



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

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ABSTRACT: Farming of Atlantic salmon *Salmo salar* has resulted in highly domesticated individuals, with notable genetic and phenotypic differences from their wild counterparts. Understanding how interbreeding with aquaculture escapees affects wild, often at-risk populations is increasingly essential to conservation efforts. Here, we used an experimental release of wild, farm, and reciprocal F₁ hybrid fry at 3 sites in the Garnish River in Newfoundland, Canada, to evaluate family and cross-specific patterns of recapture/survival, size, sex ratio, and precocial male maturation over a 28 mo period. Trends in cross type recapture changed over the study period, with the highest recapture at 3 mo in parr with wild mothers and between 15 and 28 mo in aquaculture offspring. Size trends among crosses and sites remained consistent over the study duration, with pure farm and wild-mother hybrids being consistently larger than wild individuals and 1 site displaying elevated sizes in all crosses. Rates of parr maturation differed by sex and cross type, and family-based analysis indicated family representation and size also remained consistent through time. These results indicate there is a difference in vital rates such as survival and precocial maturation between farm and wild Atlantic salmon during the freshwater early life history period, and this difference can change significantly over time. As such, an improved understanding of genetic and ecological interactions which takes this ontogenetic variation into account is likely essential to fully understand how hybridization and introgression with farm escapees are affecting wild populations.

KEY WORDS: Aquaculture escapes · Farm–wild hybridization · Atlantic salmon · Precocial maturation · Parr performance

1. INTRODUCTION

The domestication of Atlantic salmon *Salmo salar* in both North America and Europe has resulted in notable genetic differences between farm individuals and their wild counterparts (Glover et al. 2017, Wringe et al. 2019). Due to this domestication-driven divergence, introgression of farm Atlantic salmon

alleles into wild populations may result in the expression of traits maladaptive for life in the wild (Fleming & Einum 1997, Ferguson et al. 2007) and erode local adaptation by altering the frequency of wild genotypes (Verspoor et al. 2015, Karlsson et al. 2016, Glover et al. 2017, Wringe et al. 2018, Bolstad et al. 2021). In the wild, Atlantic salmon are highly adapted to their local environments (Garcia de Leaniz et al.

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2007, Fraser et al. 2011, Watson et al. 2022) and as such interbreeding of farm and wild salmon can negatively impact adaptation, leading to a reduction in fitness (McGinnity et al. 2003, Skaala et al. 2019, Sylvester et al. 2019) and population decline (Fleming et al. 2000, Bradbury et al. 2020). For this reason, investigating the different effects of selection on survival among wild, farm, and hybrid salmon in the wild is key to determining and managing the genetic and demographic impacts of escaped farm salmon on wild salmon populations.

Farm fish differ from wild fish both genetically (Besnier et al. 2015, Wringe et al. 2019) and phenotypically in a variety of traits (Fleming & Einum 1997, Wringe et al. 2016, Skaala et al. 2019, Islam et al. 2020), often through selection for increased aquaculture production (Fleming & Einum 1997, GjØen & Bentsen 1997, Harvey et al. 2016). For instance, farm Atlantic salmon typically grow faster than their wild counterparts (Fleming et al. 2000, Glover et al. 2009, Solberg et al. 2013a,b, Harvey et al. 2016, Skaala et al. 2019). In the wild, such increased growth may present an advantage in certain aspects of competitive displacement (Fleming et al. 2000, McGinnity et al. 2003, Skaala et al. 2019), but may also be detrimental, with evidence of selection against fast-growing individuals (Biro et al. 2006, Solberg et al. 2015, Glover et al. 2018). In association with growth differences, farm fish also tend to be bolder and therefore more risk-prone than their wild counterparts (Fleming & Einum 1997, Islam et al. 2020, Solberg et al. 2020), and in a pedigree structure study, families of farm origin persistently exhibited poorer survival in their early years of life (Reed et al. 2015). As such, it appears that the nature of interactions between genetics and the environment in which Atlantic salmon live can influence the impact of growth on survival (Glover et al. 2018).

However, to date, the few studies that have quantified survival and phenotypic differences among wild, farm, and hybrid individuals in the wild have been done in Europe or at limited spatial or temporal scales (e.g. Fleming & Einum 1997, Fleming et al. 2000, McGinnity et al. 2003, Skaala et al. 2019, Crowley et al. 2022). Such localized experiments may not reflect the conditions of all wild populations and landscapes (Fleming et al. 2000, Skaala et al. 2012), and the true effect of selection on genotypes over time. The goal of this study was to expand on existing research on wild, farm, and hybrid Atlantic salmon performance in the wild in southern Newfoundland to better inform predictions of population responses to escaped farm salmon in Atlantic Can-

ada. We built upon the previous findings of Crowley et al. (2022), who explored the growth and survival of wild, farm, and hybrid salmon fry 3 mo after release. Here, we assessed differences in survival and size of 4 cross types (wild, farm, and reciprocal F_1 hybrids [wild-mother and farm-mother]) and family representation across an environmental gradient in 3 river tributaries on the south coast of Newfoundland for a period of 28 mo following release. By subjecting differing cross types to common environmental conditions in 3 tributary sites, the overall goal was to isolate genetic impact on these traits and determine differences among the 4 cross types and their specific families. We hypothesized that (1) wild fish would have higher survival/recapture odds than farm individuals throughout the 28 mo study period, with hybrids being intermediate; (2) farm fish would be larger at recapture than wild fish, with hybrids being intermediate; and (3) family representation/survival and differences in size within cross types would remain constant through time.

2. MATERIALS AND METHODS

2.1. Crosses

In the late fall of 2017, 4 cross types of Atlantic salmon *Salmo salar* were produced as outlined in Crowley et al. (2022): 9 families of offspring of wild parents from the Garnish River, 6 families of offspring of parents from the Saint John River farm strain in New Brunswick (the only farm strain used in Atlantic Canada commercial aquaculture operations), 7 families of F_1 hybrids with the previously mentioned farm mothers and wild fathers (farm-mother hybrids [$F\phi$ Hyb]), and 7 families of reciprocal F_1 hybrids (wild-mother hybrids [$W\phi$ Hyb]) (Table 1). The Saint John River farm strain has been domesticated for 8–10 generations, and a multiple trait selection process including parr length, percent yearling smolt, market size, and mature size of 2-seawinter broodfish was used to select gamete donors for early generations (Glebe 1998). A low number of farm parents was used, reflecting the number of available individuals that matured by the late fall of 2017. Fin-clip samples from parents of each cross were retained in 100% ethanol for later use in parentage assignment of offspring. The Garnish River system is located on the south coast of Newfoundland near an area of intensive Atlantic salmon aquaculture on the Burin Peninsula, emptying into Fortune Bay (Fig. 1). Escapees have been previously docu-

Table 1. Number of individuals released and recaptured of each cross type and family at each site. Wild parents originated from the Garnish River in southern Newfoundland, while farm parents were from the Saint John River, New Brunswick, farm strain (the only farm strain used in Atlantic Canada commercial aquaculture operations). Release of all crosses occurred on 11 July 2018. Specific numbers of each family released at each site could not be quantified. F ϕ Hyb: farm-mother hybrids; W ϕ Hyb: wild-mother hybrids

