

1 **Early winter foraging success, swimming performance and morphology of juvenile**
2 **landlocked Atlantic salmon reared under semi-wild and hatchery conditions**

3 Aurora Hatanpää^{1,3}, Hannu Huuskonen¹, Jukka Kekäläinen¹, Raine Kortet¹, Pekka
4 Hyvärinen², Maria Letizia Vitelletti¹ and Jorma Piironen³

5
6 ¹University of Eastern Finland, Department of Environmental and Biological Sciences, P.O.
7 Box 111, FI-80101 Joensuu, Finland.

8 ²Natural Resources Institute Finland (Luke), Natural Resources, Aquatic Population
9 dynamics, Manamansalontie 90, FI-88300 Paltamo, Finland

10 ³Natural Resources Institute Finland (Luke), Natural Resources, Aquatic Population
11 dynamics, Yliopistokatu 6, FI-80100 Joensuu, Finland

12
13 Corresponding author: aurora.hatanpaa@uef.fi, tel: +358 41 5436121

14
15 Authors' e-mail addresses: hannu.huuskonen@uef.fi; jukka.s.kekalainen@uef.fi;
16 raine.kortet@uef.fi; pekka.hyvarinen@luke.fi; marialetizia.vitelletti@gmail.com;
17 jorma.piironen@luke.fi

18
19 Running title: Performance of landlocked salmon juveniles

20

21 **Abstract**

22 Several Finnish populations of salmonids have been maintained exclusively by stocking
23 hatchery-reared fish for several generations, it is crucial to know whether domestication has
24 affected fitness-related traits and to assess how the developmental environment influences
25 fish phenotypes. Here, we focused on Lake Saimaa landlocked salmon and studied the role of
26 the early rearing environment in trait formation, by comparing juveniles (fingerlings) from
27 three backgrounds: 1) semi-wild (stocked as alevins), 2) standard hatchery, and 3) enriched
28 hatchery conditions We compared juvenile morphology, swimming performance, and
29 capability of feeding on natural prey in early winter. We found no differences between
30 standard and enriched hatchery conditions. Semi-wild fish consumed more prey items, but
31 wet mass of stomach contents did not differ between backgrounds. Swimming endurance was
32 comparable between backgrounds. Semi-wild fish had slenderer body shape and longer fins
33 than hatchery-reared fish. The lack of performance differences between hatchery juveniles
34 and their semi-wild conspecifics is possibly due to reduced phenotypic plasticity caused by
35 extremely low levels of genetic diversity in this population.

36

37

38

39

40

41

42

43

44

45

46 **Introduction**

47 Many natural salmonid populations are threatened by various human activities such as
48 overharvesting and construction of hydropower dams. Dams often severely block the
49 movements of migratory fishes and thus prevent natural reproduction possibilities for these
50 species (Lundqvist et al. 2008). The vitality of impacted populations, and endangered fish
51 populations in general, is often heavily dependent on stocking of hatchery-reared fish into
52 nature (Brown and Day 2002; Fraser 2008). However, captive breeding programs expose
53 hatchery-reared fish to radically different selective forces than their wild counterparts
54 experience (Hindar et al. 1991; Waples 1991; Fleming and Gross 1993; Snyder et al. 1996;
55 Reisenbichler and Rubin 1999; Frankham 2008). This has been shown to lead to rapid
56 domestication of hatchery-reared fish stocks over as little as one generation (Christie et al.
57 2012). Crucially, this process may promote fixation of alleles that are deleterious in nature
58 (Olla et al. 1998; Lynch and O’Hely 2001; Jonsson and Jonsson 2006) and may explain why
59 apparent survival rates of hatchery-reared fishes in nature are often significantly lower than
60 those of wild conspecifics (Wang and Ryman 2001; Brown et al. 2003; Araki et al. 2007,
61 2008; Blanchet et al. 2008; Norrgård et al. 2014).

62 Current hatchery practices can cause several maladaptive changes in fish phenotype
63 and behaviour (Fleming et al. 1994; Law and Blake 1996; Berejikian et al. 2000; Johnsson et
64 al. 2001; Brockmark et al. 2010). For example, body morphology typically differs between
65 hatchery-reared and wild fish (Fleming et al. 1994; Sánchez-González and Nicieza 2017).
66 Body shape is particularly important for swimming efficiency and manoeuvrability
67 (Pakkasmaa 2001; Pakkasmaa and Piironen 2001; Ojanguren and Braña 2003). Moreover, for
68 salmonids, critical swimming speed (U_{crit} : the time and velocity when fish cannot resist the
69 current any longer, often referred to as swimming endurance) is one of the key traits likely to
70 affect survival in the wild (Plaut 2001; Pang et al. 2014). Both individual swimming ability

71 and body morphology may be associated with foraging behaviour and predation avoidance
72 (Jackson and Brown 2011; Yan et al. 2013). Hence, hatchery-induced changes in body
73 morphology can impose important fitness consequences for captive-reared fishes after release.

74 Food in the hatchery environment is often artificial and served at scheduled times with
75 little temporal or spatial variation. Natural fluctuations in feeding regime are thus often
76 completely absent. Furthermore, fish densities in hatcheries are much higher than in nature,
77 creating an unnatural social environment (Berejikian et al. 2000). In order to maximise the
78 performance of hatchery-reared fish in the wild, it is crucial to know whether stocked
79 individuals are able to learn how to feed on novel food items after release. In the wild,
80 juvenile Atlantic salmon (*Salmo salar*) feed opportunistically on drift and benthic
81 invertebrates (Amundsen and Gabler 2008; Johansen et al. 2011), requiring different skills
82 than fish acquire in hatcheries. However, enriched rearing techniques can provide solutions to
83 the issues mentioned above (e.g. Hyvärinen and Rodewald 2013; Karvonen et al. 2016).
84 Enriched rearing has recently been applied to improve the fitness of hatchery-reared Atlantic
85 salmon, as well as other salmonids (Rodewald et al. 2011).

86 Globally, many Atlantic salmon stocks are threatened and dozens of populations have
87 already been extirpated (Klemetsen et al. 2003; Rassi et al. 2010; Lumme et al. 2016; Murphy
88 et al. 2017). Therefore, maintaining populations in hatchery “refugia” has become common
89 and more work is needed to evaluate and maintain fitness-related traits for the hatchery
90 populations. Some of the known examples of Atlantic salmon refugia populations include Bay
91 of Fundy (O’Reilly and Kozfkay 2014) and Lake Ontario / Lake Champlain populations
92 (Hutchings et al. 2019). In the Eastern North America, efforts with varying degree of success
93 have been carried out, for example, to reintroduce salmon to lakes where it has been
94 extirpated and to provide supplementary stocking into declined populations (Tessier et al.
95 1997; Brunsdon et al. 2017).

96 In Finland, the Lake Saimaa landlocked salmon (*S. salar* m. *sebago*) is a critically
97 endangered unique ecomorph of the Atlantic salmon (Pursiainen et al. 1998; Lumme et al.
98 2016). The Lake Saimaa landlocked salmon has a narrow genetic background (Tonteri et al.
99 2005; Tiira et al. 2006) and has been fully dependent on stocking enhancement for the last
100 four decades, because construction of hydroelectric dams in the middle of the 1950s and early
101 1970s destroyed virtually all the natural breeding areas (Pursiainen et al. 1998). The critical
102 bottleneck was in the 1990s when less than ten parental fish were available for founding of
103 the broodstock (Tiira et al. 2006). Hence, the present stock is maintained by annual stocking
104 of hatchery-reared smolts near to their previous reproduction areas. Hatcheries are used to
105 incubate eggs and to produce smolts, and the hatchery broodstock is annually replenished by
106 collecting gametes from returning spawners. Only F1 generations have been used in the
107 hatchery propagation. The current management strategy in Finland follows the four goals for
108 conservation hatcheries (maintaining genetic diversity and effective population size, as well
109 as minimizing inbreeding and adaptation to captivity) as recommended by Fisch et al. (2015).
110 Moreover, in recent years there has been growing interest in restoring natural reproduction
111 (Soininen et al. 2019), which requires comprehensive understanding of the mechanisms
112 affecting survival of early life stages.

113 In this study, we focused on the effects of early rearing environment on fitness traits in
114 landlocked salmon by dividing offspring of shared parentage into three rearing groups: (i)
115 juveniles stocked into a natural stream as alevins in the spring, (ii) standard hatchery-reared
116 juveniles, and (iii) enriched-reared juveniles. After one summer of growth, we studied the
117 effect of early rearing conditions on swimming performance, body morphology, and the
118 ability to forage on natural prey items in 0+ fingerlings. In the standard rearing method, the
119 fish were maintained in a typical low-stimulus environment, whereas under enriched rearing,
120 natural conditions were mimicked, i.e. the tanks were supplied with shelters for fish and the

121 water velocity, depth and direction were varied, in addition to varying feeding regime
122 (Hyvärinen and Rodewald 2013). The experiments were timed for late autumn and early
123 winter as most overwinter mortality in juvenile Atlantic salmon seems to occur during this
124 period (Cunjak and Power 1987). Based on earlier observations (Jackson and Brown 2011;
125 Näslund et al. 2012; Hyvärinen and Rodewald 2013; Näslund et al. 2013), we expected to find
126 differences in all studied traits between different rearing backgrounds. In more detail, we
127 hypothesised that after spending three months in a natural stream environment, semi-wild fish
128 would differ from hatchery-reared fish. In addition, in line with earlier studies, we expected
129 the enriched-reared fish to show better performance than the standard-reared fish (Rodewald
130 et al. 2011).

