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Effects of hatchery rearing and sea ranching of parents on the life history traits of released salmon offspring

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ABSTRACT

Life-history traits such as growth, survival, sea migration and age at sexual maturity in the sea were compared between Carlin-tagged hatchery-reared Atlantic salmon smolts (*Salmo salar*) originating from hatchery broodstocks (reared) or naturally ascending spawners captured (sea ranched). The ranched parents included both wild (born in nature) and reared individuals (released as parr or smolts). All smolts were reared in similar hatchery conditions, and they were tagged and released as two-year-olds in the Simojoki River in 1986–2007. The recapture rates did not differ between the progeny groups, although the tagged smolts of the reared parents were larger than those of ranched parents at time of release. The captive salmon with ranched parents were at average heavier during their second winter at sea, but not later. Salmon with ranched parents more frequently migrated to feed in the Main Basin of the Baltic Sea, further from the home river of the salmon stock. The proportions of multi-sea-winter returners were 30% and 69% in salmon with reared and ranched parents, respectively. The different patterns of migration and sea age at maturity of these parental progeny groups suggest that differences in the life history of brood fish may cause distinct, possibly even genetic differences in the progenies.

1. Introduction

Rearing of salmonids in artificial conditions tends to change natural fish stocks due to different selective pressures acting in hatcheries compared to the natural environment (Fleming et al., 1994; Reisenbichler and Rubin, 1999). Several studies have demonstrated that reared Atlantic salmon (*Salmo salar*) may genetically and phenotypically differ from wild fish (Fleming et al., 2002; Glover et al., 2009; Hutchings and Fraser, 2008; Jonsson and Jonsson, 2006; Skaala et al., 2005). Captive reared salmon often have a lower survival rate, reproductive ability or lifetime fitness than wild fish originating from a common gene pool (Fleming et al., 2000; Jonsson et al., 2003; McGinnity et al., 1997; Saloniemi et al., 2004). The effects of domestication increase with increasing numbers of reared generations in Atlantic salmon (Fleming et al., 1994). Even culturing salmon during the juvenile part of its life-history has been observed to halve the spawning success of males compared to that of wild fish (Fleming et al., 1997). However, early release as one-year-old parr instead of smolts at the age of two years decreases the differences between wild and cultured salmon in marine survival and spawning migration (Jokikokko and Jutila, 2009; Jokikokko et al., 2006).

Various genetic hypotheses have been proposed to explain the inferior fitness of reared fish compared to wild fish. Araki et al. (2008) listed genetic changes such as the accumulation of deleterious mutations, inbreeding depression and domestication selection in captivity. The unbalanced sex ratio, small effective population size, and several generations in captivity typical of reared fish stocks increase the loss of genetic variability (Frankham, 2008; Horreo et al., 2007; Machado-Schiaffino et al., 2007). A significant question is whether hatchery rearing and stocking can have any positive contribution to the conservation of natural fish stocks, and what are the most effective methods for this (Araki et al., 2008; Blanchet et al., 2008).

Artificial production of juveniles from naturally ascending spawners is one way to supplement lost or weak natural salmon stocks. If the progeny is released in their native river after a short hatchery period, this method is called sea-ranching (Jokikokko and Jutila, 2005; Jutila et al., 2003b; McKinnell and Lundqvist, 2000). In Finland, the rearing of parental fish stocks in artificial conditions throughout their life has been common in producing hatchery-reared juveniles of Baltic Sea salmon stocks. Successive hatchery generations are unavoidable in a situation where original spawning areas in nature have been destroyed (Säisä et al., 2003), and artificial rearing has been a necessary way to protect the endangered stocks in face of the lack of reproduction areas and the excessive pressure of the mixed stock sea fishery (Jokikokko and Jutila, 2005; Jutila and Pruuki, 1988; Romakkaniemi et al., 2003). Some Baltic salmon stocks, like Iijoki and Oulujoki

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ones have been entirely maintained by broodstocks for many generations (Kallio-Nyberg et al., 2006; Koljonen, 1989).

In this study, eggs for juvenile rearing were produced by both hatchery-reared broodstocks (the same reared Simojoki parents were used for 5–7 years) and sea-ranched parents captured as returning spawners at the Simojoki River mouth (used only in the year of capture). The Simojoki River has a wild stock, but it has been supported by releases of reared parr and smolts since the mid-1980s (Jutila and Pruuki, 1988). Our aim was to compare the effects of these two types of hatchery rearing (hatchery-reared or sea-ranched parents) on the life-history traits of the resulting smolts. Both wild salmon and fish with hatchery origin (reared and released as parr or smolts) occurred among the sea-ranched parents, but these could not be separated. Fertilized eggs from both parental groups were raised in similar hatchery conditions, so we assume differences between the groups to originate from different selection pressures on parental groups during previous generations. The progeny was raised, tagged and released as two-year-old smolts, the typical age of stocked salmon in Finland.

2. Materials and methods

2.1. Salmon data

The Simojoki River (25°00′E; 65°38′N) flows into the Bothnian Bay in the northernmost part of the Baltic Sea (Fig. 1). The river supports a naturally reproducing and genetically differentiated Atlantic salmon stock (Koljonen, 2001). The natural stock of Simojoki salmon has been supported by annual releases of hatchery-reared parr and smolts from the mid-1980s to the early 2000s due to the endangered state of the natural stock in that period (Jutila and Pruuki, 1988; Jutila et al., 2003b).