Cross type	Families		Number of individuals released (2018)				Number of individuals recaptured (2018–2020)			
	Mother ID	Father ID	Site 1	Site 2	Site 3	Total	Site 1	Site 2	Site 3	Total
Wild			427	439	437	1303	83	164	195	442
	<i>W11</i>	<i>W08</i>					11	24	6	41
	<i>W13</i>	<i>W01</i>					23	30	66	119
	<i>W17</i>	<i>W22</i>					5	12	16	33
	<i>W19</i>	<i>W03</i>					5	6	13	24
	<i>W20</i>	<i>W04</i>					10	32	38	80
	<i>W23</i>	<i>W07</i>					8	15	15	38
	<i>W24</i>	<i>W08</i>					5	22	13	40
	<i>W26</i>	<i>W22</i>					6	12	10	28
	<i>W28</i>	<i>W16</i>					10	11	18	39
Farm			483	493	1471	74	164	165	403	
	<i>F01</i>	<i>F02</i>					30	56	50	136
	<i>F01</i>	<i>F03</i>					10	19	12	41
	<i>F01</i>	<i>F06</i>					17	46	34	97
	<i>F04</i>	<i>F02</i>					17	42	66	125
	<i>F05</i>	<i>F06</i>					0	1	3	4
F ϕ Hyb			483	493	1471	47	129	93	269	
	<i>F01</i>	<i>W01</i>					13	24	34	71
	<i>F01</i>	<i>W02</i>					15	39	42	96
	<i>F04</i>	<i>W08</i>					17	58	12	87
	<i>F05</i>	<i>W07</i>					2	8	5	15
W ϕ Hyb			539	551	549	1639	103	244	227	574
	<i>W11</i>	<i>F02</i>					16	36	41	93
	<i>W17</i>	<i>F02</i>					9	26	16	51
	<i>W19</i>	<i>F06</i>					17	53	49	119
	<i>W23</i>	<i>F06</i>					13	45	36	94
	<i>W24</i>	<i>F03</i>					19	29	25	73
	<i>W26</i>	<i>F02</i>					8	19	16	43
	<i>W28</i>	<i>F02</i>					21	36	44	101

mented in this system, leading to the presence of F₁ hybrids following escape events (Wringe et al. 2018, Bradbury et al. 2020). For the present experiment, all wild fish used in the crosses were genetically screened to ensure that they were pure (i.e. not introgressed).

Embryo and early fry care are described in Crowley et al. (2022). Briefly, embryos were incubated on ambient water in Heath trays at the Ocean Sciences Centre of Memorial University (St. John's, Newfoundland and Labrador, Canada), which were monitored daily, and dead embryos were removed every 4–5 d. At first feeding in late May 2018, juveniles were pooled by cross type and transferred to 470 l flow-through circular holding tanks (0.9 m diameter × 0.5 m height) on ambient water. During the first month they were fed a combination of *Artemia* and salmonid starter dry feed (EWOS-Cargill), followed by only dry feed until release.

2.2. Field methods: release and recapture

Release occurred on 11 July 2018 at 3 tributary sites of the Garnish River (Fig. 1). To distinguish generated fry from wild fish at recapture, individuals were adipose fin-clipped before release (Crowley et al. 2022). Of the 2000 fin-clipped juveniles to be released per site, some died during transport, such that 1932 were released at Site 1, 1980 at Site 2, and 1972 at Site 3. The number of individuals of each cross type released per site was relatively even (roughly 500 of each cross), although the W ϕ Hyb group had approximately 50 more fish, and the wild group roughly 50 fewer fish than the farm and F ϕ Hyb groups at each site. The fish 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

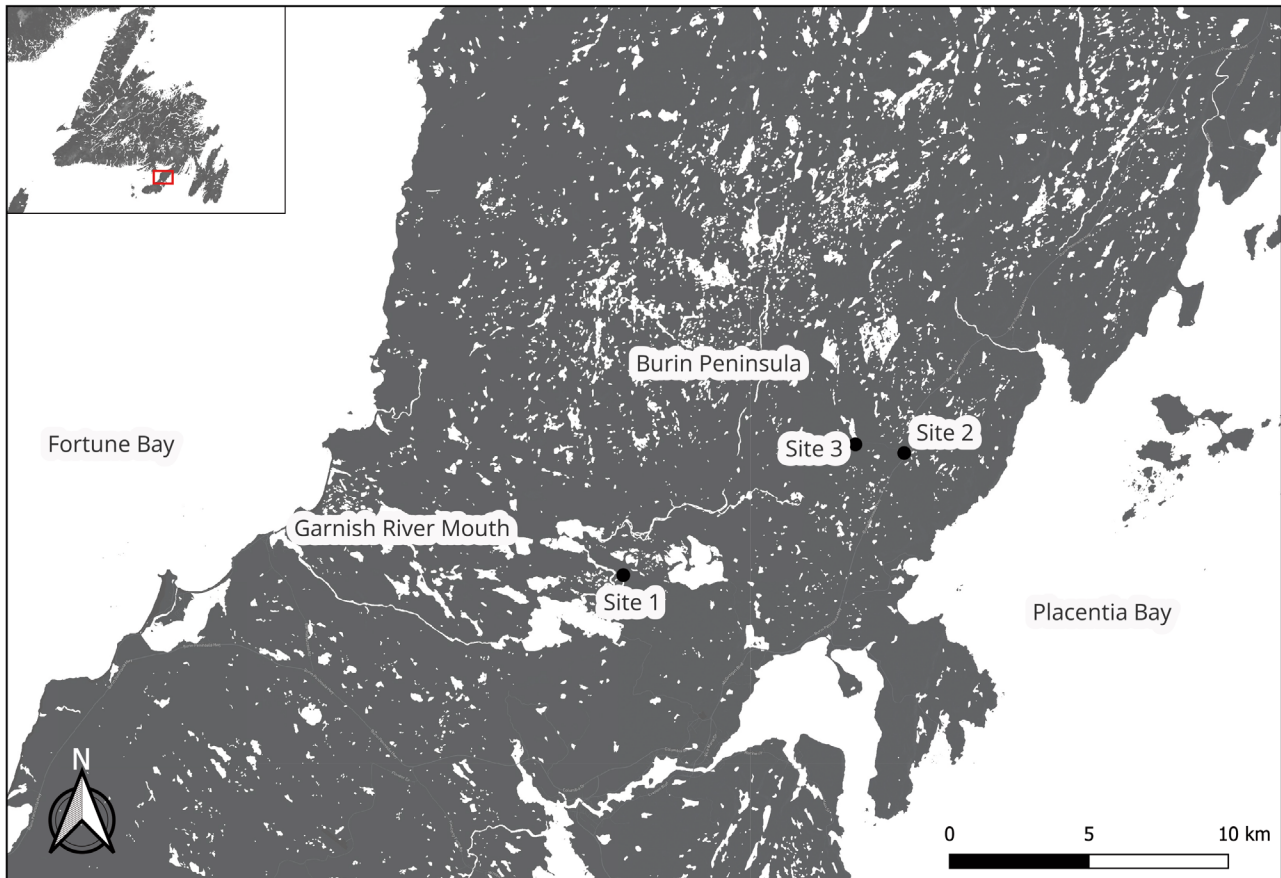


Fig. 1. The 3 tributary study sites in the Garnish River used for the release and recapture experiment with Atlantic salmon. All sites are located on the Burin Peninsula in Newfoundland, Canada. Inset: the island of Newfoundland, with box showing general study area. Map created in QGIS; map style created in Mapbox; data by OpenStreetMap under ODbL

(IACC) following Canadian Council of Animal Care (CCAC) guidelines, under protocol number 18-01-IF.

