

Novel restoration strategy using marine rearing increased fitness and genetic diversity in an endangered Atlantic salmon (*Salmo salar*) population

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ABSTRACT

Atlantic salmon (*Salmo salar*) have declined precipitously throughout most of their North American range, and many restoration strategies have been implemented to aid recovery. One such restoration strategy, implemented by the Fundy Salmon Recovery project, involves collecting endangered inner Bay of Fundy Atlantic salmon smolts from their natal rivers, rearing to maturity in modified marine sea cages, and releasing back to their natal rivers. An alternate strategy involves rearing parr collected from an isolated brook to sexual maturity at a freshwater hatchery. Releases include two approaches: release by hand (carrying fish to the water); or by carefully lowering fish into pools using a helicopter. We aimed to evaluate the efficacy of these rearing and release strategies on offspring production following release in two Fundy National Park rivers. Single nucleotide polymorphisms (SNPs) were used to match parents with their offspring using Colony, a parentage analysis software. There was no significant effect of release strategy on offspring production. Rearing strategy had a significant effect on offspring production, with marine-reared adults producing 4.1 times more offspring per individual than freshwater-reared adults. Also, the effective number of breeders was higher with wild spawning smolt-to-adult-reared Atlantic salmon. This study highlights the utility of genetic analysis to evaluate rearing and release strategies in aquaculture-aided enhancement programs.

1. Introduction

The Atlantic salmon (*Salmo salar*) is among the most recognizable species in Atlantic Canada due to its profound cultural, ecological, and economic importance to the region. Atlantic Canada is home to 16 populations of Atlantic salmon (COSEWIC, 2010). Among these, the inner Bay of Fundy (iBoF) population has a unique life history. Unlike all other populations of Atlantic salmon that migrate to the North Atlantic Ocean, the iBoF population embarks on a much shorter journey, typically staying within the Bay of Fundy and Gulf of Maine (DFO, 2010). This makes the iBoF population genetically and behaviourally distinct from all other Atlantic salmon in Atlantic Canada (Amiro et al., 2003; DFO, 2010; Vandersteen Tymchuk et al., 2010). Their limited range and precipitous population decline (only approximately 225 wild individuals remain; DFO, 2020) resulted in the population being listed as endangered under the Species at Risk Act (SARA) in 2003 (DFO, 2010).

The SARA listing prompted necessary human intervention by Fisheries and Oceans Canada (DFO) and Parks Canada (DFO, 2010).

Due to the decline of the population, restoration and conservation programs have been implemented. One such program, the Fundy Salmon Recovery (FSR) project, aims to restore wild-spawning adult populations via the release of captive-reared adults (Fig. 1). The FSR program bypasses much of the marine phase survival bottleneck by capturing out-migrating wild smolts, rearing them to maturity, before releasing them back to their natal rivers to spawn naturally (a smolt-to-adult supplementation (SAS) strategy). Uniquely, this program rears maturing smolts in the world's first marine conservation farm located in Dark Harbour on the island of Grand Manan, New Brunswick (Fig. 2), while other smolt-to-adult supplementation programs use freshwater hatcheries for rearing (see Clarke et al., 2025). Among the rivers that FSR targets, two are situated in Fundy National Park (Fig. 2), the Upper Salmon River (USR), and the Point Wolfe River (PWR), which are

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considered critical habitat for the iBoF Atlantic salmon (SARA, 2002).

In addition to the FSR program, a live gene bank is maintained by Parks Canada to conserve the unique genetic makeup of the iBoF population (Fig. 1). The live gene bank operates by capturing ~1000 salmon parr (freshwater juveniles) annually from an isolated brook. These parr are reared in captivity until maturity, where ~200 unique matings occur (surplus adults not spawned are released to the wild). Offspring (unfed fry) from these matings are released to the same isolated brook, perpetuating the cycle, and exposing the juveniles to wild conditions. This process is considered a “closed loop”, as it is assumed to be impossible for wild salmon to enter the brook and contribute to the gene pool (due to the constant isolation). In the spring, once the number of smolts needed for the live gene bank has been identified, the surplus smolts generated through this program are sent to the marine conservation farm to be reared as part of the FSR program (see Fig. 1). All adult salmon reared through this program are subsequently released to the same rivers as the FSR salmon, but salmon that were spawned by hand are held in captivity over winter to be ‘reconditioned’ before release in the subsequent year. It should also be noted that the purpose of the live gene bank is to maintain genetic composition by minimizing genetic drift-associated loss of diversity, while the FSR aims to directly restore wild populations.

A critical aim of the FSR program is to enhance the production of wild-spawned juveniles, by increasing numbers of breeders in the rivers. These naturally spawned offspring (juveniles reared completely in the wild) are free of captive exposure during their earliest life stages. This strategy is predicated on work demonstrating that juveniles with reduced captive exposure during early life stages have a greater fitness than captive bred juveniles (Clarke et al., 2016). It is therefore vital to the success of the FSR project to ensure that the restoration methods of adult rearing and release are leading to enhanced spawning in river systems.

A measure of restoration success is the number of viable offspring produced through natural spawning. The parentage of fry can be

inferred using genetic markers, by matching a parent candidate genotype to offspring genotypes. If this process is done for each adult entering the system and each fry produced, the number of offspring produced by each adult can be determined. Genetic markers like single nucleotide polymorphisms (SNPs) (Morin et al., 2004) or microsatellites (simple sequence repeats) (Bagshaw, 2017) can be measured throughout the Atlantic salmon genome, by measuring a unique panel of alleles at various loci for each individual. Although microsatellites offer more information per locus (due to their higher number of alleles per locus compared to bi-allelic SNPs), the variable mutation patterns (Morin et al., 2004) can lead to results that are difficult to compare across labs. SNPs avoid these challenges, allowing for the comparison of this SNPs dataset with SNPs of future years – which would be challenging with microsatellites.

The use of genetic markers for parentage analysis also enables assessment of the genetic diversity of populations. Maintaining a high genetic diversity is essential for restoration initiatives and the enhancement of wild populations, as it provides population-wide resilience by limiting the proportion of individuals afflicted by acute selection pressures, and by reducing the prevalence of inbreeding (Booy et al., 2000; Reed and Frankham, 2003). Current hatchery stocking practices have been associated with a loss of (Hagen et al., 2021), or change in (Crozier, 1998) genetic diversity in some Atlantic salmon populations. A commonly used metric for estimating the genetic diversity of a population is effective population size (N_e), which can help to quantify the strength of genetic drift, and loss of diversity (Hare et al., 2011; Waples, 2022).

