Fishing-induced versus natural selection in different brown trout (Salmo trutta) strains

Vainikka, Anssi

2021-11

Vainikka , A , Hyvarinen , P , Tiainen , J , Lemopoulos , A , Alioravainen , N , Prokkola , J M , Elvidge , C K & Arlinghaus , R 2021 , ' Fishing-induced versus natural selection in different brown trout (Salmo trutta) strains ' , Canadian Journal of Fisheries and Aquatic Sciences , vol. 78 , no. 11 , pp. 1586-1596 . https://doi.org/10.1139/cjfas-2020-0313

http://hdl.handle.net/10138/341886
https://doi.org/10.1139/cjfas-2020-0313

unspecified
acceptedVersion

Fishing-induced versus natural selection in different brown trout (*Salmo trutta*) strains

Anssi Vainikka[1*], Pekka Hyvärinen[2], Joni Tiainen[1,3], Alexandre Lemopoulos[1,4], Nico Alioravainen[1], Jenni M. Prokkola[1,5], Chris K. Elvidge[1, 6] & Robert Arlinghaus[7,8]

[1]Department of Environmental and Biological Sciences, University of Eastern Finland, P.O. Box 111, FI-80101 Joensuu, Finland.

[2]Natural Resources Institute Finland, Manamansalontie 90, FI-88300, Paltamo, Finland.

[3]Natural Resources Institute Finland, Latokartanonkaari 9, FI-00790 Helsinki, Finland.

[4]Current address: Department of Genetics and Evolution. University of Geneva, Geneva, Switzerland. Quai Ernest-Ansermet 30, 1205 Genève.

[5]Current address: Organismal and Evolutionary Biology Research Programme, P.O. Box 65, FI-00014 University of Helsinki, Finland

[6]Current address: Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa ON Canada K1S 5B6

[7]Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany

[8]Division of Integrative Fisheries Management, Albrecht-Daniel-Thaer Institute of Agricultural and Horticultural Sciences, Department for Crop and Animal Sciences, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Invalidenstrasse 42, 10115 Berlin, Germany

[*]Corresponding author: anssi.vainikka@uef.fi

Abstract

Wild, adfluvial brown trout (*Salmo trutta*) are iconic targets in recreational fisheries but also endangered in many native locations. We compared how fishing and natural selection affect the fitness-proxies of brown trout from two pure angling-selected strains and experimental crosses between an adfluvial, hatchery-bred strain and three wild, resident strains. We exposed age 1+ parr to predation risk under controlled conditions where their behaviour was monitored with PIT-telemetry, and stocked age 2+ fish in two natural lakes for experimental fishing. Predation mortality (16% of the fish) was negatively size-dependent, while capture probability, also reflecting survival, in the lakes (38.9% of the fish) was positively length- and condition-dependent. Angling-induced selection against low boldness and slow growth rates relative to gillnet fishing indicated gear-dependent potential for fisheries-induced evolution in behaviours and life-histories. Offspring of wild, resident fish showed slower growth rates than the crossbred strains. Strain effects suggested significant heritable scope for artificial selection on life-history traits and demonstrated that choices of fish supplementation by stocking may override the genetic effects induced by angling.

Key words: fisheries-induced selection, angling, gillnet fishing, predation, personality

Introduction

Recreational fisheries impose significant mortality on freshwater fish populations (Lewin et al. 2006). To compensate for fisheries harvest and incidental mortality or to offset natural recruitment bottlenecks, many populations are supported or entirely maintained by stocking (Hutchings and Fraser 2008; Lorenzen et al. 2012). Both fishing and hatchery-rearing practices can reduce behavioural variation with significant fitness consequences (Hutchings and Fraser 2008; Tsuboi et al. 2016, 2019). For example, high exploration tendency (Härkönen et al. 2014) and activity phenotype (Koeck et al. 2019b) associated with unintended domestication under captive breeding (Mezzera and Largiadér 2001) have been linked to increased vulnerability to angling in salmonids, implying fisheries-induced selection acts on these traits. In general, any individually consistent, repeatable and heritable behavioural (or other) trait may respond to direct or correlated selection (Réale et al. 2007; 2010; Kortet et al. 2014; Ågren et al. 2019). Adaptive behaviours may make individuals less vulnerable to fishing (Uusi-Heikkilä et al. 2008; Arlinghaus et al. 2017; Andersen et al. 2018), but limited experimental research exists on multigenerational behavioural effects of fishing in salmonids (Alioravainen et al. 2020; Prokkola et al. 2021). To alleviate the ecological and genetic risks associated with stocking, a combination of management tools enhancing natural reproduction (Aas et al. 2018) and hatchery techniques to restore behavioural and genetic diversity in stocked fish to improve their ability to form naturally reproducing populations (Hughes et al. 2008) are increasingly adopted.

For the evaluation of evolutionary impacts of fishing, the strength and direction of selection gradients from natural predation and fishing must be determined (Monk et al. 2021). Natural predation is a major survival threat to juvenile salmonids (Hyvärinen and Vehanen 2004). Studies in Northern pike (*Esox lucius*) and Atlantic cod (*Gadus morhua*) have suggested that negatively size-dependent natural selection is a potent counterforce for positively size-selective fishing (Edeline et al. 2007; Olsen and Moland 2011; Monk et al.

2021). While angling can be positively size-selective, state-dependent characteristics along with behavioural and physiological processes influence vulnerability to angling, particularly with artificial lures or flies (Lennox et al. 2017), making the interplay between predation and fishing induced selection more complex in recreational fishing than in size-selective commercial fisheries. Whilst the debate over the intrinsic or learned nature of antipredator behaviour continues, most studies agree that hatchery-rearing and unintended domestication are deleterious for natural survival-enhancing behaviours (Johnsson et al. 1996; Álvarez and Nicieza 2003; Tsuboi et al. 2019). The domestication-induced loss of intrinsic antipredator behaviour may be mitigated by crossbreeding hatchery lines with wild-provenance fish (Alioravainen et al. 2018) as long as the wild fish are genetically compatible with the hatchery fish and produce offspring with equivalent or improved fitness compared to the hatchery fish (Houde et al. 2011; Rollinson et al. 2014).

Brown trout (*Salmo trutta*) is one of the most widespread and economically valuable salmonids and a common target for intensive recreational fisheries throughout its distribution (Elliot 1989; Wills 2006). It forms resident and migratory (both anadromous and potamodromous) populations (Ferguson et al. 2019), with large-growing, migratory (adfluvial) stocks being the most valued targets in freshwater fisheries but also the most threatened (Syrjänen and Valkeajärvi 2010; Syrjänen et al. 2017). Due to the virtual absence of wild adfluvial individuals available for broodstock renewal in many areas (Syrjänen et al. 2017), it has become relevant to assess the potential of wild resident populations to mitigate domestication-effects in hatchery fish (Kallio-Nyberg et al. 2010). The potential for genetic rescue in re-introduced brown trout populations, which typically have lower fitness than wild populations (Wills 2006; Lorenzen et al. 2012), might be improved by crossbreeding captive-bred adfluvial brown trout with wild resident fish (Alioravainen et al. 2018; Kelly and Phillips

2018). Yet, little is known about how such outbreeding would affect the growth rate (Serbezov et al. 2010), survival and fishing vulnerability of the progeny.

Here, our primary aim was to examine whether parental vulnerability to angling or outbreeding influence the vulnerability of brown trout offspring to predation under seminatural conditions, or to experimental fishing in small, natural lakes. To understand the mechanisms, the angling-selected and experimentally crossed, common-garden raised study strains were monitored for survival and growth differences throughout the study. Additionally, we examined whether exploration behaviour quantified during predator exposure or size-related traits would explain capture probability by angling or gillnets in natural lakes. Bold, fast growing fish with highly angling-vulnerable parents were predicted to show the highest vulnerability to both predation and fishing (Biro and Post 2008; Philipp et al. 2009; Klefoth 2017) and that outbreeding of hatchery-strain fish with wild resident brown trout from nearby sources would increase survival under predation (Alioravainen et al. 2018). Crossbred fish were expected to demonstrate capture and growth rates intermediate to pure hatchery and wild strains in natural lakes but superior survival.

Materials and Methods

Overview of the study design

All experiments were conducted at the Kainuu Fisheries Research Station (National Resources Institute Finland) in Paltamo, Finland. Nine experimental strains of brown trout (Fig. 1., Supplementary Table S1) were created via artificial breeding in October 2015. Eggs and larval fish were monitored for survival under standard hatchery rearing conditions. 1+ fish, reared in common garden from September 2016, were exposed to predation by Northern pike under continuous passive integrated telemetry (PIT) during summer 2017 (Alioravainen et al. 2018 for a similar set-up). In July 2018, predation survivors and additional fish from the same crosses were stocked into two small natural lakes, which were experimentally fished in autumn 2018 (age 2+) and autumn 2019 (age 3+) using both angling and gillnets (Fig. 1, Supplementary Table S1). Two gear types were used to determine if angling would select different phenotypes than gillnetting that was considered relatively unselective.

Source strains and breeding design

Adult hatchery-bred trout (OUV) and wild-caught resident brown trout from River Vaarainjoki (VAA, 64° 28′ 50.510″ N/27° 34′ 17.340″ E) were first divided into high vulnerability to angling (HV, captured at least once) and low vulnerability (LV, not captured) groups by experimental fly fishing in 50 m^2 – 75 m^2 outdoor ponds during summer 2015 using two size-assorted pools per origin (Alioravainen et al. 2020, Supplementary Table S1). In addition, wild adult fish from Rivers Tuhkajoki (TUH, 64° 2′ 28.337″ N/28° 7′ 10.099″ E) and Pohjanjoki (POH, 64° 17′ 50.703″ N/28° 3′ 0.416″ E) were used for the production of outbred crosses (Lemopoulos et al. 2019a). The OUV hatchery strain was the product of 4-5 generations of captive breeding from adfluvial (migratory) brown trout originally captured in Rivers Varisjoki (~3 km downstream from VAA) and Kongasjoki (parallel in < 1 km distance with VAA; Lemopoulos et al. 2018, 2019a). By contrast, the wild strains were assumed to be residents and non-migratory (Lemopoulos et al. 2018). Wild fish were captured via electrofishing (VAA: 28–30 September 2010; 15 September–11 October 2011 and 2 October 2012; TUH: 17 September 2013; POH: 16–17 September 2015) and held in separate seminatural gravel-bottomed 50 m^2 riffle-pool ponds prior to breeding.