131

132 **Materials and Methods**

133 *The study fish and creation of experimental groups*

134 In October 2013, we artificially fertilised the eggs from a cultivated broodstock (F1 hatchery
135 generation) of Lake Saimaa landlocked salmon using 75 females from three year classes
136 (2007, 2008, and 2009) and 75 males from four year classes (2008, 2009, 2010, and 2011).
137 Fertilisation matrices were produced between five females and five males (a total of 15
138 matrices, generating 375 families). The fertilisations and early incubation occurred at the
139 Enonkoski Aquaculture Station of the Natural Resources Institute Finland (Fig. 1). Then, at
140 the eyed-egg stage, the eggs pooled from all matrices were divided into three different
141 treatments: (i) juveniles to be stocked to natural stream as alevins (i.e. semi-wild: N = 7 500
142 eggs), (ii) standard-reared (N = 7 500) and (iii) enriched-reared (N = 7 500). The semi-wild
143 fish were brought to the River Ala-Koitajoki (N 6973832 E 673569) as newly-hatched alevins
144 on 2 May 2014 and were left to grow under natural conditions until they were captured by
145 electrofishing on 12 September 2014. After capture, the fish were transported to the Kainuu

146 Fisheries Research Station (KFRS, www.kfrs.fi; Natural Resources Institute Finland (Fig. 1)).
147 The eyed eggs of the standard-reared and enriched-reared fish were transported directly to
148 KFRS. The fish were maintained under standard or enriched conditions over the summer (see
149 Table S1 and S2; Hyvärinen and Rodewald 2013; Fig. S1, S2, and S3). All experiments (see
150 below) were conducted at the KFRS in October 2014.

151 Between 12-16 September 2014 the fish were anaesthetised with benzocaine (40 mg·l⁻¹)
152 ¹), measured (total length and wet mass), and tagged with individual PIT-tags (12 mm HDX,
153 Oregon RFID). After tagging, 30 randomly selected salmon (6-10 cm total length) from each
154 rearing background were placed into six 0.4 m² circular holding tanks (two tanks per
155 background to ensure safe maintenance between the experiments). During the experimental
156 period, the hatchery-reared fish were fed with commercial dry food (Veronesi VITA, 0.5–1.0
157 mm, crude protein 55-57%) by an automatic belt feeder. Food was added twice a day, and it
158 was dispensed within the next eight hours. Semi-wild fish were provided with live zoobenthos
159 twice a week so that invertebrates were constantly available. Fish were held in the tanks
160 before and between the experiments and allowed one week of recovery between subsequent
161 experiments to mitigate potentially negative effects of handling stress. Specific growth rate
162 (SGR) of total length was calculated for the period between the tagging and the end of the
163 study by using the formula:

$$164 \quad SGR = \frac{\ln(\text{final fish length}) - \ln(\text{initial fish length})}{\text{Time interval}} * 100.$$

166 ***Foraging experiment***

167 The foraging experiments were conducted between 10-17 October 2014, using four circular
168 outdoor concrete stream ponds with gravel substrate (2-4 cm grain size), where fish were able
169 to feed on natural zoobenthos and drifting organisms (Rodewald et al. 2011). The total area of
170 each pond was 75 m², of which the stream section comprised 40 m². Water flow was

171 averaged $0.08 \text{ m}\cdot\text{s}^{-1}$ (SD ± 0.02), depth was maintained at 25 cm, and temperature followed
172 natural conditions varying between 4.2-6.2 °C (ambient temperature) during the experiment.
173 Each pond contained three to four grey plastic boxes (0.4 m^2 and $800 \times 600 \times 451 \text{ mm}$)
174 covered with lids and each end cut out and replaced with wire mesh (5 mm mesh size) to
175 allow water and drift items to flow through. The boxes were placed parallel to the flow
176 direction in the tanks. Each box was filled with 10 l of gravel (\varnothing 2-4 cm grain size). After 48
177 hrs of fasting in the holding tanks, we introduced one fish from each rearing treatment to a
178 randomly selected box (i.e. one fish per box) after transporting them individually in 10 l
179 buckets. The salmon spent 24 hours in the boxes, from introduction at 11:00 until removal at
180 11:00 the following day (Table S3).

181 We used a pulsed gastric lavage method (Kamler and Pope 2001; Braga et al. 2017) to
182 extract consumed food items from the stomachs of anaesthetised fish immediately after
183 removing them from the boxes. Stomach contents were flushed with pressurised (2.5 bar) 5
184 °C (ambient temperature) water using a 1 mm diameter metal hose. To confirm the
185 effectiveness of our stomach content analyses, we performed a pilot test where we first fasted
186 18 additional naturally-fed salmon for 0 hours, 24 hours, or 48 hours, and then inspected the
187 flushed stomach contents. After 24 hours fasting, 66% of the stomachs were empty and after
188 48 hours fasting, all stomachs were empty. Therefore, the fingerlings were fasted for 48 hours
189 prior to experimentation to ensure that the fish had completely evacuated their stomach
190 contents. After flushing, fish were left to recover for 30 minutes and then returned to their
191 original holding tanks. Stomach content samples were stored in 60% ethanol until analysis
192 under a dissecting microscope, when any invertebrates were identified to the level of order or
193 family.

194

195 *Swimming endurance experiment*

196 The swimming endurance experiment (after Vainikka et al. 2012) was conducted between 25-
197 28 October 2014 when water temperature varied between 1.1-1.2 °C following ambient
198 conditions. Using the same individuals as in the foraging experiment, the fish were fasted for
199 24 hours and then individually acclimated in 10 l buckets for 30 minutes. After the
200 acclimation period, each fish was individually placed into a swim tube. The swim tube was a
201 1200 mm long transparent tube with an inner diameter of 100 mm. Both ends of the tube were
202 covered with 5 mm mesh. Water flow in the tube was gravitational, induced by placing a
203 water input 1.4 m above the tube. The swim performance test was started after a 90 s
204 acclimation. During the test, water velocity was increased by gradually opening the input
205 valve in 5 s intervals until a maximum speed of 73.2 cm·s⁻¹ was reached in 40 s. When
206 individuals could no longer maintain position against the current (time against maximum
207 velocity varied from 1-125 s), we immediately closed the valve and removed the fish to allow
208 recovery in 10 l buckets for 15 minutes before transferring them back to their holding tanks
209 (Table S4). We used a maximum velocity of 73.2 cm·s⁻¹ because 90% of our additional pilot
210 fish (the same fish as in the pilot foraging experiment) were able to hold their position in it.
211 Some mortality occurred between experiments (4 semi-wild and 6 standard-reared fish) and
212 datapoints from dead fish were removed from the statistical models.

213

214 ***Morphology***

215 Upon completion of the swimming performance experiment, we euthanised the fish via
216 benzocaine overdose (200 mg·l⁻¹). Each fish was photographed (left lateral view) with a
217 Nikon® D80 digital camera with a Nikon® AF Zoom Nikkor 28-85 mm f/3.5-4.5N lens. The
218 photographs were taken from 25 cm distance using a fixed stand and constant camera settings
219 (ISO-800, focal length 60 mm, exposure time 1/60 sec, artificial fixed lighting, no flash). The
220 photographs were first converted into TPS files with tpsUTIL (Rohlf 2006). Using tpsDIG we

221 then selected 16 landmarks on the side view photographs and measured the following
222 morphological parameters: body length, body height 1, body height 2, body height 3, dorsal
223 fin length, head length, upper jaw length, and pectoral fin length (Fig. 2).

224

225 *Statistical analyses*

226 The sizes of the fingerlings differed between rearing backgrounds (enriched > standard >
227 semi-wild: Table 1) so size was included in statistical analyses of the experimental data (see
228 below). Differences in SGR between the rearing backgrounds were tested by one-way
229 ANOVA and paired differences were tested by Tukey HSD post hoc test.

230 The effect of rearing environment on fingerlings feeding activity (total number of
231 consumed prey items) was examined using a linear mixed-effects model (LMM with
232 restricted maximum likelihood (Bates et al. 2014)) with rearing environment and test pond as
233 categorical fixed factors, wet mass as a covariate, and test day as a random factor. The model
234 was simplified first by removing statistically insignificant interactions and then based on AIC.
235 The final model for the total number of prey items included the main effects of test pond and
236 rearing environment. The effect of the rearing environment on the total ingested prey mass
237 was studied using a generalised linear mixed model (GLMM) with negative binomial error
238 distribution and log link function. The model structure was identical with the LMM model
239 described above. GLMM was used since the response variable was not normally distributed
240 and could not be normalised with transformations. Final selection of error distribution was
241 based on lowest AIC value between four candidate distributions (negative binomial, quasi-
242 poisson, poisson, and gamma). LMM and GLMM analyses were conducted with lmerTest
243 (Kuznetsova et al. 2017) and glmmADMB (Fournier et al. 2012) packages (respectively)
244 in R version 3.2.3 (R Core Team 2015). In both models, the significance of categorical fixed

245 factors (main effects and paired differences) were tested with ANOVA function (i.e. by
246 comparing the full model against the reduced model).