The purpose of this study was to assess the efficacy of the FSR smolt-to-adult supplementation program. Specifically, the objectives of the study were: 1) to provide direct confirmation that the FSR smolt to adult supplementation strategy results in wild spawned juveniles; 2) to determine which of the current rearing and/or release strategies results in the greatest fitness among captive reared iBoF salmon; and 3) to assess the genetic diversity of the current Atlantic salmon population in the

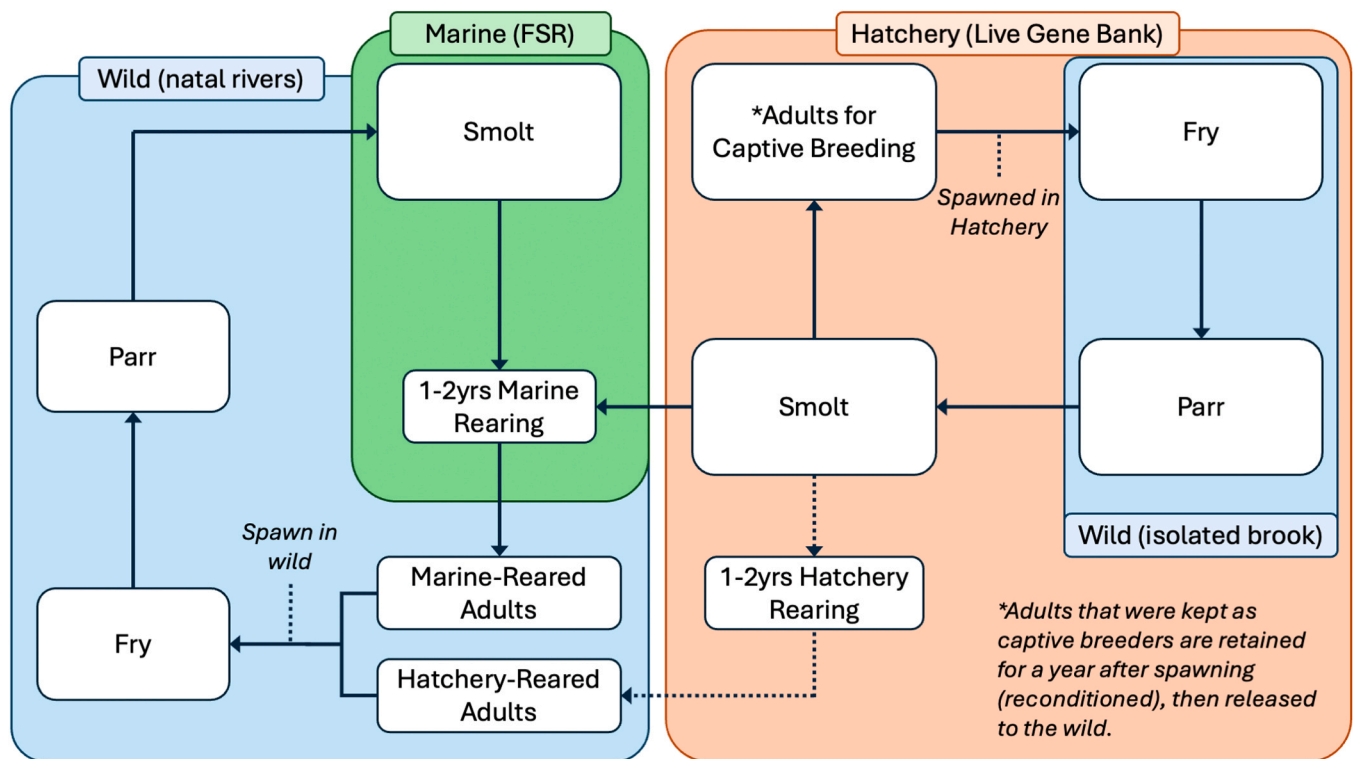


Fig. 1. Flow-chart demonstrating the Fundy Salmon Recovery (FSR) and Fundy live gene bank approaches to salmon rearing. Both programs result in the release of adult salmon to the wild. The genetic composition of the live gene bank is considered isolated from wild populations, making the program a “closed loop”, while the FSR is entirely sustained by wild spawning.

Fundy National Park river systems. We used a panel of 185 SNPs to screen all adult Atlantic salmon that were present in both the USR and PWR systems in 2020 and conducted parentage analysis to match them juveniles collected in 2021. Inferred parentage was used to provide insight into optimal methods for maximizing population enhancement through natural spawning. Assessing spawning success and genetic diversity of the current Atlantic salmon population in Fundy National Park river systems granted novel insight into the efficacy of two restoration strategies, and the genetic state of this endangered population. This information will be used to adaptively manage the FSR program and methodologies going forward to improve the efficacy of restoration strategies.

2. Methods

2.1. Program operations

All adult salmon in this project were originally collected as part of ongoing conservation efforts in Fundy National Park. Through the FSR project and Fundy's live gene bank, juvenile salmon were collected from Fundy National Park rivers to be reared to maturity to help them overcome the high marine mortality phase. Salmon are either collected as wild-hatched smolts in the spring as they exit the USR and PWR (as part of the smolt to adult supplementation program), or as fall parr/pre-smolt (Oct-Nov) from an isolated stream (Dickson Brook) preceding their year of smoltification (as part of Fundy's live gene bank program). Smolts are captured daily from April to June, using a rotary screw trap. Upon collection, wild smolts are acclimated to ocean temperatures in large, oxygenated holding tanks at a rate of 1°C/hr while being transported to

Dark Harbour. The operations of the FSR smolt-to-adult supplementation program are described in further detail in [Clarke et al. \(2025\)](#). Parr are captured by electrofishing on discrete dates which typically span from October to early November; collection ceases once a target threshold (typically 1000) individuals have been captured. Parr collected as part of the live gene bank undergo a similar acclimation process before transport to the Mactaquac Biodiversity Facility (see [Fig. 1](#)). Upon maturation, all adults (FSR and live gene bank) are sampled for genetic analysis.

2.2. Study design

This study includes all adult Atlantic salmon in the PWR and USR in 2020, collected as smolts or parr through the FSR and Fundy live gene bank programs in Fundy National Park, as well as their progeny in 2021. Caudal fin tissue samples were taken from adults prior to release and from juveniles the subsequent spring and summer (more details below). In total, 62 emigrating smolts were collected through the FSR, and 578 wild exposed parr were collected for the live gene bank ([Fig. 3, collection](#)). All smolts were reared to sexual maturity in a marine setting at Dark Harbour ([Fig. 3, rearing](#)), and wild exposed parr were reared in freshwater at the Mactaquac Biodiversity Facility until smoltification. Afterward, some were retained at the hatchery for the live gene bank, while surplus individuals were sent to Dark Harbour for marine-rearing ([Fig. 3, rearing](#)). Rearing of salmon in both programs lasted for one to two years, and 88 adults were labelled as 'reconditioned', indicating that they spawned in their first year in the hatchery, and were reared for a second year to recover before release.

