

Survival of crossbred brown trout under experimental pike predation and stocking in the wild

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Unintended domestication in hatchery broodstocks reflects a low success of supportive stocking programs. We crossbred adfluvial hatchery-stock brown trout (*Salmo trutta*) females with males from two non-native adfluvial hatchery strains and a wild but local resident strain to study survival, growth and behaviour of hybrid offspring alternatives. Experimental predation selected for larger size in wild crosses but not in the original hatchery fish. Non-native hatchery crossing reduced the survival in the predation experiment either directly or due to negatively size-selective predation. Wild crosses evaded the areas where predators were present more often than the pure hatchery origin fish in the predation experiment. Our results support an intrinsic anti-predatory behaviour in wild fish and suggest that crosses with resident fish can produce equally growing offspring that are efficient in predation avoidance. Resident, local, wild populations may be a beneficial source for improving the natural-type fitness in broodstocks affected by domestication without natural reproduction.

Introduction

Unintended domestication occurs rapidly and cumulatively in hatchery broodstocks, having particularly negative consequences when the supplementation with wild fish is impossible (Araki *et al.* 2007, Christie *et al.* 2016). Domestication impairs anti-predatory behaviours and favours bold behavioural types (Huntingford 2004). Genetic effects of hatchery-rearing reflect to low success of supportive stocking programs and failures in restoration of locally extinct populations (Ferguson 2007). Adaptation to hatchery

conditions can lead to population's mismatch with natural environment, and hatchery-breeding decreases the genetic variation in the impacted population (Aho *et al.* 2006, Araki *et al.* 2007, Besnier *et al.* 2015). Both of these processes can decrease population's ability to survive in and further adapt to a natural environment (Mäkinen *et al.* 2015).

Predation is an important natural mortality factor for released fish, particularly during the juvenile and smolt stages (Kekäläinen *et al.* 2008). Hatchery-reared fish, such as brown trout, often suffer from higher predation than the wild

fish due to the loss of learned and intrinsic anti-predatory responses (Álvarez and Nicieza 2003, Petersson and Järvi 2006) or their greater risk-taking behaviour (Biro *et al.* 2004). At individual level, high risk-taking commonly increases with growth rate (Biro and Stamps 2008, Biro and Sampson 2015), but the relationship may not always be positive in resource-limited natural environments (Adriaenssens and Johnsson 2011). However, positively size-dependent survival, that is a general and long-known phenomenon both in overwintering (Hunt 1969) and predation context (Anderson 1988, Hyvärinen and Vehanen 2004) in fish, may reduce the predation risk of fast-growth in domestic individuals compared to wild conspecifics. This is especially true if the domestic individuals maintain an ability to efficiently forage on natural food items (Solberg *et al.* 2013). On the other hand, even behavioural responses for predator may be size-dependent and lead to spatial segregation by size, as observed in the juvenile coho salmon (*Oncorhynchus kisutch*) (Reinhardt and Healey 1997). In general, hatchery-selection favours fast growth, at least unintentionally, because the larger fish simply produce more and larger eggs at a given age than the slower growing and thus smaller fish at the given age (Heath *et al.* 2003).

In southern Finland, freshwater brown trout is classified endangered (EN) due to human impact on river ecosystems (e.g. hydropower dams, agriculture, forest industry and overfishing) and the wild adfluvial brown trout are protected by law. Most migratory freshwater brown trout stocks exist only because of intensive hatchery breeding, and in most cases, there are no wild migratory fish available to replenish the hatchery broodstocks. However, local wild resident populations of brown trout still exist. These populations display slow growth, early maturation and small adult size (Huusko *et al.* 2017), which questions their suitability for a genetic enhancement of the broodstocks (Kallio-Nyberg *et al.* 2010). Result of interbreeding between migratory hatchery fish and local resident wild fish is an important question also for the conservation of many salmonids, as such interbreeding is likely to occur in natural waters receiving releases of hatchery fish. An earlier study by Kallio-Nyberg *et al.* (2010) showed

that resident \times migratory hybrids could perform similar feeding migrations as purely anadromous brown trout.

Here, we adopted an experimental approach to study if the survival of a migratory hatchery strain of freshwater brown trout could be improved by hybridizing it with other hatchery strains or a wild and local but resident and small-bodied strain of fish (cf. Kallio-Nyberg *et al.* 2010). We used regional hatchery broodstock originating from Oulujoki watershed as the model. The migratory brown trout in the area is critically endangered due to dams made by hydropower industry and overfishing that has continued for decades. Due to these factors and the extensive releases of non-native brown trout in the area, it has not been possible to replenish the hatchery broodstock with wild fish since 1970s.

We aimed to study if vulnerability to post-stocking pike predation in a river would represent a major factor determining the stocking result for the fish in addition to processes related to food availability in lakes (Hyvärinen and Huusko 2005). We crossed brown trout females from the Oulujoki watercourse (OUV hereafter) hatchery strain with males from (1) a local wild but resident strain, (2) two other geographically distinct hatchery strains, and (3) the original strain as a purebred control. We raised the offspring in a common garden set-up and tested the one-year-old juvenile trout for their behavioural and realized vulnerability to pike predation in seminatural riffle-pool system. We also released them in a natural river to test for potential differences in growth and survival. We predicted that crossbreeding with wild fish would increase survival of the offspring via increased intrinsic predator avoidance behaviour, but the benefit might come with decreased growth rate. We predicted that crossbreeding with non-native hatchery fish would not cause any benefits on predator avoidance due to congruent hatchery selection history but might because of reduced inbreeding increase in size. Finally, we tested if the studied behavioural traits were associated with growth during the predation experiment. We expected the pike predation to be negatively size-dependent (Sogard 1997).

