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Survival of reared and wild Atlantic salmon smolts: size matters more in bad years

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We compared the marine survival of Carlin-tagged wild and hatchery-reared Atlantic salmon smolts of the Simojoki river, northern Baltic Sea. All the reared and released smolts were the offspring of native spawners returning to the river. Reared smolts were adipose-fin-clipped and released from the hatchery several weeks before tagging. The wild and reared smolts were simultaneously caught and tagged at a smolt trap located at the Simojoki river mouth. The study was conducted in two years, 1991 and 1993, when post-smolt survival in the Baltic Sea was different. Tags were returned by fishermen and return rates were used to estimate the survival of the smolt groups. We applied generalized linear models with survival as response variable and the year, origin, and smolt size as explanatory variables. On average, wild smolts had a 4.5 times higher survival rate than reared fish of the same smolt size. The difference in observed tag recovery rates as such was only about twofold or less, as the larger size of the reared smolts compared with the wild ones compensated for their lower survival rate. The better survival of wild than reared smolts was more pronounced in the low-survival year (1993 smolt year class) than in the high-survival year (1991 smolt year class).

Keywords: hatchery reared, salmon, smolt size, survival, tagging, wild.

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Introduction

Several Atlantic salmon (*Salmo salar* L.) stocks of both Atlantic and Baltic rivers are endangered or have even been lost. In the Baltic Sea area the main causes of stock decline have been overexploitation and habitat loss due to the damming of rivers for hydroelectric power production. The M74 syndrome has also negatively affected salmon stocks in the Baltic Sea (Karlsson and Karlström, 1994; Anonymous, 2002).

The hatchery production of salmon is an attempt to enhance salmon stocks (Ritter, 1997; Jokikokko and Jutila, 1998; Einum and Fleming, 2001). Reared parr and smolts have been released into free-flowing rivers to augment the natural spawning population. However, the proportion of wild smolts in the Baltic Sea has been low since the 1970s due to large-scale compensatory releases (Anonymous, 2002).

The survival of reared salmon smolts is known to be inferior to that of wild smolts (e.g. Jonsson *et al.*, 1991), so it is crucial to know how many reared smolts are equivalent to a given number of wild smolts. Previous studies have also revealed that populations of reared origin do not perform as well in the natural environment as their wild counterparts. In some cases, stocking may even cause a long-term decrease in the genetic adaptation of native stocks (Fleming *et al.*, 1994, 2000; Einum and Fleming, 2001; Levin *et al.*, 2001). Wild and stocked smolts are exposed to different environmental conditions. For example, the timing of smolting under hatchery conditions is not always the same as in the wild (Soivio *et al.*, 1988). Rearing conditions, including the daylength rhythm, temperature, and the quality and amount of food, influence the growth rate, final length, physiological state, and smolting process of the fish.

In many cases the inferior performance of reared salmon in the wild is due to their long history in hatcheries, or their entirely foreign origin. In this study, we compared the survival of wild and hatchery-reared salmon that originated from the same native population of the Simojoki river. The wild smolts spent their juvenile years before smoltification in the river, and the reared smolts in the hatchery. In most tagging studies, wild salmon smolts have been caught and tagged at the river mouth in a smolt trap, whereas reared smolts have usually been tagged in the hatchery and later released into the river (e.g. Jonsson *et al.*, 1991). Due to the considerable stress caused by transportation and handling (Soivio and Virtanen, 1982; Schreck *et al.*, 1989), some reared smolts may die soon after stocking. We therefore tagged both wild and reared fish at the smolt trap in the river mouth to equalize the tagging and handling procedures. Thus, the reared fish captured at the trap had survived for several weeks in the river after their release.

We recorded smolt length at tagging, as several studies have suggested size to be important for survival in the wild (Salminen *et al.*, 1994, 1995; Kallio-Nyberg *et al.*, 1999). The study was repeated in two years, 1991 and 1993, because survival may vary considerably from year to year (McKinnell and Lundqvist, 2000). In the Finnish salmon tagging data, post-smolt mortality in the Baltic Sea was generally low in 1991 (mean recovery rate 10%) and high in 1993 (mean recovery rate 3%), while the average recovery rate was around 6% during the years 1985–2000 (Anonymous, 2002).