Reared smolts were produced by using both hatchery-reared parents (broodstocks) and returning wild or reared spawners from the Simojoki River. In this study, the parental origin is denoted as (hatchery) reared if the juveniles were produced by using a hatchery broodstock and hatchery-reared parents. Sea ranched juveniles were produced by using eggs and milt stripped from spawners that had returned to the Simojoki River. The proportion of wild and reared spawners among the ranched parents varied annually. The progenies could not be separated in relation to the breeding history of ranched parents (reared salmon released as parr or smolts, or wild salmon), but in this study they were all treated as the ranched parental group. In 1990–2001, the wild/reared ratio among multi-sea-winter (MSW) returning spawners varied from 0.120 to 1.295 (Jutila et al., 2003b).

The reared smolts included in this study were released in the Simojoki River between 1986 and 2007 (Table 1). In total, 10,180 reared smolts (14 groups) with ranched parents and 17,370 smolts, two-years-old, (21 groups) with reared parents were tagged. The juveniles were raised using similar routine methods independent on their parental origin in the northern hatcheries (Kallio-Nyberg et al., 2004). The tagged smolt groups were randomly sampled from the reared fish with several families. All smolts included in this study were marked with an individual Carlin tag in the hatchery before release. The smolt length (total body length), which was used in the analysis, was concurrently in tagging measured. The mean weight (body mass) of the sampled smolts (10% of the tagged smolts, $n \sim 100$) in each tagging group was also recorded. Salmon were tagged in the winter or spring months and mainly released in May. Due to the cold rearing water (<5 °C), growth of the tagged fish was negligible from tagging to release. The fish in this experiment were tagged according to the rules of Directive 2010/63/EU.

The fishermen along the migration routes of the Simojoki salmon in the Baltic Sea returned tags from the captured fish with information on the catch size, location and time. Salmon fishing covers the whole migration area of in the Baltic Sea (Jutila et al., 2003a). The tagging office of the Finnish Game and Fisheries Research Institute compiled

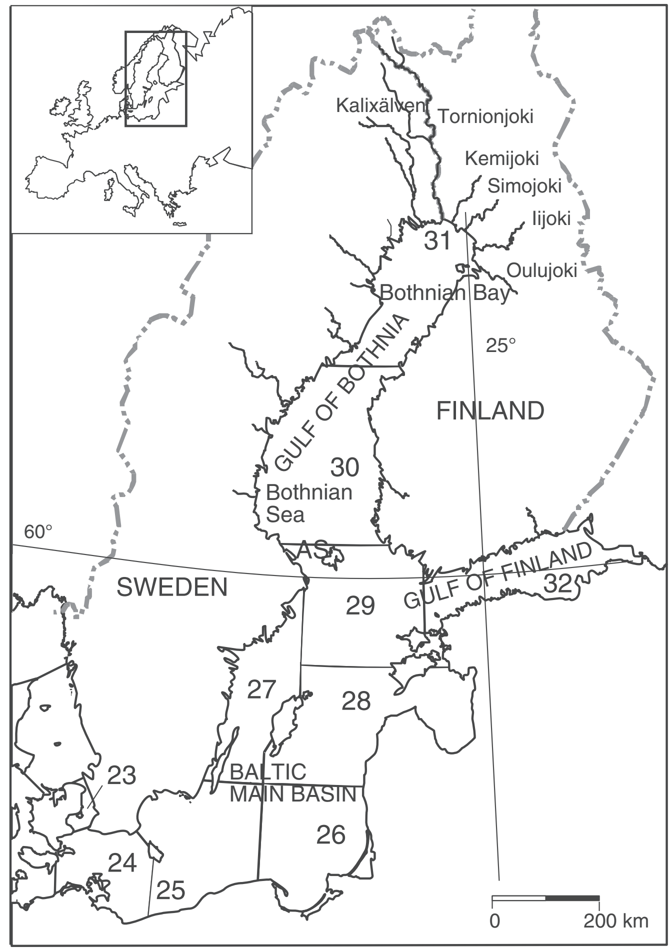

Fig. 1. The Baltic Sea showing the sub-basins (Main Basin (MB) = Baltic Proper = ICES sub-divisions 23–29; Bothnian Sea (BS) = sub-division 30; Bothnian Bay (BB) = sub-division 31; Gulf of Finland = sub-division 32 and the location of the Simojoki River and some other rivers flowing into the BB).

the data from these tags. The recruitment of salmon for fishing begins during the first winter at sea, after attaining the legal minimum landing size of 60 cm in the Baltic Sea, or 50 cm in the Bothnian Bay since 1993.

2.2. Data treatment

The recapture rate and survival analyses were based on tagging and recapture data at the group level. The mean recapture rate of tagging groups was calculated over the years 1986–2007 (SAS MEANS procedure, SAS Institute, 2002), and the trend in the recapture rate over this period was examined by using linear regression (SAS REG procedure) with year as the predictor and the proportion of recaptured fish in each tagging group as the response variable.

