



Precocial male maturation contributes to the introgression of farmed Atlantic salmon into wild populations

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ABSTRACT: The escape of domesticated Atlantic salmon *Salmo salar* from aquaculture facilities represents a continued threat to the genetic and demographic stability of wild salmon stocks. Escaped farm-origin salmon have been shown to hybridize with wild conspecifics, yet the long-term genetic impacts are generally unknown. Theoretically, life history variation, specifically precocial maturation of male hybrids, could fast-track introgression, but evidence for this has been sparse. Here, we used empirical and experimental data to examine the role of precocious male maturation in introgression. We examined hybrid class composition using juvenile sampling and genetic assignment over a 5 yr period following an escape event in southern Newfoundland, a region with high rates of natural male precocial maturation. Initially following the escape, the proportion of first-generation (F1) hybrids was high and then decreased annually, contrasting the proportion of backcross wild individuals, which increased over time. The presence and temporal distribution of backcross wild individuals supports the hypothesis that high rates of precocial maturation can fast-track the long-term impacts of escaped farmed salmon on wild populations via interbreeding. This was experimentally tested using lab-created wild, farmed, and F1 parr released and recaptured from a Newfoundland river to assess levels of precocious male maturation. Observed rates of maturation of F1 hybrids were high and similar to wild parr (77 vs. 73%, respectively), indicating that most F1 hybrids mature precocially. Our results suggest that rates of precocial male maturation should be explicitly considered in risk assessments evaluating the genetic impacts of escaped farmed salmon on wild populations.

KEY WORDS: Hybridization · *Salmo salar* · Aquaculture interactions · Precocial maturity · Alternate life history

1. INTRODUCTION

Hybridization with domestic conspecifics has been documented across the domestic production range of Atlantic salmon *Salmo salar* (Clifford et al. 1998, Glover et al. 2012, Karlsson et al. 2016, Wringe et al. 2018), and it is estimated that, globally, millions of domestic escapees enter wild environments annually

(Hansen et al. 1997, 1999, Skaala et al. 2006, Skilbrei et al. 2015, Glover et al. 2017, Keyser et al. 2018). Domesticated Atlantic salmon are genetically distinct from their wild counterparts due to several generations of direct and inadvertent domestication selection for economically important traits (Gjedrem & Baranski 2009), and accordingly, escaped domesticated Atlantic salmon and their offspring are no longer

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well adapted to the natural environment (Fleming et al. 1996, McGinnity et al. 1997, 2003, Skaala et al. 2012, Reed et al. 2015, Sylvester et al. 2019). Therefore, genetic introgression into wild populations has been identified as a major threat to wild Atlantic salmon populations (Glover et al. 2017). Interbreeding can lead to a loss of local adaptation (Taylor 1991, Einum & Fleming 1997, Bourret et al. 2011), outbreeding depression (McGinnity et al. 2003, Gilk et al. 2004, Tymchuk et al. 2007), shifts in phenology (Skaala et al. 2019, Bolstad et al. 2021, Besnier et al. 2022), changes in life history traits (Bolstad et al. 2021, Besnier et al. 2022), population decline (Sylvester et al. 2019, Bradbury et al. 2020), and in extreme cases, could result in the extinction of wild populations (Levin et al. 1996). This is supported by experimental and observational studies which report reduced survival and fitness for domestic offspring relative to wild Atlantic salmon in natural environments (Fleming et al. 2000, McGinnity et al. 2003, Skaala et al. 2012, Sylvester et al. 2019).

The ultimate magnitude of hybridization and introgression experienced by wild populations exposed to escapees may be dependent on a combination of biological and landscape characteristics (Garant et al. 2003, Glover et al. 2013, Karlsson et al. 2016, Moe et al. 2016, Sylvester et al. 2018, Diserud et al. 2022). In particular, it has been hypothesized that variation in life history such as precocial male maturation could exacerbate these impacts and accelerate the introgression of farm-origin genes into wild populations (Garant et al. 2003, Hindar et al. 2006) and subsequent population decline. Precocious maturity is a common male alternative life history where parr mature in freshwater streams as juveniles, bypassing the requirement for ocean migration to successfully reproduce (Jones 1959). Mature male parr often weigh 2 orders of magnitude less than their anadromous adult counterparts (Fleming & Reynolds 2004), adopt a sneaker strategy to achieve fertilization (Jones 1959), and display increased fertilization success in wild mating events (Hutchings & Myers 1988, Garant et al. 2003, Weir et al. 2005). As such, this life history strategy may increase the likelihood of successful reproduction and fast-track introgression by reducing the time period between hatching and reproduction, avoiding the risk of mortality associated with marine migration (Garant et al. 2003).

In southern Newfoundland, the Atlantic salmon aquaculture industry has expanded in recent years, contrasting record lows of abundance in wild salmon (DFO 2020a,b). Domestic Atlantic salmon used at aquaculture sites in this region are thought to origi-

nate from the non-local Saint John River (New Brunswick, Canada) and have undergone approximately 6–7 generations of domestication selection (Liu et al. 2017). Recent work in southern Newfoundland using genetic assignment of wild-caught juvenile salmon to genetic hybrid classes has documented extensive hybridization between wild and escaped farmed salmon and detected feral individuals (offspring of 2 domestic escapees) (Wringe et al. 2018), revealing spatial variation in hybridization (Sylvester et al. 2018) and selection against domestic offspring in the wild (Sylvester et al. 2019). However, the potential role of life history variation such as precocial male maturation in influencing levels of introgression has not been examined. In southern Newfoundland rivers, precocial males mature at 1+ yr of age, and the rates of precocial male maturation are variable but may be quite high, ranging up to 80–90% (Dalley 1978, Dalley et al. 1983, Myers 1984).