Following the sampling in October 2018 by Crowley et al. (2022), single pass electrofishing, using a LR-24 Backpack Electrofisher (Smith Root), was undertaken on 12 August and 17, 19, and 20 September 2019, as well as 30 September 2020, to recapture juveniles. The units were set at 550 V and 60 Hz, with a duty cycle of 25%. At Sites 1 and 2, recapture began roughly 100 m downstream from the first release points and continued upstream, fishing up to 250 m above the release point. At Site 3, electrofishing started at a culvert downstream from the first release point and extended until a natural barrier was reached.

Processing of recaptured fish occurred approximately 2 h after concluding electrofishing each day. Following this, fish were euthanized using MS-222 (AQUALIFE TMS, Syndel Laboratories) at a dose of 400 mg l⁻¹ buffered with an equal dose of sodium bicarbonate. To allow for later parentage analysis,

caudal fins were clipped and fin samples were stored in 100% ethanol; the rest of the fish were frozen at -20°C. All unmarked fish were released back into the stream unharmed.

2.3. Genetic analysis

To assign individuals to a family and their cross type (wild, farm, or one of the 2 hybrid groups) a panel of 31 microsatellite loci with a total of 277 alleles (multiplex panel 1a from Bradbury et al. 2018) was used, which are a subset of a larger panel of 101 loci previously utilized for Atlantic salmon in Atlantic Canada. Ultimately, 6 of these loci were excluded due to either a high percentage of missing offspring genotypes or a high estimated allelic dropout rate. Therefore, of these 31 loci, 25 were used for parentage assignment. 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 per locus 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).

A DNeasy 96 Blood and Tissue Kit (QIAGEN) was used to extract DNA following the manufacturer's protocol for purification of total DNA from animal tissues. The protocol described by Zhan et al. (2017) was followed to PCR amplify microsatellite loci, and sequencing was performed using an Illumina MiSeq and scored using MEGASAT software. Each fish was assigned to its cross type and family using COLONY (Jones & Wang 2010). To ensure the assignment sensitivity and accuracy of COLONY given the set of input parameters used, test trials included genotype data for all unique samples, parents, within-plate redundant, and cross-plate controls. Only unique samples were included in the final analysis (i.e. excluding redundant samples or controls).

2.4. Size analysis

Fork length measurements were taken from photos of all recaptured fish at each site. This was done using ImageJ software (version 1.52a), following the lateral line of the fish's body to account for body arching when present. Each recaptured sample was also weighed to the nearest hundredth of a gram. Finally, condition factor at recapture was calculated for samples collected in 2019 and 2020 by dividing the residuals of the regression of $\ln(\text{weight})$ over $\ln(\text{recapture length})$ (Bolger & Connolly 1989, Wootton 1998).

The average growth rate for the different cross types was calculated between the 3 mo post-release and 1 yr post-release recapture events, the 3 mo post-release and 2 yr post-release recapture events, and the 1 yr post-release and 2 yr post-release recapture events. This was done using the typical growth rate equation that accounts for allometry (Ostrovsky 1995), where the allometric mass exponent (b) for Atlantic salmon is 0.31 (Elliott & Hurley 1997).

2.5. Sex ratios and maturity analysis

The proportion of males and females recaptured was calculated for 2019 and 2020 recaptures based on genetic sexing. Within each category (male and female), mature versus immature individuals were distinguished, and proportion of each was also quantified.

2.6. Statistical analysis

All statistical analyses were performed in R version 4.1.1 (R Core Team 2022). The probability of recapture is the product of the probability of survival to time of recapture and the probability of being encountered at time of recapture. However, the design of this experiment did not allow these probabilities to be separated. Therefore, odds of recapture alone (proportion of fish recaptured relative to the initial number of fish released) were used as estimates of survival for cross type and family representation analyses. The estimates of survival for a given year included not only individuals recaptured that year, but also those recaptured in subsequent years given that they must have been alive in preceding years. Since the recapture (survival) data are presence/absence in form, a generalized linear model with binomial family and logit link, with odds of recapture as the response variable, was used to analyze survival. Cross type, site and year were included as fixed factors in the model in addition to all possible interaction terms.

Assumptions of normality and homoscedasticity of residuals were assessed by visual examination of residual vs. fitted plots and normal Q-Q plots of residuals. Where these assumptions were met, a general linear model was used for analysis, while a generalized linear model was used if one or more assumptions were not met. Length at recapture was examined using a linear model with cross type and site included as factors in the model. An interaction between these 2 variables was also analyzed. Recapture weight data were analyzed applying a generalized linear model with the Gamma family (identity link), as the Gamma model family is appropriate for positive continuous data.

We used analysis of deviance (McCullagh & Nelder 1989) to identify the evidential strength of different fixed factors in an experimental design of survival and size, where a normal error structure was not appropriate. We used the change in deviance to calculate a likelihood ratio (LR), a measure of strength of evidence (Royall 1997, Burnham & Anderson 2014). Where residual assumptions were met, the LR was calculated using the sums of squares of all the terms in the model. We chose not to declare decisions at a fixed error rate, consistent with best statistical practice (Läärä 2009, Wasserstein et al. 2019) and with Snedecor & Cochran (1989) in the case of interaction terms in experimental design. In addition, we chose this approach as LRs provide a measure of evidence that is invariant across experimental designs,

while the p-value does not share this property (Vieland & Hodge 1998). p-values were also reported for readers not acquainted with analysis of deviance and the evidentialist approach of Royall (1997). However, only LRs are measures of evidence. LRs provide the likelihood of the data given a model including certain variables vs. a model lacking them. An intercept-only model was used as the basis for comparisons of interest for all the terms included in each model, and the coefficient for each predictor was exponentiated to calculate odds ratios of recapture. Assessments of relative magnitude of evidence for an alternative hypothesis was given by LR = 10 indicating strong evidence, LR = 32 substantial evidence, and LR > 100 decisive evidence (Jeffreys 1961, Royall 1997).

A goodness of fit test of the number of individuals recaptured per family relative to the expected number of recaptures was used to analyze family representation through time, with proportion of individuals recaptured from each family (of the total fish recaptured at each site each year) as the response variable in the model. Cross type, site, year, and all the possible interaction terms were again included as fixed factors in the model. This same analysis was used to determine whether there was a notable skew in sex ratios of recapture samples in 2019 and 2020, as well as in the proportion of mature individuals at each site.

3. RESULTS

In 2018, a total of 1284 fish were recaptured, and 1242 were successfully genotyped and assigned parentage (Table 1). In 2019 and 2020, 407 and 39 individuals were recaptured, respectively, and all these were successfully genotyped.

