



# Fitness consequences of hybridization between wild Newfoundland and farmed European and North American Atlantic salmon

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**ABSTRACT:** Selection due to multi-generational domestication and genetically distinct origins raises concerns about potential fitness consequences of hybridization between farmed and wild Atlantic salmon. In Newfoundland (NF), Canada, the aquaculture industry uses the North American (NA) Saint John River strain, though site-specific permission has been granted to farm a European origin (EO) strain. We used complementary experiments to investigate differences in (1) dominance status and (2) growth and survival in allopatry (NF wild fish) versus sympatry (NF wild fish with NA/EO farmed individuals and related F<sub>1</sub> hybrids) in contrasting tank and semi-natural stream environments. NA farmed salmon were more dominant than NF wild individuals, with hybrids being intermediate in expression and not differing from wild fish. EO farmed salmon also tended to dominate NF wild individuals, but not significantly. Competition with farmed fish and hybrids did not affect the growth of wild fish in sympatry versus allopatry in the tank environment. However, that was not the case in one instance in the stream environment where wild fish in sympatry with NA farmed fish and hybrids outgrew those in allopatry. Within sympatric treatments, both EO and NA farmed salmon outgrew wild individuals in the tank environment, but not always in the stream environment (exception: NA farmed). Hybrids tended to display intermediate growth performance relative to farmed and wild fish in both environments. Survival did not differ among cross types in either environment. These findings suggest that irrespective of distinct origins, both EO and NA farmed salmon displayed greater dominance and growth than NF wild salmon in the tank environment. However, in the stream environment, competition imposed by NA farmed fish and related hybrids on wild fish appeared less than that imposed by the EO strain and related hybrids, as evident in growth performance. Findings thus provide valuable insight into the effects of hybridization and, consequently, fitness-related trait differences among divergent EO and NA farmed, NF wild, and F<sub>1</sub> hybrid populations of importance for the conservation and management of Atlantic salmon.

**KEY WORDS:** Hybridization · Dominance · Growth · Survival · Farmed–wild salmon interaction · *Salmo salar*

## 1. INTRODUCTION

Predicting and assessing the fitness consequences of intraspecific hybridization has long been a 2-sided debate in ecology and evolution. On one side, hybrid-

ization may lead to adaptive potential for populations by increasing heterozygosity, creating new genetic combinations, and masking deleterious alleles (Anderson & Stebbins 1954, Lynch & Walsh 1998, Frankham 2015, Chan et al. 2019). On the other side,

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hybridization between 2 reproductively isolated populations may result in the breakup of co-adapted gene complexes and/or disrupt local adaptation, which leads to outbreeding depression, a mechanism of fitness reduction (Dobzhansky 1940, Allendorf et al. 2001, Edmands 2007, Hamilton & Miller 2016). Consequently, outbreeding depression is expected when hybridization involves more genetically distant populations (Allendorf & Waples 1996, Edmands & Timmerman 2003). The resulting progeny may not be well adapted locally, as an allele that is advantageous in one environment or genetic background may be disadvantageous to overall fitness in another. Thus, there is a growing need to understand the fitness implications of hybridization among divergent populations for the conservation and management of intraspecific biodiversity.

Given rapid climate change and anthropogenic influences on the exploitation of wild living resources (Hutchings 2000, Myers & Worm 2003, Thiault et al. 2019), captive production intuitively represents an alternative means of food security (Gering et al. 2019, Houston et al. 2020). Compared with other livestock species which have been domesticated as a source of food for thousands of years (e.g. pigs, cattle, sheep, goats, and poultry were domesticated 8000–10 000 yr before present; Craig 1981), most fishes, such as Atlantic salmon *Salmo salar* L., have been domesticated for less than 16 generations (Gjedrem 2000). Atlantic salmon is an ecologically and culturally significant fish species that has been intensively farmed since 1970 and has undergone directed selection for economically important traits (e.g. faster growth, delayed maturation, and disease resistance through phenotypic and family-based selection; Gjedrem 2010). Consequently, this species is regarded as one of the most domesticated aquaculture species globally for food (Gross 1998, Teletchea & Fontaine 2014).

Behavioural traits, which often underlie growth and survival, are among the first fitness traits affected by the domestication process, where unintentional and relaxed selection alter phenotypes (e.g. aggressive, dominance, and antipredator behaviours) (Metcalfe et al. 2003, Huntingford 2004). Therefore, domesticated fish species, such as commercially bred farmed Atlantic salmon, may behave in a manner that results in a competitive advantage over their wild conspecifics in a culture environment (Einum & Fleming 1997, Fleming & Einum 1997). Moreover, social interactions and hierarchies can be influenced by body size and affect the outcome of resource competition, providing faster-growing cultured salmon with a further advantage (Abrahams & Sutterlin 1999, Biro et

al. 2004, 2006). In general, bigger, bolder, and dominant fish have better access to food and territories than smaller, shy, and submissive fish (Sundström et al. 2004). However, due to various natural selective pressures in the wild environment, cultured fish do not always show better performance in all situations (Fleming et al. 2000, McGinnity et al. 2003, Skaala et al. 2019). To date, limited research has been devoted to assessing dominance status among domesticated, wild, and related hybrid fish in the context of distinct origins (i.e. geographical and ancestral) and domestication selection among divergent populations.

One of the largest and most consistent differences in phenotypic trait expression between domesticated and wild salmon is growth, an important component of fitness (Solberg et al. 2013a, Harvey et al. 2016a, Glover et al. 2018). Recent evidence indicates that farmed salmon can display a growth rate that is over 2–3-fold higher than that of wild conspecifics when reared under identical culture environments (Solberg et al. 2013b, Harvey et al. 2016b, Glover et al. 2018). In contrast, in the natural environment, the growth of farmed salmon is only marginally higher than that of their wild counterparts (Glover et al. 2018, Skaala et al. 2019). This begs the question, why do farmed salmon outgrow wild salmon extensively in the culture environment while not in the wild? This difference may be a plastic response driven by divergent energy budgets between the 2 environments. For example, from the start of exogenous feeding, juveniles in captivity are fed high-energy commercial diets (Harvey et al. 2016b), whereas those in nature feed on a diet of natural prey. The natural prey of wild fish can vary substantially in type, form, and nutrient composition (Jonsson & Jonsson 2011). Moreover, farmed salmon may be less effective at catching prey in the wild, expend more energy in their search, and are vulnerable to starvation (Huntingford 2004). Also, there can be a trade-off between energetic gain and mortality ('high-risk, high gain'; Biro & Stamps 2008), where farmed juveniles displaying the highest growth potential are more susceptible to predation in the wild than those exhibiting lower growth potential (Solberg et al. 2020). Such a selection mechanism (growth-potential mortality) may therefore result in more similar growth among surviving farmed and wild juveniles in a natural environment. Thus, it is becoming essential to examine growth and survival responses among multi-generation domesticated farmed strains, wild populations, and related F<sub>1</sub> hybrids across the contrasting culture and natural environments.

In the past 3–4 decades, tens of millions of farmed Atlantic salmon have escaped into the wild, and con-

sequently, introgressive hybridization has been observed in wild populations over broad regions of Europe (Glover et al. 2017, Bolstad et al. 2021, Gilbey et al. 2021, Palm et al. 2021). Genetic and competitive interactions between escaped farmed and wild salmon have also been documented where the 2 coexist in Atlantic Canada (Keyser et al. 2018, Wringe et al. 2018, Sylvester et al. 2019). Currently, salmon aquaculture practices in Atlantic Canada use North American (hereafter 'NA') farmed strains that originate from the Saint John River, New Brunswick (NB). In Newfoundland (NF), permission has also been recently granted to import a strain of European (hereafter 'EO') aquaculture salmon (StofnFiskur, Iceland), domesticated from wild Norwegian populations, to be farmed as triploids. The triploidization process is not completely effective (Benfey 2016), and among any farmed salmon that may escape, a proportion may be non-triploid EO. Non-triploid escapees will be able to breed successfully and interact genetically and ecologically with wild populations (O'Reilly et al. 2006). This raises concerns that introgressive hybridization of EO-origin farmed strains into NF wild populations could be a greater threat than hybridization between NA farmed and wild salmon. Effects will depend on the distinct origins (geographical and ancestral) among the populations as well as commonalities in the effects of domestication selection. A compelling body of evidence indicates that EO farmed salmon (Norwegian) and NA farmed salmon (Saint John River strain) are highly divergent genetically ( $F_{ST} > 0.40$ ; S. J. Lehnert pers. comm. based on data from Jeffery et al. 2018). Although phenotypic and genetic differences exist among wild salmon populations within NF (e.g.  $F_{ST} = 0.12$  between Garnish and Northeast Placentia River populations; S. J. Lehnert pers. comm.), the divergence between NF wild and NA farmed salmon populations is larger ( $F_{ST} = 0.14\text{--}0.20$ ; Bradbury et al. 2018).

