

CONTRIBUTED PAPER

Postrelease exploration and stress tolerance of landlocked and anadromous Atlantic salmon and their hybrids

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Abstract

Threatened fish populations worldwide are relying on stock supplementation by hatchery-reared fish. Although stocking with non-native fish may lead to hybridization, thereby disrupting local adaptations, it could also improve the adaptive potential of small populations by increasing variability in essential behavioral traits. In this study, we crossbred the critically endangered Finnish landlocked salmon with a geographically close Baltic anadromous salmon population to compare boldness-related behavioral traits among the crossing groups. We studied postrelease exploration in seminatural streams and tested stress tolerance of the fish, as reflected by their response during swimming trials and commencement of feeding after the trials. In the stress tolerance experiments, we compared fish with different rearing backgrounds to gain insight into environmentally induced variability in stress tolerance. When compared with the anadromous salmon, the landlocked salmon showed more active postrelease exploration and higher stress tolerance. The hybrids displayed intermediate behaviors compared with the purebred salmon, indicating heritability of these traits. The landlocked salmon showed less variable exploration than the hybrids with anadromous salmon as the maternal strain, but we did not find rearing-dependent responses in stress tolerance. In summary, our findings suggest that hybridization could help in reversing likely domestication-related negative behavioral traits in the landlocked salmon.

KEYWORDS

behavior, crossbreeding, domestication, fish personality, genetic rescue, inbreeding effects, movement behavior, salmonids

1 | INTRODUCTION

Migratory salmonids worldwide have suffered from habitat destruction, overfishing, river damming and water quality deterioration, leaving original populations

threatened, critically endangered, or extirpated (Gustafson et al., 2007; Limburg & Waldman, 2009; Zaporozhets & Zaporozhets, 2004). Many endangered salmonids are thus relying on hatchery-based stock supplementation, which has indeed saved some unique

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populations from extinction (Hutchings et al., 2019; Naish et al., 2007). Stock supplementation with genetically more diverse conspecifics may benefit small, severely inbred populations by increasing local genetic diversity (Ciborowski et al., 2007; Naish et al., 2007). On the other hand, stock supplementation often fails in enhancing threatened natural populations and may even be detrimental in some cases (Christie et al., 2014; McClure et al., 2008; Zaporozhets & Zaporozhets, 2004). One especially problematic practice is the use of non-native strains, because their hybridization with native populations may lead to outbreeding depression and loss of traits important for local adaptation (Ågren et al., 2019; Ciborowski et al., 2007; Klemme et al., 2021; Miller et al., 2004).

Furthermore, populations used in supportive fish stockings are maintained in hatcheries for at least part of their life cycle. While a small founder population size and inappropriate hatchery practices may induce inbreeding, inadvertent domestication is almost inevitable when natural selection on traits beneficial in the wild is relaxed (Milla et al., 2020; Pasquet, 2018; Rollinson et al., 2014). Instead, individuals best adapted to a crowded and stressful environment are more likely to survive and produce offspring than individuals that are not able to cope with the hatchery environment (Christie et al., 2016; Pasquet, 2018). Consequently, hatchery-origin fish have been shown to be generally bolder and less affected by stress, compared with their wild conspecifics (Einum & Fleming, 1997; Islam et al., 2020; Sundström et al., 2004; Yamamoto & Reinhardt, 2003). This might be due to a competitive advantage of bolder and aggressive individuals in the hatchery environment, relative to shy and subordinate individuals (Einum & Fleming, 1997). The behavioral adaptations beneficial in hatcheries are, however, typically detrimental in the wild: bold and exploratory fish also expose themselves more likely to predation (Álvarez & Nicieza, 2003; Araki et al., 2008; Petersson & Järvi, 2006; Thompson et al., 2016). When such fish, behaviorally adapted to the hatchery environment, are stocked in large numbers into the wild, they may readily interbreed with wild individuals. This will lead to gene flow from domesticated to wild fish, with negative behavioral features becoming more prevalent also in natural populations (Ågren et al., 2019; Araki et al., 2008; Islam et al., 2020).

One population heavily reliant on hatchery propagation is the critically endangered landlocked salmon (*Salmo salar* m. *Sebago* Girard) endemic to the Vuoksi watercourse in Eastern Finland (Urho et al., 2019). Lake Saimaa is among the largest freshwater lakes of Europe, characterized by a maze of thousands of islands and interconnected basins. The landlocked salmon, therefore,

conduct an extensive feeding migration into the large lake system from the historical breeding grounds in the rivers Pielisjoki and its tributary Ala-Koitajoki (Pursiainen et al., 1998; Appendix S1). Practically all breeding grounds were destroyed in the latter half of the 20th century by river canalization and the construction of hydroelectric dams, resulting in the near extirpation of the population (Hutchings et al., 2019; Pursiainen et al., 1998; Appendix S1). The last natural landlocked salmon spawners were captured for broodstock in the 1960s, and for the next two to three generations the population was bred exclusively in captivity (Appendix S1). Since the 1970s, the population has been maintained by stocking hatchery-reared juveniles, and natural reproduction has been virtually absent (Hutchings et al., 2019; Appendix S1). Because of the population bottleneck and a continuous low effective population size, the landlocked salmon has lost most of its original genetic diversity, being therefore threatened by inbreeding (Koljonen et al., 2002; Primmer et al., 2003; Tiira et al., 2003; Tiira, Piironen, & Primmer, 2006). Following some well-known examples from conservation biology, however, it might be possible to improve the viability of the landlocked salmon by means of genetic rescue, that is, by hybridizing the population with a genetically more diverse one (Johnson et al., 2010; Madsen et al., 1999; Westemeier et al., 1998).