3.1. Recapture/survival

There was evidence for an interaction between cross type, site, and year ($p = 0.087$, LR = 13835.6) suggesting that the recapture of each cross type by site differed from year to year (0+ to 1+ to 2+) (Fig. 2, see Table S1 in the Supplement at www.int-res.com/articles/suppl/q015p323_supp.pdf). Therefore, recapture analyses were performed for each year separately. Overall, the trend of recapture shifted over time, from wild and W♀Hyb having the highest recapture rates 3 mo post-release, to farm and wild individuals having similar recapture odds 1 yr later,

and finally farm fish having the highest recapture rates and wild individuals having the lowest 2 yr post-release. In 2018 and 2019, there was also evidence for an interaction between site and cross type (2018: $p = 0.079$, LR = 289.3; 2019: $p < 0.001$, LR = 5.79×10^5), while in 2020 the evidence was strong based only on the likelihood ratio score ($p = 0.38$, LR = 24.82) (Tables S2–S4). Given these results, pairwise comparisons for odds of recapture among cross types were subsequently assessed within each site separately.

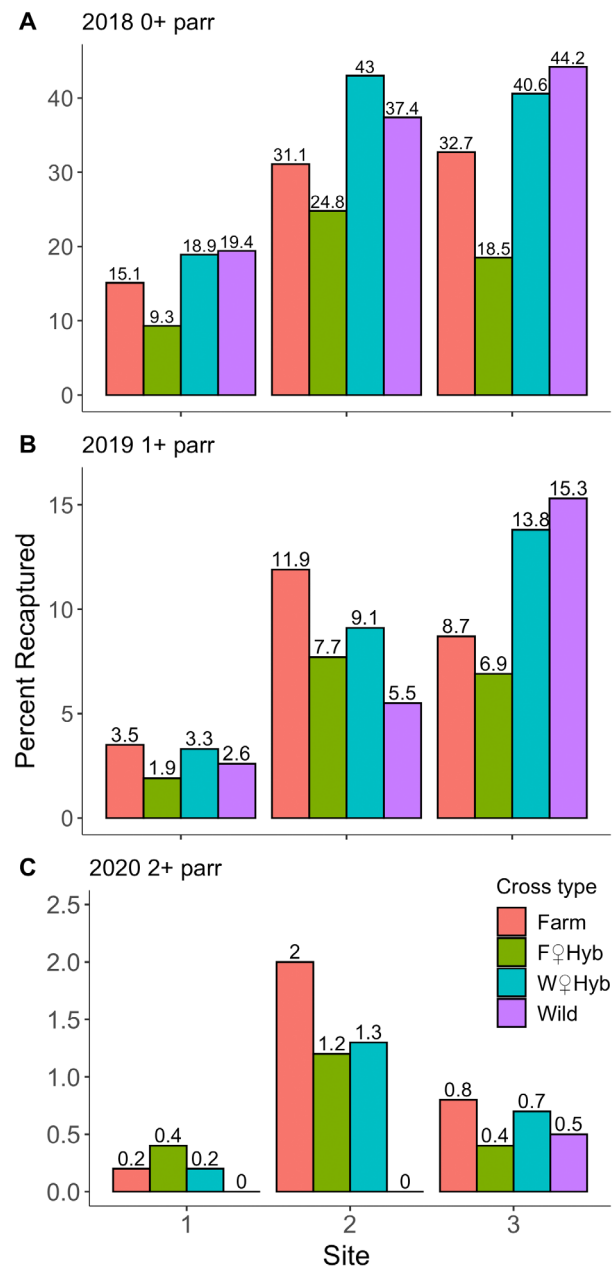


Fig. 2. Percentages of Atlantic salmon recaptured by cross type and site in (A) 2018, (B) 2019, and (C) 2020. F♀Hyb: farm-mother hybrid; W♀Hyb: wild-mother hybrid

rately. Three months post-release, wild and $W\phi$ Hyb fish had the highest and nearly identical odds of recapture across all sites (33.8 and 34.3%, respectively) (Figs. 2A & 3A). Farm and $F\phi$ Hyb individuals had overall lower rates of recapture than the other 2 crosses (26.4 and 17.6%, respectively), differing from them at Sites 2 and 3, while only $F\phi$ Hyb differed at Site 1 (Fig. 3A). Following the first year after release (3–15 mo post-release), $W\phi$ Hyb fish had the highest recapture rates across all sites (8.79%), followed by farm and wild fish with similar proportions recaptured (8.09 and 7.83%, respectively), while $F\phi$ Hyb continued to have the lowest percentage recaptured (5.51%). However, the cross types with higher recapture odds at Site 2 were different from those with higher recapture odds at Site 3 (Fig. 2B). At Site 2, farm and $W\phi$ Hyb fish had higher odds of recapture than wild individuals, and farm fish also had higher odds than $F\phi$ Hyb (Fig. 3B). At Site 3, the odds of recapture of wild and farm fish were reversed, with wild and $W\phi$ Hyb having higher odds than the other 2 cross types (Fig. 3B). In 2020, 2 yr after release (15–28 mo post-release), there were no wild fish recaptured at Sites 1 and 2 (Fig. 2C), and no differences in probability of recapture between any other cross type pairs (Fig. 3C). However, overall across the 3 sites, wild fish had substantially lower odds of recapture than farm fish (farm: 1.02%; wild: 0.15%; $p = 0.018$, LR = 149.9) (Table S5), with $W\phi$ Hyb (0.73%) and $F\phi$ Hyb (0.67%) being intermediary.

3.2. Size and condition at recapture

Length and weight at recapture varied in a similar manner across the 3 sites over the 3 yr (Figs. 4 & 5). Site 3 consistently had the largest sizes at recapture, with Sites 1 and 2 having similar sizes, except in 2018 when fish at Site 2 tended to be larger than those at Site 1. As previously reported by Crowley et al. (2022), individuals

recaptured in 2018 (3 mo after release) were largest at Site 3, which was also where the greatest pairwise differences in recapture weight and length among cross types occurred (Figs. 4A & 5A). Growth patterns also followed this trend, as growth was evidently higher at Site 3 between the 3 mo

