



International Institute for  
Applied Systems Analysis  
Schlossplatz 1  
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342  
Fax: +43 2236 71313  
E-mail: [publications@iiasa.ac.at](mailto:publications@iiasa.ac.at)  
Web: [www.iiasa.ac.at](http://www.iiasa.ac.at)

---

## Interim Report

IR-10-039

### **Divergent trends in life-history traits between Atlantic Salmon *Salmo salar* of wild and hatchery origin in the Baltic Sea**

Anssi Vainikka ([anssi.vainikka@oulu.fi](mailto:anssi.vainikka@oulu.fi))  
Irma Kallio-Nyberg ([irma.kallio-nyberg@rktl.fi](mailto:irma.kallio-nyberg@rktl.fi))  
Mikko Heino ([mikko.heino@imr.no](mailto:mikko.heino@imr.no))  
Marja-Liisa Koljonen ([marjaliisa.koljonen@rktl.fi](mailto:marjaliisa.koljonen@rktl.fi))

---

#### **Approved by**

Ulf Dieckmann  
Program Leader, EEP

July 2011

## Contents

Abstract.....	2
Introduction .....	3
Materials and methods.....	6
Data.....	6
Assignment of maturity .....	7
Correction of length-at-age.....	8
Estimation of the probabilistic maturation reaction norms .....	9
Length-at-release and length-at-age .....	11
Results .....	12
Age-at-maturation.....	12
Length-at-release .....	13
Length-at-age.....	13
Probabilistic maturation reaction norms .....	14
Discussion.....	16
Conclusions .....	21
Acknowledgements .....	22
References .....	22
Tables .....	31
Figures .....	37
Figure captions .....	42

1

2

3

## **Divergent trends in life-history traits between Atlantic**

4

## **Salmon *Salmo salar* of wild and hatchery origin in the Baltic Sea**

5

6

7

A. VAINIKKA<sup>\*†</sup>, I. KALLIO-NYBERG<sup>‡</sup>, M. HEINO<sup>§</sup> AND M-L. KOLJONEN<sup>£</sup>

8

9

<sup>†</sup>*Institute of Coastal Research, Swedish Board of Fisheries, Box 109, SE-74 222,*

10

*Öregrund, Sweden.* <sup>‡</sup>*Finnish Game and Fisheries Research Institute, Quark Fisheries*

11

*Research Station, Korsholmanpuistikko 16, FI-65100 Vaasa, Finland.* <sup>§</sup>*Department of*

12

*Biology, University of Bergen, Box 7800, NO-5020 Bergen, Institute of Marine*

13

*Research, Bergen, Norway, and International Institute for Applied Systems Analysis,*

14

*Laxenburg, Austria.* <sup>£</sup>*Finnish Game and Fisheries Research Institute, Box 2, FI-*

15

*00791, Helsinki, Finland.*

16

17

*\* Present address: Section of Ecology, Department of Biology, University of Oulu, Box*

18

*3000, FI-90014 University of Oulu, Finland.*

19

20

*\*Author to whom correspondence should be addressed: Tel.: +358 8 5531221; fax:*

21

*+358 8 5531061; e-mail:anssi.vainikka@oulu.fi.*

22

23

24

**Running headline: LIFE-HISTORY CHANGES IN ATLANTIC SALMON**

25 **ABSTRACT**

26

27 Four Atlantic salmon *Salmo salar* L. stocks in the Baltic Sea, varying in their  
28 breeding history, were studied for changes in life-history traits over years 1972–1995.  
29 Length-at-age of recaptured fish had increased throughout the study period, partly due  
30 to increased temperature and increased length-at-release, but also due to remaining  
31 cohort effects that could represent unaccounted environmental or genetic change.  
32 Simultaneously, maturation probabilities controlled for water temperature and length-  
33 at-release had increased in all stocks, but most notably in the broodstock-based River  
34 Oulujoki salmon, which also had the highest lengths-at-age. The least change was  
35 observed in the River Tornionjoki salmon that was subject only to supportive  
36 stockings originating from wild parents. These results suggest a long-term divergence  
37 between semi-natural and broodstock based salmon stocks. Increased length-at-age  
38 could not be statistically linked to advanced maturation, and it remains an open  
39 question to which extent the generally increased probabilities to mature at early age  
40 reflected underlying genetic changes.

41

42 Key words: anadromous; fishing-induced evolution; hatchery; life-history; maturation  
43 reaction norm; selection

## INTRODUCTION

44

45

46 While the exploitation rates of most Atlantic salmon *Salmo salar* L. stocks have  
47 recently decreased to ecologically sustainable levels it is still prudent to study if  
48 management practises impose selective pressures on life-history traits, thereby  
49 potentially affecting the long-term sustainability of the fishery (Allendorf *et al.*, 2008;  
50 Hard *et al.*, 2008). At population level, age and size at maturation and size-at-age  
51 commonly show temporal variation in both Atlantic and Pacific salmons due to  
52 environmental and fishing-induced demographic changes (Ricker, 1981; Quinn *et al.*,  
53 2006). Life-history traits of salmon have also been found to be highly heritable  
54 (Gjerde, 1984; 1986) and therefore potentially affected by selective fishing (Ricker,  
55 1981; Hard *et al.*, 2008). Furthermore, many salmon populations, especially in the  
56 Baltic Sea, are supported by hatchery reared smolts, and potential adaptations to  
57 captivity can influence genetics of wild populations (Frankham, 2008; Hutchings &  
58 Fraser, 2008).

59

60 Selection from fishing and hatchery breeding may operate in opposite directions:  
61 while fishery usually targets large salmon and might thereby select against fast  
62 growth, hatchery rearing and size-dependent survival of released fish may favour  
63 increased growth rates (Gjedrem, 1979). Hatchery rearing also affects age-at-  
64 maturation, migration patterns, morphology, survival and several physiological traits  
65 (Kallio-Nyberg & Koljonen, 1997; Fleming *et al.*, 2002; Handeland *et al.*, 2003;  
66 Jokikokko *et al.*, 2004; Kostow, 2004; Saloniemi *et al.*, 2004; Hutchings & Fraser,  
67 2008). However, fishery may also target grilse (1 sea-winter (SW) salmon) due to  
68 their high abundance, and the effect of hatchery rearing depends on the origin of fish

69 used in the production of the new generation. Therefore, the expected effects are case-  
70 specific and require studies how the selection regimes arising from fishing and  
71 hatchery practises affect the trait distributions in hatchery-supported fish stocks  
72 (Hutchings & Fraser, 2008).

73

74 The abundance of Atlantic salmon in the Baltic Sea decreased by the end of the 20's  
75 century not only due to damming of natal rivers but also due to heavy fishing pressure  
76 during the feeding migration (Eriksson & Eriksson, 1993; Jutila *et al.*, 2003a). In  
77 order to maintain commercial offshore salmon fishery, about 5 million hatchery-  
78 reared smolts are annually released into the Baltic Sea. Baltic salmon parr spend two  
79 to four years in the river before smoltification (Jutila & Pruuki, 1988), and the number  
80 of winters spend in the sea prior to spawning migration most commonly varies  
81 between one and three years. In 1995–2000, the average proportion of 1 sea-winter  
82 (SW), 2SW, 3SW, 4SW and repeat spawners accounted for respectively 12, 52, 30,  
83 0.4 and 6% of the River Tornionjoki catch samples (Romakkaniemi *et al.*, 2003).

84

85 Water temperature during the feeding migration in the sea has a major role in shaping  
86 the realised growth rate (*e.g.* Friedland *et al.*, 2000). Fast growth usually translates  
87 into earlier maturation in salmon (Hutchings & Jones; 1998), due to both the genetic  
88 correlation between growth and maturation and the facilitating effect of the fast  
89 phenotypic growth (Gjerde, 1984). Due to the strong impact of environmental factors  
90 on both growth and maturation of salmon, these effects need to be disentangled from  
91 possible genetic factors when assessing potentially evolutionary changes within or  
92 genetic differences between stocks. The concept of probabilistic maturation reaction  
93 norm (PMRN) offers a statistical aid that can help to disentangle genetic effects from

94 environmentally driven phenotypic variation in maturation schedules (Heino *et al.*,  
95 2002; Heino & Dieckmann, 2008). A PMRN describes a population-level probability  
96 of an average individual reaching maturity as a function of age and predominantly  
97 environmentally driven variables, such as length-at-age. Other environmental  
98 measures can readily be incorporated (Heino *et al.*, 2002; Grift *et al.*, 2007, Heino &  
99 Dieckmann, 2008), and the ability of PMRNs to reflect a genetic property depends on  
100 the degree to which the included variables can capture important sources of plasticity  
101 (reviewed by Dieckmann & Heino, 2007).

102

103 This study compares variation in two central life history traits, 1) growth rate in a  
104 hatchery (as length-at-release) and during the feeding migration (as length-at-age) and  
105 2) maturation patterns (PMRNs) over time among four Atlantic salmon stocks, Rivers  
106 Iijoki, Oulujoki, Tornionjoki and Simojoki. In total, these four stocks usually produce  
107 about 40 % of the salmon catch in the Gulf of Bothnia, and the River Tornionjoki is  
108 the most productive salmon river in the whole Baltic Sea area (ICES, 2008). These  
109 stocks represent two contrasting breeding regimes. The first two stocks ('hatchery  
110 group') are maintained entirely by continuous broodstock breeding, which has been  
111 continuing for Oulujoki salmon since 1955 and Iijoki salmon since 1965; naturally  
112 reproducing salmon populations of Rivers Oulujoki and Iijoki were lost when the  
113 rivers were dammed for the production of hydroelectricity. The current River  
114 Oulujoki stock is a mixture of several Baltic salmon stocks, including the original  
115 River Oulujoki salmon (Säisä *et al.*, 2003). The other two stocks ('semi-natural  
116 group') are maintained predominantly by natural reproduction, although hatchery-  
117 reared smolts and juveniles originating from wild-caught parents have been released  
118 supportively (Romakkaniemi *et al.*, 2003; Jutila *et al.*, 2003a). Estimated proportion

119 of stocked smolts of all smolts has varied from 0% to over 90% in the Tornionjoki  
120 and Simojoki salmon (Romakkaniemi *et al.*, 2003), but among returning adults the  
121 proportion of reared fish has been lower due to their lower survival (Jokikokko *et al.*,  
122 2006; Jokikokko & Jutila, 2009). Stocked salmon accounted 8–35% of River  
123 Tornionjoki salmon returners in 1984-2000 (Romakkaniemi *et al.*, 2003).

