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Fitness effects of assisted gene flow in an endangered salmonid population

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Abstract

Assisted gene flow is increasingly used to combat severe population declines. However, the associated risks, such as outbreeding depression, are often insufficiently assessed. Here, we studied the impact of assisted gene flow on the fitness of a highly endangered landlocked salmon population (*Salmo salar* m. *sebago*) from the lake Saimaa complex (Finland), using an anadromous Atlantic salmon population (*S. salar*) as donor. We released individuals of both parental populations and their hybrids into seminatural streams, monitoring their survival under predation risk from Northern pike (*Esox lucius*) and their growth on a natural diet. Before release, we exposed half of the salmon to the parasite *Diplostomum pseudospathaceum* to study whether assisted gene flow affects infection susceptibility, which could indirectly shape predation susceptibility and growth. The parental populations differed in both studied traits and the hybrids showed intermediate values. Relative to the target landlocked salmon population, hybrids experienced 21–26% lower survival, but 1.4–2.2% higher growth. They also carried 0.6–2.8 more parasites than the landlocked salmon, contributing to survival differences. These findings indicate that assisted gene flow can induce both negative and positive fitness effects. We propose that the overall net effects of this conservation tool need to be carefully evaluated before its implementation.

KEYWORDS

assisted gene flow, growth rate, heterosis, landlocked salmon, outbreeding depression, parasite infection, predation risk

1 | INTRODUCTION

Habitat destruction and overexploitation have led to severe population declines worldwide (e.g. Ceballos et al., 2017; Dirzo et al., 2014; Pimm et al., 2014). Small populations are vulnerable to extinction as they often carry elevated levels of genetic load, that is, they accumulate deleterious alleles as a consequence of genetic drift and inbreeding depression (Frankham, 1995; Lynch et al., 1995). This is further exacerbated by an erosion of genetic diversity, reducing adaptive potential to changing environmental conditions (Hoffmann et al., 2017; Willi et al., 2006). Small populations are also particularly vulnerable to the effects of demographic and environmental stochasticity (Lande et al., 2003). Together, these genetic, demographic and environmental factors can reinforce each other in a downward spiral, referred to as extinction vortex (Gilpin & Soulé, 1986). As a result, there is a growing demand for conservation tools that recover small and declining populations.

Assisted gene flow via the introduction of individuals from divergent populations or related species is now increasingly used in conservation efforts (Bell et al., 2019; Chan et al., 2019; Frankham, 2015; Hoffmann et al., 2021; Ralls et al., 2018). The net fitness effects of assisted gene flow, however, are complex and depend on the genetic composition and environmental conditions of the source and recipient populations. While assisted gene flow can alleviate genetic load by masking deleterious, recessive alleles and restore genetic diversity (Edmands, 2007; Fitzpatrick et al., 2020), it can also reduce the fitness of hybrids due to genetic incompatibility or maladaptation to local environmental conditions (outbreeding depression; Edmands, 2007; Frankham et al., 2011). Several studies have reported a successful reversal of population decline following assisted gene flow (e.g. Fitzpatrick et al., 2020; Hasselgren et al., 2018; Heber et al., 2013; Johnson et al., 2010; Westemeier et al., 1998), but clear evidence for outbreeding depression in other systems (e.g. Gilk et al., 2004; Goldberg et al., 2005; Huff et al., 2011; Montalvo & Ellstrand, 2001; Muhlfeld et al., 2009), makes the net outcome of this measure difficult to predict. Thus, there is need for experimental studies examining the fitness consequences of assisted gene flow to support decision-making in conservation efforts.

An important component of fitness is the ability to avoid predators. This requires cognitive skills for predator detection as well as physiological, behavioral or morphological defense traits, all of which could be hampered in small and declining populations. For example, avian prey species with low genetic diversity are known to display reduced antipredator behavior (Jiang & Møller, 2017) and experience a higher risk of predation (Møller & Nielsen, 2015). Further, inbreeding reduces the ability of *Physa acuta* snails to plastically respond to changing predation risks (Auld & Relyea, 2010). Assisted gene flow could therefore improve predator avoidance success, but at the same time, it can also cause maladaptive defensive traits. For example, natural hybrids of two cyprinid freshwater fishes are more susceptible to avian predation than either parent species, possibly due to intermediate body morphology (Nilsson et al., 2017). Growth rate is another important fitness component as it often links with survival in juveniles (e.g. Sogard, 1997) and reproductive success in mature individuals (Stearns, 2000). Positive associations between heterozygosity and growth rate have been reported in a variety of taxa (e.g. de Boer et al., 2016; Henry et al., 2003; Nielsen et al., 2012; Shi et al., 2018). However, as with predation susceptibility, there is also evidence for outbreeding depression effects on growth rate (e.g. Ågren et al., 2019; Goto et al., 2011; Granier et al., 2011; Huff et al., 2011).