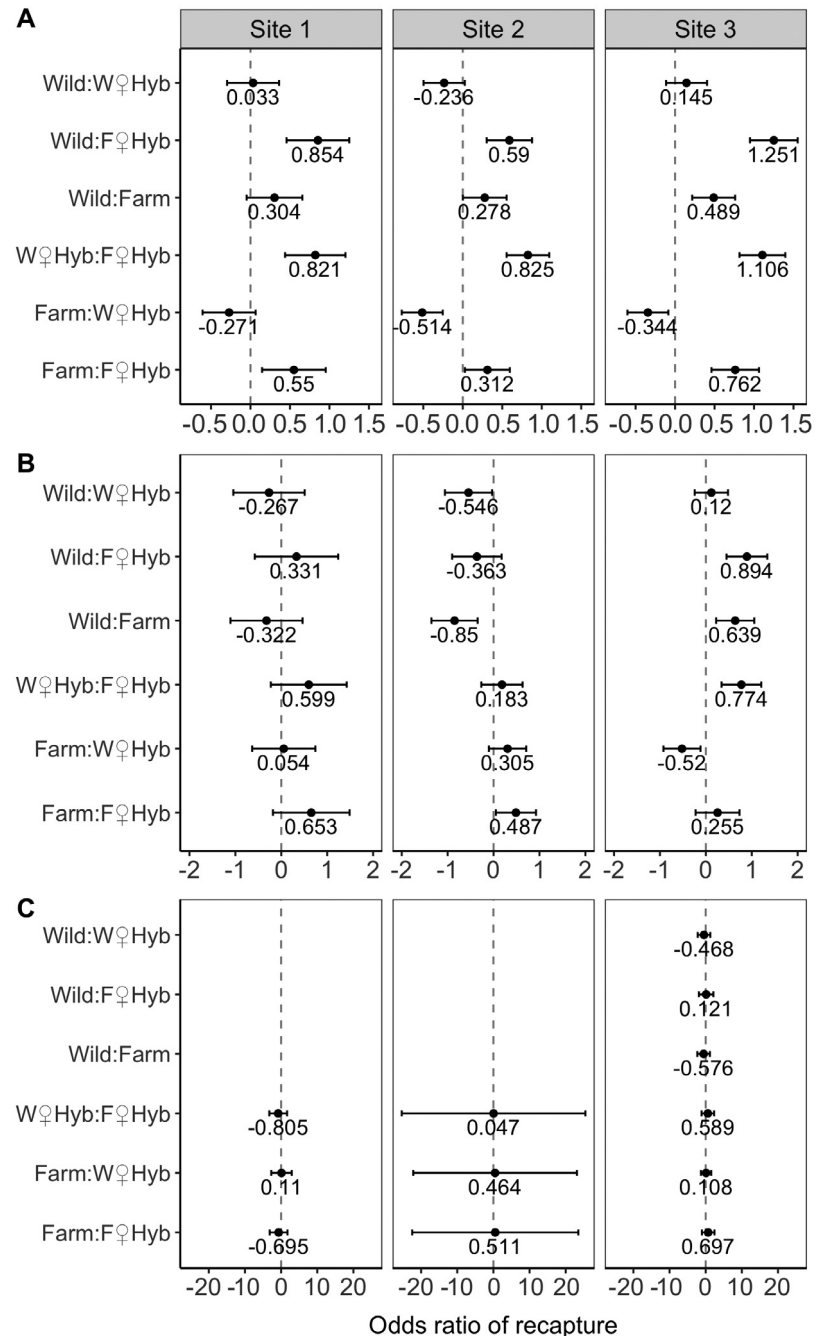


Fig. 3. Odds ratios of recapture for pairwise cross type comparisons at each site in (A) 2018, (B) 2019, and (C) 2020. Error bars represent ± 2 SE of odds ratio estimates. Odds ratios and SE were back-transformed from the logit scale. There were zero recaptures of the wild cross type at Sites 1 and 2 in 2020; therefore, pairwise comparisons relative to wild were not possible here

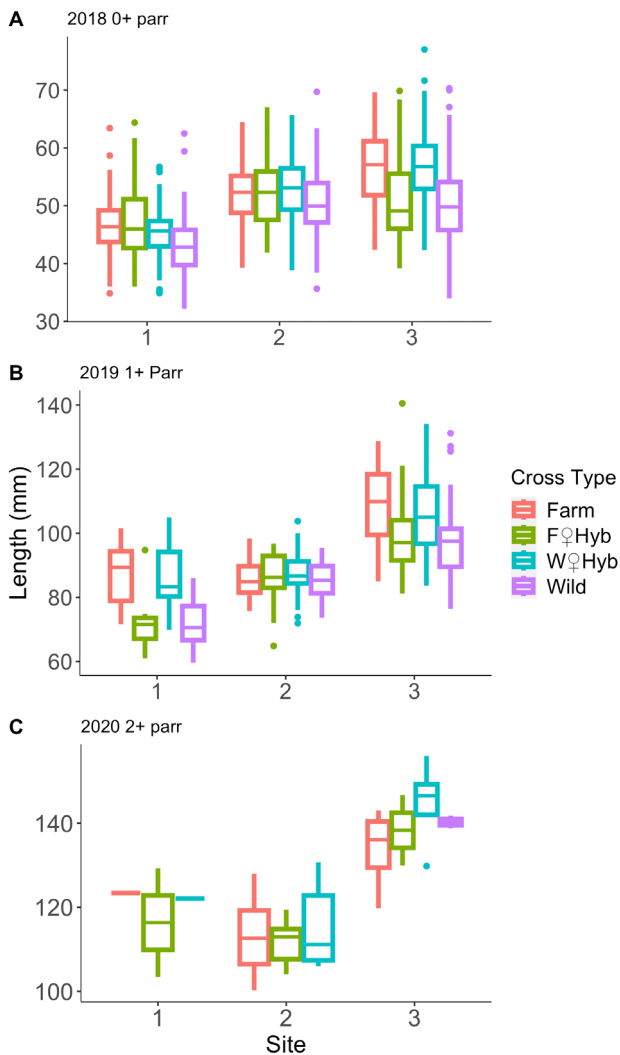


Fig. 4. Lengths of Atlantic salmon by cross type during recapture at 3 sites (A) 3 mo post-release (2018), (B) 1 yr post-release (2019), and (C) 2 yr post-release (2020). Bold lines represent median values, boxes 25 and 75 % quartiles, whiskers 1.5 times the inter-quartile range, and dots outliers

and 1 yr post-release period as well as the 3 mo and 2 yr post-release period (Fig. S1). Similarly, all cross types were notably larger at Site 3 than the other 2 sites in 2019 (length: $p < 0.01$, $LR = 6.41 \times 10^{58}$; weight: $p < 0.01$, $LR = 2.29 \times 10^8$) (Figs. 4B & 5B, Tables S6 & S7). Furthermore, there was a strong cross type \times site interaction for length ($p = 0.002$, $LR = 5.33 \times 10^4$) (Table S6), and therefore, it was analyzed at each site separately. Although the small sample size in 2020 reduced the statistical power to detect a difference in size at recapture across sites, the trend was similar to that of previous years, with fish at Site 3 being larger than those at the other sites (Figs. 4C & 5C, Tables S8 & S9). In terms of cross type differences, farm and $W\phi$ Hyb fish tended

