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Author(s): Syrjänen, Jukka; Ruokonen, Timo; Ketola, Tarmo; Valkeajärvi, Pentti

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1 **Does stocking eggs into boreal spawning rivers increase the abundance of brown trout**
2 **parr?**

3

4 Jukka Tapani Syrjänen, Timo Juhani Ruokonen, Tarmo Ketola and Pentti Valkeajärvi

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6 Correspondence:

7 Jukka Tapani Syrjänen, e-mail: jukka.t.syrjanen@jyu.fi

8 Department of Biological and Environmental Science, University of Jyväskylä, PO Box 35,

9 FI-40014 University of Jyväskylä, Finland

10 tel: +358 505454615, fax: +358 142602321

11

12 Timo Juhani Ruokonen, e-mail: timo.j.ruokonen@jyu.fi

13 Department of Biological and Environmental Science, University of Jyväskylä, PO Box 35,

14 FI-40014 University of Jyväskylä, Finland

15

16 Tarmo Ketola, e-mail: tarmo.t.ketola@jyu.fi

17 Centre of Excellence in Biological Interactions, Department of Biological and Environmental

18 Science, University of Jyväskylä, PO Box 35, FI-40014 University of Jyväskylä, Finland

19

20 Pentti Valkeajärvi, e-mail: pentti.valkeajarvi@gmail.com

21 Finnish Game and Fisheries Research Institute, Survontie 9, FI-40500 Jyväskylä, Finland

22

23 Running title: stocking brown trout eggs into boreal rivers

24

25 Abstract

26

27 Stocking with eggs has been widely used as a management measure to support degraded
28 salmonid stocks. In Finland, Atlantic salmon and both sea-migrating and lake-migrating
29 brown trout are stocked as eggs, alevins, fry, parr and smolt, while trout are also stocked as
30 mature fish. The aim of this stocking is to improve catches and to support collapsed spawning
31 stocks. We assessed the success of stocking with brown trout eggs in a study of seventeen
32 Finnish boreal forest rivers, of which nine were subject to egg stocking. All rivers contained
33 some naturally spawning trout. In sixteen rivers, including non-stocking years and unstocked
34 rivers, egg stocking did not increase total (wild and stocked) density of 0-year-old parr.
35 However, those rivers with higher existing trout densities in non-stocking years seemed to
36 benefit most from stocking, suggesting some role of river-specific extrinsic factors affecting
37 egg-to-parr survival. In one river monitored for 14 years, only a weak correlation was found
38 between the total density of 0-year-old parr and the number of eggs stocked. However in nine
39 parr samples from five rivers, the mean proportion of parr derived from stocked eggs was 40
40 %. Mean survival to first autumn parr of egg-stocked and wild individuals was 1.0 % and 3.3
41 %, respectively. Probable reasons for the detected low to moderate impact of egg-stocking are
42 1) large variation in total parr density between years and rivers, 2) low number of stocked
43 eggs, 3) placing egg boxes and egg pockets in unsuitable microhabitats, and 4) unsuitable
44 emergence time of egg-stocked individuals, or other extrinsic factors creating extra mortality.
45 We recommend field and laboratory experiments to improve and standardize stocking
46 methods, and monitoring the connection of wild spawning stocks and parr recruitment.
47 Finally, we encourage fishery authorities to create clear management goals for threatened wild
48 salmonid stocks.

49

50 Key words: alevin, Alizarin red, egg box, egg pocket, stock management, otolith, redd, *Salmo*
51 *trutta*, survival
52

53 **Introduction**

54

55 Stocking of eggs or hatched alevins has been widely used as a management measure to
56 support natural parr production of salmonid fishes in rivers (Prignon *et al.*, 1999) and lakes
57 (Bronte *et al.*, 2002) or to expand their natural distribution range. Various methods have been
58 used, including eggs in pipes that are pushed into gravel, egg boxes, and pouring eggs directly
59 onto the bottom substratum (Barlaup and Moen, 2001; Kirkland, 2012). Eggs or alevins,
60 rather than parr, have been used in stocking, as eggs are cheaper to stock than parr and are
61 easy to transport (Johnson, 2004). Moreover, egg-stocked fish go through most phases of their
62 life span in their natural environment, and thus experience natural selection, which could keep
63 the genotypes and phenotypes of populations as near to natural as possible (Kirkland, 2012).

64

65 Globally, egg stocking has been used for stocks of the genus *Salmo* for more than a century
66 (Kirkland, 2012). The success of the action could be estimated as egg-to-parr survival or as
67 comparisons between different stocking methods. However, most studies are cases of one
68 river, one year and one method (Beall *et al.*, 1994; Raddum and Fjellheim, 1995; Coghlan and
69 Ringler, 2004), or are limited only to the alevin phase (Kirkland, 2012). Barlaup and Moen
70 (2001) reviewed egg stocking or egg incubation methods, but could report egg/alevin survival
71 only until alevin hatching and emergence.

72

73 In Finland, egg or alevin stocking has been used in the stock management of Atlantic salmon
74 (*Salmo salar*), and sea-migrating and lake-migrating brown trout (*Salmo trutta*) for more than
75 a century. From the 1980s or 1990s, egg or alevin stocking has been used annually as a
76 recovery action for sea-migrating brown trout in rivers of the Finnish coast of the Baltic Sea,
77 and in some years for Atlantic salmon in Finnish and Swedish rivers of the Bothnian Bay.
78 However, the largest Finnish electrofishing dataset from egg-stocked rivers is available for

79 brown trout in the southern Lake District. There, trout is stocked annually as eggs, alevins,
80 emerged parr (fry), older parr, smolt or mature fish to improve recreational fishing catches
81 and to support spawning stocks. Currently, wild spawning stocks of trout are small, and
82 individual spawners are of small size and are probably mostly resident, non-migrating. Only
83 very few trout of 70 cm long or more, i.e. migratory individuals, are now observed in Lake
84 District rivers yearly (authors, unpublished). The mean length of the spawning redds of trout
85 in the region is clearly smaller than in other boreal rivers still holding lake-migrating stocks
86 (Syrjänen *et al.*, 2014a). These observations indicate smaller-sized, probably resident, female
87 spawners. Historically, spawners were 70 cm long and over 4 kg on average and were lake-
88 migrating, and they were abundant in spawning rivers (Syrjänen and Valkeajärvi, 2010; P.
89 Valkeajärvi, pers. comm). Thus, natural egg density is now most likely low. In Finland south
90 from the Arctic Circle, lake-migrating brown trout is classified as endangered and sea-
91 migrating trout as critically endangered in the 2010 Red List of Finnish Species (Rassi, 2010),
92 and the main reasons for this are high fishing mortality in lakes (Syrjänen and Valkeajärvi,
93 2010) and in coastal areas (Kallio-Nyberg *et al.*, 2007), along with river damming.

