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

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* and ||*Finnish Game and Fisheries Research Institute, Box 2, FI-00791, Helsinki, Finland*

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Four Atlantic salmon *Salmo salar* stocks in the Baltic Sea, varying in their breeding history, were studied for changes in life-history traits over the years 1972–1995. Total length (L_T) at age of captured (L_{TC}) fish had increased throughout the study period, partly due to increased temperature and increased L_T at release, (L_{TR}) but also due to remaining cohort effects that could represent unaccounted environmental or genetic change. Simultaneously, maturation probabilities controlled for water temperature, L_{TC} and L_{TR} had increased in all stocks. The least change was observed in the River Tornionjoki *S. salar* that was subject only to supportive stockings originating from wild parents. These results suggest a long-term divergence between semi-natural and broodstock-based *S. salar* stocks. Increased L_T at age explained advanced maturation only marginally, and it remains an open question to what extent the generally increased probabilities to mature at early age reflected underlying genetic changes.

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INTRODUCTION

While the exploitation rates of the most Atlantic salmon *Salmo salar* L. stocks have recently decreased to ecologically sustainable levels, it is still prudent to study if management practices 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 the population level, age and size at maturation and size at age commonly show temporal variation in both Atlantic and Pacific salmonids due to environmental and fishing-induced demographic changes (Ricker, 1981; Quinn *et al.*,

†Author to whom correspondence should be addressed at present address: Section of Ecology, Department of Biology, University of Oulu, Box 3000, FI-90014 University of Oulu, Finland. Tel.: +358 8 5531219; fax: +358 8 5531061; email: anssi.vainikka@oulu.fi

2006). Life-history traits of *S. salar* are highly heritable (Gjerde, 1984, 1986) and, therefore, potentially affected by selective fishing (Ricker, 1981; Hard *et al.*, 2008). Furthermore, many *S. salar* populations, especially in the Baltic Sea, are supported by hatchery-reared smolts, and potential adaptations to captivity can influence the genetics of wild populations (Frankham, 2008; Hutchings & Fraser, 2008).

Selection regimes arising from fishing and hatchery breeding may operate in opposite directions: while fishing usually targets large *S. salar* and might thereby select against fast growth and hatchery rearing, 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). Fishing, however, may also target grilse [1 sea winter (SW) *S. salar*] 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 on how the selection regimes arising from fishing and hatchery practices affect the trait distributions in hatchery-supported fish stocks (Hutchings & Fraser, 2008).

The abundance of *S. salar* in the Baltic Sea decreased towards the end of the 20th century, not only due to damming of natal rivers but also due to heavy fishing pressure during the feeding migration (Eriksson & Eriksson, 1993; Jutilla *et al.*, 2003a). To maintain a commercial offshore *S. salar* fishery, *c.* 5 million hatchery-reared smolts are released annually into the Baltic Sea. Baltic *S. salar* parr spend 2 to 4 years in the river before smoltification (Jutilla & Pruuki, 1988), and the number of winters spent in the sea before spawning migration most commonly varies between 1 and 3 years. In 1995–2000, the average proportion of 1SW, 2SW, 3SW, 4SW and repeat spawners accounted for, respectively, 12.0, 52.0, 30.0, 0.4 and 6.0% 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 (Friedland *et al.*, 2000). Fast growth usually translates into earlier maturation in *S. salar* (Hutchings & Jones, 1998), due to both the genetic correlation between growth and maturation and the facilitating effect of the fast phenotypic growth (Gjerde, 1984). Because of the strong influence of environmental factors on both growth and maturation of *S. salar*, 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 variables included can capture important sources of plasticity (Dieckmann & Heino, 2007).

This study compares variation in two central life-history traits: 1) growth rate in a hatchery [as total length (L_T) at release (L_{TR})] and during the feeding migration [as L_T at capture (L_{TC})] and 2) maturation patterns (PMRN) over time among four

S. salar stocks: Rivers Iijoki, Oulujoki, Tornionjoki and Simojoki. In total, these four stocks usually produce *c.* 40% of the *S. salar* catch in the Gulf of Bothnia, and the River Tornionjoki is the most productive *S. salar* 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 fish since 1955 and Iijoki fish since 1965; naturally reproducing *S. salar* 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 *S. salar* stocks, including the original River Oulujoki *S. salar* (Säisä *et al.*, 2003). The other two stocks (semi-natural group) reproduce predominantly naturally, but hatchery-reared smolts and juveniles originating from wild-caught parents have been released in order to support the offshore fishery (Romakkaniemi *et al.*, 2003; Jutila *et al.*, 2003a). Estimated percentage of stocked smolts of all smolts has varied from 0 to >90% in the Tornionjoki and Simojoki *S. salar* (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 *S. salar* accounted for 8–35% of River Tornionjoki returners in 1984–2000 (Romakkaniemi *et al.*, 2003).

