Common-garden comparison of relative survival and fitness-related traits of wild, farm, and hybrid Atlantic salmon *Salmo salar* parr in nature

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ABSTRACT: When escapee farmed Atlantic salmon *Salmo salar* interbreed with wild fish, the introgression of maladaptive genes can lower wild population productivity and alter key life history traits. To date, only a few European studies have compared wild, farm, and hybrid salmon under common conditions in the wild, isolating the influence of genetics on survival and fitness-related traits. Here, we examined the performance of experimentally derived Atlantic salmon fry from 4 cross types (wild, farm, and reciprocal F₁ hybrids) during the first summer of growth at 3 locations in southern Newfoundland. Overall survival was high, with the cross type rank order consistent across sites (mean percent recaptured: wild-mother hybrids 26.2% ≈ wild 26.0% > farm 19.2% > farm-mother hybrids 12.8%). Wild fish were smaller than wild-mother hybrids and farm fish, though differed less in size from farm-mother hybrids. At 2 out of 3 sites, wild-mother hybrids were larger than wild and farm-mother hybrid fish but had only a small size advantage over farm fish. Shape differences were small and mainly related to body depth, with the largest differences between wild and farm fish. Wild-mother hybrids had fewer parr marks than other cross types at a single site, and though differences in the size of marks were minimal, farm fish tended to have the narrowest marks. Overall, these results show that genetic differences exist for fitness-related traits among wild, farm, and hybrid juveniles, even over short temporal scales and under favourable environmental conditions, and may contribute to patterns of reduced farm-mother hybrid and feral farm survival in the wild.

KEY WORDS: Aquaculture escapes · Farm–wild hybridization · Introgression · Juvenile performance
risk-aversion of farm fish (e.g. Fleming & Einum 1997, Fleming et al. 2000, Bradbury et al. 2020). Therefore, investigating differences in fitness-related traits as well as differences in survival itself between wild, farm, and hybrid salmon is key to determining and managing the impacts of escaped farm salmon on wild salmon populations.

Generally, field and laboratory studies indicate that farm Atlantic salmon typically grow faster than wild conspecifics (i.e. Glover et al. 2009, 2018, Solberg et al. 2013b, Harvey et al. 2016b, Skaala et al. 2019). This may be advantageous for farm parr in competition with wild parr, as faster-growing farm fish may displace slower-growing wild fish from suitable habitat during the parr stage in the wild (Fleming et al. 2000, McGinnity et al. 2003). However, faster growth may also be a liability for farm fish in the wild, with evidence for selection against such faster-growing individuals (e.g. growth-potential mortality; Solberg et al. 2020) in addition to the lower risk-aversion of farm fish (e.g. Fleming & Einum 1997). Thus, the influence of growth on survival appears to depend on the specific nature of the ecological interactions between cross types, as well as the environment in which they live.

Differences in morphology among wild, farm, and hybrid Atlantic salmon (Fleming et al. 1994, Fleming & Einum 1997, Solem et al. 2006) may also be indicative of differential adaptation and survival capabilities. For example, differences in head size may be reflective of different feeding/foraging environments (Solem et al. 2006), while fin sizes may be reflective of the water velocities experienced by each cross type in their respective environments (Riddell & Leggett 1981), and body shape may be a result of selection pressures necessitating a certain level of swimming performance (Fleming & Einum 1997). In addition, differences in number and contrast of parr marks (the dark vertical bands on the sides of parr) between wild and hatchery strains may impact the juveniles’ abilities to camouflage against the streambed and thus avoid predators (Culling et al. 2013). Given these implications, the degree of morphological differentiation between interacting cross types has the potential to contribute to differences in performance and, ultimately, survival.

To date, just a few studies have quantified survival and phenotypic differences among wild, farm, and hybrid juveniles in the wild, and all have been done in Europe (Einum & Fleming 1997, Fleming et al. 2000, McGinnity et al. 2003, Skaala et al. 2012, 2019). In general, these studies show that farm juveniles typically have lower survival compared with their wild conspecifics, while hybrid survival is generally intermediate to the 2 pure crosses (McGinnity et al. 1997, Fleming et al. 2000, Skaala et al. 2012, 2019). However, since Atlantic salmon populations tend to be highly differentiated genetically between the eastern and western Atlantic (King et al. 2001, Lehnert et al. 2019, 2020), the nature of wild–farm interactions in these European studies may not be directly applicable to North American farm–wild interactions. It is crucial to characterize differences between farm, wild, and hybrid salmon at local scales since the extent to which farm introgression has an impact on a wild population seems often to be dependent on factors such as the demographics of the wild population in question and its original relatedness to the invading farm stock (e.g. Heino et al. 2015, Wringe et al. 2018).

This study aimed to assess differences in survival, growth, and morphology of North American first-feeding Atlantic salmon fry from 4 cross types (wild, farm, and reciprocal F1 hybrids) during the first summer of growth in multiple tributaries of a natural river on the south coast of Newfoundland. Specifically, the 4 main objectives were to compare among all cross types within each study site (1) odds of recapture, (2) recapture size (weight and length) and condition, (3) external morphology, and (4) parr marks. The overarching goal was to examine differences among these 4 cross types while isolating the influence of genetics on these traits by subjecting fish to common environmental conditions within each of 3 study sites throughout the experimental period. The use of 3 replicate experimental sites/tributaries allowed for investigation as to whether farm, wild, and hybrid fish differ from one another in their traits by the same degree in different environments. This study extends existing research on wild, farm, and hybrid Atlantic salmon performance in the wild in southern Newfoundland (Wringe et al. 2018) to better inform predictions of population responses to escaped farm salmon in Atlantic Canada (e.g. Keyser et al. 2018, Sylvester et al. 2019, Bradbury et al. 2020).

### 2. MATERIALS AND METHODS

#### 2.1. Cross, release, and recapture

Between 28 November and 21 December 2017, 4 different crosses of Atlantic salmon *Salmo salar* were generated: 8 families of wild offspring from wild parents of the Garnish River, 6 families of farm offspring...
from parents of the Saint John River farm strain, and 7 and 6 families of the reciprocal F, hybrids of the above-mentioned farm and wild parents (denoted farm-mother hybrids [Fhyb] and wild-mother hybrids [Whyb], respectively). The Garnish River system is located on the Burin Peninsula on the south coast of Newfoundland, emptying into Fortune Bay (mouth of river: 47.2353, –55.3443) and is near an area of intensive Atlantic salmon aquaculture (Fig. 1). The Saint John River (New Brunswick) strain of Atlantic salmon is, to date, the only farm strain used in Atlantic Canada commercial aquaculture operations.