Fitness consequences of population hybridizations have often been studied by comparing the mortality of purebred and hybrid offspring (in Atlantic salmon; Côte et al., 2014; Eronen et al., 2021; Houde et al., 2011). However, the effects of hybridization on behavioral patterns ultimately underlying the observed differences in fitness are not well understood (but see Ågren et al., 2019; Houde et al., 2010; Kortet et al., 2014; Islam et al., 2020). In this study, we hybridized the Finnish landlocked salmon with a geographically close Baltic anadromous salmon population to compare behavioral traits of the purebred strains and their hybridization crosses. These two populations have become geographically isolated from each other after the last glacial period, less than 10,000 years ago (Lumme et al., 2016; Tonteri et al., 2005). The anadromous salmon of our study originates from the River Neva, North-Western Russia, and it was introduced to Finland in the 1970s to compensate for lost anadromous salmon stocks (for more details, see Appendix S1). In Russia, the population had been partially supported by captive breeding since the 1940s, but natural reproduction of this anadromous salmon has occurred in the Finnish River Kymijoki since the 1980s (Titov & Sendek, 2008; Appendix S1). The captive anadromous Baltic broodstock has been regularly supplemented by wild-caught spawners that have either undergone

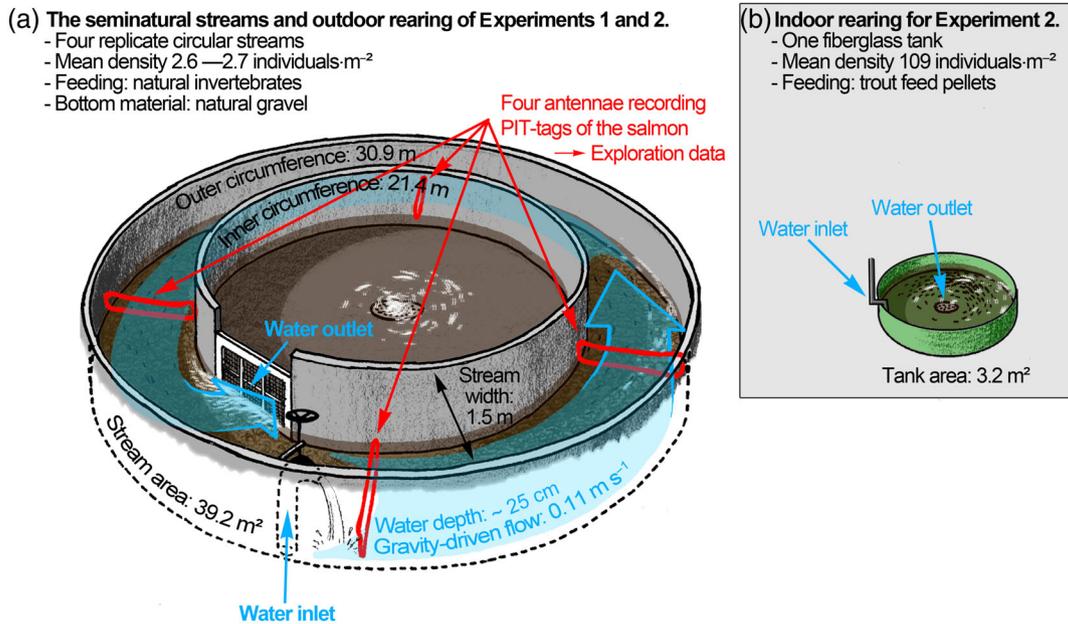
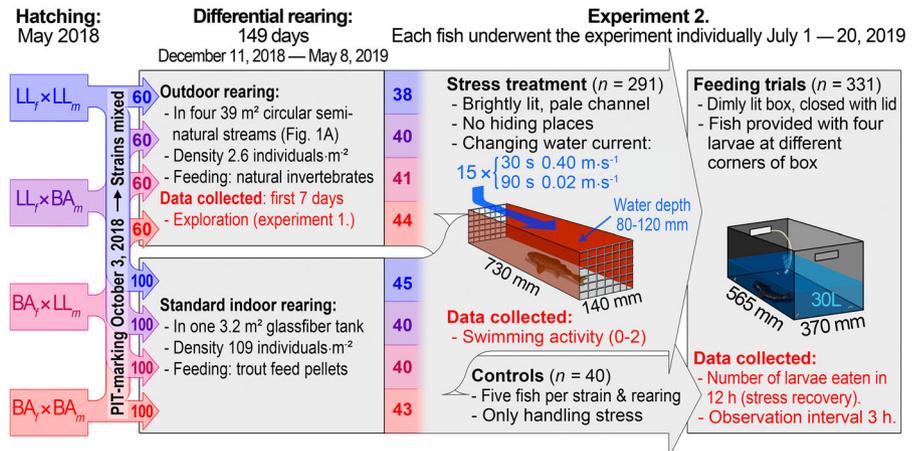


FIGURE 1 The seminatural streams (a) used for data collection in Experiment 1 (exploration data). The same streams (a) were further used in outdoor rearing for Experiment 2, while indoor rearing for Experiment 2 was conducted in fiberglass tanks (b). Both systems were fed with the same water supply from Lake Kivesjärvi.

FIGURE 2 A schematic representation of the strains, rearing backgrounds, and methods used in Experiment 2. Experimental treatments are represented by arrows from left to right. Data collected at different stages of the experiments in red. BA, Baltic anadromous salmon; f, female parent; LL, landlocked salmon; m, male parent.



a complete natural life cycle or been stocked to the river as juveniles. Both hybridized populations have a long history of captive breeding, but the landlocked salmon is characterized by significantly lower genetic diversity, relative to the Baltic anadromous salmon (Koljonen et al., 2002; Appendix S1). Observed microsatellite heterozygosity has been reported to be 0.63 in the anadromous salmon of our study but only 0.29 in the landlocked salmon (Tonteri et al., 2005). Due to its geographic proximity and a significantly higher genetic diversity, this anadromous salmon is considered a good candidate population for the genetic rescue of landlocked salmon.

