray unit were included as random intercepts. Non-significant interaction terms and covariates were removed backwards stepwise using LRTs. The model residual plots and normality check were confirmed for the final model, as for the development time, length and mass data.

Estimated marginal means (see Table S2) and Tukey-adjusted post hoc multiple comparisons (using Kenward-Roger's degrees-of-freedom method) were carried out using the 'emmeans' package (Lenth et al. 2018). This test estimated all pairwise cross type contrasts (see Tables S3 & S4) and reported parameter estimates, *t*-values (for normally distributed data), *z*-values (for binary data) and *p*-values.

3. RESULTS

3.1. Maternal body length and egg size

Overall, maternal body length varied significantly among populations ($p < 0.001$; Table 1, Fig. 3). Farm (EO) females were longer than Farm (NA) females in both years, while both farm types were longer than both wild (Wild [NA_{EO}] and Wild [NA]) types. However, there was no difference between wild types (Table 1, Fig. 3). Generally, larger females produced larger eggs than smaller females ($p < 0.001$; Table 1, Fig. 3). However, despite Farm (EO) females of both cohorts being of similar sizes, egg size of Farm15 (EO) was smaller than that of Farm16 (EO) and did not differ from Farm (NA). The relationship between maternal body length and egg size was positive within all populations (Farm [NA]: $r = 0.87$, $p < 0.001$; Wild [NA]: $r = 0.78$, $p < 0.05$; Farm16 [EO]: $r = 0.89$, $p < 0.001$; Wild [NA_{EO}]: $r = 0.91$, $p > 0.05$; Farm15 [EO]: $r = 0.39$, $p > 0.05$).

Table 1. Multiple comparisons of family-level mean differences in fitness-related traits among different Atlantic salmon cross types from the 2015 and 2016 cohorts (Tukey-adjusted pairwise comparisons). The p-values are represented by significance level, whereby *** $p < 0.001$; NS: not significant. For development time, DD: degree days. Different letters denote significant family-level trait differences among cross types (for visual representation, see Figs. 4 & 5 for cross type effects using mixed-effects models). SGR: specific growth rate. See Fig. 2 for details on cross types