Here, we used 2 complementary experiments designed to investigate differences in (1) dominance status and (2) growth and survival among divergent EO and NA farmed, NF wild, and related hybrids across contrasting tank and semi-natural stream environments. We tested the hypotheses that (1) EO and NA farmed salmon will be more dominant than NF wild salmon, and given that genetic differences between wild and farmed salmon are typically additive (Besnier et al. 2015, 2020),  $F_1$  hybrids will be intermediate in expression; (2) the growth and survival of wild fish in allopatry will be higher than that of those in sympatry (i.e. competing with farmed and related hybrids); and (3) both EO and NA farmed

strains and  $F_1$  hybrids will display higher growth and survival than wild fish within sympatry.

## 2. MATERIALS AND METHODS

### 2.1. Parental populations

The complementary dominance and growth and survival experiments were conducted across 2 yr (2016 and 2017) with 2 cohorts of fish.

The first cohort was generated in 2015 using 3 base populations. EO farmed (hereafter 'Farm.EO') is a Norwegian farmed strain that has been domesticated for 12–13 generations (Gjedrem 2010) and is produced in an Icelandic facility (StofnFiskur). Gametes were obtained from Iceland and transported by air to St John's, NF. NA farmed (hereafter 'Farm.NA') is Atlantic Canada's principal aquaculture strain that has been domesticated for 5–7 generations (Glebe 1998), originally derived from the Saint John River, New Brunswick, Canada. Farm.NA gametes were obtained from Northern Harvest Sea Farms, a local aquaculture company based on the south coast of NF. NF wild (hereafter 'Wild.NA<sub>EO</sub>', [NF wild salmon with natural evidence of EO secondary contact ~10 000 yr before present; see Bradbury et al. 2015]), were collected as adults from the Northeast Placentia River, NF (47.2408°N, 53.9566°W) on 27 July 2015 and transported to the Ocean Science Centre (OSC, Memorial University of Newfoundland), where they were held in broodstock tanks until crossing in the fall. This wild population was included in the study as it had a low level of EO admixture (on average ~1% of the genome is EO-based; I. R. Bradbury pers. obs.).

The second cohort was generated in 2016 using 2 base populations: again, Farm.EO gametes were collected from the Icelandic facility, and individuals from another NF wild population that had no signal of EO admixture (hereafter 'Wild.NA') were collected as adults from the Garnish River, NF (47.2348°N, 55.3615°W) on 9 August 2016, transported to the OSC, and held in broodstock tanks until the crosses were performed in the fall (for biological information about the parental populations, cross details and families, see Islam et al. 2021). The purpose of this second cohort was to focus on the fitness consequences of hybridization of Farm.EO with the Wild.NA salmon population having no signal of historic EO admixture and conduct reciprocal crosses.

Each year following yolk sac absorption, families were pooled by cross type. Each family consisted of ca. 200–400 juveniles (based on the number of fami-

lies per cross type to maintain similar densities); these fish were transferred into 470 l flow-through circular holding tanks (0.9 m diameter × 0.5 m high).

## 2.2. Dominance experiment

Approximately 4 wk following the onset of exogenous feeding, a dominance experiment was conducted with the juvenile fish from the 2015 and 2016 cohorts between 20 June–30 August 2016 and 25 June–4 September 2017, respectively. In 2016, we tested 175 fish: 35 from each of the 5 cross types: (1) Farm.NA, (2) Farm.NA( $\varphi$ ) × Wild.NA<sub>EO</sub>( $\sigma$ ) hybrid (Hb.NA), (3) Wild.NA<sub>EO</sub>, (4) Farm.EO( $\varphi$ ) × Wild.NA<sub>EO</sub>( $\sigma$ ) hybrid (Hb.EO), and (5) Farm.EO; in 2017, we tested 140 fish: 35 from each of the 4 cross types: (1) Wild.NA, (2) Wild.NA( $\varphi$ ) × Farm.EO( $\sigma$ ) hybrid (Hb<sub>W</sub> $\varphi$ ), (3) Farm.EO( $\varphi$ ) × Wild.NA( $\sigma$ ) hybrid (Hb<sub>F</sub> $\varphi$ ), and (4) Farm.EO. A total of 35 trials were conducted each year. Experimental protocols and conditions were the same in both years, and all observations took place between 09:00 and 17:00 h. Two trials were conducted per day using 2 experimental aquaria (70 × 45 × 36 cm) (Fig. 1). Three sides of the aquaria were covered externally to minimize disturbance, and data were recorded both manually and by video (VIXIA HF R60 HD Digital Camcorder, Canon). Before conducting each trial, experimental fish were anaesthetised with AQUALIFE TMS (MS-222; 400 mg l<sup>-1</sup>, Syndel Laboratories), saline-buffered with 0.1 M sodium bicarbonate, and measured for wet weight (mg). Fish were matched to be within 25 mg (6%) of each other to minimize the influence of size differ-

ences on their dominance status. To identify each individual during the trials, fish were marked by injecting a small amount of different coloured visible implant elastomer (Northwest Marine Technology) below the dorsal fin (both sides). The fish were deprived of food for 1 d before dominance trials, and there was no tag loss or mortality while the fish were in the experimental aquaria.

Approximately 24 h after acclimation in the experimental aquaria, the fish (one per cross type, n = 5 in 2016 and n = 4 in 2017) were tested for their dominance status. Removal tests (adopted from Adriaenssens & Johnsson 2011) were conducted to assign dominance status among the different cross types. Dominance status was calculated by a combined index using 3 indicators: (1) spatial upstream position in the aquarium, (2) feeding attempts and success, and (3) aggressive interactions. Each of the 5 observations was scored for 2 min every 15 min. At the beginning of each observation, 10–15 pellets (size: 1 mm) were delivered and spatial position was recorded (1 point for upstream). A score of 2 points was given for a feeding attempt and 1 point for consuming a pellet. Agonistic behaviours were also recorded; individuals were given 2 points for an aggressive interaction (e.g. chasing). After 5 observations, all scores were summed and the fish receiving the highest score (total score was >3 than that of other individuals) was considered dominant. After scoring, the dominant individual(s) was (were) removed from the tank and the remaining individuals were left to recover for 2 h. The procedure was then repeated with the remaining fish until dominance status (intermediate and subordinate) had been determined for all individuals. To reduce the behavioural effects of decreasing density (Adriaenssens & Johnsson 2011), the tank area was reduced after the removal of dominant individuals (Fig. 1).

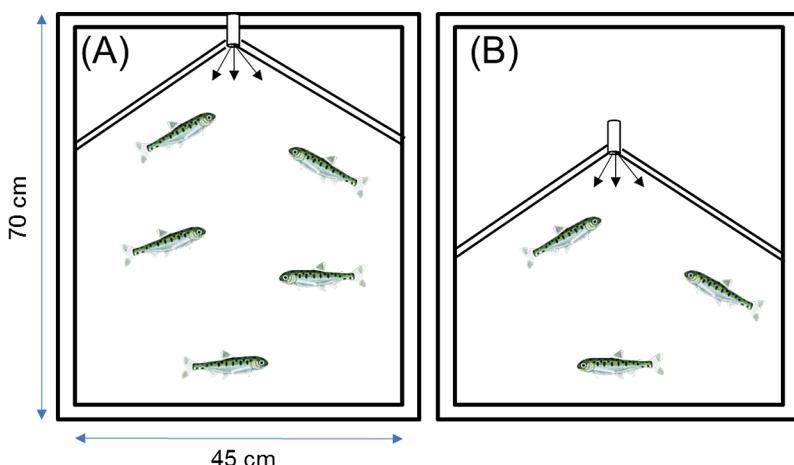


Fig. 1. Schematic representation of the experimental aquaria used for the dominance experiments with Atlantic salmon in 2016 and 2017. (A) Prior to and (B) after removal of the dominant individual(s) when the experimental area was reduced to minimize the density effects

## 2.3. Growth and survival experiments in tank and stream environments

Approximately 4 wk after the start of exogenous feeding and following pooling by cross type, farmed, wild, and hybrid fry were placed in either a tank environment consisting of 36 rectangular tanks (0.32 × 0.24 × 0.16 m), each with an independent continuous flow-through water supply or a semi-natural

stream environment consisting of 36 mesocosms ( $1.2 \times 0.22 \times 0.15$  m) (Table 1). In the latter case, the mesocosms were constructed inside 9 raceways ( $2.7 \times 0.45 \times 0.30$  m) that contained gravel substrates (5–10 cm). Each raceway had a similar flow-through water supply ( $10\text{--}15$  cm s $^{-1}$ ), and adjacent mesocosms were separated by a double-screened buffer zone. Fish were selected haphazardly from rearing tanks, anaesthetised with buffered AQUALIFE TMS (MS-222), and measured for wet weight (mg) and fork length (cm). To identify individuals to cross type, fish were marked by injecting a small amount of coloured visible implant elastomer (Northwest Marine Technology, WA, USA) below the dorsal fin. In both the tank and semi-natural stream environments in 2016, fish were placed into one of the 3 forms of competitive treatments: (1) Allopatric Wild.NA<sub>EO</sub>: 12 replicates, 30 ind. replicate $^{-1}$ , (2) Sympatric NA: 12 replicates, 30 ind. replicate $^{-1}$  (10 Wild.NA<sub>EO</sub>, 10 Hb.NA, 10 Farm.NA), and (3) Sympatric EO: 12 replicates, 30 ind. replicate $^{-1}$  (10 Wild.NA<sub>EO</sub>, 10 Hb.EO, 10 Farm.EO) (Table 1). Similarly, in 2017, 3 competitive treatments were examined: (1) Allopatric Wild.NA: 12 replicates, 30 ind. replicate $^{-1}$ , (2) Sympatric-I: 12 replicates, 30 ind. replicate $^{-1}$  (10 Wild.NA, 10 Hb<sub>W9</sub>, 10 Farm.EO), and (3) Sympatric-II: 12 replicates, 30 ind. replicate $^{-1}$  (10 Wild.NA, 10 Hb<sub>F9</sub>, 10 Farm.EO) (Table 1).