Methods

Study fish

Brown trout females ($n = 5$) from the Oulujoki watercourse broodstock (referred to as OUV, 3th–4th generation hatchery fish) were crossed with males ($n = 5$) from the same broodstock and with males ($n = 5$) from three different brown trout stocks, thus resulting in one purebred control purebred F_1 group and three F_1 crossing groups. The sires of the three crossing groups originated from (1) the Vaarainjoki ($64^{\circ}28.15737'N$, $27^{\circ}31.50062'E$) resident population (electrofished and taken to captive environment in 28–30 September 2010 and 15 September–11 October 2011), (2) the Kitkajärvi broodstock (first-generation hatchery fish, KIT hereafter), and (3) the Rautalampi watercourse broodstock (5th or 6th generation hatchery fish, RAU). Geographically, the Vaarainjoki (VAA) is situated the closest (within 5 km) to the locations where the founding individuals for OUV broodstock had originally been collected. Brown trout in the Vaarainjoki reach sexual maturity in the river at small size (< 40 cm), and there is no evidence for any lake migrations in this population. Even though the resident VAA and migratory OUV hatchery populations are geographically close they are genetically moderately differentiated ($F_{ST} = 0.109$ based on 4876 SNP loci; A. Lemopoulos unpubl. data). Other two hatchery strains originate from the other watercourses, from the ancestral populations with connection to the Baltic Sea (RAU) and to the White Sea (KIT).

All hatchery OUV broodstock and wild VAA fish were maintained in National Resources Institute of Finland's Kainuu Fisheries Research Station (www.kfrs.fi) in Paltamo at least a year prior to the breeding experiment. Milt from RAU and KIT broodstocks were brought from another National Resources Institute of Finland's hatchery in Taivalkoski. We performed the artificial fertilizations on 12 October 2011 at KFRS by producing 25 half-sib families per crossing group. The eggs were incubated until hatching in three replicates per family in floating incubation tubes placed in a 3.2 m² fibreglass tanks. After hatching on 21–23 May 2012, the fish (35 per incubation unit) were moved to 0.4-m² tanks and

fed *ad libitum* with commercial dry feeds. Due to logistic reasons, only OUV and VAA families were kept separately and in two replicates, i.e. we had fifty 0.4-m² tanks with 105 full-sib larvae in each, while KIT and RAU families were equally (7 fish from each incubation unit) pooled by female parent and raised in ten 0.4-m² tanks (105 fish per tank) per group. The rearing was terminated in 3–4 September 2012 and a sample of individuals ($n_{OUV} = 450$, $n_{OUV \times VAA} = 450$, $n_{OUV \times RAU} = 105$ and $n_{OUV \times KIT} = 108$, $n_{total} = 1116$) was tagged with 12 mm HDX PIT-tags in anaesthesia (benzocaine, 40 mg l⁻¹). After tagging, the fish were reared in three 3.2-m² tanks with daily maintenance and automated feeding until the experiments or release into the wild. The water used in the fish tanks came from the adjacent Kivesjärvi, and thus the temperature and oxygen levels varied naturally according to the ambient conditions during the study.

Pike predation experiment

As a piscivorous predator we used the northern pike (*Esox lucius*) that poses a vigorous threat on juvenile salmonids (Kekäläinen *et al.* 2008). Wild-caught pike were kept in captivity in the Kainuu Fisheries Research Station three to six years before the experiment. We anaesthetized all brown trout juveniles (benzocaine, 40 mg l⁻¹) and measured their total length (to 1 mm) and body mass (to 0.1 g) two days before the experiment started on 6 June 2013. A total of 12 semi-natural flow-through riffle-pool systems were used in pike predation experiment. Pike ($n = 2$ /pool, mean \pm SD body mass = 1.9 ± 0.5 kg) were restrained to the pool i.e. backwater section of the pond (Fig. 1). Four of the ponds had a PIT tracking device to study trout movements during the experiment (cf. Fig. 1). The intersection between the safe and pike areas was equipped with double antennas capable of detecting passive integrated transponder (PITs) when a fish swam through the antenna loops and the grid in the middle (Fig. 1). The total size of predator-free riffle area was 10.9 m², which leaves approximately 0.20 m² per individual. Due to relatively short experiment span, this territory size was assumed to be enough, since in

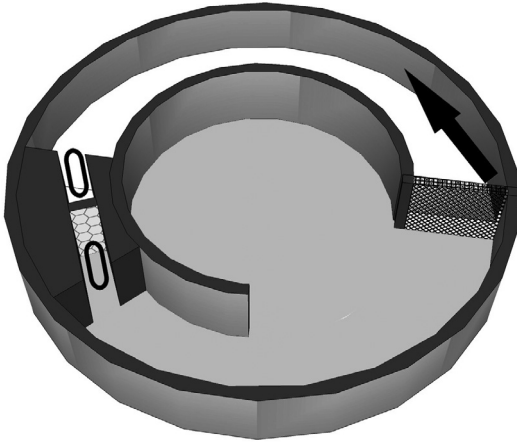


Fig. 1. Experimental seminatural flow-through riffle-pool to mimic natural parr habitat used in the pike predation experiment (Haury *et al.* 2000). White area indicates predator free riffle section with gravel bed structure ($A = 10.9 \text{ m}^2$, width 1.5 m) and grey area indicates the pool section with a presence of two pike per pond. Total area of the pond was 50 m^2 (radius: outer 4.0 m, inner 2.5 m) and the gravity flow where the depth of the riffle section was adjusted to ca. 0.3 m, and that of the pool section to 1.0 m. Honeycomb indicates the grid (45 mm) that prevents predators to swim to the riffle area and black loops present the PIT-antenna system including two antennas (stream end and back-water end). Plywood structure and metal grid (10 mm) on the other end of the riffle prevented the fish movements past the antenna channel. Gravel bed structure enabled trout parr to exploit benthic macroinvertebrate fauna as a natural food source. The black arrow points water faucet and flow direction.

field studies territory sizes of juvenile salmonids have been reported to vary approximately from 0.05 to 0.5 m^2 depending on food availability (reviewed by Grant *et al.* 2017). The double antenna design facilitated determining the direction to which a fish was swimming and the grid in between prevented the pike from reaching the refuge section of the pond. Because crossbreeding with wild fish was our main research interest, we used only OUV and OUV \times VAA fish in these ponds. Hence, we assigned 25 fish from pure OUV group and 25 fish from OUV \times VAA group to each of four pike predation ponds ($n = 50$ fish/pond, 1 from each half-sib family). In addition, ten trout from each crossing group were haphazardly dip-netted from their tanks and transferred to eight ponds ($n = 40$ per pond) without a tracking system.