Materials and methods

Study site and salmon stock

The Simojoki river (65°38′N 25°00′E) flows into the northern part of the Gulf of Bothnia in northern Finland. The mean discharge of the 175-km-long river is 38 $m^3 s^{-1}$.

All the reared salmon smolts of this study were the offspring of returning native spawners caught at the river mouth. The salmon were transported to the Finnish Game and Fisheries Research Institute's Simojoki hatchery, located on the river about 10 km from the sea. They were kept in the hatchery until stripping, and the fertilized eggs were also incubated there. The smolts were released at the age of 2 yr in spring 1991 and 1993. The smolts released in 1991 were reared 100 km north of the Simojoki, at the Vesiviljely Ky hatchery, to which they were transferred as eyed ova. In the latter year the eggs were incubated and raised to smolts at the Simojoki hatchery. In their first summer, all the fingerlings were reared in 4-m^2 fibreglass tanks in a rearing hall and thereafter outdoors in concrete ponds. The fish were fed pelleted dry feed and held at the ambient water temperature and under the natural photoperiod.

Tagging and trapping

In Simojoki river, 60 000 and 5000 2-yr smolts were stocked in 1991 and 1993, respectively (Jokikokko and Jutila, 1998). Their adipose fin had been clipped in the hatchery in the autumn prior to their release in order to distinguish them from wild fish. The smolts were anaesthetized with MS-222 during this procedure and were returned to their rearing ponds after recovery. In the spring, most of them were stocked in the Isotaini rapids, 47 km upstream from the river mouth, concurrently with the seaward migration of wild smolts. In 1991 and 1993, 1766 of these released smolts were marked with Carlin tags at the smolt trap together with 1978 wild smolts (Table 1).

The reared smolts were not released into the river before the smolt trap had been installed in the river mouth below the lowest rapid and the migration of wild smolts had started. Smolt trapping started as soon as the spring flood was over and the water level was low enough to allow the installation of the trap in the river, generally in late May. The water temperature in the river was <10°C at the beginning of trapping and 15–16°C at the end. The trapping period covered the main smolt run, which lasted for about 2 weeks in 1991 and 6 weeks in 1993. The trap was equipped with an 8-mm mesh bag and it closed about one-third of the river, which is 160–170 m wide at the trapping site. The trap was normally attended at 08:00, and on the days of peak migration for a second time in the afternoon. All the smolts were carefully removed from the trap, anaesthetized (MS-222), their origin checked, and

Table 1. Salmon smolts tagged in the river Simojoki in 1991 and 1993. The smolts of reared origin were released and subsequently tagged at the smolt trap together with wild smolts. The odds ratios (OR) are presented for wild smolts compared with reared ones in both years. The number of fish tagged and the mean length (mm), standard deviation, and percentage recovery of the smolt groups are provided.

Year	Date of tagging	Origin/Group	Number tagged	Recovery %	OR	Mean length ± s.d.
1991	June 4–17	Wild	999	21.2	1.10	161 ± 13
1991	June 4–10	Reared	998	19.7		191 ± 16
1993	May 20–July 1	Wild	979	4.6	2.14	152 ± 9
1993	May 22–June 20	Reared	768	2.2		195 ± 17

tagged. The smolts were then placed in freshwater in perforated plywood cages to recover. On the following day they were released to continue their migration towards the sea.

The total length (mm) of each tagged fish was recorded. Because of poor recoveries of very small smolts in previous tagging experiments, only smolts longer than 140 mm were tagged (Finnish Game and Fisheries Research Institute, unpublished).