We used a replicated, fully factorial 3 males × 3 females matrix breeding design to create the F_1-generation of the HV and LV selection lines and the three outcrosses with wild VAA, TUH and POH strains (Supplementary Table S1). Parental fish were randomized *a priori* from the HV and LV groups, but due to logistic constrains and non-ripe status of the randomized fish, parents were occasionally replaced with other haphazardly dip-netted fish from the same group. To minimize the risk of inbreeding, females and males within the OUV group were taken from different year classes (2008 or 2012). Within the VAA strain, males were mostly taken from the small size group (mean ± S.D. body mass 531.9 ± 249.3 g on 25 September 2015; 15 out of 18) and females from the large size group (body mass 1268.5 ± 487.6 g on 25 September 2015; 14 out of 18). Due to limited availability of mature females among the HV fish, two females that had not been captured in experimental angling had to be included as broodstock in the HV line. This resulted in 88.9% genetic contribution of strictly HV fish in the VAA HV line. Nine of the crossbred parent fish were HV fish and 15 were LV fish.

Adfluvial OUV and resident VAA strains differed genetically by F_{ST} 0.109 - 0.112, with greater diversity in the OUV versus VAA strain (Lemopoulos et al. 2019a, b). One VAA male in one replicate matrix of OUV ♀ × VAA ♂ was later genetically identified as an OUV fish despite its capture in River Vaarainjoki (i.e. VAA). This was taken into account in egg mortality calculations by strain but could not be controlled for in the other analyses. TUH and OUV strains differed by F_{ST} 0.064 - 0.074 (Lemopoulos et al. 2019a). The stocking history and migratory status of the River Tuhkajoki (TUH) population could not be confirmed, but the strain was assumed to represent wild resident fish (Lemopoulos et al. 2019a). Due to the lack of mature females in the original pool of wild-caught fish (N = 65), the OUV × POH strain was created by crossing hatchery OUV females with wild-caught POH males (Supplementary Table S1). The original F_{ST}-value between the populations was 0.119 - 0.120 (Lemopoulos et al. 2019a). No known stocking history of the POH or VAA populations suggests that they were original (Lemopoulos et al. 2019a).

Rearing of eggs and larvae with monitoring for survival

Fertilized eggs (100 per full-sib family) were incubated in family-specific mesh-bottomed floating circular tubes (diameter 10 cm) placed in 32 0.4 m^2 flow-through fibreglass tanks (5-6 tubes per tank) with daily observations of egg mortality (total average 25.5%) from 12 October 2015 to 17 May 2016. In addition, all the live eggs were counted on 15 February 2016. Fry were pooled by breeding-matrix on 17 May 2016 and reared in replicated (N = 2) 0.4 m^2 tanks (42 tanks, 225 fish in each, 9-10 fish per tank used for Alioravainen et al. 2020) until PIT-tagging over 18-21 September 2016 (50 haphazardly chosen fish per tank, N = 2105 in total). 12 mm HDX pit-tags (Oregon RFID, Oregon, USA) were inserted into the body cavity through a small scalpel incision under benzocaine (40 mg L^{-1}) anaesthesia. In the pooling of the fry, the aim was to take 25 fry from each family, but due to variability in egg mortality, the effective number of fish per family in each of the two replicates varied from 0 to 75 (Supplementary Table S1). PIT-tagged fish were further reared in four 3.2 m^2 fibreglass tanks under standard feeding regimes with commercial dry feeds (Veronesi Vita 0.5 mm – 1.5 mm, Veronesi, Italy & Hercules 1.7 mm – 2.5 mm, Raisioaqua, Finland) until transfer to two 15 m^2 indoor tanks on 14 July 2017 and finally to the predation experiment (see below) or a 50 m^2 outdoor concrete pond (21 and 28 November 2017).

Behaviour-tracked predator exposure experiment

To quantify individual boldness, behavioural responses to predator presence and vulnerability to actual predation, we conducted two batches of a 16-day experiment in replicated (N = 8) 50 m^2 seminatural riffle-pool ponds (described in Alioravainen et al. 2018). Each pond was stocked with N = 40 fish (N = 320 fish per round, N = 640 total) consisting of N = 72 fish per strain except for the OUV × POH cross (N = 64, Supplementary Table S2 for details). Fish from each strain were equally divided between the eight ponds. The ponds were equipped with plastic grids (45 mm squares) placed in half-tube chutes between the gravel-bottomed stream-like riffle area (10.9 m^2, 1.5 m wide, water depth 0.2-0.5 m) and the deeper circular inner concrete-bottomed pool area with water outlet (water depth ~0.8 m). Randomised half of the ponds were stocked with Northern pike that were released to the deep pool section. The grids were permeable to brown trout but not to pike, ensuring the safety of the trout and ethicality of the experiment. Looped PIT-antennae were installed on both sides of the grid to record (9 times per second) each fish passage and the direction of movement (see Alioravainen et al. 2018 for details). The plain text format PIT detection data were recorded using the TIRIS program (Citius solutions Oy, Kajaani, Finland). The recording computers had to be restarted twice during the first replicate batch and once during the second batch. During the offline time (10-15 min), the fish were assumed to have maintained their previous positions.

Two pike per predator pond (686.3 ± 44.0 mm, 2048 ± 300 g, mean ± SD) were transferred to the ponds on 13 July 2017 at 15:00. The original pike were returned to their rearing ponds and replaced with new pike (639.3 ± 80.2 mm, 1905 ± 686 g, mean ± SD) for the second batch on 7 August 2017. The pike were fed once per week with dead brown trout. The experimental trout were not fed during the experiment but were supplied by natural drift and benthic macroinvertebrate fauna occurring in the riffle section of the ponds (Rodewald et al. 2011). The trout were released to the riffle section of the ponds so that the grids dividing the safe (outer riffle) and risky (deep center) areas were blocked by metal gates on 13 July 2017 between 16:00 and 22:00 (escapement recorded by PIT-data). Behavioural observations started on 17 July 2017 at 10:13:00 for each pond, and the gates were removed within the next 9 minutes with the exact time recorded for each pond. PIT-data were collected continuously until 2 August 2017 at 08:00:00 after which the water level was lowered, remaining fish were dip-netted, measured for size and mass under benzocaine anaesthesia and transferred back to a 50 m^2 rearing pond. New trout were introduced to the ponds on 3 August 2017, and the gates were lifted on 7 August 2017. PIT-data were again collected for 16 days from 7 August 2017 at 10:13:00 to 23 August 2017 at 08:00:00. The barrier to prevent movement of fish between the predator and safe sides failed in one of the control ponds before the start of the trial, and though it was repaired, this pond was assigned a third category of predator treatment to account for the disturbances.

All ponds were thoroughly scanned with portable PIT-readers on 24 August 2017 and any retrieved PIT-tags were recorded as consumed by pike when found within the predator areas. No accidental tag loss was observed during the project. Each pike was also carefully PIT-scanned at removal. All missing fish were assumed to be eaten by pike, but it is possible that some fish were lost to birds or mammalian predators as the shades set on the riffle sections did not prevent terrestrial predators from accessing the ponds. Three fish were not recovered for final length and mass measurements but were later found alive and recorded as having survived. After the experiments, all fish were placed in a 50 m^2 concrete rearing pond together with other trout from the same crosses until stocking (Supplementary Table S2).

The PIT-data were analysed using custom codes in AV Bio-Statistics 5.2 software (by A.V.) for the response variables used in the final statistical analyses: 1) Entering the predator zone (or not) as binary variable, 2) Time to enter the predator zone for the first time (in minutes, maximum time if not entering), 3) Total time (min) spent in the predator section of the pond (defined only for the fish recovered alive), and 4) Number of antenna switches (requiring a minimum of 300 seconds between detections, defined only for the fish recovered alive). All variables were assumed to indicate boldness in the predator ponds and exploration tendency more generally in all ponds.

Stocking experiment

All stocked fish (N = 885 with all data, Supplementary Table S3, Supplementary Fig. S1) originated from the same breeding set-up but had varying history in behavioural tests. In addition to fish reared only for stocking (N = 325) and taken from the original 50 m^2 concrete rearing pond, 560 fish held in another similar rearing pond had previous history in behavioural experiments: N = 21 fish had been used in a behavioural study following group-behaviour in a short-term flume experiment and in a long-term seminatural migration experiment (April 2017 – June 2018, Alioravainen et al. 2021), N = 64 fish had been exposed to measurements of metabolic rate and individual behaviour under olfactory predator cues (June-July 2017, Prokkola et al. 2021) and N = 475 fish (of which 211 had been exposed to predators) were included in the predation exposure experiment described above.

The 2+ fish were dip-netted from the rearing ponds, anaesthetized with benzocaine, measured for total length (to the nearest mm) and weighed (to 0.1 g) on 11 July 2018. The availability of OUV × POH hybrids was limited compared to other strains (27 vs. 33-38 fish per strain in Lake Kylmänlampi, 44 vs. 56-78 fish per strain in Lake Koukkulampi; Supplementary Table S3). The fish were transported ~100 km in two 1.5 m^3 oxygenated tanks on a truck to Kuhmo and released at early morning on 17 July 2018 to Lake Kylmänlampi (63°58.55′ N/30°13.29′ E, 2.66 ha, 243 m above sea level) and Lake Koukkulampi (64°07.54′ N/30°16.00′ 10.099″ E, 5.71 ha, 247 m above sea level) by carrying them in batches of 30-50 fish in 50 l buckets for the last 100 – 500 m. Lake Koukkulampi received 586 trout (length 233 ± 27.2 mm, mass 136 ± 52.2 g, 101 fish ha^{-1}) and Lake Kylmänlampi 310 trout (length 246 ± 28.5 mm, mass 169 ± 78.3 g, 116 fish ha^{-1}). Lake Kylmänlampi naturally supported only ninespine stickleback (*Pungitius pungitius*), and Lake Koukkulampi naturally supported Eurasian perch (*Perca fluviatilis*) as well as stocked whitefish (*Coregonus lavaretus*).

Experimental fishing was conducted in three sessions, 1) August 2018, 2) October 2018 and 3) August 2019 (Supplementary Table S4). The main fishing methods were fly fishing from a float tube and spincasting from shore with artificial lures. In sessions 2 and 3, gillnets (30 m × 1.5-1.8 m, mesh sizes 20 mm, 25 mm, 27 mm, 30 mm, 35 mm, 40 mm and Nordic survey multimesh gillnets) were also used. Bycatch of other fishes occurred only in Lake Koukkulampi and consisted of ~250 Eurasian perch and one whitefish. For fly fishing, gear in AFTM classes 6-7 were used with sinking lines and barbless flies (woolly bugger and nymph patterns) in hook sizes 16-6 (two flies in 0.5-1 m intervals). For spincasting, 6-8' light-action rods with multifilament lines (line nominal diameter 0.10-0.15 mm) and small inline spinners and spoons with barbless hooks were used. All fish were killed immediately after landing with a sharp blow to the head. Each fishing day angling efforts were divided into 1 hr periods after which all captured fish were identified by PIT-tag, measured and weighed. A subset of fish showing gonad development were assessed visually for sexual maturity and sex, but the data did not allow proper analysis (77.6% of the dissected 85 fish were assigned as spawning in the same autumn, 60.4% of mature fish were males, no apparent differences among the strains).