The brown trout parr from the ponds without PIT-antennas were recovered between 26 and 27 June 2013, and the parr from the ponds with PIT-antennas on 22 July 2013 to ensure sufficient number of behavioural observations. We checked each pike for PIT-tags in their stomach with a handheld PIT-reader. We also collected PIT-tags from the bottom of the tank, and all PIT-tags found in the pike area were assumed to be ingested and evacuated by pike. Every PIT-tag found on the riffle area where the pike had no access were assumed to represent brown trout mortality for another reason. In total, nineteen PIT-tags were not found in ponds without antennas and these disappeared fish (potentially tags were flushed to the sink or fish got eaten by birds or minks *Neovison vison*) were excluded from the analysis. In ponds with antenna system, ten PIT-tags were not found, but we assumed that these fish had been eaten by pike based on their movement data (last detection from the pike side). Four pike died during the experiment and were replaced with new individuals the same day they were found dead. Ponds were visually checked daily. The pike were fed with dead roach once a week to ensure their wellbeing. Brown trout instead, were not fed additionally during the experiment but they were supplied by natural drift and benthic macroinvertebrate fauna naturally occurring in the riffle section of the ponds (Rodewald *et al.* 2011).

Survival in the wild

On 19 June 2013, the 467 remaining PIT-tagged fish from groups OUV \times VAA ($n = 235$) and OUV ($n = 232$), were measured for their total length (mean \pm SD = $121.7 \pm 13.6 \text{ mm}$) and body mass ($20.6 \pm 7.4 \text{ g}$) under anaesthesia (benzocaine, 40 mg l^{-1}). On the next day, the fish were transported in 100-l plastic tanks and released (together with 35 RAU and KIT fish not used in the study) in the Varisjoki, ca. 80 metres long and five to twenty metres wide riffle area (Hotelinkoski, $64^\circ 23.8685' \text{ N}$, $27^\circ 31.6375' \text{ E}$, total surface area estimated as 0.11 ha) considered an excellent parr habitat for brown trout. The fish were electrofished (on 24–25 July 2013, 2–5 August 2013 and 3–4 October 2013) in Hotelinkoski and adjacent rapids (ca. 1 km down-

stream and upstream respectively from the original release site). In electrofishing, wild or other stocked brown trout parr were more abundant than the pit-tagged study fish (> 500 non-study individuals captured in total, 443 brown trout [of age 0+ and older] in comparison with 90 PIT-tagged brown trout.

Data analyses

The PIT tag data recording was blinded by using automatic tracking devices and hence observer bias was avoided. The collected raw PIT data were configured using TIRIS data-logger program (Citius solutions Oy, Kajaani, Finland; see details in Vainikka *et al.* 2012). Antenna-specific ASCII-data were further aggregated to form spatial location data on 1-minute resolution using software PIT-data provided by www.pitdata.net. The time between 6 June at 15:45 and 22 July at 10:30 was analysed in all ponds. There was one technical break in the analysis at 28 June from 10:00 to 12:00. During this time, the fish were assumed to maintain their previous location until a new observation was made. The location data were further analysed using custom codes included in the AV Bio-Statistics 5.2 software.

First, we analysed crossing group dependency of the survival by using χ^2 -test with a binomial distribution family. We modelled the survival from pike predation using a logistic regression [*glmer* function with a logit link function in the package *lme4* (Bates *et al.* 2015)] in RStudio (version 0.99.896, R Core Development Team 2016). First detection time (time from the beginning of the experiment to a movement through the first antenna loop) were used as an indicator for exploratory behaviour. Fish length represented a covariate and the crossing group a factor. Exploration rate and body length were first ln-transformed and then standardized to meet comparability. All estimates are given as mean \pm SD, if not otherwise stated. Pike varied in size (1.9 ± 0.57 kg), as well as the number of predated trout among ponds from 15% to 65% depending on the pike size (mortality increased by pike mass among ponds; log. regr.: $z = 4.691$, $df = 518$, $p < 0.001$), but the size of the prey did not correlate with pike size (lin. regr.: $R^2 =$

0.00008, $F_{1,213} = 0.018$, $p = 0.893$). Hence, the pond id was used as a random factor in all models to control the pike size and other uncontrolled pond effects. For the ponds without movement data, we simplified the model by omitting the first detection time (exploration). For *post hoc* comparisons we used *lsmeans* R package (Lenth 2016). Possible associations between exploration rate, crossing group and length were analysed using a linear mixed effect model.