In addition to direct effects on predation susceptibility and growth, assisted gene flow could also indirectly alter these traits via changes in susceptibility to parasite infections. Populations with low genetic diversity typically suffer from higher infection susceptibility (reviewed in King & Lively, 2012) and high infection levels often associate with increased predation susceptibility (e.g. Johnson et al., 2006; Krumm et al., 2010; Mesa et al., 1994) and decreased growth (e.g. Brinker & Hamers, 2007; Karvonen & Seppälä, 2008; Lochmiller & Deerenberg, 2000). However, genetic mixing does not always improve infection resistance, as it can break down locally adapted gene complexes and result in maladaptive combinations of resistance traits (Garant et al., 2007; Moulia, 1999).

Despite clear evidence for both positive and negative effects of population mixing on predation susceptibility and growth, such effects have received little attention in the context of assisted gene flow. Here, we fill this gap with an experimental study on Saimaa landlocked salmon (LS; *Salmo salar* m. *sebago*). Many natural Atlantic salmon (AS; *S. salar*) populations are endangered worldwide (ICES, 2017), including the Saimaa LS (Hutchings et al., 2019), an endemic freshwater form inhabiting the Lake Saimaa complex in Finland. Anthropogenetic activities related to hydroelectric development during the 1950s–1970s have blocked access to spawning grounds and destroyed nursery habitats, leading to a severe genetic bottleneck (Koljonen et al., 2002). To date, the population has a small effective population size and low genetic diversity (Koljonen et al., 2002; Primmer et al., 2000; Säisä et al., 2005; Vuorinen, 1982), with clear evidence for inbreeding (Primmer et al., 2003; Tiira, Piironen, & Primmer, 2006). Given the ongoing disruption of natural reproduction, persistence of the population relies heavily on assisted breeding (Hutchings et al., 2019). For this, mature individuals are wild-caught every year from the population, and their gametes are used to produce offspring for stocking (Leinonen et al., 2020). This practice allows targeted assistance of gene flow. Previous studies have explored early life fitness consequences of this conservation measure and provided mixed results, with some evidence supporting gametic incompatibility (depending on the donor population; Eronen et al., 2021), positive effects on post-hatching survival (Eronen et al., 2021), and both positive and negative effects on post-hatching infection resistance (depending on the infective agent; Klemme et al., 2021).

We released one-year-old hybrid crosses, together with pure crosses of each parental population, to semi-natural streams. We followed their survival under predation risk by Northern pike (*Esox lucius*) and their growth while feeding on a natural diet. We also explored possible indirect effects of assisted gene flow on predation and growth by exposing half of the fish to the eye parasite *Diplostomum pseudospathaceum* before release. Relative to the Saimaa LS, hybrid crosses have reduced resistance to this parasite (Klemme et al., 2021), which is known to impair eyesight and subsequently predator avoidance (Seppälä et al., 2005) as well as growth rate (Karvonen et al., 2023; Karvonen & Seppälä, 2008). Finally, to interpret possible cross differences in survival and growth, we also monitored fish movement behavior during the experiment. This type of study is of value, not only for conserving the unique Saimaa LS, but also more generally, for decision-making related to the conservation of small and declining populations.

2 | METHODS

2.1 | Study system and animal origin

The life cycle of Saimaa LS resembles that of its anadromous ancestor, except that the entire life is spent in fresh water (Berg, 1985; Lumme et al., 2016). Parental Saimaa LS had been stocked as juveniles to the river Pielisjoki (62°42′N, 29°52′E, see Figure S1) and were caught mature from the same river. Parental AS were obtained through a breeding program of the Natural Resource Institute Finland (LUKE) and originated from a captive population from the River Neva (59°57′N, 30°13′E, Figure S1) that is regularly supplied with gametes from the original population. The expected heterozygosity for microsatellite loci of this population has been found to be twice as high ($H_{Exp} = 0.60$) than that of Saimaa LS ($H_{Exp} = 0.28$; Tonteri et al., 2005).

The experiment was conducted at LUKE's Kainuu Fisheries Research Station (64°23′N, 27°30′E, www.kfrs.fi), a flow-through experimental facility, using water from a nearby lake. To produce the experimental crosses, 15 2 × 2 factorial crossings were conducted in November 2018. Specifically, 1 LS female and 1 AS female were each crossed with 1 LS male and 1 AS male (15 replicates), resulting in 4 crosses: pure Saimaa LS, pure AS and their respective hybrids (LS × AS and AS × LS, female × male reciprocal). The eggs hatched about 160 days after fertilization, in April 2019. After hatching, the offspring were reared in 8 identical 3.2 m^2 tanks with a water depth of 20 cm, each cross in two tanks, with 480 individuals in each. In November 2019, 120 randomly selected fish from each of the 8 rearing tanks were individually marked by injection with a HDX passive integrated transponder (PIT; 12 × 2 mm, Biomark) under mild anesthesia (40 mg L^{-1} benzocaine). Subsequently, all marked fish were reared in 2 identical 3.2 m^2 tanks with a water depth of 20 cm, each containing 480 individuals (120 per cross), until the experiment commenced in July 2020. Throughout the rearing period, the fish were fed with commercial fish food (BioMar INICO plus G 0.4–0.6 mm and VITA 0.5–0.8 mm) and the light-cycle as well as water temperature corresponded to natural conditions.