MATERIALS AND METHODS

DATA

Several million 2 or 3 year-old smolts and parr, raised under standard hatchery conditions, have been released into the estuaries of the study rivers since the 1960s (Romakkaniemi *et al.*, 2003). Before the release, all fish were tagged with Carlin tags, and the L_T of each fish was recorded (L_{TR}). Tag-recovery data collected from the multinational commercial *S. salar* fishery since year 1972 were obtained from the Finnish Game and Fisheries Research Institute.

Large and old *S. salar* 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 before 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 *S. salar* 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 L_T is 600 mm except in the Bothnian Bay where it was reduced to 500 mm in 1993. Tags from undersized fish are also returned. To avoid the confounding effect of the area-specific minimum landing L_T . However, all fish having the standardized size (see below) <600 mm were excluded from the analyses involving L_{TC} . In other analyses, fish having the original L_{TC} <600 mm 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 *v.* coastal, between gear types). Most of the tags were returned from grilse, slightly fewer from 2SW fish and relatively few from 3SW fish (Table I; 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 *S. salar* 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

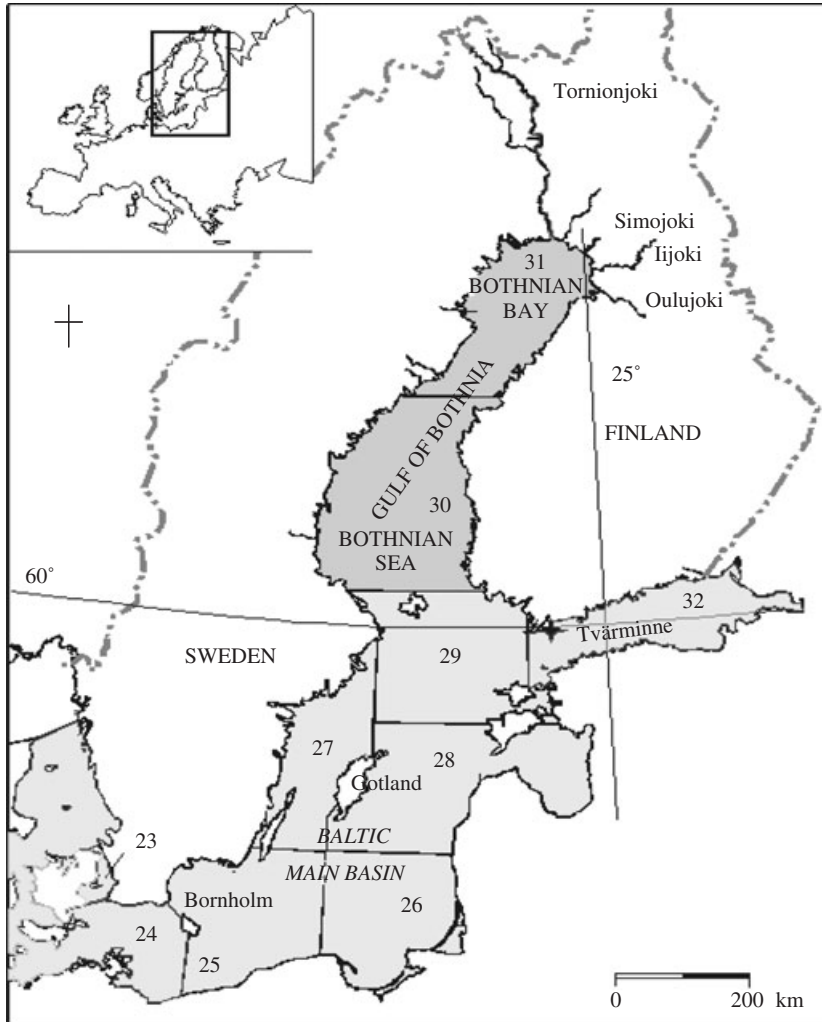


FIG. 1. Map of the study populations. *Salmo salar*, caught in ICES subdivisions (SD) 29 and 30 [i.e. migration area, (□)] with a coastal gear and *S. salar* from SD 31, were assumed to be sexually mature. All SD 21–28 [major feeding areas; (□)] fish and fish from SDs 29–30 caught with pelagic gear were assumed to be immature.

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 Baltic Main Basin [subdivision (SD) 25–29; Fig. 1] for feeding, and most of the immature *S. salar* feed in open sea areas, predominantly in the Baltic Main Basin (Kallio-Nyberg & Ikonen, 1992; Kallio-Nyberg *et al.*, 1999; Jutula *et al.* 2003b). Spawning migration to the Gulf of Bothnia begins in May and ends in August. The multi-sea-winter *S. salar* return to rivers in May or June (Jokikokko *et al.*, 2004), but male grilse return later in July or in August (Jokikokko *et al.*, 2004). The main route of the returning *S. salar* is near the Finnish coast of the Gulf of Bothnia (Kallio-Nyberg & Ikonen, 1992). Migrating *S. salar* 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

TABLE I. Percentage (%) of mature *Salmo salar* at age after 1–3 sea winters (SW) in the Baltic 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 Rivers Oulujoki and Iijoki. Numbers of fish in each group are indicated by n . Note that all <600 mm total length (L_T) *S. salar* are excluded, and the proportion of fish 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

(ICES, 2008). Based on this information, *S. salar* recaptured during the spawning migration season, from May to October, with coastal or river gears (trap nets, coastal gillnets and hook and line) north from the Åland Sea (within ICES SD 29–30) were most probably on their spawning migration and therefore classified as sexually mature fish. The *S. salar* caught from May to December in SD 21–28 or 32 and *S. salar* caught with offshore gears (baited lines and drift nets) in SD 29–30 most probably continued feeding and were classified as immature. All fish caught in SD 31 and surrounding rivers were classified mature independently of the month and gear or capture (May to December).