124

## 125 MATERIALS AND METHODS

126

### 127 DATA

128

129 Several millions of 2- or 3-year-old smolts and parr, raised under standard hatchery  
130 conditions, have been released into the estuaries of the study rivers since 1960's  
131 (Romakkaniemi *et al.*, 2003). Prior to the release, all fish were tagged with Carlin-  
132 tags, and the total length of each fish was recorded (length-at-release from here on).  
133 Tag-recovery data collected from the multinational commercial salmon fishery since  
134 year 1972 were obtained from the Finnish Game and Fisheries Research Institute.  
135 It is known that large and old salmon may migrate to the rivers before they are  
136 effectively sampled by the fishery. Because the opening date of fishery has been  
137 variably regulated since 1996 (Romakkaniemi *et al.*, 2003) only fish recaptured prior  
138 to 1996 were included in the analyses. Recaptures consisted of fish belonging to four  
139 river stocks, Rivers Oulujoki (N=3271), Iijoki (N=2632), Simojoki (N=1146), and  
140 Tornionjoki (N=487) (Fig. 1). Recaptures of the River Simojoki salmon included a  
141 number of wild fish (N=615, 53.7% of the River Simojoki fish) tagged as smolts  
142 during their migration to the sea.

143

144 All the study stocks are susceptible to mixed-stock fishery in the feeding areas of the  
145 Baltic Sea (ICES, 2008). The legal minimum landing size of salmon is 60 cm except  
146 in the Bothnian Bay where it was decreased to 50 cm in 1993. Tags from undersized  
147 fish are also returned. However, to avoid the confounding effect of the area-specific  
148 minimum landing size, all fish below 60 cm were excluded from the data. Further, for  
149 length-based PMRN analysis, all fish whose corrected length (see below) was below  
150 60 cm were omitted. An equal retention rate of the tags between the stocks, years and  
151 age groups was assumed, as well as equal return rate of tags between the different  
152 fishery segments (offshore vs. coastal, between gear types). Most of the tags were  
153 returned from grilse, slightly fewer from 2SW (SW, sea-winter) fish and relatively  
154 few from 3SW fish (Table 1, see also Romakkaniemi *et al.*, 2003). Most of the tag  
155 recoveries came from immature fish, mirroring the high fishing pressure in the  
156 feeding areas.

157

#### 158 ASSIGNMENT OF MATURITY

159

160 Maturity status of captured salmon was not directly observed and had to be inferred  
161 from the location of recapture, the type of fishing gear and the time of recapture. This  
162 was possible due to the different spatial distribution of mature and immature  
163 individuals at the time of spawning migration. Smolts migrate from the Bothnian Bay  
164 southwards, towards the Main Basin (subdivision (SD) 25–29, Fig. 1) for feeding, and  
165 most of the immature salmon feed in open sea areas, predominantly in the Main Basin  
166 (Kallio-Nyberg & Ikonen, 1992; Kallio-Nyberg *et al.*, 1999; Jutila *et al.* 2003b).  
167 Spawning migration to the Gulf of Bothnia begins in May and ends in August (Ikonen  
168 & Kallio-Nyberg, 1993). The multi-sea-winter salmon return to rivers in May or June

169 (Ikonen & Kallio-Nyberg, 1993; Jokikokko *et al.*, 2004), but male grilse return later in  
170 July or in August (Jokikokko *et al.*, 2004). The main route of the returning salmon is  
171 near the Finnish coast of the Gulf of Bothnia (Kallio-Nyberg & Ikonen, 1992).  
172 Migrating salmon are captured mainly with traps and gillnets or by active means in  
173 rivers, whereas the open sea fishery targeting feeding fish has used offshore gears,  
174 predominantly drift-nets (banned in 2008) and baited lines (ICES, 2008). Based on  
175 this information, salmon recaptured during the spawning migration season, from May  
176 to October, with coastal or river gears (trap nets, coastal gillnets, hook and line) north  
177 from the Åland Sea (within ICES SDs 29–30) were most likely on their spawning  
178 migration and therefore classified as sexually mature fish. The salmon caught from  
179 May to December in SDs 21–28 or 32 and salmon caught with offshore gears (baited  
180 lines, drift nets) in SDs 29–30 most likely continued feeding and were therefore  
181 classified as immature. All fish caught in SD31 and surrounding rivers were classified  
182 mature independently of the month and gear or capture (May-December).

183

#### 184 CORRECTION OF LENGTH-AT-AGE

185

186 Salmon staying in the feeding area grow throughout the season whereas the salmon  
187 that undertake spawning migration cease to feed and stop growing. This results in a  
188 size difference between the immature and mature fish at the same age, potentially  
189 confounding size-based analyses. To address this problem, the size observations were  
190 standardised as if all salmon were captured the same date (July 31<sup>st</sup>), accounting for a  
191 period of no growth among mature salmon. It was assumed that it would take 30 days  
192 for a maturing salmon to reach the river mouth from the feeding area (time from the  
193 Åland Sea to the Bothnian Bay, Ikonen & Kallio-Nyberg, 1993), and therefore the

194 recapture date of maturing salmon was reduced by 30 days prior to the standardisation  
195 of length. A large proportion of spawning grilse are under 60 cm in size and therefore  
196 not representatively sampled by the fishery. The within-season correction of length  
197 was based on the 2SW fish because they were assumed to be sampled most  
198 representatively for length. The observed length of 2SW salmon caught in the feeding  
199 area was modelled as a function of capture date (from 1<sup>st</sup> of January, 0-1 a) by linear  
200 regression (length = 677.5 mm + 140.4 mm yr<sup>-1</sup> × capture date;  $N = 1197$ ,  $P < 0.001$ ,  
201  $R^2 = 0.08$ ; logarithmic transformation of length did not improve the fit). Both grilse  
202 and 3SW fish were assumed to grow in equal linear proportions with the 2SW fish.  
203 Therefore, standardised length ( $L$ ) for all fish was calculated using a linear equation:  $L$   
204 = observed length / ((capture date corrected for maturity) × 0.182 yr<sup>-1</sup> + 0.879), where  
205 the coefficients are obtained by dividing the original coefficients with the mean length  
206 of the immature 2SW fish, 770.8 mm.

207

## 208 ESTIMATION OF THE PROBABILISTIC MATURATION REACTION NORMS

209

210 All salmon were assumed to spawn only once. This is justified because older than  
211 3SW fish were excluded, and because available data suggest that the proportion of  
212 returning salmon that have spawned previously is low; in River Simojoki about 0.5%  
213 of returning salmon had spawned previously (Jokikokko & Jutila, 2005). Assuming  
214 semelparity facilitated the direct estimation of PMRNs with logistic regression (Heino  
215 *et al.*, 2002; Heino & Dieckmann, 2008). Usually the PMRNs are estimated using age  
216 and some predominantly environmentally controlled variable such as size as  
217 explanatory variables (Heino & Dieckmann, 2008). Since the maturation process in  
218 salmon may start even a year before the spawning, the length at the time of recapture

219 may not be representative of the conditions that affected maturation but already  
220 affected by the maturation process itself. Therefore, PMRNs were estimated with and  
221 without information of the length at the time of capture.

222

223 The presence of spatial segregation between mature and immature fish makes them  
224 differentially susceptible to fishing. The relative probability of tag recovery is also  
225 proportional to fishing effort and gear-specific catchability that was assumed constant  
226 between the gear types. Since for the estimation of PMRNs the age- and size specific  
227 proportions of mature and immature fish need to be representative (Heino *et al.*,  
228 2002), the abundance indices of fish in the feeding and spawning migration area were  
229 used as weighting factors in the regressions and in all other GLM analyses. The  
230 abundance indices were derived from catch and effort data, and showed notable  
231 temporal variation (Fig. 2). Unfortunately, no data with correct temporal resolution  
232 (May–October) were available, and annual catch data of total landings in tonnes  
233 (ICES SDs 22–29 as immature, SDs 30–31 as mature; ICES, 2008: table 2.1.3) had to  
234 be used together with half-annual effort data (July–December, in gear hours) grouped  
235 into coastal (~mature fish) and offshore fisheries (~immature fish) (ICES, 2008). The  
236 catch statistics were available from 1972 onwards but the effort data only from 1987  
237 onwards. Therefore, mean effort for 1987–1990 was used for the years 1972–1986.  
238 The final abundance indices used as weights were formed by dividing the area-  
239 specific abundance estimates (total catches in tonnes / effort in gear hours) with the  
240 number of samples in the tag recovery data (Fig. 2). For the statistical analysis, the  
241 weights were normalised so that their mean was 1.