In the tank environment, fish were provided with a diet of commercial salmonid starter dry pellets (EWOS-Cargill) in batches 4 times per day. Feeding rates and caloric content were standardized: 75 mg of pellet in each replicate during each feeding (pellet size: crumbles 0.5 mm; composition: 55% protein, 15% fat; EWOS-Cargill) for the first 40 d. During the last 40 d (Day 41–80), the feeding rate was increased to double with 150 mg of pellet in each replicate per feeding event (pellet size: crumbles 0.7 mm; composition: 54% protein, 16% fat; EWOS-Cargill). In the stream environment, fish were provided a combination of live brine shrimp *Artemia* spp. and frozen blood worms *Chironomidae* spp. (commercial fish food supplier) as semi-natural feed. *Artemia* concentration was standardized by growing 1 000 000 cysts l $^{-1}$  and suspending the live *Artemia* from a batch into 2 l of water prior to feeding. The *Artemia* were enriched with Ori-one (0.3 g million $^{-1}$ ) and Ori-green (0.8 g million $^{-1}$ ); algae-based enrichments with highly unsaturated fatty acids and vitamins (Skretting). The caloric content of frozen blood worms was 6% crude protein, 0.5% crude fat, 0.9% crude fiber, and 89% moisture (J & L Aquatics). Feeding rates were standardized at 15 ml of semi-natural feed (80% of *Artemia* and 20% of blood worms) in each replicate

for the first 40 d and doubled (30 ml) for the last 40 d. The feeding frequency was the same as for the tank environment, and both experiments were carried out simultaneously for 80 d (between 15 June–2 September 2016, and 21 June–8 September 2017). At the termination of the experiments (Day 80), the fish were weighed (mg) and photographed for subsequent fork length (cm) measurement. There were some differences in initial size (body mass and length) among the cross types across the different treatments (allopatric vs. sympatric) within an environment (tank or semi-natural stream) (Table 1). In 2016, Wild.NA<sub>EO</sub> individuals were typically larger than Farm.NA and Hb.NA but similar in size to Farm.EO and smaller than Hb.EO. In 2017, Wild.NA individuals were similar in size to Farm.EO (except in Sympatric-II stream) and typically smaller than Hb<sub>W9</sub> but larger than Hb<sub>F9</sub>.

Experimental conditions and protocols were the same between years. The fish in both the tank and stream environments were reared under common environmental conditions (ambient water temperature: 15–17°C; pH: 5.7–6.2, dissolved oxygen: 8.0–8.5 mg l $^{-1}$ ), and the photoperiod was maintained at a 12 h light: 12 h dark schedule. 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).

#### 2.4. 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 to examine normality. To check the constancy of variance, homoscedasticity was checked visually using residuals vs. fitted values (Crawley 2005).

To assess the dominance status of the fish, which had been matched to be within 25 mg (6%) of each other, logistic regression with a binomial generalized linear model (GLM) was used. Tukey's adjusted pairwise contrasts were carried out using the 'emmeans' package (Lenth 2016) to estimate the dominance status (dominant, intermediate, and subordinate) between cross types. This test reported parameter estimates, z-values (for binary data), and p-values (see Table S1 in the Supplement at [www.int-res.com/articles/suppl/q014p243\\_supp.pdf](http://www.int-res.com/articles/suppl/q014p243_supp.pdf)).

Specific growth rates in terms of mass (SGR<sub>mass</sub>) and length (SGR<sub>length</sub>) were calculated as  $100 \times [\ln(\text{body}$

**Table 1.** Experimental design of growth and survival experiments with Atlantic salmon in tank and semi-natural stream environments (2016 and 2017). Initial number of fish per replicate, total number of fish at initial stage for each cross type, and final number of surviving fish sampled at termination for each cross type in allopatric and sympatric environments are indicated. All comparisons of initial mass and length within an environment were significant ( $p < 0.001$ ); different letters denote the significant mean trait differences among cross types. Cross types in 2016: Wild.NA<sub>EO</sub>: Newfoundland (NF) wild with a signal of European (EO) ancestry; Farm.NA: North American (NA) farmed; Hb.NA: hybrid Wild.NA<sub>EO</sub> × Farm.NA; Farm.EO: EO farmed; Hb.EO: Wild.NA<sub>EO</sub> × Farm.EO. Cross types in 2017: Wild.NA: NF wild with no signal of EO ancestry; Farm.EO: Hb<sub>WQ</sub>: Wild.NA<sub>Q</sub> × Farm.EO $\delta$ ; Hb<sub>FQ</sub>: Wild.NA $\delta$  × Farm.EO $\delta$

mass or length at termination) – ln(body mass or length at the beginning)] / time. The final Fulton's body condition factor ( $K$ ) was calculated as  $K = (\text{mass} / \text{length}^3) \times 100$ . SGR<sub>mass</sub>, SGR<sub>length</sub>, and condition were analysed using linear mixed-effects (LME) models with the 'lme4' package (Bates et al. 2015). Treatment (allopatry, sympatry) and/or cross type and environment (tank, stream) were included as categorical fixed effects. Replicate and final density (nested within replicate) were included as a random intercept. Mass data were log<sub>10</sub> transformed. The final model was selected from the full model with the 'lmerTest' package, which allowed for automatic model selection (Kuznetsova et al. 2017). The step function performed backwards selection, where non-significant random covariates were removed first. Non-significant interaction terms were eliminated before the fixed effects, and if significant interaction terms were found, all fixed covariates were included in the final model regardless of their significance level. The p-values for random effects were estimated using likelihood ratio tests (LRTs), whereas the significance values for the fixed effects were obtained using an  $F$ -test based on Satterthwaite's approximation. The final model was confirmed by using plots of the model residuals, and the normality of the fitted model residuals was confirmed visually using histograms.

Survival was analysed using a generalized linear mixed-effects model (GLMM) with a binomial distribution (logit-link function) using the 'glmer' function again in the 'lme4' package (Bates et al. 2015) using Laplace approximation to the likelihood. Again, treatment and/or cross type and environment were in-

cluded as fixed covariates, and replicate and final density nested within replicate were included as random covariates. Non-significant interaction terms and covariates were removed backwards stepwise using LRTs. The model residual plots and normality were confirmed for the final model as for the growth data.

Estimated marginal means (see Table S2) and Tukey's adjusted post hoc multiple comparisons (using Kenward-Roger's degrees-of-freedom method) were again carried out using the 'emmeans' package (Lenth 2016). 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. Dominance status

Significant differences in dominance status were observed among Farm.EO and Farm.NA strains, NF wild populations, and related hybrids in the 2016 and 2017 experiments. Farm.NA fry were more dominant and less subordinate than Wild.NA<sub>EO</sub> fry in the 2016 experiment ( $p < 0.05$ ), with Hb.NA and Hb.EO being intermediate and not differing from any other cross type ( $p > 0.05$ ; Fig. 2A, Table S1). There were no differences in intermediate status among cross types ( $p > 0.05$ ). In 2017, Farm.EO fry were more dominant and less subordinate than Hb<sub>F<sub>♀</sub></sub> ( $p < 0.05$ ) but did not differ significantly from Wild.NA and Hb<sub>W<sub>♀</sub></sub> ( $p > 0.05$ ;