94

95 Here we assess the success of stocking of brown trout eggs in forest rivers in the Finnish Lake
96 District. To reveal the impact on parr abundance, we evaluated the total autumnal density of
97 0-year-old trout in eight stocked (impact) and eight non-stocked (control) rivers. Secondly, for
98 one river with 14 years of monitoring data, we analysed the relation between the yearly parr
99 density and the number of eggs introduced. Thirdly, we estimated the proportion of stocked
100 individuals in parr populations from nine parr samples from five rivers, and compared egg-to-
101 parr survival of stocked and wild individuals in four of the five rivers.

102

103 **Materials and methods**

104

105 **Hatchery stocks**

106

107 The Finnish Game and Fisheries Research Institute (FGFRI) maintains twelve brown trout
108 hatchery stocks from Finnish inland waters. In the Finnish Lake District there are two stocks:
109 the Rautalampi stock from the Kymijoki watershed and the Vuoksi stock from the Vuoksi
110 watershed (Fig 1). The Rautalampi hatchery stock was renewed by few migratory mature fish
111 in 1990s from Lake Päijänne region, midst of the study area, but after that, no wild mature
112 lake-migrating spawners have been caught in the rivers. First hatchery generation used in egg
113 production in the beginning of 2000s were grown from the gametes of these wild fish. In
114 2000s, the hatchery stock has been renewed by wild parr sampled in the rivers of the
115 Rautalampi watercourse, such as Taikinainen and Karinkoski which are included in this study
116 as stocked rivers. Parr were grown to maturity in the hatchery. These originally wild fish were
117 also used as spawners in the hatchery, but their eggs comprised 10 % of eggs used in this
118 work, and 90 % of eggs were from the first or second hatchery generation. During 2006–
119 2011, the Rautalampi stock has produced 40–60 litres of eggs annually, one litre containing
120 6555 eggs as an average between years (SD 482) (R. Kannel, FGFRI, pers. comm.), that have
121 been stocked into some tens of rivers of the Kymijoki and the Kokemäenjoki watersheds (Fig.
122 1). Since 2008, trout eggs produced by the FGFRI have been marked by adding Alizarin red S
123 to the egg tanks to create colour marks in alevin bones. Alizarin can then be detected in the
124 fish otoliths in the laboratory, although the fish must be killed for this. The otoliths are
125 analyzed under ultraviolet light with a fluorescent microscope, and a clear fluorescent area is
126 seen in the centre of the otolith of an Alizarin-coloured fish.

127

128 **Study rivers**

129

130 The study area covers all the most important watercourses and approximately half of the most
131 important free spawning rivers for brown trout in the Finnish Lake District. Seventeen rivers
132 situated in the Kymijoki, Kokemäenjoki or Vuoksi watersheds were used in the study (Table
133 1). Some rivers were parts of the same watercourses, but were situated more than 10 km apart
134 and separated by lakes; two egg stocking rivers, Taikinainen and Karinkoski, were situated
135 only 200 m from each other but were separated by a large pool. Thus, 0-year-old brown trout
136 were presumed not to move between the rivers. Average channel width of rivers was 5 to 100
137 m and mean discharge 1 to 150 m³ s⁻¹. Twelve rivers were situated in a lake outlet and five
138 rivers 0.5 to 10 km downstream from a lake. Upstream sections of the watercourses of most
139 rivers consisted of a chain of lakes, and thus floods and movements of fine particles in the
140 channels were mild. Channel bottoms comprised mainly stones of 10–100 cm in diameter, but
141 also contained gravel. Large woody debris was sparse. All rivers were undammed. The
142 riparian zones and catchment areas were mainly forest, and water quality was good or
143 excellent. In one stocking river, Virtalankoski, lower water quality might restrict reproduction
144 of brown trout (Table 1). Bottom ice occasionally formed in channels in winter.

145

146 All rivers had been dredged by narrowing their channels and removing or blasting boulders
147 during previous centuries for timber floating, lowering lake surfaces or powering mills, but all
148 have since been restored, except Kalkkistenkoski, Saajoki and Ohrajoki. In restoration since
149 the 1980s, some boulders and stones were replaced in channels, channels were widened a
150 little, and some spawning areas were created for trout with artificial gravel (see Muotka and
151 Syrjänen, 2007). Dredging and restoration actions were usually less disruptive in large rivers
152 than in small rivers. During the study period, light channel restoration was done in three
153 stocked rivers, Taikinainen in 2002 and 2005, Karinkoski in 2002 and 2005, and Vihovuonne
154 in 2007–2008, and in one unstocked river, Läsänkoski in 2004, 2006 and 2009. Low numbers
155 of brown trout parr of 1 and 2 years old were introduced to some rivers during sampling

156 years, but no parr of 0-year-old. No other management measures were applied to the channels.
157 The availability to the study of appropriate unstocked rivers with no management measures
158 was very restricted.

159

160 **Wild fish stocks**

161

162 Brown trout reproduces naturally, but not always annually, in all seventeen rivers. Two life
163 history forms occur in most rivers, the common small-sized resident non-migrating form and
164 the rare large-sized lake-migrating form. The natural trout egg density was estimated to be
165 mainly 1–10 eggs m⁻² in riffle sections based on counts and lengths of redds (see Syrjänen and
166 Valkeajärvi, 2010). The total mean density of one year old or older parr was 4.5 individuals
167 100 m⁻² in stocked rivers and 6.0 individuals 100 m⁻² in unstocked rivers in electrofishing
168 samples taken in September or October. As the density was low to moderate, and as the lake
169 outlets supply abundant prey like filter-feeding insect larvae (Richardson and Mackay, 1991),
170 competition from older parr was presumed not to affect the density of 0-year-old parr. Other
171 fish species in the study rivers in order of appearance in electrofishing catches were bullhead
172 (*Cottus gobio*), burbot (*Lota lota*), stone loach (*Barbatula barbatula*), perch (*Perca*
173 *fluviatilis*), roach (*Rutilus rutilus*), pike (*Esox lucius*), bleak (*Alburnus alburnus*), grayling
174 (*Thymallus thymallus*), ruffe (*Gymnocephalus cernuus*) and stocked or escaped rainbow trout
175 (*Oncorhynchus mykiss* Walbaum).