Families from farmed mothers were spawned earlier (28 November–7 December) than those from wild mothers (7–21 December) due to a difference in timing of spawning-readiness of these females. Numbers of parents used in crosses were n = 3 (farm mothers and fathers, respectively), n = 9 (wild fathers), and n = 10 (wild mothers). The relatively small number of farm parents used in the crosses reflects the number of available fish that matured that year. Parents of each cross were fin-clipped, with samples stored in anhydrous ethanol for later use in parentage assignment of offspring. A sample of 10 unfertilized eggs from each female was retained and subsequently weighed and photographed for size measurements to account for potential associated maternal effects.

Embryos were incubated in Heath trays on ambient water at the Ocean Sciences Centre of Memorial University (St. John’s, Newfoundland and Labrador, Canada), where ambient water temperature was monitored daily (range: 3–8°C), and dead embryos were removed every 4–5 d. Shortly after emergence (i.e. first feeding), juveniles were pooled (22 May 2018) by cross type and transferred to 470 l flow-through circular holding tanks (0.9 m diameter × 0.5 m high). Pooled families within a cross type were roughly equal in terms of numbers of fry, with all families estimated to have at least 100 fry (except for one family from each of farm, wild, and Whyb, respectively). Juveniles were raised in ambient water and fed a combination of Artemia and salmonid starter dry feed (crumbles: 0.5 g, caloric content: 55% protein and 15% fat; EWOS-Cargill) for 1 mo, followed by only dry feed until release. Release occurred on 11 July 2018 at 3 tributary sites of the Garnish River (Fig. 1). Environmental variation was not quantified among the release sites as it was not a focus of the study; rather, the interest was in replicability of findings across different environments. Prior to release, all fry were adipose fin-clipped (anaesthetized using MS-222 at a dose of 50 mg l⁻¹ buffered with an equal amount of sodium bicarbonate) to distinguish them from wild fish upon later recapture. In addition, fish to be released at Site 2 were photographed. A total of 2000 juveniles were to be released at each site; however, since some fry died during transportation to the sites, the actual numbers released were 1932 at Site 1, 1980 at Site 2, and 1972 at Site 3. Numbers of all 4 cross types released at each site were approximately equal, though the Whyb group had ~50 more fish and the wild group ~50 fewer fish than the farm and Fhyb groups at each site. Fry were released at 4 locations approximately 50 m apart at each site.

Animal use was approved by the Memorial University of Newfoundland Institutional Animal Care Committee (IACC) following Canadian Council of Animal Care (CCAC) guidelines, under protocol number 18-01-IF.

Recapture occurred from 2–5 October 2018 using multiple pass electrofishing. For Site 3, a single electrofishing unit (LR-24 Backpack Electrofisher; Smith Root) was used; for Sites 1 and 2 (which had wider channels), 2 electrofishing units were used on opposite sides of the channel. The electrofishing
units were set at 550 V and 60 Hz, with a duty cycle of 25%. Recapture began approximately 150–200 m downstream from the first release points, over which the first ~20 m no fish were recaptured (Sites 1 and 2), or at a culvert downstream from the first release point (Site 3). Electrofishing continued up-stream until a natural barrier was reached (Site 3) or when no experimental individuals were recaptured over approximately 25 m (Sites 1 and 2). Sites 2 and 3 were each sampled on 2 different days, while Site 1 was sampled on only one day due to logistical constraints.

Recaptured fish were kept alive until processing, which occurred approximately 2 h following the end of electrofishing each day. Fish were euthanized using MS-222 (400 mg l⁻¹ buffered with an equal amount of sodium bicarbonate) and immediately photographed (Sony Alpha a5000) on the left side using a photo stand (Kaiser Reprokid digital copy stand) set at a fixed height. A size and colour standard (X-Rite Colorchecker passport) was photographed for each set of photos (i.e. at the beginning of each sampling session). All fish were then weighed (±0.01 g). The caudal fin was clipped and stored in anhydrous ethanol for later parentage analysis.

2.2. Genetic analysis

Parentage analysis was performed using caudal fin tissue samples to assign recaptured individuals to family, and therefore either wild, farm, or one of the 2 hybrid groups. Parentage analysis was done using a panel of 31 microsatellite loci with a total of 277 alleles (multiplex panel 1a from Bradbury et al. 2018), which are a subset of a larger panel of 101 loci for the Atlantic salmon genome in Atlantic Canada. Of these 31 loci, 25 were ultimately used for parentage assignment, with 6 original loci excluded due to either a high percentage of missing offspring genotypes or a high estimated allelic dropout rate. The 25 loci used included 2 with a tetranucleotide repeat sequence and 23 with a trinucleotide repeat sequence and 10–13 repeats. All loci had ≥4 alleles, with an average of 8.4 alleles locus⁻¹ over the entire panel (Bradbury et al. 2018). Additional information on locus-specific primers, repeat motifs, and chromosome numbers can be found in Table S1 of Bradbury et al. (2018).

DNA was extracted using the DNeasy 96 Blood and Tissue Kit (QIAGEN), following the manufacturer’s protocol for Purification of Total DNA from Animal Tissues. Microsatellite loci were PCR-amplified following the protocol described by Zhan et al. (2017). Sequencing was run on an Illumina MiSeq and scored using MEGASAT software (Zhan et al. 2017). Each individual fish was assigned back to its family (and therefore also its cross type) using the software program COLONY (Jones & Wang 2010). Test trials for COLONY included genotype data for all unique samples, parents, within-plate redundants, and cross-plate controls, to ensure the assignment sensitivity and accuracy of COLONY given the set of input parameters used. The final run included only unique samples (i.e. no redundants or controls).

2.3. Image analysis

Fork length measurements were taken from recapture photos of all fish at each site using ImageJ software version 1.52a (Schneider et al. 2012). In addition, 200 photos taken of fish pre-release were also measured for fork length, for a total of 50 per cross type. Care was taken to follow the lateral line of the fish’s body, to account for any body arching when present. Condition factor at recapture was calculated as the residuals taken from the regression of ln(recapture weight) on ln(recapture length) (Bolger & Connolly 1989, Wootton 1998).

For morphology analysis, landmarks were selected as in Fig. 2 and digitized using ImageJ software. All photos of fish were visually pre-screened for excess body curvature caused by fish positioning, lopsidedness, or other positioning factors that would cause problems with analysis (no recaptured fish had visible spinal deformities). Ultimately, 734 fish were landmarked, comprising 166 from Site 1, 290 from Site 2, and 278 from Site 3, of which 191 were wild, 163 were farm, 102 were Ffhyb, and 278 were Wfhyb fish. Landmarks were saved as x–y coordinates. In addition to measurements using landmarks, 120 fish (10 site−1 per cross type) were selected for pectoral fin length measurements, which were taken manually (due to variation in fin positioning) in ImageJ.