Among the hybridized strains, we examined two key behavioral traits: (1) postrelease explorative behavior in simulated stocking trials (Experiment 1, Figure 1), and (2) response to and recovery from a stressful treatment as indicators of stress tolerance (Experiment 2, Figure 2). Stress is defined here as the response to a situation perceived by the fish as harmful, reflected by escape behavior and reduced foraging. We expected more stress-tolerant fish to commence feeding activity sooner after a mildly stressful experience (handling stress and sudden changes in environmental conditions), compared with fish that are more prone to stress (Øverli et al., 2002; Wedemeyer, 1976). In animal behavior research, the

studied traits are commonly recognized as typical behavioral syndromes: suites of correlated behaviors on the boldness–shyness axis or on the exploration–avoidance axis (reviewed in fishes e.g., by Conrad et al., 2011). Thus, we assumed the examined behavioral traits to be interrelated and to reflect general boldness of the individuals: bolder fish were expected to be more explorative but also less prone to stress (Bourne & Sammons, 2008; Conrad et al., 2011; Mazué et al., 2015). Furthermore, in salmonids, increased explorative behavior and high-stress tolerance have been essentially linked to domestication (Alioravainen et al., 2020; Islam et al., 2020; Lepage et al., 2000). Therefore, these traits are also highly relevant for the fitness of hatchery-reared fish under natural conditions: bold individuals that disperse and explore more are likely less prone to stress but consequently more vulnerable to predation (Aarestrup et al., 2005; Álvarez & Nicieza, 2003; Pasquet, 2018; Thompson et al., 2016). Because most of the predation-induced mortality occurs shortly after stocking (a stressful situation), the behaviors that hatchery fish display immediately after release are critical for their survival (Aarestrup et al., 2005; Thompson et al., 2016).

Understanding the effect of genetic diversity and hybridization on behavioral traits is crucial for the conservation of endangered salmonid populations worldwide (Burridge, 2019; Fraser, 2008; McClure et al., 2008). Further, little is known about the effects of reduced genetic diversity on behavior, and specifically on the variability of behavioral responses in hatchery fish (Ågren et al., 2019; Christie et al., 2014; Milla et al., 2020; Müller & Juškauskas, 2018). In this study, we first compared explorative behavior and stress tolerance among the purebred and hybrid salmon to find possible differences in these key traits. Assuming that the level of genetic diversity may be reflected in the range of behavioral responses, we expected the landlocked salmon to show less variability in explorative behavior, compared with the Baltic anadromous salmon or their hybrids (West-Eberhard, 1989; Müller & Juškauskas, 2018). Similarly, we evaluated variability in stress tolerance among the fish that either had a seminatural rearing background or had only experienced a standard aquaculture environment (Figures 1 and 2). Seminatural background refers here to circular streams made of concrete, yet having many natural elements, such as natural water flow, stones and gravel at the bottom, and invertebrates as drifting or benthic prey for salmon juveniles (Figure 1a). Our hypothesis was that the effect of differential rearing environment would be more pronounced in anadromous salmon and hybrid fish, compared with the genetically less diverse landlocked salmon.

2 | MATERIALS AND METHODS

2.1 | Experimental fish

We studied exploration and stress tolerance in two experiments conducted at the Kainuu Fisheries Research Station in Paltamo (www.kfrs.fi). For these experiments, we hybridized the landlocked Lake Saimaa salmon (LL) with a Baltic Sea anadromous salmon (BA), to produce four strains (year classes 2018 and 2019; Table 1; Appendix S2): (1) purebred landlocked salmon ($LL_f \times LL_m$), (2) hybrids where the maternal population was landlocked salmon ($LL_f \times BA_m$), (3) hybrids where the maternal population was Baltic anadromous salmon ($BA_f \times LL_m$), and (4) purebred Baltic anadromous salmon ($BA_f \times BA_m$). Within the year-class 2019, the BA and LL parents ($n = 20$ females and 20 males) of the purebred and hybrid strains were the same, such that the strains contained half-siblings. Within the year-class 2018, however, we had to compensate for accidental mixing of the strains by taking the parental fish of the $LL_f \times LL_m$ group from partially different parents ($n = 30$ females and 30 males) than used to produce the hybrids. Within the year class 2018 the LL parents were of hatchery stock maintained at the Kainuu Fisheries Research Station (hatchery generation), whereas the LL parents of the year class 2019 were wild-caught spawners. The BA parents of both year classes originated from the Laukaa Fisheries Research and Aquaculture Station, being crosses of wild and hatchery-origin fish. For individual identification of the study fish, we marked them using passive integrated transponders (12 mm HDX+ PIT-tags, Oregon RFID, Portland, Oregon).

In Experiment 1, we released juvenile salmon of the four strains to seminatural outdoor streams in December 2018 (year-class 2018) and March 2020 (year-class 2019), recording their movements during the first 7 postrelease days (Figure 1). After spending 149 days in these seminatural streams and feeding on natural macroinvertebrate food, we transferred the year-class 2018 fish back to indoor rearing May 8, 2019. Starting July 1, 2019, we used the same fish in Experiment 2, where we studied their stress tolerance by recording stress response and recovery. We studied stress response by exposing the fish to swimming stress and observing their response in these trials (Figure 2). Thereafter we observed the commencement of feeding activity of the fish, which we assumed to reflect stress recovery (Figure 2). To gain understanding of the rearing-dependent variability in stress tolerance among the strains, we compared here fish kept in a seminatural environment with fish reared in standard indoor tanks (Figures 1 and 2). More details of the hybridizations and rearing can be found in Appendix S2.

TABLE 1 Number of (*n*), and the mean weights (g), lengths (mm), and condition indices (%) of the juvenile salmon groups used in our two experiments.