| Trait | Farm (NA) | Hyb (NA _f) | Wild (NA _{EO}) | Hyb15 (EO _w) | Hyb15 (EO _f) | Farm15 (EO) | Wild (NA) | Hyb16 (EO _w) | Hyb16 (EO _f) | Farm16 (EO) | Significance level |
|---|---------------------|---------------------------|-----------------------------|-----------------------------|-----------------------------|---------------------|---------------------|-----------------------------|-----------------------------|---------------------|-----------------------|
| Maternal traits | | | | | | | | | | | |
| Maternal body length (cm) | 77.6 ^a | | 54.3 ^b | | | 107.0 ^c | 55.5 ^b | | | 105.8 ^c | *** |
| Maternal egg size (mm) | 5.7 ^a | | 5.25 ^b | | | 5.77 ^a | 5.37 ^b | | | 6.14 ^c | *** |
| Development time (DD) | | | | | | | | | | | |
| Fertilization to eyed | 310.3 ^a | 305.2 ^b | 277.3 ^{cd} | 279.3 ^{ce} | 282 ^{de} | 284.2 ^e | 313.8 ^{af} | 318.1 ^f | 326.4 ^g | 337.9 ^h | *** |
| Eyed to hatch | 196.4 ^a | 200.7 ^a | 233.3 ^b | 233.5 ^b | 229 ^{bd} | 232.3 ^{bd} | 248.1 ^c | 222.2 ^d | 254.9 ^{ce} | 265 ^e | *** |
| Hatch to yolk absorption | 369.9 | 382.4 | 360.9 | 383 | 376.6 | 379.4 | 359.2 | 365.5 | 361.9 | 353.6 | NS |
| Overall development time | 879 ^a | 888 ^{ac} | 871 ^a | 896 ^{acd} | 887 ^{ac} | 896 ^{acd} | 927 ^{bc} | 906 ^{ab} | 943 ^{bd} | 951 ^b | *** |
| Survival (%) | | | | | | | | | | | |
| Fertilization to eyed | 80.5 ^a | 82.2 ^a | 99.7 ^b | 99.4 ^b | 82 ^a | 83.5 ^a | 90.5 ^a | 72.9 ^a | 42.3 ^c | 46.8 ^c | *** |
| Eyed to hatch | 69.9 ^{ac} | 85.7 ^{bcd} | 98.5 ^b | 97.6 ^b | 53.5 ^a | 62.7 ^{ad} | 96.3 ^b | 92.7 ^{bc} | 71.4 ^{ac} | 75.8 ^{ab} | *** |
| Hatch to yolk absorption | 93.7 ^{ab} | 90.4 ^{ab} | 82.2 ^{ab} | 96.1 ^{ab} | 85.3 ^{ab} | 89.2 ^{ab} | 97.5 ^b | 95.8 ^{ab} | 82.7 ^{ab} | 81.1 ^a | *** |
| Overall survival | 55.6 ^{ac} | 67.6 ^{bc} | 80.6 ^{bc} | 93.2 ^b | 35.0 ^{ad} | 46.1 ^{ac} | 85.2 ^{bc} | 65.6 ^{bcd} | 29.3 ^a | 30.9 ^a | *** |
| Size traits | | | | | | | | | | | |
| Length at hatch (cm) | 1.83 ^{ad} | 1.82 ^{ad} | 1.79 ^{ab} | 1.76 ^b | 1.69 ^{ce} | 1.63 ^c | 1.67 ^c | 1.84 ^d | 1.77 ^{ab} | 1.74 ^{be} | *** |
| Mass at hatch (mg) | 107.7 ^a | 106.1 ^{ac} | 95.1 ^{bd} | 98.5 ^{bce} | 88.8 ^{de} | 87.0 ^d | 102 ^{ac} | 105 ^{ac} | 118.4 ^f | 110 ^a | *** |
| Length at yolk absorption (cm) | 2.61 ^{ab} | 2.54 ^a | 2.66 ^{ab} | 2.76 ^b | 2.57 ^{ac} | 2.70 ^{bc} | 2.59 ^{ac} | 2.7 ^{bc} | 2.76 ^b | 2.68 ^{ab} | *** |
| Mass at yolk absorption (mg) | 133.7 ^a | 126.8 ^a | 120.2 ^{ab} | 136.3 ^{ac} | 96.2 ^b | 120 ^{ab} | 134.2 ^{ad} | 141.3 ^{ac} | 162.4 ^c | 155.3 ^{cd} | *** |
| Energy conversion | | | | | | | | | | | |
| SGR _{length} | 0.095 ^{ac} | 0.087 ^a | 0.104 ^{ab} | 0.115 ^{bc} | 0.105 ^{ab} | 0.13 ^b | 0.123 ^b | 0.107 ^{ab} | 0.123 ^b | 0.121 ^b | *** |
| SGR _{mass} | 0.06 | 0.05 | 0.07 | 0.08 | 0.03 | 0.09 | 0.08 | 0.09 | 0.08 | 0.09 | NS |
| Condition factor (g cm ⁻³ × 100) at hatch | 1.77 ^{ad} | 1.75 ^{ad} | 1.69 ^a | 1.81 ^{ad} | 1.83 ^{acd} | 2.0 ^{bd} | 2.24 ^b | 1.69 ^a | 2.26 ^{bc} | 2.14 ^b | *** |
| Condition factor (g cm ⁻³ × 100) at yolk absorption | 0.76 ^a | 0.77 ^a | 0.63 ^b | 0.65 ^b | 0.57 ^b | 0.59 ^b | 0.77 ^a | 0.72 ^{ab} | 0.77 ^a | 0.81 ^a | *** |
| Yolk sac volume at hatch (cm ³) | 0.077 ^{ab} | 0.061 ^a | 0.07 ^a | 0.074 ^{ab} | 0.053 ^a | 0.056 ^a | 0.069 ^a | 0.081 ^{ab} | 0.111 ^b | 0.147 ^c | *** |
| Yolk sac conversion efficiency (cm cm ⁻³) | 10.9 ^{ac} | 12.3 ^{ac} | 15.2 ^{bc} | 14.2 ^{bc} | 17.1 ^b | 18.2 ^b | 13.8 ^{bc} | 12.2 ^{ac} | 9.4 ^{ac} | 7.5 ^a | *** |

3.2. Early-life fitness-related traits

Significant differences in development time from fertilization to the eyed stage and from eyed to hatch were detected among cross types of EO and NA farmed, NA wild and related F₁ hybrids in both cohorts ($p < 0.001$; Table 1), but there was no difference from hatch to yolk absorption ($p > 0.05$; Table 1). From fertilization to the eyed stage, Wild (NA_{EO}) eggs had faster embryonic development than Wild (NA), both Farm (EO) cohorts and Farm (NA) eggs. Farm16 (EO) eggs took more cumulative DDs to reach the eyed stage than Farm15 (EO), with Farm (NA) displaying an intermediate development time that did not differ from that of Wild (NA). In general, the difference in embryonic development time among most F₁ hybrids and their maternal strains were not significant at the eyed stage. Similarly, Wild (NA_{EO})

eggs hatched earlier than Wild (NA) and Farm16 (EO) but did not differ from Farm15 (EO) and Farm (NA). Moreover, Farm16 (EO) took longer (DD) to hatch than Farm15 (EO), whereas Farm (NA) hatched earlier than both Farm (EO) cohorts. Yet again, most of the hybrids had similar hatching times as their maternal strains. Overall development time from fertilization to yolk absorption was best described by a model that included cross type (SS = 6094.3, $F = 2.59$, df = 9, 81.98, $p < 0.05$), egg size (SS = 16907.4, $F = 64.74$, df = 1, 81.84, $p < 0.0001$) and their 2-way interaction (cross-x-egg) (SS = 6148.8, $F = 2.62$, df = 9, 81.89, $p < 0.05$; Table 2). In general, Farm16 (EO) alevins had a longer development time than Farm15 (EO), Farm (NA) and Wild (NA_{EO}) alevins, which did not differ among themselves (Fig. 4A). All hybrids exhibited similar overall development time as their maternal strains.