247 The effect of rearing background on swimming performance was analysed using one-
248 way ANOVA. We used logarithmic transformation of total swimming time and removed the
249 effect of the fish size (total length) on swimming performance by using unstandardized
250 residuals of the linear regression between size and swimming time.

251 To remove the allometric variation due to differences in fish size, we performed linear
252 regression analyses between body length and all morphological measurements and used the
253 unstandardized residuals from these regressions in subsequent analyses. Unstandardized
254 residuals were first taken into a Principal Component Analysis (PCA) with Varimax rotation.
255 PCA resulted in two principal components with eigenvalues >1 , which together explained
256 80.1 % of the variation in body morphology. The first component ('body component') was
257 affected by all three body height parameters and jaw length, whereas dorsal fin length, head
258 length, and pectoral fin length formed the second component ('fin component'). Principal
259 components were analysed with one-way MANOVA using rearing background as a fixed
260 factor. The paired differences between rearing environments were tested with Tukey HSD
261 post-hoc test.

262 We tested association between the unstandardized residuals of the linear regression
263 between fish size and swimming time and PC scores in a similar model as above, but we also
264 added PC1 and PC2 separately as covariates. The interaction between covariate and rearing
265 background was not significant in both models and was removed for final analyses.
266 Univariate and multivariate ANOVAs, linear regression, and PCA were conducted using IBM
267 SPSS Statistics (version 21).

268

269 **Results**

270 ***Foraging experiment***

271 All the study fish had ingested natural prey. The dominant food items in terms of number in
272 the stomach contents were Cladocera and Diptera (Table 2), and Diptera and Trichoptera in
273 terms of biomass (Table 3). The total number of ingested prey items differed between rearing
274 environments ($\chi^2 = 8.33$, $P = 0.016$) (Table 2, Fig. 3). Pairwise comparisons indicated that
275 semi-wild salmon ingested a significantly higher number of prey items than enriched-reared
276 individuals ($t = -2.79$, $P = 0.007$, Fig. 3), with a similar trend between semi-wild and
277 standard-reared fish ($t = -1.92$, $P = 0.059$). No difference was found between standard- and
278 enriched-reared salmon ($t = -0.70$, $P = 0.484$). The effect of test pond was non-significant
279 (LMM, ANOVA function, $\chi^2 = 2.13$, $P = 0.547$).

280 The final model (GLMM) for total ingested prey mass included fish wet mass and
281 rearing environment, but both of these were statistically non-significant (wet mass: $Z = -1.65$,
282 $P = 0.099$; rearing environment: ANOVA, $P = 0.176$; Table 3).

283

284 ***Swimming endurance experiment***

285 Swimming time did not differ between rearing backgrounds (ANOVA, $F_{[2,71]} = 2.164$ and $P =$
286 0.122) (Fig. 4). PC1 (body component) and PC2 (fin component) as covariates of the
287 unstandardized residuals were not significant (PC1 $F_{[2,71]} = 0.7$ and $P = 0.406$, PC2 $F_{[2,71]} =$
288 0.008 and $P = 0.929$). Interactions between PC1 and PC2 were not significant (PC1 $P =$
289 0.337 , PC2 $P = 0.752$).

290

291 ***Morphology and SGR***

292 Both 'body component' (PC1) and 'fin component' (PC2) differed between rearing
293 backgrounds ('body component': ANOVA, $F_{[2,71]} = 13.663$ and $P < 0.001$; 'fin component':
294 ANOVA, $F_{[2,71]} = 37.402$ and $P < 0.001$, Table 4; Fig. 5). The components did not differ

295 between the enriched-reared and standard-reared fish ('body component': $P = 0.988$, 'fin
296 component': $P = 0.354$), but the semi-wild fish differed from the fingerlings originating from
297 the both hatchery-reared backgrounds ($P < 0.001$, in both cases Fig. 5). SGR of semi-wild fish
298 was lower than that of standard-reared and enriched-reared fish (Table 1). SGR differed
299 significantly between the rearing backgrounds (ANOVA, $F_{[2,76]} = 22.74$ and $P < 0.001$). The
300 rates differed between semi-wild fish and both hatchery-reared fish ($P < 0.001$) but the
301 difference between standard-reared and enriched-reared fish was non-significant ($P = 0.800$).

302

303 Discussion

304 Demanding and labile conditions of the river habitats juvenile salmonids are frequently
305 encountering, require phenotypic characteristics that suit the range of flow rates and allow
306 high-performance manoeuvrability, i.e. traits that allow juveniles to move, forage, and avoid
307 predators efficiently. Being able to feed on variable food items and to exhibit high swimming
308 endurance are probably some of the most crucial characteristics for survival in the wild
309 (Bachman 1984; Duthie 1987; Reiriz et al. 1998; Sparrevohn and Støttrup 2007; Tomiyama et
310 al. 2011). Here, we found that the semi-wild juvenile landlocked Atlantic salmon ingested a
311 higher number of food items compared to hatchery-reared fish, but there was no difference in
312 the total mass of food from stomach contents. Moreover, body morphology differed between
313 the hatchery-reared and semi-wild fish, but not between standard and enriched-reared fish.
314 Conversely, swimming endurance did not differ between any of the three different rearing
315 backgrounds.

316 Semi-wild fish were the smallest at PIT tagging and they had the slowest growth rate
317 during the experimental period as well. As our study fish had the same genetic background,
318 we can assume that the observed differences are due to growing environment. Hatchery-
319 reared fish were feeding on dry food with high energy content, whereas semi-wild fish were

320 foraging on natural food, and probably also having higher activity costs of nutrition. In the
321 feeding experiment, all fish were alone in the boxes and had equal opportunities for foraging
322 on natural food items. Contrary to our expectations, we did not find differences in the
323 ingested prey mass between the backgrounds, although semi-wild fish had consumed higher
324 number of food items. This probably indicates that semi-wild fish were feeding on smaller
325 prey items, which is plausible as the semi-wild fish were smaller than the hatchery-reared
326 fish. Whether this has any consequences for the fish nutrition is not known, but it is possible
327 that smaller prey items are digested more easily and, thus, fish could gain nutritive benefits.
328 Semi-wild fish had already learned to use natural prey before the experiment and thus they
329 could possibly have better capability in finding natural food items under semi-natural
330 conditions (Amundsen and Gabler 2008; Johansen et al. 2011). Rodewald et al. (2011) found
331 that enriched-reared Baltic salmon parr had better ability to learn to forage novel prey than
332 standard-reared parr, but we did not find differences in the ingested prey mass or number
333 between enriched and standard-reared landlocked salmon. In general, foraging performance
334 can affect post-stocking mortality, and weakened foraging ability can potentially be realised
335 as low post-release survival rates (Robert 2009; Saikkonen et al. 2011).

336 We expected to find differences in foraging and swimming performance as recent
337 social experiences and varying environments can impose carryover effects on suite of traits
338 (Jonsson and Jonsson 2014; O'Connor et al. 2014). However, swimming performance did not
339 differ between fish from different rearing backgrounds. The experiment itself tested the ability
340 to swim against strong current (burst swimming) that has biological relevance in terms of
341 ability to change location, avoid predators, and maintain position in the stream environment.
342 Other studies have reported variation in critical swimming speed (U_{crit}) with a note that
343 swimming ability decreases in colder water (see report from Peake 2008). Thus, low
344 temperatures (~ 1 °C) during the tests likely influenced our results. Even so, as the temperature

345 should affect all the fish equally, we believe that it would not have affected the inter-treatment
346 comparisons. Cold water is known to decrease swimming ability and current holding capacity
347 by 20–50 % when temperature decreases from 8 °C to below 4 °C (Rimmer et al. 1985;
348 Shustov et al. 1989). Rimmer et al. (1985) observed that current holding capacity of wild and
349 hatchery-reared Atlantic salmon fingerlings decreased similarly with temperature, although
350 the wild fingerlings were able to hold their position in stronger current than hatchery
351 conspecifics. Interestingly most winter mortality occurs during early winter (Cunjak 1988).
352 The lack of differences in swimming endurance between our study fish from different rearing
353 backgrounds indicates that mortality rates during this season could affect all rearing
354 backgrounds similarly. It is likely that in another season the overall results would have been
355 different, but to ensure that most of our study fish would survive from all of our experiments
356 we wanted to carry out physically the most demanding experiment at the end of the study
357 period.

358 Typical habitats for juvenile landlocked salmon are shallow, fast flowing areas and
359 rapids (Guay et al. 2000). From our own observations in the Lake Saimaa drainage, surface
360 velocity in these areas can be relatively fast, but current at the bottom where the fish are
361 usually found is typically close to zero. Burst swimming ability of territorial juvenile salmon
362 is still crucial for inhabiting new spots and possibly for drift foraging, as absent the ability to
363 swim against strong current the fish may not be able to maintain or return to their positions
364 (Kemp et al. 2006). Body morphology data indicated that semi-wild fish were slenderer and
365 had longer fins than their enriched or standard-reared counterparts. A slender body shape may
366 improve swimming performance whereas longer pectoral and dorsal fins can have an opposite
367 effect. Long pectoral fins may assist a fish in anchoring to the riverbed, and as fins are also
368 used for balance and orientation, they have significant influence on manoeuvrability and
369 survival under natural conditions (Arnold et al. 1991).