All the reared smolts in this study were 2 yr old. The wild smolts were mostly 2 or 3 yr old. The proportion of 2-yr smolts was over 40% in 1991 and over 50% in 1993 (Jokikokko and Jutila, 1998). Although the exact recapture time or place could not be determined for every tag, the unidentified recaptures were also included in the survival estimation. Returns to the river were extremely rare due to extensive sea fishing. Most of the tags were obtained from commercial offshore driftnet and longline fishing (Salminen *et al.*, 1994; Kallio-Nyberg *et al.*, 1999; Anonymous, 2002). Recovery data were acquired from the Finnish Game and Fisheries Research Institute, and the recoveries from all Baltic Sea countries were included. No correcting factors were used to adjust reporting rates, because we were interested in the proportions of tag returns and not the total catch.

Statistical methods

The recovery data were based on tag returns, which estimate the survival of fish. Data of this kind could be analysed by using simple χ^2 tests, or more advanced log-linear models with the year and origin included (three-dimensional contingency tables). However, length, a continuous variable, turned out to be important in understanding smolt survival. Classifying length as a discrete variable would be cumbersome and ineffective. Traditional linear models cannot be used, because our response variable is binary.

Fortunately, linear models have been generalized to cover other distributions besides the normal distribution (McCullagh and Nelder, 1989). The aim of these generalizations is to identify the relevant distribution for the data together with a "link function" connecting the observed proportions (survivals) to the values predicted by the linear model, which includes predictors such as smolt origin and length. In our case, survival naturally led to the binomial distribution and logit link, where the response variable was the number of recovered fish divided by the number of tagged fish.

The logit, or log of odds, has a natural meaning that makes the model easier to understand (for interpreting model parameters see McCullagh and Nelder, 1989, p. 110). In betting, a traditional method is to use odds, i.e. the probability of winning ($=\pi$) divided by the probability of losing ($=1-\pi$). The odds ratio or OR is a ratio of two odds that can be used to compare, for example, the likelihood of winning of two racehorses. The value predicted by our model is the log of odds ($=\log[\pi/(1-\pi)]$), where π is the proportion or probability of survivors ($=\pi$) in a group (e.g. wild smolts in 1993). Odds for differences between groups (i.e. wild and reared of the same length) can be calculated from differences between predicted values (=log odds).

The data were analysed with the SAS statistical package (version 8.10) by using the Genmod procedure. Other SAS procedures for analysis of variance and χ^2 tests were also applied (SAS Institute, 1999). The t-test was used to compare the length difference between recaptured and non-recaptured smolts.

Results

The mean length of reared smolts was greater than that of wild ones in both years (Table 1). In all groups, recovered fish had longer mean smolt lengths compared to non-recovered fish (Table 2). However, the difference was not significant in the reared group of 1991.

In the smolt year class of 1991 the mean tag recovery rate did not differ significantly between the wild and reared salmon, whereas proportionally more wild than reared fish were recovered from the smolt year class of 1993 (d.f. = 1, $\chi^2 = 7.14$, $p = 0.007$). The recovery rate was higher among fish tagged in 1991 than in 1993 in both groups (Table 1). The odds of tag recovery (1.10) of the 1991 year class were very similar for wild and reared smolts, but in the 1993 year class, the wild fish had 2.14 times better odds for returning (OR in Table 1). These odds values are based on recoveries only, and smolt length has not been taken into account.

In the generalized linear approach of Table 3, we continued the analysis of survival by including smolt length (mm) in the model besides origin (reared and wild smolts) and the release years. All factors and their interactions showed statistically significant effects on survival. Odds ratios from the model indicate that wild smolts have on average 4.5 times better survival rate than the reared smolts of identical size for both years combined. Table 3 shows that when size is taken into account, the odds ratio increases to 1.48 (from OR = 1.1 in Table 1) for the 1991 release,

Table 2. The mean smolt length (mm) of recovered and non-recovered wild and reared salmon tagged in 1991 and 1993. The probability of the length difference is based on t-test.

	Recovered			Non-recovered			
	n	Mean	s.d.	n	Mean	s.d.	p
Wild 1991	212	162	12	787	160	13	0.017
Reared 1991	197	193	17	801	191	16	0.216
Wild 1993	45	155	9	934	152	9	0.025
Reared 1993	17	208	14	751	195	17	0.001

Table 3. Effect of origin (wild, reared), year, logarithmic length, and interactions on the survival rate of smolts. The odds ratios (OR) when differences in size distribution are taken into account are shown. The four OR are given in the order of wild vs. reared for the whole data set, the tagging years 1991 and 1993 compared, and wild vs. reared fish separately for the tagging years 1991 and 1993.