In total, 640 adults were released in 2020, with 311 to the PWR and



Fig. 2. Map of the Bay of Fundy region, with locations relevant to the Fundy Salmon Recovery and the Fundy live gene bank programs marked. The mouths of the Upper Salmon (USR) and Point Wolfe (PWR) Rivers are marked in blue, and are within Fundy National Park (FNP). The Mactaquac Biodiversity Facility (MBF) hatchery and the Dark Harbour conservation farm are marked in red.

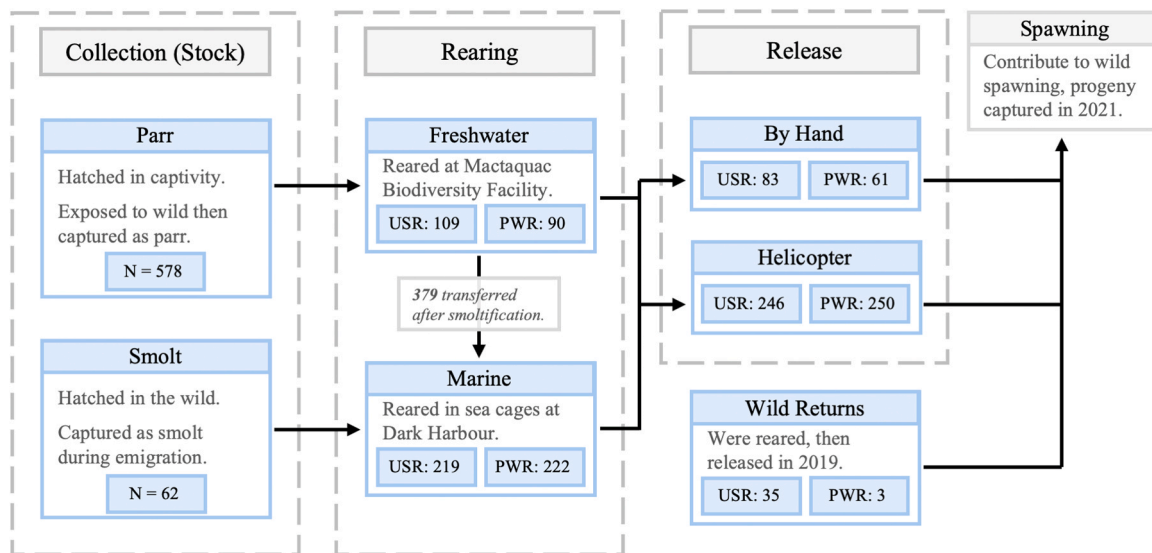


Fig. 3. Flow-chart of the study design. Relevant numbers are indicated below each step in the adult release process to indicate how many individuals underwent each treatment. USR indicates adults released to the Upper Salmon River, PWR indicates adults released to the Point Wolfe River.

329 to the USR (Fig. 3, release). A portion of the salmon were slowly reintroduced by hand, using a water-filled rubber tube (also known as a “boot”) to transport them to the river, where they were released into a suitable pool. This was done for 61 PWR-bound salmon (41 from Dark Harbour and 20 from hatchery), and 61 USR-bound salmon (41 from Dark Harbour and 20 from hatchery) between September 9th – October 1st, 2020 (Fig. 3, Table 1). The remaining mature adults (USR: 246; PWR: 250) were transported to the release sites in a large water-filled, oxygenated, insulated transport tank via helicopter on October 6th, 2020 (Table 1). Upon reaching the site, the tank was gently lowered into a deep pool, where a river crew would slowly release the fish. Additionally, 22 hatchery adults were released by hand to the USR on October 6th, 2020.

In addition to the adults released into the river system, naturally returning adults were considered as candidate parents. All FSR adults released into iBoF river systems are tagged with a 23 mm half-duplex passive integrated transponder (PIT) tag, allowing each individual to be identified. Returning salmon in 2020 were identified using a large PIT antenna system at the mouth of both rivers, which they must pass through as they enter the river. In total, 3 adults returned to the PWR, and 35 adults returned to the USR. All identified returning adults were released into the USR in 2019 through the FSR project or Fundy live gene bank.

Tissue samples were taken from the upper caudal fin of all adults prior to their release in 2020. The adults were anaesthetized using 80 ppm tricaine methanesulfonate (MS 222), and a < 1 cm² section from the tip of the upper caudal fin was taken. These samples were promptly placed in vials containing 95% ethanol and stored at 4 °C until analysis. Tissue samples from naturally returning adults were previously collected from adults released in 2019 using the same method. A total of

Table 1
Number of adults released through the Fundy Salmon Recovery project to the Upper Salmon River (USR) and the Point Wolfe Rivers (PWR) in 2020, using each method of release, and rearing strategy.

USR			PWR		
Rearing	Release	Adults	Rearing	Release	Adults
Freshwater	Helicopter	71	Freshwater	Helicopter	71
	By Hand	40		By Hand	20
Marine	Helicopter	175	Marine	Helicopter	173
	By Hand	40		By Hand	40

634 adult samples from 2020 (PWR: 307; USR: 327) were used in this study (this included 4 replicate samples for quality control). In addition to these, 37 of the 38 samples from 2019 were used.

In the summer of 2021, both the PWR and the USR were surveyed from head of tide to the upstream natural waterfall barriers for salmon fry by electrofishing fry habitat. The backpack electrofishing unit was set at a standard power output of 80 W. Fry collected at a given site were sampled quickly to reduce stress by anaesthetizing using clove oil (80 ppm), collecting a caudal fin clip for genetic material (<5 mm² from the upper caudal fin). Tissue samples were stored in 95% ethanol at 4 °C. A total of 415 fry tissue samples from the PWR and 66 fry tissue samples from the USR were used in this study.

2.3. SNP genotyping

The optimal genotyping strategy for this study was implemented based on previous simulations by the Pavey Lab (see Pavey, 2016). It was determined that a 185 SNP panel (Roth et al., 2025) would provide sufficient power for a parentage analysis, given our sample sizes. Fry and adult tissue samples were sent to the Pavey Lab for inventory and packaging. A total of 1153 (672 adult, 481 fry) tissue samples were cut and packaged using LGC, Biosearch Technologies’ BioArk sampling kits. Samples were then shipped to the LGC, Biosearch Technologies lab in Hoddesdon, UK, which performed the SNP genotyping using their KASP genotyping method (Alvarez-Fernandez et al., 2021). SNPs were acquired for 185 loci in the Atlantic salmon genome.