The proportion of recaptured fish in each group was assumed to indicate survival in the group, which is correct if natural mortality mainly occurs during the first sea year before recruitment to fishing. This is the case in the northern Baltic Sea, where the great majority of the released smolts have been found to die in the post-smolt stage (Salminen et al., 1995). The marine survival of the Simojoki salmon was analysed in relation to parental origin and smolt length using a linear regression model (SAS MIXED procedure) with the repeated option for the release groups of the same year and with the proportion of recaptured in each tagging group as the dependent variable, as previously applied by Kallio-Nyberg et al. (2006) (SAS

Table 1
Number of fish tagged and recapture rate (rate = the recaptured proportion of the tagged smolts) of hatchery-reared Simojoki salmon smolts released in 1986–2007 in the Simojoki River. All years with any reared or ranched groups are shown on separate lines with tagging groups pooled (if > 1 groups per year, their number is shown under the Tagged column). The smolt length is calculated for recaptured salmon. The parental origin (parents: ranched; reared), number of smolt tagged per parental group per year (Tagged), recapture rate (Rate) and mean smolt length of recaptured fish ($x \pm$ SD) are presented. The common smolt years (1986, 1988, 1989, 1990, 1994 and 1995) for both parental groups are marked with an asterisk.

Year	Parents	Tagged	Rate	Smolt length (mm)		
		n (groups)	%	*n*	*x*	±SD
*1986	Ranched	635 (2)	2.4	15	193	25
*1986	Reared	653 (2)	1.9	13	251	36
1987	Ranched	798 (2)	5.5	44	219	33
*1988	Ranched	984 (2)	6.4	63	159	9
*1988	Reared	499	19.2	97	205	29
*1989	Ranched	999	4.8	56	177	44
*1989	Reared	1454 (2)	16.8	241	213	31
*1990	Ranched	997	6.3	63	174	11
*1990	Reared	498	3.2	28	151	8
1991	Ranched	997	12.9	405	182	16
1992	Ranched	999	3.4	89	185	18
1993	Ranched	999	2.3	206	190	18
*1994	Ranched	996	5.6	123	173	14
*1994	Reared	1000	4.8	76	162	13
*1995	Ranched	996	4.8	256	165	11
*1995	Reared	898	0.6	6	248	21
1996	Reared	2463 (3)	1.7	42	232	43
1997	Reared	992	4.0	41	170	13
1998	Reared	1997 (2)	2.2	43	171	12
2000	Reared	999	2.8	121	187	23
2001	Reared	999	0.3	301	179	14
2002	Reared	997	1.1	12	181	12
2003	Reared	999	2.5	26	199	21
2004	Reared	926	0.1	30	197	25
2005	Reared	997	0.4	72	196	18
2006	Ranched	780	0.4	70	219	25
2007	Reared	999	0.6	98	237	32

Institute, 2002). The proportion of recaptured fish in each group, i.e. the response variable, was normalized using arcsine transformation. Only the common smolt years (1986, 1988, 1989, 1990, 1994, 1995) for both parental origin groups were included. The number of (tagging) groups in the survival model was eight for ranched and eight for reared parental salmon, because there were 3–4 tagging groups in 1986, 1988 and 1989.

The growth analyses were based on individual recaptured fish. First, the mean catch length and weight of parental groups were compared using *t*-tests (SAS TTEST). The fish caught after 12–18 months at sea in the Main Basin (MB) and in the Bothnian Sea (BS) were included. The sample consisted of both fish returning after the first winter and of fish continuing their feeding migration. Next, we compared fish captured in the MB and BS in the second winter (19–23 months at sea) and in the third summer and winter (24–36 months at sea). The 95% confidence limits (CL) for the group mean (x) are given the equations $(\text{CL} - 95\%) = \text{x} - t_{0.05} \quad (n - 1) * (s / \sqrt{n})$ and $(\text{CL} + 95\%) = \text{x} + t_{0.05}\ (n - 1) * (s / \sqrt{n})$, where t is 1.96 (the normal distribution), n is sample and s is variance. Due to the low annual number of recaptured fish (Table 1), the years were pooled within the parental groups. Because ranched groups were mainly released in the 1980s and 1990s, we first compared the parental groups released in 1986–2007, and after that groups released in 1986–1999.

The increase in weight was analysed in a linear regression model (SAS MIXED), in which we used the logarithm of weight to achieve normality of the residuals. The predictors were the classified variables origin (ranched/reared) and year (only the years when both origin groups had been used to produce smolts, i.e. 1986, 1988, 1989, 1990, 1994), and the continuous variable was the time at sea in months. The year 1995 was omitted because of the low number of recaptures in the parental reared group. All variables were fixed, and interactions between the variables were included in the model if they were statistically significant. Month was not nested under year, partly due to the limited data set, and partly because we assumed the strong seasonality of the Baltic Sea to make the within-year growth curves quite similar, even if the average growth of salmon differed between years. After the predicted growth curves were plotted as graphs, we back-transformed weight to linearity, which produced a nonlinear curve. We first examined growth after the first winter (12–18 months at sea), and then in the second winter and third summer (19–30 months). The recaptures from the MB and Gulf of Bothnia were included.

The spatial distribution of the recaptures of salmon with reared and ranched parents during the feeding seasons was compared by applying the SAS FREQ procedure with the χ^2 test (SAS Institute, 2002). The salmon recaptured in the MB and BS in the winter months (19–23 months at sea = second winter; 31–35 months at sea = third winter) were assumed to be undertaking the feeding migrating. Simojoki salmon and other Bothnian Bay (BB) salmon stocks mainly migrate to feed in the MB of the Baltic Sea (migration distance about 800–1400 km from the home river), but some salmon may also feed in the BS, in the southern part of the Gulf of Bothnia (about 500–600 km), depending on the annual food resources available there (Jutila et al., 2003a; Kallio-Nyberg et al., 1999; Salminen et al., 1994) (Fig. 1). Only the common smolt years (1986, 1988, 1989, 1990, 1994, 1995) for both parental origin groups were included.