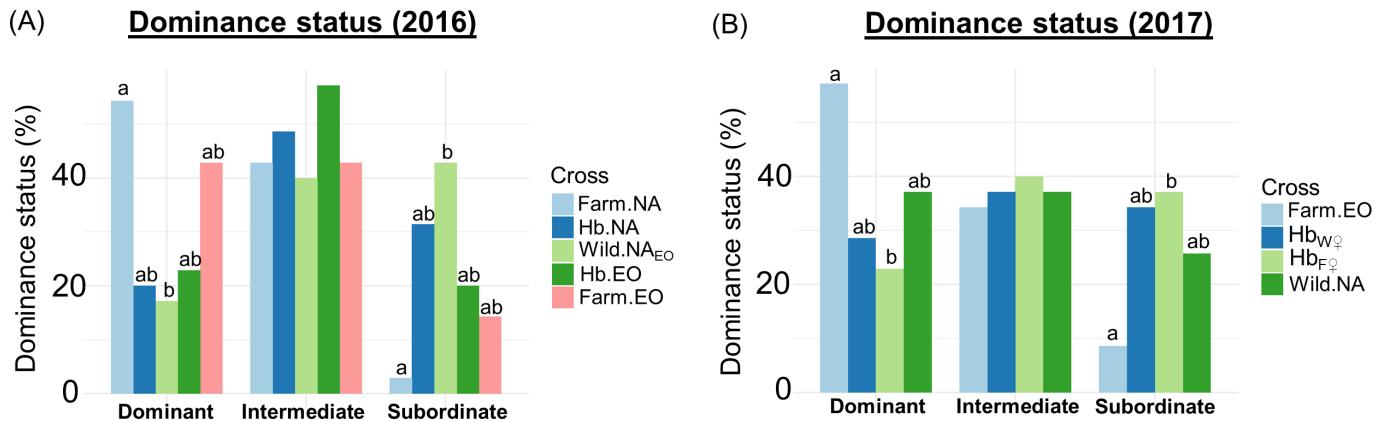


Fig. 2. Dominance status (%) among different cross types in the (A) 2016 and (B) 2017 dominance experiments with Atlantic salmon. Different letters indicate significant differences in dominance status among cross types. See Table S1 for Tukey-adjusted pairwise contrasts of different cross types for the estimation of dominance status. Cross types in 2016: Farm.NA: North American (NA) farmed; Hb.NA: hybrid Wild.NAEAO × Farm.NA; Wild.NAEAO: Newfoundland (NF) wild with a signal of European (EO) ancestry; Hb.EO: Wild.NAEAO × Farm.EO; Farm.EO: EO farmed. Cross types in 2017: Farm.EO: EO farmed; Hb<sub>W<sub>♀</sub></sub>: Wild.NA<sub>♀</sub> × Farm.EO<sub>♂</sub>; Hb<sub>F<sub>♀</sub></sub>: Wild.NA<sub>♀</sub> × Farm.EO; Wild.NA: NF wild with no signal of EO ancestry

Fig. 2B, Table S1). No differences in intermediate status were observed.

### 3.2. Growth and condition in tank and stream environments 2016

A significant effect of cross type on growth ( $\text{SGR}_{\text{mass}}$  and  $\text{SGR}_{\text{length}}$ ) and body condition was detected in both the tank and stream environments in 2016 (Tables 2 & 3, Fig. 3A–F). In order to assess the effect of competition on the wild fish, we compared their performance

in allopatry versus sympatry with farmed and hybrid fish. We found that in the tank environment, the growth ( $\text{SGR}_{\text{mass}}$  and  $\text{SGR}_{\text{length}}$ ) of Wild.NA<sub>EO</sub> fish in allopatry did not differ from those in either sympatric treatment (Table 3, Fig. 3A,B). However, in the stream environment, Wild.NA<sub>EO</sub> fish in the Sympatric NA treatment had higher growth ( $\text{SGR}_{\text{mass}}$  and  $\text{SGR}_{\text{length}}$ ) than Wild.NA<sub>EO</sub> fish in allopatry and in the Sympatric EO treatment (Table 3, Fig. 3D,E). In contrast, no differences in condition were observed between allopatric and sympatric Wild.NA<sub>EO</sub> fish in either the tank or stream environments (Table 3, Fig. 3C,F).

**Table 2.** Linear mixed-effects model selection for examining growth variation (specific growth rate in terms of mass and length [ $\text{SGR}_{\text{mass}}$ ,  $\text{SGR}_{\text{length}}$ ], and condition) in Atlantic salmon between treatments, environments, and cross types from the 2016 and 2017 growth experiments (superscript a and b, respectively). Significant fixed effects (p-values in **bold**) were retained in the final model. \*Insignificant fixed effects were also retained in the final model as the interaction terms were significant. Significant random effects (final density nested within replicate) were also retained in the final model. df: degrees of freedom based on Satterwaite's approximations. C: cross types; E: environments; T: treatments

Treatment	Variable	Growth experiment (2016) <sup>a</sup>				Variable	Growth experiment (2017) <sup>b</sup>			
		SS	df	F	p		SS	df	F	p
Allopatric Wild vs. Sympatric Wild	<b>SGR<sub>mass</sub></b>					<b>SGR<sub>mass</sub></b>				
	T	0.67	2, 55	16.35	<b>&lt;0.0001</b>	T	0.07	2, 66	4.43	<b>&lt;0.05</b>
	E	8.71	1, 55	424.5	<b>&lt;0.0001</b>	E	5.78	1, 66	94.3	<b>&lt;0.0001</b>
	T × E	0.28	2, 55	6.71	<b>&lt;0.001</b>	T × E	0.17	2, 66	1.42	0.25
	<b>SGR<sub>length</sub></b>					<b>SGR<sub>length</sub></b>				
	T	0.05	2, 55	7.06	<b>&lt;0.01</b>	T	0.00	2, 66	4.29	<b>&lt;0.05</b>
	E	0.76	1, 55	213.0	<b>&lt;0.0001</b>	E	0.45	1, 66	109.2	<b>&lt;0.0001</b>
	T × E	0.06	2, 55	7.86	<b>&lt;0.001</b>	T × E	0.01	2, 66	1.02	0.37
	<b>Condition</b>					<b>Condition</b>				
Sympatric NA <sup>a</sup> /Sympatric-I <sup>b</sup>	<b>SGR<sub>mass</sub></b>					<b>SGR<sub>mass</sub></b>				
	C	0.11	2, 48.61	2.46	0.09*	C	1.93	2, 66	15.80	<b>&lt;0.0001</b>
	E	9.60	1, 51.12	436.1	<b>&lt;0.0001</b>	E	7.29	1, 66	119.1	<b>&lt;0.0001</b>
	C × E	0.58	2, 44.78	13.29	<b>&lt;0.0001</b>	C × E	0.10	2, 66	0.80	0.45
	<b>SGR<sub>length</sub></b>					<b>SGR<sub>length</sub></b>				
	C	0.01	2, 57.92	1.80	0.17*	C	0.10	2, 44.87	22.89	<b>&lt;0.0001</b>
	E	0.62	1, 60.06	280.1	<b>&lt;0.0001</b>	E	0.15	1, 65.31	63.53	<b>&lt;0.0001</b>
	C × E	0.04	2, 53.55	9.94	<b>&lt;0.001</b>	C × E	0.04	2, 51.17	7.71	<b>&lt;0.01</b>
	<b>Condition</b>					<b>Condition</b>				
Sympatric EO <sup>a</sup> /Sympatric-II <sup>b</sup>	<b>SGR<sub>mass</sub></b>					<b>SGR<sub>mass</sub></b>				
	C	0.77	2, 55	14.83	<b>&lt;0.0001</b>	C	3.24	2, 53.17	55.82	<b>&lt;0.0001</b>
	E	9.46	1, 55	365.4	<b>&lt;0.0001</b>	E	6.40	1, 61.66	220.3	<b>&lt;0.0001</b>
	C × E	0.08	2, 55	1.52	0.22	C × E	1.23	2, 47.85	21.25	<b>&lt;0.0001</b>
	<b>SGR<sub>length</sub></b>					<b>SGR<sub>length</sub></b>				
	C	0.08	2, 51.56	11.37	<b>&lt;0.0001</b>	C	0.20	2, 55	33.74	<b>&lt;0.0001</b>
	E	0.82	1, 52.62	226.6	<b>&lt;0.0001</b>	E	0.69	1, 55	234.1	<b>&lt;0.0001</b>
	C × E	0.02	2, 51.67	2.84	0.07	C × E	0.12	2, 55	20.64	<b>&lt;0.0001</b>
	<b>Condition</b>					<b>Condition</b>				
C	0.12	2, 66	14.71	<b>&lt;0.0001</b>	C	0.07	2, 66	1.33	0.12	
E	0.16	1, 66	37.76	<b>&lt;0.0001</b>	E	0.08	1, 66	9.35	<b>&lt;0.01</b>	
	C × E	0.00	2, 66	0.40	0.67	C × E	0.04	2, 66	2.17	0.12

**Table 3.** Cross type effects on fitness-related traits in Atlantic salmon between competitive treatments in tank and stream environments (2016 and 2017) using mixed-effects models (controlled for random intercept). Significant values after sequential Bonferroni correction (\* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ; \*\*\*\* $p < 0.0001$ ; NS: not significant). Different letters denote significant differences in estimated marginal mean traits among cross types. Cross types in 2016: Wild.NA<sub>EO</sub>: Newfoundland (NF) wild with a signal of European (EO) ancestry; Farm.NA: North American (NA) farmed; Hb.NA: hybrid Wild.NA<sub>EO</sub> × Farm.NA; Farm.EO: Farm.NA<sub>EO</sub> × Farm.EO farmed; Hb.EO: Wild.NA<sub>EO</sub> × Farm.EO. Cross types in 2017: Wild.NA: NF wild with no signal of EO ancestry; Farm.EO: Hb<sub>WFg</sub>: Wild.NA $\delta$  × Farm.EO $\delta$ ; SGR<sub>mass</sub>: specific growth rate in terms of mass and length SGR<sub>length</sub>: specific growth rate in terms of mass and length