Growth and condition

Instantaneous (specific) growth rate was calculated for each fish in the predation experiment and for each fish captured during the stocking experiment as:

$$IGR_{100} = 100\,\frac{\ln(M_{stocking}) - \ln(M_{capture})}{days\ between}, \qquad (1)$$

where *M* is body mass (g). This common metric (Lugert et al. 2016) was chosen despite its complex unit as it was normally distributed and efficiently controls for different capture dates among the fish (Pearson's correlation between capture date and IGR, $R = 0.057$, $N = 340$, $P = 0.297$). Condition factor (CF) was calculated for the stocked fish as:

$$CF = 100\,000 \frac{M_{stocking}}{L_{stocking}^{3.2752}}, \tag{2}$$

where L is the fish total length (mm) and the exponent 3.2752 was empirically derived from the pooled size (total length and mass) measurements at stocking using non-linear regression. Mean-standardized selection gradients β_μ were calculated as instructed by Matsumura et al. (2012).

Statistical analyses for egg and juvenile survival

To account for potential failure to fertilize all eggs, egg batches with zero survival (N = 6) were excluded from the analysis, and the egg and alevin survival was analysed for two time periods: I: from fertilizations to eyed-egg stage (14 October 2015 to 15 February 2016) and II from eyed-egg stage to the counting of live fry (15 February 2016 to 17 May 2016). Survival proportions were arcsine square root (egg, alevin and fry survival) and logit-transformed (fingerling survival) to meet normality and analysed for strain differences using linear mixed effect models (LME, eggs) and linear models (GLM, larvae). In the LME, male and female parent ID's and their interaction (dropped from the final models due to being non-significant) were included as random factors, and strain, male body mass and female body mass as fixed factors and variables. The GLM was based on the tanks as independent statistical units, and strain was the only fixed factor.

Statistical analyses for the predation experiment

Survival likelihood in predator experiment was determined through logistic regression with backward model selection based on log-likelihood ratio tests. Fish strain, predator presence, original length, batch and strain × original length were first entered as explanatory terms.

Behavioural measures were not included as they were confounded with the other factors. The raw survival frequencies were supplementarily tested using a χ^2 test (Preacher 2001). Latency time to enter the predator section was analysed for all the successfully tested fish (N = 600) using Cox regression in the *coxme* package (Therneau et al. 2003) in R 3.5.2 (The R Foundation for Statistical Computing). The initial model included the random effect of pond (ponds of the second batch treated as new ponds), factors strain, predator presence and predator presence × strain -interaction, and covariates initial fish length and the interaction between length and strain (Alioravainen et al. 2018), but the interaction terms were dropped from the final models (AICs 5844.8, 5834.4 and 5824.9 in the order of simplification). Among the fish that survived the predation experiment, the three response variables (time to enter the predator section, time spent in the predator section and the total count of section switches) were subject to principal component analysis (PCA) to extract the common boldness/exploration-related variation. The extracted PC scores (by regression) were further analysed using LME models with pond × batch as a random factor, predator presence and strain as fixed effects and initial total length as covariate. The predator × strain interaction was omitted as it was non-significant, $P = 0.119$. A model without the strain term was used to derive the model residuals (named boldness scores from here on) used to represent the boldness of fish later stocked for fishing experiments. LME was also used to determine if strain explained specific growth rate during the predation experiment among surviving fish.

Statistical analyses for the stocking experiment

Fully factorial GLMs with rearing pond, stocking lake and strain as fixed factors were used to examine if the stocked fish differed in size or condition. Levene's tests were used to assess homoscedasticity of variances, but violations were accepted as biologically indicative of different variances among groups. Independent samples *t*-tests were used to compare group means between stocking lakes. Cox regression with lake as stratum (and to confirm results, separately by lake) was used to examine which factors contributed to vulnerability to capture defined by time until capture (days) and final status (captured or not) by 1) all gear, and 2) angling gear only among 1) fish included in the predation experiment, 2) all fish and 3) fish captured by angling or by gillnets, and thus confirmed to be alive. The initial model including strain (with deviance contrasts, i.e. factor level specific differences from the mean effect), rearing pond (capturing use in previous experiments), length at stocking, condition factor at stocking and boldness score was simplified with backward likelihood-ratio model selection. IGR_{100} was included in the model for the fish confirmed to be alive. Logistic regression of capture status was used to determine probability of capture by gillnet in data excluding the fish captured and removed from the lakes by angling before gillnetting. Captures in angling were assumed to primarily reflect differences in vulnerability to angling, while captures in gillnetting were assumed to primarily reflect differences in survival due to the small size of the lakes and large number of gillnets used.

Histograms of variables and residuals were visually examined for normality. All analyses were conducted using IBM SPSS statistics 25.0.0.1 (IBM Corporation) unless otherwise stated.

Ethics approval

All animal experimentation was conducted under licenses (ESAVI/3443/04.10.07/2015 and ESAVI/3385/2018) from the Animal Experiment Board (ELLA) of Finland. All animal rearing and experimentation complied with the *Canadian Council on Animal Care guidelines*, and Finnish laws and regulations. Introducing a new species to the used natural lakes lacking migration corridors to other waterbodies was approved by ELY-centre of Lapland (permit no. LAPELY 508 / 5711-2018). All other fishing was forbidden in the study lakes by decision of

ELY-centre of Lapland (LAPELY 507 / 5710-2018), and all fishing rights to the study lakes were rented from Metsähallitus, a state-owned organization responsible for the management of state-owned land and waterbodies in Finland (contract #43245). Fishing against the prevailing regulations was conducted under permission (LAPELY 166 / 5713-2017) of the ELY-centre of Lapland. The experiments did not threaten the endangered wild populations of brown trout in Finland. All collection of wild brown trout for the establishment of the study strains was conducted under licences from local shareholder associations managing the respective waters and ELY-centre of Kainuu (dnro 1013 / 5713-2012).

Results

Egg-stage and first-summer survival

Strains did not differ in egg survival until eyed-egg stage (78.7% ± 27.3%, mean ± S.D., LME, $F_{8,73.89} = 1.509$, $P = 0.169$), but sire mass had a negative effect (LME, estimate -0.00025, $F_{1,60.44} = 8.538$, $P = 0.005$) and maternal mass a positive effect (LME, estimate 0.00013, $F_{1,76.52} = 4.238$, $P = 0.043$) on egg survival. Random sire effect and maternal effect were both statistically significant (sire variance estimate 0.0581, Wald's $Z = 4.143$, $P < 0.001$; maternal effect, variance estimate 0.0358, Wald's $Z = 3.862$, $P < 0.001$). Eggs hatched during the two first weeks of April 2016. The survival from eyed-egg stage to fry stage was not explained by any of the studied factors (97.3% ± 0.075%, mean ± S.D, LME, strain $F_{8,64.61} = 1.102$, $P = 0.374$, sire mass $F_{1,57.09} = 0.324$, $P = 0.572$, maternal mass $F_{1,60.17} = 3.209$, $P = 0.078$), but maternal random effect was statistically significant (variance estimate 0.0101, Wald's $Z = 4.078$, $P < 0.001$). There were no strain-specific differences in the survival of the fingerlings during the first summer prior to pit-tagging (92.6% ± 0.06%, mean ± S.D., GLM, $F_{8,\ 757.348} = 1.375$, $P = 0.243$).

Survival in predator exposure experiment

Two fish (0.63%) died in the control treatment and 51 fish (15.94%) in the predator treatment with no frequency differences among the strains (χ^2 = 4.64, df = 8, P = 0.795, Supplementary Table S2). Pooled across origins, mortality was 16.7% in the hatchery group, 14.8% in the outbred group and 18.1% in the wild group. The strains showed statistically significant but biologically small differences in length at the beginning of the predation exposure experiment (July-August 2017, ANOVA, $F_{8, 578}$ = 4.97, P < 0.001, Supplementary Fig. S1a). Pike presence and original length of the fish were the only statistically significant predictors of survival (strain: Wald's χ^2 = 5.88, df = 8, P = 0.661; batch: χ^2 = 0.176, df = 1, P = 0.675; strain × length: χ^2 = 7.09, df = 8, P = 0.527). Predator presence tripled the risk of mortality (exp(B) = 2.901, χ^2 = 18.78, df = 1; P < 0.001) and large size decreased the risk of mortality 3% per each mm (exp(B) = 0.970, χ^2 = 10.77, df = 1, P = 0.001).

Predator-induced selection and behavioural change

Pooled over the strains, predation-induced mean-standardized selection gradient for length was β_μ = 0.677 (S = 1.33 mm, μ = 143.28 mm, σ_P = 16.78 mm, Matsumura et al. 2012). Predator presence did not affect likelihood to enter the deep pool sections (χ^2 = 1.503, df = 1, P = 0.220; average entrance with predators at 105.9 h (84.4 % of the fish) and without predators at 78.6 h (90.0 % of the fish) from the beginning of the experiment). Larger fish were less likely to enter the predator sections than smaller fish (exp(B) = 0.988, z = -4.23, P < 0.001), and the length effect was independent of strain (interaction, χ^2 = 6.317, df = 8, P = 0.612). The statistically significant strain effect (χ^2 = 23.731, df = 8, P = 0.003) indicated that wild-strain fish had increased tendency to enter the pool section (compared to OUV HV reference, VAA HV: exp(B) = 1.636, VAA LV: exp(B) = 1.987, P < 0.01). This effect was observed both with and without predators because the predator presence × strain interaction was non-significant (χ^2 =

5.234, df = 8, P = 0.732). Brown trout spent 45.2 ± 75.4 h in the deep sections without predators and 55.7 ± 73.5 h with predators.

Principal component analysis yielded only one component (from here on boldness score) explaining 45.9% of variance in time to enter the pike sections (loading -0.572), total time spent in the pike sections (loading 0.683) and total activity (loading 0.763). Predator presence decreased boldness score ($F_{2, 12.95}$ = 5.214, P = 0.022), and the control ponds did not differ from the control pond with the broken gate ($t_{12.696}$ = -0.057, P = 0.955). Fish length was negatively related to boldness ($F_{1, 568.44}$ = 7.037, P = 0.008, R = -0.096, N = 640, P = 0.020) but strain did not have a statistically significant effect ($F_{8, 563.56}$ = 0.364, P = 0.939, Fig. 2a). The origin effect was not significant even when simplified to hatchery, wild and hybrid groups ($F_{2, 572.87}$ = 1.241, P = 0.290).