370 The studied traits could be condition dependent, which requires future attention. While
371 it is known that hatchery fish show higher condition indices than fish in natural conditions, it
372 is unknown whether it gives them advantage in overwintering in nature. Stress is another
373 factor that can affect fish physiology and performance (Kortet et al. 2019). In our study, the
374 fish had similar handling procedures, but we cannot rule out that semi-wild fish could have
375 experienced higher stress levels due to the greatest change from their growing environment.

376

377 *Conclusions and management implications*

378 The results confirmed our prediction that early rearing conditions can modify the performance
379 of landlocked juvenile salmon. In previous studies more notable differences between standard
380 and enriched-rearing methods have been detected (Rodewald et al. 2011; Näslund et al. 2012,
381 2013; Hyvärinen and Rodewald 2013). Lack of differences between enriched rearing and
382 standard rearing has been documented in relatively few previous studies (Brockmark et al.
383 2010; Rosengren et al. 2017). We expect that although phenotypic plasticity is not completely
384 lost, lack of genetic variation in our stock could explain the small variation between the
385 hatchery rearing backgrounds, whereas natural environmental conditions may influence
386 morphology, potentially enhancing survival in the wild. According to Tonteri et al. (2005),
387 the Lake Saimaa landlocked salmon population had the lowest allelic diversity and observed
388 heterozygosity among 23 North European Atlantic salmon populations.

389 Attempting to reintroduce viable populations of species at risk back to nature is
390 always challenging (Robert 2009; Bouzat 2010; Piccolo et al. 2012; Johnsson et al. 2014).
391 Efforts to undo domestication or rewild a fish population after decades of hatchery rearing are
392 even more difficult (Soininen et al. 2019). However, our results demonstrate some remaining
393 phenotypic plasticity in a domesticated Lake Saimaa salmon stock, and in our opinion the
394 next step is to study how well the semi-wild fish survive under natural conditions during

395 smolt migration and if they return to spawn. Stocking fry to rivers can be a useful method to
396 reintroduce species where it has been extirpated, but it should be the last resort in
397 conservation (Johnsson et al. 2014). Hatchery environments seem to favour fish that might
398 not be the best individuals to survive in nature, although mortality in the wild is much higher
399 than under hatchery conditions as numerous previous studies have shown (Robert 2009;
400 Saikkonen et al. 2011; Johnsson et al. 2014).

401 To conclude, short exposure of Lake Saimaa landlocked salmon juveniles to artificial
402 hatchery conditions in either standard or enriched environments did not lead to notable
403 differences in early winter foraging patterns or swimming endurance between hatchery-reared
404 juveniles and their semi-wild conspecifics. However, morphological traits of juveniles
405 differed significantly. Future studies should focus on the survival of the semi-wild and wild
406 fish to identify reasons behind the low survival. Better understanding of the mechanisms
407 behind domestication could suggest solutions to improve conservational hatchery rearing.

408

409 **Acknowledgements**

410 We thank the staff of the Kainuu Fisheries Research Station (KFRS) and the Enonkoski
411 Aquaculture Station of the Natural Resources Institute of Finland for their help during the
412 studies. We thank Tuuli Pietinen and Ninni Rissanen for their assistance during the
413 experiments. Also, we thank Alexandre Lemopoulos, Chris Elvidge, Nico Alioravainen,
414 Laura Härkönen, and three anonymous reviewers for their helpful comments on the
415 manuscript. The study was financially supported by the Natural Resources Institute of
416 Finland, Ministry of Agriculture and Forestry of Finland, and the Raija and Ossi Tuuliainen
417 Foundation. Experimental procedures followed ABS/ASAB guidelines for ethical treatment
418 of animals and comply with current Finnish legislation. The experiments were conducted
419 under license from the Finnish Animal Experiment Board (ESAVI/5361/04.10.07/2013).

420
421
422
423
424
425
426
427
428
429
430
431
432
433
434
435
436
437
438
439
440
441
442
443
444

References

- Amundsen, P.-A., and Gabler, H.-M. 2008. Food consumption and growth of Atlantic salmon *Salmo salar* parr in sub-Arctic rivers: empirical support for food limitation and competition. *J. Fish Biol.* **73**: 250–261. doi:10.1111/j.1095-8649.2008.01932.x.
- Araki, H., Cooper, B., and Blouin, M.S. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* **318**(5847): 100–103. doi:10.1126/science.1145621.
- Araki, H., Berejikian, B.A., Ford, M.J., and Blouin, M.S. 2008. SYNTHESIS: Fitness of hatchery-reared salmonids in the wild. *Evol. Appl.* **1**(2): 342–355. doi:10.1111/j.1752-4571.2008.00026.x.
- Arnold, G.P., Webb, P.W., and Holford, B.H. 1991. The role of the pectoral fins in station-holding of Atlantic salmon parr (*Salmo salar* L.). *J. Exp. Biol.* **156**: 625–629. doi:http://dx.doi.org/10.1108/01437720810878897.
- Bachman, R.A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. *Trans. Am. Fish. Soc.* **113**(1): 1–32. doi:10.1577/1548-8659(1984)113<1:FBOFWA>2.0.CO;2.
- Bates, D., Mächler, M., Bolker, B., and Walker, S. 2014. Fitting Linear Mixed-Effects Models using lme4. *J. Stat. Softw.* **67**(1): 1–48. doi:10.18637/jss.v067.i01.
- Berejikian, B.A., Tezak, E.P., Flagg, T.A., LaRae, A.L., Kummerow, E., and Mahnken, C.V.W. 2000. Social dominance, growth, and habitat use of age-0 steelhead (*Oncorhynchus mykiss*) grown in enriched and conventional hatchery rearing environments. *Can. J. Fish. Aquat. Sci.* **57**(3): 628–636. doi:10.1139/cjfas-57-3-628.
- Blanchet, S., Páez, D.J., Bernatchez, L., and Dodson, J.J. 2008. An integrated comparison of captive-bred and wild Atlantic salmon (*Salmo salar*): Implications for supportive

- 445 breeding programs. *Biol. Conserv.* **141**(8): 1989–1999.
446 doi:10.1016/j.biocon.2008.05.014.
- 447 Bouzat, J.L. 2010. Conservation genetics of population bottlenecks: the role of chance,
448 selection, and history. *Conserv. Genet.* **11**: 463–478. doi:10.1007/s10592-010-0049-0.
- 449 Braga, R.R., Ribeiro, V.M., Bornatowski, H., Abilhoa, V., and Vitule, J.R.S. 2017. Gastric
450 lavage for dietary studies of small fishes: Efficiency, survival and applicability. *Acta*
451 *Ichthyol. Piscat.* **47**(1): 97–100. doi:10.3750/AIEP/02079.
- 452 Brockmark, S., Adriaenssens, B., and Johnsson, J.I. 2010. Less is more: Density influences
453 the development of behavioural life skills in trout. *Proc. R. Soc. B Biol. Sci.* **277**(1696):
454 3035–3043. doi:10.1098/rspb.2010.0561.
- 455 Brown, C., and Day, R.L. 2002. The future of stock enhancements: Lessons for hatchery
456 practice from conservation biology. *Fish Fish.* **3**(2): 79–94. doi:10.1046/j.1467-
457 2979.2002.00077.x.
- 458 Brown, C., Davidson, T., and Laland, K. 2003. Environmental enrichment and prior
459 experience of live prey improve foraging behaviour in hatchery-reared Atlantic salmon.
460 *J. Fish Biol.* **63**: 187–196. doi:10.1046/j.1095-8649.2003.00208.x.
- 461 Brunsdon, E.B., Fraser, D.J., Ardren, W.R., and Grant, J.W.A. 2017. Dispersal and density-
462 dependent growth of Atlantic salmon (*Salmo salar*) juveniles: clumped versus dispersed
463 stocking. *Can. J. Fish. Aquat. Sci.* **74**(9): 1337–1347. doi:10.1139/cjfas-2015-0488.
- 464 Christie, M.R., Marine, M.L., French, R.A., and Blouin, M.S. 2012. Genetic adaptation to
465 captivity can occur in a single generation. *Proc. Natl. Acad. Sci.* **109**(1): 238–242.
466 doi:10.1073/pnas.1111073109.
- 467 Cunjak, R.A. 1988. Physiological Consequences of Overwintering in Streams: The Cost of
468 Acclimitization? *Can. J. Fish. Aquat. Sci.* **45**: 443–452. doi:10.1139/f88-053.
- 469 Cunjak, R.A., and Power, G. 1987. The feeding and energetics of stream-resident trout in