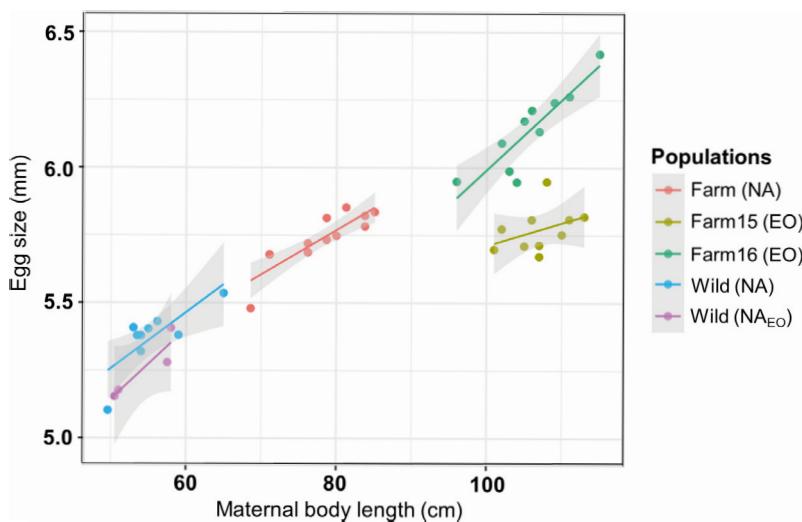


Fig. 3. Regression plot of egg size in relation to maternal body length for the different farmed and wild populations. See Fig. 2 for details. Shaded areas: 95 % CI

Significant differences in survival at the 3 different early-life stages examined (eyed, hatch and yolk absorption) were detected among cross types ($p < 0.001$; Table 1). From fertilization to the eyed stage, Wild (NA_{EO}) embryos had higher survival than Wild (NA), both Farm (EO) cohorts and Farm (NA) embryos. No detectable differences in embryo survival were observed among Wild (NA), Farm (NA) and Farm15 (EO), but Farm16 (EO) had significantly lower survival than other cross types. The differences in embryonic survival between F₁ hybrids and their maternal strains were not significant at the eyed stage. From eyed to hatch, both Wild populations had higher survival than Farm (NA) and Farm15 (EO) but did not differ from Farm16 (EO) embryos. Again, all F₁ hybrids had similar survival as their maternal strains at this stage. From hatch to yolk absorption, no significant differences in alevin survival were detected among cross types, except that Farm16 (EO) had lower survival than Wild (NA). In terms of overall survival, the significant terms retained after model selection were cross type ($\chi^2 = 99.2$, $p < 0.0001$), egg size ($\chi^2 = 3.54$, $p < 0.05$) and the cross- \times -egg interaction term ($\chi^2 = 34.0$, $p < 0.0001$) (Table 3). In general, both wild populations had higher survival than Farm16 (EO) but did not differ from Farm (NA) and Farm15 (EO) (Fig. 4B). There was no difference in overall survival between F₁ hybrids and their related maternal strains.

Significant differences in size (body length and mass) were detected among EO and NA farmed strains, NA wild populations and related hybrids at hatch and yolk absorption ($p < 0.001$; Table 1). At

hatch, Wild (NA) and Farm15 (EO) alevins were shorter than Wild (NA_{EO}), Farm (NA) and Farm16 (EO) alevins. Farm (NA) alevins were longer than Farm16 (EO) but did not differ from Wild (NA_{EO}), which in turn did not differ from Farm16 (EO). There was no difference in alevin length between F₁ hybrids and their related maternal strains, except Hyb16 (EO_{fq}) > Wild (NA). In terms of body mass at the same stage, Farm15 (EO) alevins weighed less than Wild (NA), Farm (NA) and Farm16 (EO) but were no different than Wild (NA_{EO}). There was no difference in alevin mass between F₁ hybrids and their respective maternal strains, except Hyb16 (EO_{fq}) > Farm16 (EO). For fry length at yolk absorption, egg size (SS = 0.36, $F = 132.51$, df = 1, 41.35, $p < 0.0001$) and the cross- \times -egg interaction term (SS = 0.06, $F = 2.27$, df = 9, 55.40, $p < 0.05$) (Table 2) were significant and therefore retained in the final model. As the higher-order interaction term was significant, the lower-order, non-significant fixed-term cross type was also retained in the final model. There was no difference in fry length at yolk absorption among farmed strains and wild populations (Fig. 5A). However, Hyb16 (EO_{fq}) and Hyb15 (EO_{wq}) were larger than Hyb (NA_{fq}), Hyb15 (EO_{fq}) and Wild (NA). For mass at yolk absorption, the model terms cross type (SS = 491.4, $F = 6.0$, df = 9, 33.34, $p < 0.0001$), egg size (SS = 1150.8, $F = 126.5$, df = 1, 26.86, $p < 0.0001$) and their interaction (SS = 491.7, $F = 6.0$, df = 9, 31.65, $p < 0.0001$) were significant and therefore retained in the final model (Table 2). The random effect term dam was also significant (LR = 18.58, $p < 0.0001$) and retained in the final model. Farm16 (EO) fry weighed more than Farm15 (EO), Farm (NA) and Wild (NA_{EO}) but did not differ from Wild (NA) (Fig. 5B). No difference in fry mass was observed between F₁ hybrids and their respective maternal strains.