Adult salmon undergo a return migration in the BB during the spawning season (April–October), which takes place 12–18 months after release for one-sea-winter (1SW) salmon and 24–30 months after release for 2SW fish. The age distribution of the two parental origin groups was compared using a χ^2 test (SAS FREQ), selecting both fish that were caught in the Gulf of Bothnia (GB) (including BS and BB) and those that were only caught in the BB in the spawning seasons. Because salmon return from the MB to the GB when they begin their spawning migration, the age distribution in the gulf was expected to reveal the sea age at sexual maturity of the parental groups. The distributions were examined in both the GB and BB, because it is possible that some salmon may have migrated to feed in the southern GB during the spawning migration (Jutila et al., 2003a; Salminen et al., 1994). Moreover, the number of fish recaptured was small only in the BB. Four spawning migration seasons were included: 12–18, 24–30, 36–42 and 48–54 months after release for 1SW–4SW fish. Only the common smolt years (1986, 1988, 1989, 1990, 1994, 1995) for both parental origin groups were included.

3. Results

3.1. Recapture rate and survival of the parental origin groups

Altogether, 4.7% (±3.3, $n = 14$ tagging groups) of the salmon with ranched parents and 3.3% (±4.6, $n = 21$) of those with reared parents were recaptured (*t*-test: $P =$ ns) (Table 1). The recapture rate did not show an increasing or decreasing trend during the study years in the group with ranched parents (predicted linear regression: rate = 287 − 0.142 ∗ year; $F_{(1,12)} = 0.6$, $P =$ ns, $r^2 = 0.051$), but a recaptures decreased with time in the reared parent group (rate = 756 − 0.381 ∗ year; $F_{(1,18)} = 6.8$, $P = 0.018$, $r^2 = 0.274$). However, the release years differed somewhat between the parental origin groups, as there was hardly any ranching during the last ten years of the study period (Table 1).

For years when fish were released with both reared and ranched parents, survival did not differ between the parental origin groups, and was not connected with the smolt length: the recapture rate for the ranched group was 4.6% (293/6387 individuals) and that for the reared group 4.8% (337 / 6998; χ^2 test).

3.2. Smolt size and marine growth of parental origin groups

The mean smolt length (16.9 ± 1.9 cm; $n = 576$ for recaptured individuals) for ranched parental progeny was lower than that of the progeny of reared parents (20.1 ± 3.7 cm; $n = 461$; $P < 0.001$). Furthermore, the mean smolt weight for ranched parental smolts was lower (37 ± 9 g; $n = 10$ groups; recaptured and non-recaptured smolts pooled) compared to reared parental ones (79 ± 43 g; $n = 8$ groups; $P < 0.05$).

The mean catch length and weight of the groups differed after the first sea winter (12–18 months at sea); the captured progeny of reared parental salmon was on average 7 cm longer and 800 g heavier than ranched ones (reared: length: $n = 31$, 73 ± 11 cm; weight: $n = 27$, 3.9 ± 1.5 kg, ranched: $n = 31$, 66 ± 10 cm; $n = 42$, 3.2 ± 1.4 kg) recaptured in the feeding areas (MB + BS; smolt groups 1986–2007) (Fig. 2). In the second and third sea winters, the catch length of the MSW salmon with reared parents tended to be longer, but non-significantly different from those with ranched parents (19–23 months: ranched 76.6 ± 10.9 cm, $n = 43$; reared: 75.0 ± 7.6 cm, $n = 34$; and 24–36 months, ranched: 78.4 ± 10.5 cm, $n = 34$; reared: 77.6 ± 11.1 cm, $n = 19$). In contrast, the mean catch weight was greater for salmon with ranched parents (5.6 ± 1.9 kg, $n = 53$) than for those with reared parents in the second winter (4.7 ± 1.9 kg, $n = 43$; $P = 0.021$) ($P < 0.05$), but there was subsequently (24–36 months) no difference in catch weight ($P > 0.05$; Fig. 2). The trends for length and weight were similar, if only smolts released in the 1980s and 1990s were included. The ranched parental salmon were captured on average one month later ($n = 28$; 15.6 ± 1.4 months at sea) than the reared ones ($n = 82$, 14.6 ± 1.7; t-test: $P < 0.05$).

The increase in the log-transformed weight was analysed using linear regression and by using parental origin (ranched, $n = 27$; reared, $n = 82$), time at sea (12–18 months) and release year as explanatory variables (Table 2). The growth of the ranched group was rapid and the mean weight reached the weight of the reared group by the end of the first spawning migration season (Fig. 3). The years differed somewhat, with growth being better in 1994 and worse in 1990, but there was no interaction between year and origin. Growth during the second winter and third summer (ranched, $n = 62$; reared, $n = 58$; months 19–30) was analysed in the same way as in the first summer (Table 2). The weight of the parental groups did not differ, but the effect of year and its interaction with origin became more important (Table 2).