- 470 winter. *J. Fish Biol.* **31**: 493–511. doi:10.1111/j.1095-8649.1987.tb05254.x.
- 471 Duthie, G.G. 1987. Observations of poor swimming performance among hatchery-reared
472 rainbow trout, *Salmo gairdneri*. *Environ. Biol. Fishes* **18**(4): 309–311.
- 473 Fisch, K.M., Kozfkay, C.C., Ivy, J.A., Ryder, O.A., and Waples, R.S. 2015. Fish Hatchery
474 Genetic Management Techniques : Integrating Theory with North American Journal of
475 Aquaculture Fish Hatchery Genetic Management Techniques : Integrating Theory with
476 Implementation. *North Am. J. Fish. Manag.* **77**(3): 343–357.
477 doi:10.1080/15222055.2014.999846.
- 478 Fleming, I.A., and Gross, M.R. 1993. Breeding success of hatchery and wild coho salmon
479 (*Oncorhynchus kisutch*) in competition. *Ecol. Appl.* **3**(2): 230–245. doi:10.1016/0304-
480 4203(95)00013-H.
- 481 Fleming, I.A., Jonsson, B., and Gross, M.R. 1994. Phenotypic divergence of sea-ranched,
482 farmed, and wild salmon. *Can. J. Fish. Aquat. Sci.* **51**(12): 2808–2824. doi:10.1139/f94-
483 280.
- 484 Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen,
485 A., and Sibert, J. 2012. AD Model Builder: Using automatic differentiation for statistical
486 inference of highly parameterized complex nonlinear models. *Optim. Methods Softw.*
487 **27**(2): 233–249. doi:10.1080/10556788.2011.597854.
- 488 Frankham, R. 2008. Genetic adaptation to captivity in species conservation programs. *Mol.*
489 *Ecol.* **17**(1): 325–333. doi:10.1111/j.1365-294X.2007.03399.x.
- 490 Fraser, D.J. 2008. How well can captive breeding programs conserve biodiversity? A review
491 of salmonids. *Evol. Appl.* **1**(4): 535–586. doi:10.1111/j.1752-4571.2008.00036.x.
- 492 Guay, J.C., Boisclair, D., Rioux, D., Leclerc, M., Lapointe, M., and Legendre, P. 2000.
493 Development and validation of numerical habitat models for juveniles of Atlantic salmon
494 (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **57**: 2065–2075. doi:10.1139/f00-162.

- 495 Hindar, K., Ryman, N., and Utter, F. 1991. Genetic Effects of Cultured Fish on Natural Fish
496 Populations. *Can. J. Fish. Aquat. Sci.* **48**: 945–957. doi:10.1139/f91-1111.
- 497 Hutchings, J.A., Ardren, W.R., Barlaup, B.T., Bergman, E., Clarke, K.D., Greenberg, L.A.,
498 Lake, C., Piironen, J., Sirois, P., Sundt-Hansen, L.E., and Fraser, D.J. 2019. Life-History
499 Variability and Conservation Status of Landlocked Atlantic Salmon. *Can. J. Fish. Aquat.*
500 *Sci.* **0**(0): 1–58. doi:https://doi.org/10.1139/cjfas-2018-0413.
- 501 Hyvärinen, P., and Rodewald, P. 2013. Enriched rearing improves survival of hatchery-reared
502 Atlantic salmon smolts during migration in the River Tornionjoki. *Can. J. Fish. Aquat.*
503 *Sci.* **70**: 1386–1395. doi:10.1139/cjfas-2013-0147.
- 504 Jackson, C.D. and Brown, G.E. 2011. Differences in antipredator behaviour between wild and
505 hatchery-reared juvenile Atlantic salmon (*Salmo salar*) under seminatural conditions.
506 *Can. J. Fish. Aquat. Sci.* **68**: 2157–2166. doi:10.1139/f2011-129.
- 507 Johansen, M., Erkinaro, J., and Amundsen, P.A. 2011. The when, what and where of
508 freshwater feeding. *In Atlantic Salmon Ecology. Edited by Ø. Aas, S. Einum, A.*
509 *Klemetsen, and J. Skurdal.* pp. 89–114. doi:10.1002/9781444327755.ch4.
- 510 Johnsson, J.I., Höjesjö, J., and Fleming, I.A. 2001. Behavioural and heart rate responses to
511 predation risk in wild and domesticated Atlantic salmon. *Can. J. Fish. Aquat. Sci.* **58**(4):
512 788–794. doi:10.1139/f01-025.
- 513 Johnsson, J.I., Brockmark, S., and Näslund, J. 2014. Environmental effects on behavioural
514 development consequences for fitness of captive-reared fishes in the wild. *J. Fish Biol.*
515 **85**: 1946–1971. doi:10.1111/jfb.12547.
- 516 Jonsson, B., and Jonsson, N. 2006. Cultured Atlantic salmon in nature: a review of their
517 ecology and interaction with wild fish. *J. Mar. Sci.* **63**(7): 1162–1181.
518 doi:10.1016/j.icesjms.2006.03.004.
- 519 Jonsson, B., and Jonsson, N. 2014. Early environment influences later performance in fishes.

- 520 (151): 151–188. doi:10.1111/jfb.12432.
- 521 Kamler, J.F., and Pope, K.L. 2001. Nonlethal Methods of Examining Fish Stomach Contents.
522 Rev. Fish. Sci. **9**(1): 1–11. doi:10.1080/20016491101663.
- 523 Kemp, P.S., Gilvear, D.J., and Armstrong, J.D. 2006. Variation in performance reveals
524 discharge-related energy costs for foraging Atlantic salmon (*Salmo salar*) parr. Ecol.
525 Freshw. Fish **15**(4): 565–571. doi:10.1111/j.1600-0633.2006.00200.x.
- 526 Klemetsen, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O’Connell, M.F.,
527 and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L.
528 and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecol.
529 Freshw. Fish **12**(1): 1–59. doi:10.1034/j.1600-0633.2003.00010.x.
- 530 Kortet, R., Laakkonen, M.V.M., Tikkanen, J., Vainikka, A., and Hirvonen, H. 2019. Size-
531 dependent stress response in juvenile Arctic charr (*Salvelinus alpinus*) under prolonged
532 predator conditioning. Aquac. Res. **50**(5): 1482–1490. doi:10.1111/are.14023.
- 533 Kuznetsova, A., Brockhoff, P.B., and Christensen, R.H.B. 2017. lmerTest Package : Tests in
534 Linear Mixed Effects Models. J. Stat. Softw. **82**(13): 1–26. doi:10.18637/jss.v082.i13.
- 535 Law, T.C., and Blake, R.W. 1996. Comparison of the Fast-Start Performances of Closely
536 Related, Morphologically Distinct Threespine Sticklebacks (*Gasterosteus* spp.). J. Exp.
537 Biol. **199**(Pt 12): 2595–604. doi:10.1111/j.1095-8649.2005.00788.x.
- 538 Lee, C.G., and Farrell, A.P. 2003. Excess post-exercise oxygen consumption in adult sockeye
539 (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon following critical speed swimming.
540 J. Exp. Biol. **206**(18): 3253–3260. doi:10.1242/jeb.00548.
- 541 Lumme, J., Ozerov, M., Veselov, A., and Primmer, C. 2016. The Formation of Landlocked
542 Populations of Atlantic Salmon. In Evolutionar Biology of the Atlantic Salmon. Edited
543 by T. Vladic and E. Pettersson. CRC Press. pp. 26–43. doi:10.1201/b18721-4.
- 544 Lundqvist, H., Rivinoja, P., Leonardsson, K., and McKinnell, S. 2008. Upstream passage

- 545 problems for wild Atlantic salmon (*Salmo salar* L.) in a regulated river and its effect on
546 the population. *Hydrobiologia* **602**(1): 111–127. doi:10.1007/s10750-008-9282-7.
- 547 Lynch, M., and O’Hely, M. 2001. Captive breeding and the genetic fitness of natural
548 populations. *Conserv. Genet.* **2**(4): 363–378. doi:10.1023/A:1012550620717.
- 549 Murphy, M.H., Ringler, N.H., and Stewart, D.J. 2017. Comparison of growth and survival of
550 sea-run and landlocked strains of Atlantic salmon *Salmo salar* in the Lake Ontario
551 watershed. *J. Great Lakes Res.* **43**(5): 953–962. doi:10.1016/j.jglr.2017.06.007.
- 552 Näslund, J., Aarestrup, K., Thomassen, S.T., and Johnsson, J.I. 2012. Early enrichment effects
553 on brain development in hatchery-reared Atlantic salmon (*Salmo salar*): no evidence for
554 a critical period. *Can. J. Fish. Aquat. Sci.* **69**(9): 1481–1490. doi:10.1139/f2012-074.
- 555 Näslund, J., Rosengren, M., Del Villar, D., Gansel, L., Norrgård, J.R., Persson, L.,
556 Winkowski, J.J., and Kvingedal, E. 2013. Hatchery tank enrichment affects cortisol
557 levels and shelter-seeking in Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.*
558 **70**(4): 585–590. doi:10.1139/cjfas-2012-0302.
- 559 Norrgård, J.R., Bergman, E., Greenberg, L.A., and Schmitz, M. 2014. Effects of feed quality
560 and quantity on growth, early maturation and smolt development in hatchery-reared
561 landlocked Atlantic salmon *Salmo salar*. *J. Fish Biol.* **85**(4): 1192–1210.
562 doi:10.1111/jfb.12523.
- 563 O’Connor, C.M., Norris, D.R., Crossin, G.T., and Cooke, S.J. 2014. Biological carryover
564 effects : linking common concepts and mechanisms in ecology and evolution. *Ecosphere*
565 **5**(3): 1–11. doi:doi.org/10.1890/ES13-00388.1.
- 566 O’Reilly, P.T.O., and Kozfkay, C.C. 2014. Use of microsatellite data and pedigree
567 information in the genetic management of two long-term salmon conservation programs.
568 *Rev. Fish Biol. Fish.* **24**: 819–848. doi:10.1007/s11160-014-9347-9.
- 569 Ojanguren, A.F., and Braña, F. 2003. Effects of size and morphology on swimming