Significant differences in growth, body condition, yolk sac volume and YCE were observed among cross types ($p < 0.001$; Table 1). In terms of SGR_{length}, cross type (SS = 0.45, $F = 15.11$, df = 9, 42.32 $p < 0.0001$) and egg size (SS = 0.001, $F = 12.28$, df = 1, 25.87, $p < 0.01$) were significant (Table 2) and therefore retained in the final model. The random covariate dam was also significant (LR = 6.39, $p < 0.05$) and retained. Of the pure crosses, Farm15 (EO), Farm16 (EO) and Wild (NA) had the highest SGR_{length} from hatch to yolk

Table 2. Summary of linear mixed-effects model selection for investigating differences in overall Atlantic salmon development time, body length and mass at yolk absorption, specific growth rate (SGR) length and mass, condition factor at yolk absorption, yolk sac volume at hatch and yolk sac conversion efficiency for different cross types of the 2015 and 2016 cohorts. Maternal identity (dam), paternal identity (sire) and Heath tray unit (for position effect) were included as random intercepts. Significant fixed effects (p-values in **bold**) were retained in the final model; significant random effects (dam, sire, Heath tray unit) were also retained in the final model. Denominator df based on Satterwaite's approximations

| Variable | SS | Num. df | Den. df | F | p |
|--|---------|---------|---------|--------|-------------------|
| Overall development time | | | | | |
| Cross | 6094.3 | 9 | 81.98 | 2.59 | <0.05 |
| Egg | 16907.4 | 1 | 81.84 | 64.74 | <0.0001 |
| Cross × egg | 6148.8 | 9 | 81.89 | 2.62 | <0.05 |
| Length at yolk absorption | | | | | |
| Cross | 0.05 | 9 | 55.61 | 1.97 | 0.06 ^a |
| Egg | 0.36 | 1 | 41.35 | 132.51 | <0.0001 |
| Cross × egg | 0.06 | 9 | 55.40 | 2.27 | <0.05 |
| Mass at yolk absorption | | | | | |
| Cross | 491.4 | 9 | 33.34 | 6.0 | <0.0001 |
| Egg | 1150.8 | 1 | 26.86 | 126.5 | <0.0001 |
| Cross × egg | 491.7 | 9 | 31.65 | 6.0 | <0.0001 |
| SGR_{length} | | | | | |
| Cross | 0.45 | 9 | 42.32 | 15.11 | <0.0001 |
| Egg | 0.001 | 1 | 25.87 | 12.28 | <0.01 |
| Cross × egg | 0.001 | 9 | 35.46 | 1.25 | 0.30 |
| SGR_{mass} | | | | | |
| Cross | 0.01 | 9 | 55.86 | 0.86 | 0.57 |
| Egg | 0.02 | 1 | 63.03 | 13.91 | <0.0001 |
| Cross × egg | 0.01 | 9 | 53.42 | 0.92 | 0.52 |
| Condition factor at yolk absorption | | | | | |
| Cross | 0.05 | 9 | 61.86 | 3.17 | <0.01 |
| Egg | 0.002 | 1 | 66.68 | 1.02 | 0.32 ^a |
| Cross × egg | 0.05 | 9 | 58.89 | 3.10 | <0.01 |
| Yolk sac volume at hatch | | | | | |
| Cross | 0.004 | 9 | 30.57 | 4.40 | <0.001 |
| Egg | 0.005 | 1 | 22.35 | 48.9 | <0.0001 |
| Cross × egg | 0.004 | 9 | 30.50 | 4.36 | <0.01 |
| Yolk sac conversion efficiency | | | | | |
| Cross | 668.77 | 9 | 34.45 | 25.97 | <0.0001 |
| Egg | 173.65 | 1 | 28.99 | 107.45 | <0.0001 |
| Cross × egg | 23.24 | 9 | 32.99 | 1.60 | 0.16 |

^aCross (length at yolk absorption) and egg (condition factor at yolk absorption) were also retained in the final model as the interaction terms were significant

absorption, which differed significantly from Farm (NA), with Wild (NA_{EO}) being intermediate between the former pure crosses and Farm (NA) (Fig. 5C). There was no difference in SGR_{length} between F₁ hybrids and their respective maternal strains. For SGR_{mass}, the only significant term retained in the final model was egg size (SS = 0.02, F = 13.91, df = 1, 63.03, p < 0.0001) (Table 2). We did not find any

significant differences in SGR_{mass} among cross types (Tables 1 & 2).