For parr mark measurements, 10 fish from each site × cross type combination were chosen randomly for analysis (total: 120 fish). Parr marks were counted manually, and each mark was measured width-wise across its widest point parallel to the lateral line and lengthwise perpendicular to the lateral line from the lateral line to the bottom of the mark. Measurements of marks were performed using ImageJ.
2.4. Statistical methods

2.4.1. Models for recapture, weight, and parr marks

All statistical analyses were performed in R version 4.0.2 (R Core Team 2020). The probability of recapture is the product of 2 probabilities: the probability of survival to time of recapture and the probability of being encountered at time of recapture (Skalski et al. 2009). However, since the design of this experiment did not allow for the separation of these 2 probabilities, probabilities and odds of recapture were used as estimates of survival here. Since the recapture (survival) data is presence-absence in form, a generalized linear model with binomial family and logit link was used for the analysis, with odds of recapture as the response.

For comparisons of release length, a linear model was used for analysis with cross type included as a factor. Recapture length and condition factor were also analyzed using linear models. All recapture size models included site and cross type as factors in addition to mean egg weight (for each mother × cross type × site combination) as a covariate and all possible interaction terms. Assumptions of normality and homoscedasticity of residuals were assessed by visual examination of residual-fit plots and normal Q–Q plots of residuals, and assumptions were met for all models ultimately used. As diagnostic plots indicated a general linear model was not a good fit for recapture weight data, a generalized linear model with the gamma family (identity link) was used since the gamma model family is also appropriate for positive continuous data. The analysis of the parr mark data used linear models to test for the effects of site and cross type on (1) number of parr marks, (2) mean width of marks, and (3) mean length of marks below the lateral line. Parr mark length and width were ln transformed before model analysis, and ln-transformed standard length was included as a covariate. Finally, the linear model for pectoral fin length (ln transformed) also included standard length (ln transformed), site, and cross type.

Although we do report p-values for model parameters, based on the recommendations of Wasserstein et al. (2019) we do not use the terms ‘statistically significant’ or ‘non-significant’ (or indeed, ‘difference vs. no difference’) with the p-value of 0.05 serving the delineator of this dichotomy. Instead, the relative evidence for the data given the models and their parameter estimates was assessed using likelihood ratios (LRs), with assessments of relative magnitude of evidence given with LR = 8 indicating ‘strong’ evidence, and LR = 32 for ‘quite strong’ evidence (Royall 1997) (though note that these designations are not meant to be ‘cut-offs’ or confer a decision-making rule). In this paper, all LRs greater than 8 will be referred to as ‘strong’ evidence. LRs give the likelihood of the data given 2 different/competing models (Glover & Dixon 2004); that is, the likelihood of the data given a model including a specific variable vs. given a model lacking it. For generalized linear models, LRs were calculated using the change in deviance (e.g. Christensen 1990) from an analysis of deviance on the given generalized linear model. For linear models, LRs were calculated using the sums of squares and were corrected for number of model parameters as in Glover & Dixon (2004). Finally, the
The \( W_f \)hyb and wild cross types had the highest percentages recaptured across all sites (26.2 and 26.0\%, respectively), followed by pure farm (19.2\%), and then \( F_f \)hyb (12.8\%) (Fig. 3A). However, only certain cross type pairs had consistently large differences from one another in their recapture odds across all 3 sites (Fig. 3B). Wild and \( W_f \)hyb had nearly identical odds of recapture at all sites. \( W_f \)hyb and wild had higher odds of recapture than \( F_f \)hyb at all 3 sites, and \( W_f \)hyb also had higher odds than farm at 2 out of 3 sites. On the other hand, differences in recapture odds for wild vs. farm were slightly less than that of \( W_f \)hyb vs. farm, with error bars overlapping the 1:1 odds ratio line at 2 out of 3 sites (i.e. indicating a result of no difference in recapture odds for these pairs was also reasonably likely).

### 3.2. Release length

There was strong evidence for the effect of cross type on length at release \((F_{3,196} = 5.53, LR = 147.6, p = 0.001)\). However, differences were very small overall, with the largest mean difference in release length between any cross type being 2.03 mm (equivalent to only 6.3\% of mean release length for all cross types; see Fig. 4b).

### 3.3. Size at recapture

There was insufficient evidence for an effect of cross type on egg weight \((LR = 0.49, p = 0.081)\), with a mean (\( \pm \)SD) egg weight from farm mothers of 94.0 ± 19.3 mg and that of wild mothers, 91.6 ± 11.5 mg. However, results of the linear model indicated there was strong evidence for an effect on mother identity nested within cross type on egg weight \((LR = 8.53 \times 10^{39}, p < 0.001)\). Therefore, mean egg weight for each individual mother was included as a covariate in the models for recapture weight, length, and condition. There was strong evidence for an effect of mean egg weight \((LR = 1.63 \times 10^{10}, p < 0.001)\), site \((LR = 4.97 \times 10^{11}, p < 0.001)\), and cross type \((LR = 212.41, p < 0.001)\) on offspring recapture weight, as well as for the interactions of mean egg weight \( \times \) cross type \((LR = 82.11, p < 0.001)\), and site \( \times \) cross type \((LR = 23.78, p < 0.001)\) (Table S2). For offspring length, there was also strong evidence for an effect of mean egg weight \((LR = 68.75, p < 0.001)\), site \((LR = 4.97 \times 10^{11}, p < 0.001)\), and cross type \((LR = 212.41, p < 0.001)\) on offspring recapture weight, as well as for the interactions of mean egg weight \( \times \) cross type \((LR = 82.11, p < 0.001)\), and site \( \times \) cross type \((LR = 23.78, p < 0.001)\) (Table S2). For offspring length, there was also strong evidence for an effect of mean egg weight \((LR = 1.63 \times 10^{10}, p < 0.001)\), site \((LR = 4.69 \times 10^{10}, p < 0.001)\), and cross type \((LR = 1.64 \times 10^{10}, p < 0.001)\), as well as for the egg weight \( \times \) cross type interaction \((LR = 9.25 \times 10^{10}, p < 0.001)\) and the site \( \times \) cross type interaction.
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(LR = 1.37 × 10^5, p < 0.001) (Table S3). Given the evidence for the site × cross type interaction term, pairwise comparisons in mean recapture weights and lengths among cross types were subsequently assessed within each site separately. These comparisons were made at the grand mean value for egg weight (93.2 mg), thereby taking into account the effect of egg weight on recapture size.