Growth in predator exposure experiment

The original LME suggested that none of the included explanatory factors or variables were statistically significant in explaining IGR_{100}, so the model was simplified by dropping off terms one by one (1. predator presence × origin, $F_{16, 541.86}$ = 0.556, P = 0.916; 2. predator presence, $F_{2, 12.64}$ = 0.051, P = 0.951; 3. fish length, $F_{1, 567.35}$ = 0.169, P = 0.681). The final model including only strain had marginal statistical significance ($F_{8, 558.95}$ = 1.946, P = 0.051, Fig. 2a). When the origin effect was compared only between the hatchery, wild and crossbred fish, the effect was significant ($F_{2, 565.00}$ = 5.680, P = 0.004) with offspring of wild parents having slower growth rate (0.029 ± 0.084 × 100 ln g d^{-1}, mean + S.E.) than hatchery parents (0.169 ± 0.084 × 100 ln g d^{-1}) or the crossbred fish (0.175 ± 0.079 × 100 ln g d^{-1}).

Capture rates by strain and individual traits

For the length and condition information of the stocked fish, see the statistics and Fig. S1 in Supplementary Materials. In total, 345 trout were captured during the experimental fishing sessions (297 in 2018 and 48 in 2019) resulting in a 38.8% recovery rate (77.9% in Lake Kylmänlampi and 18.2% in Lake Koukkulampi, Fig. 2. For lake-specific results see Supplementary Figs. S2 and S3). Fish captured in Lake Kylmänlampi were, on average, significantly longer (t_{342} = -4.901, P < 0.001) and heavier (t = -6.250, df = 206.58, P < 0.001) than fish captured in Lake Koukkulampi (278.6 mm and 228.3 g vs 261.1 mm and 171.4 g, respectively). For strain-specific capture sizes see Supplementary Table S3. The catch per unit effort (CPUE, number of fish per hour of fishing) decreased rapidly over time and was lower in Lake Koukkulampi than in Lake Kylmänlampi (Supplementary Table S4). Of the captured fish, 119 were caught with artificial lures, 117 by fly fishing and 109 with gillnets (including 12 with Nordic survey gillnets).

Condition factor and length at stocking but not strain or boldness score explained vulnerability to capture among the fish included in the predation exposure experiment (N = 475, of which 163 were captured; Table 1). The model explaining the vulnerability to angling (115 fish out of 475) did not differ qualitatively and produced very similar results (Table 1). When only captured fish were included, boldness score was the only retained variable but was not statistically significant in explaining angling vulnerability (Table 1).

Cox regression indicated that strain or previous use in experiments did not explain vulnerability to capture (340 captured fish) among all fish (882 in total; Supplementary Table S5). Strain was dropped from the model even when simplified to three categories of origin (χ^2 = 4.266, df = 2, P = 0.112). The strain effect was close to significant (P = 0.096) in model explaining vulnerability to angling among all stocked fish (Supplementary Table S5), and strain-specific odd ratios revealed that the OUV HV line had the highest probability for becoming captured by angling (Supplementary Table S3). When the strain effect was simplified to three groups, the hatchery strain (OUV) showed increased vulnerability to angling (1.354 × the probability in crossbred group, 39.3% capture rate) and the wild strain (VAA) decreased vulnerability (0.749 × the probability in crossbred group, 33.8% capture rate; Supplementary Table S5). The crossed groups had the highest recapture rate (40.7%) but, due to the influence of covariates, intermediate risk to become captured. When the model was limited to fish confirmed to be alive (captured), only length at stocking was retained in the model although its effect was not statistically significant (Supplementary Table S5). When the analysis for the fish confirmed to be alive was conducted separately for the lakes, length appeared to be the main determinant of vulnerability to angling in Lake Koukkulampi and condition factor the main determinant in Lake Kylmänlampi (Supplementary Table S5).

Fishing-induced selection

Comparison of boldness score, length, condition and IGR_{100} between the angled and non-angled fish among the fish confirmed to be alive revealed statistically significant angling selection on boldness and IGR_{100} (Table 2). Logistic regression fitted on the non-angled fish to predict vulnerability to gillnet fishing (survival from angling and natural mortality), the model selection procedure retained only condition factor (exp(B) = 18596.49, $\chi^2 = 4.73$, df = 1, P = 0.030) and lake effects (exp(B) = 0.054 for Lake Koukkulampi, $\chi^2 = 132.40$, df = 1, $P < 0.001$). The final model predicted 86.9% of the fish to the correct capture category. Pooled over the strains, mean-standardized selection gradient for length-at-stocking was $\beta_\mu = -1.556$ assuming that all non-captured fish survived, and $\beta_\mu = 2.480$ assuming that all non-captured fish died for natural reasons.

Growth in natural lakes

IGR_{100} among captured fish was negatively influenced by length at stocking (GLM, $F_{1, 327}$ = 56.81, P < 0.001, estimate -0.0068 × 100 ln g day^{-1} mm^{-1}). The strain × length at stocking interaction was non-significant (GLM, $F_{8, 319}$ = 1.86, P = 0.066). The final model indicated that there were differences among strains ($F_{8,327}$ = 4.48, P < 0.001; Fig. 3c), that fish captured by angling had slower growth rates (0.016 ± 0.026 × 100 ln g day^{-1}, mean ± S.E.) than fish captured with gillnets (0.115 ± 0.037 × 100 ln g day^{-1}), that fish used in other experiments had faster growth rates (0.125 ± 0.028 × 100 ln g day^{-1}) than untouched fish (0.005 ± 0.035 × 100 ln g day^{-1}) and that fish in Lake Kylmänlampi grew faster (0.371 ± 0.025 × 100 ln g day^{-1}) than fish in Lake Koukkulampi (-0.241 ± 0.038 × 100 ln g day^{-1}). Growth rate was not correlated with boldness scores (Pearson's r = 0.022, N = 340, P = 0.783) or time until capture (r = 0.057, N = 340, P = 0.297) indicating that differences between fish captured by angling vs gillnets were not explained by the inherently longer times until capture by gillnet (confirmed by including capture date as a covariate in the GLM).

When the comparison of growth rates was simplified to hatchery, hybrid and wild fish, the patterns remained qualitatively similar (simple strain effect, $F_{2, 333}$ = 12.40, P < 0.001; captured via angling, $F_{1,333}$ = 4.31, P = 0.039; lake, $F_{1, 333}$ = 198.16, P < 0.001; background pond, $F_{1, 333}$ = 9.64, P = 0.002). Crossbred fish had the fastest (0.116 ± 0.028 × 100 ln g day^{-1}, mean ± S.E.) growth rates but these were not significantly different from the hatchery fish with average IGR_{100} (0.111 ± 0.044 × 100 ln g day^{-1}). Wild fish had the slowest IGR_{100} (-0.140 ± 0.048 × 100 ln g day^{-1}).

Discussion

Crossbreeding did not improve survival during predation exposure, but crossbred strains showed good growth rates with the hatchery female × wild male crosses demonstrating fastest growth (Fig. 3c). Hatchery origin of brown trout appeared to increase post-release capture rate as both pure hatchery strain fish and crossbred fish showed higher angling capture rates than the pure wild-strain fish in small natural lakes. However, offspring of angling-selected parents did not show any detectable transgenerational responses to fishing. Individual vulnerability to angling was best yet statistically non-significantly explained by boldness score, but compared to fish captured by gillnets, angled fish showed lower boldness scores and slower growth rate suggesting strong fishing-induced selection on these traits. Overall capture rates were explained by length (especially in Lake Koukkulampi with poor recapture rate) and condition factor (especially in Lake Kylmänlampi with excellent recapture rate) at stocking suggesting that post-release survival, potentially related to better starvation-resistance of large fish (Anderson 1988) played a role in explaining capture rates while vulnerability to angling could also have been condition- and state-dependent, and potentially mediated by individual behavioural differences (Lennox et al. 2017).

Body size was the most important predictor of survival in the predation exposure and capture probability in the natural lakes. Strain-specific variation in growth also demonstrated considerable heritable scope for selection on growth-related traits. Pike predation was negatively size-dependent partly due to size-dependent behaviour (Alioravainen et al. 2018), while capture probability in lakes was positively size-dependent and thus supporting the pattern of conflicting natural and fishing-induced selection (Edeline et al. 2007; Olsen and Moland 2011; Monk et al. 2021; but see Edeline et al. 2009; Klefoth 2017). Comparison of the selection pressures suggests that negatively-size-dependent predation mortality is a potent counterforce (β_{μ} = 0.677) for positively size-selective fishing (β_{μ} = -1.017). However, the total selection gradient for length-at-stocking was -1.556 - 2.480 depending on the unknown survival rate of the uncaptured fish. While fish that displayed high tendency to take risks likely suffered from predation in the predator exposure experiment, angling selected against fish that avoided risks in the predator exposure experiment suggesting that behaviour may play a role in mediating selection but not as simply as often predicted.

Potential for assisted genetic rescue

Crossbreeding of hatchery fish with wild fish was expected to improve the survival of the offspring at the potential cost of genetic incompatibility issues (Houde et al. 2011; Neff et al. 2011; Frankham 2015). We did not observe mortality differences among the study strains at egg, alevin, fry or fingerling stages suggesting that any potential issues with genetic compatibility at the first generation were marginal at most (see also Ågren et al. 2019). Interestingly, we detected a negatively size-dependent paternal effect on early egg survival, and a less surprising positively size-dependent maternal effect on early egg survival. Brown trout are known to express some parental effects in offspring (Petersson and Järvi 2007), but male size has not previously been found to explain egg survival (Jacob et al. 2007). Because the body size of the sire did not explain survival of the eyed-eggs and alevins, it is likely that the size-dependent sire effect arose via effect on fertilization success in this study and should thus be interpreted with caution. Maternal effects mediated via egg size are known to diminish quickly in hatchery environments (Einum and Fleming 1999), and the maternal size effect was statistically non-significant already on the survival of alevins and fry. However, our experimental design did not allow formal analysis to separate phenotypic maternal and paternal effects from purely genetic effects on offspring performance.

Unlike Alioravainen et al. (2018) but supporting the results of Petersson and Järvi (2006), we did not observe any survival benefits from crossbreeding during predator exposure.

Surprisingly, the fish did not appear to demonstrate intrinsic predator avoidance as nearly all fish entered the risky pool sections both with and without predators. The offspring of wild fish were the most likely to enter the risky predation section, potentially due to size-dependent within-group dominance behaviours. Although this effect was somewhat bound to the faster pool side entrance of the wild offspring in the control ponds, the data did not support earlier findings of wild or hatchery × wild crosses being less bold than pure hatchery strain fish (Alioravainen et al. 2018; Ågren et al. 2019; Prokkola et al. 2021). Instead, fish reduced their demonstrated boldness, most likely through learning in response to predator presence independent of strain. Due to the large size of the pike, negatively size-dependent mortality cannot be explained by gape-limitation but may at least partly relate to faster entrances to the risky areas by smaller brown trout (Alioravainen et al. 2018).