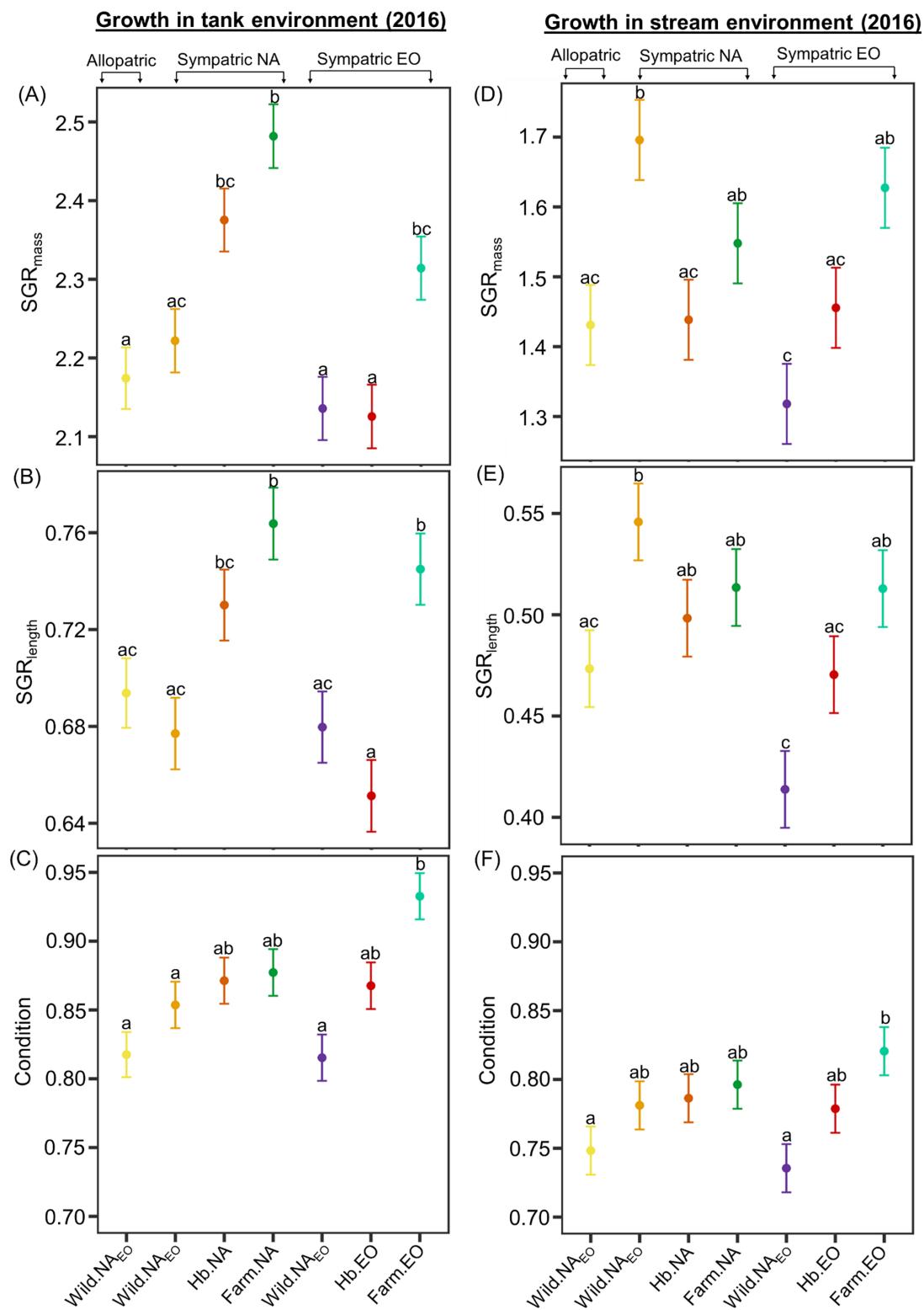


Fig. 3. (A–F) Cross type effects on Atlantic salmon growth differences in tank and stream environments (2016) using mixed-effects models. Displayed are marginal means  $\pm$  SE. Different letters denote significant differences in estimated marginal mean traits among cross types. The axes differ between panels for specific growth rates in terms of mass ( $SGR_{mass}$ ) and length ( $SGR_{length}$ ). See Table S2 for estimated marginal means and Table S3 for Tukey-adjusted pairwise contrasts among cross types fitted in the final models. See Fig. 2 for cross types

In the Sympatric NA treatment, growth ( $SGR_{mass}$  and  $SGR_{length}$ ) of Farm.NA was higher in the tank environment than Wild.NA<sub>EO</sub>, with Hb.NA being intermediate and not differing from the other 2 (Table 3, Fig. 3A,B). However, in the stream environment, Wild.NA<sub>EO</sub> exhibited higher  $SGR_{mass}$  than Hb.NA, with Farm.NA being intermediate and not differing from the other 2, while there was no difference in  $SGR_{length}$  among cross types (Table 3, Fig. 3D,E). There were also no differences in condition observed among cross types within the Sympatric NA treatment for either the tank or stream environments (Table 3, Fig. 3C,F). In the Sympatric EO treatment, Farm.EO had higher growth ( $SGR_{mass}$ ,  $SGR_{length}$ ) performance than both Wild.NA<sub>EO</sub> and Hb.EO in the tank environment, which did not differ between themselves (Table 3, Fig. 3A,B). In the stream environment, however, Farm.EO exhibited a higher growth performance than only Wild.NA<sub>EO</sub>, with Hb.EO being intermediate and not differing from the other 2. Wild.NA<sub>EO</sub> had lower condition than Farm.EO, with Hb.EO being intermediate in both environments.

### 3.3. Growth and condition in tank and stream environments 2017

Significant differences in growth ( $SGR_{mass}$  and  $SGR_{length}$ ) were observed among the Farm.EO strain, Wild.NA population, and related hybrids in both the tank and stream environments in 2017, but not in terms of body condition (Tables 2 & 3, Fig. 4). When assessing the effect of competition on the wild fish in allopatry versus sympatry with farmed and hybrid fish, we found no differences in growth performance ( $SGR_{mass}$  and  $SGR_{length}$ ) or condition in either the tank or stream environments (Table 3, Fig. 4).

In the Sympatric-I treatment (Wild, Hb<sub>W9</sub>, Farm.EO), Farm.EO and Hb<sub>W9</sub> had higher  $SGR_{mass}$  than Wild.NA in the tank environment, and the pattern was similar in terms of  $SGR_{length}$ , except that Hb<sub>W9</sub> was intermediate (Table 3, Fig. 4A,B). In the stream environment, Farm.EO had higher  $SGR_{mass}$  than Wild.NA, with Hb<sub>W9</sub> being intermediate (Table 3, Fig. 4D). The pattern was similar for  $SGR_{length}$ , except that Hb<sub>W9</sub> had higher growth than Wild.NA (Fig. 4E). There were no differences in condition among cross types in both the tank and stream environments (Table 3, Fig. 4C,F). In the Sympatric-II treatment (Wild, Hb<sub>F9</sub>, Farm.EO), Farm.EO had higher growth performance ( $SGR_{mass}$  and  $SGR_{length}$ ) than Wild.NA in the tank environment, with Hb<sub>F9</sub> having intermediate performance that did

not differ from the other 2 (Table 3, Fig. 4A,B). In the stream environment, the pattern was similar, except that the intermediate growth performance of Hb<sub>F9</sub> now differed significantly from that of both the farmed strain and wild population (Table 3, Fig. 4D,E). No differences in condition were detected among cross types both in the tank and stream environments (Table 3, Fig. 4C,F).

### 3.4. Growth plasticity across environments

Significant interactions of competitive treatment or cross type with environment were detected in both 2016 and 2017 (Table 2), indicative of treatments/cross types responding differently to environments in a plastic manner, resulting in differing growth reaction norms (Fig. 5A–D). In terms of slopes in  $SGR_{mass}$  between environments (2016), Wild.NA<sub>EO</sub> in the Sympatric NA treatment displayed a flatter reaction norm slope than those in the Allopatric and Sympatric EO treatments (Fig. 5A). For  $SGR_{length}$ , slopes for Wild.NA<sub>EO</sub> were similar among Allopatric, Sympatric NA and EO (Fig. 5B). Within the Sympatric NA treatment (2016), the  $SGR_{mass}$  and  $SGR_{length}$  slopes were flatter for Wild.NA<sub>EO</sub> than that for Farm.NA and Hb.NA. However, within the Sympatric EO treatment (2016), similar plastic responses/growth reaction norms in terms of  $SGR_{mass}$  and  $SGR_{length}$  were observed across the environments. In contrast, similar growth reaction norms across environments were observed for the Allopatric vs. Sympatric Wild treatments in 2017 (Table 2, Fig. 5C,D). Within the Sympatric-I treatment of 2017,  $SGR_{mass}$  reaction norms were similar among cross types across the environments, while there was significant a cross × environment interaction for  $SGR_{length}$ , indicative of differing reaction norms across the environments. In the latter case, Wild.NA showed a steeper slope than Hb<sub>W9</sub> and Farm.EO. Within the Sympatric-II treatment of 2017, for both  $SGR_{mass}$  and  $SGR_{length}$ , Wild.NA and Farm EO showed flatter slopes than Hb<sub>F9</sub>.