For the infection treatment, a common freshwater parasite, the eye fluke *D. pseudospathaceum* was used. This parasite establishes in the eye lens of its second intermediate fish host, where it causes considerable tissue damage, resulting in eye cataracts that impair host vision (Karvonen, 2012). Infective larval stages (cercariae) of *D. pseudospathaceum*, used for the parasite exposures, were collected from 20 shedding *Lymnaea stagnalis* snails (first intermediate host). The naturally infected snails had been collected from Lake Konnevesi (62°36′N, 26°33′E) and Lake Veijonjärvi (61°57′N, 25°41′E) 1 week before the exposures and were subsequently maintained in individual containers with lake water at 4°C. It is important to note that *D. pseudospathaceum* does not show a detectable genetic population structure in the snail host across a large geographical scale (Louhi et al., 2010), suggesting that the origin of the parasites was unlikely to affect the cross-specific infection susceptibility. Before the exposures, the snails were transferred to room temperature for 4 h, after which average cercarial density in the combined solution of all snails was estimated using 10 1 ml aliquots.

The Northern pike inhabits lakes and slow-flowing rivers, and is one of the most important predators of salmonids (Jonsson & Jonsson, 2011). For the predation experiment, 12 pike were used. They had been wild caught in Lake Oulujärvi (64°28′N, 27°21′E) several years before the experiment and kept in captivity at Kainuu Fisheries Research Station.

The experiments were carried out with permission from the Finnish Regional State Administrative Agency (license no. ESAVI/5184/04.10.07/2017 and ESAVI/8187/2018) and complied with the animal care legislation of Finland.

2.2 | Experimental procedure

The experiment was conducted during July–September 2020, when the experimental crosses were 1 year old. The experimental design included manipulation of parasite infection status before release to seminatural streams (infected vs. uninfected salmon) and manipulation of predation risk from pike in the streams (predator present vs. absent).

To manipulate infection status, 640 fish (160 per cross) were randomly selected in July 2020 and exposed to *D. pseudospathaceum* ($N = 320$, 80 per cross) or sham-exposed ($N = 320$). Specifically, all experimental fish were evenly divided among 16 80 L tanks ($N = 40$ fish per tank) filled with aerated lake water (17.7°C). Half of the tanks received a small amount of lake water with 12,000 infective cercariae (300 per fish) and the other 8 tanks received lake water without cercariae. After 25 min of exposure, all individuals from the same exposure treatment were transferred to a 3.2 m^2 tank for recovery. Six days after the exposures, all 640 experimental fish were measured for total length and body mass under mild anesthesia (40 mg L^{-1} benzocaine) and then transferred to seminatural outdoor streams.

The round outdoor streams (50 m^2) consisted of a ring-shaped section at the outer edge (width 1.5 m) and a round pool section (35 m^2) in the middle, separated by a C-shaped wall (Figure 1). The outer section simulated a shallow river section with moderate water flow. It was covered with coarse gravel (ø 50–70 mm) and larger stones (ø 200 mm); the water depth was set to 22 cm and the inflow to about 4 L/s. The pool resembled deeper river areas with slowly flowing or stagnant water. The pool did not contain any structures, had a water depth of 78 cm and contained the water outlet. During the experiment, the fish relied on natural food resources, consisting of benthic and drifting invertebrates. The shallow outer sections of the streams were covered with camouflage nets to prevent bird predation.

To manipulate predation risk, 3 pike (1.4–3.0 kg) were transferred to the pool section of each of 4 randomly selected streams before the start of the experiment. The remaining 4 streams remained predator-free. In all 8 streams, 2 plastic mesh grids were placed vertically between the C-shaped inner wall and the outer wall. The grids had a mesh size of 50 mm, allowing salmon to pass, but preventing pike from entering the shallow section and thus, providing a predator-free refuge. Two PIT-based radio frequency identification antennas were installed on each side of the grid walls (4 antennas per stream), which recorded the identity of passing fish with a recording frequency of 9 times per second. To ensure sufficient food availability for the pike, they were fed with 1 dead roach (*Rutilus rutilus*) each once a week.

Each of the 8 streams was stocked with 80 salmon, 20 from each cross, of which half had been exposed to the parasite. The salmon were first placed for 24 h into 2 large flow-through boxes (80 × 60 × 45 cm, 40 fish per box) within the shallow section to acclimate, after which they were simultaneously released. The streams were left undisturbed for 53 days, after which all remaining salmon were caught and euthanized with an overdose of benzocaine (200 mg L^{-1}). They were identified, measured for total length and body mass and their eyes were dissected for parasite counts. The pike were also caught and returned to their maintenance tank.