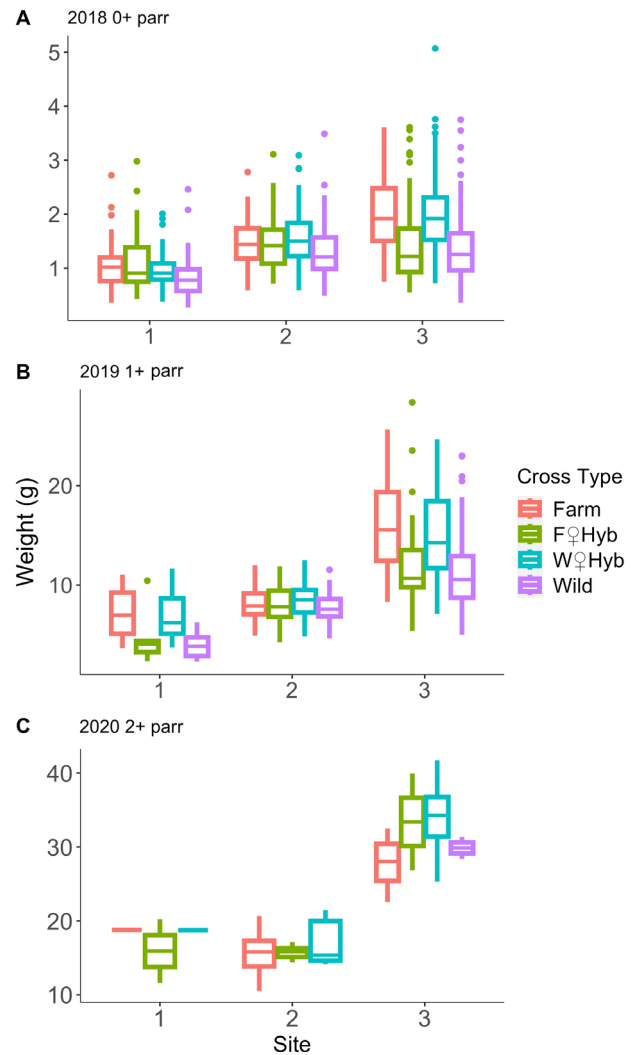


Fig. 5. Weights of Atlantic salmon by cross type during recapture at 3 sites (A) 3 mo post-release (2018), (B) 1 yr post-release (2019), and (C) 2 yr post-release (2020). Bold lines represent median values, boxes 25 and 75 % quartiles, whiskers 1.5 times the inter-quartile range, and dots outliers

to be consistently the largest across sites in 2018 and 2019, with wild and $F\phi$ Hyb typically being the smallest. Specifically, in 2018, $W\phi$ Hyb and farm were the largest at Sites 2 and 3, followed by wild, while at Site 1 farm and $F\phi$ Hyb were larger than the other 2 crosses (Crowley et al. 2022). This was again consistent with growth patterns between the 2018 and 2019 recapture periods, where farm and $W\phi$ Hyb had higher growth rates than the other 2 crosses (Fig. S1). In 2019, although farm and $W\phi$ Hyb were larger than the other 2 crosses across all sites, the evidence only pointed to an actual difference in size at Sites 1 and 3, where farm and $W\phi$ Hyb were longer and heavier (Fig. 6, Tables S7 & S10, respectively). However, in 2020, the differences among

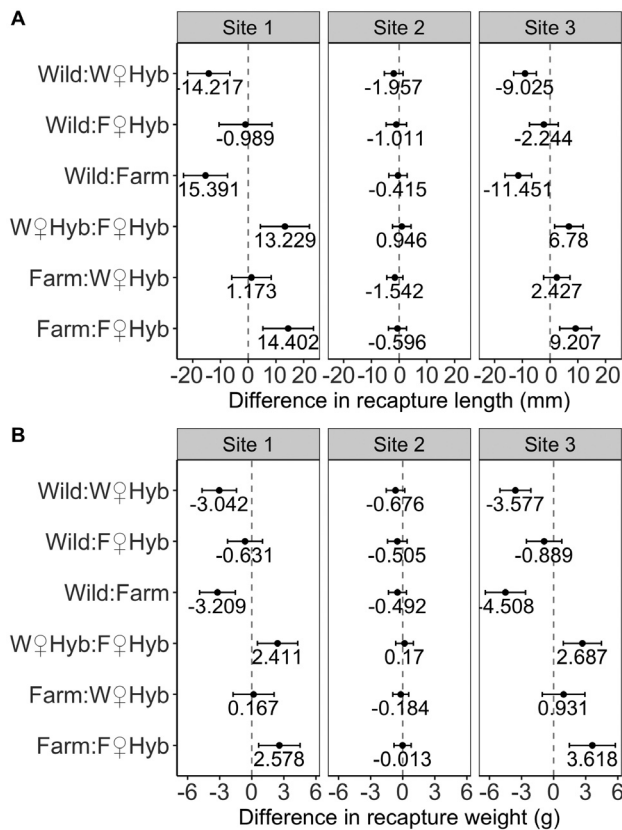


Fig. 6. Pairwise differences in mean (A) length and (B) weight at recapture at each site 1 yr post-release (2019). Error bars represent ±2 SE of difference estimates

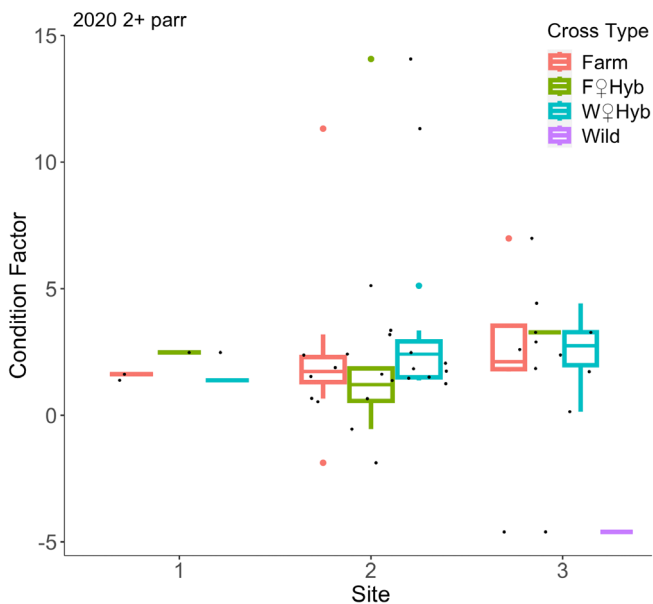


Fig. 7. Condition of Atlantic salmon at recapture in 2020 for each cross type by site pairing. Two wild samples recaptured only in Site 3. Bold lines represent median values, boxes 25 and 75% quartiles, whiskers 1.5 times the inter-quartile range, and dots outliers (coloured dots represent outliers, black dots are individual data points)

cross types were less detectable, which again may in part be due to low statistical power.

In 2018, wild parr had lower condition than all other cross types at Sites 2 and 3, with no differences between any crosses at Site 1 (as reported previously by Crowley et al. 2022). There was, however, little evidence for an effect of cross type, site, or any interaction between these variables in 2019 ($p = 0.77$, $LR = 5.41$), and no notable differences in condition between cross type pairs and across sites. Nonetheless, in 2020, there was a decisive effect of cross type on the condition of recaptured salmon, with wild fish again having a lower condition than the other 3 cross types (Fig. 7, Table S11).

3.3. Sex ratios and maturity

Overall, there was little to no evidence for a deviation from an even sex ratio (i.e. 50:50) in either 2019 or 2020 ($p = 0.104$, $LR = 3.74$ and $p = 0.0406$, $LR = 8.13$, respectively). The proportion of mature males in 2019 increased from Site 1 to 3 (30.3 to 69.7 to 81.6%), reflecting differences in size among the sites. Additionally, there was decisive evidence for a difference in maturation rates among cross types ($p = 0.0117$, $LR = 245.06$, Table S12). W♀Hyb and wild parr had similarly high proportions of mature males (82.1 and 70.2%, respectively), while farm males had the lowest (56.1%), with F♀Hyb males being intermediate (65.6%). The only substantial pairwise contrast, however, was between W♀Hyb and pure farm fish. Size also strongly affected the proportion of mature males for W♀Hyb and wild parr ($p < 0.001$, $LR = 526.10$ and $p < 0.001$, $LR = 13725.35$, respectively), but not for the other 2 crosses. In 2020, all recaptured males were mature, while all recaptured females both years remained immature.