We tested how the crossing group of fish or size affected fish movement behaviour by fitting a linear mixed effect model by using *lme4* R package (Bates *et al.* 2015). We analysed four different types of behaviours: exploration, activity, risk-taking behaviour and finally predator avoidance. We determined (1) the first detection time by antenna (exploration), (2) number of total movements between the sections (activity) (3) the total time the individual brown trout spent in the pike section (risk-taking behaviour), and (4) the last detection time as a rough proxy for the timing of decease, and to test whether survived utilize both sections successfully throughout the experiment. Activity and risk-taking behaviour were only feasible for the individuals whom survived alive through the experiment. For the analyses, all behavioural variables were standardized and ln-transformed, and the pond was used as a random factor. Measure for length before the experiment and growth rate were also standardized for the analysis to achieve comparability. We calculated growth rate g with the formula $g = \ln(L_2/L_1)/\Delta t$, where Δt is the number of days between stocking and the recapture

The recapture probability of stocked parr in the Varisjoki was studied using logistic regression (*nlme* R package, Pinheiro *et al.* 2016) analysis with standardized length at release as a covariate and crossing group and their interaction term as factors. For fish that were recaptured on July–August ($n = 70$), individual growth rate g until recapture was compared between the populations using one-way ANOVA.

Compliance with ethical standards

All the experiments described in this paper were

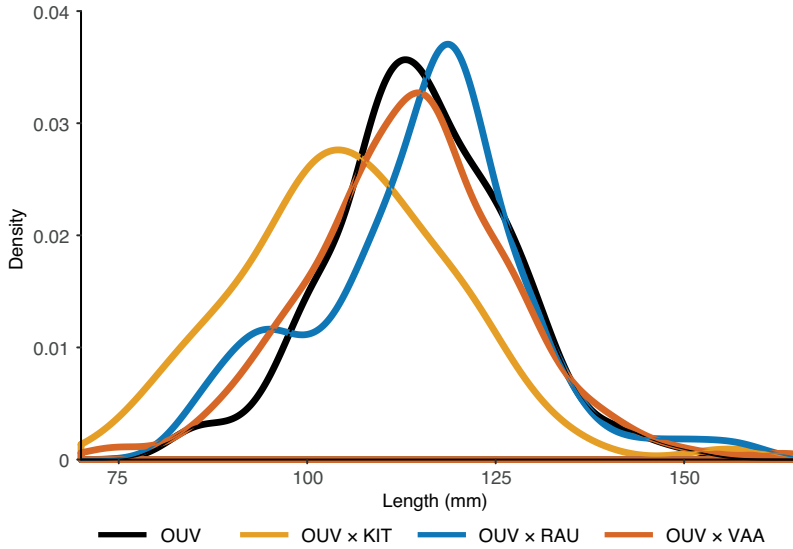


Fig. 2. Length distribution of fish used in pike predation experiment. OUV × KIT crosses were significantly smaller than any other crossing groups.

conducted under an animal experiment license (ESAVI/2458/04.10.03/2011) granted by ELLA (Animal Experiment Board of Finland) and in compliance with *Guidelines for the treatment of animals in behavioural research and teaching* (Anon. 2012). Before fish learn predator avoidance, the presence of pike unlikely causes stress to naïve trout that do not necessarily show intrinsic responses towards predator cues (Brown and Smith 1998). Brown trout juveniles were stocked to the predator-free area and not forced to swim to the predation risk area. Brown trout were able to swim back to refuge area. Predation risk area was large ($A \sim 40 \text{ m}^2$) which also enabled brown trout to hide and escape predation even within it. Predators were fed during the experiment to ensure their wellbeing, which potentially also reduced predators' motivation to feed on live prey.

Results

Survival in predation experiment

Total survival was 59% in the pike exposure ponds without PIT-antennas and 57% in the longer exposure with PIT-antennas. Crossing groups differed in average total body length before the experiment: OUV × KIT fish were smaller than fish from any other crossing group (Fig. 2 and Table 1). In general, survival was crossing group dependent in the part of the experiment with four crossing groups ($\chi^2 = 8.54$, $df = 3$, $p < 0.05$) but only marginally in the experiment with two crossing groups ($\chi^2 = 3.40$, $df = 1$, $p = 0.07$; Fig. 3). Based on the mixed effects logistic regression models, survival was positively size-dependent in OUV × KIT

Table 1. The simultaneous tests for general linear hypotheses estimating the pairwise size differences among each group.

Post hoc comparisons	Estimate	SE	z	p
OUV vs. OUV × KIT	10.962	2.165	5.064	< 0.001
OUV vs. OUV × RAU	1.389	2.179	0.638	0.920
OUV vs. OUV × VAA	4.275	2.165	1.975	0.200
OUV×KIT vs. OUV × RAU	-9.573	2.179	-4.394	< 0.001
OUV×KIT vs. OUV × VAA	-6.687	2.165	-3.086	0.010
OUV×RAU vs. OUV × VAA	2.886	2.179	1.324	0.550