2.3 | Statistics

At the end of the experiment, 311 out of the initial 320 salmon were recovered from predator-free streams, and 146 out of the initial 320 salmon from streams with predators. Among the streams with predators, 2 recovered salmon were excluded from the data analyses due to technical issues, resulting in 144 out of 318 recovered fish for this group. Additionally, 5 of the not recovered

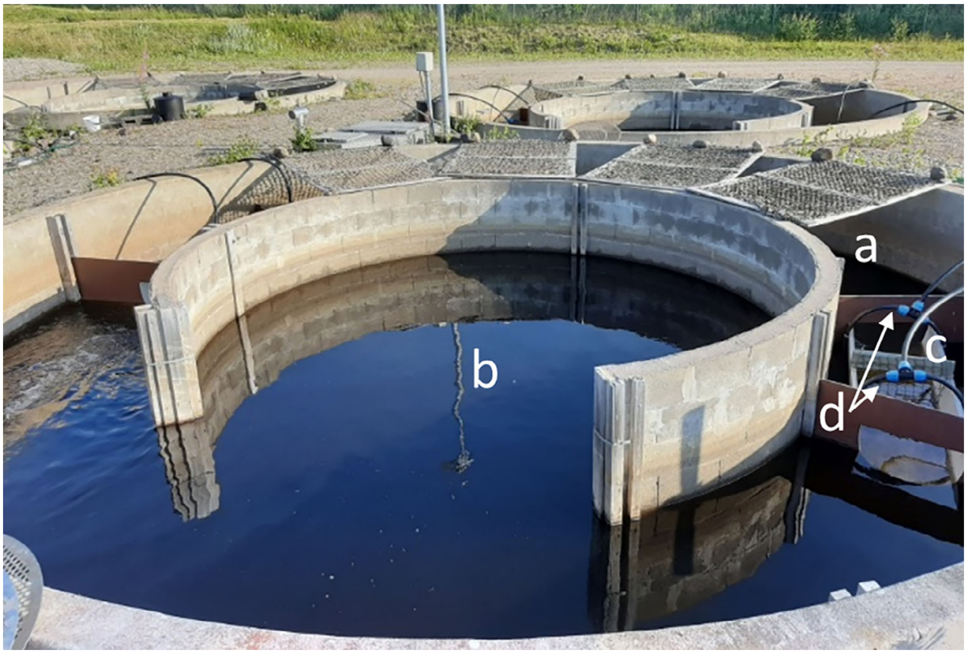

FIGURE 1 Seminatural outdoor stream, consisting of a shallow predator-free section (a, covered section in the back) and a deeper pool section (b, front and middle) containing predatory pike in half of the streams. The sections were separated by a mesh grid wall (c) on either side of the shallow section that allowed salmon to pass, but restricted pike to the pool section. On each side of each mesh grid wall, two passive integrated transponder (PIT) antennas (d) recorded the identity of bypassing fish. Photo credit: Pekka Hyvärinen.

salmon from the predator streams were excluded, because they were never observed entering the pool section. Consequently, the final sample size for the predator streams was 144 recovered salmon out of the initial 313.

All models were fitted in SAS v. 9.4. A generalized linear model (GLM) was used to explore the effects of cross on parasite load (negative binomial error). This analysis included only parasite-exposed individuals and only those recovered from predator-free streams to prevent possible predation bias ($N = 155$). Thus, cross was the only fixed factor. Another GLM was fitted to compare parasite load between fish recovered from predator-free streams and predator streams, and here predator treatment was the only fixed factor.

Survival during the predation experiment was analyzed using mixed effects Cox-regression including all salmon in predator streams ($N = 313$). The last observed change from the predator-free to the predator section was used as an estimate for time of death (minutes since start of the experiment). Cross and infection status were entered as explaining factors and stream identity as a random factor. Mortality in non-predator streams was very low (9/320 fish) and thus, not formally analyzed. These nine fish included one to five individuals from each cross and 5 parasite-exposed and 4 unexposed individuals.

Generalized linear mixed models with Satterthwaite's computation of degrees of freedom (df) were fitted to explore the effects of cross, infection status and predation risk on growth in length ($N = 454$), change in body condition ($N = 453$) and movement behavior ($N = 624$). All models included stream identity as a random factor. Percentage change in length [specific growth rate G; $G = 100 \times (\ln \text{length}_{\text{end}} - \ln \text{length}_{\text{beginning}})$] and absolute change in body condition [Fulton's condition factor $K_{\text{end}} - K_{\text{beginning}}$; $K = \text{mass (g)}/\text{length}^3 \text{ (cm)} \times 100$] were calculated across 53 days in the outdoor streams and fitted with a normal error distribution. Movement behavior was extracted from signal detections at PIT antennas, which were filtered to a 1 s resolution using the PIT Data software package (http://pitdata.net/). Three behavioral variables were determined for each salmon. First, the latency to the first entry of the pool section after release (minutes, negative binomial error). Second, the proportional time spent in the pool section of the total time in the experiment, that is, until the time of death or the end of the experiment (binomial error). Third, as a proxy for activity, the average number of completed half rounds per hour in the experiment, that is, until the time of death or the end of the experiment. This variable was determined as the number of consecutive detections in both antenna pairs in either direction (normal error). Significance values of post hoc comparisons were Bonferroni-corrected.

3 | RESULTS

3.1 | Parasite load

All parasite exposed individuals that were recovered after the experiment ($N = 212$) carried infections. Among the 243 unexposed individuals, 6 were infected with a single *D. pseudospathaceum* parasite, likely from exposure to infective parasite stages before the experiment. These infections were considered negligible due to the low prevalence and intensity, that is, these individuals were treated as 'uninfected'.

