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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
Web: www.iiasa.ac.at

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

Approved by

Ulf Dieckmann
Program Leader, EEP

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A. VAINIKKA*[†], I. KALLIO-NYBERG[‡], M. HEINO[§] AND M-L. KOLJONEN[£]

[†]*Institute of Coastal Research, Swedish Board of Fisheries, Box 109, SE-74 222, Öregrund, Sweden.* [‡]*Finnish Game and Fisheries Research Institute, Quark Fisheries Research Station, Korsholmanpuistikko 16, FI-65100 Vaasa, Finland.* [§]*Department of Biology, University of Bergen, Box 7800, NO-5020 Bergen, Institute of Marine Research, Bergen, Norway, and International Institute for Applied Systems Analysis, Laxenburg, Austria.* [£]*Finnish Game and Fisheries Research Institute, Box 2, FI-00791, Helsinki, Finland.*

* Present address: *Section of Ecology, Department of Biology, University of Oulu, Box 3000, FI-90014 University of Oulu, Finland.*

*Author to whom correspondence should be addressed: Tel.: +358 8 5531221; fax: +358 8 5531061; e-mail:anssi.vainikka@oulu.fi.

Running headline: LIFE-HISTORY CHANGES IN ATLANTIC SALMON

ABSTRACT

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

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

INTRODUCTION

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

Selection from fishing and hatchery breeding may operate in opposite directions: while fishery usually targets large salmon and might thereby select against fast growth, hatchery rearing and size-dependent survival of released fish may favour increased growth rates (Gjedrem, 1979). Hatchery rearing also affects age-at-maturation, migration patterns, morphology, survival and several physiological traits (Kallio-Nyberg & Koljonen, 1997; Fleming *et al.*, 2002; Handeland *et al.*, 2003; Jokikokko *et al.*, 2004; Kostow, 2004; Saloniemi *et al.*, 2004; Hutchings & Fraser, 2008). However, fishery may also target grilse (1 sea-winter (SW) salmon) due to their high abundance, and the effect of hatchery rearing depends on the origin of fish used in the production of the new generation. Therefore, the expected effects are case-specific and require studies how the selection regimes arising from fishing and hatchery practises affect the trait distributions in hatchery-supported fish stocks (Hutchings & Fraser, 2008).

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

Water temperature during the feeding migration in the sea has a major role in shaping the realised growth rate (*e.g.* Friedland *et al.*, 2000). Fast growth usually translates into earlier maturation in salmon (Hutchings & Jones; 1998), due to both the genetic correlation between growth and maturation and the facilitating effect of the fast phenotypic growth (Gjerde, 1984). Due to the strong impact of environmental factors on both growth and maturation of salmon, these effects need to be disentangled from possible genetic factors when assessing potentially evolutionary changes within or genetic differences between stocks. The concept of probabilistic maturation reaction norm (PMRN) offers a statistical aid that can help to disentangle genetic effects from environmentally driven phenotypic variation in maturation schedules (Heino *et al.*, 2002; Heino & Dieckmann, 2008). A PMRN describes a population-level probability of an average individual reaching maturity as a function of age and predominantly environmentally driven variables, such as length-at-age. Other environmental measures can readily be incorporated (Heino *et al.*, 2002; Grift *et al.*, 2007, Heino & Dieckmann, 2008), and the ability of PMRNs to reflect a genetic property depends on the degree to which the included variables can capture important sources of plasticity (reviewed by Dieckmann & Heino, 2007).