176

177 **Egg stocking methods**

178

179 All egg stockings were actual management actions, not experimental treatments. The eggs
180 were fertilized in hatcheries in September or October. The eggs of the Rautalampi stock were
181 produced by the FGFRI Laukaa Fish Farm and used in the Kymijoki and Kokemäenjoki

182 watersheds, and the eggs of the Vuoksi stock were produced by FGFRI Saimaa Fisheries
183 Research and Aquaculture and used in the Vuoksi watershed. Stocking was done by hatchery
184 personnel, by local river fishery organisers, or in some cases by research personnel, usually in
185 March when eggs were in the “eyed” phase. Only some experts among the stocking personnel
186 had experience of observing real trout redds in rivers. A tree sprout pipe of 60 mm in diameter
187 and Whitlock-Vibert© plastic egg stocking boxes were used as stocking methods, often
188 simultaneously in the same river, or only one method in one river through the study
189 (Supplementary data). Both methods allow alevins to swim out freely. When using the pipe,
190 some tens of egg pockets were created in the gravel beds in riffle sections of the upper parts
191 of the rivers, and 100–200 mL of eggs were introduced into each hole in the gravel at a depth
192 of 5–10 cm. With egg boxes, 100–200 mL of eggs were laid into each box, but not gravel.
193 Each box was buried partly inside gravel and between stones of 10–20 cm of diameter, or just
194 laid on the bottom surface with a weight. 10–30 egg boxes were used in each river. Water
195 depth was 15–50 cm at sites with pipe egg pockets or egg boxes.

196

197 In both methods, 6 000–30 000 (approximately 0.9–4.6 L) of eggs were used per river and
198 year, and the stocking density was 1–10 eggs m⁻² for riffle sections. The number of stocked
199 eggs per river corresponds to the number of eggs from approximately 5–22 kg of mature
200 female trout biomass including eggs, or from 1–5 migrating females with mean size of 4–5
201 kg. The mean wet mass of eggs produced by FGFRI hatchery females is 15 % of the mass of a
202 large female including eggs, and the mean wet mass of an egg of a large female is 0.11 g
203 (Turkka and Arkko, 2004).

204

205 In the box stocking method, the boxes were removed from the channels in June, when the
206 number of dead eggs or alevins was always 20 or less per box. No accumulation of fine
207 particles in boxes was detected in any river.

208

209 **Collection of three data sets**

210

211 In the sixteen-river dataset, the total (wild + stocked) density of 0-year-old parr was used as
212 the dependent variable. Density was estimated by electrofishing two to five constant sampling
213 areas, total 300–800 m² per river, mainly by the three-pass-removal method, in September or
214 October. River-specific catchability values were used. The gears used were backpack
215 Geomega FA4 or FA3, backpack Deka Lord 3000, and Lugab with aggregator. The same gear
216 was used in each river through the study. Approximately 80 % of the artificial egg pockets
217 and egg boxes were situated inside the electrofishing sampling areas or less than 20 m
218 upstream, and the other 20 % were located 20–50 m upstream. Data were collected from 2000
219 to 2011, but the number of sampling years per river was 4–12. The number of stocking years
220 and the number of non-stocking years were both 2–10 per stocked river. Unstocked rivers
221 were sampled in exactly the same years as stocked rivers. Thus, yearly fluctuation in
222 environmental factors, like river flow at the time of electrofishing, should not have any
223 noticeable effect on the final results of the impact, as regional floods or droughts occur
224 simultaneously in most or all of the study rivers. The total number of density observations
225 was 122.

226

227 In the Simunankoski data set, electrofishing was done in 1996 and from 1999 to 2011. In this
228 river, there were ten stocking years and four non-stocking years, and 10 000–30 000 eggs
229 were stocked per stocking year. This corresponds to the egg number of 2–5 migrating
230 females.

231

232 In the otolith dataset, nine parr samples yielding a total of 198 individuals of 0-year-old parr
233 were taken from five rivers (Table 1) in September-October 2009 to 2012, each sample

234 consisting of 5–30 fish. The otoliths were removed and analyzed in the laboratory, and the
235 proportions of individuals derived from stocked eggs and of wild individuals were calculated.
236 To estimate survival of egg-stocked and wild individuals, the size of habitat area suitable for
237 0-year-old parr was estimated for four rivers from map measurements and field observations
238 made during electrofishing and redd counting, but Kalkkistenkoski Rapids was too large
239 (Table 1) and spatially too complicated for such estimates. Each of the four rivers was
240 bordered by a lake or a large pool at its upper and lower end, so each river length was
241 measured precisely. The size of suitable habitat area was calculated using the Internet service
242 Paikkatiетоikkuna (www.paikkatiетоikkuna.fi) by three field assistants independently, and
243 average values were used. Riffle area shallower than 1 m was classified as suitable habitat,
244 but boat routes were excluded. The numbers of egg-stocked and wild parr were estimated by
245 multiplying the density estimates for both groups from electrofishing samples by the size of
246 the suitable habitat area.

247

248 The sample size of otoliths per river was restricted because we limited killing a threatened
249 species, as wild individuals were also expected to occur in the samples. Thus, discussion of
250 results from proportional occurrence and survival estimates is mainly on the means among the
251 five rivers.

252

253 The number of wild eggs was estimated by redd counting and measuring, done by wading in
254 the same four rivers and for the same year classes in October–November, prior to egg stocking
255 in March. Three rivers were waded completely, and Simunankoski to a depth of 1–1.5 m, by
256 experienced personnel. Redd tail lengths were measured with a ruler stick. Clear redd-shaped
257 pits were classified as redds, but small and unclear pits were carefully dug out, and if 1–2
258 eggs were found the pit was identified as a redd (see Syrjänen *et al.*, 2014a). The fork length
259 of a spawned female trout (L , cm) was estimated for each redd from the redd tail length (q ,

260 cm) as $\ln L = 0.60 \cdot \ln q + 0.86$ (modified from Crisp and Carling, 1989). The egg number (E)
261 buried by the female in her redd was calculated from the female fork length (L , mm) as $E =$
262 $0.006266 \cdot L^{2.048}$ (Elliott 1995). Egg numbers in redds were summed for each river. To
263 account for mortality of wild eggs during winter, 90 % of wild eggs were assumed to survive
264 until March (see Syrjänen *et al.*, 2008), the time of egg stocking. Survival was calculated as
265 the proportion of parr numbers in autumn from egg number in March, separately for wild and
266 stocked eggs and parr.

267

268 **Data analysis**

269

270 The data from sixteen rivers were first analysed using a general linear model with maximum
271 likelihood (ML) and restricted maximum likelihood (REML) (IBM SPSS statistics v20)
272 methods. The total (wild + stocked) density of 0-year-old parr was explained by the fixed
273 effect of the river type (stocked, unstocked). The fixed effect of stocking year (stocking, non-
274 stocking) was nested within a river type, as only the stocked rivers were stocked. To control
275 for regional conditions, such as water quality, weather or fishing restrictions that could affect
276 general trout abundance within the region, river pair was fitted as a fixed factor, a pair
277 meaning a stocked river and a nearby unstocked river. General yearly variation was taken into
278 account by fitting year as a fixed factor. To control for the non-independence of the
279 subsequent observations from the same rivers over time, identity of the river was fitted as a
280 random factor. Models were chosen by AIC (from ML models), and parameter estimates were
281 obtained with REML. The model selection was performed on the subset of possible models
282 that contained factors relevant to our study questions (stocking). As stocking was nested
283 within the river type, no model contained effects of stocking without river type. The egg
284 stocking method (pipe or box) could not be included as a factor, as the data were unbalanced
285 for this factor, and both methods were often used simultaneously (Supplementary data).