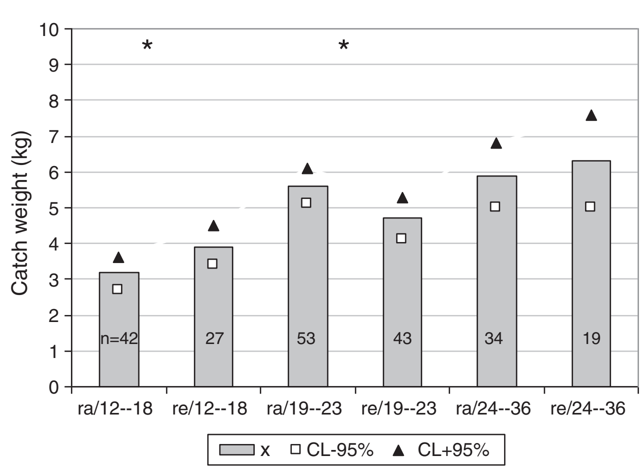

Fig. 2. Mean catch weight of the parental ranched (ra) and reared (re) groups after the first winter at sea during first return migration (12–18 months at sea), the second winter (19–23 months) and in the third summer and winter (24–36 months) in smolt groups released in 1986–2007 and recaptured in the MB and BS included. The 95% confidence limits (CL − 95% and CL + 95%) for the group mean (x) are shown. Significant differences in t-tests of age-specific catch weights between parental origin groups shown above the bars (* = $P < 0.05$).

Table 2
Individual-specific growth models for tagged smolts from tag return data in relation to parental origin (ranched, reared), months at sea and release year (1986, 1988, 1989, 1990, 1994) for salmon captured after the first winter at sea (12–18 months) and later from the second winter to the third summer (19–30 months at sea). The response variable was catch weight.

Model	Predictor	Num, *df*	Den, *df*	*F* value	*P*
12–18 months	Origin	1	102	11.11	0.0012
	Month	1	102	81.58	<0.001
	Year	4	102	3.62	0.008
	Origin * month	1	102	8.98	0.003
19–30 months	Origin	1	109	0.16	0.692
	Month	1	109	1.14	0.288
	Year	4	109	2.28	0.065
	Origin * year	4	109	4.10	0.004

3.3. Migration and length of sea period

The feeding migration area of the parental reared and ranched progeny groups differed significantly in the second sea winter (19–23 months at sea) during the six-year period when both parental groups were available. The salmon with ranched parents more frequently migrated further to the MB (83%) than the salmon with reared parents (52%; χ^2 test: $P < 0.01$). A large proportion (48%) of salmon with reared parents was caught close to the BS in the second winter (Fig. 4). Later, during the third winter, the spatial distributions of progeny groups with reared or ranched parents did not differ.

After the first winter at sea (12–18 months at sea), the salmon with ranched parents were caught more frequently (65%) in the MB than those of reared parents (41%; χ^2 test: $P < 0.01$) (Fig. 5). After the second winter at sea (24–30 months after release), the parental origin had no significant effect on the spatial distribution (Fig. 5).

The sea age distributions of the ranched and reared progeny groups differed significantly during the return migration seasons (χ^2 test: $P < 0.001$; estimated from the recoveries in the GB or BB). The reared parental salmon returned earlier than the ranched ones. The proportion of grilse was 66–70% in the reared parental group compared with 23–31% in the group with ranched parents (recaptures in the GB or BB) (Fig. 5). In the reared parental group, 3–4SW fish were rare (2%), but in the ranched group, 20–23% of the returners were 3–4SW fish (Fig. 6).

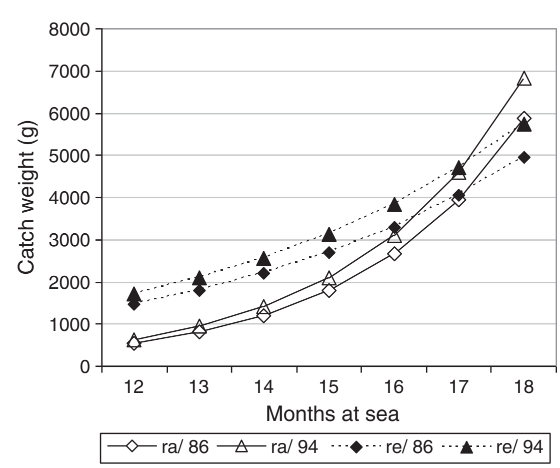

Fig. 3. Predicted catch weight of salmon with ranched (open symbol) and reared (solid) parents in relation to the number of months spent at sea in the smolt year 1986 and 1994 according to a linear regression model. The time period is from 12 to 18 months after release (the first return migration season) and the recapture site is the Main Basin and Gulf of Bothnia of the Baltic Sea. The sample sizes were 28 for salmon with ranched parents and 82 for those with reared parents. Five years (1986, 1988, 1989, 1990, 1994) were included in the model, but only two are shown. Predictors in the model are log-transformed, but in the figure are transformed back to linearity.

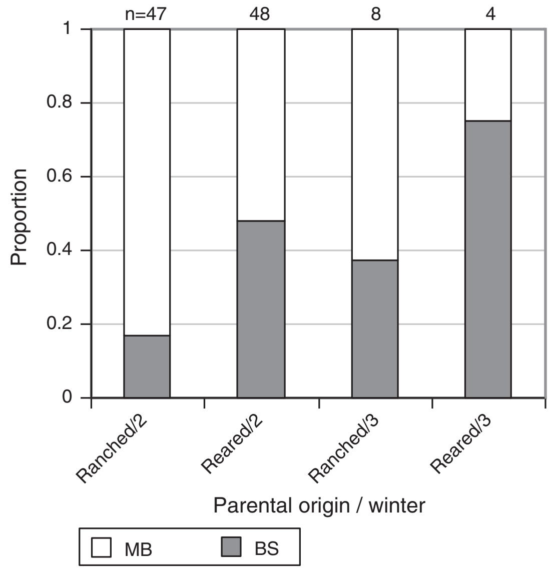

Fig. 4. Spatial distribution of salmon with ranched and reared parents in the second and third sea winters (19–23 and 31–35 months at sea) in the Main Basin (MB) and in the Bothnian Sea (BS). The number of recoveries is indicated above the column.