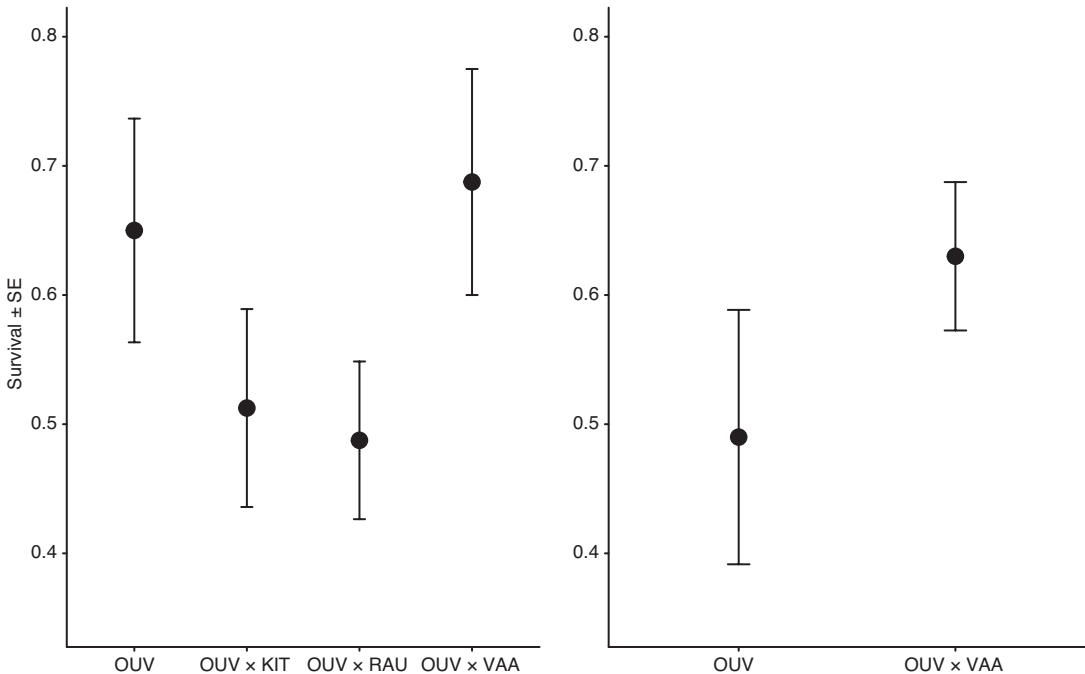


Fig. 3. Mean survival of brown trout parr in the predation experiment. The left panel represents the ponds without behavioural tracking and the right panel the ponds with behavioural tracking.

and OUV × VAA fish (Table 2 and Fig. 4). The size-adjusted survival probability was significantly higher in OUV × VAA compared to OUV × RAU crossing groups (Fig. 3 and Table 3). In ponds where we observed behaviour as well, survival was positively size-dependent only in OUV × VAA crosses. The crossbreeding effect was mere (Table 2).

Behavioural differences and growth of survived fish during predation experiment

Neither crossing group nor the length of fish explained the first detection time (Table 4). However, OUV × VAA fish were less active and spent less time in risky pike area than pure OUV fish (Table 4 and Fig. 5). Smaller fish were found to stay longer in pike area than larger individuals. Fish body length did not explain activity during the experiment, but high activity related to a decrease in growth during the experiment (Table 4). Strain or size of the fish did not explain the last visit to the pike side. Interestingly, the sur-

vival delayed the last time in the pike side indicating that fish used both sides of the experimental pond throughout the experiment (Table 4).

Survival and growth in the wild

Wild crossed OUV × VAA (mean ± SD = 120.8 ± 13.5 mm) offspring were slightly smaller at the time of releasing than purebred OUV offspring (123.2 ± 13.3 mm; one-way ANOVA: $F_{1,465} = 3.918$, $p < 0.05$). In total 18.0% of released fish were detected or recaptured: 70 by electrofishing in July/August 2013 and 14 additional individuals (26 in total) by electrofishing in October 2013. Only 5 individuals were recaptured elsewhere than the original stocking site, from the rapids upstream and all of them were OUV × VAA crosses. Based on the logistic regression analysis, crossing group, length at release or their interaction did not explain recapture probability (crossing group: $z = 1.107$, $df = 464$, $p = 0.268$; length at release (standardized): $z = 0.374$, $df = 465$, $p = 0.708$; interaction: $z = -0.691$, $df = 463$, $p = 0.490$).

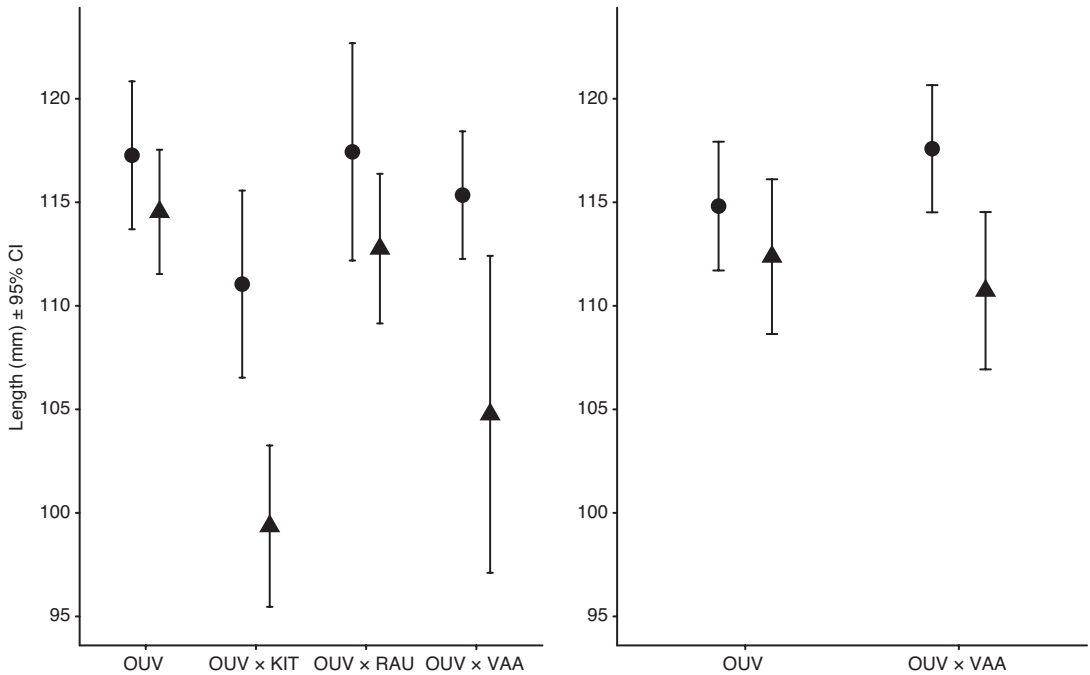


Fig. 4. Initial total length of survived (circles) and predated (triangles) brown trout in ponds without behavioural tracking (left) and in the ponds with behavioural tracking (right).

The fish recaptured in July/August ($n = 70$) by electrofishing did not differ in growth rate with respect to the breed ($F_{1,68} = 2.112, p = 0.15$). The average July/August length of OUV \times VAA

crosses was 144.0 ± 13.3 mm and that of pure-bred OUV fish was 145.1 ± 12.0 mm. The respective growth rates were $0.54 \pm 0.53\%/d$ and $0.39 \pm 0.12\%/d$.