This study compares variation in two central life history traits, 1) growth rate in a hatchery (as length-at-release) and during the feeding migration (as length-at-age) and 2) maturation patterns (PMRNs) over time among four Atlantic salmon stocks, Rivers Iijoki, Oulujoki, Tornionjoki and Simojoki. In total, these four stocks usually produce about 40 % of the salmon catch in the Gulf of Bothnia, and the River Tornionjoki is the most productive salmon river in the whole Baltic Sea area (ICES, 2008). These stocks represent two contrasting breeding regimes. The first two stocks (‘hatchery group’) are maintained entirely by continuous broodstock breeding, which has been continuing for Oulujoki salmon since 1955 and Iijoki salmon since 1965; naturally reproducing salmon populations of Rivers Oulujoki and Iijoki were lost when the rivers were dammed for the production of hydroelectricity. The current River Oulujoki stock is a mixture of several Baltic salmon stocks, including the original River Oulujoki salmon (Säisä *et al.*, 2003). The other two stocks (‘semi-natural group’) are maintained predominantly by natural reproduction, although hatchery-reared smolts and juveniles originating from wild-caught parents have been released supportively (Romakkaniemi *et al.*, 2003; Jutila *et al.*, 2003a). Estimated proportion of stocked smolts of all smolts has varied from 0% to over 90% in the Tornionjoki and Simojoki salmon (Romakkaniemi *et al.*, 2003), but among returning adults the proportion of reared fish has been lower due to their lower survival (Jokikokko *et al.*, 2006; Jokikokko & Jutila, 2009). Stocked salmon accounted 8–35% of River Tornionjoki salmon returners in 1984-2000 (Romakkaniemi *et al.*, 2003).

MATERIALS AND METHODS

DATA

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

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

ASSIGNMENT OF MATURITY

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

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

CORRECTION OF LENGTH-AT-AGE

Salmon staying in the feeding area grow throughout the season whereas the salmon that undertake spawning migration cease to feed and stop growing. This results in a size difference between the immature and mature fish at the same age, potentially confounding size-based analyses. To address this problem, the size observations were standardised as if all salmon were captured the same date (July 31st), accounting for a period of no growth among mature salmon. It was assumed that it would take 30 days for a maturing salmon to reach the river mouth from the feeding area (time from the Åland Sea to the Bothnian Bay, Ikonen & Kallio-Nyberg, 1993), and therefore the recapture date of maturing salmon was reduced by 30 days prior to the standardisation of length. A large proportion of spawning grilse are under 60 cm in size and therefore not representatively sampled by the fishery. The within-season correction of length was based on the 2SW fish because they were assumed to be sampled most representatively for length. The observed length of 2SW salmon caught in the feeding area was modelled as a function of capture date (from 1st of January, 0-1 a) by linear regression (length = 677.5 mm + 140.4 mm yr^{-1} × capture date; $N = 1197$, $P < 0.001$, $R^2 = 0.08$; logarithmic transformation of length did not improve the fit). Both grilse and 3SW fish were assumed to grow in equal linear proportions with the 2SW fish. Therefore, standardised length (L) for all fish was calculated using a linear equation: L = observed length / ((capture date corrected for maturity) × 0.182 yr^{-1} + 0.879), where the coefficients are obtained by dividing the original coefficients with the mean length of the immature 2SW fish, 770.8 mm.

ESTIMATION OF THE PROBABILISTIC MATURATION REACTION NORMS

All salmon were assumed to spawn only once. This is justified because older than 3SW fish were excluded, and because available data suggest that the proportion of returning salmon that have spawned previously is low; in River Simojoki about 0.5% of returning salmon had spawned previously (Jokikokko & Jutila, 2005). Assuming semelparity facilitated the direct estimation of PMRNs with logistic regression (Heino *et al.*, 2002; Heino & Dieckmann, 2008). Usually the PMRNs are estimated using age and some predominantly environmentally controlled variable such as size as explanatory variables (Heino & Dieckmann, 2008). Since the maturation process in salmon may start even a year before the spawning, the length at the time of recapture may not be representative of the conditions that affected maturation but already affected by the maturation process itself. Therefore, PMRNs were estimated with and without information of the length at the time of capture.