At the grand mean egg weight value, all cross types were their smallest (weight and length) at Site 1 and largest at Site 3 (Figs. 5A & 6A, Table S4). Wild individuals were smallest on average consistently across all 3 sites. At Sites 2 and 3, W\textsubscript{hyb} were largest, followed by farm and then F\textsubscript{hyb}. However, at Site 1, the order of cross types from largest to smallest was farm > F\textsubscript{hyb} > W\textsubscript{hyb} > wild.

The largest pairwise differences in recapture weight and length between cross types occurred at Site 3, except for the wild: F\textsubscript{hyb} pairing, for which the largest difference was at Site 1 (Figs. 5B & 6B). W\textsubscript{hyb} and farm were consistently larger than wild across all sites. On the other hand, farm and W\textsubscript{hyb} were similar in size at all sites (and error bars overlapped zero difference in recapture size), as were
3.4. Condition factor at recapture

There was strong evidence for an effect of site (LR = 9.83 × 10^{15}, p < 0.001), cross type (LR = 3.40 × 10^{7}, p < 0.001), and all interactions except egg weight × site on condition factor (Fig. 7A, Table S5). Pairwise differences were very similar for each cross type pair at Sites 2 and 3, with wild having lower condition than all other cross types and farm having higher condition than W_\text{hyb} (Fig. 7B). By contrast, the ±2 SE bars for all pairwise comparisons at Site 1 spanned zero difference in condition factor.

3.5. Morphology

Initially, a linear model with centroid size, site, cross type, and all possible interaction terms was run on the Procrustes coordinates. The LRs for centroid size
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(F_{1,727} = 85.71, LR = 2.27 \times 10^{14}, p < 0.001), site (F_{2,727} = 35.42, LR = 3.00 \times 10^{12}, p < 0.001), and cross type (F_{3,727} = 27.78, LR = 9.26 \times 10^{15}, p < 0.001) were >100, and these terms were thus selected for a reduced model (all other terms had LRs < 1) (Table S6). LRs for the effects of centroid size, site, and cross type provided strong evidence for their inclusion in the reduced model; however, the size of their effects on shape was small. Centroid size explained 8.9% of the variation in the data, site explained 6.3%, and cross type explained 8.6% (Table S6). Pairwise comparisons of distances between least-squares means of overall shape were made between cross types and between sites (Table 1), after accounting for centroid size. For cross type comparisons, distances between means were largest for farm vs. wild and smallest for farm vs. F\_\text{hyb}; for sites, distances were largest between Sites 1 and 2 and smallest between Sites 2 and 3. The largest cross type differences appeared to be for landmarks associated with body depth, with wild having smaller depths than other cross types; however, once again it is important to note that overall differences were small.

Fig. 5. (A) Weights of each Atlantic salmon at recapture for each cross type × site pairing, and (B) pairwise differences in mean recapture weight for each cross type by site pairing. Boxplot parameters in (A): lines: median values; upper and lower hinges: third and first quartiles (respectively); upper and lower whiskers extend to furthest value no more than 1.5 times the interquartile range above and below the upper and lower hinges (respectively). Error bars on pairwise differences in (B) ± 2 SE of the difference estimate.
For pectoral fin length, after accounting for the effect of fish standard length ($F_{1,96} = 483.4$, $LR = 7.04 \times 10^{35}$, $p < 0.001$), there was strong evidence for an effect of site on this trait ($F_{2,96} = 19.5$, $LR = 2.19 \times 10^6$, $p < 0.001$), but insufficient evidence for an effect of cross type or any interactions ($LR < 1$, $p > 0.1$). Predicted pectoral fin lengths were back-calculated from ln-transformed emmeans predictions: 11.59 mm (Site 2), 10.48 mm (Site 3), and 10.38 mm (Site 1). All site predictions were calculated at the grand mean fish standard length of 43.8 mm (which was also back-calculated from the ln-transformed mean output by the model).

3.6. Parr mark number and size

There was insufficient evidence for the standard length covariate term ($F_{1,97} = 3.26$, $LR = 1.7$, $p = 0.074$) as well as the site term and its interactions with standard length ($LR < 1.0$) on number of parr marks. However, there was evidence for the cross type term ($F_{3,97} = 2.53$, $LR = 16.3$, $p = 0.062$) as well as its interaction with site ($F_{6,97} = 1.93$, $LR = 263.6$, $p = 0.083$) on parr mark number. Therefore, pairwise comparisons of mean numbers of marks between cross types were conducted separately within each site. The largest overall pairwise differences occurred

![Fig. 6. Same as Fig. 5, but for (A) lengths of each Atlantic salmon at recapture for each cross type by site pairing, and (B) pairwise differences in mean recapture length for each cross type by site pairing](image)
at Site 3, with Wₒhyb having fewer parr marks than all 3 of the other crosses (differences all >1.7 marks; Fig. 8A, Table S7). In contrast, differences for all other pairs were <1.2 marks, with their 2*SE marks spanning zero difference in number of marks.

There was strong evidence for an effect of standard length and site on mean mark length and width (Table 2). The largest differences in mean mark length at the grand mean of standard length (44.7 mm; back-calculated from ln-transformed grand mean length output by emmeans function) were at Site 1 for Fₒhyb : Wₒhyb and farm: Wₒhyb (Fig. 8B). However, difference in size of marks for all pairs was small overall, with error bars for difference estimates spanning zero difference across all sites. One consistent result across all sites though was that farm fish tended to have narrower marks than the other cross types (Fig. 8C, Table S7).

4. DISCUSSION

We found a consistent pattern of relative cross type survival across multiple study sites, with survival higher for parr from wild mothers than those from farm mothers. We also found differences in size at
recapture among cross types, with environment also influencing patterns of growth. Morphology differences existed between sites and cross types, though very small in general. Overall, our results extend previous findings of proportional change in cross type abundances in southern Newfoundland (Wringe et al. 2018, Sylvester et al. 2019), as well as size and shape differences (Perriman et al. 2022) among offspring following a large aquaculture escape event in 2013, thereby contributing additional population-specific data to the body of research on wild–farm interactions.