### 3.5. Survival

No significant differences in survival were observed among Farm.EO and Farm.NA strains, NF wild populations, or related hybrids in the tank and stream environments in 2016 and 2017 ( $p > 0.05$ ; Table 4, Fig. 6A–D). In the Allopatric Wild vs. Sympatric Wild treatments in 2016 and 2017, the only

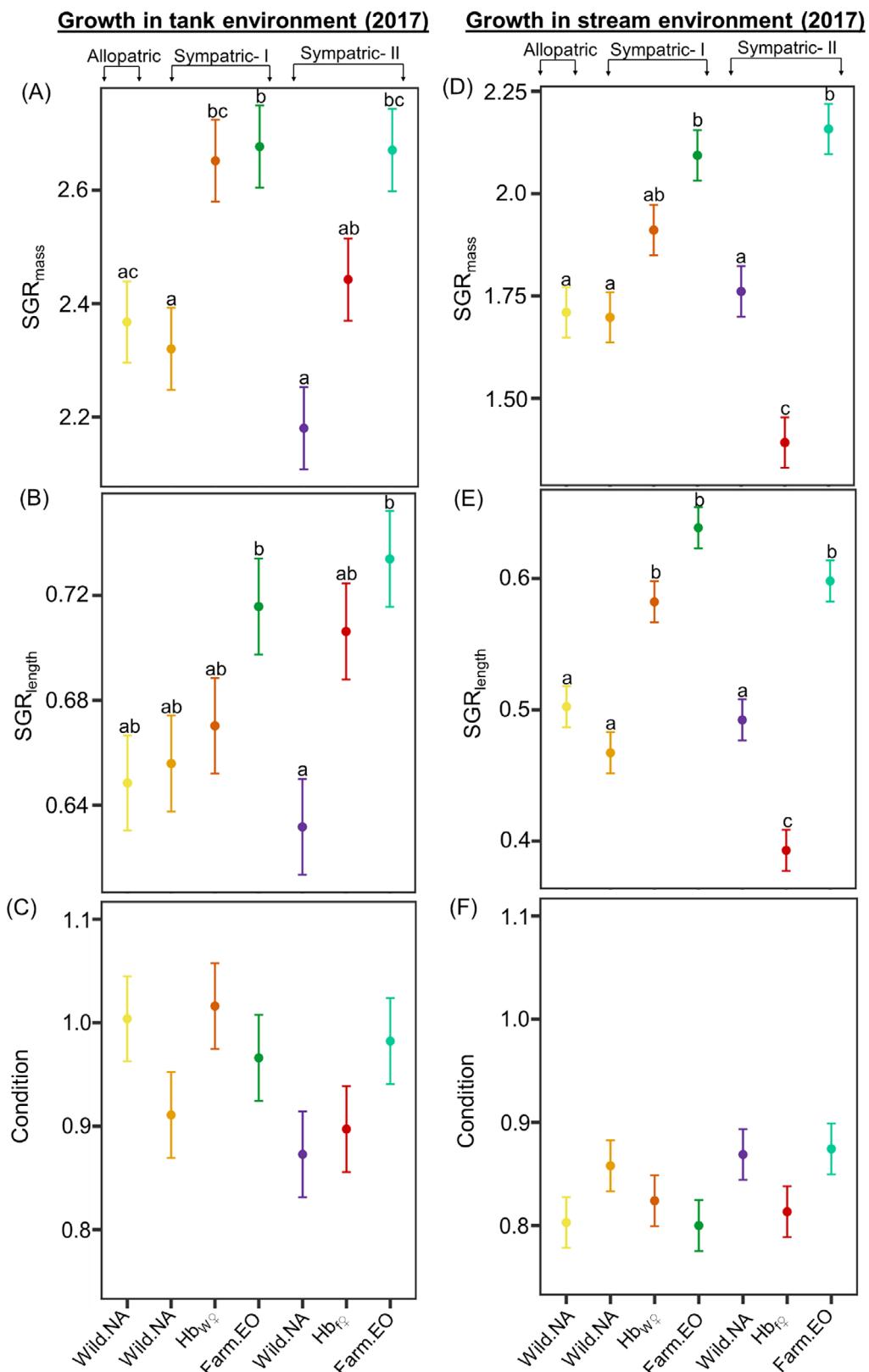


Fig. 4. (A–F) Cross type effects on Atlantic salmon growth differences in tank and stream environments (2017) using mixed-effects models. See Table S2 for estimated marginal means and Table S3 for Tukey-adjusted pairwise contrasts among cross types fitted in the final models. See Fig. 2 for cross types

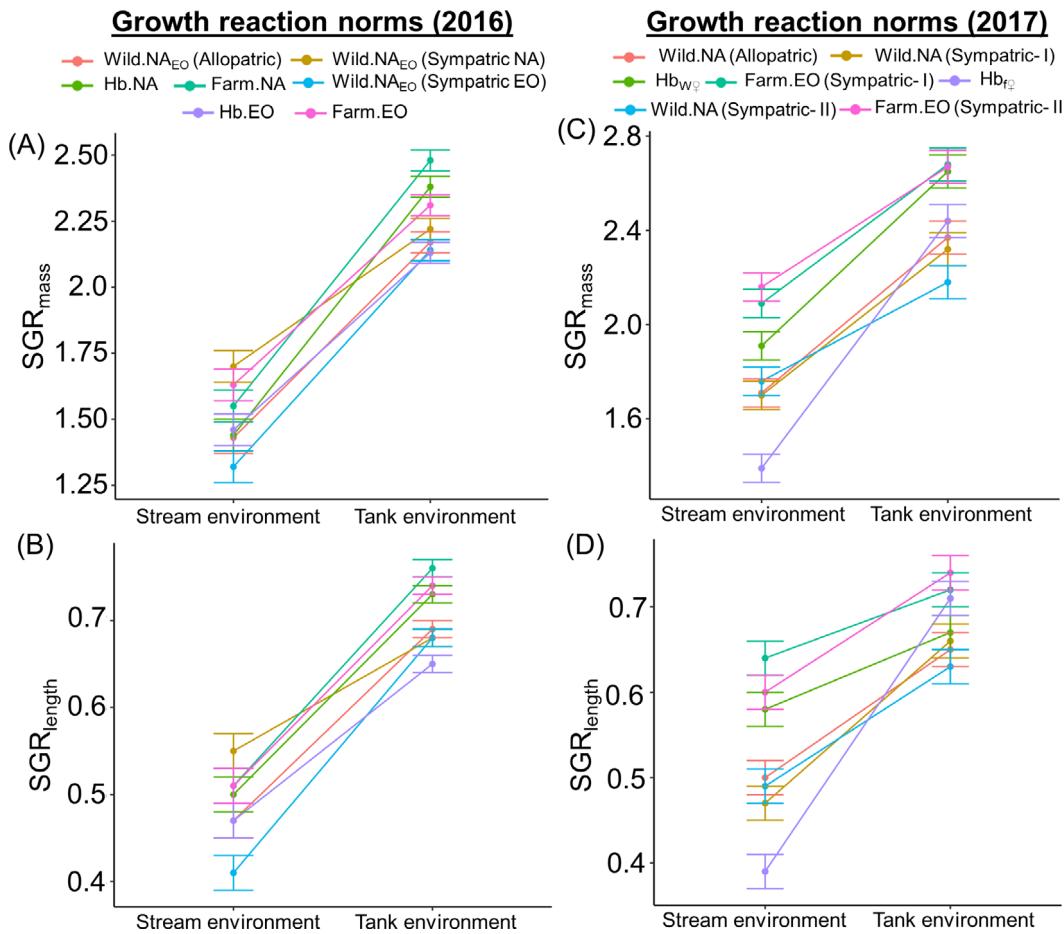


Fig. 5. (A–D) Growth reaction norms of Atlantic salmon between environments (tank environment with pellet feed; stream environment with semi-natural feed) among cross types in 2016 and 2017 experiments. Displayed are marginal means  $\pm$  SE. The axes differ between panels. See Fig. 2 for cross types

model term that was significant and retained in the final model was environment ( $\chi^2 = 7.65$ ,  $p < 0.05$  and  $\chi^2 = 9.76$ ,  $p < 0.01$ , respectively; Table 4). The only case of a significant effect of environment was for the Sympatric-II treatment in 2017 ( $\chi^2 = 4.40$ ,  $p < 0.05$ ; Table 4), which was therefore retained after model selection.