Post-release survival as estimated by gillnet capture rate in the natural lakes did not differ between crossbred and purebred groups, but vulnerability to angling appeared to be greater in the hatchery strain compared to the wild strain while the crossbred group showed intermediate vulnerability (sensu Mezzera and Largiadér 2001). Domestication has been shown to increase vulnerability to angling in common carp (*Cyprinus carpio*) (Beukema 1969; Klefoth et al. 2012) but decrease it in ayu (*Plecoglossus altivelis*) (Tsuboi et al. 2019). The changes in vulnerability to fishing were likely mediated through strain-specific variation in heritable personality traits (Kortet et al. 2014; Ågren et al. 2019; Alioravainen et al. 2020).

The crossbred strains demonstrated good growth rates (~7-11 cm y^{-1} in length, comparable to most Finnish adfluvial brown trout stocks, Huusko et al. 2017) both in the predation experiment and in the natural lakes, particularly when the female parent was from the hatchery strain and the male was from a wild strain (Fig. 3). The strong effect of maternal strain could be explained by the maternal inheritance of mitochondria and their important role in explaining growth rates in brown trout (Salin et al. 2019). Also earlier experiments have shown that migratory × resident crosses of brown trout display growth rates comparable to those of pure migratory strains (Kallio-Nyberg et al. 2010; Alioravainen et al. 2018; Ågren et al. 2019). Crossbreeding of migratory strains with resident strains might lead to early maturation, but the data collected here did not indicate any major effects as fish from the pure hatchery strain also showed signs of sexual maturation at smaller size than typical for migratory brown trout (Huusko et al. 2017).

Overall, our results are conditionally positive for the use of slow-growing resident strains of brown trout to help the recovery of wild-type behavioural trait value distributions in hatchery broodstocks (McClelland and Naish 2007, Kelly and Phillips 2018). As such these results support earlier studies in anadromous brown trout (Kallio-Nyberg et al. 2010). However, as our study was limited to F1-generation hybrids, there may be potential outbreeding depression effects that would only manifest in subsequent generations (McClelland and Naish 2007; Neff et al. 2011). In addition, the impact of crossbreeding on maturation schedules of brown trout should be systematically evaluated under natural conditions before adopting crossbreeding in conservational hatchery programs. Nevertheless, stocking should not be continued beyond the first introduction of crossbred, genetically heterogenous individuals to allow the introduced fish to adapt to their new environment (Boulding and Hay 2001; Aprahamian et al. 2003; Aas et al. 2018).

Fishing-induced selection versus natural selection

The groups selected for high or low vulnerability to angling within the hatchery and wild strains (Alioravainen et al. 2020) did not differ in any examined trait thus demonstrating a lack of a measurable evolutionary response to fly fishing. As predicted (Philipp et al. 2009), the hatchery origin high vulnerability line (OUV HV) showed the highest angling capture rate in the natural lakes but the statistical difference to the other strains was small, and the wild strain high vulnerability line (VAA HV) had the lowest vulnerability to angling (Supplementary Table S3). Strong environmental effects over two summers of hatchery rearing and behavioural conformity (Webster and Ward 2010) within groups may have partially diminished any inherited differences between the HV and LV lines (see also Prokkola et al. 2021). Thus, our results do not provide strong support for the absence of any response to fly fishing or falsify behavioural results obtained in first-summer (described in Alioravainen et al. 2020) or second-summer juveniles (Prokkola et al. 2021).

Even though we did not find a transgenerational response to fly-fishing in the F1 generation, fish captured in the natural lakes were generally larger than the non-captured fish. Because we could not confirm that the non-captured fish were alive, this observation does not directly imply positively size-selective fishing mortality. When the effect of size and condition on the survival of the fish was controlled by focusing the vulnerability analysis only on the captured fish (confirmed to be alive), vulnerability to angling was (marginally) explained only by boldness score (in survivors of the predation experiment, $P = 0.099$) and length (all fish, $P = 0.150$). Comparison of trait means in angled and gillnetted fish (Table 2) further revealed that angling-imposed selection against slow growth and low boldness relative to gillnetted fish (c.f. Klefoth et al. 2017). These differences could not be explained by the intrinsically later captures via gillnets.

Slow growth rate could be an indication of high level of hunger, and thus rather indicate a state-dependent vulnerability to angling rather than strong selection on life-history traits. Largemouth bass (*Micropterus salmoides*) with high vulnerability to angling are known to have higher metabolic rates (but see Prokkola et al. 2021 for brown trout) and food consumption than bass with low vulnerability to angling (Cooke et al. 2007; Redpath et al. 2010). Thus, in resource-limited natural lakes fish with high vulnerability to be captured by angling should show increased energy demands and thus greater feeding motivation, but lower realized growth rates due to the lack of suitable food (Lennox et al. 2017). Another potential explanation for our results lies in gillnet selection against active behaviour (Alós et al. 2012), as gillnet fishing is highly selective for bold behaviour and fast growth (Biro and Post 2008). However, these explanations are not necessarily mutually exclusive, as angling could have targeted the fish that had the highest intrinsic growth capacity and thus the highest foraging motivation while the gillnet-captured fish were more successful at foraging and had lower motivation to strike the flies and lures.

We defined boldness score as tendency to spend time in the predator sections of the study ponds but whether these scores actually reflected boldness, exploration or tendency to avoid competition in the riffle section is not clear (Alioravainen et al. 2018). Thus, angling targeted low-activity individuals that preferably occupied the predator-free riffle areas in the predation experiment. A feasible alternative explanation is that angling selected against qualities like dominance that made fish successful in obtaining a feeding territory in the riffle sections (Alioravainen et al. 2018). No matter what the actual behavioural mechanism is, the link between behaviours under predation risk and vulnerability to angling adds to the evidence that fishing can induce selection on ecologically relevant behavioural traits (Olsen et al. 2012; Klefoth et al. 2017; Arlinghaus et al. 2017).

Resolving how behavioural and size-dependent traits in general affect vulnerability to fishing in varying environments remains a challenge (Uusi-Heikkilä et al. 2008; Lennox et al. 2017). Obviously, the net result of conflicting size-selection from natural and human-induced sources, as acting on released fish, is affected both the post-release survival rate and the intensity of harvesting (Edeline et al. 2007; Olsen & Moland 2011). Changes in growth may not be likely due to angling-selection, while natural selection might not be producing a similar counterforce for angling-induced behavioural changes as for size-selection induced by positively size-selective fishing gear (Monk et al. 2021).

The relationships between growth rate, personality, body size, survival and physiology are generally environment-dependent rendering the interpretation of observational results challenging. Gillnet capture was assumed to reflect survival more than vulnerability to this type of fishing as gillnet fishing for brown trout in small lakes is extremely efficient (Borgstrøm 1992). The findings of large size and high condition factor at stocking being the major determinants of capture suggest that the stocking lakes were challenging environments for the fish (Carlson et al. 2008). In the shallow, clearwater Lake Koukkulampi, length at stocking was the main predictor of angling vulnerability. In the deeper and more resource-rich Lake Kylmänlampi, fish with high condition factor at stocking were most vulnerable to angling. Because the study lakes did not support natural piscivorous fishes, size- and condition-dependent survival must have arisen from other reasons such as starvation resistance and/or very high water temperatures that occurred in summer 2018 right after stocking. Catch rates by angling decreased rapidly with increases in cumulative fishing effort (similar to Koeck et al. 2019a), while overall, we recorded high capture rates in the smaller Lake Kylmänlampi compared to significantly lower capture rates in the larger Lake Koukkulampi. Despite the better capture rates and acutely better growth rates in Lake Kylmänlampi, the Lake Koukkulampi fish showed better growth in length from the stocking year to the next year. Any direct gear selectivity effects are unlikely to explain the results on growth because identical angling (lures and flies) gear and gillnets with multiple mesh sizes were used in both lakes and even the smallest trout stocked were catchable with the gears used.

Conclusions

This study compared the effects of angling-induced selection to strain-specific variation in brown trout. Overall, our results show that the strain differences (e.g., domesticated vs. wild fish) are much stronger than those induced by angling over a single generation. Thus, hatchery impacts on brown trout stocks are expected to override fishing-induced effects (Hutchings and Fraser 2008) while gillnet fishing may induce stronger undesired selection on production-related traits than angling (Handford et al. 1977). Fishing-induced selection may be at least partly contradictory to hatchery-induced selection as the pure hatchery group was the most vulnerable to angling, and hatchery-reared brown trout typically show increased boldness over wild brown trout (Ågren et al. 2019; Alioravainen et al. 2020). Fishing may select against hatchery fish and wild × hatchery hybrids (Mezzera and Largiadér 2001), further reducing risk of introgressive hybridization in wild brown trout populations receiving hatchery-reared fish (Wills 2006; Koeck et al. 2019b). The offspring of wild resident fish clearly experienced slower growth both in the predation experiment and in the natural lakes, while crossbred groups performed relatively well. Our results suggest that migratory hatchery female × resident wild male crosses could be used in stockings intended to create new, naturally reproducing populations or be further selectively bred for the restoration of pre-domestication fitness in hatchery broodstocks.

Conflict of Interest

The authors declare no conflicts of interest.

Acknowledgements

We thank Paavo Niemi, Petro Penttinen, Pyry Pihlasvaara, Robin Tahvanainen, Juha Väisänen and Lauri Peippo for their help in experimental fishing in Kuhmo. Kanerva Korhonen, Nicolas Tanrattana and Michelle Kozlova assisted with transporting the fish to the experimental lakes. Pekka K. Korhonen, Tapio Laaksonen, Markku Hyvönen, Ari Leinonen, Erja Konttinen and Aarne Toivonen were invaluable in maintaining the two generations of fish throughout the study. Financial support was provided via grants from the Academy of Finland (No. 286261) and the Finnish Ministry of Agriculture and Forestry to A.V., and from the European Maritime and Fisheries Fund (decision #43521) to P.H.

References

Aas, Ø., Cucherousset, J., Fleming, I.A., Wolter, C., Höjesjö, J., Buoro, M., Santoul, F., Johnsson, J.I., Hindar, K., and Arlinghaus, R. 2018. Salmonid stocking in five North Atlantic jurisdictions: Identifying drivers and barriers to policy change. Aquat. Conserv. Mar. Freshw. Ecosyst. **28**: 1451-1464. doi: 10.1002/aqc.2984.

Ågren, A., Vainikka, A., Janhunen, M., Hyvärinen, P., Piironen, J., and Kortet, R. 2019. Experimental crossbreeding reveals strain-specific variation in mortality, growth and personality in the brown trout (*Salmo trutta*). Sci. Rep. **9**: 2771. doi:10.1038/s41598-018-35794-6.