### 4.1. Survival

We observed significant cross type-related differences in recapture odds that were consistent across a range of environmental conditions. In line with previous work, we saw that wild offspring had higher recapture/survival than farm offspring (McGinnity et al. 1997, 2003, Fleming et al. 2000, Skaala et al. 2012, 2019). While our results for hybrid relative survival did not follow the generally observed cross type survival trend (wild > hybrids > farm), it is important to note that some previous studies have reported results of relative survival at the cohort and/or family level that do not agree with the overall cross type pattern, and our results do correspond to some of these findings. For example, McGinnity et al. (2003) found a fairly high farm:wild relative survival value (farm ~84 % of wild) for one 0+ cohort, which falls within the range of our farm:wild percent recaptured estimates (farm: 66–85 % of wild). In addition, results which correspond to our finding of high W\textsubscript{hyb} survival include McGinnity et al. (1997), who found W\textsubscript{hyb} had the highest overall survival for one cohort of 0+ parr and spring smolts, and Skaala et al. (2012), who found that for one experimental cohort, W\textsubscript{hyb} fish had essentially the same relative survival as pure wild. Though the relatively small numbers of parents (especially of farmed origin) used in our study may not reflect within-cross type diversity to the same degree as in studies using greater numbers of families, our results nevertheless emphasize the potential for certain families to over- or under-perform relative to their overall cross type. In particular, instances of higher-than-expected hybrid success may be critical given that most escaped farm fish that breed do so with wild rather than other farm fish, meaning hybrid offspring are more likely to occur than pure feral farm offspring (e.g. Fleming et al. 1996, 2000). Therefore, it is the relative performance of hybrid offspring that will be especially important for predicting future impacts of escapees on wild populations.

It should be expected that differences in temporal scale between previous studies and this one would contribute to differences in relative recapture results. Results of studies that quantified freshwater survival at the smolt stage (Skaala et al. 2012, 2019) reflect patterns of survival over a longer period of time and a broader range of environmental conditions (perhaps most notably, winter) than those experienced by our fish. In addition, studies that began at earlier life stages would have had early-life (i.e. egg, larval) mortality, and potentially parental spawning success influence their 0+ recapture numbers, while our study looks exclusively at relative survival over the first summer of growth and controls for these factors. For example, compared with our results, the larger proportion of F\textsubscript{hyb} 0+ recaptures relative to W\textsubscript{hyb} found by Fleming et al. (2000) (who began their study at the breeding stage) appeared to be largely due to F\textsubscript{hyb} being the more likely of the 2 F1 hybrid groups given differential parental spawning success (Fleming et al. 1996). In addition, the fact that we found a smaller farm:wild survival differential than McGinnity et al. (1997) (farm: 51–53 % of wild) and Fleming et al. (2000) (farm: ~70 % of wild), could be because our study does not reflect mortality during the egg and larval stages, which these 2 other studies do.

Factors other than cross type, such as egg size, may also be an important influence on the relative survival of juvenile Atlantic salmon, and the influence of egg size may vary among populations and studies. Skaala...
Crowley et al. (2012), whose farm eggs were slightly larger than those from wild fish, found that when the effect of egg size was controlled for, farm juveniles had lower survival overall from egg to smolt stage than both wild and hybrids; however, when it was not controlled for, the families with the highest and lowest overall survival were both farm in origin. On the other hand, Skaala et al. (2019) used farm eggs that were smaller than wild, and found that while egg–smolt survival of farm fish was lower than that of wild overall, it was relatively higher after controlling for egg size than before. In our study, it was not possible to include egg weight as a covariate in the survival model since the number of fry from each mother initially released was unknown. However, there was substantial variation in egg weight among mothers, though

Fig. 8. Differences in (A) mean number of parr marks; (B) mean ln(parr mark length) below lateral line; and (C) mean ln(parr mark width) for each cross type pair of Atlantic salmon at each site. Error bar: ±2 SE of the difference estimate. Differences were calculated at the grand mean of standard length (45.20 mm)
Overall, more work is needed to investigate cross type differences in the North American wild to ultimately determine if the patterns of relative survival we observed here are broadly representative of North American populations. To date, North American studies comparing performance of farm, wild, and hybrid juveniles in the lab have found varying results in comparison to European studies. Hamoutene et al. (2017) found that North American F₁ hybrids, while potentially the most likely of the F₁ hybrids to occur (Fleming et al. 1996), had the highest mortality rates at the egg and fry stages in a lab environment, similar to our findings for relative survival of this cross type in the wild. However, other North American lab studies have found that relative survival of F₁ hybrids compared to parent populations can be environment-dependent (Fraser et al. 2008), therefore a broader survey of North American rivers/populations would be prudent and beneficial. Nevertheless, in general, our results corroborate previous research globally showing that fish from farm mothers tend to have lower survival than those from wild mothers, and differences from previously established general patterns that we see are reflective of the need for more population-specific work in order to account for this variability.

4.2. Size

We did not find evidence that larger size consistently confers higher survival for cross types as a group (though it is important to note that we were not able to investigate a link between individual size at recapture and survival within cross type groups). While Wょhyb were the largest cross type at Sites 2 and 3 and had the highest relative survival overall, this link between larger size and higher survival did not extend to the other cross types. In particular, wild parr having the second-highest survival but being

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Table 2. ANOVA results of the linear model for mean Atlantic salmon parr mark length below lateral line, and mean mark width by site and cross type. The standard length covariate was ln transformed prior to model analysis. LR: likelihood ratio

| Source                        | df | SS   | MS  | F    | p         | LR    | SS   | MS  | F    | p         | LR    | SS   | MS  |
|-------------------------------|----|------|-----|------|-----------|-------|------|-----|------|-----------|-------|------|-----|
| Standard length               | 1  | 4.600| 4.400| 487.24| <0.001 | 6.74×10¹⁰| 5.376| 5.376| 467.870| <0.001 | 4.1×10¹⁷|
| Site                          | 2  | 0.159| 0.079| 8.392 | <0.001 | 377.404| 0.275| 0.137| 11.958 | <0.001 | 7078.48|
| Cross type                    | 3  | 0.004| 0.002| 0.155 | 0.927   | 0.043 | 0.089| 0.030| 2.567 | 0.059   | 1.902 |
| Standard length × site        | 2  | 0.009| 0.004| 0.463 | 0.631   | 0.153 | 0.020| 0.010| 0.884 | 0.416   | 0.248 |
| Standard length × cross type  | 3  | 0.083| 0.028| 2.932 | 0.037   | 2.539 | 0.083| 0.028| 2.420 | 0.071   | 1.327 |
| Site × cross type             | 6  | 0.008| 0.001| 0.133 | 0.992   | 0.006 | 0.015| 0.003| 0.219 | 0.970   | 0.001 |
| Standard length × site × cross type | 6  | 0.088| 0.015| 1.556 | 0.168   | 0.030 | 0.053| 0.009| 0.771 | 0.394   | 0.002 |
| Residuals                     | 97 | 0.916| 0.009|       |         |       | 1.115| 0.012|       |         |       |
smallest at all 3 sites suggests that being small does not automatically confer a relative survival disadvantage over the first summer. Even if wild parr were being displaced from beneficial habitat by larger farm fish (Fleming et al. 2000, McGinnity et al. 2003), it does not seem to have been overly detrimental during this time period. In addition, the lack of evidence for larger size of farm fish conferring higher survival is also consistent with results of previous studies finding evidence for at least some selection against fast-growing farm fish in the wild (e.g. Glover et al. 2018), as larger farm fish may be bolder and therefore more risk-prone than their wild counterparts (Fleming & Einum 1997, Islam et al. 2020, Solberg et al. 2020). Ultimately, our results suggest that relative size rankings of cross types cannot be used as a reliable predictor of their relative survival across a range of environmental conditions.