#### 4. DISCUSSION

The present study demonstrated fitness-related trait (dominance and growth) differences among divergent Farm.EO and Farm.NA strains, NF wild populations, and related F<sub>1</sub> hybrid salmon and provides insight into the potential fitness effect of hybridization. The main findings can be summarized in 5 key points. (1) Farm.NA fish were more dominant and less subordinate than NF wild conspecifics. Hybrids were intermediate in expression and did not

differ from wild fish. Farm.EO fish also tended to dominate NF wild fish, though the difference was not significant. (2) Competition with farm and hybrid fish did not affect the growth of wild fish in sympatry versus allopatry with the exception of wild fish in the Sympatry NA treatment of the stream environment outgrowing those in allopatry. (3) Within sympatric treatments, farmed fish outgrew wild fish in all comparisons except in the Sympatry NA treatment in the stream environment. (4) F<sub>1</sub> hybrids tended to exhibit intermediate growth performance relative to those of the pure farmed strains and native wild populations both in tank and stream environments. (5) No survival difference was detected among cross types in either the tank or stream environments. These findings suggest that irrespective of EO or NA ancestry, farmed salmon display greater dominance and growth than wild salmon in a tank environment. However, in the stream environment, competition imposed by Farm.NA fish and related hybrids on

Table 4. Generalized linear mixed-effects model (GLMM) selection for investigating differences in survival of Atlantic salmon using likelihood ratio tests between treatments, environments, and cross types from the 2016 and 2017 survival experiments. Final density nested within replicate was included as a random intercept. AIC: Akaike's information criterion. C: cross type; E: environment; T: treatment; <sup>a</sup>retained final model. Significant fixed effects (p-values in **bold**) were retained in the final model

Treatment	Model no.	Terms included in GLMM model	Terms tested	Versus model no.	Log likelihood	AIC	df	$\chi^2$	p
<b>Survival experiment (2016)</b>									
Allopatric Wild vs.	0	T + E + T: E			-88.51	193.01	8		
Sympatric Wild	1 <sup>a</sup>	T + E	T: E	0	-88.78	188.32	6	0.55	0.76
	2	T	E	1	-89.16	189.56	5	7.65	<b>&lt;0.05</b>
	3	E	T	1	-92.60	193.21	4	0.76	0.38
Sympatric NA	Survival								
	0	C + E + C: E			-66.11	148.21	8		
	1	C + E	C: E	0	-66.21	144.43	6	0.22	0.90
	2	C	E	1	-66.22	142.44	5	0.01	0.92
	3 <sup>a</sup>	E	C	1	-66.53	141.06	4	0.63	0.73
	4	Intercept only	C + E	1	-66.53	139.06	3	0.62	0.89
Sympatric EO	Survival								
	0	C + E + C: E			-80.11	176.21	8		
	1	C + E	C: E	0	-80.26	172.53	6	0.31	0.86
	2 <sup>a</sup>	C	E	1	-80.27	170.54	5	0.02	0.90
	3	E	C	1	-82.41	172.83	4	4.30	0.12
	4	Intercept only	C + E	1	-82.42	170.84	3	4.32	0.23
<b>Survival experiment (2017)</b>									
Allopatric Wild vs.	0	T + E + T: E			-70.64	153.34	8		
Sympatric Wild	1 <sup>a</sup>	T + E	T: E	0	-68.67	153.28	6	3.94	0.14
	2	T	E	1	-75.52	161.04	5	9.76	<b>&lt;0.01</b>
	3	E	T	1	-71.33	150.65	4	1.38	0.50
Sympatric-I	Survival								
	0	C + E + C: E			-49.63	112.10	8		
	1	C + E	C: E	0	-48.05	111.27	6	3.17	0.21
	2	C	E	1	-49.64	109.29	5	0.02	0.90
	3 <sup>a</sup>	E	C	1	-49.84	107.69	4	0.41	0.81
	4	Intercept only	C + E	1	-49.85	105.70	3	0.43	0.93
Sympatric-II	Survival								
	0	C + E + C: E			-74.19	164.38	8		
	1 <sup>a</sup>	C + E	C: E	0	-74.49	160.98	6	0.60	0.73
	2	C	E	1	-76.69	163.38	5	4.40	<b>&lt;0.05</b>
	3	E	C	1	-77.80	163.60	4	0.52	0.76

wild fish was less than that imposed by the Farm.EO strain and related hybrids, as evident in growth performance.

#### 4.1. Differences in dominance status

Our findings are consistent with the observations of earlier farmed-wild dominance studies (Einum & Fleming 1997, Fleming & Einum 1997, Houde et al. 2010a) in that farmed fish tend to dominate wild fish, and hybrids are frequently intermediate. This is not surprising, as behavioural traits (e.g. dominance) are believed to be among the first traits to respond to domestication (Price 1984, Huntingford 2004). More-

over, both Farm.NA and Farm.EO fish showed similar patterns in dominance status, suggesting common domestication effects as observed previously in terms of exploratory behaviour, novel object response, boldness under predation risk, and aggression (Islam et al. 2020). These effects are likely to be at least partly genetic, given that the fish were reared and tested under common environmental conditions.

#### 4.2. Growth and survival differences in tank and stream environments

Interestingly, we found no growth difference in wild fish (Wild.NA<sub>EO</sub> and Wild.NA) when reared in

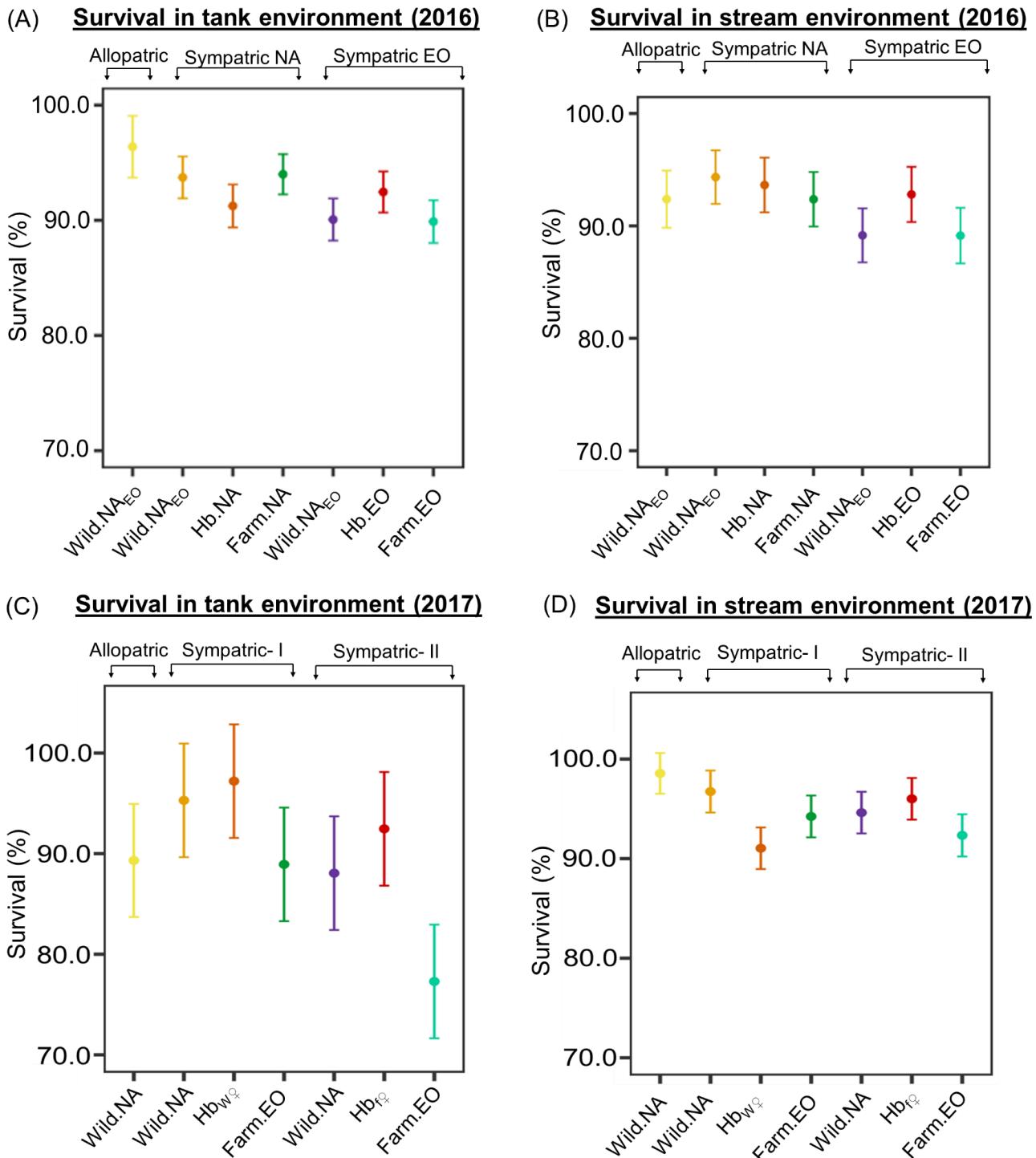


Fig. 6. (A–D) Cross type effects on Atlantic salmon survival differences in tank and stream environments (2016 and 2017 experiments) using mixed-effects models. Displayed are marginal means  $\pm$  SE. See Table S2 for estimated marginal means and Table S4 for Tukey-adjusted pairwise contrasts among cross types fitted in the final models. See Fig. 2 for cross types

allopatry versus sympatry in the tank environment; however, in the stream environment, Wild.NA<sub>EO</sub> in sympathy (Sympatric NA; i.e. competing with Farm.NA and Hb.NA) outgrew their counterparts in allopatry.