Factor	d.f.	χ^2	OR
Origin	1	26.8***	4.52***
Year	1	8.5**	29.9***
Origin × year	1	14.2***	1991: 1.49*
			1993: 13.77***
Length	1	19.9***	
Length × year	1	7.4**	
Deviation	3 738		

$p < 0.001$ = ***; $p < 0.01$ = **; $p < 0.05$ = *.

and to 13.8 (from OR = 2.1 in Table 1) for the smolts released in the year 1993.

The difference in survival between wild and reared smolts increased with increasing smolt size as illustrated in Figure 1. The model shows, for example, that among fish tagged in 1991 the survival of a 202-mm reared smolt was equal to that of a 161-mm wild smolt, which was the mean length of wild fish tagged in 1991 (Table 1). Similarly, in 1993, 219-mm-long reared smolts and 152-mm wild smolts had an equal probability of survival. The longer smolts tended to have a higher survival rate, but size alone could not explain the survival difference between origin groups. The survival difference was especially apparent in the unfavourable release year of 1993, as seen in Figure 1.

Discussion

Our model suggests that the marine survival of Atlantic salmon in the Baltic Sea area is dependent on the smolt length and origin of the smolts (wild/reared) and the year of release. We found a significant association between survival and origin, as earlier reported by Jonsson *et al.* (1991), but we also demonstrated that the effect of length on survival, and the difference between wild and reared smolts, is dependent on the release year.

Among the Gulf of Bothnia salmon stocks, the survival of the smolt year classes 1993 and 1990 was the lowest of the years 1986–1995. The most favourable stocking years of this period were 1988, 1989, and 1991 (Anonymous, 2002). In our study, survival of longer smolts was higher both in reared and wild smolts in the year 1991. Year 1993 was so unfavourable for reared smolts that their larger size compared to wild smolts could not compensate for their weaker ability to survive in the wild.

A positive association between the recovery rate and smolt size has been observed several times in earlier studies (Eriksson, 1989; Virtanen *et al.*, 1991; Salminen *et al.*, 1995; Kallio-Nyberg *et al.*, 1999). The larger size of reared than wild smolts compensated for their poorer survival, thus substantially reducing the difference in recovery rates. However, even though the reared smolts were longer than the wild fish, the latter had a roughly twofold higher recovery rate.

Carlin tags and associated handling are known to increase mortality, especially in small smolts (Isaksson and Bergman, 1978; Hansen, 1988). This means that wild smolts were likely to suffer more due to the tag, so the higher recovery rate of the wild than of the reared fish indicates an even greater difference in survival between them.

Crozier and Kennedy (1993), Romakkaniemi *et al.* (2000), and Jutila *et al.* (2003) have studied the spawning-stock composition of Atlantic salmon. They have found a higher proportion of wild salmon among ascending spawners than among smolts migrating to the sea showing a better survival of wild smolts in the sea phase. Fleming *et al.* (2000) observed that the lifetime reproductive success (adult to adult) of farmed fish in the wild was 16% of that of native salmon. Jonsson *et al.* (1991) concluded that the juvenile experience appears to explain the differences in behaviour between reared and wild fish. Juvenile survival in hatcheries is higher than in the natural environment, where only the fittest individuals will survive. Reared fish lack experience of predators, and their response to them differs from that of wild fish (Johnsson *et al.*, 2001). Thus, predation on recently stocked reared fish is more intense than that on wild fish.