242

243 Logistic regression models describing the probability of being mature ( $o$ ) were  
244 compared based on AIC values and proportion of correctly classified individuals, and  
245 the two following models were chosen as the most parsimonious:

246

$$247 \text{Logit}[o(a,s,l,c,r)] \sim \alpha_0 + \alpha_{1-2} a + \alpha_{3-5} r + \alpha_6 c + \alpha_7 l + \alpha_8 s + \alpha_9 t + \alpha_{10-12} r \times c \quad (1)$$

$$248 \text{Logit}[o(a,s,c,r)] \sim \alpha_0 + \alpha_{1-2} a + \alpha_{3-5} r + \alpha_6 c + \alpha_7 s + \alpha_8 t + \alpha_{9-11} r \times c, \quad (2)$$

249

250 where the  $\alpha$  are the estimated coefficients,  $l$  is the standardized length-at-age,  $s$  is  
251 length-at-release (smolt length),  $c$  is cohort,  $r$  is river,  $a$  is age (treated as a factor),  
252 and  $t$  is sea water temperature measured near the Tvärminne Zoological Station one  
253 year before the capture (mean between April and August, measured by the Finnish  
254 Institute of Marine Research, Fig. 1, 2). Any temporal shifts were assumed to be  
255 linear, and the cohort effect was entered as a continuous variable.

256

## 257 LENGTH-AT-RELEASE AND LENGTH-AT-AGE

258

259 Changes in length-at-release were analysed using ANCOVA, where cohort was  
260 entered as a covariate and smolt age (years of rearing before release) and river as  
261 factors. A model with cohort as a factor and without interaction terms was used to  
262 output the estimated marginal cohort-wise means of length-at-release. To examine if  
263 the standardised length-at-age of salmon varied between the stocks, an analysis of  
264 covariance was applied separately for each sea age class (SW). Cohort, length-at-  
265 release and mean sea water temperature (see above) were entered as covariates.  
266 Factors included river and the interactions of cohort with river and maturity status.  
267 The model structure was chosen based on biological information about the

268 relationships and significance of parameters in more complex candidate models. An  
269 additional model with cohort as a factor, and without interactions terms, was used to  
270 output cohort-wise marginal mean estimates of length-at-age.

271

272 Due to missing values for some cohort  $\times$  river and cohort  $\times$  maturity interactions,  
273 Type IV estimation of sums of squares was used in all ANCOVA analyses. Pairwise  
274 Bonferroni *post hoc* tests were used to analyse the pairwise differences between the  
275 rivers. All the analyses were weighted by the abundance indices (see above). The  
276 statistical analyses were performed in SPSS 16.0.1 for Windows (SPSS Inc. USA)  
277 and R (R Development Core Team 2008).

278

279

## RESULTS

280 AGE-AT-MATURATION

281

282 Proportion of mature individuals at age in raw data was used as the first proxy of  
283 maturation, although the proportions are influenced by changes in fishing pressure  
284 between the feeding and migration areas. Average proportion of salmon maturing as  
285 grilse was higher in the hatchery group (River Iijoki and River Oulujoki salmon) than  
286 in the supportively stocked wild salmon group (River Simojoki and River Tornionjoki  
287 salmon) across the time series, and correspondingly larger proportion of older fish  
288 were mature in the latter group (Table 1, Fig. 3). There were relatively many  
289 immature 3SW salmon in the hatchery group (Table 1), which indicates spawning  
290 even later in life or a potential reproductive failure. On the other hand, considerable  
291 proportions of mature grilse were not included in the Fig. 3 as they were excluded  
292 from the data due to the 60 cm size limit.

293

294 LENGTH-AT-RELEASE

295 Length-at-release of stocked salmon had increased over time in all rivers (Fig. 4),  
296 indicating improved conditions in hatcheries but potentially also improved intrinsic  
297 growth rate. There were consistent differences between the rivers, but also divergent  
298 trends over time as indicated by the statistically significant river x cohort interaction  
299 term (Table II). The least change occurred in River Simojoki salmon (12.7 %  
300 increase) and the largest change in the River Iijoki salmon (62.1 % increase). All the  
301 rivers except for rivers Tornionjoki and Iijoki differed statistically significantly from  
302 each other (Bonferroni pairwise *post hoc* tests,  $P < 0.001$ ). Estimated as marginal  
303 means (cohort = 1982), the River Oulujoki smolts were the largest (219 mm), river  
304 Iijoki (211 mm) and river Tornionjoki (210 mm) of intermediate size, and River  
305 Simojoki smolts the smallest (204 mm); the large proportion of clearly smaller wild  
306 smolts in the River Simojoki contributed to the small average size in that river. Size-  
307 at-release increased as a function of smolt age (estimated as marginal means, cohort =  
308 1982), being 151 mm after one year, 180 mm after two years, 214 mm after three  
309 years and 299 mm after four years. Length-at-release, corrected for the time in  
310 hatchery, did not increase more in populations produced by long-term broodstock  
311 breeding programmes (rivers Oulujoki and Iijoki) than in supported naturally  
312 reproducing populations (rivers Tornionjoki and Simojoki) (ANCOVA, parameter  
313 estimates for the slope: Oulujoki, 1.6 mm yr<sup>-1</sup>; Iijoki, 3.2 mm yr<sup>-1</sup>; Simojoki, 0.8 mm  
314 yr<sup>-1</sup>; Tornionjoki, 2.8 mm yr<sup>-1</sup>) (Fig. 4).

315

316 LENGTH-AT-AGE

317

318 Most of the variation in the standardised length-at-age was explained by length-at-  
319 release (correlation between length-at-release and length-at-age, Pearson's  $r = 0.111$ ,  
320  $N = 2981$ ;  $P < 0.001$  for grilse;  $r = 0.104$ ,  $N = 2281$ ,  $P < 0.001$  for 2SW fish;  $r =$   
321  $0.053$ ,  $N = 383$ ,  $P > 0.05$  for 3SW fish), water temperature, and cohort in interaction  
322 with river and maturity status (Table III). The significant positive main effect of  
323 cohort (for the reference river Tornionjoki) indicated a residual increasing trend in the  
324 length-at-age of 1SW fish, not explained by changes in water temperature, maturation  
325 schedules or in length-at-release. However, when length-at-release and water  
326 temperature were controlled, the estimated temporal trends in the length-at-age of  
327 mature grilse were negative for all stocks except for River Tornionjoki salmon (Fig.  
328 5).

329

330 The length-at-age of 2SW fish increased significantly less in rivers Iijoki and  
331 Simojoki than in the River Tornionjoki or Oulujoki salmon (Fig. 5b) (parameter  
332 estimates for the slope of temporal change in mature fish: Oulujoki,  $6.6 \text{ mm yr}^{-1}$ ;  
333 Iijoki,  $1.9 \text{ mm yr}^{-1}$ ; Simojoki,  $3.0 \text{ mm yr}^{-1}$ ; Tornionjoki,  $4.8 \text{ mm yr}^{-1}$ ). The length-at-  
334 age of 3SW fish showed less change than the length at younger ages in relative terms  
335 but was still increasing over time in all stocks (Fig. 5c) (parameter estimates for the  
336 slope of temporal change: Oulujoki,  $14.0 \text{ mm yr}^{-1}$ ; Iijoki,  $9.7 \text{ mm yr}^{-1}$ ; Simojoki,  $1.8$   
337  $\text{mm yr}^{-1}$ ; Tornionjoki,  $0.9 \text{ mm yr}^{-1}$ ). According to Bonferroni comparisons, mature  
338 fish of all stocks were significantly smaller than immature fish after one and two sea-  
339 winters,  $P < 0.001$ ), but significantly larger after three sea winters (919 mm vs. 803  
340 mm,  $P < 0.001$ ).

341

342 PROBABILISTIC MATURATION REACTION NORMS

343

344 The most complex logistic regression model capturing all biologically relevant  
345 relationships (Eq. 1) predicted 74.7% of salmon to a correct maturity class without  
346 weighting, and 72.0% with weighting (after the correction for the abundance of  
347 mature and immature fish). Increasing age had the expected positive effect on  
348 maturation probability (Table IV). Water temperature a year before capture also had a  
349 positive effect on maturation probability, but the positive effect of length-at-release  
350 was only marginally significant and the effect of length-at-capture was negative  
351 (Table IV). The main effect of cohort effect was positive indicating an increased  
352 maturation probability in the reference river Oulujoki (Table IV). Negative river  $\times$   
353 cohort interaction terms indicated that the temporal changes were less prominent in all  
354 the other rivers, the River Tornionjoki stock showing the least change (Tables IV, V).  
355 There were also consistent differences between the rivers throughout the study period  
356 (Tables IV, V). Interactions of length-at-capture and length-at-release with cohort  
357 were non-significant and were omitted from the final model.

358

359 Without the effect of length (data missing for some years), more fish could be  
360 included in the analysis. However, the results remained qualitatively the same (Table  
361 IV), and the predicted increases of maturation probabilities according to the weighted  
362 model varied between -12% and 187% (Table V). Without weighting, the simple  
363 PMRN model (Eq. 2) predicted 76.7% of salmon to correct maturity class while the  
364 respective precision for the weighted model was 68.6%. Contrary to the expectation,  
365 the length-at-release did not have a significant effect on the probability to mature  
366 (Table IV). Interaction of length-at-release with cohort was non-significant and was  
367 omitted from the final model.