The result of wild parr being smallest on average across all sites is consistent with results from similar European studies (e.g. Einum & Fleming 1997, Fleming & Einum 1997, Fleming et al. 2000, Glover et al. 2009, Solberg et al. 2013b, Harvey et al. 2016). In contrast, while a few recent studies on Newfoundland Atlantic salmon juveniles have found wild fish to be largest at certain early life stages, it is likely that a cross type-based maternal egg size effect contributed to these results, and likely did not play a role in our study. For example, Perriman et al. (2022) found wild fish to be largest overall at first-feeding and 80 d later in a semi-natural environment as well as being larger than hybrids at age 0+ in the wild. Hamoutene et al. (2017) found wild to be largest at hatch in a hatchery environment, and Islam et al. (2021) found wild fish were longer than farmed (though not heavier) at first feeding in a lab environment. Authors of all 3 of these studies attributed the larger relative size of their wild juveniles to the fact that the eggs they used from wild females were larger than those from farmed females. In contrast, in our study there was little difference in average egg size of wild and farmed mothers, therefore wild juveniles as a group would not be expected to have this particular size advantage initially (and indeed, wild juveniles were also the smallest cross type at release). Overall, our size results for the pure crosses are in line with results of previous research, demonstrating that farmed fish tend to outgrow wild across a range of environmental conditions, though to a lesser extent in more challenging growth conditions (reviewed by Glover et al. 2018).

A potentially notable result we report is the apparent size advantage of W’hyyb observed at 2 sites, since hybrids have typically been found to be intermediate in size between pure crosses (e.g. Einum & Fleming 1997, Fleming & Einum 1997, Fleming et al. 2000, Glover et al. 2009, Solberg et al. 2013a, Harvey et al. 2016). Nevertheless, our observations are supported by the results of Skaala et al. (2012), who found that for a cohort using hybrids from wild mothers, the hybrids were indeed the largest cross type as smolts, while in 2 other cohorts using hybrids from farm mothers, the hybrids were either intermediate to the pure crosses or smallest as smolts. There is often variability in growth among populations of the same cross type, and certain populations under certain environmental conditions may over- or under-perform relative to their overall cross type (e.g. Harvey et al. 2016); therefore, it is possible that the particular parental crosses used in our study resulted in a W’hyyb strain that was a particularly good performer under specific conditions (i.e. Sites 2 and 3). Alternatively, since W’hyyb were also the largest cross type at release, their relative size at recapture could be reflective of their initial size; though since farm and F’hyyb fish outgrew W’hyyb at Site 1, initial size is likely to be only a partial influencer of recapture size and/or only an important factor under certain environmental conditions.

4.3. Morphology

Though wild Atlantic salmon populations have been found to be genetically distinct from one another (e.g. Fraser et al. 2011, Bourret et al. 2013), the degree to which variation in morphology is related to genetics vs. environment is not yet clear. Our results indicate that there is evidence for effects of both environment and cross type on body morphology, with the largest differences in shape being for landmarks associated with body depth; however, overall shape differences were small. Fleming & Einum (1997) also found that tank-reared Norwegian farmed juveniles had deeper bodies than tank-reared wild juveniles did, as did Perriman et al. (2022) for tank-reared Newfoundland juveniles at 80 d post-first-feeding. Aquaculture selection for greater weight in salmonids has potentially resulted in a corresponding increase in body depth (Gjerde & Schaeffer 1989), and the aquaculture environment may 'release' farmed fish from the natural selection pressures for a more streamlined body that is often associated with stronger swimming performance (Fleming & Einum 1997). These genetic-based morphological differences between cross types may be
less expressed phenotypically in the wild vs. culture (e.g. Solem et al. 2006), and instances of morphological convergence among cross types with increasing time spent in a wild environment have also been observed (e.g. Fleming et al. 1994, Von Cramon-Taubadel et al. 2005, Perriman et al. 2022, results which are in line with our observations of small overall differences in the wild. In addition, the lack of evidence for a cross type effect but strong evidence for a site effect on pectoral fin length suggests that environment plays a stronger role in shaping this trait than does genetics, perhaps through differences in flow characteristics of the 3 sites. Overall, our results suggest that any genetic differences in morphological traits between the wild and farmed populations we used are not strongly expressed in a wild environment, at least over the first summer.

4.4. Parr marks

Our results show strong evidence for an effect of cross type as well as a site × cross type interaction on number of parr marks, corroborating previous studies showing that both genetics and environment play a role in determining parr mark numbers. Juvenile salmon in different environments are likely to experience selection for certain parr mark patterns because this trait influences their ability to camouflage against the riverbed and thus hide from predators (Donnelly & Dill 1984, Culling et al. 2013). Boulding et al. (2008) found 3 quantitative trait loci that influenced parr mark numbers, a finding which was supported by the results of their common-garden experiment finding different numbers of marks on fish from different genetic backgrounds raised in a common environment. Since we found that Wohyb had the fewest parr marks and outgrew the other cross types by the largest margin at Site 3, it is possible that they had an environment-specific genetic advantage for parr mark number (i.e. enabling better camouflage, allowing more energy to be spent on feeding and less on predator avoidance). At the other 2 sites, cross type differences in parr mark number were minimal, despite Wohyb remaining the cross type with highest recapture odds. This suggests that the influence of parr mark number on overall survival is not particularly strong, or perhaps this trait interacts with others in varying ways under different conditions to influence survival.

On the other hand, for parr mark size (length and width), there was a lack of evidence for a cross type effect but strong evidence for a site effect, suggesting that plasticity plays a larger role than genetics for this trait. Indeed, Jørgensen et al. (2018) found that the environment played a larger role in determining spot pigmentation patterns on Atlantic salmon than did genetics (though the latter did still have an effect). In general, our results for parr mark number and size were quite variable, and pairwise differences between cross types were small. We observed the largest pairwise cross type differences for parr mark size at Site 1 (where pure farm fish had narrower marks than both hybrids), which was also the site with the lowest growth overall. This perhaps suggests that selection for parr mark size (and thus camouflage ability) operates more strongly under more challenging growth conditions, potentially due to trade-offs in energy allocation for feeding vs. predator avoidance.