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

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

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

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

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

LENGTH-AT-RELEASE AND LENGTH-AT-AGE

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

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

RESULTS

AGE-AT-MATURATION

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

LENGTH-AT-RELEASE

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

LENGTH-AT-AGE

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

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

PROBABILISTIC MATURATION REACTION NORMS

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

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

DISCUSSION

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

What could explain the increased growth rates over time? Likely, environmental factors and improved aquaculture methods had contributed to the overall phenotypic increase in the growth rate of all stocks. However, common conditions cannot explain divergent trends between the stock types. Fishing can impose selective pressures only on stocks with natural or supported reproduction (here, River Simojoki and River Tornionjoki) but all the study stocks are exposed to selection within hatcheries. Fast growth rate is selected for in a hatchery environment even without intentional selection, because the survival and fecundity of fish in hatcheries is dependent on food intake rates, and there is no or little mortality cost for high foraging and feeding rates. In addition, survival of released smolts is positively size-dependent (Saloniemi *et al.*, 2004; Kallio-Nyberg *et al.*, 2006; 2007) which may lead to the overrepresentation of fast growing salmon genotypes among individuals that return to spawn or become new broodstock (here, River Simojoki and River Tornionjoki). Therefore, both selection within hatcheries and natural mortality of released smolts in the sea favour fast growth. These mechanisms might explain some of the observed increases in the length-at-age of salmon. However, the current results do not clearly distinguish the intensities of selection within and outside hatcheries since the length-at-age of 2SW salmon increased most in the River Tornionjoki (the largest wild Baltic salmon stock) and River Oulujoki (hatchery stock). On the other hand, the size of 3SW salmon increased significantly more in the hatchery stocks than in the supported wild stocks suggesting that the within hatchery selection might, however, be stronger than the selection arising from the size-dependent survival of released smolts.

Fishing may also be an important selective agent acting to an opposite direction than the positively size-dependent survival of smolts. The drift-net fishery in the Baltic Main Basin has been size- and age-selective, so that fast-growing and late-maturing fish have been selected against. Further, highly abundant male grilse spawning before reaching the minimum legal length of 60 cm (since 1993, 50 cm in the Bothnian Bay) reproduce before recruiting to the offshore fisheries (McKinnell & Lundqvist, 1998). Therefore, early maturity despite the small body size at the time of spawning may be favoured by protecting grilse from fishing. It is worth noting that early maturity would be selected for by favouring fast growth if the genetic correlation between growth rate and age at maturation was, as often observed, negative (Gjerde, 1984; Gjedrem, 2000). This would suggest that both size-selective fishing and hatchery selection (due to the genetic correlation) might favour fast growth (at least until maturation as grilse) and early maturation. Instead of increasing, the size of mature grilse had decreased especially in the broodstock-based stocks. This does not contradict the prediction for faster growth (until maturation), but might simply indicate an energetic cost of early reproduction. Further, this may indicate that the unintentional selection within hatcheries is stronger than the selection imposed by fishing.

Although growth and maturation are linked at both the genetic and phenotypic level, the analyses of probabilistic maturation reaction norms in this study failed to account for increased growth rates. This occurred since young mature fish were smaller than immature fish, although the theory and existing data would predict the opposite (Gjerde, 1984; Hutchings & Jones, 1998). There are several reasons to expect why the mature fish in reality might have not been smaller than their immature conspecifics. First, variation in growth rate of salmon is high (Larsson, 1984), and catch date within a year explained only about 8 % of the size of recaptured salmon. This made it difficult to control for the longer time immature fish had for growth in comparison to maturing fish that had ceased feeding. It is also unknown when the growth of maturing salmon in the Baltic Sea starts to differ from the growth of immature fish. The whole spring time growth might already be affected by sex hormones and the energy reserved for migration and gamete production. This would imply that the salmon that initiated maturation in previous year were larger than the salmon that remained immature but became smaller than the immature feeding salmon prior to the time of sampling, as has been observed for mature parr (McKinnell & Lundqvist, 1998 and references therein). Since all fish below highest minimum size limit (60 cm) were excluded, the size limit *per se* cannot explain the observed differences, although it efficiently excluded all small immature salmon but also large proportions of small mature males (Christensen & Larsson, 1979). Indeed, as all salmon less than 60 cm in length were excluded from the analysis, it might be that the marked increases of maturation probabilities at young age were still underestimates. Moreover, this exclusion makes the estimates for the size of grilse unreliable.