CORRECTION OF L_T AT AGE

Salmo salar staying in the feeding area grow throughout the season, whereas the individuals 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 standardized as if all *S. salar* were captured on the same date (31 July), accounting for a period of no growth among mature fish. It was assumed that it would take 30 days for a maturing fish to reach the river mouth from the feeding area (time from the Åland Sea to the Bothnian Bay), and, therefore, the recapture date of maturing fish was increased by 30 days before the standardization of L_T . A large proportion of spawning grilse are <600 mm in size and not representatively sampled by the fishery (Christensen & Larsson, 1979). The within-season correction of L_T was based on the 2SW fish, because they were assumed to be sampled most representatively for L_T . The observed L_T of 2SW *S. salar* caught in the feeding area was modelled as a function of capture date (from 1 January) by linear regression ($L_T = L_0 + Gt$, where L_0 is the L_T at 1 January, 677.5 mm, G the growth rate, 140.4 mm year⁻¹, and t the time of the capture in years; $n = 1197$, $P < 0.001$, $r^2 = 0.08$; ln transformation of L_T did not improve the fit). Both grilse and 3SW fish were assumed to grow in equal linear proportions with the 2SW fish. Therefore, the standardized L_T (L_{TS}) for all fish was calculated using the equation: $L_{TS} = L_T(t_C G_C + L_{0C})^{-1}$, where t_C is the time of the capture corrected for the 30 days growth difference between the immature and maturing fish in years (see above), G_C the scaled growth rate 0.182 year⁻¹ and L_{0C} is the scaled size at the beginning of the year, 0.879. The scaled dimensionless coefficients were obtained by dividing the original coefficients by the mean L_T of immature 2SW fish, 770.8 mm.

ESTIMATION OF THE PROBABILISTIC MATURATION REACTION NORMS

All *S. salar* were assumed to spawn only once. This is justified because older than 3SW fish were excluded, and because available data suggest that the percentage of returning fish that have spawned previously is low; in River Simojoki *c.* 0.5% of returning individuals had spawned previously (Jokikokko & Jutila, 2005). Assuming semelparity facilitated the

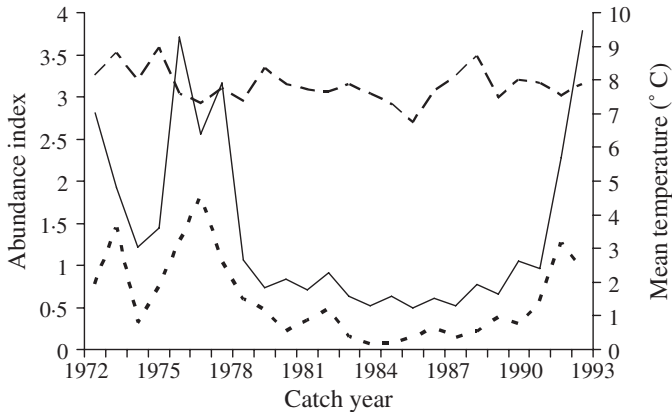


FIG. 2. Abundance indices of Atlantic salmon *Salmo salar* (——, mature; - - -, immature) used as weights in the logistic regressions for probabilistic maturation reaction norms (PMRN) and in other statistical models, and the mean temperature (— · —) between April and August measured in Tvärminne (SD 29, Fig. 1).

direct estimation of PMRN by logistic regression (Heino *et al.*, 2002; Heino & Dieckmann, 2008). Usually PMRN are estimated using age and some predominantly environmentally controlled variable such as size as explanatory variables (Heino & Dieckmann, 2008). Since the maturation process in *S. salar* may start as much as a year before the spawning, the L_T at the time of recapture may not be representative of the conditions that affected maturation but may already be affected by the maturation process itself. Therefore, PMRN were estimated with and without information of the L_{TS} 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 PMRN, 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 logistic regressions and in all other general linear models (GLM). 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 to October) were available, and annual catch data of total landings in t (ICES SD 22–29 as immature, SD 30–31 as mature; ICES, 2008) had to be used together with half-annual effort data (July to December, in gear hours) grouped into coastal (*c.* mature fish) and offshore fisheries (*c.* 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 t per effort in gear hours) by the number of samples in the tag-recovery data (Fig. 2). For the statistical analysis, the weights were normalized so that their mean was 1.