Experiment 1. Postrelease exploration								
Trial	Strain ^a	<i>n</i>	Body weight	SD	Body length	SD	Condition index	SD
December 2018	LL _f × LL _m	60	5.9	1.8	83	8	103	5
	LL _f × BA _m	60	6.1	1.5	84	7	101	6
	BA _f × LL _m	60	5.9	1.6	84	8	101	5
	BA _f × BA _m	60	6.3	1.7	86	8	101	5
March 2020	LL _f × LL _m	100	13.4	4.6	112	13	97	7
	LL _f × BA _m	99	14.0	4.9	112	15	99	7
	BA _f × LL _m	99	12.8	5.3	108	16	100	7
	BA _f × BA _m	100	12.6	4.5	108	14	102	8
Experiment 2. Stress response and recovery								
Strain ^a	Treatment background	<i>n</i>	Body weight	SD	Body length	SD	Condition index	SD
LL _f × LL _m	Indoor	45	28.4	7.1	144	12	100	7
	Outdoor	38	22.6	8.7	131	17	101	9
LL _f × BA _m	Indoor	40	28.6	8.4	143	16	102	10
	Outdoor	40	22.7	7.9	131	17	102	8
BA _f × LL _m	Indoor	40	28.7	8.7	144	15	98	7
	Outdoor	41	23.3	8.5	132	18	102	8
BA _f × BA _m	Indoor	43	31.9	6.7	149	11	102	6
	Outdoor	44	24.4	8.6	138	20	95	8

^aBA, Baltic anadromous salmon; f, female parent; LL, landlocked salmon; m, male parent.

2.2 | Experiment 1: Postrelease exploration

The first experiment comprised two separate trials, which we conducted starting on December 11, 2018 (for year-class 2018; the outdoor group used subsequently for Experiment 2; Figures 1 and 2) and March 16–23, 2020 (year-class 2019). For the first trial, we divided 60 eight-month-old salmon per strain into four mixed-strain groups of 60 individuals (15 salmon × 4 strains × 4 groups for a total $n = 240$; Table 1). For the second trial, we divided 99–100 ten-month-old salmon per strain into four mixed-strain groups of 99–100 individuals (24–25 salmon × 4 strains × 4 groups for a total $n = 398$; Table 1).

In both trials, the groups were released into four seminatural circular outdoor streams (Figure 1a). Density of the fish in the streams was 2.7 and 2.6 individuals·m⁻² in the 2018 and 2020 trials, respectively. The streams in the 2018 trials also contained anadromous salmon of another hybridized strain that were not included in our present data. Water temperature of the inflowing lake water varied naturally, being on average +2.8°C (range +2.6 to +3.0°C) in both exploration trials. We did not feed the fish, since the gravel bottom and the inflowing water

contained macroinvertebrate fauna, which the fish could feed on (Hatanpää et al., 2020). Each stream was equipped with four evenly spaced custom-made antennae capable of reading PIT tags and recording the movement of all the individuals at an accuracy of 0.25 rounds. Because movement practically ceased after the first 5 days, we only used data recorded for the first 7 postrelease days, that is, 168 h. We considered that the movement activity of the fish during these first days reflected exploration and dispersal in a novel environment, after which the individuals settled into their feeding territories.

2.3 | Experiment 2: Stress tolerance

We performed the stress treatments and subsequent feeding trials July 1–20, 2019. Half of the fish used in the second experiment had been exposed to seminatural outdoor conditions during Experiment 1 (outdoor fish; Figure 1a). They had thus gained experience in feeding on natural invertebrates for 149 days by the time they were moved back to indoor rearing tanks 2 months before Experiment 2. The other half of the experimental fish had experienced only standard aquaculture rearing,

feeding on Veronesi Vita 0.8 dry feed pellets (indoor fish; Figure 1b). Each of the eight experimental groups, that is, four strains \times two rearing backgrounds, comprised 38–45 individuals (331 in total; Table 1 and Figure 2). These included five control fish per group, which were excluded from the stress treatment and brought directly to the feeding trials (Figure 2). We transferred the abovementioned experimental fish into a 15 m² storage tank prior to the start of the stress tolerance trials.

Thereafter, we caught 24 fish per day haphazardly from the storage tank and transferred them in groups of four fish into fasting cages within a separate tank. After fasting in the cages for 18–23 h, we exposed the fish individually to a 30 min stress treatment in pale, brightly lit channels with a rapidly changing water current (Figure 2; see also Hyvärinen et al., 2004). During this treatment, as a response to stress, most salmon settled to the bottom of the channel refusing to move, but notes were made if an individual was observed swimming against the current at least once during the first (0–15 min from start) and/or second (15–30 min) half of the treatment.

Immediately after the stress treatment, we moved the fish into the feeding trials to observe how rapidly they recovered from stress, that is, started feeding. Here we placed the fish individually into dark and dimly lit plastic boxes filled with 30 L of water oxygenated by an aquarium oxygenator (Figure 2). In the box, the fish was provided novel food comprising four fly larvae (commercially produced *Lucilia sericata*) placed at different corners of the plastic box. We performed the feeding trials always in groups of four fish placed in four boxes, starting between 8:30 and 13:00 and inspected all boxes at intervals of 3 h (at 12:00, 15:00, 18:00, and 21:00), and at the end of each trial (exactly 12 h after the start), noting the number of larvae eaten by each individual at each time interval. The temperature of the inflowing water during our stress tolerance experiments was +15.5°C to +17.0°C and the oxygen content varied between 7.8 and 8.6 mg·L⁻¹. After the experiments, we anesthetized the fish and measured their body lengths and weights on July 21, 2019 (Table 1).