- 570 performance in juvenile brown trout (*Salmo trutta* L.). *Ecol. Freshw. Fish* **12**: 241–246.
- 571 Pakkasmaa, S. 2001. Morphological differentiation among local trout (*Salmo trutta*)
572 populations. *Biol. J. Linn. Soc.* **72**: 231–239. doi:10.1111/j.1095-8312.2001.tb01313.x.
- 573 Pakkasmaa, S., and Piironen, J. 2001. Water velocity shapes juvenile salmonids. *Evol. Ecol.*
574 **14**(8): 721–730. doi:10.1023/A:1011691810801.
- 575 Pang, X., Yuan, X.-Z., Cao, Z.-D., and Fu, S.-J. 2014. The effects of fasting on swimming
576 performance in juvenile qingbo (*Spinibarbus sinensis*) at two temperatures. *J. Therm.*
577 *Biol.* **42**: 25–32. doi:10.1016/j.jtherbio.2014.02.014.
- 578 Peake, S.J. 2008. Swimming performance and behavior of fish species endemic to
579 Newfoundland and Labrador: A literature review for the purpose of establishing design
580 and water velocity criteria for fishways and culverts. *In* Canadian Manuscript Report of
581 Fisheries and Aquatic Sciences. doi:10.1016/J.TVJL.2013.02.020.
- 582 Piccolo, J.J., Norrgård, J.R., Greenberg, L.A., Schmitz, M., and Bergman, E. 2012.
583 Conservation of endemic landlocked salmonids in regulated rivers: A case-study from
584 Lake Vänern, Sweden. *Fish Fish.* **13**(4): 418–433. doi:10.1111/j.1467-
585 2979.2011.00437.x.
- 586 Plaut, I. 2001. Critical swimming speed: Its ecological relevance. *Comp. Biochem. Physiol. -*
587 *A Mol. Integr. Physiol.* **131**(1): 41–50. doi:10.1016/S1095-6433(01)00462-7.
- 588 Pursiainen, M., Makkonen, J., and Piironen, J. 1998. Maintenance and exploitation of
589 landlocked salmon, *Salmo salar* m. *sebago*, in the Vuoksi Watercourse. *In* Stocking and
590 introduction of fish, *Fishing Ne. Edited by* I.G. Cowx. Blackwell, London. pp. 946–958.
- 591 Rassi, P., Hyvärinen, E., Juslén, A., and Mannerkoski, I. (Editors). 2010. The 2010 Red List
592 of Finnish species. *In* Ympäristöministeriö & Suomen ympäristökeskus. Available from
593 www.environment.fi/redlist.
- 594 Reiriz, L., Nicieza, A.G., and Braña, F. 1998. Prey selection by experienced and naive

- 595 juvenile Atlantic salmon. *J. Fish Biol.* **53**(1): 100–114. doi:10.1006/jfbi.1998.0688.
- 596 Reisenbichler, R.R., and Rubin, S.P. 1999. Genetic changes from artificial propagation of
597 Pacific salmon affect the productivity and viability of supplemented populations. *J. Mar.*
598 *Sci.* **56**: 459–466. doi:10.1111/j.1467-8292.1988.tb01527.x.
- 599 Rimmer, D.M., Saunders, R.L., and Paim, U. 1985. Effects of temperature and season on the
600 position holding performance of juvenile Atlantic salmon (*Salmo salar*). *Can. J. Zool.*
601 **63**: 92–96. doi:doi.org/10.1139/z85-017.
- 602 Robert, A. 2009. Captive breeding genetics and reintroduction success. *Biol. Conserv.*
603 **142**(12): 2915–2922. doi:10.1016/j.biocon.2009.07.016.
- 604 Rodewald, P., Hyvärinen, P., and Hirvonen, H. 2011. Wild origin and enriched environment
605 promote foraging rate and learning to forage on natural prey of captive reared Atlantic
606 salmon parr. *Ecol. Freshw. Fish* **20**(4): 569–579. doi:10.1111/j.1600-0633.2011.00505.x.
- 607 Rohlf, F.J. 2006. A comment on phylogenetic correction. *Soc. Study Evol.* **60**(7): 1509–1515.
608 doi:10.1554/05-550.1.
- 609 Rosengren, M., Kvingedal, E., Näslund, J., Johnsson, J.I., and Sundell, K. 2017. Born to be
610 wild : effects of rearing density and environmental enrichment on stress , welfare , and
611 smolt migration in hatchery-reared Atlantic salmon. *Can. J. Fish. Aquat. Sci.* **74**: 396–
612 405.
- 613 Saikkonen, A., Kekäläinen, J., and Piironen, J. 2011. Rapid growth of Atlantic salmon
614 juveniles in captivity may indicate poor performance in nature. *Biol. Conserv.* **144**(9):
615 2320–2327. doi:10.1016/J.BIOCON.2011.06.010.
- 616 Sánchez-González, J.R., and Nicieza, A.G. 2017. Phenotypic convergence of artificially
617 reared and wild trout is mediated by shape plasticity. *Ecol. Evol.* **7**(15): 5922–5929.
618 doi:10.1002/ece3.3156.
- 619 Shustov, Y.A., Shchurov, N.L., and Veselov, A.E. 1989. Effect of temperature on the physical

- 620 properties of juvenile lake salmon, *Salmo salar sebago*. J. Ichthyol. **29**: 125–127.
- 621 Snyder, N., Derrickson, S., Beissinger, S., Wiley, J.W., Smith, T.B., Toone, W.D., and Miller,
622 B. 1996. Limitations of captive breeding in endangered species recovery. Conserv. Biol.
623 **10**(2): 338–348. doi:10.1111/j.1523-1739.2008.01163.x.
- 624 Soininen, N., Belinskij, A., Vainikka, A., and Huuskonen, H. 2019. Bringing back ecological
625 flows: migratory fish, hydropower and legal maladaptivity in the governance of Finnish
626 rivers. Water Int. **44**: 321–336. doi:10.1080/02508060.2019.1542260.
- 627 Sparrevohn, C.R., and Støttrup, J.G. 2007. Post-release survival and feeding in reared turbot.
628 J. Sea Res. **57**(2–3 SPEC. ISS.): 151–161. doi:10.1016/j.seares.2006.08.010.
- 629 Tessier, N., Bernatchez, L., and Wright, J.M. 1997. Population structure and impact of
630 supportive breeding inferred from mitochondrial and microsatellite DNA analyses in
631 land-locked Atlantic salmon *Salmo salar* L. Mol. Ecol. **6**(8): 735–750.
632 doi:10.1046/j.1365-294X.1997.00244.x.
- 633 Tiira, K., Piironen, J., and Primmer, C.R. 2006. Evidence for reduced genetic variation in
634 severely deformed juvenile salmonids. Can. J. Fish. Aquat. Sci. **63**: 2700–2707.
635 doi:10.1139/F06-154.
- 636 Tomiyama, T., Watanabe, M., Kawata, G., and Ebe, K. 2011. Post-release feeding and growth
637 of hatchery-reared Japanese flounder *Paralichthys olivaceus*: Relevance to stocking
638 effectiveness. J. Fish Biol. **78**(5): 1423–1436. doi:10.1111/j.1095-8649.2011.02949.x.
- 639 Tonteri, A., Titov, S., Veselov, A., Zubchenko, A., Koskinen, M.T., Lesbarrères, D.,
640 Kaluzhin, S., Bakhmet, I., Lumme, J., and Primmer, C.R. 2005. Phylogeography of
641 anadromous and non-anadromous Atlantic salmon (*Salmo salar*) from northern Europe.
642 Ann. Zool. Fennici **42**(1): 1–22. From <http://www.jstor.org/stable/23736697>.
- 643 Vainikka, A., Huusko, R., Hyvärinen, P., Korhonen, P.K., Laaksonen, T., Koskela, J., Vielma,
644 J., Hirvonen, H., Salminen, M., and Grant, J. 2012. Food restriction prior to release

- 645 reduces precocious maturity and improves migration tendency of Atlantic salmon (*Salmo*
646 *salar*) smolts. *Can. J. Fish. Aquat. Sci.* **69**(12): 1981–1993. doi:10.1139/f2012-119.
- 647 Wang, J., and Ryman, N. 2001. Genetic effects of multiple generations of supportive
648 breeding. *Conserv. Biol.* **15**(6): 1619–1631. doi:10.1046/j.1523-1739.2001.00173.x.
- 649 Waples, R.S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from
650 the Pacific Northwest. *Can. J. Fish. Aquat. Sci.* **48**(S1): 124–133. doi:10.1139/f91-311.
- 651 Yan, G.J., He, X.K., Cao, Z.D., and Fu, S.J. 2013. An interspecific comparison between
652 morphology and swimming performance in cyprinids. *J. Evol. Biol.* **26**(8): 1802–1815.
653 doi:10.1111/jeb.12182.

654

655

656

657 **Figure captions**

658

659 **Figure 1.** Map of Finland with the Lake Saimaa basin. The locations of Enonkoski
660 Aquaculture Station (A) and Kainuu Fisheries Research Station (B) and the rivers Pielisjoki
661 and Ala-Koitaajoki (C) are given.