286

287 To explore further the determinants of stocking success, we analysed whether the overall parr
288 density in non-stocking years (proxy for natural parr density of the river), number of eggs
289 stocked and their interaction could affect parr density in stocked rivers. After standardization
290 to a mean of zero, these effects were fitted as continuous covariates. This REML model
291 included also a random effect of river identity, and year as a fixed factor. Note that since non-
292 stocked rivers were not considered in this analysis, fitting a regional factor was not
293 meaningful (i.e. since fitting single site within each region).

294

295 In the Simunankoski data set, the correlation of the total (wild + stocked) autumnal density of
296 0-year-old parr and the number of eggs stocked was analyzed in 14 observation years.

297

298 In the otolith dataset, survival between egg-stocked and wild individuals was analysed with
299 paired samples t-test, and correlation in survival between the two groups was analyzed with
300 seven observations (Kalkkistenkoski excluded).

301

302 **Results**

303

304 We used the sixteen-river dataset to test several different combinations of explanatory factors;
305 using AIC as a selection criterion, the best model contained effects of river identity, river
306 type, and stocking nested within river type (Table 2). We therefore restrict our results and
307 discussion to this model, which is sufficiently parsimonious but still captures the details of
308 our setup (effects of stocking and effects due to control and stocked rivers).

309

310 Among the sixteen rivers, the type of river (stocked, unstocked) did not affect trout density
311 ($F_{[1,18.056]} = 0.003$, $P = 0.959$); mean density (from estimated marginal means) was 11.3 in

312 stocked rivers and 11.6 individuals 100 m⁻² in unstocked rivers. Moreover, the effect of
313 stocking was weak in the stocked rivers ($F_{[1,111.760]} = 0.850$, $P = 0.430$); mean density was
314 12.9 in stocking years and 9.7 in non-stocking years (Fig. 2). Thus, the average, but non-
315 significant, effect of egg stocking was approximately 3 individuals 100 m⁻² (see also
316 Supplementary data). River identity affected densities (variance 85.87, standard error of the
317 mean 37.76, Wald $Z = 2.274$ $P = 0.023$) and the variation in the parr density between rivers
318 and years was large (Fig. 2).

319

320 We also found that higher levels of egg stocking (number of eggs) increased parr densities in
321 stocked rivers ($b = 0.00578$, $SE = 0.00205$, $F_{1, 11.432} = 7.984$, $P = 0.016$), although the average
322 natural parr density did not indicate a significant effect on yearly parr density ($b = 0.919$, SE
323 $= 0.637$, $F_{1, 4.105} = 2.085$, $P = 0.221$). However, interaction of stocking and natural density
324 indicated that at high natural densities the egg stocking was more effective in increasing the
325 total parr density ($b = 0.000102$, $SE = 2.164 \times 10^{-5}$, $F_{1, 9.972} = 22.341$, $P = 0.001$). River identity
326 did not affect variation in parr density (Wald $Z = 1.338$, $P = 0.181$), but we did find an effect
327 of year ($F_{1, 8.602} = 4.373$, $P = 0.021$).

328

329

330 In Simunankoski Rapids, the Spearman correlation coefficient between the number of eggs
331 stocked and the total (wild + stocked) parr density was positive but non-significant when the
332 four non-stocking years were included ($r = 0.434$, $P = 0.121$, $n = 14$), or excluded ($r = 0.523$,
333 $P = 0.121$, $n = 10$) (Fig. 3).

334

335 According to otolith analysis, the average proportion of individuals originating from egg
336 stocking was 39.9 %, (range 0–100 %) in the nine samples from five rivers. In three samples,
337 the proportion was remarkably high, 77–100 % (Table 3). Average egg-to-parr survival of

338 egg-stocked and wild individuals from time of egg stocking (usually March) to September-
339 October was 1.0 %, (range 0–2.6) and 3.3 % (0–9.0), respectively (Table 3). No difference
340 was detected in survival between egg-stocked and wild trout ($t_6 = 1.57$, $P = 0.168$). If the two
341 samples smaller than 20 fish were excluded, the average proportion of egg-stocked
342 individuals was 49.2 % (range 5.0–100), and the average egg-to-parr survival of egg-stocked
343 and wild individuals was 1.2 % (0.3–2.6) and 2.3 % (0–6.8), respectively. The survival
344 estimates for egg-stocked and wild individuals did not correlate (Spearman $r = -0.179$, $P =$
345 0.702 , $n = 7$).

346

347 **Discussion**

348

349 **Efficiency of trout egg stocking**

350

351 Using a 12-year dataset of egg-stocking and population estimates from 16 rivers, and a data
352 set of ten stocking years from one river of these, we found rather low average effectiveness of
353 brown trout egg stocking in rivers in the Finnish Lake District. Moreover, according to otolith
354 analysis the egg-to-parr survival was low, even though the proportion of marked otoliths in
355 parr samples was higher than expected with respect to the two other data sets.

356

357 Although egg stocking is widely used, its effectiveness at increasing parr abundance has
358 rarely been assessed. In another field experiment with brown trout eggs made in northern
359 Finland, stocking had a positive impact on parr density, but only in sites without natural parr
360 (Niva *et al.*, 2012). However, the design of this earlier study lacked non-stocking years at
361 stocked rivers, and the eggs were poured directly to the channel substratum.

362

363 **Why is egg-stocking apparently ineffective in Finland?**

364

365 There are several possible reasons for the low to moderate average effectiveness of egg
366 stocking. First, large annual and spatial variation in total parr density lowered the possibility
367 to detect an impact of stocking by reducing the test power. The variation is probably due to
368 annual variation in egg-to-parr survival of wild and/or egg-stocked individuals and in wild
369 egg production. Survival in the hatching and/or emergence period may be particularly affected
370 by temporal and spatial fluctuations in factors like water temperature (Jensen and Johnsen,
371 1999; Sternecker *et al.*, 2014), floods (Jensen and Johnsen, 1999), food supply, and fish
372 predation (Brännäs, 1995). In addition, distribution of 0-year-old salmonids may be patchy
373 (Beall *et al.*, 1994; Einum *et al.*, 2011), and the location of high and low density patches may
374 change from year to year. Catchability during electrofishing is affected by river flow level at
375 the time of sampling (Ugedal *et al.*, 2008), but our sixteen-river design included river pairs
376 with nearby control rivers, which should have decreased any effects of interannual differences
377 in discharge. Enlarging the total sampling areas electrofished would also diminish this
378 problem by producing more accurate information about yearly parr densities, but labour
379 resources for this are usually not available.