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

$$\text{Logit}[o(a, s, l, c, r)] \sim \alpha_0 + \alpha_{1-2}a + \alpha_{3-5}r + \alpha_6c + \alpha_7L_{TS} + \alpha_8L_{TR} + \alpha_9t + \alpha_{10-12}r \times c \quad (1)$$

$$\text{Logit}[o(a, s, c, r)] \sim \alpha_0 + \alpha_{1-2}a + \alpha_{3-5}r + \alpha_6c + \alpha_7L_{\text{TR}} + \alpha_8t + \alpha_{9-11}r \times c, \quad (2)$$

where the α are the estimated coefficients, L_{TS} is the standardized L_{T} at age, L_{TR} is the L_{T} at release, 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 1 year before the capture (mean between April and August, measured by the Finnish Institute of Marine Research; Figs 1 and 2). Any temporal shifts were assumed to be linear, and the cohort effect was entered as a continuous variable.

L_{T} AT RELEASE (L_{TR}) AND L_{T} AT AGE

Changes in L_{TR} 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 L_{T} at release. To examine whether the L_{TS} of *S. salar* varied between the stocks, an ANCOVA was applied separately for each sea age class (SW). Cohort, L_{TR} and mean sea water temperature a year before capture (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 L_{TS} at age.

Due to missing values for some cohort \times river and cohort \times maturity interactions, type IV estimation of sums of squares was used in all ANCOVA analyses. Pair-wise Bonferroni *post hoc* tests were used to analyse the pair-wise 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.; www.spss.com) and R (R Development Core Team; www.r-project.org).

RESULTS

AGE AT MATURATION

The proportion of mature individuals at age in the 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 *S. salar* maturing as grilse was higher in the hatchery group (Rivers Iijoki and Oulujoki) than in the supportively stocked wild fish group (Rivers Simojoki and Tornionjoki) across the time series, and correspondingly larger proportion of older fish were mature in the latter group (Table I and Fig. 3). There were relatively many immature 3SW *S. salar* in the hatchery group (Table I), 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 Fig. 3 as they were excluded from the data due to the 600 mm size limit.

L_{T} AT RELEASE (L_{TR})

The L_{TR} of stocked *S. salar* 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

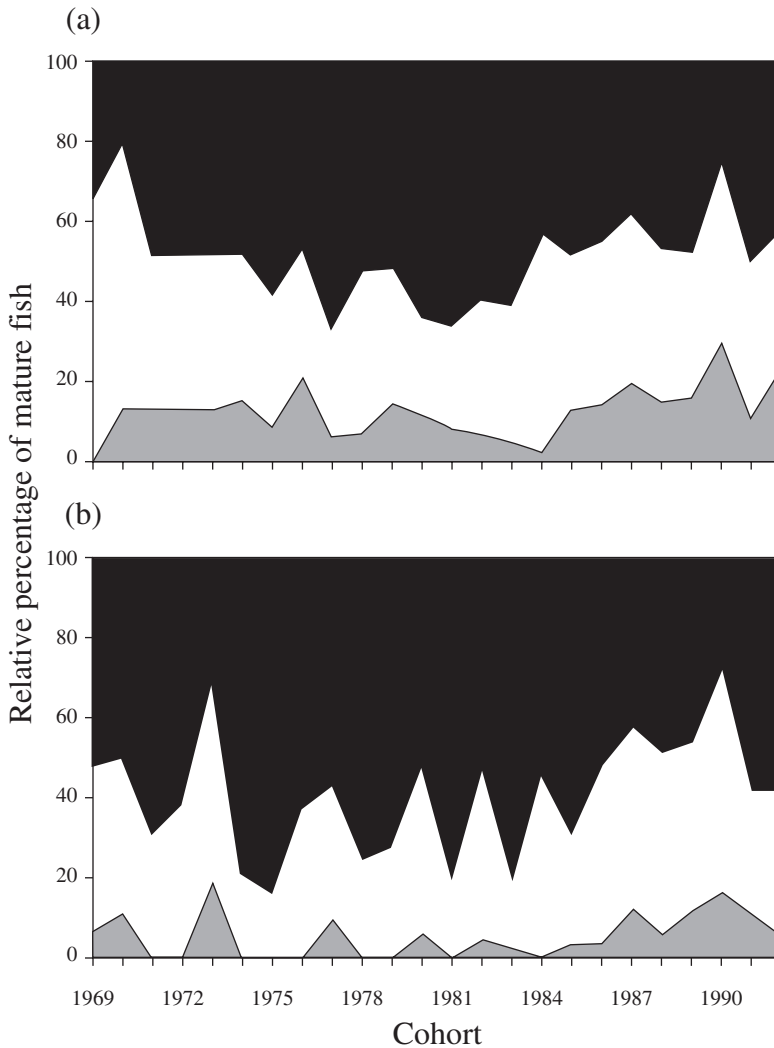


FIG. 3. Temporal changes in relative frequencies of mature *Salmo salar* (■, grilse; □, 2 sea winters (SW); ■, 3SW) from (a) hatchery stocks of Rivers Oulujoki and Iijoki and (b) supported wild stocks of Rivers Simojoki and Tornionjoki. Missing data for some individual cohort and age groups are replaced 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) *S. salar* from Rivers Tornionjoki and Simojoki].