662

663 **Figure 2.** Landmarks and lines used in morphometric measurements of juvenile landlocked
664 Atlantic salmon (*Salmo salar*) raised under three different background conditions.

665

666 **Figure 3.** Feeding activity (number of prey items \pm SE) of juvenile landlocked Atlantic
667 salmon (*Salmo salar*) from three different rearing backgrounds. Different letters indicate
668 statistically significant differences between backgrounds.

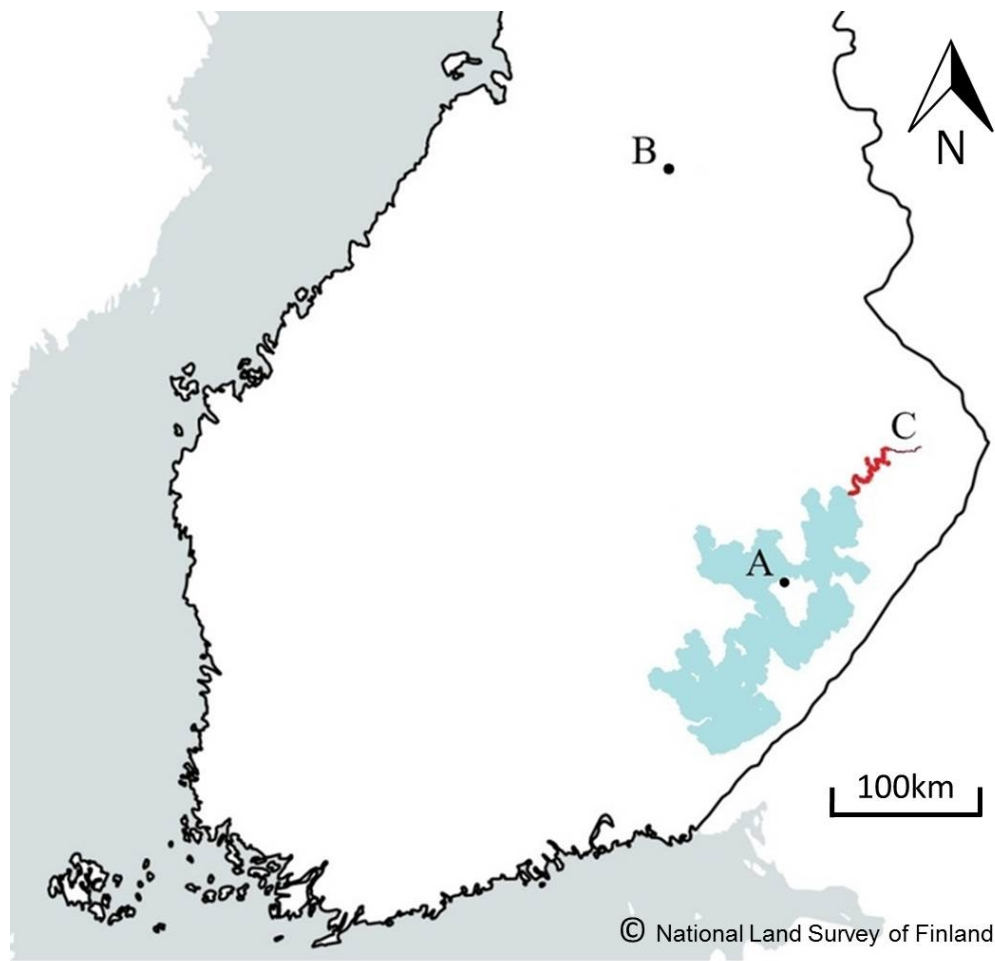
669

670 **Figure 4.** Swimming endurance (unstandardized residuals \pm SE) of juvenile landlocked
671 Atlantic salmon (*Salmo salar*) from three different rearing backgrounds. Letters indicate lack
672 of statistically significant differences between the backgrounds.

673

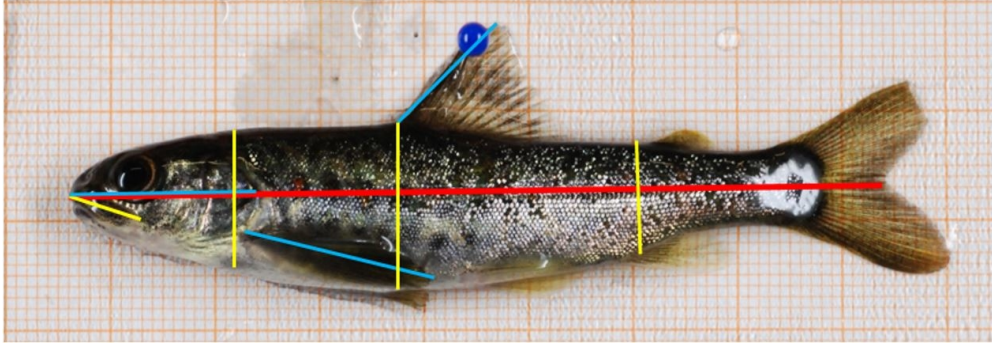
674 **Figure 5.** Principal components with eigenvalue > 1 (left: PC1 \pm SE; right: PC2 \pm SE) from
675 morphometric analysis of juvenile landlocked Atlantic salmon (*Salmo salar*) from three
676 different rearing backgrounds. Different letters indicate statistically significant differences
677 between rearing backgrounds.

678



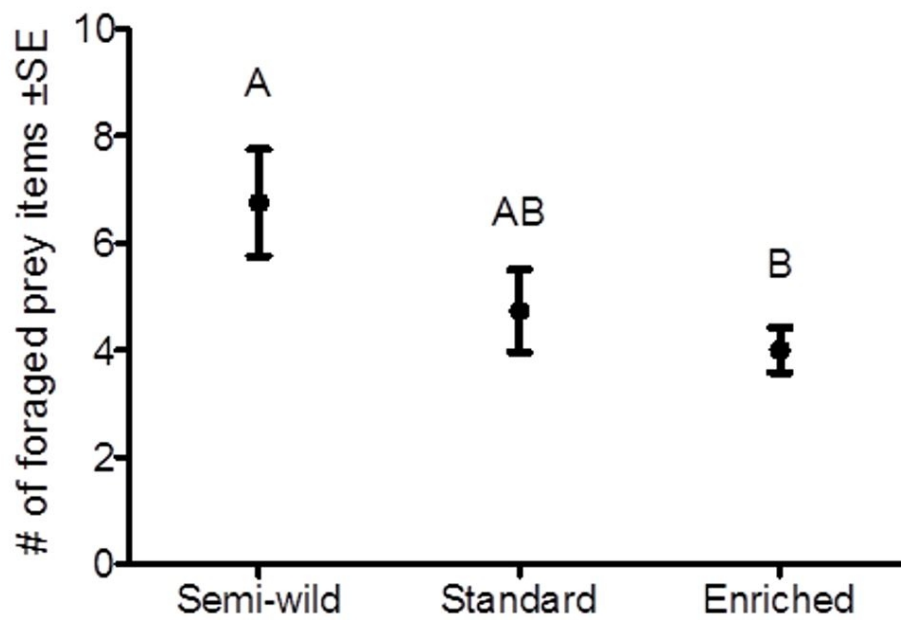
Map of Finland with the Lake Saimaa basin. The locations of Enonkoski Aquaculture Station (A) and Kainuu Fisheries Research Station (B) and the rivers Pielisjoki and Ala-Koitajoki (C) are given.

178x171mm (150 x 150 DPI)



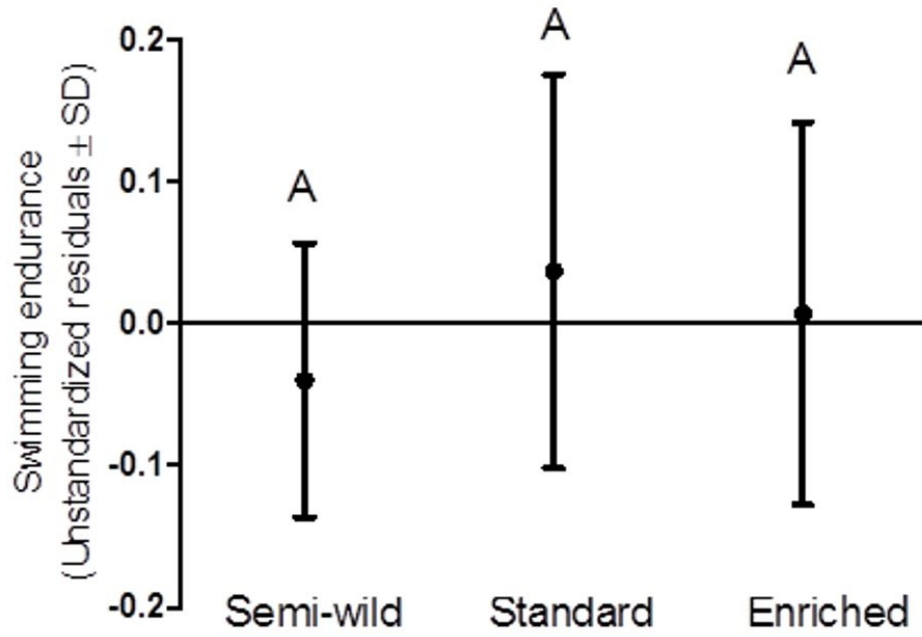
Landmarks and lines used in morphometric measurements of juvenile landlocked Atlantic salmon (*Salmo salar*) raised under three different background conditions.