2.4. Parentage analysis

The quality of SNP data for each individual was assessed based on genotype completeness (percent missing loci), and samples that were inadequate for our analyses were removed. Individuals with less than an 80% complete SNPs dataset (as a result of loci being uncalleable, bad, and/or not measured) were removed from the study. As a result, a total of 617 adult samples and 443 fry samples were used in the parentage analysis. To prevent ambiguity in parentage assignment, the data were scanned for any individuals with identical genotypes; no identical genotypes were present.

Parents were assigned to each fry using the parentage analysis program Colony (Jones and Wang, 2010). The mating system was set to male and female polygamy with no inbreeding or cloning, the analysis method was set to Full-Likelihood, with medium likelihood precision,

and the species was set to be dioecious and diploid. The run was set to update allele frequencies, with sibship scaling, and a random number seed of 1234 (the default). Sibship prior was set to weak, with maternal and paternal sibship sizes both set at 1. The run-time was set to long. Following the parent-assignment, parent-offspring pairs assigned with less than 95% confidence were removed.

2.5. Data analysis

To assess which rearing and release strategy of iBoF adults led to the greatest spawning success, a generalized linear model (Equation 1) was used. A Shapiro-Wilk test was done to assess the normality of the offspring count data (Shapiro and Wilk, 1965). The offspring count data for both rivers were significantly non-normal ($p < 0.001$). To mitigate the effects of non-normality, a Poisson distribution was used. This model included the fixed effect caused by the rearing strategy of the adult, the fixed effect caused by release type, the fixed effect caused by the life history of the adult, and the fixed effect caused by the stock origin. This model was used for the USR and the PWR separately due to the large discrepancy in collected offspring for the two rivers. The model was run in R (version 3.6.2) (R Core Team, 2021) (Equation 1). Pairwise comparisons were made using Tukey HSD tests after the models were fitted.

$$Y_{ijkl} = \mu + L_i + R_j + H_k + S_l + \epsilon_{ijkl}$$

Equation 1. Generalized linear model, where:

Y_{ijk} = The measured number of offspring produced by an adult under treatment ijk .

μ = The mean parameter (average number of offspring any iBoF salmon would produce).

L_i = The fixed effect caused by release type, i (by hand, helicopter, or a natural return).

R_j = The fixed effect caused by rearing strategy, j (hatchery, or Dark Harbour).

H_k = The fixed effect caused by life history, k (reared for 1 year, 2 years, or 2 years and reconditioned).

S_l = The fixed effect caused by the stock origin of the adult, l (wild smolt, or wild exposed parr).

ϵ_{ijkl} = The error term.

To overcome an observed bias toward zero-spawning, and an observed discrepancy between reconditioned adults and non-reconditioned adults, additional tests were conducted. The generalized linear model (Equation 1) was used to analyze the effects among only spawning adults on the USR to overcome the bias toward zero. Additionally, a Welch two sample t -test (Welch, 1947) was used to determine whether there was a significant difference in offspring production between reconditioned (adults who were previously artificially spawned at the Mactaquac Biodiversity Facility hatchery) and non-reconditioned adults.

A randomization test (Fisher, 1935) was done after results were obtained from the linear models and Welch two sample t -tests. This test was done to simulate the null hypothesis (that there is no difference in number of offspring produced between two groups), by randomly shuffling the response variable (number of offspring) among all individuals, then measuring the pairwise differences in average number of offspring for each group. This process was repeated 3000 times, producing a normally distributed curve of differences. Then, the probability of finding differences greater than or equal to our findings (p -value) was calculated using this curve of differences. The script used to complete this test is available at https://github.com/JackNason/RandomizationTest_Feb2024.git (written in Python 3.9), the package Pandas (The pandas development team, 2024) was used.

Linear regressions were used to determine whether larger parents

produced more offspring, using Fulton's Condition Factor (CF) as the independent variable, and number of offspring as the response. This was done for both male and female spawners. Additionally, a linear regression was used to determine whether more fecund females produced more viable offspring, where Equation 2 was used to estimate fecundity (Jones et al., 2005). Hatchery-reared females were excluded due to their adverse effect on the equal spread of residuals, excluding them was necessary to validate the assumption of equal-variances for the linear regression. Diagnostic plots of residuals were produced and assessed for each regression (see Supplemental Figure 1).

$$Fec. = 431.3e^{0.037l}$$

Equation 2. Equation to estimate fecundity (number of eggs) developed by Jones et al. (2005) using Big Salmon River females (an iBoF river), where:

l = the fork length of the female salmon in cm.

2.6. Linkage disequilibrium effective population size (LDNe)

Effective number of breeders (N_b) was estimated with Linkage Disequilibrium (LD) using the software NeEstimator (Do et al., 2014). The adult samples were used to estimate N_b . Before N_b was calculated, full siblings were identified among the adults using Colony (Jones and Wang, 2010). Sibling assignments with less than 95% confidence were ignored. For each full-sibling family, one representative was randomly selected to be used in the LDNe calculation, the rest were removed. Any individuals who had no identifiable full siblings (with confidence 95% or above) were included in the calculation.

The LDNe calculation was completed twice, once for hatchery-spawned adults, which were captured as wild-exposed parr, then again for all adults (including wild-spawned, wild smolt origin adults). Adults captured as parr were assumed to be within a "closed-loop" live gene bank, as they are all captured from a small isolated stream (Dickson Brook). Unfed fry from the Mactaquac Biodiversity Facility hatchery are released to Dickson Brook each spring, then parr (>9 cm) are collected every fall. Dickson Brook flows directly into the Bay of Fundy and is assumed to be impassible to adult salmon (during normal conditions). The remainder of the adults (captured as wild smolts) are considered to be part of an "open-loop", due to the possibility of genetic input from immigrants from other systems.

2.7. Adult morphometrics

The length, weight, CF, and fecundity for all marine reared adults and freshwater reared adults were assessed before analysis (Table 2). This was done for both rivers, in order to highlight the physiological differences between groups within the two systems. Equation 3 was used to calculate CF (Ricker, 1977), which will be used as a numeric representation of the adult's overall size. Two adults were missing measurements for either weight or length and were omitted from morphometric analyses.

$$CF = \frac{100w}{l^3}$$

Equation 3. Fulton's condition factor (CF) (Ricker, 1977), where:

w = the mass of the salmon in g.

l = the fork length of the salmon in cm.

To explore the relationship between spawning and CF further, the average CF of successful spawners was compared to the average CF of all adults. Additionally, histograms were produced to compare the distribution of all adult CFs, and spawner CFs. This was done to determine whether there was an ideal CF for spawning success.