Table 2. Final logistic regression models explaining the survival probability against control group OUV in pools without (residual df = 308) and with behavioural data (residual df = 187). Length of the fish is nested within crossing group to indicate differential size-dependent mortality among crosses.

Fixed effect	Effect size	SE	z	p
Without behaviour data				
Intercept	0.617	0.357	1.730	0.08
OUV \times KIT	-0.103	0.401	-0.258	0.8
OUV \times RAU	-0.697	0.362	-1.925	0.05
OUV \times VAA	0.377	0.379	0.993	0.32
OUV:Length	0.281	0.326	0.859	0.39
OUV \times KIT:Length	0.913	0.317	2.881	0.004
OUV \times RAU:Length	0.454	0.260	1.744	0.08
OUV \times VAA:Length	0.801	0.299	2.675	0.007
With behaviour data				
Intercept	-0.018	0.334	-0.055	0.96
OUV \times VAA	0.588	0.316	1.859	0.06
First detection time	0.489	0.172	2.851	0.004
OUV:Length	0.225	0.229	0.983	0.33
OUV \times VAA:Length	0.644	0.262	2.457	0.01

Discussion

Crossbreeding with non-native hatchery-stock fish induced survival differences in pike exposure, and these differences were explained differentially by size in each group. Survival in the pike predation experiment was positively size-dependent, but the recapture probability in the wild was not predicted by size. Experimental predation selected also against fast explorers — individuals that were detected first, were also most vulnerable to predation and unlikely survived. Even though we did not find strong

evidence that crossbreeding with wild fish would improve survival of hatchery strain fish under predation risk in a short-term exposure, we found that the offspring of wild-crossed hatchery trout (wild crosses hereafter) avoided pool area where predators were present and displayed lower activity than the pure hatchery-bred offspring (purebreds). This indicates either better intrinsic predator avoidance or differential habitat preferences, since pike predation is naturally higher in pool sections than in rapidly running riffles in rivers. Despite the smaller size of the wild crosses and negatively size-dependent natu-

Table 3. Simultaneous tests for general linear hypotheses of pairwise comparison of the size adjusted trout survival in pike predation experiment among four crossing groups

<i>Post hoc</i> comparisons	Estimate	SE	<i>z</i>	<i>p</i>
OUV vs. OUV×KIT	0.101	0.401	0.253	0.90
OUV vs. OUV×RAU	0.696	0.362	1.926	0.22
OUV vs. OUV×VAA	-0.378	0.379	-0.997	0.75
OUV×KIT vs. OUV×RAU	0.595	0.394	1.509	0.43
OUV×KIT vs. OUV×VAA	-0.480	0.414	-1.158	0.65
OUV×RAU vs. OUV×VAA	-1.074	0.376	-2.858	0.02

Table 4. Linear mixed effect models explaining exploration, activity, risk-taking behaviour and predator avoidance, and growth during the pike predation experiment (type III ANOVA with Satterthwaite approximation for degrees of freedom). Individual length before the experiment or at the release were used as a covariate in all models. All continuous variables were standardized to help interpretation.

Fixed effect	Effect size	df	SE	<i>t</i>	<i>p</i>
First detection time					
Intercept	-0.001	4.43	0.164	-0.007	1
OUV vs. OUV×VAA	0.012	191.05	0.139	0.086	0.93
Length [before the experiment]	-0.036	193.43	0.072	-0.494	0.62
Activity					
Intercept	0.276	8.80	0.163	1.698	0.13
OUV vs. OUV×VAA	-0.525	103.76	0.187	-2.808	0.006
Length [before the experiment]	-0.080	104.81	0.098	-0.858	0.39
Risk-taking behaviour					
Intercept	0.203	9.16	0.144	1.410	0.192
OUV vs. OUV×VAA	-0.386	103.97	0.185	-2.084	0.04
Length [before the experiment]	-0.254	104.98	0.097	-2.634	0.01
Last movement					
Intercept	-0.233	17.68	0.135	-1.730	0.1
Survival	0.428	146.84	0.151	2.842	0.005
OUV vs. OUV×VAA	0.017	168.76	0.147	0.114	0.91
Length [before the experiment]	0.125	170.90	0.083	1.516	0.13
Growth rate					
Intercept	-0.018	3.84	0.272	-0.068	0.95
OUV vs. OUV×VAA	0.044	102.42	0.162	0.271	0.787
Activity	-0.257	102.76	0.082	-3.127	0.002