## DISCUSSION

368

369

370 River Oulujoki salmon, with the longest history of hatchery breeding (Säisä *et al.*,  
371 2003), had the largest grilse size, and the seminatural stocks of rivers Simojoki and  
372 Tornionjoki the smallest length-at-age in general. Length-at-age had increased in all  
373 the observed salmon stocks, including the River Tornionjoki that supports the largest  
374 wild Baltic salmon population, in contrast to the observations of decreasing length-at-  
375 age in Pacific salmon (Ricker, 1981). Maturation probabilities had increased over time  
376 at all ages in all stocks, but significantly more at early ages and in stocks relying  
377 exclusively on broodstock breeding programmes. River Oulujoki salmon had started  
378 to mature significantly earlier than the salmon from the seminatural stocks or River  
379 Iijoki hatchery stock, while the River Tornionjoki salmon showed the least change.  
380 These results agree with the prediction that hatchery-rearing may increase growth rate  
381 and the likelihood of early maturity (Gjedrem, 1979; Petersson *et al.*, 1993; Fleming  
382 *et al.*, 1994; Kallio-Nyberg & Koljonen, 1997; McGinnity *et al.*, 1997).

383

384 What could explain the increased growth rates over time? Likely, environmental  
385 factors and improved aquaculture methods had contributed to the overall phenotypic  
386 increase in the growth rate of all stocks. However, common conditions cannot explain  
387 divergent trends between the stock types. Fishing can impose selective pressures only  
388 on stocks with natural or supported reproduction (here, River Simojoki and River  
389 Tornionjoki) but all the study stocks are exposed to selection within hatcheries. Fast  
390 growth rate is selected for in a hatchery environment even without intentional  
391 selection, because the survival and fecundity of fish in hatcheries is dependent on  
392 food intake rates, and there is no or little mortality cost for high foraging and feeding

393 rates. In addition, survival of released smolts is positively size-dependent (Saloniemi  
394 *et al.*, 2004; Kallio-Nyberg *et al.*, 2006; 2007) which may lead to the  
395 overrepresentation of fast growing salmon genotypes among individuals that return to  
396 spawn or become new broodstock (here, River Simojoki and River Tornionjoki).  
397 Therefore, both selection within hatcheries and natural mortality of released smolts in  
398 the sea favour fast growth. These mechanisms might explain some of the observed  
399 increases in the length-at-age of salmon. However, the current results do not clearly  
400 distinguish the intensities of selection within and outside hatcheries since the length-  
401 at-age of 2SW salmon increased most in the River Tornionjoki (the largest wild Baltic  
402 salmon stock) and River Oulujoki (hatchery stock). On the other hand, the size of  
403 3SW salmon increased significantly more in the hatchery stocks than in the supported  
404 wild stocks suggesting that the within hatchery selection might, however, be stronger  
405 than the selection arising from the size-dependent survival of released smolts.  
406  
407 Fishing may also be an important selective agent acting to an opposite direction than  
408 the positively size-dependent survival of smolts. The drift-net fishery in the Baltic  
409 Main Basin has been size- and age-selective, so that fast-growing and late-maturing  
410 fish have been selected against. Further, highly abundant male grilse spawning before  
411 reaching the minimum legal length of 60 cm (since 1993, 50 cm in the Bothnian Bay)  
412 reproduce before recruiting to the offshore fisheries (McKinnell & Lundqvist, 1998).  
413 Therefore, early maturity despite the small body size at the time of spawning may be  
414 favoured by protecting grilse from fishing. It is worth noting that early maturity would  
415 be selected for by favouring fast growth if the genetic correlation between growth rate  
416 and age at maturation was, as often observed, negative (Gjerde, 1984; Gjedrem,  
417 2000). This would suggest that both size-selective fishing and hatchery selection (due

418 to the genetic correlation) might favour fast growth (at least until maturation as grilse)  
419 and early maturation. Instead of increasing, the size of mature grilse had decreased  
420 especially in the broodstock-based stocks. This does not contradict the prediction for  
421 faster growth (until maturation), but might simply indicate an energetic cost of early  
422 reproduction. Further, this may indicate that the unintentional selection within  
423 hatcheries is stronger than the selection imposed by fishing.

424

425 Although growth and maturation are linked at both the genetic and phenotypic level,  
426 the analyses of probabilistic maturation reaction norms in this study failed to account  
427 for increased growth rates. This occurred since young mature fish were smaller than  
428 immature fish, although the theory and existing data would predict the opposite  
429 (Gjerde, 1984; Hutchings & Jones, 1998). There are several reasons to expect why the  
430 mature fish in reality might have not been smaller than their immature conspecifics.  
431 First, variation in growth rate of salmon is high (Larsson, 1984), and catch date within  
432 a year explained only about 8 % of the size of recaptured salmon. This made it  
433 difficult to control for the longer time immature fish had for growth in comparison to  
434 maturing fish that had ceased feeding. It is also unknown when the growth of  
435 maturing salmon in the Baltic Sea starts to differ from the growth of immature fish.  
436 The whole spring time growth might already be affected by sex hormones and the  
437 energy reserved for migration and gamete production. This would imply that the  
438 salmon that initiated maturation in previous year were larger than the salmon that  
439 remained immature but became smaller than the immature feeding salmon prior to the  
440 time of sampling, as has been observed for mature parr (McKinnell & Lundqvist,  
441 1998 and references therein). Since all fish below highest minimum size limit (60 cm)  
442 were excluded, the size limit *per se* cannot explain the observed differences, although

443 it efficiently excluded all small immature salmon but also large proportions of small  
444 mature males (Christensen & Larsson, 1979). Indeed, as all salmon less than 60 cm in  
445 length were excluded from the analysis, it might be that the marked increases of  
446 maturation probabilities at young age were still underestimates. Moreover, this  
447 exclusion makes the estimates for the size of grilse unreliable.

448

449 Water temperature measured in one point location within the salmon distribution area  
450 had a positive effect on maturation probability but could not fully explain the  
451 observed changes. Moreover, it would be difficult to track the ambient temperature  
452 each individual fish have actually experienced. Increased length-at-release had the  
453 expected positive effect on maturation, but surprisingly it appeared non-significant  
454 when the effect of length-at-capture was not included in the model. Future studies  
455 could examine the potential for a genetic change by estimating experimentally the  
456 maturation reaction norm of salmon: as a function of size-at-release and growth rate  
457 after smoltification, and then simulating the phenotypic changes expected through the  
458 time series given the observed environmental variables and the experimentally  
459 estimated PMRN.

460

461 Estimation of maturity status was based on capture data and spatial segregation  
462 between juvenile and mature parts of the population, which is potentially problematic.  
463 For example, increased growth rates during the feeding migration are known to  
464 decrease the length of feeding migration in stocked salmon (Kallio-Nyberg *et al.*,  
465 1999; Jutila *et al.*, 2003b). However, all salmon, except for some River Simojoki  
466 smolts, originated from stockings and non-genetic effects of hatchery-rearing cannot  
467 explain the differences between the river types in this study. The lack of information

468 on the sex of the sampled salmon prevented the estimation of sex-dependent effects,  
469 which is a clear disadvantage when male and female life-histories are known to differ  
470 (Christensen & Larsson, 1979). The catchability of salmon also differs greatly  
471 between the open sea feeding areas and spawning migration routes. In this study, the  
472 effects of varying catchability was minimised by excluding salmon caught year 1996  
473 onwards, since prior to this year the fishery used somewhat invariable methods (Jutila  
474 *et al.*, 2003a). There are also error sources related to the tag retention rates between  
475 different fishery segments (Michielsens *et al.*, 2006). Due to potential violations of  
476 numerous assumptions in this study, the PMRN estimates of the current study should  
477 be interpreted with caution, and only the differences between stocks are relatively  
478 immune to these problems given comparable feeding migration routes between the  
479 stocks. However, given the high heritability of growth and maturation in salmon  
480 (Powell *et al.*, 2008), these results support the earlier findings of Kallio-Nyberg &  
481 Koljonen (1997) and Säisä *et al.* (2003) reporting life-history divergence between  
482 salmon from wild and reared parents and directly observed temporal genetic changes  
483 in the study stocks. The current results are also in line with the direct genetic evidence  
484 demonstrating consistent differences between the stocks studied (Koljonen *et al.*,  
485 1999).

486

487 Many salmon populations have become endangered due to multiple anthropogenic  
488 factors (Parrish *et al.*, 1998). One reason for the declines may be domestication  
489 selection (Fleming & Einum, 1997; Fleming *et al.*, 2000; Kallio-Nyberg *et al.*, 2007).  
490 The survival of stocked smolts has not decreased only in the Baltic Sea (Michielsens  
491 *et al.*, 2006; Koljonen, 2006), but also in the whole North Atlantic during the 1980s  
492 and 1990s (Jonsson *et al.*, 2003). Captive breeding might result in an evolutionary

493 divergence of the reared stock and the wild stock (Petersson *et al.*, 1993; Fleming *et*  
494 *al.*, 2000), and reduce genetic diversity within the stock (Koljonen *et al.*, 2002; Säisä  
495 *et al.*, 2003). Consequently, interbreeding of domesticated salmon with wild  
496 specimens threatens local adaptations of wild populations (Fraser *et al.*, 2008).  
497 Domestication effects in gene transcription profiles have been found to be rapid in  
498 farmed Atlantic salmon (Roberge *et al.*, 2006). Further, genes controlling for genome  
499 transcription seem to be inherited in non-additive manner leading to surprisingly large  
500 differences in individuals originating from interbreeding of farmed and wild salmon  
501 (Roberge *et al.*, 2008). Therefore, if even the major life-history traits may change over  
502 time, as suggested by the present study, it is possible that the decreased survival of  
503 released fish is related to the deterioration of the gene pool of the captively bred  
504 salmon.