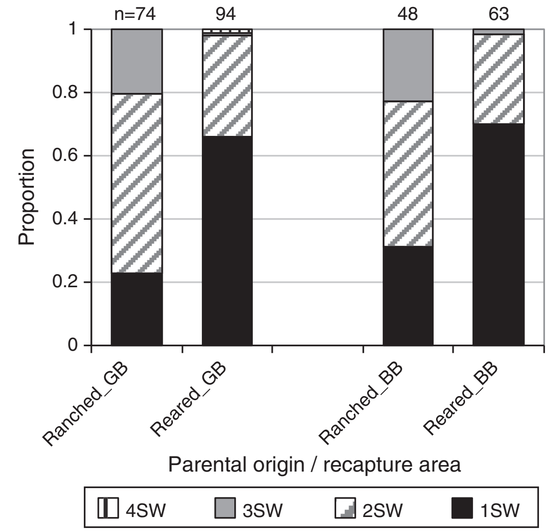

Fig. 6. Sea age (1SW–4SW) of recaptured salmon with ranched and reared parents in the Gulf of Bothnia (GB, including BS and BB) and in the Bothnian Bay (BB) in the return migration seasons (April–October; 12–18 and 24–30 months at sea). The number of recoveries is shown above the column.

4. Discussion

4.1. Survival

In this study, the compared progeny groups were reared in similar conditions and no differences were found in their survival measured in terms of recapture rates. The results do not suggest selection on survival to differ between the progenies of the two parental groups, but the effects on the life-history traits cannot be excluded. In comparison to studies conducted on wild salmon, the survival of the reared groups (parental origin groups pooled) was found by Kallio-Nyberg et al. (2011) to be lower. Factors like inbreeding or age of parents may also affect the survival of progenies (Fleming, 1998; Kallio-Nyberg et al., 2007b), but in this study we could not examine the effect of the specific parental traits on the progenies.

Despite the larger size of the smolts with reared parents, the recapture rate in this study was similar for both parental origin groups. The high growth rate of the reared parental salmon in the hatchery is not necessarily a benefit in nature, although larger smolts released after hatchery rearing have survived better than smaller ones in earlier studies (Jokikokko et al., 2006; Kallio-Nyberg et al., 2009; McKinnell and Lundqvist, 2000). Saikkonen et al. (2011) observed that rapid growth of salmon juveniles in captivity may indicate poor performance in nature.

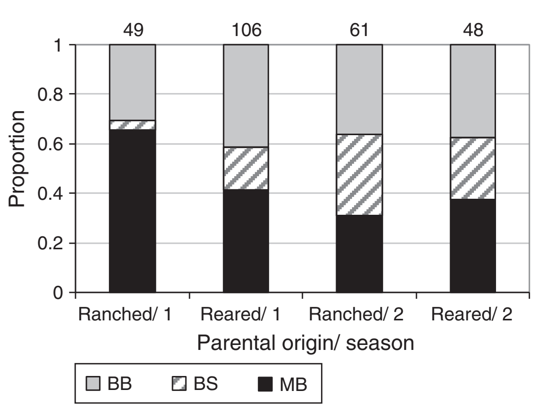

Fig. 5. Spatial distribution of salmon during the first (1) and second (2) return migration seasons (12–18 and 24–30 months at sea) with sea-ranched and hatchery-reared parents. The number of recoveries is indicated above the column.

Reared salmon have had lower survival rates than wild ones in the natural environment when the wild and reared smolts have come from the same gene pool (Jonsson et al., 2003; Saloniemi et al., 2004). Even the larger smolt size of the reared salmon does not compensate for their decreased survival (Saloniemi et al., 2004). Artificial selection affect antipredator responses and thereby increase the risk of being preyed on (Johnsson et al., 2001), a trait that has changed after only one hatchery generation (Fritts et al., 2007).

The domestication may reduce the reproductive ability. Hindar et al. (2006) reported that sea-ranched salmon had a higher (0.51–0.91) relative spawning success in natural breeding environments compared to cultured salmon (0.13–0.44). In the Simojoki salmon, wild smolts survived better from smolt to ascending adult salmon compared to salmon released as two-year-old smolts or parr (0.68 vs. 0.20–0.29) (Jokikokko and Jutila, 2009). In this river, the strengthening of fishing regulation together with releases of hatchery-reared juveniles increased the spawning stock in years when natural production was very low (Jutila et al., 2003b).

Tagging may reduce the survival of smolts (Hansen, 1988), and when survival is estimated from recapture data, also the proportion of lost and returned tags may affect the results. As the reporting activity is likely to be lower than the presence of marks in the catch (WGBAST, 2011) or for fish under the legal size (<60 cm) (Kallio-Nyberg et al., 2007a) the observed recapture rate is a minimum estimate.