Parasite load among infected individuals recovered from predator-free streams differed between the crosses ($N = 155$, $X^2 = 29.5$, $df = 3$, $p < .001$). LS showed the lowest estimated mean parasite load (30.4 ± 1.6). On average, the hybrids carried 2.8 (LS × AS) and 0.6 (AS × LS) parasites more than LS (both $p > .999$), and AS carried 12.8 parasites more than LS ($p < .001$).

3.2 | Predation susceptibility

Survival in the predator streams was affected by infection status (Wald $X^2 = 7.00$, $df = 1$, $p = .008$), with infected salmon showing 52% higher mortality than uninfected salmon [Hazard ratio (HR) = 1.52, 95% CI 1.11–2.06; Figure 2a]. LS had the lowest mortality (Figure 2b). The mortality of the hybrids was 26% (LS × AS, HR = 1.26, 0.81–1.97) and 21% (AS × LS, HR = 1.21, 0.77–1.90) higher, while that of AS was 42% higher (HR = 1.42, 0.92–2.19). However, the cross effect was not statistically significant (Wald $X^2 = 2.50$, $df = 3$, $p = .474$). The interaction between infection treatment and cross was also not significant (Wald $X^2 = 0.74$, $df = 3$, $p = .863$), although cross differences were caused mainly by the infection (Figure 2c,d). Among uninfected individuals, mortality relative to LS was 12% (LS × AS), 0% (AS × LS), and 24% (AS) higher, while it was 43% (LS × AS), 47% (AS × LS), and 62% (AS) higher among infected individuals.

We also observed that infected fish recovered from predator streams ($N = 57$) carried on average 8.1 parasites fewer than those recovered from predator-free streams ($N = 155$; 26.3 ± 3 vs. 34.4 parasites, $X^2 = 24.9$, $df = 1$, $p < .001$). This suggests that predation likely focused on individuals with the highest parasite loads (assuming equal parasite loads in the predation treatments before the experiment).

3.3 | Growth in length and change in body condition

Growth in length during 53 days in the outdoor streams was explained by cross, infection status and predation