Here, we further explored the effect of hybridization and introgression on wild populations of Atlantic salmon in southern Newfoundland. First, using empirical data on changes in hybrid class composition from southern Newfoundland over a 5 yr period encompassing offspring from a known large escape event in 2013 (Wringe et al. 2018, Sylvester et al. 2019) and a known smaller escape event in 2015, we examined evidence for rapid increases in the presence of backcross wild (BCW) individuals consistent with precocial male maturation in hybrids. Second, using experimental data on lab-created wild, farmed, and first-generation (F1) hybrid crosses released and recaptured in a southern Newfoundland river, we assessed rates of precocial male maturation in a natural river. This study provides evidence of a clear role of precocial male maturation in introgression experienced by wild Atlantic salmon populations interbreeding with escaped farmed salmon.

2. MATERIALS AND METHODS

2.1. Southern Newfoundland river sampling and genotyping

Atlantic salmon parr were sampled from 19 rivers in southern Newfoundland by electrofishing during the summer months between 2014 and 2018 (Fig. 1, see Table 1). Sampling was conducted under a Fisheries and Oceans Canada experimental license and collections permit, and fish were euthanized either by a lethal dose of MS-222 or brain pithing. Captured fish were assigned to age class (young of the year

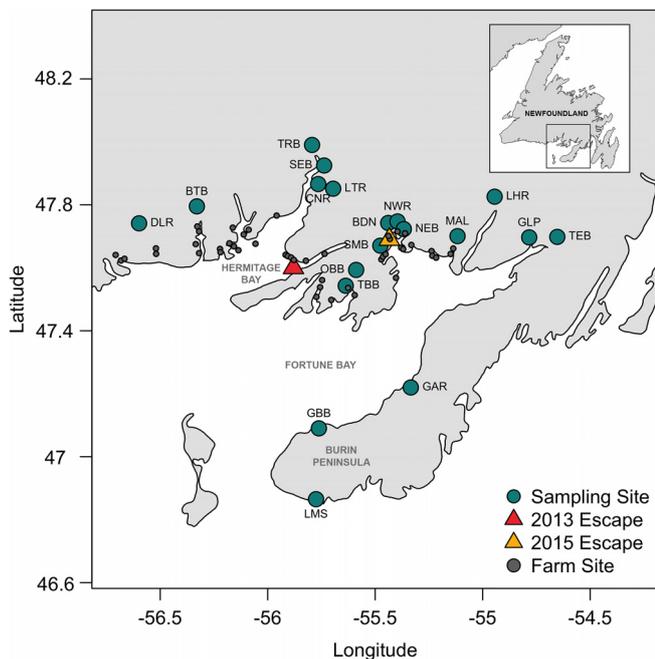


Fig. 1. Atlantic salmon parr sampling sites in southern Newfoundland relative to the large 2013 escape event and smaller 2015 escape event. Farm sites indicate close proximity to wild salmon populations. See Table 1 for river abbreviations

[YOY], 1+ parr, 2+ parr, smolt) based on fork length (see Sylvester et al. 2019), and a fin clip was collected and preserved in 95% ethanol for subsequent DNA extraction. High-confidence wild-caught samples and samples of known farmed origin of various year classes from the region, therefore likely to represent escapee genotypes, were also genotyped for use as an allele frequency baseline for pure wild and domestic populations, respectively (Table S1 in the Supplement at www.int-res.com/articles/suppl/q014p205_supp.pdf) (Wringe et al. 2018). DNA was extracted using methods outlined in Sylvester et al. (2019), but briefly, DNA was extracted using QIAmp 96 DNA QIAcube HT Kit (Qiagen) and quantified using QuantiT PicoGreen dsDNA Assay Kit (Invitrogen), following manufacturer protocols. Samples from the YOY age class were initially genotyped with Fluidigm single nucleotide polymorphism (SNP)-type assays for 96 diagnostic SNP markers previously shown to assign individuals to hybrid class (herein called the primary panel) (Wringe et al. 2018). Quality control filtering was performed, and fish with a sample call rate ≥ 0.9 were retained for subsequent analysis. Individuals assigned to any one of the 4 hybrid genetic classes (see Section 2.4) based on this primary panel were selected for genotyping on an additional 95 SNP panel for fish collected in 2014, 2015, and 2016 (Wringe et al. 2019) or 96 SNP panel

for 2017 and 2018 fish. This 96 SNP panel was redeveloped to include several more informative SNP loci to reflect population changes over the time series; however, the 2 panels are similar as they have an overlap of 83 SNPs. These additional panels were developed to confirm hybrid genetic class and improve assignment power when analyzed in combination with the primary panel (herein called the secondary panel).

2.2. Genetic class analysis

Genetic data manipulation was performed using PLINK v.1.9 (Purcell et al. 2007, Chang et al. 2015) and the package 'genepopedit' (Stanley et al. 2017) in R (R Core Team 2019). The program 'NEWHYBRIDS' (Anderson & Thompson 2002), run in parallel using the R package 'parallelnewhybrid' (Wringe et al. 2017a), was used to categorize samples into one of 6 genetic classes. Samples could be classified as pure wild, pure farmed (indicating feral offspring), F1 hybrid, or one of several second-generation hybrids that are further introgressed (F2, BCW, backcross farm/feral [BCF]). NEWHYBRIDS uses a Bayesian model-based clustering analysis to calculate the posterior probability, using Markov chain Monte Carlo sampling for each individual. As each river was run independently to reduce the chance of inter-river genetic variation being misinterpreted as introgression, high-confidence pure wild individuals (posterior probability of assignment ≥ 0.995) specific to that river were used in the baseline where possible. For the primary SNP panel analysis, each river had 150 genotypes of wild origin for use in the baseline, and when possible, all 150 were high-confidence river-caught individuals representing pure wild genotypes from the specific river being analyzed. Where an insufficient number of high-confidence river-caught pure wild fish had been sampled and genotyped, the allele frequency baseline was supplemented with simulated and centred wild genotypes, generated using individuals identified as pure wild, using the 'hybriddetective' package (Table S1) (Karls-son et al. 2014, Wringe et al. 2017b). The wild fish used to produce the simulated wild baseline individuals were collected from multiple rivers and are therefore representative of the southern Newfoundland region rather than a specific river. The farmed baselines used in the analysis were the same for each river and included 143 simulated and centred individuals based on samples collected from nearby aquaculture sea cages and 57 high-confidence pure feral fish collected within rivers representing the genotypes of escapees.