380

381 Second, number of stocked eggs per occasion was low, corresponding to only few large
382 females. Third, mean survival of stocked eggs to first autumn parr was low. This may be
383 partly a consequence of placing egg boxes and egg pockets in unsuitable microhabitats,
384 producing extra mortality. The stocking procedure was not standardized, as stocking
385 personnel changed between rivers and years, and the skills of the persons varied.
386 Alternatively, the timing of hatching and/or of emergence of egg-stocked individuals may
387 differ from the natural population, as the timing of egg fertilization is decided by hatchery
388 personnel, perhaps starting the egg incubation period before or after the peak spawning period
389 of natural populations. As a result, the timing of emergence in spring may differ between the

390 egg-stocked population and the natural population, which may result in different survival
391 between the two groups depending on temporal fluctuation of mortality factors. In addition,
392 the length of the “spawning period” of hatchery fish, i.e. the time when the fish are milked
393 and eggs are fertilized, is normally only some hours, but the length of the spawning period of
394 a natural brown trout stock may well be weeks. Thus, the emergence period could be shorter
395 in an egg-stocked population (see Syrjänen *et al.* 2008) than in a natural population in the
396 same river, which in turn may create more yearly fluctuation in mortality of the egg-stocked
397 population at emergence. In other words, if environmental factors during the short emergence
398 period happen to be optimal, so that water temperature and discharge are optimal, prey are
399 abundant and fish predation is low, then egg stocking may be effective. But if the
400 environmental factors during emergence are sub-optimal, egg stocking may have only a
401 negligible impact on the total parr density. In a natural population, the longer emergence
402 period could equalize the impact of these temporally varying mortality factors. Indeed in our
403 parr otolith data, the large temporal and spatial variation in proportion of egg-stocked
404 individuals in samples (Table 3) and the lack of correlation between survival of wild and egg-
405 stocked individuals support these hypotheses.

406

407 Interestingly, we also found that those rivers that already had higher natural density of trout
408 seemed to benefit most from stocking. This suggests a role for external factors that reduce
409 survival of both wild eggs and/or parr, but also effectiveness of egg stocking. This result
410 could indicate that the parr densities are far from carrying capacity in the study rivers. If
411 carrying capacity is a limiting factor, we would expect to see negative or diminishing effects
412 of stocking on overall density in rivers with high natural reproduction. Then in some cases,
413 egg stocking may be very important to maintain parr production, as the highest proportions of
414 egg-stocked parr were 77–100 % in three otolith samples. In extreme cases (such as
415 Myllynkoski), without egg stocking the species might even disappear from the river (Table 3).

416

417 **Egg-to-parr survival of stocked and wild individuals**

418

419 In six published egg stocking case studies of rivers, the survival estimates for Atlantic salmon
420 from egg to first fall parr vary strongly, as the range was approximately 0–20 % (Table 4).
421 However, many of these stockings were probably experimental actions done by skilful
422 experts, not hatchery personnel perhaps partly lacking knowledge of the proper microhabitat
423 for eggs. Our result for average egg-to-parr survival of 1 % is low, but not unusual, compared
424 to the published results. In wild populations in the other six studies, the survival of brown
425 trout or Atlantic salmon from egg to first fall parr was mainly 1–5 % (Table 4), so the mean
426 survival in our study of 3 % is well within the published range. Hence the survival estimates
427 for wild and stocked individuals seem to be quite similar, but encompass a wide natural range.
428 Thus in general, egg stocking could be a valid method to boost degraded stocks.

429

430 Unfortunately, we could not observe survival during the alevin or emergence period, but
431 Syrjänen *et al.* (2008) observed high survival of eggs until hatching (83–98 %) in an egg
432 incubation experiment in rivers Arvajanjoki and Rutajoki in the Kymijoki watershed with
433 eggs from the same Rautalampi hatchery stock as used in this work. In that earlier study, eggs
434 were again mainly from the first or second hatchery generation, but survival was very high. In
435 Barlaup and Moen's (2001) review, average survival of salmonid eggs, mainly of the genus
436 *Salmo*, was 67 %, (range 6–98 %, n of sites/rivers=31) to hatching, and 57 % (range 5–98 %,
437 n=10) to emergence. In our study, egg boxes never included appreciable numbers of dead
438 eggs or alevins in June, but some dead eggs or alevins may have decomposed and disappeared
439 from the boxes. However, the occurrence of significant mortality could rather occur during
440 and immediately after the emergence period (Brännäs, 1995). The boxes might not have
441 mimicked natural egg pockets, especially in their shallow burial. In this scenario, when

442 alevins leave the boxes they might occupy the surface of gravel beds instead of being inside
443 beds between particles. On the gravel surface they could then face higher predation or
444 unsuitably high water velocity.

445

446 We could not compare results from different stocking methods. Harshbarger and Porter
447 (1982) compared the pipe and the box methods, and concluded that pipes produced higher
448 average egg-to-parr survival than Whitlock-Vibert© boxes (29 % vs. 8 %, respectively).
449 However in that study, boxes accumulated large amounts of sand, and the sediment volume
450 correlated positively with egg mortality. Rigorous comparisons of different methods by field
451 experiments and in artificial channels with reasonable spatial and temporal scales are needed.

452

453 **Stock-recruitment connections**

454

455 Only local information about the number of eggs laid by the natural spawning stock and about
456 the stock-recruitment relationship can provide an accurate basis for egg or parr stocking into a
457 particular river, but unfortunately this information is usually lacking, as it is for our study
458 rivers. Supportive egg stocking will increase parr abundance only if the number of eggs
459 produced by the natural spawners is clearly less than the number that yields the highest parr
460 abundance. Globally, only few appropriate stock-recruitment curves have been created for the
461 genus *Salmo*. In Black Brows Beck, sea-migrating brown trout parr density peaked at 60 eggs
462 m^{-2} (Elliott, 1994). In the River Imsa, Atlantic salmon smolt number was highest at both 6 and
463 60 eggs m^{-2} (Jonsson, Johnson and Hansen, 1998). In the Nivelle River, Atlantic salmon parr
464 density was highest at 5 eggs m^{-2} of riffle habitat (Dumas and Prouzet, 2003), and in Girnock
465 Burn, an egg density of 3.4 eggs m^{-2} yielded the highest smolt number (Buck and Hay, 1984).
466 A wide range in the optimal egg density estimates between studies and rivers may result from
467 variation in sampling methods, quality of physical parr habitats, prey supply, smoltification

468 age, or survival between rivers. In the Finnish Lake District, annual monitoring of spawning
469 stocks, estimates of egg-to-parr survival for both wild and stocked individuals, and creation of
470 stock-recruitment estimates are needed for better management of collapsed salmonid stocks.