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

Estimation of maturity status was based on capture data and spatial segregation between juvenile and mature parts of the population, which is potentially problematic. For example, increased growth rates during the feeding migration are known to decrease the length of feeding migration in stocked salmon (Kallio-Nyberg *et al.*, 1999; Jutila *et al.*, 2003b). However, all salmon, except for some River Simojoki smolts, originated from stockings and non-genetic effects of hatchery-rearing cannot explain the differences between the river types in this study. The lack of information on the sex of the sampled salmon prevented the estimation of sex-dependent effects, which is a clear disadvantage when male and female life-histories are known to differ (Christensen & Larsson, 1979). The catchability of salmon also differs greatly between the open sea feeding areas and spawning migration routes. In this study, the effects of varying catchability was minimised by excluding salmon caught year 1996 onwards, since prior to this year the fishery used somewhat invariable methods (Jutila *et al.*, 2003a). There are also error sources related to the tag retention rates between different fishery segments (Michielsens *et al.*, 2006). Due to potential violations of numerous assumptions in this study, the PMRN estimates of the current study should be interpreted with caution, and only the differences between stocks are relatively immune to these problems given comparable feeding migration routes between the stocks. However, given the high heritability of growth and maturation in salmon (Powell *et al.*, 2008), these results support the earlier findings of Kallio-Nyberg & Koljonen (1997) and Säisä *et al.* (2003) reporting life-history divergence between salmon from wild and reared parents and directly observed temporal genetic changes in the study stocks. The current results are also in line with the direct genetic evidence demonstrating consistent differences between the stocks studied (Koljonen *et al.*, 1999).

Many salmon populations have become endangered due to multiple anthropogenic factors (Parrish *et al.*, 1998). One reason for the declines may be domestication selection (Fleming & Einum, 1997; Fleming *et al.*, 2000; Kallio-Nyberg *et al.*, 2007). The survival of stocked smolts has not decreased only in the Baltic Sea (Michielsens *et al.*, 2006; Koljonen, 2006), but also in the whole North Atlantic during the 1980s and 1990s (Jonsson *et al.*, 2003). Captive breeding might result in an evolutionary divergence of the reared stock and the wild stock (Petersson *et al.*, 1993; Fleming *et al.*, 2000), and reduce genetic diversity within the stock (Koljonen *et al.*, 2002; Säisä *et al.*, 2003). Consequently, interbreeding of domesticated salmon with wild specimens threatens local adaptations of wild populations (Fraser *et al.*, 2008). Domestication effects in gene transcription profiles have been found to be rapid in farmed Atlantic salmon (Roberge *et al.*, 2006). Further, genes controlling for genome transcription seem to be inherited in non-additive manner leading to surprisingly large differences in individuals originating from interbreeding of farmed and wild salmon (Roberge *et al.*, 2008). Therefore, if even the major life-history traits may change over time, as suggested by the present study, it is possible that the decreased survival of released fish is related to the deterioration of the gene pool of the captively bred salmon.

CONCLUSIONS

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

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Table I. Proportions of mature salmon at age after 1-3 sea winters (SW) in the sea across the cohorts 1969–1992 in respect to the origin of the fish (number of all mature fish divided by the number of all fish at age). Wild stocks refer to rivers Simojoki and Tornionjoki and hatchery stocks are those from rives Oulujoki and Iijoki. Numbers of fish in each group are indicated by N. Note that all <60 cm salmon are excluded, and 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

Table II. Variables affecting the variation in length-at-release (in mm) in released Baltic salmon for cohorts 1967–1992 according to ANCOVA, where cohort was entered as a continuous variable. Effect size (η^2) describes the total variance that is 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 × cohort	3	<0.001	0.06
Corrected model	10	<0.001	0.35
Error	7525		
Total	7536		