Representative fish from the main producers were chosen for this baseline and supplemented with pure domestic fish encountered in the wild. Given that escapes are often detected without reported escape events, this strategy was chosen to accurately capture variation present in the aquaculture fish. The high-confidence farmed individuals ($n = 57$) from the wild were largely (93%) juveniles. All baseline individuals were run in *NEWHYBRIDS* with the 'z' option indicating prior knowledge of that individual's genetic class due to known origin, and simulated baseline individuals were also run with the 's' option indicating these individuals were not sampled from the mixture of interest (Anderson & Thompson 2002). *NEWHYBRIDS* was run using a burn-in of 50 000 and 100 000 sweeps with individuals from all sampling years included for each river. Posterior probability of assignment for each genetic class was calculated for each individual, representing the level of certainty that the individual belongs to that genetic class. Each individual was then classified as either pure wild, pure farmed/feral, or hybrid based on which genetic class had the highest posterior probability, with the hybrid class being the sum of the F1, F2, BCW, and BCF posterior probabilities. Individuals that did not pass the posterior probability threshold of 0.8 within the pure wild or pure farmed/feral genetic classes were removed from the data set, while all individuals identified as a hybrid were selected for further genotyping regardless of passing this threshold.

Individuals initially identified as a hybrid genetic class from the *NEWHYBRIDS* analysis using the primary SNP panel were reanalyzed using SNPs from the primary and secondary SNP panels. *NEWHYBRIDS* was run using the same methodology outlined above, with individuals collected from 2014–2016 run together and 2017–2018 run together within their respective rivers due to the minor panel redesign. However, all wild and farmed baselines were simulated due to reduced numbers of high-confidence wild and farmed individuals genotyped on the secondary panel (see Table S1 for details). Again, individuals were removed from the data set if they did not pass a posterior probability threshold of 0.8 for one of the 4 hybrid genetic classes. The proportions of each genetic class were scaled for river population size using axial river length, as axial length is a proxy for the population size in Newfoundland (Porter et al. 1974), for each sampling year to represent the total proportion of each genetic class for southern Newfoundland rivers.

The efficiency and accuracy of the secondary panel were estimated to assess the performance of the panel at assigning individuals to the appropriate

genetic class, specifically the hybrid genetic classes. This was done using the 'hybridPowerComp' function in 'hybriddetective' (Wringe et al. 2017b). Efficiency is the proportion of individuals in a genetic class that were correctly identified, while accuracy is the proportion of individuals assigned to a certain genetic class that actually belong to that class (Vähä & Primmer 2006). Efficiency and accuracy were estimated using known high-confidence wild and farmed baseline samples to simulate 125 individuals for each of the 6 genetic classes, creating 3 simulations with 3 replicates each for a total of 9 data sets. These data sets were then run through the same *NEWHYBRIDS* workflow above to assign each simulated individual to a genetic class.

2.3. Precocial maturation in a wild environment

In order to assess the occurrence of precocial maturation of F1 hybrids in wild environments, lab-crossed pure wild, pure farmed, and F1 hybrids released in a southern Newfoundland river had their sex and maturation status subsequently categorized upon recapture. Crosses were created at the Ocean Sciences Centre in St. John's, Newfoundland, in November and December 2017 and reared in a flow-through system until release in the Garnish River (Fortune Bay) system at 3 sites in July 2018 (see Crowley et al. 2022). At the time of release, the fish were of similar size (Crowley et al. 2022). Wild parents used in the crosses were from the Garnish River and farmed parents were from the Saint John River aquaculture strain, the strain used at aquaculture sites in southern Newfoundland. In total, 27 family crosses were created: 9 pure wild, 6 pure farmed, and 12 F1 wild–farmed hybrid crosses, 6 families of each reciprocal cross. Before release, an adipose fin was removed from offspring for future identification of these experimental fish, and fish were recaptured in September 2019 via electrofishing. Internal examination via dissection was performed to determine sex and maturation status, and fish fork length and weight were also recorded. A tissue sample from both parents and recaptured offspring was extracted with the DNeasy Blood and Tissue Kit (Qiagen) and genotyped for 25 microsatellite markers (a subset from Bradbury et al. 2018) to establish parentage and thus genetic class. Parentage assignment was performed using *COLONY* (Jones & Wang 2010) for known parental individuals and 401 recaptured offspring from 23 family crosses, of which 189 were female and 212 male (Table S2).

Analysis of recaptured males was performed within hybrid genetic class to assess differences in maturation status. For the 212 recaptured male parr, a binary phenotypic trait was recorded: mature or not mature. Proportions of mature and not mature males for all 3 cross types were estimated based on the recaptured individuals both by release–recapture site and combined for the entire river. Weight and length were highly correlated (adjusted R^2 : 0.942, $p < 0.001$), therefore weight was chosen as the variable for analysis, but weight was ln transformed to conform to a normal distribution (Shapiro-Wilk normality test, $p > 0.1$). ANOVAs were performed to test for differences between weight at different release–recapture sites and differences in weight between the cross types. To test for differences in maturation status (precocially mature, not mature) between the cross type (wild, hybrid, farmed) a chi-squared test for independence was performed. Fisher's exact test was used for post hoc analysis to determine significant differences in maturation status between the genetic cross type.