over time as indicated by the statistically significant river \times cohort interaction term (Table II). The least change occurred in River Simojoki *S. salar* (12.7% increase) and the largest change in the River Iijoki *S. salar* (62.1% increase). All the rivers except Tornionjoki and Iijoki showed statistically significant differences from each other (Bonferroni pair-wise *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

TABLE II. Variables affecting the variation in total L_T at release (L_{TR} ; mm) in released Baltic *Salmo salar* 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.	P	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		

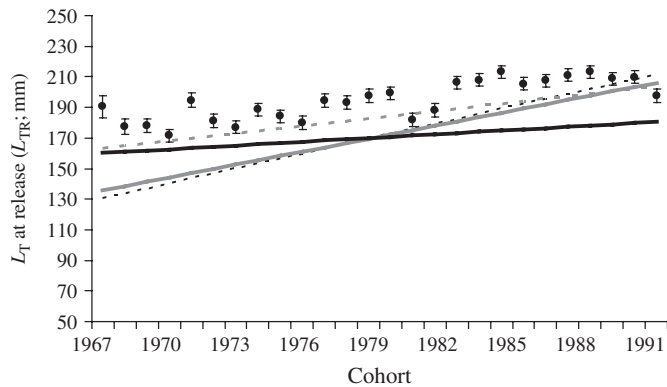


FIG. 4. Temporal variation in the total length (L_T)-at-release (smolt L_T) of *Salmo salar* according to ANCOVA (cohort-wise marginal means \pm s.e.), and the estimated river-specific trends at constant hatchery age (2 years) (---, River Iijoki; - · - ·, River Oulujoki; —, River Tornionjoki; ———, River Simojoki).

smolts the smallest (204 mm); the large proportion of clearly smaller wild smolts in the River Simojoki contributed to the small average L_T in that river. The L_{TR} increased as a function of smolt age (estimated as marginal means, cohort = 1982), being 151 mm after 1 year, 180 mm after 2 years, 214 mm after 3 years and 299 mm after 4 years. The L_{TR} , 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, coefficient estimates for the slope: Oulujoki, 1.6 mm year⁻¹; Iijoki, 3.2 mm year⁻¹; Simojoki, 0.8 mm year⁻¹; Tornionjoki, 2.8 mm year⁻¹) (Fig. 4).

L_{TS} AT AGE

Part of the variation in the standardized L_T -at-capture was explained by L_{TR} (correlation between L_{TR} and L_{TC} , Pearson's $r = 0.169$, $n = 2266$, $P < 0.001$ for

TABLE III. Factors affecting the standardized total length (L_{TS} , in mm) of recaptured Baltic *Salmo salar* for cohorts 1969–1992 according to ANCOVA, where cohort, L_T at release (L_{TR} ; mm) and the mean temperature ($^{\circ}$ C) between April and August measured at Tvärminne a year before recapture are entered as continuous variables: (a) for grilse, (b) for 2 sea winter (SW) fish, and (c) for 3SW fish

Source of variation	d.f.	<i>P</i>	Effect size	Coefficient
(a)				
Intercept	1	<0.001	0.008	−3110
River	3	<0.05	0.004	
Maturity	1	<0.001	0.007	−2130*
L_{TR}	1	<0.001	0.021	0.26
Temperature	1	<0.001	0.017	14.4
Cohort (for River Tornionjoki)	1	<0.001	0.012	1.82
River × cohort	3	<0.05	0.004	
Maturity × cohort	1	<0.001	0.007	1.09*
Corrected model	11	<0.001	0.156	
Error	2254			
Total	2266			
(b)				
Intercept	1	<0.01	0.002	−10900
River	3	<0.001	0.006	
Maturity	1	<0.001	0.009	5380*
L_T at release	1	<0.001	0.016	0.472
Temperature	1	<0.001	0.008	18.2
Cohort (for River Tornionjoki)	1	<0.001	0.016	5.77
River × cohort	3	<0.001	0.006	
Maturity × cohort	1	<0.001	0.009	−2.72*
Corrected model	11	<0.001	0.154	
Error	2163			
Total	2175			
(c)				
Intercept	1	>0.05	0.004	642
River	3	<0.001	0.058	
Maturity	1	<0.05	0.015	11400*
L_T at release	1	>0.05	0.002	−0.250
Temperature	1	>0.05	0.005	17.5
Cohort (for River Tornionjoki)	1	<0.05	0.014	0.126
River × cohort	3	<0.001	0.057	
Maturity × cohort	1	<0.05	0.016	−5.83*
Corrected model	11	<0.001	0.281	
Error	359			
Total	371			

*, value for immature fish in relation to mature fish.

grilse; $r = 0.164$, $n = 2175$, $P < 0.001$ for 2SW fish; $r = 0.007$, $n = 371$, $P > 0.05$ 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 L_{TS} at capture of grilse,

not explained by changes in water temperature, maturation schedules or in L_{TR} . In the River Oulujoki *S. salar*, however, the trend was negative and statistically significantly different from the other stocks ($-0.68 \text{ mm year}^{-1}$) (Table III and Fig. 5).