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

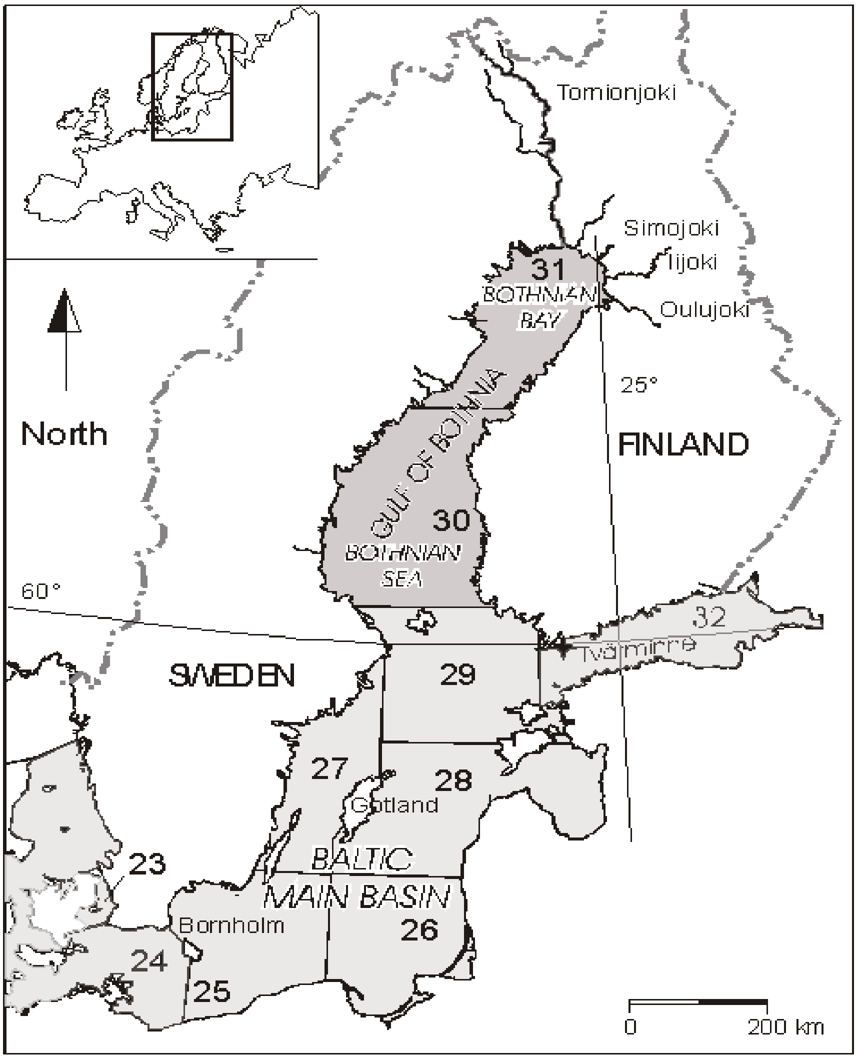
Table IV. Comparison between logistic regression models explaining the probability of salmon becoming mature, i.e. a probabilistic maturation reaction norm (PMRN). The most complex model a) was build based on biological knowledge on expected relationships, the model b) was simplified due to missing length values. Length and 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