3. RESULTS

3.1. River sampled genetic class analysis

A total of 3950 fish of the 4204 genotyped YOY individuals from all 5 collection years (Table 1) exceeded the posterior probability threshold of 0.8 for one of the 6 genetic classes after genotyping on

either the primary or secondary SNP panels. For each collection year, the proportion of pure wild, pure feral, and hybrid parr were estimated for each river using axial length as a proxy for population size (Fig. 2) and then, more specifically, the proportion of the 4 hybrid genetic categories (Fig. 3), to observe temporal variation in hybrid classes. In 2014, the year immediately following the large escape event, many rivers had a high proportion of pure feral and hybrid fish, specifically F1 hybrids (Fig. 4). The general trend observed was a steady increase in the proportion of pure wild YOY fish with the exception of the 2017 sampling year, where there was a slight decrease with a reciprocal increase in hybrid genetic classes (Fig. 4A). Within the hybrid genetic classes, there was a sharp increase in the proportion of BCW individuals following the escape event, and BCW remained the predominant hybrid class in subsequent years (Fig. 4B). The overall proportion of BCW fish increased from 0.10 in 2014 to a maximum of 0.84 in 2017, with a slight dip to 0.81 in 2018. A decrease in the proportion of F1 fish was also observed, with a high of 0.78 in 2014 dropping to the lowest at a proportion of 0.06 in 2017 (Fig. 4B). The F1 proportion slightly increased in 2018 to 0.1, mirroring the slight decrease in BCW in that year.

However, several rivers in the study area deviated from the general trend of increasing pure wild and BCW proportions. One river, Lamaline Salmonier River, located at the extreme edge of the survey area, had only pure wild individuals sampled across all

Table 1. Southern Newfoundland rivers sampled for juvenile Atlantic salmon and associated river codes (see Fig. 1), latitudinal and longitudinal coordinates, and number of sampled and successfully genotyped young of the year parr for each year

River name	River code	Lat	Long	2014	2015	2016	2017	2018
Bay du Nord River	BDN	47.782	−55.445	0	55	50	33	13
Bottom Brook	BTB	47.795	−56.329	32	3	46	8	0
Conne River	CNR	47.866	−55.765	370	20	81	53	71
Dollard's Brook	DLR	47.741	−56.599	25	22	67	62	10
Garnish River	GAR	47.239	−55.353	199	56	102	41	79
Grand Bank Brook	GBB	47.091	−55.763	42	15	3	39	4
Grand LaPierre	GLP	47.695	−54.782	118	14	7	6	0
Lamaline Salmonier River	LMS	47.780	−54.948	40	89	59	54	41
Little River	LTR	47.851	−55.696	130	0	86	56	40
Long Harbour River	LHR	46.865	−55.775	137	49	49	41	8
Mal Bay Brook	MAL	47.701	−55.116	17	36	0	0	0
Northeast Brook	NEB	47.723	−55.367	115	1	50	67	3
Northwest River	NWR	47.749	−55.395	41	0	80	52	29
Old Bay Brook	OBB	47.593	−55.588	18	0	34	66	73
Simms Brook	SMB	47.670	−55.476	69	20	87	55	27
Southeast Brook	SEB	47.924	−55.741	31	0	0	16	10
Tailrace Brook	TRB	47.992	−55.792	80	9	50	50	25
Taylor Bay Brook	TBB	47.543	−55.637	120	0	3	16	1
Terrenceville Brook	TEB	47.671	−54.711	120	9	48	46	5