In terms of Fulton's K at hatch, Wild (NA) and Farm16 (EO) had the highest K, followed by Farm15 (EO), which did differ from Farm (NA); Wild (NA_{EO}) had the lowest K but did not differ from Farm (NA). There was no difference in K at hatch between F₁ hybrids and their respective maternal strains, except Hyb16 (EO_{wg}) < Wild (NA). With regards to K at yolk absorption, cross type (SS = 0.05, F = 3.17, df = 9, 61.86, p < 0.01) and the cross-×-egg interaction term (SS = 0.05, F = 3.10, df = 9, 58.89, p < 0.01) were significant and retained in the final model (Table 2). As the 2-way interaction term was significant, the fixed term egg size was also retained. Farm16 (EO) fry had the highest K at yolk absorption, which did not differ from that of Farm (NA) and Wild (NA) (Fig. 5D), whereas Farm15 (EO) had the lowest K of the pure crosses and did not differ from Wild (NA_{EO}). There were no differences in fry K between F₁ hybrids and their respective maternal strains. With respect to yolk sac volume at hatch, both cross type (SS = 0.004, F = 4.40, df = 9, 30.57, p < 0.001), egg size (SS = 0.005, F = 48.9, df = 1, 22.35, p < 0.0001) and their interaction (SS = 0.004, F = 4.36, df = 9, 30.50, p < 0.01) were significant and therefore retained after model selection (Table 2). The random covariate dam was also significant (LR = 4.87, p < 0.05) and also retained. Farm16 (EO) alevins had the largest yolk sac volume at hatch (Fig. 5E). There was no difference in yolk sac volume among Farm (NA), Farm15 (EO) and both Wild populations. No differences in alevin yolk sac volume were observed between F₁ hybrids

and their respective maternal strains, except Hyb16 (EO_{f9}) < Farm16 (EO). In terms of YCE, cross type (SS = 668.77, F = 25.97, df = 9, 34.45, p < 0.0001) and egg size (SS = 173.65, F = 107.45, df = 1, 28.99, p < 0.0001) were significant and retained in the final model (Table 2). Of the pure crosses, Farm15 (EO) had the largest YCE, followed by both Wild populations, which did not differ from Farm15 (EO) and

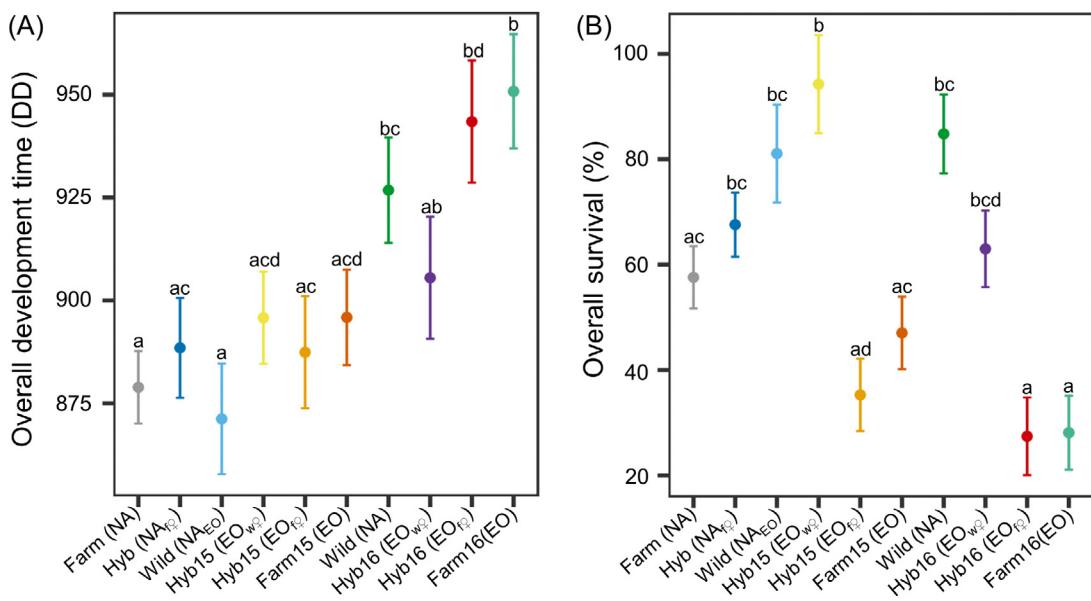


Fig. 4. Cross-type effects on (A) overall development time (degree-days, DD), and (B) overall survival of Atlantic salmon using mixed-effects models. Displayed are marginal means \pm SE. Different letters denote significant differences in estimated marginal mean (family-level) traits among cross types. Both the units and axes differ between panels. See Table S2 for estimated marginal means, and Tables S3 and S4 for Tukey-adjusted pairwise contrasts among cross types fitted in the final models. Cross types: Farm (NA); Hyb (NA_{f0}); Wild (NA_{EO}); Hyb15 (EO_{w0}); Hyb15 (EO_{f0}); and Farm15 (EO) from the 2015 cohort. Cross types: Wild (NA); Hyb16 (EO_{w0}); Hyb16 (EO_{f0}); and Farm16 (EO) from the 2016 cohort

Farm (NA) (Fig. 5F). Farm16 (EO) had the lowest YCE and differed from all other pure crosses except Farm (NA). Again, no difference was observed in alevin YCE between F₁ hybrids and their related maternal strains.