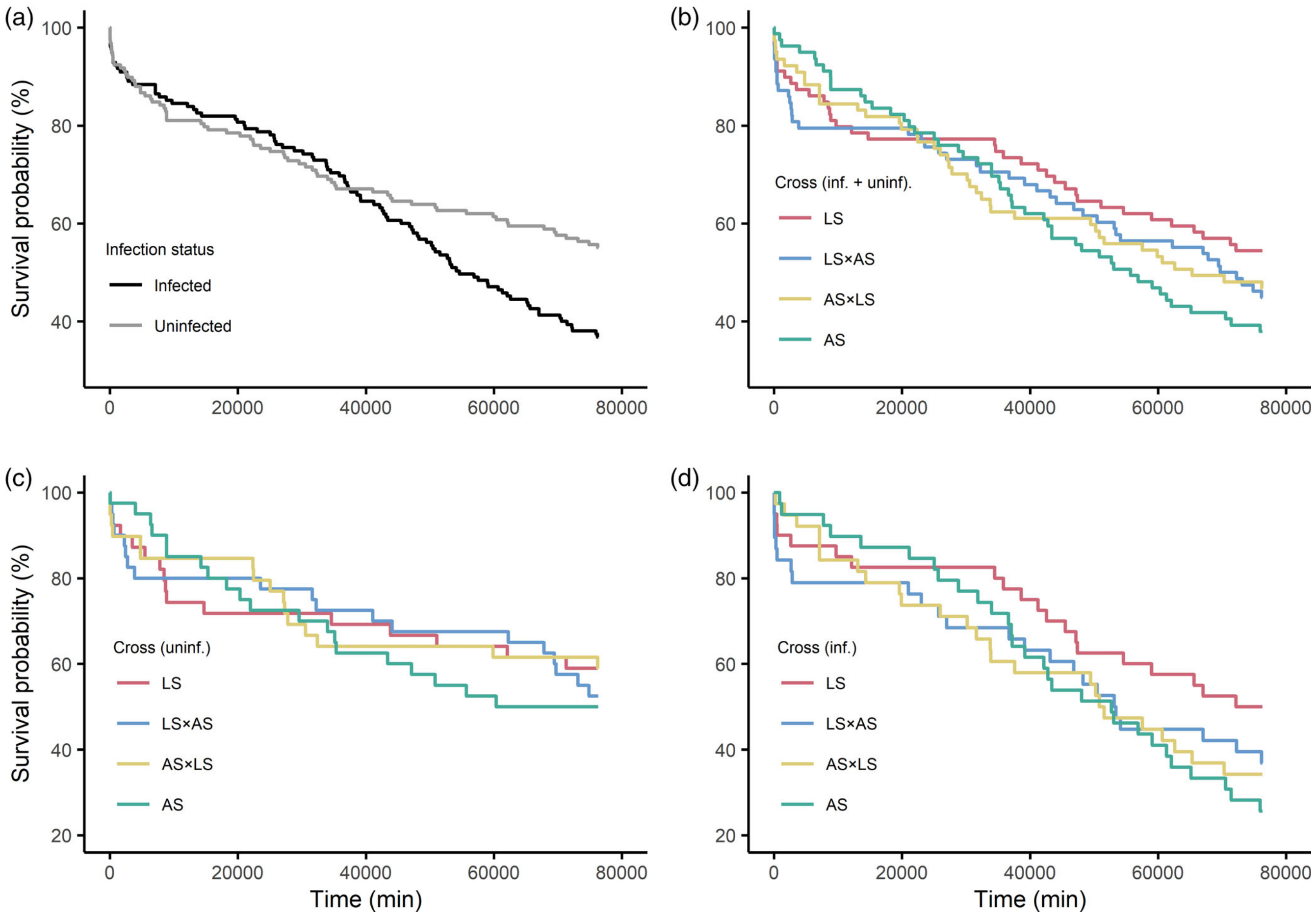

FIGURE 2 Survival probability of salmon under predation by pike during 53 days in seminatural outdoor streams. Survival curves are shown in relation to (a) infection status (infected with *Diplostomum pseudospathaceum* or uninfected); (b) cross (landlocked salmon [LS], Atlantic salmon [AS], and their hybrids, dam × sire); (c) cross of uninfected salmon; and (d) cross of infected salmon. Note that the figure shows the raw survival data.

TABLE 1 *F*-test results from a generalized linear mixed model on growth in length (%, $N = 454$) and body condition change (Fultons K, $N = 453$) of four salmon crosses, either uninfected or infected with the trematode *Diplostomum pseudospathaceum*, during 53 days in eight seminatural outdoor streams (random factor), half of which contained pike predators.

Trait	Term	*df*	*ddf*	*F*	*p*
Δ Length %	Cross (C)	3	432	31.91	<.001
	Infection status (I)	1	432	9.27	.003
	Predation risk (P)	1	6	18.52	.005
	C × I	3	432	0.15	.931
	C × P	3	432	1.48	.220
	I × P	1	432	2.80	.095
	C × I × P	3	432	0.85	.465
Δ Condition *K*	Cross (C)	3	431	30.08	<.001
	Infection status (I)	1	431	14.58	<.001
	Predation risk (P)	1	6	4.10	.089
	C × I	3	431	1.17	.320
	C × P	3	431	3.41	.018
	I × P	1	431	4.23	.040
	C × I × P	3	431	0.45	.720

risk (Table 1, Figure 3a). Specifically, LS had the lowest estimated growth in length. The hybrids grew 2.2% (LS × AS) and 1.4% (AS × LS) more than LS ($p < .001$ and $p = .037$, respectively), and AS grew 5.1% more than LS ($p < .001$). Infection and predator presence had a negative effect on growth in all four crosses. On average, infected individuals experienced a 1.1% reduction in growth compared to uninfected individuals, while individuals in streams with predator presence experienced a reduction of 2.8% compared to individuals in streams without predators. All interactions were not significant.

Change in body condition was explained by interactions between cross and predation risk, and between infection status and predation risk (Table 1, Figure 3b). Overall, condition decreased in all crosses after transfer to the seminatural streams. The presence of predators further reduced body condition in all crosses except AS. LS showed the greatest reduction in condition compared to other crosses regardless of predator presence (all pairwise $p < .004$). Reduction in condition was also higher in infected salmon compared to uninfected in all crosses. The condition of uninfected fish was further reduced by the presence of predators ($p = .006$), while this was not observed in infected salmon ($p = .301$).

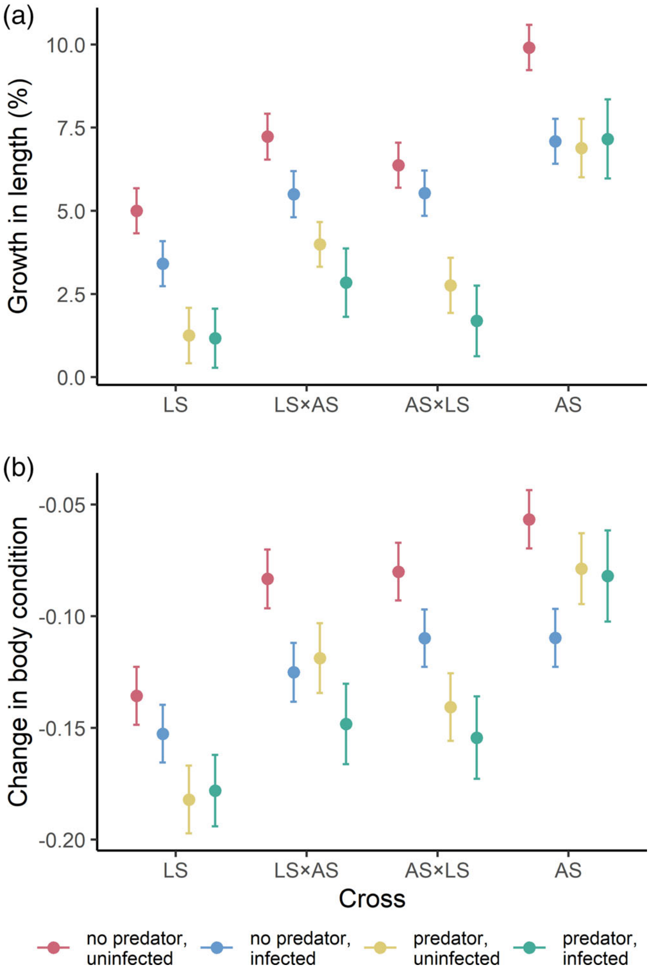

FIGURE 3 Predicted mean (±SE) of (a) growth in length and (b) change in body condition of four salmon crosses during 53 days in seminatural streams. Crosses included the endangered landlocked salmon (LS), an anadromous Atlantic salmon population (AS) and their hybrids (dam × sire). The streams were either predator-free or contained pike predators. Before release to the streams, half of the salmon had been exposed to the eye parasite *Diplostomum pseudospathaceum*.