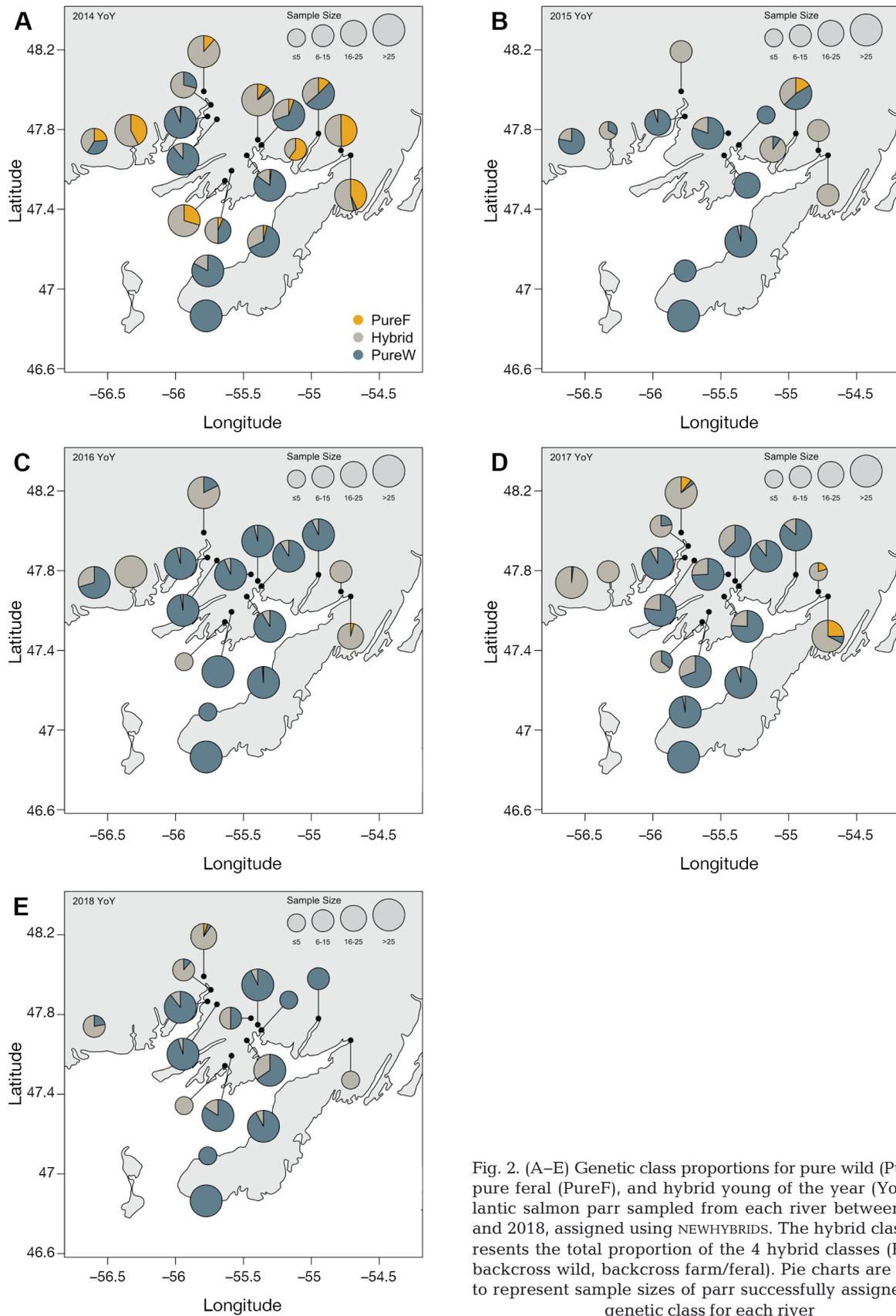


Fig. 2. (A–E) Genetic class proportions for pure wild (PureW), pure feral (PureF), and hybrid young of the year (YoY) Atlantic salmon parr sampled from each river between 2014 and 2018, assigned using NEWHYBRIDS. The hybrid class represents the total proportion of the 4 hybrid classes (F1, F2, backcross wild, backcross farm/feral). Pie charts are scaled to represent sample sizes of parr successfully assigned to a genetic class for each river

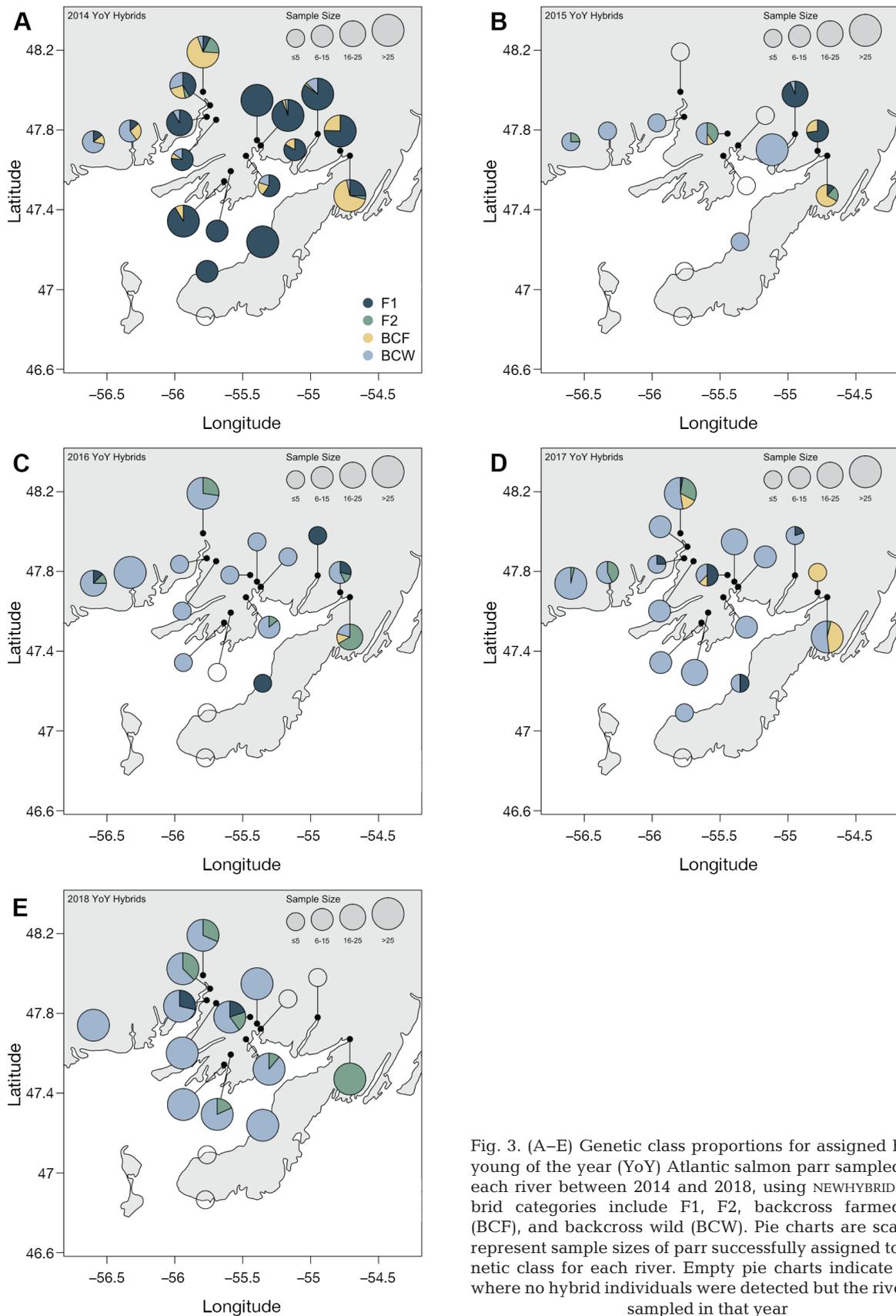


Fig. 3. (A–E) Genetic class proportions for assigned hybrid young of the year (YoY) Atlantic salmon parr sampled from each river between 2014 and 2018, using NEWHYBRIDS. Hybrid categories include F1, F2, backcross farmed/feral (BCF), and backcross wild (BCW). Pie charts are scaled to represent sample sizes of parr successfully assigned to a genetic class for each river. Empty pie charts indicate rivers where no hybrid individuals were detected but the river was sampled in that year