Table 2

Average fork length, weight, Fulton’s Condition Factor (CF), and fecundity of all adults released to the Upper Salmon River (USR) and the Point Wolfe Rivers (PWR) in 2020, (\pm standard deviations). Length and weight were assessed at maturity, at both Dark Harbour (DH) and the Mactaquac Biodiversity Facility (MBF).

Source	Sex	DH		MBF	
		Male	Female	Male	Female
USR	Length (cm)	58.6 \pm 9.3	62.6 \pm 10.8	56.1 \pm 6.6	54.9 \pm 5.0
	Weight (kg)	2.797 \pm 1.583	3.629 \pm 2.020	2.185 \pm 0.730	2.090 \pm 0.557
	CF (g/cm ³)	1.28 \pm 0.19	1.34 \pm 0.25	1.23 \pm 0.28	1.25 \pm 0.20
	Fecundity	-	4662 \pm 1831	-	3346 \pm 687
PWR	Length (cm)	60.0 \pm 10.0	64.6 \pm 8.9	55.8 \pm 7.5	56.4 \pm 6.5
	Weight (kg)	3.017 \pm 1.692	3.897 \pm 1.642	2.187 \pm 0.850	2.349 \pm 0.827
	CF (g/cm ³)	1.30 \pm 0.13	1.37 \pm 0.19	1.24 \pm 0.27	1.27 \pm 0.18
	Fecundity	-	5027 \pm 1495	-	3577 \pm 916

3. Results

3.1. Parentage analysis

Of the 443 offspring that were used in the parentage analysis, 222 were successfully matched with adult parent candidates in Colony, with a minimum probability of 95%. The average number of offspring produced by a successfully spawning individual was 3.46. A total of 103 offspring were matched with both mother and father candidates. The average full-sibling family size (not including half-siblings) among offspring was 2.82 individuals. There were 115 offspring matched with female parent candidates, but not male parent candidates. These 115 mother-only offspring were attributed to 30 mothers. In comparison, only 4 offspring were contributed from fathers, whose female mating partner could not be identified (each produced one offspring).

The parentage analysis found that 120 adults contributed to spawning in 2020, out of the 617 adults that were sampled and analysed. On the USR, only 50 of the 340 (14.7%) sampled adults produced progeny. On the PWR, 70 out of the 277 (25.3%) sampled adults produced progeny. In total, 31 of the 173 (17.9%) hatchery adults produced fry, and 89 of the 444 (20.0%) marine-reared adults produced fry. Of all mating pairs (only spawning events where both parents were identified) there were no instances of two hatchery-reared adults mating together. Additionally, most mating pairs consisted of two marine-reared adults (Fig. 4).

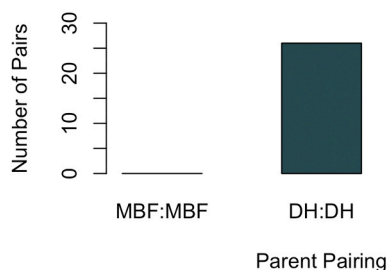


Fig. 4. Number of unique mating pairs, of hatchery (MBF) and marine (DH) rearing origin in two Fundy National Park rivers in 2020. DH reared salmon tended to pair together most frequently, and MBF reared salmon always paired up with a DH reared salmon. There were no instances of two MBF salmon pairing.

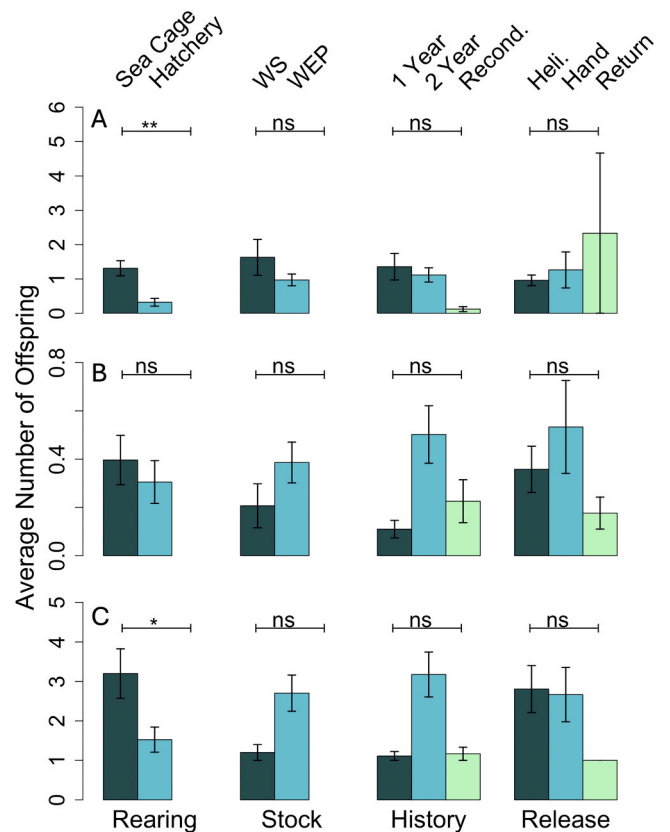


Fig. 5. The average number of offspring produced by captive-reared Atlantic salmon (*Salmo salar*) after their release to the wild in 2020. Groups within factors are denoted above (WS: wild smolt, WEP: wild exposed parr, Recond: reconditioned, Heli: helicopter, Return: returning adult). (A) Average number of offspring produced by adults in the Point Wolfe River. Rearing strategy was found to have a significant effect on the number of offspring. (B) Average number of offspring produced by adults in the Upper Salmon River. No factors had a significant effect on the number of offspring. (C) Average number of offspring produced by adults that spawned (does not include adults with zero offspring). Rearing strategy was found to have a significant effect on the number of offspring. Significance was determined using a generalized linear model, using a Poisson distribution. “ns” indicates no significant effect, “*” indicates a p-value less than 0.05, “***” indicates a p-value less than 0.01. Error bars represent the standard error.

3.2. Point Wolfe river

All Point Wolfe River (PWR) adults were analyzed using the generalized linear model (Equation 1). A Tukey HSD test found a significant difference between marine-reared and hatchery-reared salmon (p-value: 0.006), but no differences between other levels (Fig. 5(A)). On average, marine-reared (sea cage) adults produced 1.312 ± 0.220 (standard error) offspring while hatchery-reared adults produced 0.321 ± 0.113 offspring on average. Among spawning adults only, marine-reared adults produced an average of 4.492 ± 0.572 offspring while hatchery-reared adults produced an average of 2.083 ± 0.499 offspring.