505

## 506 CONCLUSIONS

507

508 Taken together, consistent differences between the stocks were found, and increased  
509 growth rate in hatchery and early maturation were linked with a long breeding history  
510 of the stock, although the hatchery-based River Iijoki salmon more resembled wild  
511 stocks than the River Oulujoki stock. Whether there were evolutionary changes in the  
512 maturation schedules or growth rate of the wild supported stocks remains open, but  
513 the study provides reasonable evidence to suggest that the captive bred salmon have  
514 genetically diverged from the wild stocks in their life-history traits, thus supporting  
515 the earlier results (Kallio-Nyberg & Koljonen, 1997). Understanding of relative  
516 importance of fishing selection and hatchery selection is an important applied and

517 fundamental research question, and further comparative studies on life-history traits  
518 between wild and released salmon are warranted.

519

## 520 **Acknowledgements**

521

522 This study has been carried out with financial support from the European  
523 Commission, as part of the Specific Targeted Research Project Fisheries-induced  
524 Evolution (FinE, contract number SSP-2006-044276) under the Scientific Support to  
525 Policies cross-cutting activities of the European Community's Sixth Framework  
526 Programme. It does not necessarily reflect the views of the European Commission and  
527 does not anticipate the Commission's future policy in this area. AV and MH also  
528 acknowledge funding through the Marie Curie Research Training Network FishACE  
529 (MRTN-CT-2004-005578), funded by EC's Sixth Framework Programme. MH  
530 acknowledges support from the Norwegian Research Council (project 173417/S40)  
531 and the Bergen Research Foundation. For helpful discussions during the manuscript  
532 preparation A. Romakkaniemi, and for comments on the manuscript two anonymous  
533 referees are acknowledged.

534

## 535 **References**

536

- 537 Allendorf, F.W., England, P.R., Luikart, G., Ritchie, P.A. & Ryman, N. (2008).  
538 Genetic effects of harvest on wild animal populations. *Trends in Ecology &*  
539 *Evolution* **23**, 327-337. doi: 10.1016/j.tree.2008.02.008.
- 540 Christensen, O. & Larsson, P.-O. (1979). Review of Baltic salmon research. *ICES*  
541 *Cooperative Research Report* **89**.

542 Dieckmann, U. & Heino, M. (2007). Probabilistic maturation reaction norms: their  
543 history, strengths, and limitations. *Marine Ecology Progress Series* **335**, 253-  
544 269. doi: 10.3354/meps335253.

545 Eriksson, T & Eriksson, L.-O. (1993). The status of wild and hatchery propagated  
546 Swedish salmon stocks after 40 years of hatchery releases in the Baltic rivers.  
547 *Fisheries Research* **18**, 147-159.

548 Fleming, I.A., Jonsson, B. & Gross, M.R. (1994). Phenotypic divergence of sea-  
549 ranched, farmed and wild salmon. *Canadian Journal of Fisheries and Aquatic*  
550 *Sciences* **51**, 2808-2824.

551 Fleming, I. A. & Einum, S. (1997). Experimental test of genetic divergence of farmed  
552 from wild Atlantic salmon due to domestication. *ICES Journal of Marine*  
553 *Science* **54**, 1051-1063. doi:10.1016/S1054-3139(97)80009-4.

554 Fleming, I.A, Agustsson, T., Finstad, B., Johnsson, J. & Björnsson, B.T. (2002).  
555 Effects of domestication on growth physiology and endocrinology of Atlantic  
556 salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*  
557 **59**, 1323-1330.

558 Fleming, I.A., Hindar, K., Mjølnerød, Jonsson, B., Balstad, T. & Lamberg, A. (2000).  
559 Lifetime success and interactions of farm salmon invading a native population.  
560 *Proceedings of the Royal Society of London, Series B* **267**, 1517-1523. doi:  
561 10.1098/rspb.2000.1173.

562 Frankham, R. (2008). Genetic adaptation to captivity in species conservation  
563 programs. *Molecular Ecology* **17**, 325-333. doi: 10.1111/j.1365-  
564 294X.2007.03399.x..

565 Fraser, D.J., Cook, A.M., Eddington, J.D, Bentzen, P. & Hutchings, J.A. (2008).  
566 Mixed evidence for reduced local adaptation in wild salmon resulting from

567 interbreeding with escaped farmed salmon: complexities in hybrid fitness.  
568 *Evolutionary Applications* **1**, 501-512. doi: 10.1111/j.1752-  
569 4571.2008.00037.x.

570 Friedland, K.D., Hansen, L.P., Dunkley, D.A., & MacLean, J.C. (2000). Linkage  
571 between ocean climate, postsmolt growth, and survival of Atlantic salmon  
572 (*Salmo salar* L.) in the North Sea area. *ICES Journal of Marine Science* **57**,  
573 419–429. doi: 10.1006/jmsc.1999.0639.

574 Gjedrem, T. (1979). Selection for growth rate and domestication in Atlantic salmon.  
575 *Zeitschrift für Tierzucht und Zuchtungsbiologie*. **96**, 56-59.

576 Gjedrem, T. (2000). Genetic improvement of cold-water fish species. *Aquaculture*  
577 *Research* **31**, 25-33. doi: 10.1046/j.1365-2109.2000.00389.x.

578 Gjerde, B. (1984). Response to individual selection for age at sexual maturity in  
579 Atlantic salmon. *Aquaculture* **38**, 229-240.

580 Gjerde, B. (1986). Growth and reproduction in fish and shellfish. *Aquaculture* **57**, 37-  
581 55.

582 Grift, R.E., Heino, M., Rinjdsorp, A.D., Kraak, S.B.M. & Dieckmann, U. (2007).  
583 Three-dimensional maturation reaction norms for North Sea plaice. *Marine*  
584 *Ecology Progress Series* **334**, 213-224. doi: 10.3354/meps334213.

585 Handeland, S.O., Björnsson, B. Th., Arnesen, A.M. & Stefansson, S.O. (2003).  
586 Seawater adaptation and growth of post-smolt Atlantic salmon (*Salmo salar*)  
587 of wild and farmed strains. *Aquaculture* **220**, 367-384. doi: 0.1016/S0044-  
588 8486(02)00508-2.

589 Hard, J.J., Gross, M.R., Heino, M., Hillborn, R., Kope, R.G., Law, R. & Reynolds,  
590 J.D. (2008). Evolutionary consequences of fishing and their implications for

591 salmon. *Evolutionary Applications* **1**, 388-408. doi: 10.1111/j.1752-  
592 4571.2008.00020.x..

593 Heino, M. & Dieckmann, U. (2008). Detecting fisheries-induced life-history  
594 evolution: an overview of the reaction norm approach. *Bulletin of Marine  
595 Science* **83**, 69-93.

596 Heino, M., Dieckmann, U. & Godø, O.R. (2002). Measuring probabilistic reaction  
597 norms for age and size at maturation. *Evolution* **56**, 669-678.

598 Hutchings, J.A. & Fraser, D.J. (2008). The nature of fisheries- and farming-induced  
599 evolution. *Molecular Ecology* **17**, 294-313. doi: 10.1111/j.1365-  
600 294X.2007.03485.x..

601 Hutchings, J.A. & Jones, M.E.B. (1998). Life history variation and growth rate  
602 thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of  
603 Fisheries and Aquatic Sciences* **55**, 22-47.

604 ICES. (2008). Report of the Baltic salmon and trout assessment working group  
605 (WGBAST), 1-10 April 2008, ICES Headquarters, Copenhagen. ICES  
606 CM2008/ACOM:05. 267 pp.

607 Ikonen, E. & Kallio-Nyberg, I. (1993). The origin and timing of the coastal return  
608 migration of salmon (*Salmo salar*) in the Gulf of Bothnia. Anadromous and  
609 Catadromous Fish Committee. ICES C.M. 1993/M:34.

610 Jokikokko, E. & Jutila, E. (2005). Effect of fishing regulation on the occurrence of  
611 repeat spawners and age distribution of Atlantic salmon in a northern Baltic  
612 river. *Fisheries Management and Ecology* **12**, 3341-347. doi: 10.1111/j.1365-  
613 2400.2005.00457.x..

614 Jokikokko, E. & Jutila, E. (2009). Numbers of ascending wild and reared Atlantic  
615 salmon adults in relation to smolt output of the Simojoki river in the northern  
616 Baltic Sea. *Fisheries Management and Ecology* **16**, 165-167.

617 Jokikokko, E., Kallio-Nyberg, I. & Jutila, E. (2004). The timing, sex and age  
618 composition of the wild and reared Atlantic salmon ascending the Simojoki  
619 River, northern Finland. *Journal of Applied Ichthyology* **20**, 37-42.

620 Jokikokko, E., Kallio-Nyberg, I., Saloniemi, I. & Jutila, E. (2006). The survival of  
621 semi-wild, wild and hatchery-reared Atlantic salmon smolts of the Simojoki  
622 River in the Baltic Sea. *Journal of Fish Biology* **68**, 430-442. doi:  
623 10.1111/j.0022-1112.2006.00892.x..

624 Jonsson, N., Jonsson, B. & Hansen, L.P. (2003). The marine survival and growth of  
625 wild and hatchery reared Atlantic salmon. *Journal of Applied Ecology* **40**, 900-  
626 911. doi: 10.1046/j.1365-2664.2003.00851.x.

627 Jutila, E. & Pruuki, V. (1988). The enhancement of the salmon stocks in the Simojoki  
628 and Tornionjoki rivers by stocking parr in the rapids. *Aqua Fennica* **18**, 93-99.

629 Jutila, E., Jokikokko, E., and Julkunen, M. (2003a). Management of Atlantic salmon  
630 in the Simojoki river, northern Gulf of Bothnia: effect of stocking and fishing  
631 regulation. *Fisheries Research* **64**, 5-17.