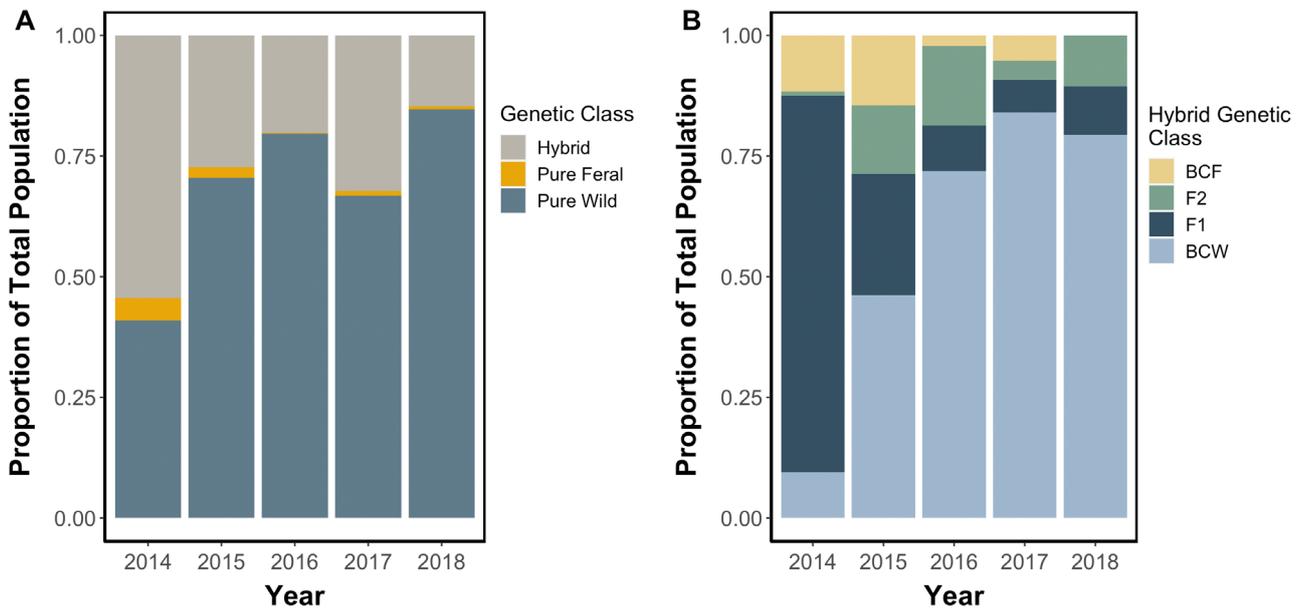


Fig. 4. Proportions of genetic classes for the total southern Newfoundland population of Atlantic salmon scaled by river axial length as a proxy for population size, for each year sampled. (A) total proportions for pure wild, pure feral, and hybrid genetic classes, where hybrid cumulatively represents all 4 hybrid categories. (B) Total proportions for the hybrid genetic classes, backcross farmed/feral (BCF), F2, F1, and backcross wild (BCW), for the hybrid proportion indicated in (A)

years. In contrast, several small rivers did not show an increase in the proportion of pure wild and appeared to be dominated by hybrids and/or feral fish. These rivers, Taylor Bay Brook, Grand LaPierre, and Terrenceville Brook, displayed patterns of hybrid swarms as many of the YOY fish sampled in these rivers were highly admixed.

The ‘hybriddetective’ accuracy and efficiency analysis demonstrated the ability of the secondary panel to clearly assign the river sampled individuals to genetic class. The panel demonstrated high accuracy for all genetic classes, and accuracy ranged from 1 (pure feral) to 0.970 (F1), while efficiency ranged from 0.995 (pure feral) to 0.720 (F2) at the posterior probability threshold of 0.8 (Fig. S1). Specifically, the accuracy of assignment of BCW individuals was 0.986, and the efficiency was 0.933. The secondary panel, therefore, demonstrated high accuracy and efficiency at assigning individuals to all genetic classes.

3.2. Precocial maturation rates between crosses

Of the 401 recaptured and genetically assigned experimental 1+ parr from the release experiment, 212 were males (51 wild, 99 F1 hybrid, and 62 farmed) of which 146 (69%) were fully mature or in the process of maturing (Fig. 5). Across all 3 release sites, F1 hybrids had the highest percentage of

mature parr (77%), followed by pure wild (73%) and pure farmed (53%). There were some notable differences among the 3 sites; e.g. Site 1 had lower proportions of precocial parr for all cross types, and Site 3 had higher proportions, which could be attributed to differences in male parr weight between sites (ANOVA, $p < 0.001$). There were no significant differences in the weight of fish from different genetic class crosses (ANOVA, $p = 0.377$), indicating equal distribution of sizes between the crosses; however, weight was significantly different between immature and mature fish ($p < 0.01$), with mature fish having a higher average weight. A chi-squared test was performed to test the relationship between maturation status (immature–mature) and genetic cross type, and a statistically significant association was detected ($p < 0.01$). Fisher’s exact test was used for post hoc analysis and indicated that significant differences existed in the maturation status between farmed and F1 hybrids ($p < 0.05$), where F1 males had higher proportions of mature parr (see Fig. 5), but there was no difference between farmed and wild crosses and wild and F1 crosses.

4. DISCUSSION

Genetic interactions between domesticated and wild Atlantic salmon have been widely documented