3.4. Family representation through time and size

There was little evidence for an effect of year of recapture on family representation ($p = 0.992$, $LR = 1.01$) (Table S13), with no notable effects of selection for or against any specific families (i.e. from 2018 to 2019 and then to 2020) (Fig. S2). Even though certain families had substantially higher recapture rates than others, this difference among families remained constant through the years sampled (2018–2020). Similarly, the effect of family on weight was substantial in the first 2 sampling periods, also having an interaction with site (2018: $p < 0.001$, $LR = 4929.5$;

2019: $p < 0.001$, LR = 40.04) (Tables S14 & S15). For this reason, weight was analyzed for each site individually both years. Family and site had a strong effect on length 3 mo post-release ($p < 0.001$, LR = 13.08 and $p < 0.001$, LR = 13.43, respectively), but had no interaction (Table S16). In contrast, there was little evidence of an influence of family or site on weight in 2020, or on length in 2019 and 2020 (Tables S17, S18 & S19, respectively). Overall, the differences in weight among families appeared to decrease over time until there was insufficient power, due to small sample size, to detect any difference in 2+ parr. Certain families tended to be larger than others; however, these differences again remained constant throughout the sampling periods.

4. DISCUSSION

Given substantial genetic and phenotypic differences between highly domesticated farm Atlantic salmon *Salmo salar* and their wild counterparts, understanding how interbreeding can affect local adaptation and fitness of wild, often at-risk salmon populations has become essential to conservation efforts. Here, we found that the odds of recapture of different cross types varied significantly across the study period. There was a transition from pure wild offspring initially having higher recapture rates than farm parr, to farm offspring gradually having the highest recaptures of all crosses 15–28 mo post-release. The proportion of mature individuals differed by cross type, but overall, there was not a difference in sex ratios either recapture year. We observed high rates of precocial male maturation in the dominant hybrid group (W ϕ Hyb), indicating that the risk of introgression (backcrossing) is high. This, along with the evidence for elevated hybrid survival, suggests that the risk of wild populations being negatively impacted by farm escapees may be high. Overall, our results build on findings from Crowley et al. (2022) and expand on previous work studying cross type performance in the wild (McGinnity et al. 1997, 2003, Fleming et al. 2000, Skaala et al. 2012, 2019). More specifically, we provide novel insight into the impacts of hybridization and interactions of farmed with wild salmon in southern Newfoundland.

4.1. Survival

We observed a notable difference in rates of recapture/survival of Atlantic salmon from year to year.

Crowley et al. (2022) studied recapture odds of these experimentally released individuals in 2018 (3 mo post-release) and determined that, in accordance with previous studies, wild offspring had higher recapture odds than farm offspring (McGinnity et al. 1997, 2003, Fleming et al. 2000, Skaala et al. 2012, 2019). They found an overall survival trend of wild > hybrids > farm, although W ϕ Hyb had substantially high survival not too dissimilar to wild. Here we found that in the subsequent year (3–15 mo), farm offspring reached overall survival rates analogous to those of wild salmon, and only slightly lower than W ϕ Hyb. Specifically, there were no differences in relative survival at Site 1 among any cross types, while farm and W ϕ Hyb had higher survival than wild fish at Site 2, and in contrast, wild and W ϕ Hyb had greater survival than farm and F ϕ Hyb at Site 3. Two years post-release (15–28 mo), few wild individuals were recaptured, and these were only encountered at one site. Farm offspring had higher recapture odds than both wild and W ϕ Hyb, though this difference was not substantial. This could suggest that selection against farm fish primarily occurs during the first year (0+) where results follow the generally observed trend (wild > hybrids > farm) (McGinnity et al. 1997, 2003, Fleming et al. 2000). Our results not only differ from the 3 mo post-release sampling, but also from a broad-scale study of the change in proportions of wild, feral, and hybrid offspring following an escape event in southern Newfoundland, where wild salmon were implicated to have the highest annual survival rates over the first 2+ years in the river and pure farm offspring the lowest (Sylvester et al. 2019). However, our findings are in line with previous results from European studies, where evidence of differential survival after the 0+ stage was scarce (McGinnity et al. 1997, 2003, Fleming et al. 2000), and hybridization of domestic salmon decreased the production of wild salmon smolts and therefore wild adult abundance, through resource competition in freshwater (Skaala et al. 2019).

This analysis extends the time scale evaluated in Crowley et al. (2022), where only the 3 mo post-release period was studied, not accounting for survival during the winter months. Studies have shown that survival during the winter season tends to be lower relative to summer months in several salmonids due to unfavourable conditions and thus may be an important selective event in the salmon life history (Beamish et al. 2004, Finstad et al. 2004, Piou & Prévost 2013). Here, larger farm salmon did not appear to incur a differential survival cost over the winter relative to wild salmon, and W ϕ Hyb continued to have the highest overall survival among cross

types. Additionally, since selection against farm individuals can be more pronounced during early life (McGinnity et al. 1997, 2003, Fleming et al. 2000), as we saw during the first 3 mo post-release, the weakest individuals may die, leaving the most fit to persist. This could account for the change in survival patterns among cross types over the 3 yr period. Factors beyond cross type may also substantially influence recapture odds, such as the role limiting resources can have on mortality, growth and population dynamics (e.g. Keeley 2001, Finstad et al. 2009). Here, survival trends differed across sites; Site 1 had the fewest recaptures relative to the other 2 sites in all sampling years, and this site appeared the least abundant in resources of the 3 tributary sites, as reflected in fish body size, particularly in 2018 and 2019. Resource availability could therefore also be affecting the survival of all cross types, impacting the smaller wild and F ϕ Hyb salmon more heavily, which might explain the effects seen at Site 1 in 2019 and 2020. Furthermore, offspring in this experiment were released at river sites during early development. However, previous studies found the difference in survival between wild and farm juveniles is the most notable between eyed egg stage and the first summer (McGinnity et al. 1997, Fleming et al. 2000). Thus, if farm individuals had experienced natural conditions from hatch, their mortality rates might have been higher in the first year and many individuals may not have survived as far as the third summer.

Modelling studies in Atlantic Canada also support the hypothesis that introgression between wild and escaped domestic individuals can reduce population viability and genetically alter wild salmon (e.g. Sylvestre et al. 2019, Bradbury et al. 2020). Yet, specifically in North America, studies on the long-term effects of farm escapes on the survival of local populations are still scarce and inconclusive, highlighting the need for further study on this topic. Overall, our results combined with those of Crowley et al. (2022) show that there is, in fact, a difference in survival among crosses of Atlantic salmon, and this effect changes over time and varies spatially. Here, the shifting site-specific pattern of survival over the 3 yr following release ultimately differs from previously established general patterns, further emphasizing the contrasts among location and populations, and the need for additional population focused work over longer time series.

A major challenge of our experiment was characterizing parr dispersal, as we could not separate the probability of survival to time of recapture and the probability of being encountered at time of recapture from each other. This means that parr dispersal was

unaccounted for in our survival estimates. Therefore, it is also plausible that differences observed in recapture rates among cross types could be a function of and attributable to dispersal. It has been shown that environmental factors such as water velocity can influence dispersal of young salmon, such that higher velocities could lead to an increase in passive dispersal of parr in the downstream direction (Gowan et al. 1994, Heggenes & Dokk 2001). Furthermore, density-dependent growth and mortality could have also prompted parr dispersal as a way to avoid these costs (Grant & Imre 2005, Grossman et al. 2012). It is also possible that a few of the largest parr may have smoltified and migrated at age 2+ (O'Connor & Ash 1993), prior to the third recapture event. Thus, it is possible that rates of dispersal were different among crosses and were influenced by environmental variation of traits that were not quantified across our tributary sites. These were not measured as this was not a focus of the study; rather, our interest was in replicability of findings across different environments. Still, parr movement does not discount the possibility that survival can differ substantially among cross type groups, or of an interaction between survival and dispersal that could be further explored.