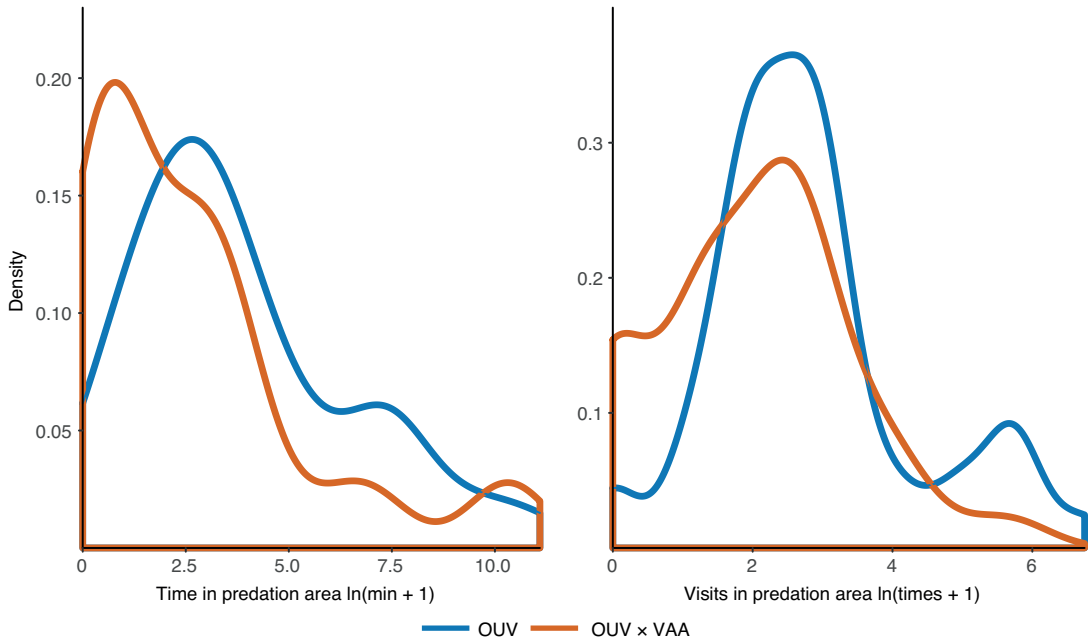


Fig. 5. The observed density distribution of ln-transformed total time (min) spent in the pool (pike) side and total visits.

ral predation, they displayed equal survival probability compared to purebred hatchery fish that probably avoided predation by being larger. Wild crosses also showed higher survival than the fish from the hatchery crossbred OUV \times RAU crosses. Nevertheless, we did not observe any difference between crossed and hatchery purebred individuals in their post-stocking survival or growth. Thereby, crossbreeding with wild but resident strain fish probably does not seem to restrict the growth rate of adfluvial brown trout at the juvenile stage.

The predation data alone indicate that pike-induced mortality was clearly negatively size-dependent, which translates to strong predator-induced natural selection for fast growth in juvenile phase. Negative size-dependency of pike predation was not explained by pike size, since the evidence of previous studies confirms that pike used in experiment were massive compared to the prey size and, on the other hand, the pike would have been expected to prefer larger brown trout with better nutritional value (Nilsson and Brönmark 2000). Experimental studies actually show that positively size-dependent survival can rather be explained by post-attack events, such as

pike's prey handling time rather than pre-attack prey size preferences (Nilsson and Brönmark 1999). However, detailed analysis revealed that pike predation was significantly size-dependent only within two crosses (OUV \times KIT and wild crossed OUV \times VAA). Size-dependency in predation mortality could have arisen via at least two mechanisms. First, large individuals may have had a better ability to escape the pike predation attacks. Second, large individuals may have avoided pike area more efficiently than the small individuals. Indeed, the latter mechanism was supported by the movement data. In contrast to our study where food was probably more abundant in predator-free section, Tymchuk *et al.* (2007) studied crossed domestic \times wild rainbow trout (*Oncorhynchus mykiss*) and found a potential trade-off between growth and survival under the risk of predation.

By adding a behavioural perspective, we found that among the individuals that survived from predation experiment, purebred hatchery brown trout parr were, independently of the size-related behavioural correlations, more active and willing to take risks than wild crosses. Because survival seemed to delay the last detection time

in the pike area, we assume that the survived fish did not completely start to avoid the predation area but used both sides of the ponds throughout the experiment. Interestingly, the exploration as such was barely correlated with size and did not vary between pure hatchery and wild crossed offspring, which indicates that high exploration tendency has a high cost independently of other traits. High exploration is previously linked also with high vulnerability to angling (Härkönen *et al.* 2014), suggesting a potential double cost for the exploration tendency. These behavioural traits are heritable also in brown trout, although at low levels (Kortet *et al.* 2014), which support the idea that they can evolve due to hatchery- or fishing-induced selection. Previous studies on various taxa show that natural selection favours less active individuals that can adjust their habitat use and behaviour under predation risk (Quinn *et al.* 2012, Niemelä *et al.* 2012, Alós *et al.* 2012, David *et al.* 2014).

In line with the predator exposure experiment, no survival differences were detected in the natural river between the purebreds and wild crosses. Unlike a previous study (Jokikokko *et al.* 2006), we did not observe positively size-dependent recapture rates in the wild. Despite being smaller at the time of release, the wild crosses did not differ in growth or size at the recapture in the wild by the end of the summer compared to the purebred hatchery fish. In our experiment, both wild crosses and purebred hatchery juveniles were naïve to natural environment, thus similar growth rates suggest equal-like intrinsic feeding capacity in the wild. Juvenile brown trout with divergent life histories are not known to differ in their size for first summer (Jonsson and Gravem 1985), which leaves us without an answer about the plausible migration behaviour of wild crosses.

Our study was not the first to examine and fail to find clear survival differences between hatchery-reared and wild or wild crossed fish, and their crosses originating from the same genetic background (Dannewitz *et al.* 2003, Dahl *et al.* 2006). However, in contrast with these earlier studies, we used fish from a hatchery broodstock without natural selection effects for 3–4 generations but originating from the study river. In the former studies, strains with limited

time in hatchery breeding were used, which suggested that hatchery rearing itself would be unlikely to cause survival differences, but that changes would accumulate over time through genetic changes. Other dissimilarity to previous studies on predation was that most studies by now had used an artificial predator and/or measured predator avoidance behaviour without the actual chance of becoming predated (Peterson and Järvi 2006, Solberg *et al.* 2015, Peterson *et al.* 2015). Artificial predator encounters lack the natural-like predator-prey interaction which might result a failure in detecting potential effects on survival and manifestation of anti-predatory behaviour. In our common garden experiment, behavioural predator avoidance was different among the crosses for intrinsic reasons but alone could not predict the realized survival. Antipredator responses associate usually with prior experience in juvenile salmonid species (Salvanes 2017), but our results indicate differences either in intrinsic predator avoidance behaviour or in ability to adopt avoidance behaviour rapidly after novel predator experience. Despite the avoidance behaviour did not translate to survival benefit at population level, our study suggests that avoidance and exploration behaviour are highly important traits at individual level and have the potential to affect the survival independently of body size (cf. Hyvärinen and Vehanen 2004). Thus, our study can be used to further design experiments to measure meaningful behavioural variation without the need to expose fish to realized predation that in experimental context can be considered ethically questionable. Due to the mixed breeding design, we cannot omit family-effects, but we can consider such effects randomised, since within the pond, fish were only half-siblings.