4. DISCUSSION

The present study has demonstrated early-life fitness-related trait differences among divergent EO and NA farmed strains, NA wild populations and related F₁ hybrids, and these differences can provide insight into the impact of hybridization in the wild.

The main findings can be summarized in 4 key points: (1) significant differences were detected in development time (except from hatch to yolk absorption), survival, size and energy conversion among EO and NA farm, wild and F₁ hybrid offspring during early life; (2) fitness-related traits differed between Farm (EO) and Farm (NA) and also between Wild (NA) and Wild (NA_{EO}); (3) few differences in fitness-related traits between F₁ hybrids and their respective maternal strains were detected; and (4) significant associations were found between the maternal effects of egg size and many of the traits measured. These findings suggest that geographical and ancestral relationships and maternal effects were more

Table 3. Summary of generalized linear mixed-effects model (GLMM) selection using likelihood ratio tests for investigating difference in overall survival for different cross types of the 2015 and 2016 Atlantic salmon cohorts. AIC: Akaike's information criterion

| Model no. | Terms included in GLMM model | Term tested | Versus model no. | Log likelihood | AIC | df | χ^2 | p |
|----------------|----------------------------------|--------------------|------------------|----------------|--------|----|----------|---------|
| 0 ^a | Cross + egg + cross \times egg | | | -799.09 | 1644.2 | 23 | | |
| 1 | Cross + egg | Cross \times egg | 0 | -816.09 | 1660.2 | 14 | 34.0 | <0.0001 |
| 2 | Cross | Egg | 1 | -817.86 | 1661.7 | 13 | 3.54 | <0.05 |
| 3 | Egg | Cross | 1 | -865.70 | 1741.1 | 5 | 99.2 | <0.0001 |