5. CONCLUSIONS

Overall, our results showed that there are differences among farmed, wild, and hybrid Atlantic salmon parr for fitness-related traits and survival even at small temporal scales under favourable environmental conditions. We showed that plasticity for these traits exists within cross types, with differing relative performance in terms of size and morphology at replicate study sites. The fact that the pattern of relative survival was consistent across sites but was not obviously linked to patterns in any of the fitness-related traits suggests that other traits (unexamined here) may differ among cross types and influence survival, or perhaps multiple traits combine to have a cumulative effect on survival. Ultimately, as the first North American wild-environment study of its kind, this work could serve as a lead-in for additional research on these specific populations in the wild, especially to further investigate potentially critical findings such as the possibility of wild-mother hybrid vigour. Such research provides key data for these populations in areas of high aquaculture activity and will help to inform predictive modeling of escapee impacts and subsequent management decisions.

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LITERATURE CITED

Adams DC, Collyer ML, Kaliontzopoulou A (2020) geomorph: software for geometric morphometric analyses Version 3.3.1. https://github.com/geomorphR/geomorph

Baskett ML, Burgess SC, Waples RS (2013) Assessing strategies to minimize unintended fitness consequences of aquaculture on wild populations. Evol Appl 6:1090–1108

Besnier F, Glover KA, Lien S, Kent M, Hansen MM, Shen X, Skåla Ø (2015) Identification of quantitative genetic components of fitness variation in farmed, hybrid and native salmon in the wild. Heredity 115:47–55

Bolger T, Connolly PL (1989) The selection of suitable indices for the measurement and analysis of fish condition. J Fish Biol 34:171–182

Boulding EG, Culling M, Glebe B, Berg PR, Lien S, Moen T (2008) Conservation genomics of Atlantic salmon: SNPs associated with QTLs for adaptive traits in parr from four trans-Atlantic backcrosses. Heredity 101:381–391

Bourret V, Kent MP, Primmer CR, Vasmégni A and others (2013) SNP-array reveals genome-wide patterns of geographical and potential adaptive divergence across the natural range of Atlantic salmon (Salmo salar). Mol Ecol 22:532–551

Bradbury IR, Wringe BF, Watson B, Paterson I and others (2016) Genotyping-by-sequencing of genome-wide microsatellite loci reveals fine-scale harvest composition in a coastal Atlantic salmon fishery. Evol Appl 11:918–930

Bradbury IR, Duffy S, Lehnert SJ, Jóhannsson R and others (2020) Model-based evaluation of the genetic impacts of farm-escaped Atlantic salmon on wild populations. Aquacult Environ Interact 12:45–59

Christensen R (1990) Log-linear models and logistic regression, 2nd edn. Springer, New York, NY

Collyer ML, Adams DC (2018) RRPP: an R package for fitting linear models to high-dimensional data using residual randomization. Methods Ecol Evol 9:1772–1779

Collyer ML, Adams DC (2020) RRPP: linear model evaluation with randomized residuals in a permutation procedure. Version 0.6.1. https://github.com/mlcollyer/RRPP

Culling M, Freamo H, Patterson K, Berg PR, Lien S, Boulding EG (2013) Signatures of selection on growth, shape, parr marks, and SNPs among seven Canadian Atlantic salmon (Salmo salar) populations. Open Evol J 7:1−16

Donnelly WA, Dill LM (1984) Evidence for crypsis in coho salmon, Oncorhynchus kisutch (Walbaum), parr: substrate colour preference and achromatic reflectance. J Fish Biol 25:183–195

Einum S, Fleming IA (1997) Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. J Fish Biol 50:634–651

Fleming IA, Einum S (1997) Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. ICES J Mar Sci 54:1051–1063

Fleming IA, Jonsson B, Gross MR (1994) Phenotypic divergence of sea-ranched, farmed, and wild salmon. Can J Fish Aquat Sci 51:2808–2824

Fleming IA, Jonsson B, Gross MR, Lamberg A (1996) An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (Salmo salar). J Appl Ecol 33:893–905

Fleming IA, Hindar K, Mjolnerod IB, Jonsson B, Balstad T, Lamberg A (2000) Lifetime success and interactions of farmed salmon invading a native population. Proc R Soc B 267:1517–1523

Fraser DJ, Cook AM, Eddington JD, Bentzen P, Hutchings JA (2008) Mixed evidence for reduced local adaptation in wild salmon resulting from interbreeding with escaped farmed salmon: complexities in hybrid fitness. Evol Appl 1:501–512

Fraser DJ, Weir LK, Bernatchez L, Hansen MM, Taylor EB (2011) Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. Heredity 106:404–420

Garcia de Leaniz C, Fleming IA, Einum S, Verspoor E and others (2007) A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. Biol Rev Camb Philos Soc 82:173−211

Gjerde B, Schaeffer LR (1989) Body traits in rainbow trout: II. Estimates of heritabilities and of phenotypic and genetic correlations. Aquaculture 80:25–44

Glover S, Dixon P (2004) Likelihood ratios: a simple and flexible statistic for empirical psychologists. Psychon Bull Rev 11:791–806

Glover KA, Otterå H, Olsen RE, Slinde E, Taranger GL, Skåla ø (2009) A comparison of farmed, wild and hybrid Atlantic salmon (Salmo salar L) reared under farming conditions. Aquaculture 286:203−210

Glover KA, Solberg MF, McGinnity P, Hindar K and others (2017) Half a century of genetic interaction between farmed and wild Atlantic salmon: status of knowledge and unanswered questions. Fish Fish 18:890–927

Glover KA, Solberg MF, Bennier F, Skåla ø (2016) Cryptic introgression: evidence that selection and plasticity mask the full phenotypic potential of domesticated Atlantic salmon in the wild. Sci Rep 8:13966

Gower JC (1975) Generalized Procrustes analysis. Psychometrika 40:33–51

Hamoutene D, Perez-Casanova J, Burt K, Lush L, Caines J, Collier C, Hinks R (2017) Early life traits of farm and wild Atlantic salmon Salmo salar and first generation hybrids in the south coast of Newfoundland. J Fish Biol 90:2271–2288

Harvey AC, Glover KA, Taylor MI, Creer S, Carvalho GR (2016) A common garden design reveals population-specific variability in potential impacts of hybridization between populations of farmed and wild Atlantic salmon, Salmo salar L. Evol Appl 9:435–449