471

472 **Parr abundance of boreal lake-migratory stocks**

473

474 Historically in the Finnish Lake District rivers, egg density was most probably much higher
475 than now, as there were annually tens or hundreds of lake-migrating female spawners per
476 river, and the mean female size was over 4 kg (Syrjänen and Valkeajärvi, 2010; P.
477 Valkeajärvi pers. comm). Currently, fishing mortality in lakes prevents the maturation and
478 spawning of lake-migrating individuals. In rivers, observations of large (i.e. migratory)
479 individuals returning from lakes are very few (authors, unpublished). Syrjänen *et al.* (2014b)
480 marked 5762 stream trout of length 14–65 cm and mainly wild, with Carling or t-anchor tags
481 in rivers of the Kymijoki watercourse . As tag controls, 933 tag observations were made on
482 marking rivers prior to possible lake migration, 107 observations on lakes, and 1 observation
483 of a mature fish in the marking river returned from lake migration to spawn. In lake tag
484 returns, the average length of caught trout was 47 cm, and no fish reached a length of 70 cm.
485 Thus, the egg number is most likely limiting the parr number now, but other factors, like
486 environmental conditions or predation, will also affect egg and parr survival. The highest
487 reported average densities of 0-year-old brown trout in autumn electrofishing samples over
488 several years in Finland were 120 individuals 100 m⁻² in the Kivikoski Rapids in Arvajanjoki
489 in 1984–1993 (Syrjänen and Valkeajärvi, 2010) and 43 individuals 100 m⁻² in the River
490 Kitkajoki in the northern Oulankajoki watershed in 1987–1994 (Mäki-Petäys *et al.*, 2000). In
491 both cases, the female spawners were mainly lake-migrating and 50–80 cm (1.5–7 kg) in size.
492 In the upper part of Vindelälven in North Sweden, the average density of 0-year-old brown
493 trout was 61 individuals 100 m⁻² in the 6 km long main reproduction site of a lake-migrating

494 brown trout stock in 2006–2012 (M. Bidner, Ekom AB, Sweden, pers. comm.). In six
495 tributaries of Lake Vättern in Sweden, the among-river average was 61 individuals 100 m⁻²,
496 but 146 in the best river Röttleå, in 2000–2012, and spawners were mainly migratory from
497 Lake Vättern (Olsson and Johansson, 2013). In our study including the best trout rivers in the
498 Finnish Lake District, the average density was only 11 individuals 100 m⁻² including egg-
499 stocked individuals.

500

501 **Management goals for wild migratory salmonids**

502

503 To conclude, our results emphasize that collapsed and strongly harvested stocks of migratory
504 salmonids cannot easily be stimulated by egg stocking alone. The action might raise parr
505 density significantly if higher numbers of eggs were used, and if the stocking methods were
506 improved. However, stocking of tens of litres of eggs per river would need financial and
507 labour resources not available, and the current supply of eggs in hatcheries is insufficient. But
508 standardization of the egg stocking methods, as has been done in egg incubation experiments
509 by developing standardized egg sandwich (Pander *et al.*, 2009) and floating box (Pander *et*
510 *al.*, 2010) methods, could produce more accurate information about the effect of the action, or
511 perhaps higher survival of egg-stocked individuals. On the other hand, continuous stocking of
512 eggs, parr or smolts into waters where individuals could reproduce naturally, raises question
513 about the goals of fishery management (see Youngson *et al.*, 2003). Stocking, even of eggs,
514 may change the genotype of stocks if the practice continues for decades or centuries.

515

516 In Finland, the benefits of current egg stocking practices are at best moderate. Moreover,
517 stocking of parr and smolts has only produced weak yields during recent decades according to
518 tag returns from trout in the Finnish Lake District (Syrjänen *et al.*, 2011) or in the Finnish
519 coast of the Baltic Sea (Kallio-Nyberg *et al.* 2007), or from Atlantic salmon in the Baltic Sea

520 (Kallio-Nyberg *et al.* 2013). Nor has another common management action, channel
521 restoration, succeeded in restoring brown trout spawning stocks, or raising parr abundance
522 (Muotka and Syrjänen, 2007; Syrjänen and Valkeajärvi, 2010; Vehanen *et al.*, 2010), or
523 appreciably improving parr habitat quality (Huusko and Yrjänä, 1997; Korsu *et al.*, 2010). If
524 wild salmonids stocks in Finland are to recover, we recommend that fishery administrations
525 should create clear management goals for wild salmonid stocks, and decrease fishing
526 mortality by regulation of lake or coastal sea fishing effort.

527

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529

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539

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541

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- 672

673 **Table 1.** The rivers used in the different study designs (16r=16 rivers, SR=Simunankoski
 674 Rapids, o=otolith analysis), pair number in design 16s, watershed (K=Kymijoki,
 675 Ko=Kokemäenjoki, V=Vuoksi), location in lake outlet (y=yes, n=no), geographical location,
 676 size, and selected mean water chemistry characteristics in the 17 study rivers in southern
 677 Finland in 2000–2011. Tot-P values may be overestimations for Ohrajoki (tributary), as water
 678 samples were taken from its main river Pengerjoki.

River	Used in design	River pair	Water-shed	Lake outlet	Latitude (N)	Longitude (E)	Mean channel width (m)	River order	pH	Tot-P ($\mu\text{g}\cdot\text{l}^{-1}$)
Stocked rivers										
Kalkkistenkoski	16r, o	1	K	y	61° 17'	25° 35'	105	6	7.2	7
Myllynkoski	16r, o	2	K	y	61° 44'	26° 08'	15	4	7.0	8
Muuramenjoki	16r, o	3	K	y	62° 08'	25° 41'	19	4	6.9	9
Taikinainen	16r	4	K	y	62° 36'	26° 19'	90	4	6.9	6
Karinkoski	16r	5	K	n	62° 36'	26° 19'	90	4	6.9	6
Simunankoski	16r, SR, o	6	K	y	62° 23'	26° 11'	42	5	6.9	7
Virtalankoski	16r	7	Ko	n	62° 18'	24° 44'	14	4	5.9	23
Vihovuonne	16r	8	V	y	62° 24'	28° 43'	85	5	6.9	6
Unstocked rivers										
Läsänkoski	16r	1	K	y	61° 54'	26° 54'	38	4	6.8	11
Arvajanjoki	16r	2	K	y	61° 41'	25° 10'	12	3	6.6	4
Saajoki	16r	3	K	n	61° 59'	25° 24'	4	3	6.1	16
Koivujoki	16r	4	K	n	63° 23'	26° 23'	15	3	6.8	13
Ohrajoki	16r	5	K	n	62° 22'	25° 06'	7	3	6.0	26
Huopanankoski	16r	6	K	y	63° 33'	25° 02'	20	4	6.9	12
Multianjoki	16r	7	Ko	y	62° 25'	24° 44'	10	3	6.2	14
Puuskankoski	16r	8	K	n	61° 34'	26° 43'	25	5	7.0	5
Additional stocked river										
Sahankoski	o		K	y	63° 08'	25° 57'	40	4	7.0	12

679

680

681 **Table 2.** Model selection for the best predictive model for the total density of 0-year-old
 682 brown trout parr across 16 rivers. -2LL denotes twice the log likelihood whereas AIC denotes
 683 Akaike information criteria (smaller is better). The best model is highlighted with bold.