2.4 | Statistical analysis

All analyses were conducted in R (version 4.0.3, R core team, 2020) using the R studio interface. Within both experiments, we conducted preliminary analyses on mean body size and condition index (Ricker, 1975) among experimental groups using analysis of variance (Details in Appendix S3). In all models, we included the fixed factors based on their significance ($\alpha \leq .05$) and chose the most relevant interaction terms based on AIC criteria. Final model fits were graphically evaluated using

residual plots and paired differences were based on Šidák corrected post hoc tests from the package emmeans (Lenth, 2020). To evaluate the generalized models, we used simulated residuals obtained using the package DHARMA (Hartig, 2020).

We modeled postrelease exploration using a linear mixed effect model with a restricted maximum likelihood estimation method in the R-package nlme (Pinheiro et al., 2020). Due to a right-skewed distribution we log-transformed the response variable, that is, total rounds moved in either direction in the circular streams. In the final model, we used strain and trial (December 2018 and March 2020) as fixed factors, body weight and its interactions with the trial as fixed covariates, and seminatural stream as a random factor. Additionally, we evaluated the heterogeneity of behavioral variance among the strains using a log-likelihood ratio test for alternative models with common and separate residual variances (package lme4; Zeileis & Hothorn, 2002).

To model the proportion of fish that started actively swimming against the water current in the stress treatment (stress response indicator in Experiment 2), we coded the behavior of the fish as follows: 0 = no active swimming, 1 = active swimming against the current at either half of the treatment, and 2 = active swimming against the current at both halves. Since the data consisted of counts and most of the fish did not move during the experiment, we fitted on the data a generalized linear mixed model with a Poisson distribution using the R-package glmmTMB (Brooks et al., 2017). We used strain, rearing background and their interactions as fixed factors choosing body weight as a fixed covariate (without interactions).

In the feeding trials (stress recovery indicator in Experiment 2), we treated the binomial response (if the fish started to feed or not) as four Bernoulli trials, the outcome of which we coded into two columns for the number of observations made before and after the fish started to feed. Thereafter, we fitted on the data a generalized linear mixed model with a beta-binomial distribution using the R-package glmmTMB (Brooks et al., 2017). We used again strain and rearing background with interactions as fixed factors and chose the condition index (without interactions) as a fixed covariate. Further, we applied a survival analysis to model the median time the fish from different groups started to feed (Appendix S5).

2.5 | Statement on animal subjects

All animal experimentation reported meets the ABS/ASAB guidelines for ethical treatment of animals and complies with the current Finnish legislation. Animal use permit no: ESAVI/3385/2018.

TABLE 2 Results of the linear mixed effects model on postrelease exploration, with response: Log-converted total rounds moved in circular seminatural streams during the first 7 postrelease days.

	df _{num}	df _{den}	F	Effect size ^a	p
Intercept	1	625	145.580	0.19	<.001
Strain	3	625	36.343	0.15	<.001
Trial, i.e., year	1	6	2.435	0.29	.170
Weight, g	1	625	50.498	0.07	<.001
Trial × Weight, g	1	625	9.048	0.01	.003
Strain ^b	Mean	95% CI	Variance ^c	Back-converted mean ^d	Post hoc group ^e
LL _f × LL _m	4.224	3.143–5.305	1.000	1786	a
LL _f × BA _m	3.822	2.744–4.901	0.993	1195	b
BA _f × LL _m	4.028	2.939–5.117	1.250	1468	ab
BA _f × BA _m	3.104	2.030–4.179	1.045	583	c

Note: More specifically the significances of the pairwise comparisons are: a vs. b $p = .0024$ a vs. ab $p = .4766$ a vs. c $p < .0001$ b vs. ab $p = .4125$ b vs. c $p < .0001$ ab vs. c $p < .0001$.

^a η^2 .

^bBA, Baltic anadromous salmon; f, female parent; LL, landlocked salmon; m, male parent.

^cStandard deviations.

^dTotal distance (m) moved during the first 7 postrelease days.

^eGroup assigned in pairwise tests of Šidák corrected means at $p < .05$.

3 | RESULTS

3.1 | Experiment 1: Postrelease exploration

The strains used in the 2018 trial did not differ statistically in their mean body weights, lengths or condition indices (Table 1 and Appendix S3). The 10-month-old salmon in the 2020 trial were on average 118% heavier and 31% longer, but had a 2.2% lower condition index, compared with the 8-month-old salmon in the 2018 trial. In the 2020 trial, the mean weights and lengths did not differ among strains, but LL_f × LL_m had a 5.1% lower condition index than BA_f × BA_m.

After correcting for the significant effect of body weight, the strains differed significantly in exploration, whereas trial (i.e., year) had no statistically significant effect (Table 2). BA_f × BA_m explored less than any other group, whereas LL_f × BA_m explored less than LL_f × LL_m (Table 2; Figure 3). The hybrids showed intermediate exploration, but the differences between the two hybrid strains, as well as between BA_f × LL_m and LL_f × LL_m, were statistically insignificant. We found a significant positive association between exploration and body weight, and the association was more pronounced for the smaller fish in the 2018 trial (interaction term in Table 2). A log-likelihood ratio test indicated that the model with separate residual variances among strains gave a better fit than the model with a common residual variance ($\chi^2 = 170.8$, $df = 3$, $p < .001$). The variances of

exploration were thus heterogeneous among the strains, with the hybrid strain BA_f × LL_m showing clearly more variable explorative behavior than the other strains (Table 2). In the 2018 trial, exploration of the fish occurred during the first 24 h only, whereas in 2020 explorative behavior was distributed over 4 days (Figure 3 and Appendix S4).