632 Jutila, E., Jokikokko, E., Kallio-Nyberg, I., Saloniemi, I., Pasanen, P. (2003b).  
633 Differences in sea migration between wild and reared Atlantic salmon (*Salmo*  
634 *salar* L.) in the Baltic Sea. *Fisheries Research* **60**, 333-343.

635 Kallio-Nyberg, I. & Ikonen, E. (1992). Migration pattern of two salmon stocks in the  
636 Baltic Sea. *ICES Journal of Marine Science*, **49**, 191-198.

637 Kallio-Nyberg, I. & Koljonen, M.-L. (1997). The genetic consequence of hatchery-  
638 rearing on life-history traits of the Atlantic salmon (*Salmo salar* L.): a

639 comparative analysis of sea-ranched salmon with wild and reared parents.  
640 *Aquaculture* **153**, 207-224. doi: 10.1016/S0044-8486(97)00023-9.

641 Kallio-Nyberg, I., Peltonen, H. & Rita, H. (1999). Effects of stock-specific and  
642 environmental factors on the feeding migration of Atlantic salmon (*Salmo*  
643 *salar*) in the Baltic Sea. *Canadian Journal of Fisheries and Aquatic Sciences*  
644 **56**, 853-861.

645 Kallio-Nyberg, I., Jutila, E., Jokikokko, E. & Saloniemi, I. (2006). Survival of reared  
646 Atlantic salmon and sea trout in relation to marine conditions of smolt year in  
647 the Baltic Sea. *Fisheries Research* **80**, 295-304.

648 Kallio-Nyberg I., Saloniemi I. & Koljonen M-L. (2007). Effects of parental and smolt  
649 traits on the marine survival of released Atlantic salmon (*Salmo salar*).  
650 *Aquaculture* **272**, 254-266. doi: 10.1016/j.aquaculture.2007.08.048.

651 Koljonen, M.-L. (2006). Annual changes in the proportions of wild and hatchery  
652 Atlantic salmon (*Salmo salar*) caught in the Baltic Sea. *ICES Journal of*  
653 *Marine Science* **63**, 1274-1285. doi: 10.1016/j.icesjms.2006.04.010.

654 Koljonen, M.-L., Jansson, H., Paaver, T., Vasin, O. and Koskiniemi, J. (1999).  
655 Phylogeographic lineages and differentiation pattern of Atlantic salmon in the  
656 Baltic Sea with management implications. *Canadian Journal of Fisheries and*  
657 *Aquatic Sciences* **56**, 1766-1780.

658 Koljonen, M.-L., Tähtinen, J., Säisä, M. & Koskiniemi, J. (2002). Maintenance of  
659 genetic diversity of Atlantic salmon (*Salmo salar*) by captive breeding  
660 programmes and the geographical distribution of microsatellite variation.  
661 *Aquaculture* **212**, 69-92. doi: 10.1016/S0044-8486(01)00808-0.

662 Kostow, K.E. (2004). Differences in juvenile phenotypes and survival between  
663 hatchery stocks and a natural population provide evidence for modified

664 selection due to captive breeding. *Canadian Journal of Fisheries and Aquatic*  
665 *Sciences* **61**, 577-589.

666 Larsson, P-O. (1984). Growth of Baltic salmon *Salmo salar* in the sea. *Marine*  
667 *Ecology Progress Series* **17**, 215-226.

668 McGinnity, P., Stone, C., Taggart, J.B., Cooke, D., Cotter, D., Hynes, R., McCamley,  
669 C., Cross, T. & Ferguson, A. (1997). Genetic impact of escaped farmed  
670 Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling  
671 to assess freshwater performance of wild, farmed and hybrid progeny in a  
672 natural river environment. *ICES Journal of Marine Science* **54**, 998-1008. doi:  
673 10.1016/S1054-3139(97)80004-5.

674 McKinnell, S. & Lundqvist, H. (1998). The effect of sexual maturation on the spatial  
675 distribution of Baltic salmon. *Journal of Fish Biology* **52**, 1175-1185.

676 Michielsens, C.G.J., McAllister, M.K., Kuikka, S., Pakarinen, T., Karlsson, L.,  
677 Romakkaniemi, A., Perä, I. & Mäntyniemi, S. (2006). A Bayesian state-space  
678 mark-recapture model to estimate exploitation rates in mixed-stock fisheries.  
679 *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 321-334.

680 Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D. & Reeves, G.H. (1998).  
681 Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of*  
682 *Fisheries and Aquatic Sciences* **55**, 281-287.

683 Petersson, E., Järvi, T., Steffner, N.G. & Ragnarsson, B. (1993). The effect of  
684 domestication on some life history traits of sea trout and Atlantic salmon.  
685 *Journal of Fish Biology* **48**, 776-791.

686 Powell, J., White, I., Guy, D. & Brotherstone, S. (2008). Genetic parameters of  
687 production traits in Atlantic salmon (*Salmo salar*). *Aquaculture* **274**, 225-231.  
688 doi: 10.1016/j.aquaculture.2007.11.036.

689 Quinn, T.P., McGinnity, P. & Cross, T.F. (2006). Long-term declines in body size and  
690 shifts in run timing of Atlantic salmon in Ireland. *Journal of Fish Biology* **68**,  
691 1713-1730. doi: 10.1111/j.0022-1112.2006.01017.x.

692 R Development Core Team (2008). *R: A Language and Environment for Statistical*  
693 *Computing*. R Foundation for Statistical Computing, Vienna, Austria  
694 (<http://www.R-project.org>).

695 Ricker, W. E. (1981). Changes in the average size and average age of Pacific salmon.  
696 *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1636-1656.

697 Roberge, C., Einum, S., Guderley, H. & Bernatchez, L. (2006). Rapid parallel  
698 evolutionary changes of gene transcription profiles in farmed Atlantic salmon.  
699 *Molecular Ecology* **15**, 9-20. doi: 10.1111/j.1365-294X.2005.02807.x.

700 Roberge, C., Normandeau, E., Einum, S., Guderley, H. & Bernatchez, L. (2008).  
701 Genetic consequences of interbreeding between farmed and wild Atlantic  
702 salmon: insights from the transcriptome. *Molecular Ecology* **17**, 314-324. doi:  
703 10.1111/j.1365-294X.2007.03438.x..

704 Romakkaniemi, A., Perä, I., Karlsson, L., Jutila, E. Carlsson, U. & Pakarinen, T.  
705 (2003). Development of wild Atlantic salmon stocks in the rivers of the  
706 northern Baltic Sea in response to management measures. *ICES Journal of*  
707 *Marine Science* **60**, 329-342. doi: 10.1016/S1054-3139(03)00020-1.

708 Säisä, M., Koljonen, M-L. & Tähtinen, J. (2003). Genetic changes in Atlantic salmon  
709 stocks since historical times and the effective population sizes of a long-term  
710 captive breeding programmes. *Conservation Genetics* **4**, 613-627.

711 Saloniemi, I., Jokikokko, E., Kallio-Nyberg, I., Jutila, E. & Pasanen, P. (2004).  
712 Survival of reared and wild Atlantic salmon smolts: size matters more in bad

713 years. *ICES Journal of Marine Science* **61**, 782-787. doi:  
714 10.1016/j.icesjms.2004.03.032.

715 **Table I.** Proportions of mature salmon at age after 1-3 sea winters (SW) in the sea  
716 across the cohorts 1969–1992 in respect to the origin of the fish (number of all mature  
717 fish divided by the number of all fish at age). Wild stocks refer to rivers Simojoki and  
718 Tornionjoki and hatchery stocks are those from rives Oulujoki and Iijoki. Numbers of  
719 fish in each group are indicated by N. Note that all <60 cm salmon are excluded, and  
720 the proportions of salmon maturing as grilse are underestimates due to this exclusion.

Group	1SW	2SW	3SW	N
Wild	9%	48%	69%	1611
Hatchery	13%	39%	55%	5902
N	4184	2811	518	7513

721

722 **Table II.** Variables affecting the variation in length-at-release (in mm) in released  
 723 Baltic salmon for cohorts 1967–1992 according to ANCOVA, where cohort was  
 724 entered as a continuous variable. Effect size ( $\eta^2$ ) describes the total variance that is  
 725 attributed to an effect.

Source of variation	d.f.	Sig.	Effect size
Intercept	1	<0.001	0.13
River	3	<0.001	0.05
Years in hatchery	3	<0.001	0.12
Cohort	1	<0.001	0.13
River $\times$ cohort	3	<0.001	0.06
Corrected model	10	<0.001	0.35
Error	7525		
Total	7536		

726 **Table III.** Factors affecting the length (in mm) of recaptured Baltic salmon for  
727 cohorts 1969–1992 according to ANCOVA, where cohort, length-at-release (mm) and  
728 the mean temperature (°C) between April and August measured in Tvärminne a year  
729 before recapture are entered as continuous variables. a) for grilse, b) for 2SW fish, c)  
730 for 3SW fish. \*value for immature fish in relation to mature fish.

a)

Source of variation	d.f.	Sig.	Effect size	Param.
Intercept	1	<0.001	0.01	-630
River	3	<0.001	0.00	
Maturity	1	<0.001	0.03	-5841*
Length-at-release	1	<0.001	0.01	0.22
Temperature	1	<0.001	0.02	17.1
Cohort	1	<0.001	0.01	0.54
River × cohort	3	<0.001	0.00	
Maturity × cohort	1	<0.001	0.03	2.99*
Corrected model	11	<0.001	0.41	
Error	2969			
Total	1981			

b)