^aRetained final model

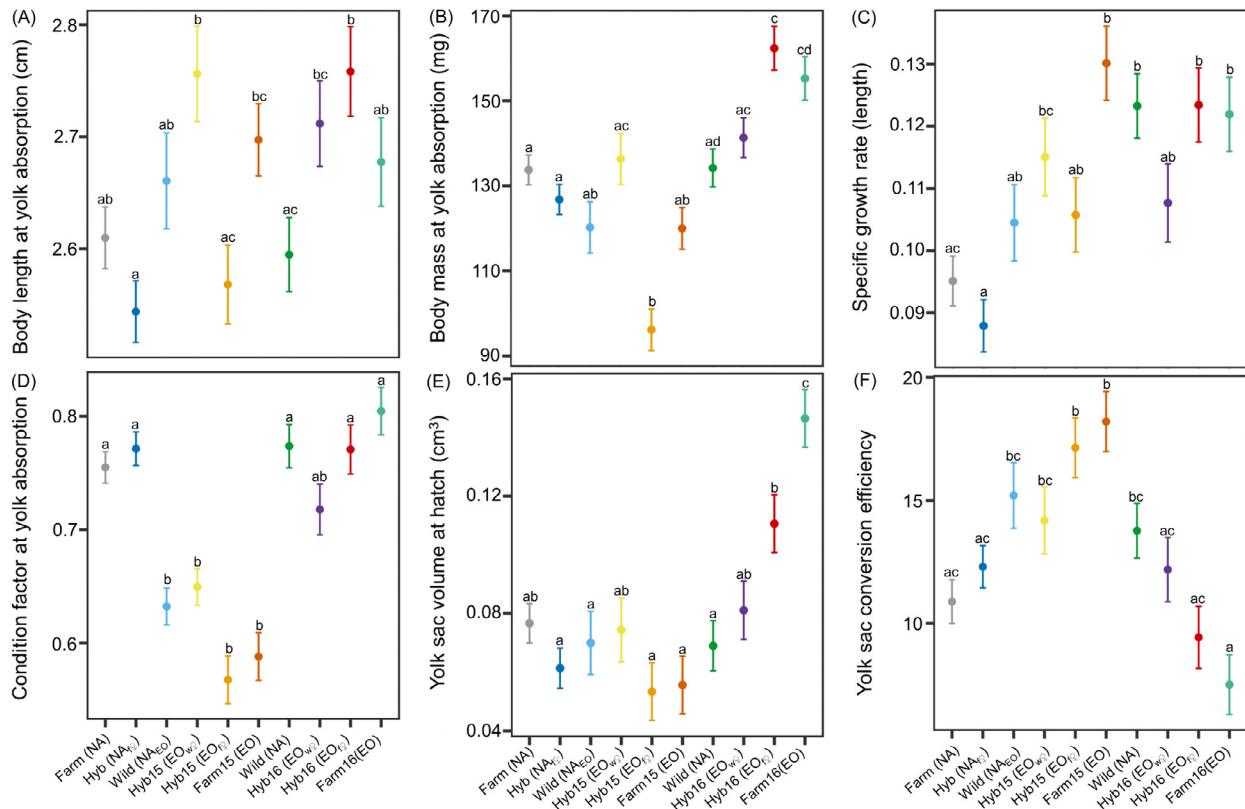


Fig. 5. Cross-type effects on Atlantic salmon (A) length at yolk absorption; (B) mass at yolk absorption; (C) specific growth rate (length); (D) condition factor at yolk absorption; (E) yolk sac volume at hatch; and (F) yolk sac conversion efficiency using mixed-effects models. Displayed are marginal means \pm SE. Different letters denote significant differences in estimated marginal mean (family-level) traits among cross types. Both the units and axes differ among panels. See Table S2 for estimated marginal means, and Table S3 for Tukey-adjusted pairwise contrasts for different cross types fitted in the final models. Cross types: Farm (NA); Hyb (NA_{fq}); Wild (NA_{EO}); Hyb15 (EO_{wq}); Hyb15 (EO_{fq}); and Farm15 (EO) from the 2015 cohort. Cross types: Wild (NA); Hyb16 (EO_{wq}); Hyb16 (EO_{fq}); and Farm16 (EO) from the 2016 cohort

important in generating early-life trait differences among farmed, wild and their related hybrids than the effects of domestication selection.

We found significant differences in development time to the eyed and hatch stages in salmon of farmed, wild and hybrid origin, which was not unexpected based on previous observations of other domesticated salmonid populations (Beacham & Murray 1987, Donaghy & Verspoor 1997, Fraser et al. 2010b, Solberg et al. 2014). However, we did not find a significant difference in development time from hatch to yolk absorption among cross types. It is possible that the increases in temperature at this latter incubation stage might decrease among-population differences in development time, given that temperature variation does not necessarily affect all life stages equally (Thorn & Morbey 2018). Moreover, developmental trait differences were not always the same at different developmental stages (eyed, hatch and yolk absorption) in each farmed, wild and F₁ hybrid cross

comparison. Overall, however, Farm16 (EO) had a longer developmental time than the other farm strains, which appears likely to be related to the larger egg size of Farm16 (EO) females. Wild (NA) displayed intermediate development time in each of the 3 early-life developmental phases. Wild (NA_{EO}) always had the shortest development time and smallest egg size; however, despite these characteristics, its overall development time did not differ from that of Farm (NA).

All hybrid fry exhibited similar development times to yolk absorption as their respective maternal strains, which implies that maternal effects, likely associated with egg size (Hendry et al. 1998, Einum & Fleming 2004, Green 2008), were important determinants of development time (Thorpe et al. 1984, Beacham & Murray 1985, 1987, Einum & Fleming 2000b). It is also possible that maternal transcript factors contributed to this pattern (Bougas et al. 2013, Bicskei et al. 2016, Biziayehu et al. 2019). Emergence timing,

which will be affected both by adult spawning time and embryo development time, is likely to affect competitive ability due to prior residency (Cutts et al. 1999, Kvingedal & Einum 2011). Thus, the extended developmental time of Farm16 (EO) and the related maternal hybrid (Hyb16 [EO_{f_g}]) may be maladaptive, compromising survival and growth in the wild (Einium & Fleming 2000a). Put simply, the delayed emergence of Farm16 (EO) offspring may inhibit introgressive hybridization. However, this effect seems to be cohort-specific, as a delayed emergence was not observed in Farm15 (EO).

Our results demonstrated significant differences in early-life survival among farmed, wild and F₁ hybrid conspecifics, which is consistent with the observations of other salmonid populations (Granath et al. 2004, Fraser et al. 2010a, Houde et al. 2013, 2015, Falica et al. 2017). The survival differences were consistent at different stages in each farmed, wild and F₁ hybrid cross comparison. In general, both Wild (NA) and Wild (NA_{EO}) had the highest survival, Farm (NA) had intermediate survival and both Farm (EO) cohorts had the lowest survival. We cannot rule out the possibility of an egg quality effect on early-life survival, as gametes of both wild parental populations were derived from adults stripped immediately prior to fertilization on site, while gametes of the farm strains were stripped at their respective facilities (Iceland and south coast NF) and shipped immediately to St. John's. Such egg quality effects would be expected to be most evident during the early developmental stage, when Farm16 (EO) had the lowest survival from fertilization to the eyed stage followed by the Farm (NA) and Farm15 (EO) strains. As with development time, survival of F₁ hybrids was most similar to that of their respective maternal strains, indicative of maternal effects, though the effect here appears to be more likely related to egg quality than size.