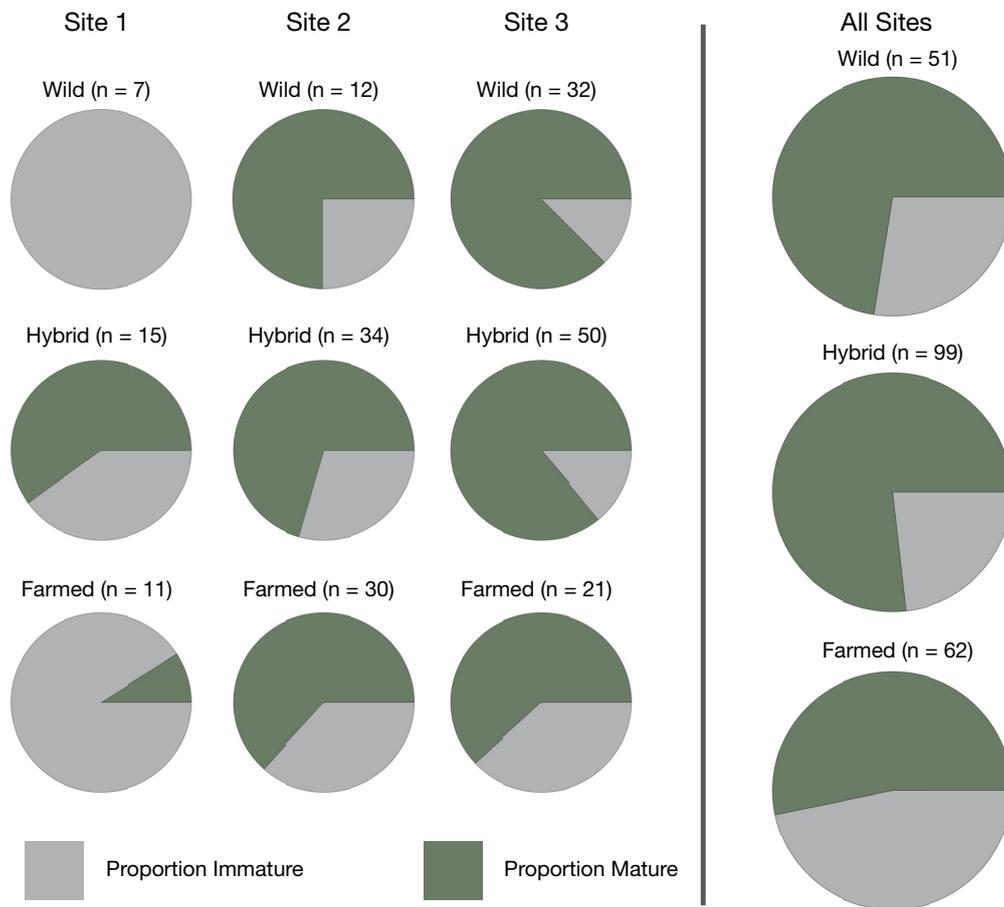


Fig. 5. Proportions of immature and mature male Atlantic salmon parr from 3 genetic class cross types (pure wild, F1 hybrid, and pure farmed) experimentally placed in the Garnish River in southern Newfoundland. Lab-created crosses were made in late 2017 and released at 3 sites within the Garnish River in July 2018 and resampled in September 2019

(Hindar et al. 2006, Glover et al. 2017, Keyser et al. 2018) and are consistently identified as a significant threat to the persistence of salmon in the wild. Although the extent of genetic introgression has been associated with the number and proportion of domestic escapees (Glover et al. 2013, Heino et al. 2015, Karlsson et al. 2016, Diserud et al. 2022), the role of other mechanisms such as levels of precocial male maturation, which may influence the rate of introgression, remain less clear. Understanding these mechanisms will be critical to predicting and mitigating the impacts of escapees on wild populations. Here, we built on the existing research and explored the potential role of precocial maturation on introgression using a combination of empirical and experimental data. Our results demonstrate that (1) increases in the proportion of BCW individuals following escape suggests precocial maturation is a significant driver of introgression; and (2) F1 hybrid male parr mature in natural environments at similar

rates to wild male parr. Our results support a clear role for precocial male maturation in determining the rate of introgression experienced by wild salmon populations interbreeding with escaped farmed salmon and extends previous observations of introgression in the region (Wringe et al. 2018, Sylvester et al. 2019).

4.1. Change in hybrid classes

Our results identified significant temporal differences in the proportions of the different hybrid classes present across southern Newfoundland during the sampling period. In the year immediately succeeding the 2013 escape event, our results support previous observations that YOY F1 hybrids were the most prevalent hybrid classes detected in rivers, and that hybrids comprised the majority of parr sampled. In the following years, the proportion of F1 hybrids

appears to have decreased drastically, consistent with a large influx of escapees in 2013. However, the low but continued presence of F1 hybrids in the latter years of monitoring also points to continuing smaller escape events, which is consistent with counting fence data that have detected mature escapees entering southern Newfoundland rivers (Bradbury et al. 2020).

In contrast to the decrease in F1 hybrids observed here, the proportion of BCW individuals appeared to have increased rapidly in subsequent years as initially suggested by Wringe et al. (2018) and Sylvester et al. (2019). This study significantly extends previous work by increasing the monitoring timeline and number of loci used for hybrid assignment. There are 2 potential routes for the generation of the observed BCW individuals. Firstly, hybrid males could have matured precocially and successfully reproduced with wild individuals. Secondly, F1 hybrids could have both successfully smolted and returned from the sea following the marine migratory stage. Our results suggest that the proportion of BCW parr peaked in 2017 and 2018, thus would have to have been spawned in 2016 and 2017, when F1 parr produced from the large escape event would have been 2+ and 3+ yr of age and unlikely to have successfully returned from sea. In this region of southern Newfoundland, the majority of Atlantic salmon juveniles spend 3–4 yr in river environments before smoltification and downstream migration (DFO 2006) and typically spend one winter at sea (DFO 2018). A previous study indicated that hybrids may spend more time at sea than wild conspecifics from the same river environment (McGinnity et al. 2003), where wild adults returned after one sea winter (1SW) similar to our population of study. In contrast, Bolstad et al. (2021) found that increased levels of introgression decreased the overall age of maturity in both males and females, specifically by reducing smolt age. However, it may be important to note the population Bolstad et al. (2021) has both 1SW and 2SW adults, which may illustrate population-level differences. This, however, does not negate the possibility that some hybrid F1s may have returned from sea in the following years and reproduced in this population. There is some evidence of hybrid smolts migrating out of 2 of these sampled river systems and thus likely also contributing to further introgression if successfully able to return to spawning grounds as adults. Overall, due to the short timelines and the likely high at-sea mortality, it seems much more plausible that precocial hybrid male maturation explains the increase in BCW individuals observed here.