Alioravainen, N., Hyvärinen, P., Kortet, R., Härkönen, L., and Vainikka, A. 2018. Survival of crossbred brown trout under experimental pike predation and stocking in the wild. Boreal Environ. Res. **23**: 267–281.

Alioravainen, N., Hyvärinen, P., and Vainikka, A. 2020. Behavioural effects in juvenile brown trout in response to parental angling selection. Can. J. Fish. Aquat. Sci. **77**: 365-374. doi: 10.1139/cjfas-2018-0424.

Alioravainen, N., Prokkola, J.M., Lemopoulos, A., Härkönen, L., Hyvärinen, P. and Vainikka, A. 2021. Postrelease exploration and diel activity of hatchery, wild, and hybrid strain brown trout in seminatural streams. Can. J. Fish. Aquat. Sci. **77**: 1772-1779. doi: 10.1139/cjfas-2019-0436.

Alós, J., Palmer, M., and Arlinghaus, R. 2012. Consistent selection towards low activity phenotypes when catchability depends on encounters among human predators and fish. PLoS ONE, **7**: e48030. doi:10.1371/journal.pone. 0048030.

Álvarez, D., and Nicieza, A.G. 2003. Predator avoidance behaviour in wild and hatchery-reared brown trout: the role of experience and domestication. J. Fish Biol. **63**: 1565–1577. doi:10.1111/j.1095-8649.2003.00267.x.

Andersen, K.H., Marty, L., and Arlinghaus, R. 2018. Evolution of boldness and life history in response to selective harvesting. Can. J. Fish. Aquat. Sci. **75(2)**: 271–281. doi:10.1139/cjfas-2016-0350.

Anderson, J.T. 1988. A Review of Size Dependent Survival During Pre-Recruit Stages of Fishes in Relation to Recruitment. J. Northw. Atl. Fish. Sci. 8: 55-66.

Aprahamian, M.W., Martin Smith, K., McGinnity, P., McKelvey, S., and Taylor, J. 2003. Restocking of salmonids—opportunities and limitations. Fish. Res. **62**: 211–227. doi:10.1016/S0165-7836(02)00163-7.

Arlinghaus, R., Laskowski, K.L., Alós, J., Klefoth, T., Monk, C.T., Nakayama, S. and Schröder, A. 2017. Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. Fish Fish. **18**(2): 360-373. doi: 10.1111/faf.12176.

Beukema, J.J. 1969. Angling experiments with carp (*Cyprinus carpio* L.) I. Differences between wild, domesticated and hybrid strains. Neth. J. Zool. **19**: 596-609.

Biro, P.A., and Post, J.P. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proc. Nat. Am. Sci. **105**(8): 2919-2922. doi: 10.1073/pnas.0708159105.

Borgstrøm, R. 1992. Effect of Population Density on Gillnet Catchability in Four Allopatric Populations of Brown Trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. **49**(8): 1539-1545. doi: 10.1139/f92-170.

Boulding, E.G.. and Hay, T. 2001. Genetic and demographic parameters determining population persistence after a discrete change in the environment. Heredity, **86**(3): 313-324. doi: 10.1046/j.1365-2540.2001.00829.x.

Carlson, S.M., Olsen, E.M., and Vøllestad, L.A. 2008. Seasonal mortality and the effect of body size: a review and an empirical test using individual data on brown trout. Func. Ecol. **22**: 663-673. doi: 10.1111/j.1365-2435.2008.01416.x.

Cooke, S.J., Suski, C.D., Ostrand, K.G., Wahl, D.H., and Philipp, D.P. 2007. Physiological and Behavioral Consequences of Long-Term Artificial Selection for Vulnerability to Recreational Angling in a Teleost Fish. Phys. Biochem. Zool. **80(5)**: 480-490. doi: 10.1086/520618.

Edeline, E. Carlson, S.M., Stige, L.C., Windfield, I.J., Fletcher, J.M., James, J.B., Haugen, T.O., Vøllestad, L.A., and Stenseth, N.C. 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. Proc. Nat. Am. Sci. **104**: 15799-15804. doi: 10.1073/pnas.0705908104.

Einum, S., and Fleming, I.A. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. Proc. R. Soc. Lond. B. **266**: 2095-2100. doi: 10.1098/rspb.1999.0893.

Elliot, J.M. 1989. Wild brown trout *Salmo trutta*: an important national and international resource. Freshw. Biol. **21**(1): 1-5. doi: 10.1111/j.1365-2427.1989.tb01343.x.

Ferguson, A., Reed, T.E., Cross, T.F., McGinnity, P., and Prodöhl, P.A. 2019. Anadromy, potamodromy and residency in brown trout *Salmo trutta*: the role of genes and the environment. J. Fish. Biol. **95**: 692-718. doi: 10.1111/jfb.14005.

Frankham, R. 2015. Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. Mol. Ecol. **24**(11): 2610-2618. doi: 10.1111/mec.13139.

Handford, P., Bell, G., and Reimchen, T. 1977. A Gillnet Fishery Considered as an Experiment in Artificial Selection. Can. J. Fish. Aquat. Sci. **34**(7): 954-961. doi: 10.1139/f77-148.

Härkönen, L., Hyvärinen, P., Paappanen, J., and Vainikka, A. 2014. Explorative behavior increases vulnerability to angling in hatchery-reared brown trout *Salmo trutta*. Can. J. Fish. Aquat. Sci. **71**: 1900-1909. doi: 10.1139/cjfas-2014-0221.

Houde, A.L.S., Fraser, D.J., O´Reilly, P., and Hutchings, J.A. 2011. Relative risks of inbreeding and outbreeding depression in the wild in endangered salmon. Evol. Appl. **4**(5): 634-647. doi: 10.1111/j.1752-4571.2011.00186.x.

Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N., and Wellend, M. 2008. Ecological consequences of genetic diversity. Ecol. Lett. **11**(6): 609-623. doi: 10.1111/j.1461-0248.2008.01179.x.

Hutchings, J.A., and Fraser, D.J. 2008. The nature of fishing- and farming-induced evolution. Mol. Ecol. 17: 294-313. doi: 10.1111/j.1365-294X.2007.03485.x.

Huusko, A., Vainikka, A., Syrjänen, J., Orell, P., Louhi, P., and Vehanen, T. 2017. Life-History of the Adfluvial Brown Trout (*Salmo trutta* L.) in Eastern Fennoscandia. In Brown Trout (eds J. Lobón-Cerviá and N. Sanz). doi:10.1002/9781119268352.ch12.

Hyvärinen, P. and Vehanen, T. 2004. Effect of brown trout body size on post-stocking survival and pike predation. Ecol. Freshw. Fish. **13**: 77-84.

Jacob, A., Nusslé, S., Britschgi, A., Evanno, G., Müller, R., and Wedekind, C. 2007. Male dominance linked to size and age, but not to 'good genes' in brown trout (*Salmo trutta*). BMC Evol. Biol. 7: 207. doi: 10.1186/1471-2148-7-207.

Johnsson, J.I., Petersson, E., Jönsson, E., Björnsson, B.T., and Järvi, T. 1996. Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. Can. J. Fish. Aquat. Sci. **53**: 1546-1554.

Kallio-Nyberg, I., Jutila, E., Koljonen, M-L., Koskiniemi, J., and Saloniemi, I. 2010. Can the lost migratory *Salmo trutta* stocks be compensated with resident trout stocks in coastal rivers? Fish. Res. **102**(1-2): 69-79. doi: 10.1016/j.fishres.2009.10.011.

Kelly, E., and Phillips, B.L. 2018. Targeted gene flow and rapid adaptation in an endangered marsupial. Cons. Biol. **33**(1): 112-121. doi: 10.1111/cobi.13149.

Klefoth, T., Skov, C., Krause, J. & Arlinghaus, R. 2012. The role of ecological context and predation risk-stimuli in revealing the true picture about the genetic basis of boldness evolution in fish. Behav. Ecol. Sociobiol. **66**: 547-559. doi: 10.1007/s00265-011-1303-2

Klefoth, T. 2017. The phenotypic correlates of individual vulnerability to angling. PhD thesis, Humboldt-Universität zu Berlin, 233 pp.

Klefoth, T., Skov, C., Kuparinen, A. & Arlinghaus, R. 2017. Toward a mechanistic understanding of vulnerability to hook-and-line fishing: Boldness as the basic target of angling-induced selection. Evol. Appl. **10**(10): 994-1006. doi: 10.1111/eva.12504

Koeck, B., Wallerius, M.L., Arlinghaus, R., and Johnsson, J.I. 2019a. Behavioural adjustment of fish to temporal variation in fishing pressure affects catchability: an experiment with angled trout. Can. J. Fish. Aquat. Sci. **77**(1): 188-193. doi: 10.1139/cjfas-2019-0064.

Koeck, B., Závorka, L., Aldvén, D., Näslund, J., Arlinghaus, R., Thörnqvist, P-O., Winberg, S., Björnsson, T., and Johnsson, J.I. 2019b. Angling selects against active and stress-resilient phenotypes in rainbow trout. Can. J. Fish. Aquat. Sci. **76**(2): 320-333. doi: 10.1139/cjfas-2018-0085.

Kortet, R., Vainikka, A., Janhunen, M., Piironen, J., and Hyvärinen, P. 2014. Behavioral variation shows heritability in juvenile brown trout *Salmo trutta*. Behav. Ecol. Sociobiol. **68**: 927-934. doi: 10.1007/s00265-014-1705-z.

Lemopoulos, A., Uusi-Heikkilä, S., Huusko, A., Vasemägi, A., and Vainikka, A. 2018. Comparison of migratory and resident populations of brown trout reveals candidate genes for migration tendency. Genom. Biol. Evol. **10**: 1493-1503. doi: 10.1093/gbe/evy102.

Lemopoulos, A., Prokkola, J.M., Uusi-Heikkilä, S., Vasemägi, A., Huusko, A., Hyvärinen, P., Koljonen, M-L., Koskiniemi, J., and Vainikka, A. 2019a. Comparing RADseq and microsatellites for estimating genetic diversity and relatedness - implications for brown trout conservation. Ecol. Evol. **9**(4): 2106-2120. doi: 10.1002/ece3.4905.

Lemopoulos, A., Uusi-Heikkilä, S., Hyvärinen, P., Alioravainen, N., Prokkola, J.M., Elvidge, C.K., Vasemägi, A., and Vainikka, A. 2019b. Association Mapping Based on a Common-Garden Migration Experiment Reveals Candidate Genes for Migration Tendency in Brown Trout. G3 (Bethesda) 9: 2887-2896. doi: 10.1534/g3.119.400369.

Lennox, R.J., Alós, J., Arlinghaus, R., Horodysky, A., Klefoth, T., Monk, C.T., and Cooke, S.J. 2017. What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. Fish & Fish. **18**: 986-1010. doi: 10.1111/faf.12219.