Due to the observed discrepancy in offspring production between reconditioned and non-reconditioned adults in the PWR, a Welch two sample t-test was done to compare the two groups. The average number of offspring produced by a non-reconditioned adult in the PWR (1.158 ± 0.184), was significantly greater than the average number produced by a reconditioned adult (0.121 ± 0.072) ($t = 5.242$, p-value < 0.001).

Additionally, a randomization test was completed to assess pairwise differences in number of offspring produced (Table 3). The results of the randomization supported the findings of the generalized linear model and t-test. Notably, a significant difference was found when comparing

Table 3

Pairwise comparisons of each level of the four main factors included in this study. The measured difference in average number of offspring produced is reported, and the probability of finding a difference this extreme, or more extreme, under the assumption that there is no difference between the groups was listed as a p-value. These values were determined using a randomization test. The levels of each factor were abbreviated as follows: WS: wild smolt; WEP: wild exposed parr; Recond: reconditioned; Heli: helicopter; Return: returning adult.

Factor	Comparison	Measured Difference (Number of Offspring)	p-value
Rearing Strategy	Sea Cage - Hatchery	0.991	< 0.001
Stock Origin	WS - WEP	0.657	0.116
Life History	1 Year - 2 Year	0.240	0.298
	1 Year - Recond.	1.236	0.020
	2 Year - Recond.	0.996	0.009
Release Type	Hand - Heli.	0.304	0.224
	Hand - Return	-1.070	0.186
	Heli. - Return	-1.374	0.146

sea-cage (marine) reared adults to hatchery (freshwater), and reconditioned adults were found to have significantly fewer offspring than both 1-year, and 2-year adults (Table 3).

3.3. Upper Salmon river

A Tukey HSD test using the fitted generalized linear model (Equation 1) found no significant differences between any levels in each factor of the model (Fig. 5(B)). This test included all adults released into the USR that year, and all naturally returning individuals. This was done to account for differences in sample sizes for the different factors, since the majority of adults contributed zero offspring.

A Tukey HSD test using the model (Equation 1), including only the successfully spawning adults from the USR found that there was a significant difference between marine-reared and hatchery-reared salmon (p-value: 0.014), but no differences among levels of any other factors (Fig. 5(C)). The average number of offspring produced by a marine-reared (sea cage) spawning adult was 3.200 ± 0.626 (standard error), while the average number of offspring produced by a hatchery-reared spawning adult was 1.526 ± 0.319 .

Due to the observed discrepancy between reconditioned versus non-reconditioned adults, a further test was used to compare the average number of offspring produced by these two groups. Including all adults, using a Welch two sample t-test (Welch, 1947), no significant difference was observed in the USR between reconditioned and non-reconditioned

adults ($t = 1.297$ p-value: 0.197). An additional t-test was used to compare the average number of offspring produced by reconditioned and non-reconditioned adults among those that spawned. This t-test found a significant difference ($t = 3.180$, p-value: 0.003) between the two groups among spawning adults, where non-reconditioned spawners produced an average of 2.744 ± 0.467 offspring, whereas reconditioned spawners produced an average of 1.167 ± 0.167 offspring.

3.4. Linkage disequilibrium effective population size

The N_b estimates were found to increase significantly with the inclusion of wild-spawned adults, compared to the only live gene bank origin adults. N_b was estimated to be 57.1 (95% confidence interval (CI): 54.2 – 60.2) for the live gene bank adults, whereas N_b was estimated to be 65.2 (95% CI: 62.2 – 68.4) for the whole group of adults (live gene bank, and wild-spawned origin). The original breeding program used to repopulate the USR and the PWR from 2011 to 2013 was comprised of 70 total breeders (35 males, 35 females), indicating a theoretical maximum starting N_b of 70 (but likely lower than this).

3.5. Adult morphometrics

Neither males nor females showed a significant linear relationship between condition factor (CF) and viable offspring production (Fig. 6 (A); fathers p-value: 0.949, multiple R^2 : < 0.001, and F-statistic: 0.004; mothers p-value: 0.180, multiple R^2 : 0.047, and F-statistic: 1.862). The linear regression found no significant linear relationship between fecundity and number of viable offspring (Fig. 6(B); p-value: 0.169, multiple R^2 : 0.037, and F-statistic: 1.945).

The average CF of all adults was determined to be 1.300, with a variance of 0.048 (Supplemental Figure 2 (A)). The average CF of successfully spawning adults was found to be 1.331, with a variance of 0.104 (Supplemental Figure 2 (B)). We thus found no discernable ideal CF for spawning among FSR adults in 2020. The large discrepancy in variance between the spawners and the whole group is thought to be caused by the large difference in sample sizes (Supplemental Figure 2 (A, B)). To mitigate the effects of sample size differences, the histograms were recreated using only individuals from the PWR. There was no discernable difference between the total population of the PWR and the spawning population of the PWR (Supplemental Figure 2 (C, D)). The group mean CFs were 1.313 and 1.345, and their variances were 0.038 and 0.078 respectively.

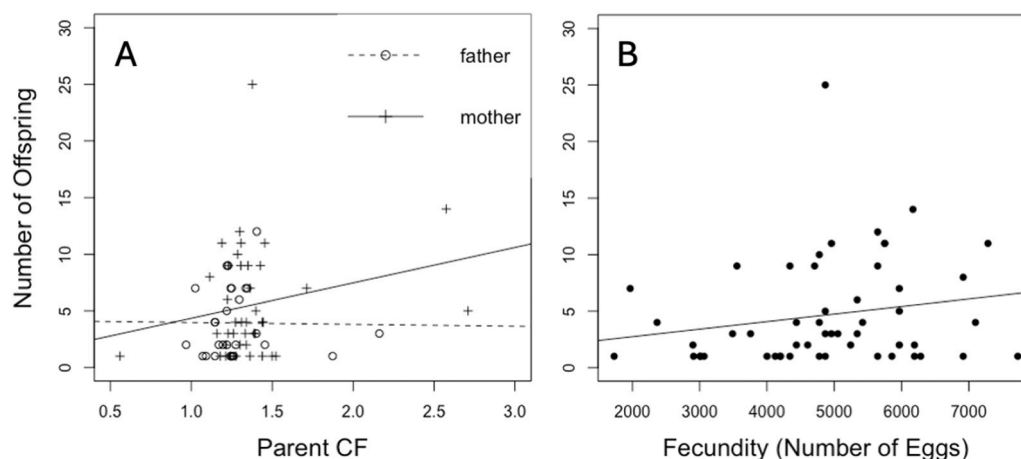


Fig. 6. The effects of (A) Fulton’s condition factor (CF) of both mothers and fathers on viable offspring and (B) number of viable offspring was plotted against the fecundity of sea-cage reared females, who spawned successfully. Linear regressions were used to measure correlation for both mothers and fathers, they found no significant correlation between CF and number of offspring (p-value > 0.05). A linear regression was used to measure correlation between fecundity and number of offspring, no significant correlation was found (p-value > 0.05).