Also of note, several rivers appeared to be dominated by mixtures of hybrids, specifically BCF and F2 genetic classes as well as feral individuals. These rivers were generally the smaller rivers surveyed and therefore also have small wild populations that could potentially easily be swamped by an influx of escaped domestic salmon, as shown in several Norwegian rivers (Glover et al. 2013, Heino et al. 2015). These rivers may represent examples of hybrid swarms, where there is extensive mixture of wild and farmed genotypes, and in extreme circumstances, pure genotypes may no longer be present in the population (Allendorf et al. 2001). However, it is important to recognize that the power of the genetic assignment to hybrid class presented here was likely limited to first (i.e. F1) or second-generation hybrids (i.e. F2 or first-generation backcrosses), and any later-generation hybrids could have been misassigned or had lower assignment success (Pritchard et al. 2016). A larger SNP panel would likely be required to quantify the presence of these later stages of introgression potentially present in some of these smaller, more impacted populations.

4.2. F1 hybrid male parr precocially mature in wild environments

To evaluate the role that precocial maturation may play in driving the observed patterns of introgression in southern Newfoundland rivers, we conducted experimental releases of laboratory-crossed individuals. These transplants of lab-crossed pure wild, pure farmed, and F1 hybrid Atlantic salmon showed that males of all 3 genetic classes have the ability to precocially mature in a wild environment, and in fact, that most F1 male parr matured by their second year. This is consistent with high rates of precocial male maturation observed throughout southern Newfoundland and the demonstrated ability for 1+ aged parr to mature (Dalley et al. 1983, Myers 1984). There were some notable differences in the proportion of mature parr of the same genetic class between the release sites, indicating that rates of precocial maturation can differ within areas of the same river, possibly due to differences in food resources, as weight significantly differed between sites. Additionally, it is important to note that within this river system there may be migration of juveniles to lake habitats which could bias these estimates of precocial parr maturation, as lacustrine and riverine growth rates differ (Hutchings 1986), especially if migration occurs differentially between cross types. However, we do not

have data at this point to evaluate the effect of lake-ward migration on precocial maturation rates, but high recapture rates in this study provide confidence in the rates of precocial maturation between cross types. Previous studies have focused on farmed and hybrid precocial parr fertilization success (Garant et al. 2003, Weir et al. 2005, Hindar et al. 2006) after early introgression work suggested mature farmed escapee parr contributed to spawning (Clifford et al. 1998), but little work has been done to demonstrate the proportion of parr maturation in natural environments as presented in this study. Although it is possible that some of the fish matured during the first year, this has been thought to be very unlikely for salmon in the region (Dalley 1978).

Here, we show that F1 hybrids are capable of precocially maturing in wild environments and that the proportion of mature F1 male parr did not differ from wild males under the same environmental conditions. This is contrary to a previous laboratory-based study which found F1 hybrids to have reduced levels of maturity compared to wild conspecifics (Debes & Hutchings 2014, Yates et al. 2015) and the suggestion that early maturation is directly selected against in domestic breeding programs (O'Flynn et al. 1992, Gjedrem 2000). Moreover, this is also counter to 2 experimental studies which reported reduced male parr maturity in domestic offspring compared to hybrid and wild parr in 0+ aged parr (Imsa, Norway) and 1+ parr (Burishoole, Ireland) (McGinnity 1997, Fleming et al. 2000, McGinnity et al. 2003, Hindar et al. 2006). Growth has previously been shown to influence the incidence of precocial maturation (Saunders et al. 1982, Letcher & Gries 2003), and recent research indicates that the probability of early maturation is reduced beyond a growth threshold (Moreau & Fleming 2012, Harvey et al. 2018). In riverine environments, where competition for food resources exists and accelerated growth may not occur, this growth threshold may not be exceeded, resulting in the precocial maturation of F1 hybrids (I. A. Fleming pers. obs.). However, it also should be noted that population and strain-level differences have been documented in precocial maturation studies (Aubin-Horth & Dodson 2004, Aubin-Horth et al. 2006, Piché et al. 2008), and strains with similar growth have shown differences in rates of precocial maturation (Harvey et al. 2018), leading to differences between these studies. Also, as the crosses here involved contributions from wild Newfoundland Atlantic salmon, where the probability of male parr maturation is likely high, there may also be a genetic predisposition to precocial hybrid male maturation here.

4.3. Implications

Our results suggest that consideration of the reproductive contribution of F1 hybrid precocial male parr may be an important component of monitoring introgression and predicting impacts. As demonstrated here, hybrid precocial male maturation can directly impact the level of introgression as (1) the number of BCW hybrids has been shown to increase shortly following escape events and (2) we have confirmed that most F1 hybrid male parr mature in southern Newfoundland rivers. It seems reasonable to conclude that the rate of precocial maturation of a river should be taken into consideration when developing introgression risk assessments, as it will influence both the rate and magnitude of changes experienced by wild populations. As rates of precocial maturation can vary among populations (Myers et al. 1986) as well as differences between North American and European precocial maturation rates (Valiente et al. 2005), levels of risk due to precocial maturation are likely specific to particular regions. Integrating the precocial maturation rate with other risk factors (see Glover et al. 2020) will provide a more accurate estimate of the potential genetic and demographic impact of domestic introgression. Future studies that could further explore the hypothesis that hybrids fast-track introgression could determine the maternal lineage of BCW fish, as many F1 hybrid individuals have farmed origin dams (Fleming et al. 1996, 2000), using mitochondrial markers for matrilineal tracing (Newman 1997, Karlsson et al. 2010a,b).

5. CONCLUSIONS

Precocial male hybrids have been hypothesized to fast-track introgression, and here we provide both empirical and experimental evidence to contribute to this evolving body of knowledge and directly support this hypothesis. Empirically, we detected a large proportion of BCW fish of the YOY age class shortly following a large escape event, indicative of F1 hybrids maturing precocially and successfully spawning as 1+ parr. Experimentally, we also demonstrated that most male F1 hybrid 1+ parr mature precocially in a southern Newfoundland river. Therefore, we suggest that rates of precocial male maturation in the wild be explicitly considered in risk assessments evaluating the genetic impacts of escaped farmed salmon on wild populations. The continued monitoring of genetic classes in the region will show the genetic impacts of aquaculture escapees and will help inform manage-

ment decisions regarding the currently threatened southern Newfoundland Atlantic salmon populations.

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