Lewin, W-C., Arlinghaus, R., and Mehner, T. 2006. Documented and Potential Biological Impacts of Recreational Fishing: Insights for Management and Conservation. Rev. Fish. Sci. **14**(4): 305-367. doi: 10.1080/10641260600886455.

Lorenzen, K., Beveridge, M.C.M., and Mangel, M. 2012. Cultured fish: integrative biology and management of domestication and interactions with wild fish. Biol. Rev. **87**(3): 639-660. doi: 10.1111/j.1469-185X.2011.00215.x.

Lugert, V., Thaller, G., Tetens, J., Schulz, C., and Krieter, J. 2016. A review on fish growth calculation: multiple functions in fish production and their specific application. Rev. Aquac. **8**: 30-42. doi: 10.1111/raq.12071.

Matsumura, S., Arlinghaus, R., and Dieckmann, U. 2012. Standardizing Selection Strengths to Study Selection in the Wild: A Critical Comparison and Suggestions for the Future. BioScience **62**: 1039-1054. doi: 10.1525/bio.2012.62.12.6.

McClelland, E.K., and Naish, K.A. 2007. What is the fitness outcome of crossing unrelated fish populations? A meta-analysis and an evaluation of future research directions. Cons. Gen. **8**: 397-416.

Mezzera, M., and Largiadér, C.R. 2001. Evidence for selective angling of introduced trout and their hybrids in a stocked brown trout population. J. Fish Biol. **59**: 287-301. doi: 10.1006/jfbi.2001.163.

Monk, C.T., Bekkevold, D., Klefoth, T., Pagel, T. Palmer, T. & Arlinghaus, R. 2021. The battle between harvest and natural selection creates small and shy fish. Proc. Nat. Ac. Sci. **118**: e2009451118. doi: 10.1073/pnas.2009451118.

Neff, B.D., Garner, S.R., and Pitcher, T.E. 2011. Conservation and enhancement of wild fish populations: preserving genetic quality versus genetic diversity. Can. J. Fish. Aquat. Sci. **68**(6): 1139-1154. doi: 10.1139/f2011-029.

Olsen, E.M., and Moland, E. 2011. Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. Evol. Ecol. **25**: 695-710. doi: 10.1007/s10682-010-9427-9.

Olsen, E.M., Heupel, M.R., Simpfendorfer, C.A., and Moland, E. 2012. Harvest selection on Atlantic cod behavioral traits: implications for spatial management. Ecol Evol. **2(7)**: 1549-1562. doi: 10.1002/ece3.244.

Petersson, E., and Järvi, T. 2006. Anti-predator response in wild and sea-ranched brown trout and their crosses. Aquaculture **253**: 218-228. doi: 10.1016/j.aquaculture.2005.08.012.

Petersson, E., and Järvi, T. 2007. Characteristics of brown trout males influence growth and survival of their offspring. J. Fish Biol. **71**: 493-509. doi: 10.1111/j.1095-8649.2007.01501.x.

Philipp, D.P., Cooke, S.J., Claussen, J.E., Koppelman, J.B., Suski, C.D., and Burkett, D.P. 2009. Selection for Vulnerability to Angling in Largemouth Bass. Trans. Am. Fish. Soc. **183**(1): 189-199. doi: 10.1577/T06-243.1.

Preacher, K. J. 2001. Calculation for the chi-square test: An interactive calculation tool for chi-square tests of goodness of fit and independence [Computer software]. Available from http://quantpsy.org.

Prokkola, J.M., Alioravainen, N., Mehtätalo, L., Hyvärinen, P., Lemopoulos, A., Metso, S. and Vainikka, A. 2021. Does parental angling selection affect the behavior or metabolism of brown trout parr? Ecol. Evol. in press. doi: 10.1002/ece3.7220.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T., and Dingemanse, N.J. 2007. Integrating animal temperament within ecology and evolution. Biol. Rev. **82**(2): 291-318. doi: 10.1111/j.1469-185X.2007.00010.x

Redpath, T.D., Cooke, S.J., Suski, C.D., Arlinghaus, R., Couture, P., Wahl, D.H. and Philipp, D.P. 2010. The metabolic and biochemical basis of vulnerability to recreational angling after three generations of angling-induced selection in a teleost fish. Can. J. Fish. Aquat. Sci. **67**: 1983-1992. doi: 10.1139/F10-120.

Rodewald, P., Hyvärinen, P., and Hirvonen, H. 2011. Wild origin and enriched environment promote foraging rate and learning to forage on natural prey of captive reared Atlantic salmon parr. Ecol. Freshw. Fish. 20(4): 569-579. doi: 10.1111/j.1600-0633.2011.00505.x.

Rollinson, N., Keith, D.M., Houde, A.L., Debes, P.V., McBride, M.C., and Hutchings, J.A. 2014. Risk assessment of inbreeding and outbreeding depression in a captive-breeding program. Conserv. Biol. **28**(2): 529-540. doi: 10.1111/cobi.12188.

Salin, K., Villasevil, E.M., Anderson, G.J., Lamarre, S.G., Melanson, C.A., McCarthy, I., Selman, C., and Metcalfe, N.B. 2019. Differences in mitochondrial efficiency explain individual variation in growth performance. Proc. R. Soc. Lond. B. 286: 20191466. doi: 10.1098/rspb.2019.1466.

Serbezov, D., Bernatchez, L., Olsen, E.M., and Vøllestad, L.A. 2010. Quantitative genetic parameters for wild stream-living brown trout: heritability and parental effects. J. Evol. Biol. **23**: 1631-1641. doi: 10.1111/j.1420-9101.2010.02028.

Syrjänen, J., and Valkeajärvi, P. 2010. Gillnet fishing drives lake-migrating brown trout to near extinction in the Lake Päijänne region, Finland. Fish. Man. Ecol. 17(2): 199-208. doi: 10.1111/j.1365-2400.2010.00738.x.

Syrjänen, J., Vainikka, A., Louhi, P., Huusko, A., Orell, P., and Vehanen, T. 2017. History, Conservation and Management of Adfluvial Brown Trout Stocks in Finland. In Brown Trout (eds J. Lobón-Cerviá and N. Sanz). doi:10.1002/9781119268352.ch28

Therneau, T., Grambsch, P., and Pankratz, V.S. 2003. Penalized survival models and frailty, *J. Comp. Graph. Stat.* **12**: 156-175.

Tsuboi, J-I., Morita, K., Klefoth, T., Endou, S., and Arlinghaus, R. 2016. Behaviour-mediated alteration of positively size-dependent vulnerability to angling in response to historical fishing pressure in a freshwater salmonid. Can. J. Fish. Aquat. Sci. **73**(3): 461-468. doi: 10.1139/cjfas-2014-0571.

Tsuboi, J-I., Kaji, K., Baba, S., and Arlinghaus, R. 2019. Trade-offs in the adaptation towards hatchery and natural conditions drive survival, migration, and angling vulnerability in a territorial fish in the wild. Can. J. Fish. Aquat. Sci. 76: 1757-1767. doi: 10.1139/cjfas-2018-0256.

Uusi-Heikkilä, S., Wolter, C., Klefoth, T., and Arlinghaus, R. 2008. A behavioral perspective on fishing-induced evolution. Trends Ecol. Evol. **23**(8): 419-421. doi: 10.1016/j.tree.2008.04.006.

Webster, M.M., and Ward, A.J.W. 2010. Personality and social context. Biol. Rev. **86**(4): 759-773. doi: 10.1111/j.1469-185X.2010.00169.x.

Wills, T.C. 2006. Comparative Abundance, Survival, and Growth of One Wild and Two Domestic Brown Trout Strains Stocked in Michigan Rivers. North. Am. J. Fish. Man. **26**: 535-544. doi: 10.1577/M05-053.1.

Table 1. Cox regression results on vulnerability to capture by I: all fishing gear, II: by angling among the subset of fish that were included in the predation experiment and III: by angling only among the fish confirmed to be alive after stocking (captured by either method and tested for boldness).

Subset	Factor / variable	Loss of χ^2	d.f.	Sig.	Wald	d.f.	Sig.	Exp(B)
I	Strain	6.162	8	0.629				
	Boldness score	0.941	1	0.332				
	Length at stocking	3.107	1	0.078	3.11	1	0.078	1.006
	Condition factor	7.416	1	0.006	7.28	1	0.007	1311.22
II	Strain	9.112	8	0.333				
	Boldness score	0.178	1	0.674				
	Length at stocking	4.464	1	0.035	4.493	1	0.034	1.008
	Condition factor	5.582	1	0.018	5.506	1	0.019	1683.11
III	Strain	9.623	8	0.293				
	Length at stocking	0.151	1	0.698				
	Condition factor	0.237	1	0.626				
	SGR	0.095	1	0.758				
	Boldness score	2.874	1	0.090	2.729	1	0.099	0.819

Table 2. Selection imposed by angling on fish confirmed to be alive after stocking via capture by angling or by gillnets. Mean-standardized selection gradient β_μ is calculated according to Matsumura et al. (2012). *Not corrected for average, because of arbitrary scale and negative average boldness score (-0.0287). S.D. refers to standard deviation.

	Captured			Non-captured					
Trait	Average	S.D.	N	Average	S.D.	N	t	Sig.	β_μ
Boldness score	-0.143	0.744	117	0.245	1.004	49	2.75	0.007	0.383*
Stocking length (mm)	245.2	23.2	232	242.0	22.6	108	-1.207	0.228	-1.017
Condition factor	0.248	0.026	232	0.246	0.026	108	-0.585	0.559	-0.446
IGR_{100} 100 ln g d^{-1}	0.135	0.534	232	0.250	0.364	108	2.326	0.021	0.039

Figure captions

Fig. 1. Schematic outline of the experiments. Breeding design was based on 3 males/females × 3 males/females matrix except for OUV × POH due to lack of mature POH females. The initial rearing of strains occurred in replicated tanks but was fully common-garden since PIT-tagging in autumn 2016. Experimental fishing in the two natural lakes was started by angling and finished with gillnets in both years.

Fig. 2. Realized total frequencies of different outcomings by strain in the stocking experiment pooled over the two natural lakes. See Supplementary Figures S2-S3 for lake-specific results.

Fig. 3. Estimated marginal mean (model-predicted average) strain differences (± 95% confidence intervals) in (a) boldness scores in the predation exposure experiment, (b) growth rates in the predation exposure experiment ($IGR_{100,}$ see the main text for the calculation), and (c) realized post-stocking growth rates (IGR_{100}) of the captured fish in the natural lakes. The first strain acronym indicates the maternal origin and the latter the sire origin.