The L_{TS} at capture of 2SW fish increased significantly less in the River Iijoki stock than in the other rivers [Fig. 5(b)] (coefficient estimates for the slope of temporal change in mature fish: Oulujoki, 5.6 mm year^{-1} ; Iijoki, 2.5 mm year^{-1} ; Simojoki, 3.7 mm year^{-1} ; Tornionjoki, 5.8 mm year^{-1}). The L_{TS} at capture of 3SW fish increased statistically significantly more in the stocks of hatchery group than in the stocks of semi-natural group [Fig. 5(c)] (coefficient estimates for the slope of temporal change: Oulujoki, $12.6 \text{ mm year}^{-1}$; Iijoki, $10.7 \text{ mm year}^{-1}$; Simojoki, 2.3 mm year^{-1} ; Tornionjoki, 0.1 mm year^{-1}). According to Bonferroni comparisons, mature fish of all stocks were significantly smaller than immature fish after 1SW, $P < 0.001$ (653 v. 676 mm), but significantly larger after 2SW (776 v. 763 mm) and 3SW (946 v. 817 mm) ($P < 0.01$ and $P < 0.001$, respectively).

PROBABILISTIC MATURATION REACTION NORMS

The most comprehensive logistic regression model capturing all biologically relevant relationships (equation 1) assigned 75.9% of *S. salar* to the correct maturity class without weighting, and 68.6% 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, cohort and the L_{TS} at capture had a positive effect on the maturation probability indicating an increased maturation probability in all rivers independently of the controlled environmental variables (Table IV). River \times cohort interaction terms or the main effects of rivers were not significant indicating that the maturation probabilities increased in all rivers more or less equally (Table V). Interactions of L_{TS} at capture and L_{TR} with cohort were non-significant and were omitted from the final model.

Without the effect of L_{TS} at capture (data missing for some individuals), more fish could be included in the analysis. The results, however, 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 (equation 2) assigned 76.7% of *S. salar* to the correct maturity class, while the respective precision for the weighted model was 68.6%. Contrary to the expectation, the L_{TR} did not have a significant effect on the probability to mature (Table IV). Interaction of L_{TR} with cohort was non-significant and was omitted from the final model.

DISCUSSION

River Oulujoki *S. salar*, with the longest history of hatchery breeding (Säisä *et al.*, 2003), showed the greatest increases in the probability to mature at early age and L_{TS} at capture over the period of three decades. The L_{TS} at capture had increased in all the observed *S. salar* stocks, including the River Tornionjoki that supports the largest wild Baltic *S. salar* population, in contrast to the observations of decreasing L_T at age in Pacific salmon *Oncorhynchus* spp. (Ricker, 1981). Maturation probabilities had increased over time at all ages and in all stocks except for River Tornionjoki,