Source of variation	d.f.	Sig.	Effect size	Param.
Intercept	1	<0.001	0.032	-8963
River	3	0.000	0.013	
Maturity	1	0.000	0.027	10187*
Length-at-release	1	0.000	0.009	0.37
Temperature	1	0.004	0.004	13.0
Cohort	1	0.005	0.004	4.81
River × cohort	3	0.000	0.013	
Maturity × cohort	1	0.000	0.027	-5.13*
Corrected model	11	0.000	0.249	
Error	2269			
Total	2281			

c)

Source of variation	d.f.	Sig.	Effect size	Param.
Intercept	1	0.169	0.005	-977
River	3	<0.001	0.066	
Maturity	1	0.001	0.030	16013*
Length-at-release	1	0.432	0.002	-0.21
Temperature	1	0.143	0.006	18.2
Cohort	1	0.098	0.007	0.89
River × cohort	3	<0.001	0.066	
Maturity × cohort	1	0.001	0.030	-8.14*
Corrected model	11	<0.001	0.409	
Error	371			
Total	383			

731  
732  
733

734 **Table IV.** Comparison between logistic regression models explaining the probability  
735 of salmon becoming mature, i.e. a probabilistic maturation reaction norm (PMRN).  
736 The most complex model a) was build based on biological knowledge on expected  
737 relationships, the model b) was simplified due to missing length values. Length and  
738 smolt length are measured in millimetres, and temperature in degrees of Celsius.

a) Variable, the weighted most complex model	Estimate	S.E.	Sig.
Intercept	-218	27.0	<0.001
age 2	2.10	0.11	<0.001
age 3	3.73	0.23	<0.001
River Iijoki vs. River Oulujoki	107	36	0.003
River Simojoki vs. River Oulujoki	122	34	<0.001
River Torniojoki vs. River Oulujoki	164	68	0.016
Cohort	0.11	0.01	<0.001
Length-at-capture	-0.005	0.000	<0.001
Length-at-release	0.003	0.002	0.057
Temperature a year before capture	0.46	0.10	<0.001
River Iijoki x cohort vs. River Oulujoki x cohort	-0.05	0.02	0.003
River Simojoki x cohort vs. River Oulujoki x cohort	-0.06	0.02	<0.001
River Tornionjoki x cohort vs. R. Oulujoki x cohort	-0.08	0.03	0.015

b) Variable, the weighted simple model	Estimate	S.E.	Sig.
Intercept	-118	20.5	<0.001
age 2	1.50	0.08	<0.001
age 3	1.99	0.14	<0.001
River Iijoki	20.9	29.6	0.480
River Simojoki	32.9	27.9	0.237
River Torniojoki	130	60.4	0.032
Cohort	0.06	0.01	<0.001
Length-at-release	0.001	0.001	0.513
Temperature a year before capture	0.30	0.08	<0.001
River Iijoki x cohort vs. River Oulujoki x cohort	-0.01	0.01	0.484
River Simojoki x cohort vs. River Oulujoki x cohort	-0.02	0.01	0.239
River Tornionjoki x cohort vs. R. Oulujoki x cohort	-0.07	0.03	0.032

739

740

741

742

743

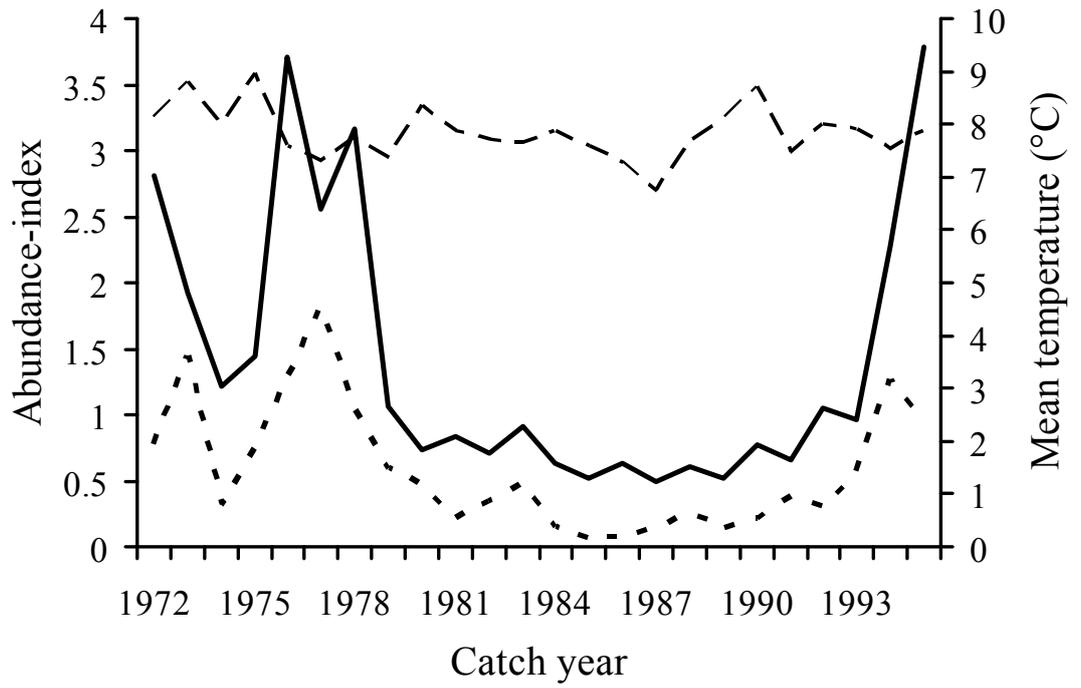
744

745 **Table V.** Probabilities of salmon from cohorts 1967 and 1992 maturing at a given age  
 746 (sea winters) at fixed length-at-release 190 mm, at fixed length of 676, 783 and 924  
 747 mm for ages 1-3, respectively, and at fixed temperature 6.76 °C (mean values over the  
 748 study period) assuming a linear temporal change and PMRN model of Table IVa or  
 749 IVb (complex vs. simple PMRN model).

River	Age	Full weighted model			Simple weighted model		
		P-1967	P-1992	%	P-1967	P-1992	%
Simojoki	1	0.17	0.40	139	0.20	0.41	107
Tornionjoki	1	0.24	0.38	60	0.39	0.34	-12
Iijoki	1	0.16	0.44	169	0.20	0.44	125
Oulujoki	1	0.09	0.62	554	0.15	0.42	187
Simojoki	2	0.55	0.80	46	0.52	0.75	44
Tornionjoki	2	0.65	0.79	20	0.74	0.70	-5
Iijoki	2	0.55	0.83	52	0.53	0.78	49
Oulujoki	2	0.39	0.91	133	0.43	0.76	76
Simojoki	3	0.76	0.91	20	0.64	0.83	30
Tornionjoki	3	0.83	0.91	9	0.82	0.79	-4
Iijoki	3	0.76	0.93	22	0.64	0.85	33
Oulujoki	3	0.62	0.96	54	0.56	0.84	51