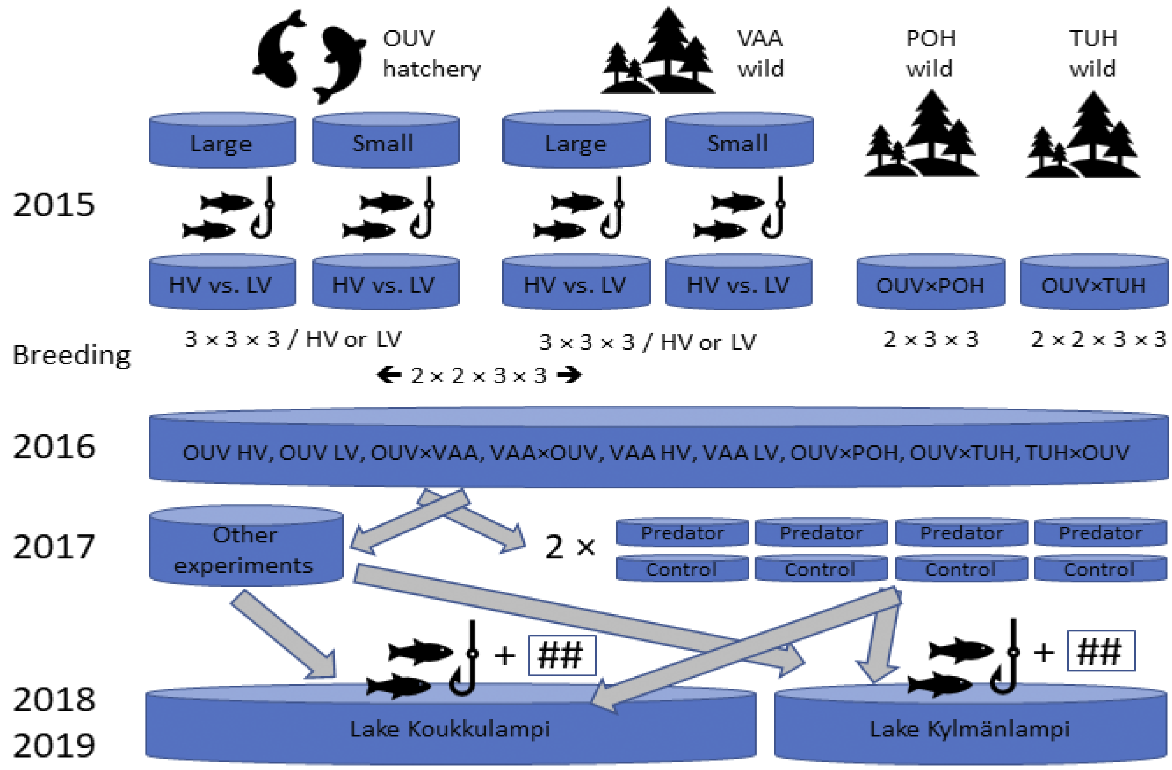
OUV
hatchery
VAA
wild
POH
wild
TUH
wild
Large
Small
Large
Small
2015
HV vs. LV
HV vs. LV
HV vs. LV
HV vs. LV
OUV×POH
OUV×TUH
Breeding
3 × 3 × 3 / HV or LV
3 × 3 × 3 / HV or LV
2 × 3 × 3
2 × 2 × 3 × 3
2 × 2 × 3 × 3
2016
OUV HV, OUV LV, OUV×VAA, VAA×OUV, VAA HV, VAA LV, OUV×POH, OUV×TUH, TUH×OUV
2017
Other experiments
2 ×
Predator
Predator
Predator
Predator
Control
Control
Control
Control
+ ##
+ ##
2018
2019
Lake Koukkulampi
Lake Kylmänlampi

Figure 1.

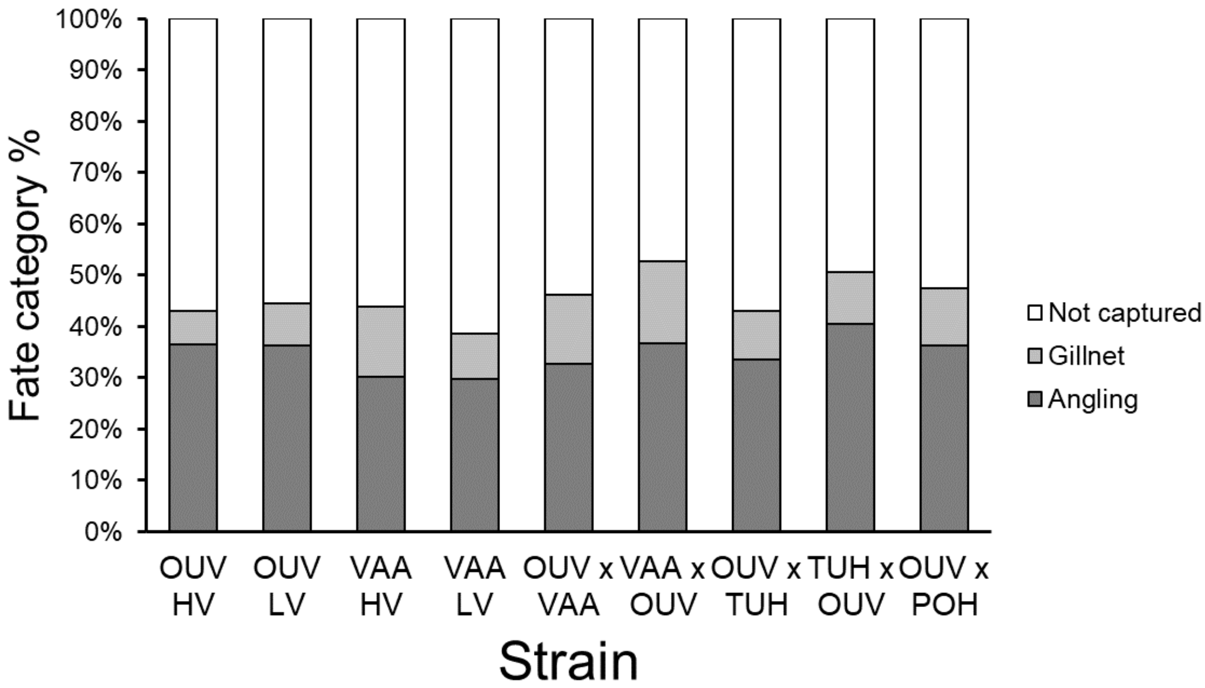
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Fate category %
Not captured
Gillnet
Angling
OUV HV
OUV LV
VAA HV
VAA LV
OUV x VAA
VAA x OUV
OUV x TUH
TUH x OUV
OUV x POH
Strain

Figure 2.

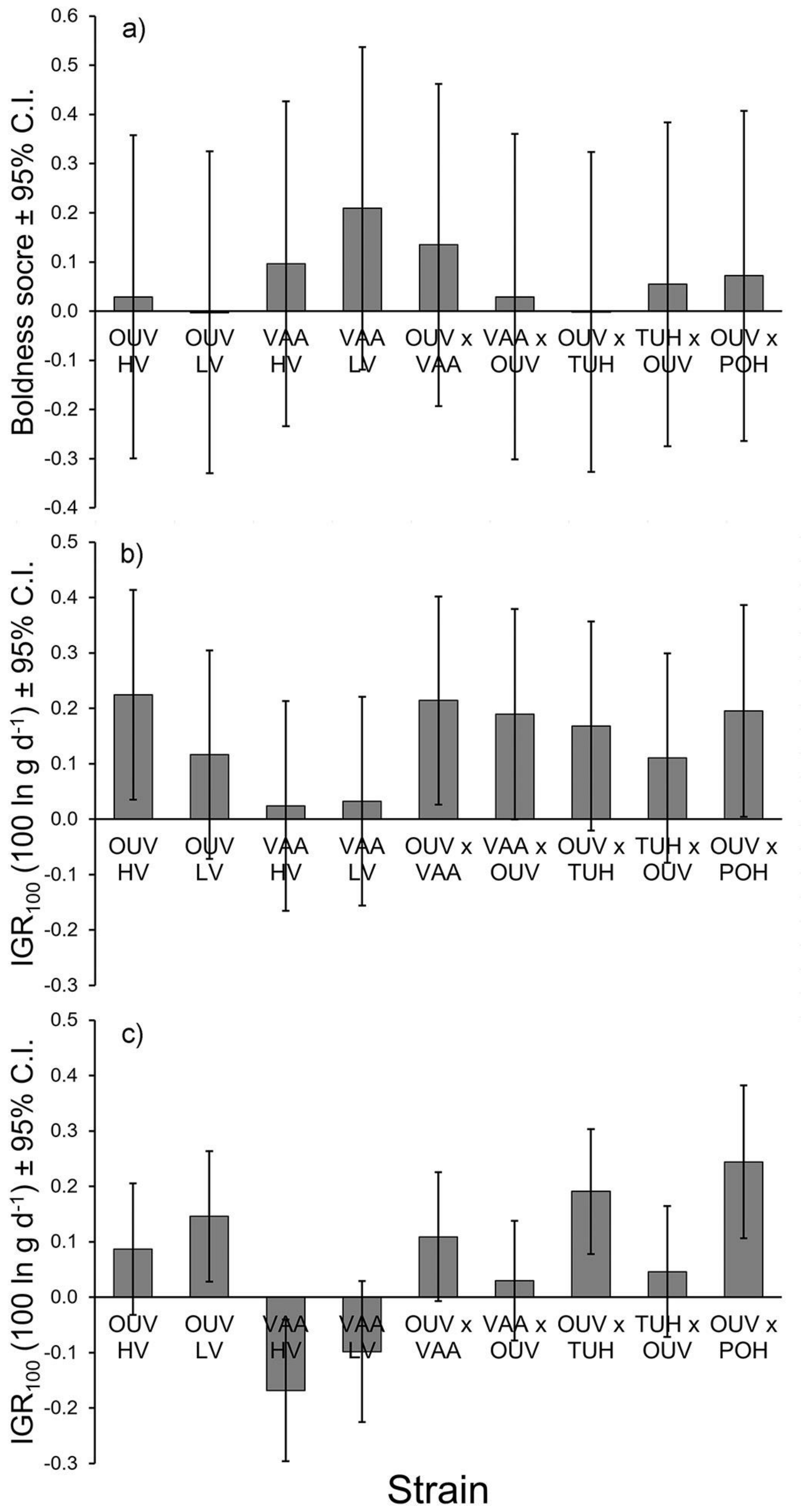
a)
Boldness socre ± 95% C.I.
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
OUV HV
OUV LV
VAA HV
VAA LV
OUV x VAA
VAA x OUV
OUV x TUH
TUH x OUV
OUV x POH
b)
IGR100 (100 ln g d-1) ± 95% C.I.
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
c)
IGR100 (100 ln g d-1) ± 95% C.I.
Strain

Figure 3.