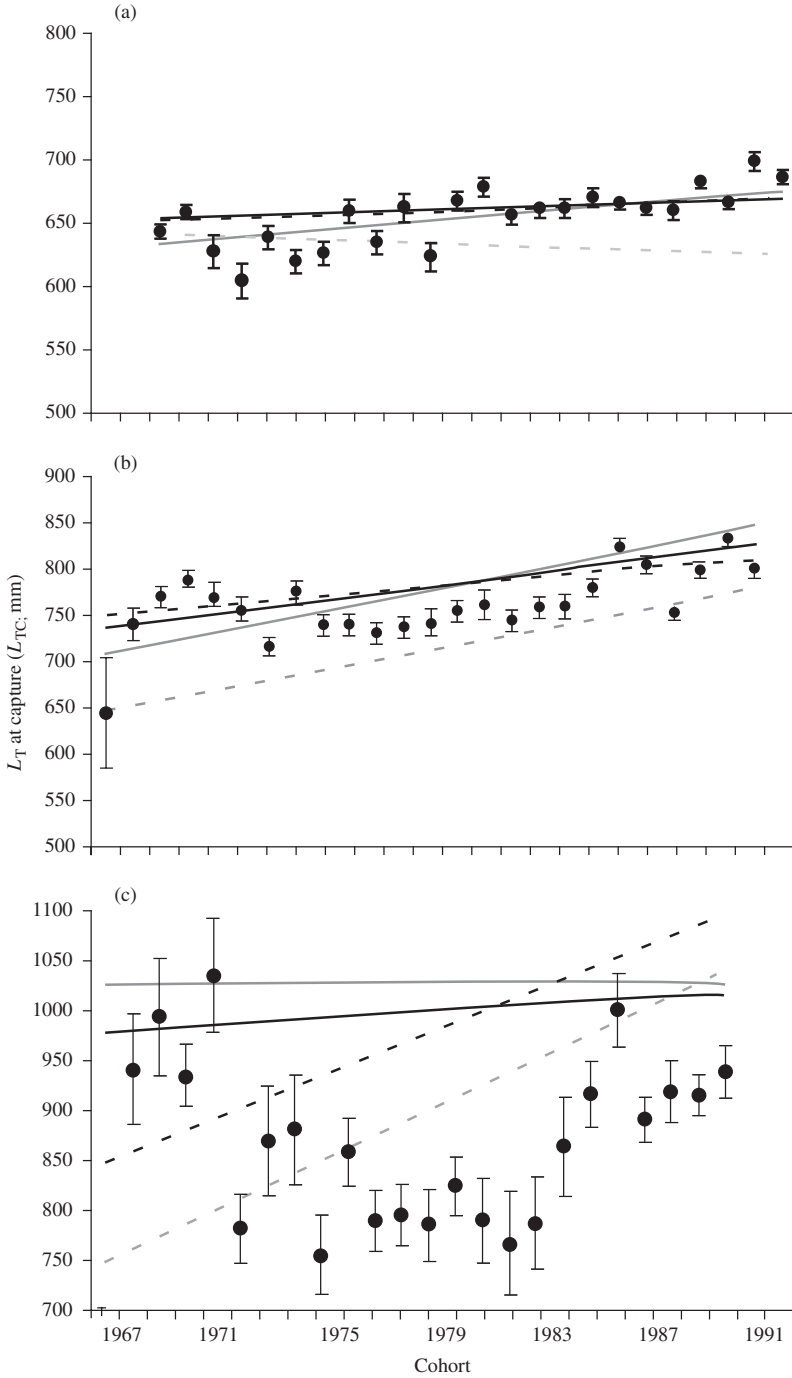


FIG. 5. Temporal variation (marginal means derived from ANCOVAs) in the mean \pm s.e. standardized total length (L_{TS}) at age of *Salmo salar*: (a) grilse, (b) 2 sea winter (SW) fish and (c) 3SW fish. The trend lines (---, River Iijoki; - · -, River Oulujoki; —, River Simojoki; — — —, River Tornionjoki) show estimated (according to ANCOVA) temporal trends for mature individuals at mean L_{TR} (for sea-ages 1 to 3 years, 194.4, 185.9 and 182.6 mm, respectively) and temperature (7.8 °C).

TABLE IV. Comparison of logistic regression models explaining the probability of *Salmo salar* becoming mature, *i.e.* probabilistic maturation reaction norms (PMRN). The most comprehensive model (a) was built based on biological knowledge on expected relationships and the model (b) was simplified due to missing standardized total length (L_{TS}) at capture values. L_T at release (L_{TR}) and L_{TS} at capture are measured in mm, temperature in °C and cohort is in years

(a) Variable, the weighted comprehensive model	Estimate	S.E.	P
Intercept	-121	34.0	<0.001
Age 2	1.77	0.12	<0.001
Age 3	2.50	0.24	<0.001
River Iijoki <i>v.</i> River Oulujoki	21.0	41.0	>0.05
River Simojoki <i>v.</i> River Oulujoki	36.0	40.0	>0.05
River Torniojoki <i>v.</i> River Oulujoki	106.0	70.0	<0.05
Cohort	0.058	0.017	<0.01
L_{TS} at capture	0.0011	0.0006	<0.05
L_{TR}	0.0032	0.0019	>0.05
Temperature a year before capture	0.39	0.10	<0.001
River Iijoki \times cohort <i>v.</i> River Oulujoki \times cohort	-0.010	0.021	>0.05
River Simojoki \times cohort <i>v.</i> River Oulujoki \times cohort	-0.018	0.020	>0.05
River Tornionjoki \times cohort <i>v.</i> River Oulujoki \times cohort	-0.053	0.035	>0.05
(b) Variable, the weighted simple model	Estimate	S.E.	P
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	>0.05
River Simojoki	32.9	27.9	>0.05
River Torniojoki	130.0	60.4	<0.05
Cohort	0.058	0.010	<0.001
L_{TR}	0.0010	0.0015	>0.05
Temperature a year before capture	0.30	0.08	<0.001
River Iijoki \times cohort <i>v.</i> River Oulujoki \times cohort	-0.010	0.015	>0.05
River Simojoki \times cohort <i>v.</i> River Oulujoki \times cohort	-0.017	0.014	>0.05
River Tornionjoki \times cohort <i>v.</i> River Oulujoki \times cohort	-0.065	0.030	<0.05

but significantly more at early ages and in stocks relying exclusively on broodstock breeding programmes. 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? Probably, environmental factors and improved aquaculture methods had contributed to the overall phenotypic increase in the growth rate of all stocks. Common conditions, however, cannot explain divergent trends between the stock types. Fishing can impose selective pressures only on stocks with natural or supported reproduction (here, Rivers Simojoki and 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 are dependent on food intake rates, and there is little or no mortality cost for high foraging and feeding

TABLE V. Probabilities of *Salmo salar* from cohorts 1967 and 1992 maturing at a given age (sea winters) at fixed total length at release (L_{TR}) 190 mm, at fixed standardised total length (L_{TS}) of 644, 768 and 919 mm for ages 1 to 3 years, respectively, and at fixed temperature 7.77° C (mean values over the study period) assuming a linear temporal change and PMRN model of Table IV(a) or (b) (comprehensive *v.* simple PMRN model)