3.2 | Experiment 2: Stress tolerance

Fish of different strains did not differ statistically in their mean body weights or condition indices. Instead, the indoor fish were on average 26% heavier and 8% longer than the outdoor fish (Table 1 and Appendix S3). Within the outdoor-reared group, particularly BA_f × BA_m had a lower condition index than the other groups (Table 1 and Appendix S3). Strain and body weight affected significantly the probability of swimming against the current in the stress treatment, that is, the stress response (Table 3 and Figure 4a). The rearing background or its interaction with strain, however, had no effect on stress response (Table 3). Post hoc comparisons revealed that BA_f × BA_m were more likely to swim against the water current (mean probability of swimming against current 23.0% and 95% confidence interval (95% CI): 9.0% to 58.6%) than either LL_f × LL_m (mean 1.9% and CI: 0.4%–9.0%) or LL_f × BA_m (mean 1.9% and CI: 0.4%–9.4%). BA_f × LL_m showed intermediate swimming activity (mean 5.3%

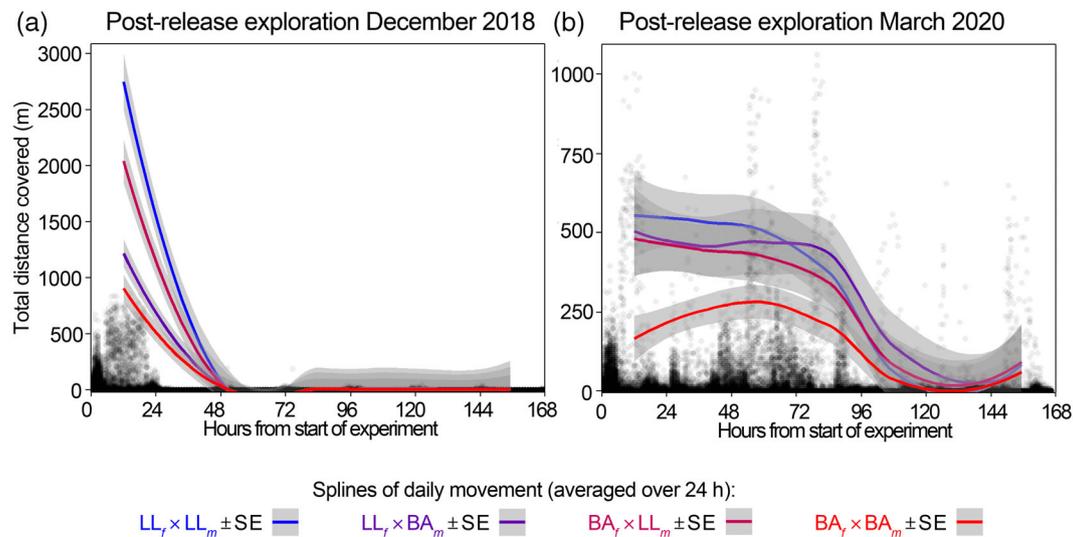


FIGURE 3 Results of Experiment 1, the postrelease exploration trials. Exploration of the different salmon strains during the first 7 days after release into seminatural streams in December 2018 (a) and March 2020 (b). The semitransparent background points represent all hourly movement signals, and the loess regression curves indicate daily strain-specific movement averaged over 24 h. BA, Baltic anadromous salmon; f, female parent; LL, landlocked salmon; m, male parent. Note the different scales of the y-axes.

TABLE 3 Results of the generalized linear mixed model on stress response, that is, swimming activity during the stress treatment (response: number of nonstationary swimming observations, 0–2).

	Wald χ^2	df	$p > \chi^2$
Strain	20.119	3	<.001
Rearing background	0.166	1	.683
Strain \times Rearing background	0.489	3	.921
Weight, g	7.625	1	.006

and CI: 1.5%–18.9%) and did not differ in this respect from the other three strains (Figure 4a). Further, the model indicated that bigger individuals were less likely to start swimming against the water current than smaller ones.

Strain also affected the probability of starting to feed during the 12-h stress recovery trials (Table 4 and Figure 4b). Rearing background as such, again did not affect stress recovery. Yet, we found a marginally significant interaction between rearing background and strain. Pairwise comparisons revealed that $LL_f \times LL_m$ had a significantly higher probability (mean 55.5% and 95% CI: 43.2%–67.1%) to start feeding during the 12-h trial than either $BA_f \times BA_m$ (mean 34.9% and CI: 24.9%–46.6%) or $BA_f \times LL_m$ (mean 36.6% and CI: 26.2%–48.3%; Figure 4b). Feeding probability of $LL_f \times BA_m$ was again intermediate (mean 40.2% and CI: 28.9%–52.6%) between the purebred strains and did not differ statistically from the other three strains. Our model also revealed a

significant negative association between the condition factor and the probability to start feeding; individuals with higher condition index were less likely to start feeding, than individuals with a lower condition index. The survival analysis indicated that $LL_f \times LL_m$ started feeding significantly earlier (median 5.05–5.38 h), than $BA_f \times BA_m$ (median 8.79–12.81 h), when the effect of rearing background was statistically controlled (Appendix S5). Within $LL_f \times BA_m$, the fish with outdoor background started feeding significantly later (median: 17.52 h) than the fish reared indoors (median: 5.22 h).