4. Discussion

This study measured the efficacy of the Fundy Salmon Recovery (FSR) restoration initiative for enhancing wild spawning in Fundy National Park's endangered Atlantic salmon (*Salmo salar*) population. We determined that in 2020, in the Point Wolfe River (PWR), adults that were reared in a marine environment produced greater than four-times as many offspring per individual as their live gene bank, freshwater-reared conspecifics. Additionally, the process of spawning salmon in captivity, reconditioning, and releasing them back to their natal river appears to have a detrimental effect on wild spawning in the year of release, as non-reconditioned adults (*i.e.*, newly released first time spawners) produced ten-times more offspring per individual than reconditioned adults in the PWR. The incorporation of wild spawning has rendered the N_b , a measure of genetic diversity, significantly higher than when considering only live gene bank-origin adults. Finally, no relationship was discerned between fecundity, size, and/or progeny production among marine- and freshwater-reared adults.

4.1. Captive rearing effects

Marine-reared Atlantic salmon produced more offspring than their hatchery-reared conspecifics. This observed fitness discrepancy may be indicative of lasting impacts caused by differences in rearing environments and/or program objectives (*i.e.*, direct wild supplementation via the FSR versus the maintenance of genetic diversity via the live gene bank). Many studies (Clarke et al., 2016; Evans et al., 2014; Jonsson et al., 2019) have shown that hatchery captivity can lead to reduced success in riverine environments, although the effects of marine captivity have less characterization in this context. Clarke et al. (2016) found that Fundy National Park females produced smaller, less successful eggs after increased juvenile hatchery exposure. Rearing-related effects have also been shown to have a direct consequence on repeat spawning, mortality, and fitness in other Atlantic salmon populations (Bordeleau et al., 2018). These negative impacts may be attributable to heritable epigenetic changes (Rodríguez Barreto et al., 2019; Wellband et al., 2021) or potential captivity-driven selection for traits (Araki et al., 2008; Christie et al., 2012) imparted on hatchery-reared salmon, which are yet to be characterized for FSR marine-reared adults. We do not suggest that the FSR marine-reared salmon are immune to the captivity-related erosion of fitness, but they had greater reproductive success (*i.e.*, increased juvenile production) compared to their hatchery counterparts in 2020, suggesting some mitigation of these captivity-related effects through program objectives and modified rearing techniques.

Direct offspring of hatchery broodstock salmon (*i.e.*, wild exposed parr origin adults) did not have a significant reduction in offspring production, contrary to prior findings (Araki et al., 2008; Milot et al., 2013) and the predictions of Bowlby and Gibson (2011). However, rearing salmon from smolt to adult in the hatchery for the purposes of a live gene bank yielded a reduction in fitness (*i.e.*, decreased wild offspring production) compared to marine-reared salmon. This study occurred only 9 years after the founding of Fundy's live gene bank, while Bowlby and Gibson (2011) predicted a genetically deleterious effect after 15–20 years of live gene bank rearing. It is therefore possible that these negative genetic effects have not yet emerged. Overall, these findings suggest that the marine-rearing strategy employed by the FSR project may be able to, at least partially, mitigate the reduction in fitness that is often associated with captive rearing (Araki et al., 2008; Bordeleau et al., 2018; Bowlby and Gibson, 2011; Jonsson et al., 2019).

Although the exact mechanism behind the observed fitness differences between marine-reared and hatchery-reared adults is unknown, we hypothesize that the fitness discrepancy could be related to the more wild-mimicking properties of the marine-rearing strategy, as environmental enrichment tends to increase fitness-related traits in fishes (Galloway et al., 2025; He et al., 2026; Jonsson et al., 2014; Salvanes

et al., 2013). The two rearing programs employ similar feeding regimes, but the marine-rearing pens are open to the ocean, allowing for exposure to wild food sources (*e.g.*, macroinvertebrates). Exposure to wild macroinvertebrate prey is generally beneficial to the rearing of juvenile salmonids (Brown et al., 2003; Czerniawski et al., 2011). Additionally, there are likely differences in stress imparted on the salmon in the two programs, which can cause reductions in growth (Jentoft et al., 2005; McCormick et al., 1998) and alter immune responses in salmonids (Fast et al., 2008; Martorell-Ribera et al., 2022). There are many captive-rearing related factors which this study cannot account for, so it is difficult to determine the precise mechanism by which marine-reared salmon out-performed their hatchery conspecifics. This study, however, demonstrated that FSR marine rearing practices produced fitter salmon than the hatchery, leading to greater population enhancement.

4.2. Genetic diversity

Effective number of breeders (N_b) was greater with the inclusion of wild produced smolt origin adults, demonstrating the importance of wild spawning in the maintenance of genetic diversity and restoration success. The “open loop” smolt to adult strategy includes adults originating from the live gene bank but relies on natural mate selection and spawning by mature adults and precocious parr in the wild, as well as immigration from neighbouring rivers. Although all FSR salmon stem from the same original group of 70 founders, the inclusion of wild spawning (through the smolt-to-adult supplementation program) has allowed the FSR to retain a higher overall genetic diversity in comparison to the live gene bank-reliant program. N_b is directly proportional to N_e (Ferchaud et al., 2016), as N_e can be approximated by multiplying N_b by the generation time (Waples, 1989). N_b is therefore an appropriate approximation of genetic diversity, and the strength of genetic drift. The observed maintenance of genetic diversity could be attributed to asymmetric gene flow from neighbouring rivers, as has been shown in other populations (Consuegra et al., 2005; Palstra et al., 2007) in addition to other wild-spawning related factors.

Genetic diversity could be enhanced as a result of the smolt-to-adult supplementation strategy for reasons beyond gene flow from other rivers. Sexually mature male (precocious) parr (see Fleming, 1996) have been shown to increase the number of effective breeders in river systems, helping to maintain genetic diversity across generations (Bouchard et al., 2022; de Mestral et al., 2012; Johnstone et al., 2013; Martinez et al., 2000). Mature male parr are likely contributing to the wild breeding pool (Alannah Bartlett, Fort Folly Habitat Recovery; unpublished), but are unable to contribute to the live gene bank (as they are not currently part of the mating plan). Their contribution to the mating pool is potentially corroborated by the large number of unpaired female spawners in this study, which may have spawned with precocious parr. Additionally, captive breeding programs prevent natural mate selection, which promotes heterozygosity in major histocompatibility complex (MHC)-related genes (Consuegra and Garcia De Leaniz, 2008; Landry et al., 2001) which may contribute to genetic diversity and fitness in the wild.