Heino M, Svenstad T, Wennevik V, Glover KA (2015) Genetic introgression of farmed salmon in native populations: quantifying the relative influence of population size and frequency of escapees. Aquacult Environ Interact 6:185−190

Islam SS, Wringe BF, Bradbury IR, Fleming IA (2020) Behavioural variation among divergent European and North American farmed and wild Atlantic salmon (Salmo salar) populations. Appl Anim Behav Sci 230:105029

Islam SS, Wringe BF, Bøe K, Bradbury IR, Fleming IA (2021) Early-life fitness trait variation among divergent European and North American farmed and Newfoundland wild Atlantic salmon populations. Aquacult Environ Interact 13:323–337

Jones OR, Wang J (2010) COLONY: a program for parentage and sibship inference from multilocus genotype data. Mol Ecol Resour 10:551–555
Jørgensen KM, Solberg MF, Besnier F, Thorsen A and others (2018) Judging a salmon by its spots: environmental variation is the primary determinant of spot patterns in *Salmo salar*. BMC Ecol 18:14

Karlsdotter S, Moen T, Lien S, Glover KA, Hindar K (2011) Generic genetic differences between farmed and wild Atlantic salmon identified from a 7K SNP-chip. Mol Ecol Resour 11:247−253

Keyser F, Wringe BF, Jeffery NW, Dempson JB, Duffy S, Bradbury IR (2018) Predicting the impacts of escaped farmed Atlantic salmon on wild salmon populations. Can J Fish Aquat Sci 75:506−512

King TL, Kalinowski ST, Schill WB, Spidle AP, Lubinski BA (2001) Population structure of Atlantic salmon (*Salmo salar* L.): a range-wide perspective from microsatellite DNA variation. Mol Ecol 10:807−821

Le Luyer J, Laporte M, Beacham TD, Kaukinen KH and others (2017) Parallel epigenetic modifications induced by hatchery rearing in a Pacific salmon. Proc Natl Acad Sci USA 114:12964−12969

Lehnert SJ, Bentzen P, Kess T, Lien S, Horne JB, Clément M, Bradbury IR (2019) Chromosome polymorphisms track trans-Atlantic divergence and secondary contact in Atlantic salmon. Mol Ecol 28:2074−2087

Lehnert SJ, Kess T, Bentzen P, Clément M, Bradbury IR (2020) Divergent and linked selection shape patterns of genomic differentiation between European and North American Atlantic salmon (*Salmo salar*). Mol Ecol 29:2160−2175

Lenth R (2020) emmeans: estimated marginal means. Version 1.4.8. https://github.com/rvlenth/emmeans

McGinnity P, Stone C, Taggart JB, Cooke D and others (1997) Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. ICES J Mar Sci 54:998−1008

McGinnity P, Prodöhl P, Ferguson A, Hynes R and others (2003) Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proc R Soc B 270: 2443−2450

Perriman BM, Bentzen P, Wringe BF, Duffy SJ and others (2022) Morphological consequences of hybridization between farm and wild Atlantic salmon (*Salmo salar*) under both experimental and wild conditions. Aquacult Environ Interact (in press), doi:10.3354/aei00429

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Riddell BE, Leggett WC (1981) Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 38:308−320

Rohlf FJ (2015) The tps series of software. Hystrix 26:9−12

Rohlf FJ, Slice D (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. Syst Biol 39:40−59

Royall R (1997) Statistical evidence: a likelihood paradigm. CRC Press, Boca Raton, FL

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 23 years of image analysis. Nat Methods 9: 671−675

Skaala O, Taggart JB, Gunnes K (2005) Genetic differences between five major domesticated strains of Atlantic salmon and wild salmon. J Fish Biol 67:118−128

Skaala Ø, Glover KA, Barlaup BT, Svåsand T, Besnier F, Hansen MM, Borgstrøm R (2012) Performance of farmed, hybrid, and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. Can J Fish Aquat Sci 69: 1994−2006

Skaala Ø, Besnier F, Borgstrøm R, Barlaup B and others (2019) An extensive common-garden study with domesticated and wild Atlantic salmon in the wild reveals impact on smolt production and shifts in fitness traits. Evol Appl 12:1001−1016

Skalski JR, Buchanan RA, Grisvold J (2009) Review of marking methods and release-recapture designs for estimating the survival of very small fish: examples from the assessment of salmonid fry survival. Rev Fish Sci 17:391−401

Solberg MF, Skaala Ø, Nilsen F, Glover KA (2013a) Does domestication cause changes in growth reaction norms? A study of farmed, wild and hybrid Atlantic salmon families exposed to environmental stress. PLOS ONE 8:e54469

Solberg MF, Zhang Z, Nilsen F, Glover KA (2013b) Growth reaction norms of domesticated, wild and hybrid Atlantic salmon families in response to differing social and physical environments. BMC Evol Biol 13:234

Solberg MF, Robertsen G, Sundt-Hansen LE, Hindar K, Glover KA (2020) Domestication leads to increased predation susceptibility. Sci Rep 10:1929

Solem Ø, Berg OK, Kjesnes AJ (2006) Inter- and intra-population morphological differences between wild and farmed Atlantic salmon juveniles. J Fish Biol 69:1466−1481

Sylvestor EVA, Wringe BF, Duffy SJ, Hamilton LC and others (2019) Estimating the relative fitness of escaped farmed salmon offspring in the wild and modelling the consequences of invasion for wild populations. Evol Appl 12: 705−717

Taylor E (1991) A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185−207

Von Cramon-Taubadel N, Ling EN, Cotter D, Wilkins NP (2005) Determination of body shape variation in Irish hatchery-reared and wild Atlantic salmon. J Fish Biol 66: 1471−1482

Wasserstein RL, Schirm AL, Lazar NA (2019) Moving to a world beyond ‘p < 0.05’. Am Stat 73:1−19

Winans GA (1984) Multivariate morphometric variability in Pacific salmon: technical demonstration. Can J Fish Aquat Sci 41:1150−1159

Wootton RJ (1998) Ecology of teleost fishes. Kluwer Academic, Boston, MA

Wringe BF, Jeffery NW, Stanley RRE, Hamilton LC and others (2018) Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. Commun Biol 1:108

Wringe BF, Anderson EC, Jeffery NW, Stanley RRE, Bradbury IR (2019) Development and evaluation of SNP panels for the detection of hybridization between wild and escaped Atlantic salmon (*Salmo salar*) in the western Atlantic. Can J Fish Aquat Sci 76:692−704

Zhang L, Paterson IG, Fraser BA, Watson B and others (2017) MEGASAT: automated inference of microsatellite genotypes from sequence data. Mol Ecol Resour 17:247–256