It cannot either be totally ruled out that the captures of the parental origin groups are reported in a different way due to their different sizes or behaviour. For example, large smolts are able to feed on other fish instead of only invertebrates at an earlier age (Salminen, 1997; Salminen et al., 1994). In addition, Salminen et al. (1995) demonstrated that large salmon smolts are more vulnerable to fishing than small smolts. Variation in the reporting activity may particularly affect the estimates of the feeding distances of salmon. An earlier comparative study of Atlantic salmon (*S. salar*) in Kemijoki estuary demonstrated that hatchery-reared progenies of reared sea-ranched parents have higher recapture rates than hatchery-reared progenies of wild parents (Kallio-Nyberg et al., 2007b). The decreased parr maturation rate (precocity) of the progenies with sea-reared parents partly explained their higher marine survival, because mature males had a lower marine survival than immature males (Kallio-Nyberg et al., 2007b).

In Finnish tagging experiments, the recapture rate of tagged salmon smolts decreased in the Baltic Sea from approximately 10% in the 1980s to 1% in the 2000s (Kallio-Nyberg et al., 2006, 2009). The decline in the recruitment of Atlantic salmon is a global phenomenon (Friedland et al., 2009; Jonsson et al., 2003). All Finnish salmon stocks in the Baltic Sea have generally been supported by releasing two-year-old hatchery-reared smolts in the coastal rivers (Romakkaniemi et al., 2003; Salminen et al., 2007). A possible negative influence of hatchery rearing on the viability of the fish stocks is likely, but environmental changes could also explain part of the decrease in marine survival, as the declining recapture rate in both parental origin groups in this study suggests.

4.2. Growth

Broodstock rearing tends to select fish with a higher growth rate. In this study, the progeny of reared parents attained a larger size as smolts and during the first return migration season compared to those of ranched parents. This is consistent with the previous studies (Fleming et al., 2002; Glover et al., 2009; Kallio-Nyberg and Koljonen, 1997).

At sea, the growth difference between parental groups changed. After 12–18 months after release the reared parental 1SW salmon were yet larger (Figs. 2 and 3), but during the second sea winter (19–23 months at sea) the ranched fish gained on them in mean size (Fig. 2). However the other analysis with several other predictors as the parental origin showed that the catch weight of the parental groups that had spent 19–30 months at sea did not differ (linear regression, Table 2). Data on sea growth may be influenced by factors such as growth ability, the selectivity of fishing, behaviour, and the sea age at maturity. However, the growth model using common smolt years did not suggest a link with annual environmental factors. A large proportion of the salmon with a reared parental origin attained maturity after one sea winter (Fig. 5). Most mature 1SW Baltic salmon are males (Romakkaniemi et al., 2003), and most of these 1SW spawners do not survive to the second sea migration (Jokikokko et al., 2006). The parental ranched salmon group continued to grow in the sea and passed the first return migration season, but the 1SW larger males either died or lost weight due to spawning, and so the size difference between the parental groups changed.

It is possible that the growth curves of the parental groups also differ due to different feeding conditions. The parental ranched salmon more frequently migrated to feed in the MB, where the prey fish abundances are highest in the Baltic Sea, while a large proportion of parental reared salmon migrated to feed in the more barren BS.

Over the long-term from 1972 to 1995, the growth rate of salmon stocks originating from the BB rivers increased (Vainikka et al., 2010). This increase in the growth rate could partly be explained by the higher sea surface temperature and partly by the larger release size of hatchery-grown fish. However, the observation that the growth rate has changed more in broodstock-based stocks (Oulujoki, Iijoki) than in semi-wild (both natural and reared stock) stocks (Tornionjoki, Simojoki) supports the contention that selection in hatcheries may partly explain the increase in the growth rate (Vainikka et al., 2010).

4.3. Migration

The progenies of the hatchery-reared broodstock had shorter feeding migration distances than those with sea-ranched or wild parents. This is consistent with earlier observations that wild salmon migrate to feed more frequently about 500 km further to the MB, while reared salmon more often remain in the BS (Jutila et al., 2003a; Kallio-Nyberg et al., 2011). Domestication selection in the parental generation appears to shorten the feeding migration distance. A short migration distance might be linked to the high number of 1SW males that return to spawn after a short sea migration (Jokikokko et al., 2004; Jonsson et al., 1990). A bigger size in the post smolt phase also causes feeding distance differences when salmon of reared origin more often remain in the BS instead of migrating to the MB (Jutila et al., 2003a; Kallio-Nyberg et al., 2011; Salminen, 1997).

4.4. Sea age at sexual maturity

The salmon with reared parents returned as maturing salmon to the GB at a younger age than the salmon with ranched parents. This may be linked to differences in the freshwater growth and different selection pressures of the parental generation. A trend towards increased growth under domestication, earlier reported by Fleming et al. (2002), was apparent here, as the broodstock-based smolts were larger. As a consequence of early growth, the proportion of grilse is high among the returning salmon (Salminen, 1997; Skilbrei, 1989). There appears to be a negative correlation between the growth rate and sea age at maturity (Gjerde, 1984). An earlier experiment with Baltic salmon compared reared captive progenies of sea-ranched and wild parents. Progeny of wild parents had higher sea age at maturity, but progenies of captive parents grew faster (Kallio-Nyberg and Koljonen, 1997). In another study, the rearing was found to reduce the proportion of MSW salmon as compared with wild smolts (Kallio-Nyberg et al., 2011). Rearing may thus change the age structure of salmon stocks, as reported earlier for steelhead (*Oncorhynchus mykiss*) (Kostow, 2004). Hatchery fish were nearly uniform in smolt age and age at first spawning, whereas naturally produced fish of this salmonid species were highly variable (Kostow, 2004).