The Fundy National Park live gene bank has succeeded in maintaining the genetic diversity of iBoF salmon. Two reports of the effective number of breeders, N_b , exist for the Fundy National Park salmon population. One estimate occurred at the beginning of the FSR program, estimating a N_b of 51 (95% CI = 48–54) with LDNe and 56 (95% CI = 40–81) using Colony (Thais et al., 2016). This study used emigrating smolts, captured in 2015, which were offspring of adults released in 2011 to calculate N_b (at the conception of the smolt to adult supplementation program). Prevost and Fraser (2018) estimated N_b to be 56 (95% CI = 52–60). Both prior estimates clearly overlap with the effective number of breeders reported in this study, indicating no significant loss of genetic diversity.

4.3. Release method

There was no observable difference in fitness between fish released by hand or by helicopter transport. This is contrary to the perception that helicopter transport would be more stressful, and thus detrimental to fitness. Many common acute stressors, like heat stress and hypoxia can lead to lasting negative consequences in Atlantic salmon (Hvas et al., 2025). However, these factors were intentionally mitigated in all transport methods used in this study. As it pertains to release methodology, it has recently been shown that acclimation can at least partially mitigate handling-related physiological changes in salmon (Roberts et al., 2024). Additionally, Hoem and Tveten (2023) reported no observable change in stress-related gene expression in salmon related to transportation. We therefore conclude that the mitigation of density, temperature shock, and oxygen levels used in both release methods in this study likely prevented any significant difference in fitness, despite the difference in perceived gentleness.

4.4. Life history effects

The importance of stock origin and life history appear to be limited with respect to reproductive success during the captive-reared salmon's first adult year in the wild. This contrasts with previous findings, which have shown that the negative impacts of hatchery rearing on juvenile survivorship increase with hatchery-rearing time (Clarke et al., 2016; Evans et al., 2014). In this study, no significant effect was caused by stock origin, which is directly related to time in captivity at juvenile ages (as parr-origin adults will be reared for longer than smolt-origin adults). It should be noted that even the live gene bank program is designed to minimize early captive exposure and to subject offspring to wild exposure from the unfed fry to pre-smolt stage, and as Clarke et al. (2016) noted, reducing captive exposure during this period increases fitness. These findings suggest that rearing during the smolt to adult maturation period of the salmon lifecycle may have a greater impact on fitness and restoration success than previously thought. No difference was observed between one-year and two-years reared adults, which may suggest a greater dependency on rearing environment than rearing time.

The adults that had been spawned in captivity at the Mactaquac Biodiversity Facility hatchery, then reconditioned and released the subsequent year produced far fewer offspring in the year of release than non-reconditioned adults in the PWR. Similarly, Bordeleau et al. (2018) demonstrated that artificially spawning Atlantic salmon in captivity causes a reduction in survival and fitness to fish released in the wild. Contrary to these findings, reconditioned adults have recently been shown to return to rivers at a much higher rate than their non-reconditioned counterparts in the years following release (Morrissey, 2024). This may suggest that their fitness is not diminished, but that they may spawn more in subsequent years rather than in their first year following release to the wild. Additionally, the value of maintaining the live gene bank, while still releasing these captive-spawned salmon is likely worth the observed reduction in wild spawning in the year of release.

Despite being considered the most important factors in spawning success (Fleming, 1996), fecundity and size had no effect on fitness. These key factors in wild spawning may be overshadowed by potential behavioural, genetic, or epigenetic effects which linger as a result of captive rearing practices (Araki et al., 2008; Clarke et al., 2016; de Mestral et al., 2013; Rodriguez Barreto et al., 2019; Wellband et al., 2021). Behavioural factors like redd placement and mate selection could have a large enough effect on progeny survival to obfuscate the effects of size, though our study has no way of determining this. Among males, human-reared Atlantic salmon have been shown to fail at producing typical dominance hierarchies, and fail to release sperm reliably during mating (Weir et al., 2004), which may be implicated in the lack of size-dependency in this study.

4.5. Conclusion

Population restoration and fisheries management efforts relying on stocking, or captive rearing should place a strong emphasis on mimicking wild life-history, and promoting wild spawning. Many fish species (including several species of salmonids) are supplemented via rearing and stocking practices (see Araki and Schmid, 2010), which commonly fail to expose individuals to life stage specific stimuli that they would experience in the wild. As wild conditions worsen as a result of human activity and climate change (see Priya et al., 2023), continued conservation effort will need to be taken for many fish species. Our recommendation to the designers of these programs is to promote spawning in the wild where possible, to maintain a high genetic diversity, increasing the longevity and self-reliance of the population. Programs should be designed to shift captive exposure to later life stages, prioritize the quality of rearing conditions, and release reared adults to maximize wild spawning.

Population enhancement efforts in Fundy National Park have helped facilitate the return of adult salmon, increasing juvenile production and genetic diversity. Restoration programs should prioritize methods that release the most fit individuals possible to promote wild spawning, hastening the recovery of the population. Continued evaluation of each restoration approach (*i.e.*, smolt-to-adult supplementation vs live gene bank) will aid managers in tailoring restoration/enhancement strategies accordingly. This study has demonstrated that the marine-rearing smolt-to-adult supplementation method employed by the FSR project successfully increases wild hatched juvenile salmon abundance, and helps to maintain wild genetic diversity. Ongoing evaluation plays a crucial role in the success of recovery measures and adjusting enhancement strategies in response to changing ecological conditions.

CRedit authorship contribution statement

Kyle Wellband: Writing – review & editing, Methodology. **Kurt M. Samways:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **John M. Whitelaw:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **John W. Robinson:** Writing – review & editing, Methodology, Investigation, Data curation. **Scott A. Pavay:** Writing – review & editing, Supervision, Resources, Methodology. **Nason Jack Spencer James:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation.

Ethical statement

All work described herein was conducted in accordance with the regulations set by the Canadian Council on Animal Care. All procedures in this study were approved by the University of New Brunswick's Animal Care Committee (Animal Use Protocol 2021–1R-02).

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Kurt M. Samways reports financial support and equipment, drugs, or supplies were provided by Parks Canada. Kurt M. Samways reports equipment, drugs, or supplies was provided by Cooke Aquaculture Inc. If

there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2026.107762](https://doi.org/10.1016/j.fishres.2026.107762).

Data availability

Data will be made available on request.

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