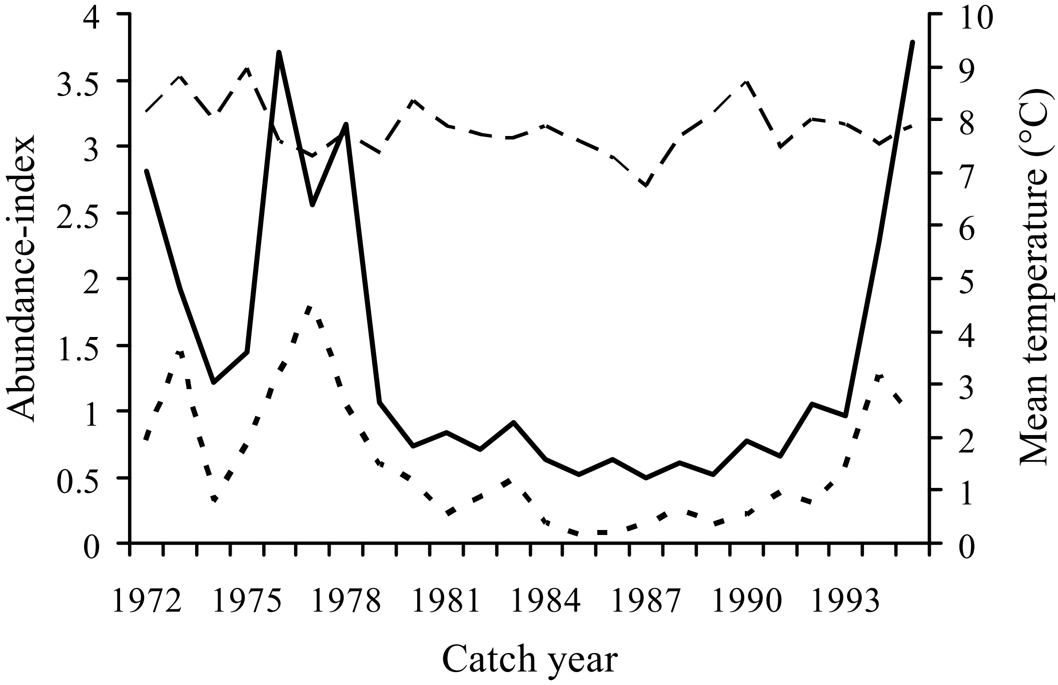
b) Variable, the weighted simple model	Estimate	S.E.	Sig.
Intercept	-118	20.5	<0.001
age 2	1.50	0.08	<0.001
age 3	1.99	0.14	<0.001
River Iijoki	20.9	29.6	0.480
River Simojoki	32.9	27.9	0.237
River Torniojoki	130	60.4	0.032
Cohort	0.06	0.01	<0.001
Length-at-release	0.001	0.001	0.513
Temperature a year 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

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

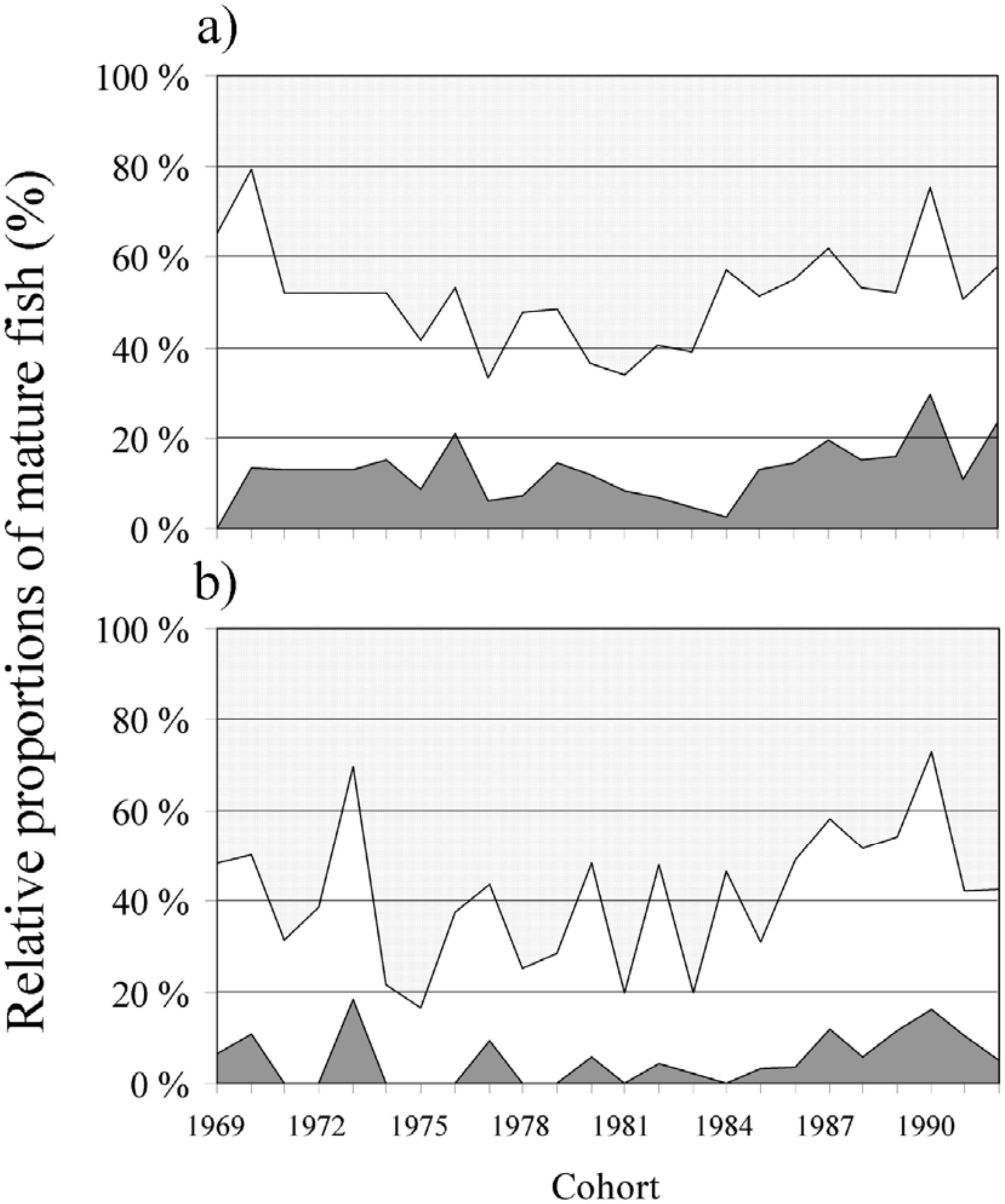
River	Age	Full weighted model			Simple weighted model		
		P-1967	P-1992	%	P-1967	P-1992	%
Simojoki	1	0.17	0.40	139	0.20	0.41	107
Tornionjoki	1	0.24	0.38	60	0.39	0.34	-12
Iijoki	1	0.16	0.44	169	0.20	0.44	125
Oulujoki	1	0.09	0.62	554	0.15	0.42	187
Simojoki	2	0.55	0.80	46	0.52	0.75	44
Tornionjoki	2	0.65	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