750  
 751  
 752  
 753  
 754  
 755  
 756  
 757  
 758  
 759  
 760  
 761

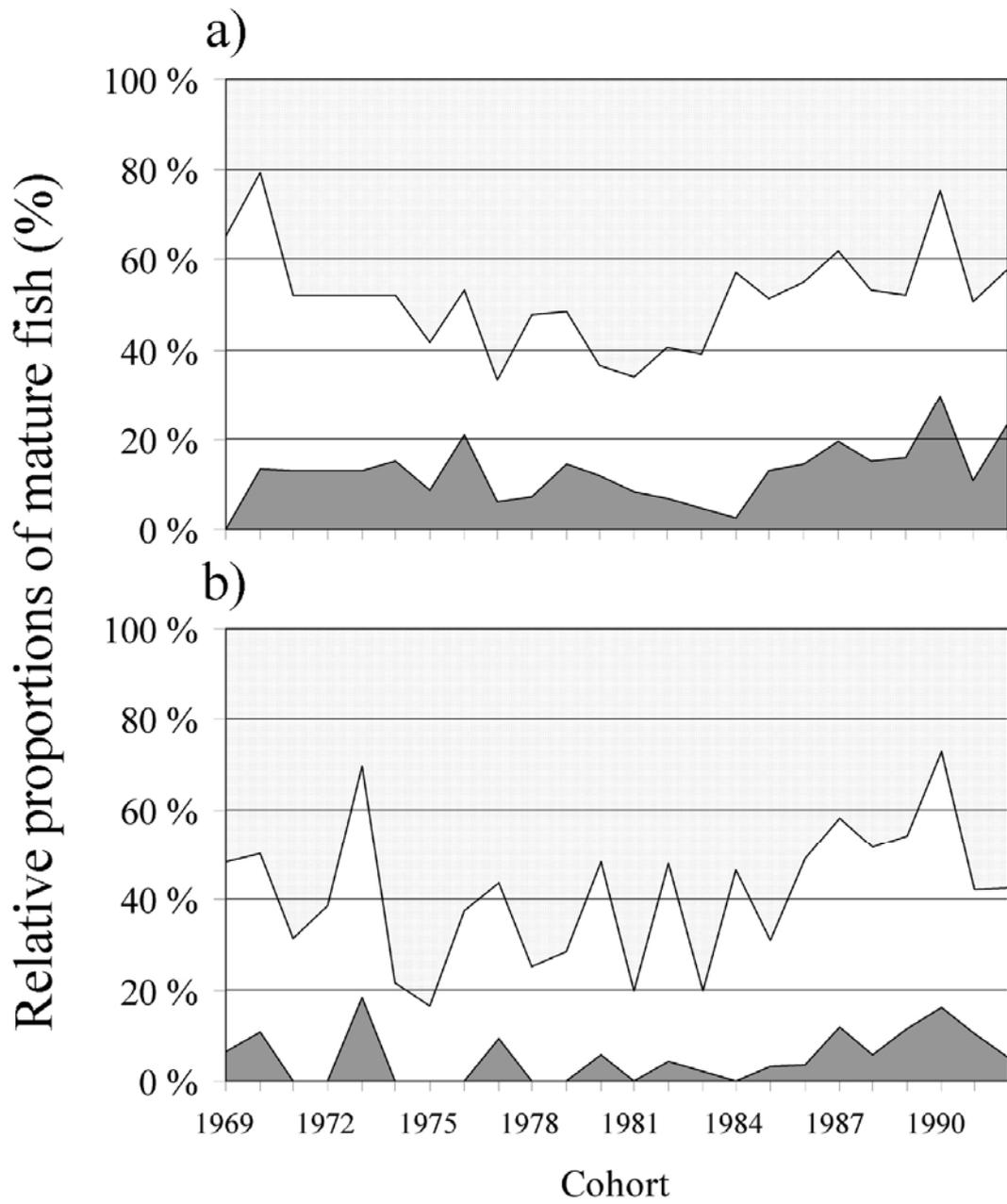




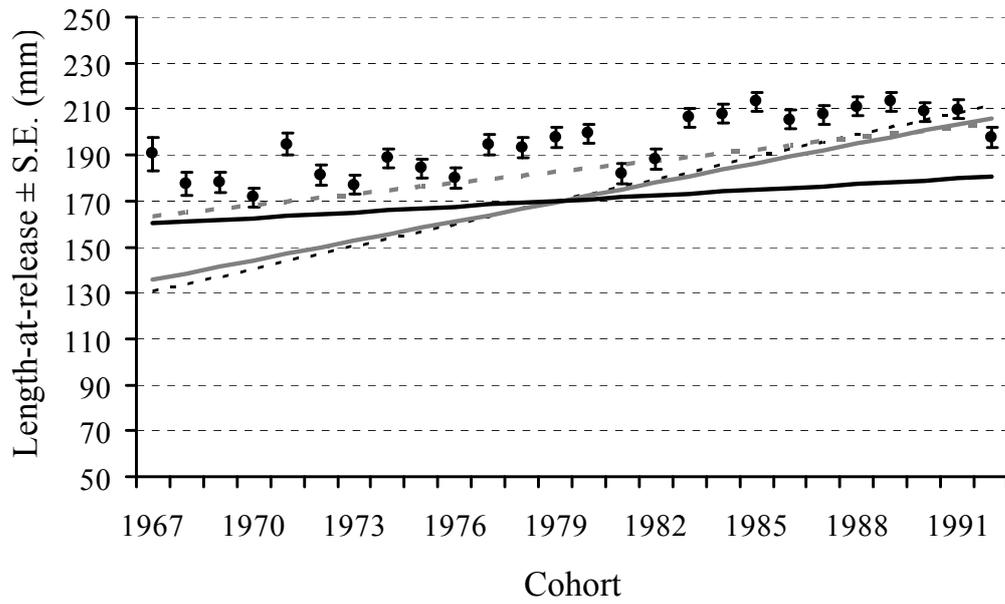
787

788

Vainikka et al. Fig. 2.



792



793

794

Vainikka et al. Fig. 4.

795

796

797

798

799

800

801

802

803

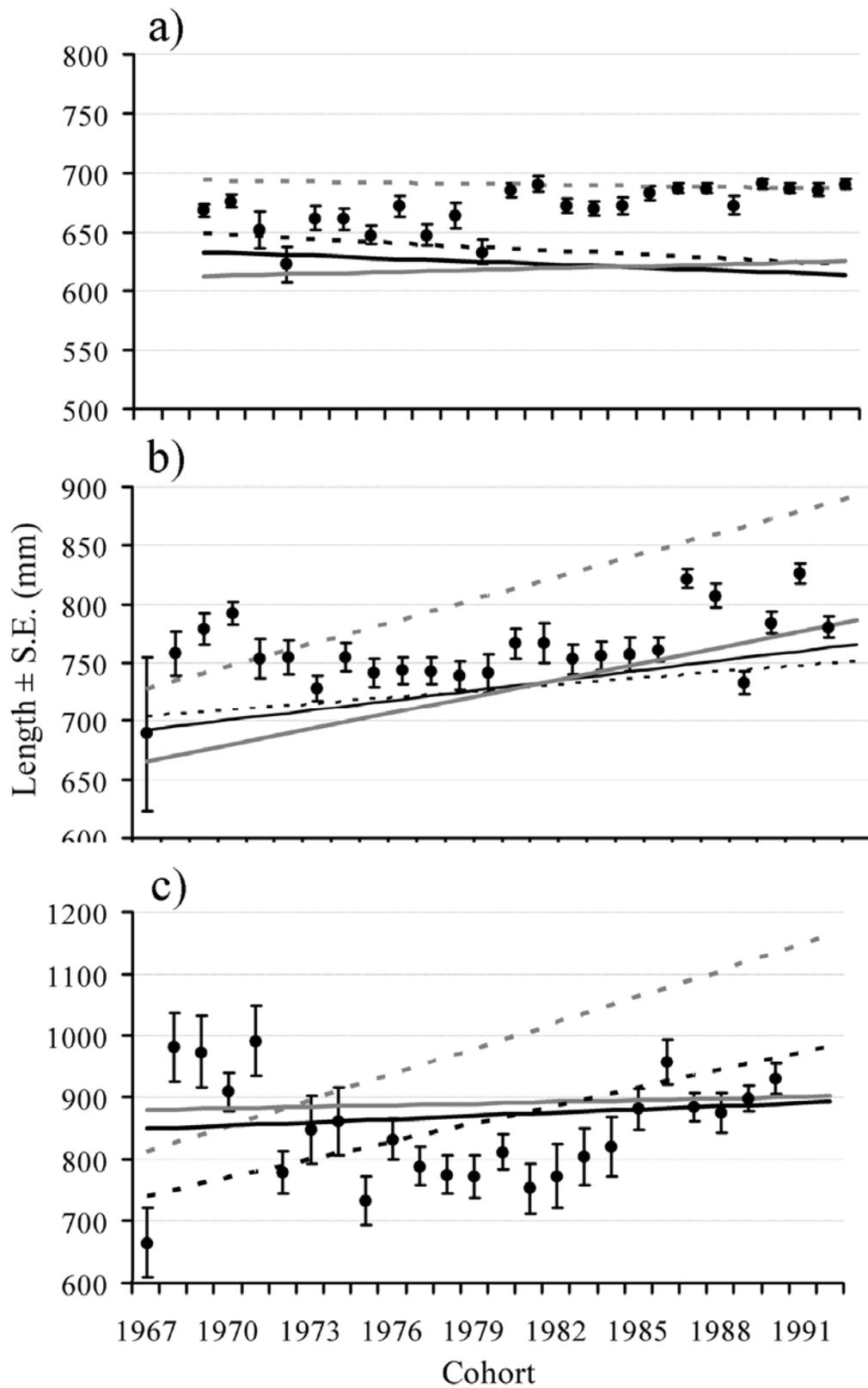
804

805

806

807

808



809

810

Vainikka et al. Fig. 5.

811 **Figure captions**

812

813 **Fig. 1.** Map of the study populations. Atlantic salmon *Salmo salar* caught in ICES  
814 subdivisions (SDs) 29 and 30 (i.e., ‘migration area’, indicated by dark grey) with a  
815 coastal gear and salmon from SD 31 were assumed to be sexually mature. All SD 21-  
816 28 (major feeding areas indicated by light grey) salmon and salmon from SDs 29-30  
817 caught with a pelagic gear were assumed to be immature.

818

819 **Fig. 2.** Abundance indices of Atlantic salmon *Salmo salar* (continuous line for mature  
820 and dotted line for immature) used to weight the logistic regressions for PMRNs and  
821 the mean temperature (long dotted line) between April and August measured in  
822 Tvärminne (SD 29, Fig. 1).

823

824 **Fig. 3.** Temporal changes in relative frequencies of mature Atlantic salmon *Salmo*  
825 *salar* (grey: grilse, white: 2SW and shaded: 3SW) from a) hatchery stocks of Rivers  
826 Oulujoki and Iijoki and b) supported wild stocks of Rivers Simojoki and Tornionjoki.  
827 Missing data for some individual cohort & age groups is replaced by mean over the  
828 whole time period (cohorts 1969 (3SW), 1971-1973, 1974 (3SW), 1991 (3SW) and  
829 1992 (2-3SW) for Rivers Oulujoki and Iijoki, and cohorts 1991 (3SW) and 1992 (2-  
830 3SW) salmon from Rivers Tornionjoki and Simojoki).

831

832 **Fig. 4.** Temporal variation in the length-at-release (smolt length) of Atlantic salmon  
833 *Salmo salar* according to ANCOVA (cohort-wise marginal means with error bars  
834 representing standard error of the mean), and the estimated river-specific trends at

835 constant hatchery age (two years). Dotted black: River Iijoki; dotted grey: River  
836 Oulujoki; continuous grey: River Tornionjoki; solid black: River Simojoki.

837

838 **Fig. 5.** Temporal variation (marginal means derived from ANCOVAs) in the length-  
839 at-age of the Atlantic salmon *Salmo salar* a) grilse, b) 2SW fish, and c) 3SW fish. The  
840 trend lines (dotted black, River Iijoki; dotted grey, River Oulujoki; continuous black,  
841 River Simojoki; continuous grey, River Tornionjoki) show estimated (according to  
842 ANCOVAs) temporal trends for mature individuals at constant size-at-release (195  
843 mm) and temperature (7.8 °C).