Model	Model equation	-2 LL	AIC
1	y=river pair+river type+stocking(river type)+year+riverID	937.219	985.219
2	y=river type+stocking(river type)+year+riverID	943.154	977.154
3	y=river pair+river type+stocking(river type)+riverID	958.602	984.602
4	y=river pair+river type+year+riverID	939.536	983.536
5	y=river type+stocking(river type)+riverID	963.669	975.669

684

685

686 **Table 3.** Number of sampled 0-year-old brown trout (N) per river, proportion of individuals
 687 originating from egg stocking (E), and estimated survival of egg-stocked (S_E) and wild (S_W)
 688 individuals from March through to September-October. ND = No data.

River	Year	N	E (%)	S_E (%)	S_W (%)
Myllynkoski	2011	22	100	0.3	0.0
Muuramenjoki	2011	30	77	1.1	0.4
Muuramenjoki	2012	30	27	1.7	6.8
Sahankoski	2010	5	0	0.0	9.0
Sahankoski	2011	26	31	0.8	1.5
Simunankoski	2009	28	25	0.7	3.9
Simunankoski	2010	30	80	2.6	1.2
Kalkkistenkoski	2009	20	5	ND	ND
Kalkkistenkoski	2010	7	14	ND	ND
Mean			40	1.0	3.3

689

690 **Table 4.** Mean survival estimates (S, %) from egg until first fall parr of egg-stocked and wild
 691 individuals of brown trout or Atlantic salmon in published papers. LAS=landlocked Atlantic
 692 salmon, AS=Atlantic salmon, BT=brown trout. *=until first winter, †=until 1st July.

Species	River	S (%)	Author
Egg-stocked			
LAS	Salmon River	0	Coghlan and Ringler, 2004
AS	Beaver Brook	0.8	Johnson, 2004
AS	a Scottish stream	11.1–14.8	Egglshaw and Shackley, 1980
AS	Bjørnbettelva	2–24	Einum and Nislow, 2005
AS	Ekso	c.a. 10–20	Raddum and Fjellheim, 1995
AS	a French stream	11.8*	Beall <i>et al.</i> , 1994
Wild			
BT	Rutajoki	0.7–5.1	Syrjänen, Sivonen and Sivonen, 2014a
BT	Black Brows Beck	2–5	Elliott, 1994
BT	Wilfin Beck	1–5	Elliott, 1994
BT	Kernec Brook	5	Bagliniere <i>et al.</i> , 1994
AS	Tobique River	3.8	Gibson <i>et al.</i> , 2009
AS	Nivelle River	1.0	Dumas and Prouzet, 2003
AS	Catamaran Brook	30.7†	Cunjak and Therrien, 1998

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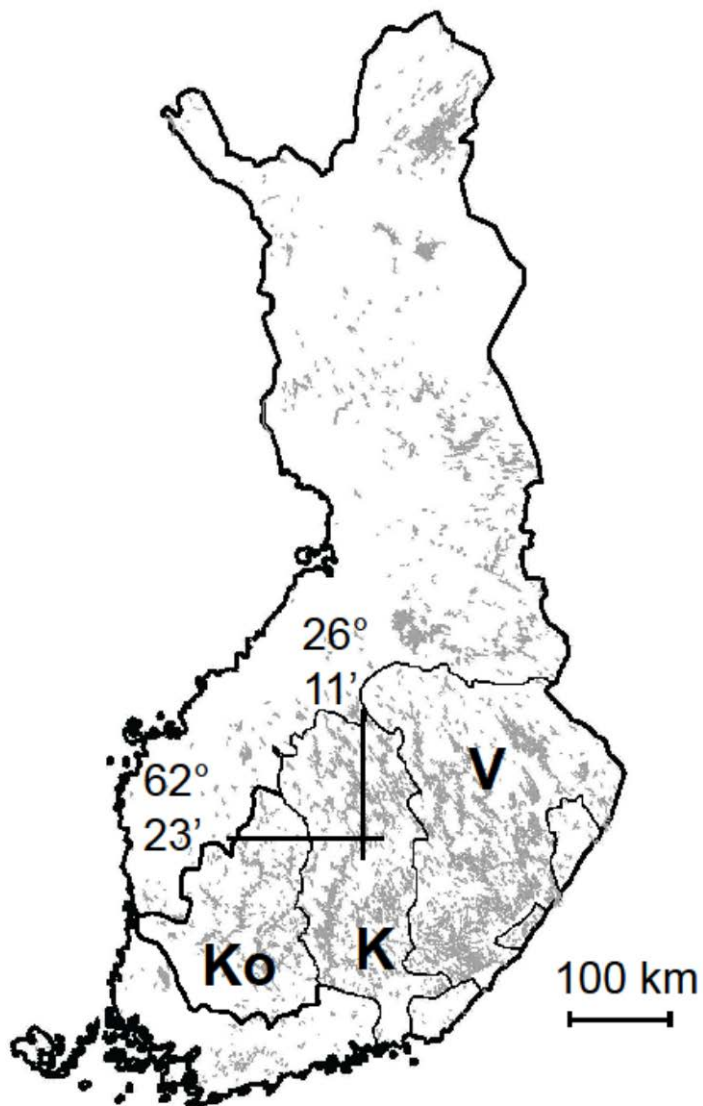
695 **Supplementary data.** Total (wild and egg-stocked) density of 0-year-old brown trout
 696 (individuals per 100 m²) in eight stocked rivers and eight unstocked rivers in southern Finland
 697 in egg stocking (s) years and non-stocking (non-s) years in design 16r, number of observation
 698 years (N), and stocking method used.