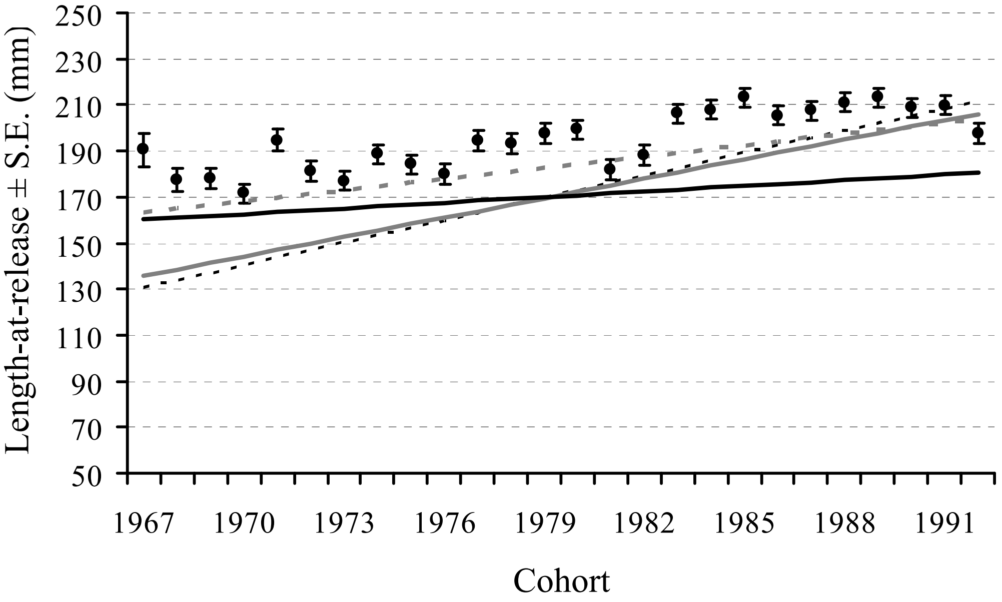
Vainikka et al. Fig. 1.