4.2. Size

Our overall results are in line with previous findings from both the first summer of this experiment (Crowley et al. 2022), and studies throughout Europe (e.g. Einum & Fleming 1997, McGinnity et al. 1997, Fleming et al. 2000), where wild parr tended to be the smallest of the crosses, and farm fish were larger across various environmental conditions. Unlike the changing survival patterns, the size trend remained constant throughout the sampling periods, with Site 3 typically having the largest individuals, and farm and W ϕ Hyb fish also being generally larger than wild and F ϕ Hyb. In contrast, recent studies in Newfoundland have failed to find evidence for a consistent growth and size pattern across freshwater life stages. For instance, Hamoutene et al. (2017) reported that egg size of wild females relative to that of farmed females was notably larger, which likely produced larger wild offspring at hatch. Similarly, Perriman et al. (2022) detected a significant difference in size between pure wild and pure farm individuals, where, under tank and semi-natural conditions, wild fish were larger than both farm and hybrid salmon at first feeding. However, since this difference disappeared by Day 80, it was again attributed to maternal

effects of egg size. These contrasting results could be associated with the different wild populations studied and/or differences in rearing experiences of juveniles. On the other hand, Crowley et al. (2022) reported that there was little difference in average egg size of wild and farmed mothers in the fish used for this experiment, and wild juveniles were the smallest cross type at release.

Although the design of this experiment did not allow us to study a link between size at recapture and survival within cross type groups, there appears to be a correlation between these 2 variables. We were only able to detect a difference in size among cross types in 2018 and 2019, due to a small sample size in 2020. Nevertheless, farm and W ϕ Hyb were generally larger than the other 2 cross types, and also exhibited overall higher rates of recapture (W ϕ Hyb) or increasing odds relative to wild individuals through time (farm). However, these patterns of recapture may not completely reflect survival; it is possible that the generally larger farm and W ϕ Hyb individuals displaced the smaller wild fish from these sites when competing for resources. Offspring of escaped farm salmon have been found to negatively impact wild populations through competition, as faster-growing farm parr may competitively displace wild parr from suitable environments in the wild (Fleming et al. 2000, McGinnity et al. 2003, Skaala et al. 2019) and can induce mortality (Roberston et al. 2019). Additionally, increased aggression has been observed in farm salmon (Fleming & Einum 1997, Fleming et al. 2002, Islam et al. 2022), which may further be advantageous to these already larger fish in competitive encounters. Yet the possibilities that wild fish were displaced out of the tributary sites and that their survival is lower over time are not mutually exclusive, as the impact of this displacement on wild individuals is dependent on whether displaced parr can survive downstream. Even so, previous research has also indicated that farm Atlantic salmon offspring risk a substantially higher level of predation exposure and that fast-growing salmonids have greater vulnerability to fishing due to their greater appetite and, correspondingly, greater foraging activity rates and boldness (Einum & Fleming 1997, Biro & Post 2008, Solberg et al. 2020).

Site had a strong effect on differences in size all years, as fish of all cross types were larger at Site 3 than individuals of the same cross at Sites 1 and 2. This likely reflects differences in available forage, though this was not quantified. However, this is where wild and W ϕ Hyb had decisively higher survival than farm and F ϕ Hyb in 2019, which further

suggests that resource availability and competition could affect odds of recapture of smaller cross types over time (Fleming et al. 2000, McGinnity et al. 2003, Skaala et al. 2019).

4.3. Sex ratios and maturity

Although there was no evidence for a biased sex ratio in our recapture samples, the effect of sex on maturation rates was notable. A recent study in southern Newfoundland determined that precocial male maturation may play a key role in the observed increasing presence of backcrossed individuals over time following an escape event and thus genetic introgression (Holborn et al. 2022). Consistent with this observation, we found that the proportion of mature hybrid male parr was high at age 1+ and did not differ from that of wild males under the same environmental conditions, while that of farm parr was lower. Additionally, growth has been previously found to influence rates of precocial maturation (Letcher & Gries 2003, Jonsson & Jonsson 2011), with some findings suggesting that exceedingly high growth rates can cause individuals to outgrow the size threshold for early maturation (Moreau & Fleming 2012, Harvey et al. 2018). However, here, size had a strong effect on the maturation rates of wild and W ϕ Hyb parr, even though W ϕ Hyb were substantially larger than wild individuals, suggesting they might have differing growth rate thresholds for maturation. Moreover, we observed an increase in the proportion of mature males from Sites 1 to 3, likely reflecting differences in size among the sites. Rates of introgression will be further influenced by differences among cross types in the relative reproductive success of males that mature precocially, which has been shown to differ previously, with farm and hybrid males having superior success to wild males (Garant et al. 2003). Thus, the high rates of male precocial maturation observed here, particularly among hybrid males, will likely lead to high rates of introgression of farm genotypes into wild Atlantic salmon populations.

4.4. Family representation and size

Survival and selection at the family level have been studied less frequently than cross type survival. Here we found that certain families outperformed others regardless of their body size relative to each other. Moreover, this difference in survival rates

remained consistent throughout the 3 yr of sampling, and families that differed in size did not always differ in odds of recapture. This consistent survival pattern could indicate that family-level selection occurred prior to the first recapture event. Results similar to these have been observed previously in a European study, where families that were highly represented at the 0+ parr stage in the experiment were also highly represented at the 1+ parr stage, implying consistent performance differences in the wild (Reed et al. 2015). This was despite the finding that offspring with 1 or 2 farm parents exhibited poorer survival in their first and second year of life compared with those with 2 wild parents. Similarly, Skaala et al. (2019) found that families with high egg to smolt survival also had high smolt to adult survival.

The relatively small family numbers used in this study per cross type were due to the limited number of farmed parents that matured by the time breeding occurred. This could present a challenge in our ability to draw certain conclusions regarding cross type survival as the performance of one or a few families within a cross type could weigh heavily on the average performance of that cross. However, the proportion of individuals of one family would still have to be substantially higher than the rest at each site if it were to disproportionately increase the odds of recapture of an entire cross type group over another. Since we found that the families with greater representation were the same over the 3 yr, which was not the case for cross types, it is therefore unlikely that the effect of family numbers heavily affected cross type survival results.

5. CONCLUSIONS

Our overall results indicate that relative differences in survival among wild, farm, and hybrid Atlantic salmon parr change during the freshwater period. Here, selection against farm individuals appears to be stronger during the first summer after release (0+ parr) and shifts over time. Moreover, rates of male precocial maturation can be high already in the second year of life, particularly among hybrid individuals. We show that vital rates such as survival and precocial maturation of wild, hybrid, and farm offspring can change during their life span. Therefore, improved understanding of this variation is needed to determine, predict, and manage the genetic and demographic impacts of farm escapees on wild salmon populations.

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