4 | DISCUSSION

We found that the purebred landlocked salmon explored the novel environment more than the anadromous salmon or hybrids with landlocked salmon as the maternal population when the positive relationship between fish size and exploration was accounted for. In relation to the parental strains, the levels of exploration in hybrid strains were intermediate but higher than in purebred anadromous salmon. The low exploration tendency of the anadromous salmon may refer to general shyness or increased stress after release in the new environment. The high exploration tendency of the landlocked salmon, on the contrary, could indicate boldness and a reduced stress reaction in a novel environment. Since the strain-specific differences in exploration were consistent between trials (years), we expect that differing backgrounds of the LL parents (wild-caught vs. hatchery fish)

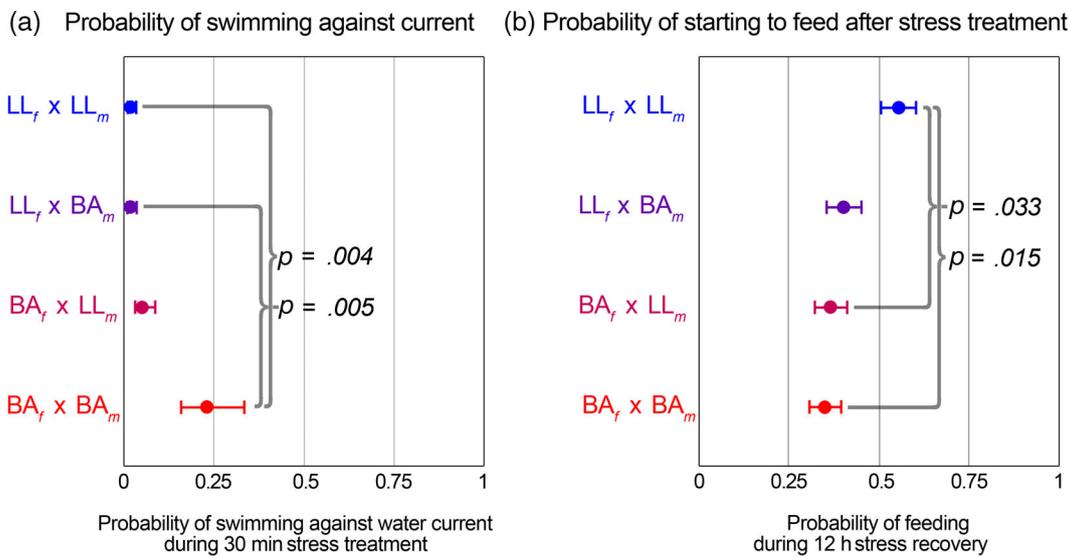


FIGURE 4 Results of Experiment 2, the stress tolerance trials. Modeled and back-converted probabilities and standard errors of swimming against current in the stress treatment (a) and starting to feed during the 12 h stress-recovery experiment (b). Response in (a) is the number of observations where the fish started swimming against the current and response in (b) is the binomial count of observations before and after starting to feed. The curly brackets in the figure mark statistically significant pairwise comparisons with their p -values. BA, Baltic anadromous salmon; f, female parent; LL, landlocked salmon; m, male parent.

TABLE 4 Results of the generalized linear mixed model on stress recovery, that is, probability of feeding during 12 h following the stress treatment (response: binomial counts of observations before and after starting to feed on larvae after stress treatment, 0–4).

	Wald χ^2	df	$p > \chi^2$
Strain	11.218	3	.011
Rearing background	1.137	1	.286
Strain \times Rearing background	6.967	3	.073
Condition index	16.059	1	<.001

in our hybridizations did not affect the results. The salmon might have exhibited more active exploration if we had conducted these trials during warmer waters and not in winter. In the December 2018 trial, postrelease exploration in all strains was much shorter in duration than in the March 2020 trial (Figure 3 and Appendix S4). This is likely related to the very short days and the darkness in December, compared with significantly longer days in March. The differences in the duration of peak exploration could also be partly explained by the larger size of the fish in 2020 than in the 2018 trial (average difference of body weight was over twofold).

In addition to exploration, we found differences in stress tolerance among the strains. The landlocked salmon swam less actively against the current during the stress treatment and fed more actively afterwards, compared with the anadromous salmon. Again, the hybrid

groups were intermediate to the purebred strains in both stress-related features. Despite these clear strain-dependent differences, no difference in stress recovery emerged between the control fish and those that underwent the stress treatment. It is possible that relatively small differences in stress level may have remained undetected due to the low number of controls ($n = 40$) in relation to the fish exposed to the treatment ($n = 291$). Furthermore, the control fish were also affected by unavoidable handling stress when transferred to the feeding trials (Lepage et al., 2000; Wedemeyer, 1976). Individuals with higher condition index seemed to be less eager to start feeding, compared with individuals with a lower condition index, which might indicate a trade-off between good condition and stress tolerance. In fish stockings, this would mean that well-fed fish with a higher condition index may behave more carefully in the presence of predators. Fish with a lower condition index, instead, may be forced by hunger to take higher risks.

Partially in line with our hypotheses, we found that hybrids with anadromous salmon as their maternal population showed more variable postrelease exploration than the purebred landlocked salmon (Table 2). Hybridization may thus not only reduce explorative behavior in landlocked salmon but also increases interindividual variation, presumably as a result of increased genetic variation. More variable behavior could enhance the adaptive potential of hybrids in relation to the purebred landlocked salmon (West-Eberhard, 1989; Whiteley et al., 2015). Contrary to our expectations,

however, stress tolerance was unaffected by rearing background in all salmon strains studied. Hence, despite being genetically more diverse, neither the purebred anadromous nor hybrid salmon showed more variable stress tolerance than the landlocked salmon. Yet, the rearing background-dependent behavioral differences among the strains may have remained undetected because of the relatively long time period (2 months) between differential rearing and the following trials. Furthermore, the survival analysis that we conducted additionally on the same data, indicated a possible difference between indoor and outdoor-reared $LL_f \times BA_m$ -hybrids (Appendix S5). The effect of genetic diversity on the variability of behavioral responses, however, remains ambiguous in our study. Future studies should include individual or family-based genetic data to get a better understanding of the association of genetic diversity with phenotypic plasticity.