335x115mm (96 x 96 DPI)



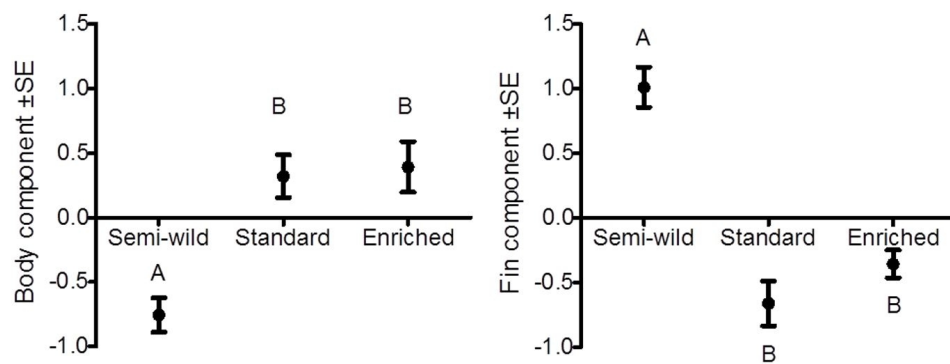
Feeding activity (number of prey items \pm SE) of juvenile landlocked Atlantic salmon (*Salmo salar*) from three different rearing backgrounds. Different letters indicate statistically significant differences between backgrounds.

279x187mm (96 x 96 DPI)



Swimming endurance (unstandardized residuals \pm SE) of juvenile landlocked Atlantic salmon (*Salmo salar*) from three different rearing backgrounds. Letters indicate lack of statistically significant differences between the backgrounds.

254x184mm (96 x 96 DPI)



Principal components with eigenvalue > 1 (left: PC1 \pm SE; right: PC2 \pm SE) from morphometric analysis of juvenile landlocked Atlantic salmon (*Salmo salar*) from three different rearing backgrounds. Different letters indicate statistically significant differences between rearing backgrounds.

380x156mm (96 x 96 DPI)

1 **Table 1.** Mean (\pm SE) sizes of juvenile landlocked Atlantic salmon (*Salmo salar*) from three
 2 different rearing backgrounds. Specific growth rate (SGR) of total length during the
 3 experimental period is also given.

| | Semi-wild | Standard | Enriched | Total |
|----------------------------------|------------------|------------------|------------------|------------------|
| N | 24 | 22 | 30 | 76 |
| Total length (mm) | 78.9 \pm 1.3 | 83.1 \pm 1.4 | 85.2 \pm 1.6 | 82.6 \pm 0.9 |
| Fresh mass (g) | 4.9 \pm 0.2 | 6.0 \pm 0.3 | 6.7 \pm 0.4 | 5.9 \pm 0.2 |
| SGR (% \cdot d ⁻¹) | 0.04 \pm 0.009 | 0.10 \pm 0.007 | 0.11 \pm 0.007 | 0.08 \pm 0.006 |

4

5

6 **Table 2.** Numbers of different prey items ingested by juvenile landlocked Atlantic salmon
 7 (*Salmo salar*) from three different rearing backgrounds during the foraging experiment. The
 8 total number of individuals is shown on the second line.

| | Semi-wild | Standard | Enriched | Total |
|------------------------------|-----------|----------|----------|-------|
| Number of fish | 24 | 22 | 30 | 76 |
| Turbellaria | | | | |
| <i>Planaria</i> spp. | 0 | 1 | 1 | 2 |
| Bivalvia | | | | |
| <i>Pisidium</i> spp. | 0 | 1 | 0 | 1 |
| Crustacea | | | | |
| Cladocera | | | | |
| <i>Bosmina</i> spp. | 0 | 0 | 2 | 2 |
| <i>Daphnia</i> spp. | 44 | 48 | 59 | 151 |
| <i>Leptodora</i> spp. | 24 | 8 | 2 | 34 |
| Cyclopoida | 7 | 9 | 11 | 27 |
| Amphipoda | 1 | 0 | 0 | 1 |
| Isopoda | | | | |
| <i>Asellus aquaticus</i> | 0 | 0 | 2 | 2 |
| Hexapoda | | | | |
| Collembola | 0 | 1 | 0 | 1 |
| Insecta | | | | |
| Ephemeroptera | | | | |
| <i>Leptophlebia</i> spp. | 0 | 0 | 1 | 1 |
| <i>Paraleptophlebia</i> spp. | 2 | 1 | 0 | 3 |
| Ephemeroptera, unidentified | 1 | 1 | 1 | 3 |
| Odonata | | | | |
| Zygoptera | 1 | 0 | 0 | 1 |
| Trichoptera | | | | |
| Polycentropodidae | 5 | 2 | 9 | 16 |
| Limnephilidae | 1 | 0 | 0 | 1 |
| Trichoptera, unidentified | 5 | 4 | 3 | 12 |
| Diptera | | | | |
| <i>Chaoborus</i> spp. | 38 | 16 | 21 | 75 |
| <i>Chironomidae</i> spp. | 20 | 12 | 8 | 40 |
| <i>Psychodidae</i> spp. | 1 | 0 | 0 | 1 |
| Unidentified prey | 5 | 5 | 11 | 21 |
| Total | 149 | 109 | 131 | 389 |
| Average per background | 6.2 | 5.0 | 4.4 | 5.1 |
| SD per background | 4.9 | 3.6 | 2.3 | 3.8 |

9

10 **Table 3.** Total fresh mass (mg) of prey items consumed by juvenile landlocked Atlantic salmon
 11 (*Salmo salar*) from three different rearing backgrounds in the foraging experiment. The total
 12 number of individuals is shown on the second line.

| | Semi-wild | Standard | Enriched | Total |
|------------------------------|-----------|----------|----------|-------|
| Number of fish | 24 | 22 | 30 | 76 |
| Turbellaria | | | | |
| <i>Planaria</i> spp. | 0 | 5.5 | 3.6 | 9.1 |
| Bivalvia | | | | |
| <i>Pisidium</i> spp. | 0 | < 0.1 | 0 | < 0.1 |
| Crustacea | | | | |
| Cladocera | | | | |
| <i>Bosmina</i> spp. | 0 | 0 | < 0.1 | < 0.1 |
| <i>Daphnia</i> spp. | < 0.1 | < 0.1 | < 0.1 | < 0.1 |
| <i>Leptodora</i> spp. | 6.2 | < 0.1 | < 0.1 | 6.2 |
| Cyclopoida | < 0.1 | < 0.1 | < 0.1 | < 0.1 |
| Amphipoda | 10.7 | 0 | 0 | 10.7 |
| Isopoda | | | | |
| <i>Asellus aquaticus</i> | 0 | 0 | 4.2 | 4.2 |
| Hexapoda | | | | |
| Collembola | 0 | < 0.1 | 0 | < 0.1 |
| Insecta | | | | |
| Ephemeroptera | | | | |
| <i>Leptophlebia</i> spp. | 0 | 0 | 0.3 | 0.3 |
| <i>Paraleptophlebia</i> spp. | 1.6 | 0.7 | 0 | 2.3 |
| Ephemeroptera, unidentified | < 0.1 | < 0.1 | < 0.1 | < 0.1 |
| Odonata | | | | |
| Zygoptera | 4.8 | 0 | 0.1 | 4.8 |
| Trichoptera | | | | |
| <i>Polycentropodidae</i> | 6.9 | < 0.1 | 6.4 | 13.3 |
| <i>Limnephilidae</i> | 2.6 | 0 | 0 | 2.6 |
| Trichoptera, unidentified | 2.7 | 4.4 | 0.3 | 7.4 |
| Diptera | | | | |
| <i>Chaoborus</i> spp. | 29.3 | 8.6 | 4.5 | 42.4 |
| <i>Chironomidae</i> spp. | 6.9 | 3.6 | 1.1 | 11.6 |
| <i>Psychodidae</i> spp. | 0.6 | 0 | 0 | 0.6 |
| Unidentified prey | 19.9 | 10.6 | 15.4 | 45.9 |
| Total | 92.2 | 33.4 | 35.8 | 161.4 |
| Average per background | 3.8 | 1.5 | 1.2 | 2.1 |
| SD per background | 5.0 | 2.4 | 2.1 | 3.5 |

13
 14
 15

16 **Table 4.** Principal component analysis with Rotated Component Matrix of morphometric
 17 measurements of juvenile landlocked Atlantic salmon (*Salmo salar*) from three different rearing
 18 backgrounds. Two components ('body' component and 'fin' component) with eigenvalues > 1
 19 were identified. Loadings < 0.3 are not shown in the matrix.

| | Rotated Component Matrix | |
|---------------------|--------------------------|--------|
| | 1 | 2 |
| Body height 1 | 0.776 | |
| Body height 2 | 0.940 | |
| Body height 3 | 0.951 | |
| Dorsal fin length | | 0.929 |
| Head length | 0.860 | |
| Upper jaw length | 0.684 | |
| Pectoral fin length | | 0.854 |
| Eigenvalues | 4.125 | 1.484 |
| Total variance % | 58.924 | 21.198 |
| Cumulative % | 58.924 | 80.121 |

20