Intensive rearing in the hatchery may affect traits that are genetically correlated with the maturation time of anadromous salmon. Lower age at maturity at sea was observed in the hatchery reared Iijoki and Oulujoki salmon stocks compared with the wild salmon stocks (Rivers Simojoki and Tornionjoki) supported by provisional releases of hatchery-reared parr and smolt (Vainikka et al., 2010). The sea age at first maturity (number of sea winters of the returning salmon) in semi-wild Simojoki salmon was stable during 1972–1995 (Vainikka et al., 2010). The Iijoki and Oulujoki salmon stocks have multiple hatchery generations (Säisä et al., 2003), but Simojoki broodstocks have been maintained by using only ranched or wild salmon (Jutila et al., 2003b).

The sea-age distribution of adult Simojoki salmon partly depends on size-selective fishing and fishing regulations. Jutila et al. (2003b) have shown that early summer regulation of fishing in the Gulf of Bothnia has affected the size and structure of the ascending spawning stock. During a period of strict fishing regulation (1997–2003), the proportion of MSW spawners increased in the spawning population compared to the earlier period of slight regulation (1990–1996).

4.5. Management implications

The principal reason for using hatchery rearing and smolt releases in the enhancement of the Simojoki salmon stock was an alarming decrease in natural parr and smolt production observed since the 1970s (Jutila and Pruuki, 1988). In 1986–1988, when rearing and stocking began, the natural smolt production was only a few thousand smolts per year. The goal of the supportive stockings using parr and smolt releases was to increase the ascending spawning stock in the river. Both wild and ranched reared spawners have been used in breeding since the 1980s (Jutila et al., 2003b). The released juveniles have been imprinted on the spawning areas of the river (Jokikokko and Jutila, 1998), and the wild and reared fish have probably spawned together in the wild. To avoid intra-specific competition of parr in the river, smolts were also released in large numbers in the most critical years.

However, hatchery rearing includes the risks of losing or changing the adaptive diversity of the reared stock and other stocks adapted to neighbouring rivers (Hindar et al., 2006; Horreo et al., 2007; Koljonen et al., 2002). Large-scale hatchery rearing may hinder, rather than aid, the recovery of the endangered population (Levin et al., 2001). For the Simojoki salmon, the risk of extinction and the loss of genetic diversity due to the small effective population size were regarded as greater threats than the possible change in adaptive diversity (Koljonen, 2001; Koljonen et al., 1999). Captive breeding has maintained genetic diversity at a level that is at least at the same as or higher than in the smallest wild stocks in the Baltic Sea (Koljonen et al., 1999). However, supportive breeding has been found to erode the original genetic variability in other salmon stocks (Blanchet et al., 2008; Machado-Schiaffino et al., 2007). The observed differences in life-history traits between the progenies of reared and ranched parents suggest that selection pressures in the parental generation may differ between reared and ranched groups. However, the reared and released salmon independent on their breeding history, encounter high natural and fishing mortality (WGBAST, 2011), and very few are able to spawn the next generation (Jokikokko and Jutila, 2009). Although the progenies may differ in their life-history traits, these differences will not obviously be transmitted to the next generation, and genetic studies would be needed to demonstrate whether these changes are temporary or permanent.

The acquisition of eggs for hatchery rearing by using reared broodstocks reduces the annual needs for catching returning spawners in the river, because the broodstock parents can be stripped in the hatchery in 5–7 successive years. On the other hand, the use of the same parents in production over several years differs considerably from the situation in natural spawning. In nature, females usually only spawn once, but with up to 16 different males (Weir et al., 2010). In the breeding of Simojoki salmon, the eggs of one female have mostly been fertilized using the milt of three males. In addition, many generations overlap in natural spawning (Jokikokko and Jutila, 2005), but in an artificial broodstocks mating females and males more often belong to the same generation. The ranched parents are a sample from the ascending spawners and thus differ less from the natural stock.

In conclusion, the results indicate that phenotypic and genetic changes may have occurred in the progeny generation of the Simojoki salmon both with broodstock-reared and ranched parents. However, a large proportion of the released salmon in the Simojoki River were stocked as one-summer-year old or one-winter-year old parr, which were more similar to the wild salmon (Jokikokko et al., 2006; Kallio-Nyberg et al., 2011). The Simojoki salmon stock has now partly recovered, producing 20,000–40,000 smolts annually in the early 2000s, while the annual natural smolt production was estimated to be 55,000–65,000 smolts in the 1960s (Jutila and Pruuki, 1988). Consequently, the enhancement of the salmon stock using releases of hatchery-reared parr and smolts ended in 2003. Despite the present observations of possible genetic changes in the life-history traits of salmon differing in parental breeding history, the releases have succeeded in conserving and maintaining the Simojoki salmon stock during the most critical periods (Jokikokko, 2006). The small number of spawners and low natural smolt production in the 1980s (Jutila et al., 2003b) might have affected the variation more than hatchery rearing after this. In certain cases, however, hatchery-reared broodstocks and stocking with reared smolts may be the only method to maintain the salmon stock until more potent alternatives such as fishing regulations and habitat restoration are realized. Due to the potential genetic changes affecting the progeny, the use of hatchery brood stocks in enhancement stocking should be restricted to a minimum or completely avoided.

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