We cannot completely exclude the impact of territoriality for our results, even though the hatchery-reared fish typically are far less territorial than wild fish (Deverill *et al.* 1999). Territorial individuals of brown trout tend to be more aggressive and have larger home ranges than subordinate individuals (Näslund and Johnsson 2016). Lahti *et al.* (2001) showed that brown trout populations differ in the level of aggressiveness. Territorial individuals can simply occupy higher quality habitats, such as the pred-

ator free riffle sections in our experiment. Thus, it is not certain if individuals in our experiment accepted the risk by their own choice, or if they were forced to move to the risky area by aggressive encounters by the dominant individuals. Because the territory size correlates with individual size, it might partially explain the observed size-dependent mortality in wild crosses, but also in OUV \times KIT, since Kitkajärvi strain has only a short history of hatchery rearing (Grant and Kramer 1990, Grant *et al.* 2017). Hatchery-reared brown trout are shown to be more aggressive than wild ones, failing at territory acquisition and suffering from lower growth rates in semi-natural environments (Deverill *et al.* 1999), but the intensity of aggression can be highly context-dependent (Ruzzante 1994). Because we observed differences amongst the crosses and purebreds when controlled for individual body sizes, it is very unlikely that the size was the major determinant of space use, but differences in space use aroused from the genetic background. Hatchery fish might suffer from increased mortality due to failures in territory acquisition in natural conditions, but size alone is very unlikely to explain the differences in area preferences among the crosses and purebred offspring in our pike predation experiment. Also, if the large fish had obtained territories in the safe area, we should have been able to detect the size-related correlation of the last visiting time to risky area, which we did not observe.

Contrary to some expectations (Stamps 2007, Réale *et al.* 2010), high moving activity had a negative effect on the growth of brown trout during the predation experiment. Thus, our results are in line with those of Härkönen *et al.* (2014) and support the findings by Metcalfe (1986) according to whom fish with high activity rates acquire less resources for growth as they waste energy in swimming. Adriaenssens and Johnsson (2011) showed that low activity can be associated with fast growth in brown trout in the wild. Recently, it was proposed that growth rate could be linked either to high activity or to the size of the home range (Zavorka, *et al.* 2015). Thus, how growth rate associates with activity is not yet completely clear in brown trout. Biro *et al.* (2004) observed that predation selected against high growth rates in domestic popula-

tions of rainbow trout. In our experiment, we were unfortunately only able to compare activity and growth among individuals that survived the pike exposure in the experiment.

Crossbreeding with non-native strains caused survival effects either directly (OUV \times RAU) or due to small body size (OUV \times KIT) as these fish differed from the purebred fish in our predation experiment. Even though the survival difference between OUV \times RAU and purebred fish was not statistically significant, the relatively high effect size indicates the strong predation pressure on the crosses despite their equal body size. OUV \times KIT crosses were significantly smaller than any other crosses or purebred fish, which very likely yields to high mortality due to strong size-dependent predation. Even though stocking programs aim to support endangered wild populations, they can also unintentionally harm the locally adapted, wild populations through introgression (Levin *et al.* 2001, Hansen 2002). Hatchery-reared fish often display lower survival and fitness than their wild conspecifics (Fleming and Petersson 2001). Some of the fish, even when released directly to lakes or coastal areas, may still spawn in neighbouring rivers and negatively affect the original gene pools (Fleming and Petersson 2001, Borgström *et al.* 2002). Our pairwise result on higher size-independent mortality in OUV \times RAU crosses than in wild crosses fish indicated that difference in behaviour might translate to survival differences. Both OUV and RAU broodstocks have a noticeably long hatchery-rearing history, which is known to favour high growth rates (Heath *et al.* 2003) and dampen the innate anti-predatory responses (Petersson and Järvi 2006). From applied perspective, it is noticeable that the RAU fish are generally used in stocking in the Oulujärvi watershed. Our results show that the RAU fish will likely have a poor offspring fitness in nature even if they interbred with local fish. Thus, crossing different hatchery populations does not improve the stocking result and should rather be avoided in all normal circumstances. Plausible reasons for this could be that all the hatchery populations embody alike phenotypes due to uniform hatchery selection. Further mixing of hatchery broodstocks may strengthen maladaptation to natural conditions (Muhlfeld *et al.* 2009, O'Toole *et al.* 2015).

Conclusions

We showed that crossbreeding of hatchery strain of brown trout with wild and local but resident individuals improved behavioural predator avoidance without causing limited growth during their first post-release summer. Pike predation was negatively size-dependent in two of the crossing groups and acted against high exploration and risk-taking in general. We propose that if predictions about survival are simply derived from predation data, we could have not detected that behavioural differences between crossing groups potentially would lead to mortality differences in the long run. Our results suggest that for sustainable management of the wild populations, an update of migratory hatchery broodstocks with wild but resident fish could be plausible solution to reduce harmful domestication effects caused by hatchery selection, but such practises must be considered case-wise as there a risk for losing local adaptation that are not yet fully understood. Long-term hatchery rearing without continuous transfer of genetic material from the natural environments can lead to cumulative domestication effects that likely decreases the survival and fitness of the stocked fish. The resident fish might offer a feasible genetic source for fitness-improving, but genetic information is yet pending for future studies. Future work should address also the effects of interbreeding on growth and migration of the hybrid offspring.

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