Given the difference in dominance, one might necessarily expect a growth difference between allopatric and sympatric wild in the tank environment, as the tank environment is somewhat more benign than

that of the stream environment, but the inter-strain competition for food may remain in the sympatric treatment. However, the high densities of commercial aquaculture tend to suppress social interaction and hierarchies (Laursen et al. 2015, Johnsson & Näslund 2018). Our results indicate that the effects of intra-strain competition, or lack thereof, for wild fish in the tank environment are no different than that of inter-strain competition with farmed and hybrid fish, a pattern that has also been observed with Norwegian populations (Solberg et al. 2013b). There was just one difference in growth between wild fish in allopatry and sympathy in the stream environment: wild fish in Sympatry NA (i.e. with Farm.NA and Hb.NA) but not in Sympatry EO (i.e. with Farm.EO and Hb.EO) outgrew those in allopatry. This is indicative of intra-strain competition for Wild.NA<sub>EO</sub> fish being greater than that of inter-strain competition with Farm.NA and Hb.NA. It also suggests that the different genetic origins of the farmed strains and other factors associated with semi-natural stream conditions may influence the outcome of competition between wild fish in allopatry and sympathy in the stream environment.

Within sympathy, both Farm.EO and Farm.NA fish outgrew wild fish in the tank environment, as was expected based on previous observations of other domesticated salmonid populations (Einum & Fleming 1997, Solberg et al. 2013a, Harvey et al. 2016a, Glover et al. 2018). In our study, the 2 farmed strains used are historically genetically divergent but have both experienced inadvertent domestication selection and directional selection for economically important traits; thus, an outstanding question that remained was whether these 2 farmed strains would display fitness-related trait (e.g. growth) differences between each other. In this study, both Farm.NA and Farm.EO fish equally outgrew Wild.NA<sub>EO</sub> and Wild.NA in the tank environment. It has been previously suggested that domesticated Atlantic salmon display increased consumption, metabolism, and potentially feed conversion efficiency when presented with excess and high-energy diet that results in 2–3-fold greater growth than wild conspecifics under farming conditions (Solberg et al. 2013b, Harvey et al. 2016b, Glover et al. 2018). However, this was not necessarily the same in the stream environment, as in at least one instance (i.e. Sympatric NA) Wild.NA<sub>EO</sub> outgrew Hb.NA and tended to do so relative to Farm.NA as well, though not significantly. This suggests that the impact of competition with Farm.NA and associated hybrids is less than that imposed by the Farm.EO strain. It is worth pointing out that different wild pop-

ulations as well as different cohorts of Farm.EO salmon were used in the 2 years of this study. Despite all fish growing slightly faster in 2017 than 2016, patterns of relative differences in growth between Farm.EO and the wild populations were similar between years. Condition did not differ among cross types in 2016 and 2017, except in the Sympatric EO treatment of both the tank and stream environments, where the pattern of significant differences matched those in growth. A previous study comparing domestic, wild, and hybrid rainbow trout *Oncorhynchus mykiss* in culture and semi-natural environments also found that the patterns of final body condition among cross types matched those in growth rate (Tymchuk et al. 2007). In the present study, F<sub>1</sub> hybrids tended to display intermediate growth performance relative to those of pure farmed strains and native wild populations in both the tank and stream environments—though not in all cases, which was consistent with earlier studies (Einum & Fleming 1997, McGinnity et al. 1997, 2003, Fleming et al. 2000, Houde et al. 2010a, Solberg et al. 2013a,b, Harvey et al. 2016a,b, Skaala et al. 2019).

In the present study, we found that growth was consistently better in the tank than stream environment, yet both treatments and cross types responded somewhat differently to the 2 contrasting environments in a plastic manner, resulting in different growth reaction norms. As suggested previously, such plasticity is mediated through the lack of available energy (Glover et al. 2018) or, as has been shown in brown trout *Salmo trutta*, the accessibility/use of energy (Sundt-Hansen et al. 2009), which may lead to growth-potential mortality (Solberg et al. 2013b, Glover et al. 2018) in the natural environment. It is possible that fish were unable to obtain and utilize the correct balance of nutrients to maximize growth in the stream environment. Although, unlike true natural environment with live prey and the presence of predators, in our stream study, we provided a semi-natural diet of a combination of brine shrimp and frozen blood worms in the absence of predation, where they had to seek food in a horizontally flowing environment where establishment and defence of territories may be important. We, therefore, tentatively suggest that growth in the semi-natural stream may be influenced mainly by competition for food and nutrients.

We found no survival difference among Farm.EO and Farm.NA strains, NF wild populations, and F<sub>1</sub> hybrids in both the tank and stream environments. Several previous studies have reported higher survival of wild fish in natural environments (McGinnity

et al. 1997, 2003, Fleming et al. 2000, Skaala et al. 2012, 2019, Sylvester et al. 2019), although the differences in viability may be most pronounced at the earliest life stages, and after reaching a certain size (e.g. parr), differences in survival may be less apparent (e.g. Einum & Fleming 1997, Fleming et al. 2000, Crowley et al. 2022, but see Wacker et al. 2021). Moreover, the current study was conducted in predator-free tank and stream environments, so we are less likely to see growth-potential mortality (Biro et al. 2006, Solberg et al. 2015, Glover et al. 2018) or mortality associated with differences in risk sensitivity (Einium & Fleming 1997, Fleming & Einum 1997, Houde et al. 2010b, Solberg et al. 2020). Furthermore, the experiments were undertaken for a short period of time (less than 3 mo), which may have made it difficult to identify survival differences.

#### 4.3. Implications

Extensive introgressive hybridization of escaped farmed salmon into wild populations has been recently documented in Norway (Glover et al. 2017, Bolstad et al. 2021) as well as in other regions of Europe (e.g. Scotland, Gilbey et al. 2021; Sweden, Palm et al. 2021) and throughout salmon farming regions of Atlantic Canada (O'Reilly et al. 2006, Keyser et al. 2018, Wringe et al. 2018). A persistent concern about the successful breeding of escaped farmed salmon with local wild populations and the resultant hybridization is the fitness impacts and consequent threat to local adaptation. It was unknown, however, whether the competitive and fitness consequences posed by escaped Farm.EO fish would be greater than that of escaped Farm.NA fish for local NF wild populations. The fitness-related trait (dominance and growth) differences that were observed in the current study validate these concerns of a potential threat posed by escaped farmed fish, whether they be NA or EO in origin, to local NF wild fish. Moreover, intermediate trait expression (with a few exceptions) of F<sub>1</sub> hybrids between wild and farmed fish infer that farm-wild hybridization can lead to the disruption of local adaptation, as could farm dominance in trait expression (Garcia de Leaniz et al. 2007, Fraser et al. 2011). As offspring of escaped farmed salmon have already been detected in 17 out of 18 wild salmon rivers in southern NF (Wringe et al. 2018), it is likely that a high number of hybrids will alter the trait expression patterns relative to wild fish (Sylvester et al. 2019). For example, there has been a decline in the abundance of wild salmon in southern

NF of ~45% between 1996 and 2010, particularly near the main farming area (e.g. ~70% decline in the Conne River), and these wild populations have been designated as threatened (COSEWIC 2010). In our study, we found that the performance and consequence of hybridization were similar for Farm.NA and Farm.EO strains except in the stream environment, where Farm.NA and the related hybrid were outperformed by the wild fish across the 12 replicates. The latter may suggest that concerns of introgressive hybridization for local NF wild populations could be greater from EO than NA farm escapes.

#### 5. CONCLUSIONS

In general, the present study has demonstrated that multi-generation domestication selection has generated fitness-related trait differences among divergent Farm.EO and Farm.NA strains, NF wild populations, and F<sub>1</sub> hybrids. Briefly, common domestication effects appear to be responsible for both Farm.NA and Farm.EO fish tending to dominate their NF wild conspecifics in the tank environment. Similarly, such effects are likely responsible for both farm strains outgrowing their NF wild conspecifics in the tank environment, but this was not always the same scenario in the stream environment. Also, we found that F<sub>1</sub> hybrids tended to exhibit intermediate performance when competing with farmed and wild juveniles. Moreover, extensive interbreeding of escaped farmed salmon with wild populations can influence lifetime fitness and threaten native populations (Fleming et al. 1996, 2000, McGinnity et al. 1997, 2003, Skaala et al. 2012, 2019). Our findings suggest that irrespective of their origins, both escaped Farm.EO and Farm.NA salmon displayed greater dominance and growth than wild fish in a tank environment. However, the impact of competition for NF wild salmon was less from Farm.NA and related hybrids than that of Farm.EO salmon in the stream environment. As such, understanding the effect of hybridization and, consequently, fitness-related trait differences among divergent farmed, wild, and F<sub>1</sub> hybrid populations can provide valuable insights for the conservation and management of Atlantic salmon.

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