River	River pair	Density in s years			Density in non-s years			Egg stocking method
		Mean	Range	N	Mean	Range	N	
Stocked rivers								
Kalkkistenkoski	1	9	3–14	2	15	15–16	2	Box, pipe
Myllynkoski	2	8	2–20	6	2	0–4	2	Box, pipe
Muuramenjoki	3	10	6–14	2	14	1–23	10	Box
Taikinainen	4	7	6–8	2	2	0–4	2	Box, pipe
Karinkoski	5	10	2–19	2	13	7–19	2	Box, pipe
Simunankoski	6	38	16–58	9	22	14–38	3	Pipe, box
Virtalankoski	7	2	0–6	3	2	0–4	9	Box
Vihovuonne	8	2	0–4	2	6	1–10	3	Box, pipe
Mean		11			9			
Unstocked rivers								
Läsänkoski	1	8	1–14	2	8	0–15	2	
Arvajanjoki	2	17	2–30	6	20	16–24	2	
Saajoki	3	3	1–5	2	5	0–15	10	
Koivujoki	4	12	5–19	2	8	7–9	2	
Ohrajoki	5	12	0–24	2	10	6–14	2	
Huopanankoski	6	7	1–14	9	5	1–11	3	
Multianjoki	7	19	6–40	3	35	4–77	9	
Puuskankoski	8	3	0–5	2	2	0–3	3	
Mean		10			11			

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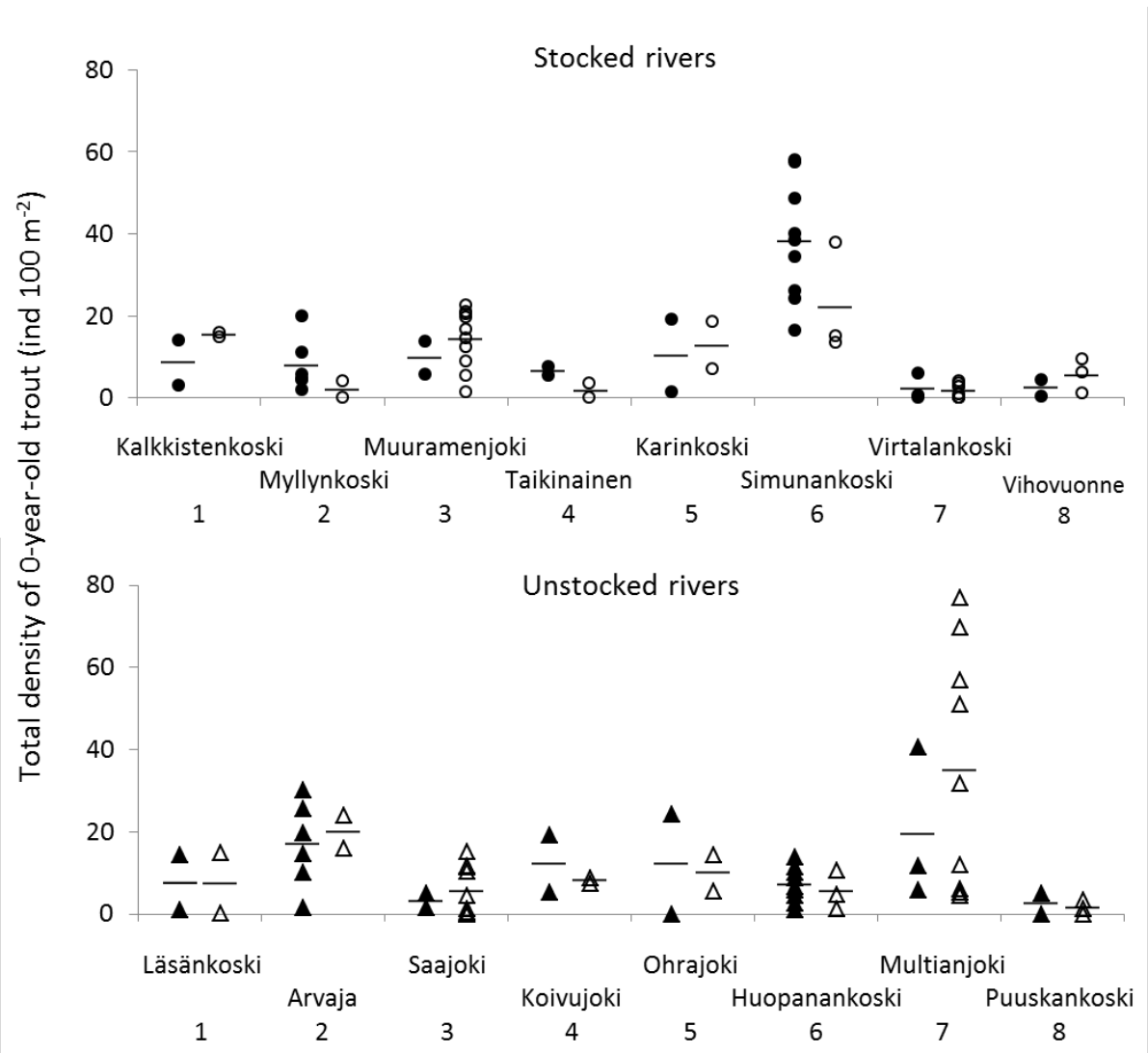
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702

703 **Figure 1.** Location of the the Kokemäenjoki (Ko), Kymijoki (K) and Vuoksi (V) watersheds
704 in southern Finland. The location of the Simunankoski Rapids is shown with latitude and
705 longitude values. Lakes are shown in grey.

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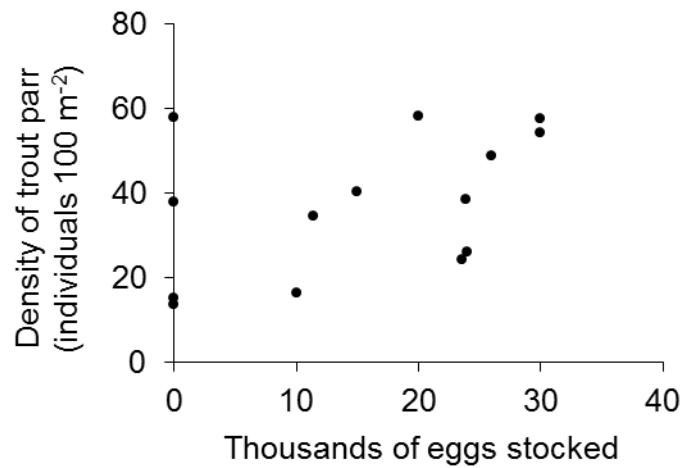


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708

709 **Figure 2.** Total (wild and egg-stocked) autumnal density of 0-year-old brown trout parr in
 710 sixteen rivers in the Finnish Lake District in 2000–2011. Black symbols indicate yearly parr
 711 density in stocked and unstocked (control) rivers in stocking years, and open symbols indicate
 712 parr density in non-stocking years. Line symbols indicate average values in each river in
 713 stocking years and non-stocking years. Numbers below river names indicate river pairs.

714



715

716 **Figure 3.** Total (wild and egg-stocked) annual density of 0-year-old brown trout parr related
717 to the number of eggs stocked in Simunankoski Rapids in years 1996 and 1999–2011.
718 Spearman $r = 0.434$, $P = 0.121$. Eggs were stocked in spring and the river was electrofished in
719 the following autumn of the same calendar year.