3.4 | Movement behavior

The latency to the first entry of the pool section (containing predators in predator streams) was affected by cross, infection status and predation risk (Table 2). Specifically, the estimated time of first entry to the pool for LS was at 1431.8 ± 427.9 min, which was later than in all other crosses. The hybrids entered the pool on average 261.3 min (LS × AS) and 540.7 min (AS × LS) earlier (both $p > .999$) and AS 895.3 min earlier ($p = .040$). Uninfected salmon (645.2 ± 153.6 min) entered the pool earlier than infected (1387.4 ± 331.5 min), and salmon in predator-free streams (379.0 ± 107.9 min) earlier than those in predator streams (2361.5 ± 671.1 min).

The proportional time spend in the pool section was explained by predation risk (Table 2). The pool section was the preferred habitat in predator-free streams (estimated proportional time = 0.93 ± 0.03), but was actively avoided in predation streams (0.13 ± 0.04).

Activity was explained by infection status and the interaction between cross and predation risk (Table 2). Uninfected salmon completed, on average, 0.080 ± 0.017 half rounds h^{-1}, while infected salmon completed only about half of that (0.037 ± 0.017 half rounds h^{-1}). Among predator-free streams, LS showed the lowest activity with an estimated number of 0.030 ± 0.020 half rounds h^{-1}. The hybrids completed on average 0.017 (LS × AS) and 0.061 (AS × LS) half rounds h^{-1} more (both $p > .353$) and AS 0.150 half rounds h^{-1} more than LS ($p < .001$). In streams with predators, activity was reduced and no differences were observed between the crosses.

4 | DISCUSSION

Conservationists have repeatedly appealed for the use of assisted gene flow in rescue attempts of small endangered populations (Chan et al., 2019; Frankham, 2015; Ralls et al., 2018). However, the fitness consequences of such actions are often difficult to predict. Our experimental study, mimicking assisted gene flow to an endangered LS

TABLE 2 *F*-test results from a generalized linear mixed model ($N = 624$) on latency to the first entry of the pool (min), proportional time spend in the pool, and completed half rounds h^{-1} of four salmon crosses, either uninfected or infected with the trematode *Diplostomum pseudospathaceum*, during 53 days in 8 seminatural outdoor streams (random factor), half of which contained pike predators.

Trait	Term	*df*	*df*	*F*	*p*
First entry	Cross (C)	3	602	2.77	.041
	Infection status (I)	1	602	8.91	.003
	Predation risk (P)	1	6	20.69	.004
	C × I	3	602	1.49	.216
	C × P	3	602	0.85	.469
	I × P	1	602	1.57	.212
	C × I × P	3	602	2.51	.058
Time in pool	Cross (C)	3	602	1.50	.213
	Infection status (I)	1	602	0.42	.519
	Predation risk (P)	1	6	74.74	<.001
	C × I	3	602	0.32	.813
	C × P	3	602	0.84	.475
	I × P	1	602	0.97	.325
	C × I × P	3	602	0.50	.681
Half rounds h^{-1}	Cross (C)	3	602	2.82	.039
	Infection status (I)	1	602	7.05	.008
	Predation risk (P)	1	6	1.01	.354
	C × I	3	602	1.20	.309
	C × P	3	602	8.12	<.001
	I × P	1	602	3.28	.071
	C × I × P	3	602	2.22	.084

population, explored the consequences of this conservation measure on predation susceptibility and growth in seminatural conditions. We found clear differences in all studied traits between the parental populations and the hybrids were an additive blend of parental characteristics. Relative to the targeted landlocked population, the hybrids had a lower survival under predation (though statistically non-significant), but a higher growth rate. Our results suggest that assisted gene flow can induce both negative and positive fitness effects in the F1 generation.

The presence of pike predators clearly increased salmon mortality, suggesting that predator avoidance skills were decisive for survival. Low genetic diversity has previously been associated with decreased predator avoidance (Auld & Relyea, 2010; Jiang & Møller, 2017; Møller & Nielsen, 2015). However, in the present study, LS had the lowest mortality, while the hybrids showed 21–26% higher predation risk. Although these cross differences were not statistically significant, they are likely to be of biological importance. Because natural reproduction is almost completely absent, assisted gene flow in the Saimaa LS population would be implemented by the stocking of hatchery-reared hybrids. Fish stocking is typically associated with high mortality, caused mainly by predation (Henderson & Letcher, 2003; Olla et al., 1998). Thus, any potential fitness advantage of the hybrids due to increased genetic diversity may be erased by a higher mortality following stocking.