Nevertheless, both experiments revealed clear behavioral differences between the landlocked salmon and the Baltic anadromous salmon. Since we expected bolder fish to explore more and to be less prone to stress, the two experiments gave consistent results: compared with the anadromous salmon, the landlocked salmon showed both higher explorative tendency and lower stress tolerance. The observed consistency between active exploration and high-stress tolerance conforms to the theory of behavioral syndromes (Conrad et al., 2011). Reaction to novelty, for example, is commonly seen as one measure of boldness and it is likely correlated with the tendency to explore a novel habitat (Bourne & Sammons, 2008; Conrad et al., 2011; Mazué et al., 2015). Similarly, bolder fish may be less stressed by novel or uncomfortable situations and thus commence feeding sooner after a stressful experience (Conrad et al., 2011; Øverli et al., 2002; Vaz-Serrano et al., 2011). Considering these previous studies and our experiments, the average landlocked salmon individual could thus be expected to be bolder than the average anadromous salmon individual. Since the hybrids showed intermediate behavior to the purebred strains, the strain-specific behavioral traits seemed to be heritable. Stress tolerance, exploration, and boldness have been shown to have a heritable basis in several salmonid species (Islam et al., 2020; Kortet et al., 2014; Lucas et al., 2004; Øverli et al., 2002).

The strain-specific behaviors we found can partly result from inherent physiological or ecological differences between the investigated populations, reflecting thousands of years of divergent evolution (Lumme et al., 2016; Tonteri et al., 2005). On the other hand, the strains have similar life histories, involving juvenile stages in rivers and feeding migrations of up to hundreds of kilometers either in an extensive freshwater lake

system or in a brackish water sea (Hutchings et al., 2019; Kallio-Nyberg & Ikonen, 1992; Appendix S1). Furthermore, even though the breeding rivers Neva and Pielisjoki differ greatly in size, they belong to the same watershed and may resemble each other ecologically. These similarities could indicate that also genetic drift, especially among the genetically impoverished landlocked salmon, may have played an important role in facilitating behavioral divergence of the studied salmon strains. Because there are hardly any original spawning or nursery areas remaining in either river, it is impossible to reconstruct the original natural conditions in these salmon habitats (Hutchings et al., 2019; Titov & Sendek, 2008; Appendix S1).

The behavioral differences between the strains may also be the consequence of domestication, as both our studied populations have a long history of captive breeding. Christie et al. (2016) demonstrated in rainbow trout (steelhead) that already first hatchery generation fish differed in their gene expression from wild-origin fish, and at least some of these differentially expressed genes were related to stress tolerance. Previous research has indicated that more domesticated fish, including salmon, are less sensitive to stress induced for example by novel objects, transfer to a new environment, or a simulated attack by a predator, compared with wild-origin fish (Álvarez & Nicieza, 2003; Einum & Fleming, 1997; Johnsson et al., 2001; Lepage et al., 2000). Hatchery fish have also been shown to disperse more readily than wild fish after stocking and to be bolder than their wild-origin conspecifics (Alioravainen et al., 2020; Horká et al., 2015; Islam et al., 2020; Sundström et al., 2004). Considering these studies, the behavioral differences we found between the purebred strains would suggest that the landlocked salmon might be more domesticated than the studied anadromous salmon. The genetic bottleneck along with multiple generations of captive rearing and the absence of natural reproduction for decades may have led to domestication in the landlocked salmon (Koljonen et al., 2002; Tiira et al., 2003; Appendix S1).

The high explorative tendency we observed in the landlocked salmon can be expected to reflect dispersion in a novel environment, which could prove disadvantageous in the presence of predators (Aarestrup et al., 2005; Thompson et al., 2016). Similarly, a reduced stress response in a new environment might be associated with boldness and the likelihood of foraging under the threat of predation, which may increase predation risk even further (Álvarez & Nicieza, 2003; Petersson & Järvi, 2006). Multiple generations of hatchery influence together with reduced genetic diversity and genetic drift might, therefore, have led to negative behavioral changes in the landlocked salmon (Koljonen et al., 2002; Tiira et al., 2003;

Tiira, Laurila, et al., 2006; Appendix S1). Thus, the behavioral features we observed in our experiments, may expose the stocked landlocked salmon juveniles to elevated mortality, which could partly explain their low stocking success (Pursiainen et al., 1998; Appendix S1).

4.1 | Implications

Our results suggest that, in addition to restoring genetic diversity, hybridization with anadromous salmon could reverse negative and possibly domestication-related behavioral features in the landlocked salmon. Carefully planned, partial hybridization could thus support efforts to restore the viability of this critically endangered salmon population, albeit at the cost of genetic uniqueness (see also Burrige, 2019). It needs to be emphasized, however, that further research into the subject is still needed, especially because possible outbreeding depression may not become apparent before the second-generation back-crosses and because we cannot rule out the possibility of some of the observed behavioral differences being local adaptations (Klemme et al., 2021; Whiteley et al., 2015).

For the anadromous salmon, on the other hand, the behavioral consequences of hybridization with landlocked salmon could be expected to be negative. Thus, our results also support the growing body of evidence that important behavioral adaptations of fish populations can be disturbed when they are stocked and hybridize with foreign and possibly domesticated populations, or with fish with reduced genetic diversity (Ågren et al., 2019; Alioravainen et al., 2020; Islam et al., 2020; Klemme et al., 2021). This could partially explain many of the negative outcomes of supportive stockings (Christie et al., 2014; McClure et al., 2008; Zaporozhets & Zaporozhets, 2004).

Finally, our results could be potentially applied in the production of more profitable hybridized landlocked salmon stocks for put-and-take fisheries utilization. This might benefit commercial and recreational fisheries management in lakes isolated from Lake Saimaa, where natural reproduction cannot occur and where such fisheries are already practiced. These purely hatchery-based put-and-take landlocked salmon fisheries with notable economic importance are already utilized in several Finnish lakes.

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DATA AVAILABILITY STATEMENT

All data for this study is archived online in the Dryad digital repository (DOI <https://doi.org/10.5061/dryad.9ghx3ffmg>).

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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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