River	Age (years)	Comprehensive weighted model			Simple weighted model		
		P-1967	P-1992	%	P-1967	P-1992	%
Simojoki	1	0.21	0.42	101	0.20	0.41	107
Tornionjoki	1	0.33	0.36	8	0.39	0.34	-12
Iijoki	1	0.19	0.44	128	0.20	0.44	125
Oulujoki	1	0.11	0.35	215	0.15	0.42	187
Simojoki	2	0.64	0.83	29	0.52	0.75	44
Tornionjoki	2	0.77	0.79	3	0.74	0.70	-5
Iijoki	2	0.62	0.84	36	0.53	0.78	49
Oulujoki	2	0.46	0.78	71	0.43	0.76	76
Simojoki	3	0.82	0.92	13	0.64	0.83	30
Tornionjoki	3	0.89	0.90	1	0.82	0.79	-4
Iijoki	3	0.80	0.93	16	0.64	0.85	33
Oulujoki	3	0.67	0.90	33	0.56	0.84	51

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 *S. salar* genotypes among individuals that return to spawn or become new broodstock (here, Rivers Simojoki and 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 L_{TS} at age of *S. salar*. The current results, however, do not clearly distinguish the intensities of selection within and outside hatcheries since the L_{TS} at age of 2SW *S. salar* increased most in the River Tornionjoki (the largest wild Baltic stock) and River Oulujoki (hatchery stock). On the other hand, the size of 3SW *S. salar* increased significantly more in the hatchery stocks than in the supported wild stocks, suggesting that the within-hatchery selection might 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 to 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 caught before their first spawning run. Furthermore, highly abundant male grilse spawning before reaching the minimum legal L_T of 600 mm (since 1993, 500 mm 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. 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. Furthermore, 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 levels, the analyses of probabilistic maturation reaction norms in this study failed to account for increased growth rates. This occurred because 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 *S. salar* is high (Larsson, 1984), and catch date within a year explained only *c.* 8% of the size of recaptured fish. This made it difficult to control for the longer time immature fish had for growth in comparison with maturing fish that had ceased feeding. It is also unknown when the growth of maturing *S. salar* 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 fish that initiated maturation in previous year were larger than the fish that remained immature, but became smaller than the immature feeding fish before the time of sampling, as has been observed for mature parr (McKinnell & Lundqvist, 1998). Since all fish below highest minimum size limit (600 mm) were excluded, the size limit *per se* cannot explain the observed differences, although it efficiently excluded all small immature *S. salar* but also large proportions of small mature males (Christensen & Larsson, 1979). Indeed, as all *S. salar* <600 mm in L_T 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 L_T of grilse unreliable.

Water temperature measured at one point of location within the *S. salar* 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 has experienced. Increased L_{TR} had the expected positive effect on maturation, but surprisingly it appeared non-significant when the effect of L_{TS} 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 *S. salar*: as a function of L_{TR} 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 *S. salar* (Kallio-Nyberg *et al.*, 1999; Jutila *et al.*, 2003b). All *S. salar*, except for some River Simojoki smolts, however, 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 *S. salar* 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 *S. salar* also differs greatly between the open sea feeding areas and spawning migration routes. In this study, the

effects of varying catchability were minimized by excluding fish caught from year 1996 onwards, since before 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. Given the high heritability of growth and maturation in *S. salar* (Powell *et al.*, 2008), however, these results support the earlier findings of Kallio-Nyberg & Koljonen (1997) and Säisä *et al.* (2003) reporting life-history divergence between *S. salar* from wild and reared parents and directly observed temporal genetic changes in the studied stocks. The current results are also in line with direct genetic evidence demonstrating consistent differences between the stocks studied (Koljonen *et al.*, 1999).

Many *S. salar* populations have become endangered due to multiple anthropogenic factors (Parrish *et al.*, 1998). One reason for the declines may be domestication selection (Fleming & Enum, 1997; Fleming *et al.*, 2000; Kallio-Nyberg *et al.*, 2007). The survival of stocked smolts has not only decreased in the Baltic Sea (Koljonen, 2006; Michielsens *et al.*, 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 reduces genetic diversity within the stock (Koljonen *et al.*, 2002; Säisä *et al.*, 2003). Consequently, interbreeding of domesticated *S. salar* with wild fish threatens local adaptations of wild populations (Fraser *et al.*, 2008). Domestication effects in gene transcription profiles have been found to be rapid in farmed *S. salar* (Roberge *et al.*, 2006). Furthermore, 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 *S. salar* (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 captive-bred *S. salar*.

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 *S. salar* more resembled wild stocks than the River Oulujoki stock. Whether there were evolutionary changes in the maturation schedules or growth rate of the supported wild stocks remains open, but the study provides reasonable evidence to suggest that the captive-bred *S. salar* have genetically diverged from the wild stocks in their life-history traits, thus supporting the earlier results (Kallio-Nyberg & Koljonen, 1997). Understanding the relative significance 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 fishes are warranted.

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