Predation susceptibility was increased by infection with the eye parasite *D. pseudospathaceum*, at least in the second half of the experiment (Figure 2a). This time coincides with the formation of parasite-induced eye cataracts, typically observed 4–6 weeks post exposure (Seppälä et al., 2005). The cataracts reduce host vision, which likely impairs predator detection. As infection intensity predicts cataract size (Karvonen et al., 2004) and cataract size predicts predation risk (Seppälä et al., 2005), a higher infection intensity should be associated with a higher risk of predation. This was also suggested by the present study, as infected salmon recovered from predator streams carried fewer parasites than those recovered from predator-free streams. Although previously observed increased infection intensities in hybrids, relative to LS (Klemme et al., 2021), were less evident in the present study, cross-specific differences in predation risk were mostly observed among infected salmon. Thus, our results suggest that by increasing infection susceptibility, assisted gene flow may indirectly impact survival under predation.

Cross-specific differences in movement behavior may additionally have contributed to survival differences. LS exhibited more cautious behaviors than the other crosses, showing lower swimming activity and longer latency to the first pool habitat entry. While all crosses clearly responded to predator presence by reducing their activity and delaying entry to the predator section, cross-specific differences for the latter trait remained under predation. It is possible that these behavioral differences were driven by heterozygosity levels. Brown trout (*Salmo trutta*), for example, show a positive association between heterozygosity and bold behavior under predation risk (Vilhunen et al., 2008). This finding seems counterintuitive, as boldness generally increases predation risk (Hulthen et al., 2017; Sih et al., 2012; Smith & Blumstein, 2008). However, heterozygosity in brown trout is also positively associated with competitive ability (Tiira, Laurila, et al., 2006). It is possible that bold behavior under predation and competitive ability belong to a suite of correlated traits (behavioral syndrome; Sih et al., 2004) and are therefore linked via genetic effects (pleiotropy, linkage disequilibrium) or neuroendocrine mechanisms. Furthermore, these behavioral correlations typically generate trade-offs, which can result in suboptimal behaviors in some situations (Sih et al., 2004). Thus, inbred LS may experience a lower predation risk due to more cautious behaviors, but could at the same time suffer from decreased competitive ability.

Juvenile salmon occupy feeding territories that are aggressively defended (Keenleyside & Yamamoto, 1962) and competitive ability predicts growth rate (Metcalfe, 1998). Landlocked salmon had the lowest growth rate and the highest condition loss in the present study, suggesting that this population was indeed competitively inferior. While lower growth rates could also indicate inbreeding effects on feeding efficiency, previous studies on Saimaa LS have demonstrated that low genetic variability is associated with low aggression levels (Tiira et al., 2003) and low foraging rates under competition (Primmer et al., 2003). A negative effect of inbreeding on competitive ability has also been reported in other taxa, such as plants (Cheptou et al., 2001) and birds (de Boer et al., 2016). The hybrids, on the other hand, showed enhanced growth and better maintenance of energy reserves, suggesting that assisted gene flow can improve fitness-associated traits, such as competitive ability.

To summarize, assisted gene flow to an endangered LS population had negative fitness effects in terms of reduced survival under predation, but also positive effects in terms of improved growth. Similar contrasting effects have also been demonstrated for early life fitness measures in this system (Eronen et al., 2021; Klemme et al., 2021). Together these studies suggest that the overall net benefit of assisted gene flow may be small. To reduce the risk of outbreeding depression and achieve lasting positive effects in assisted gene flow attempts, several recommendations regarding the selection of donor populations have been proposed (Frankham et al., 2011). One of them concerns the time of isolation between the donor and recipient populations, which should not exceed 500 years (Frankham et al., 2011). However, such populations are not always available. The Saimaa LS became isolated within the Lake Saimaa area after the last glacial period about 10,000 years ago (Berg, 1985; Lumme et al., 2016), which may be one reason for the observed outbreeding depression. However, another study employing admixture of neighboring AS populations has revealed evidence for outbreeding depression even in much smaller genetic distances between populations (Houde et al., 2011).

We propose that the fitness effects of assisted gene flow need to be carefully evaluated before implementing this practice, also incorporating, when possible, different developmental stages. Future studies should also explore fitness effects beyond the F1 generation. For example, some adverse recombination effects, such as the disruption of co-adapted gene complexes, might not be expressed until the F2 generation or later (Hufford & Mazer, 2003). Further, the highest level of heterosis, that is, hybrid vigor, is seen in the F1 generation. In addition to the risk of outbreeding, assisted gene flow can also potentially lead to a loss of native ancestry and, consequently, of unique traits (Bell et al., 2019; Chan et al., 2019). Nevertheless, in cases where species are highly threatened by a lack of genetic diversity, assisted gene flow may represent the only viable option for averting extinction and conserving at least a portion of the ancestral genome (Chan et al., 2019). Ultimately, however, the success of assisted gene flow depends on overcoming the factors that led to the decline of the population. In the case of the Saimaa LS, habitat restoration efforts are in progress and the first results suggest that natural reproduction can be successfully restored (Hatanpää et al., 2021; Leinonen et al., 2020).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data associated with this manuscript are available at The University of Jyväskylä data repository JYX: https://doi.org/10.17011/jyx/dataset/92356.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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