The farmed, wild and F₁ hybrid offspring also differed significantly in early-life size (in terms of both length and mass) at hatch and yolk absorption. Moreover, with regards to growth rate, both cohorts of the Farm (EO) strain had higher SGR_{length} and SGR_{mass} than Farm (NA), while Wild (NA) had higher SGR_{length} than Wild (NA_{EO}). Our study was designed to discern the degree to which farmed-wild early-life fitness trait differences may be attributable to the domestication selection and the ancestral relationship among the populations. In our study, the 2 farmed strains used are historically genetically divergent but have undergone multiple generations of domestication selection, albeit for differing lengths of time (Farm [EO]: 10–12 generations; Farm [NA]: 5–7

generations); thus, a question that remains is whether these 2 farmed strains would display similar early-life fitness traits (e.g. growth). However, while these 2 farmed strains have likely experienced similar domestication selection, there was not strong evidence of similarities in early-life traits, which contrasts with observations of their behaviour as young-of-the-year juveniles, where both Farm (EO) and Farm (NA) fish showed similar patterns (Islam et al. 2020). Moreover, it does not appear that the differences can be explained by the maternal effects of egg size, as Farm (NA) and Farm15 (EO) had similar egg sizes, though smaller than Farm16 (EO). While we cannot entirely rule out the possibility that the different numbers of generations of domestication selection have influenced the differences between these 2 farmed strains, inconsistencies in their differences relative to the wild populations (i.e. not always differing in the same direction) suggest that their distinct geographical and ancestral origins are more important in explaining the patterns observed.

F₁ hybrids had similar overall growth to their maternal strains, and we also found a significant dam effect (for mass at yolk absorption and SGR_{length}), which again suggests that maternal effects, likely due to egg size, largely determine this pattern, as also seen in earlier studies (Houde et al. 2011, Debes et al. 2013, Solberg et al. 2014). However, there was still cross type effect for SGR_{length} (although not for SGR_{mass}), even after controlling for egg size and the dam effect in the model. Energy conversion (i.e. utilization of endogenous yolk resources; YCE) also differed significantly among cross types, even after controlling for the effects of egg size, in contrast with some earlier studies that did not find differences between farmed strains and wild populations (Debes et al. 2013, Solberg et al. 2014). There were also differences in yolk sac volume at hatch, with Farm16 (EO) having the greatest volume (and largest initial egg size) compared to other cross types, while no differences were observed among Farm (NA) and the 2 wild populations despite differences in initial egg size. Taken together, although it appeared that there were significant differences in growth and energy conversion, our findings provide little indication that domestication selection has resulted in changes in early alevin size, growth and endogenous resource utilization, but rather suggest that distinct geographic and ancestral relationships of the farmed strains and maternal effects have mainly contributed to early-life growth differences.

In conclusion, the differences in the early-life fitness traits observed among divergent EO and NA

farmed, wild and F₁ hybrid populations appear to largely reflect the influence of geographic and ancestral relationships of the farmed strains and maternal effects and less so domestication selection. Briefly, although the traits nearly always differed significantly among cross types, the differences were not necessarily consistent among the different early-life stages. Moreover, we did not see many consistent trait differences among farmed strains relative to the wild populations, suggesting that domestication selection had relatively less effect on fitness at this relatively early life stage than maternal effects, likely due to differences in egg size. Along the same line, one of our main hypotheses was that interbreeding will cause F₁ hybrids to display altered fitness (reflected in differences in fitness-related traits) relative to farm and wild populations. However, we observed few differences in fitness-related traits between F₁ hybrids and their respective maternal farmed/wild strains. As the principal route of hybridization/introgression is likely to occur through farm females rather than males because of sex differences in their reproductive capabilities (Fleming et al. 1996, 2000), the maternal contributions of farm females will be important in understanding the fitness consequences of interbreeding. Escaped farmed salmon have been detected in rivers in Southern NF (Keyser et al. 2018, Wringe et al. 2018), and successful breeding between farmed and wild salmon was detected in 17 out 18 rivers studied. Wringe et al. (2018) also detected successful reproduction of pure farm individuals (i.e. production of feral offspring) in a number of rivers, which is of particular note given the results presented in this study. It has long been clear that successful breeding of escaped farmed salmon within wild populations can have fitness impacts (e.g. on growth and survival) at subsequent life stages, influencing lifetime success and threatening the native wild populations (McGinnity et al. 1997, 2003, Fleming et al. 2000, Skaala et al. 2019). Thus, understanding the effect of hybridization—and consequently, early-life fitness trait differences among divergent farmed, wild and F₁ hybrid populations—can provide valuable insight for the conservation and management of Atlantic salmon.

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This experiment was carried out in accordance with the Memorial University institutional guidelines and was approved under Animal Care and Use Protocol (15-21-IF).

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