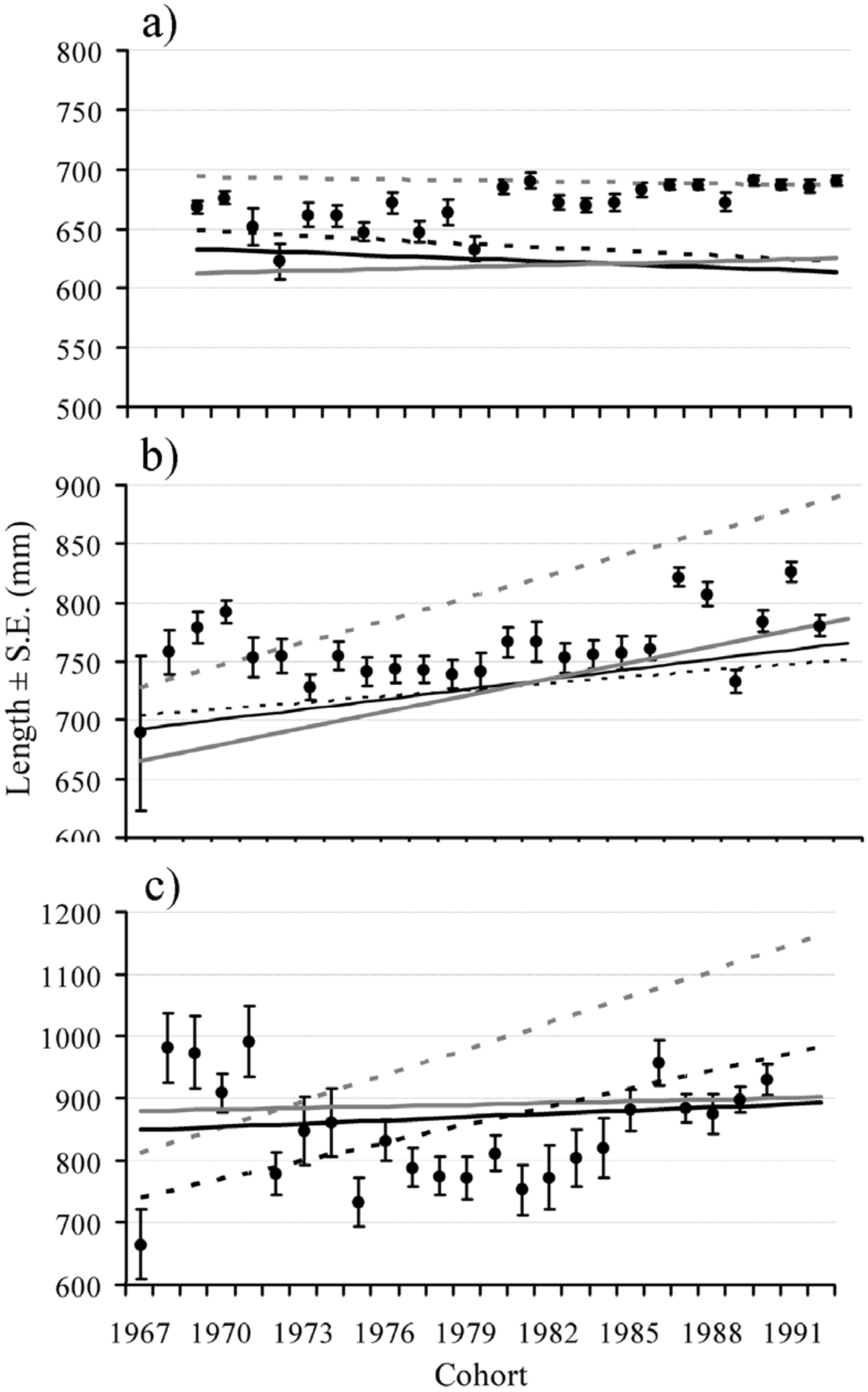
Vainikka et al. Fig. 2.



Vainikka et al. Fig. 3.



Vainikka et al. Fig. 4.



Vainikka et al. Fig. 5.

Figure captions

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

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

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

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

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

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