Jonsson *et al.* (1991) reported earlier that the survival rate from smolt to adult in the wild was about twice as high for wild as for reared Atlantic salmon, but they did not take smolt length into account. It is important to note that the tagged reared smolts in our study represented the most viable reared fish, because they had survived to reach the trap despite considerable stress from handling, transportation, and stocking (see Soivio and Virtanen, 1982;

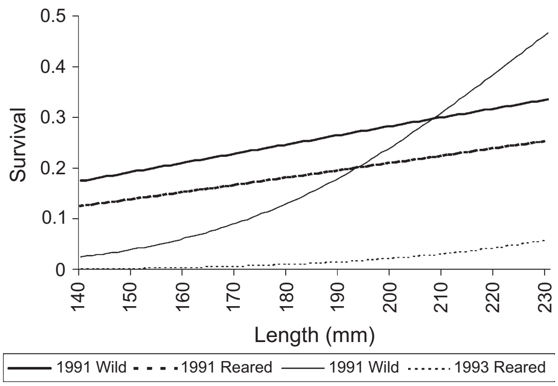

Figure 1. Probability of survival as a function of smolt size according to the model presented in Table 3. Survival is shown for wild and reared smolts tagged in 1991 and 1993.

Schreck *et al.*, 1989). The difference between wild and reared groups would have been even higher if tagging of reared smolts had been performed in the hatchery, as is usually the practice.

The tagging length of the reared individuals recaptured as adults was similar to that of non-recaptured fish stocked in 1991, when post-smolt mortality at sea was low and return rate was high. Thus, a greater length did not significantly increase the survival of reared smolts, showing that their mean length of 19 cm was close to the upper limit at which length can provide any survival advantage. In the Gulf of Finland, among stocked Neva salmon, this limit has been about 22 cm at tagging (Salminen *et al.*, 1995). By contrast, in the more unfavourable stocking year of 1993, survival was more size dependent. Although reared smolts could benefit from their greater size in unfavourable conditions, their size could not compensate for their increased mortality. Potential risks could be mitigated by rearing bigger smolts, but this has several partly conflicting economical and ecological consequences such as earlier maturation and earlier recruitment to a size-selective offshore fishery (Salminen, 2000). Wild smolts survived proportionally better than reared smolts in both years. The smaller mean size of wild smolts compared with stocked smolts indicated that there are also other factors besides size affecting the survival.

Hansen and Jonsson (1989), Virtanen *et al.* (1991), Vehanen *et al.* (1993), and Salminen *et al.* (1995) all assumed size/survival relationships to be associated with predation. Larger smolts may have fewer predators than smaller ones, which are exposed to size-dependent predation for a longer time than larger smolts. Skilbrei *et al.* (1994) compared two size groups in their study and found small smolts (<14–15 cm) but no large smolts (18–20 cm) in the stomachs of gill-netted predators. Smolt size may also have an effect on the spatial distribution of salmon and, thus, on the recapture rate (Salminen *et al.*, 1994; Kallio-Nyberg *et al.*, 1999). Vehanen *et al.* (1993) assumed that the availability of potential food items was better for larger than for smaller fish. The availability of different prey types varies between sea areas, but e.g. in the southern Gulf of Bothnia, small post-smolt salmon first feed on terrestrial insects and marine invertebrates near the water surface, and later in summer on young herring of the same year (Salminen, 2000). When smolts reach the sea, the larger ones are in advantage, as they are able to include more fish in their diet (Jutila and Toivonen, 1985; Salminen, 2000).

In several earlier studies, reared salmon had been kept in hatcheries for several generations, and in some cases non-native salmon have been used for stocking (reviewed by Fleming and Petersson, 2001). In our study the parents of the hatchery-reared salmon had been caught from the same river 3 years before stocking, and all the tagged smolts were released into their native waters. We have no reason to assume that the parents of the reared and the wild salmon groups differed genetically. Nevertheless, the different experiences and unintentional selection of the wild and reared fish have caused most of the differences in salmon growth, survival, and behaviour (see Jonsson *et al.*, 1991).

In conclusion, our results show that the marine survival of Atlantic salmon in the Baltic Sea area is dependent on the smolt length and origin of the smolts (wild/reared) and the year of release. In our data, survival of wild smolts was over four times higher than that of hatchery-reared smolts released in 1991 and 1993 in their natural environment, the Simojoki river. Furthermore, our results suggest that in good years bigger size of hatchery-reared smolts may compensate for their inferior performance compared to wild smolts, but in bad years wild smolts are superior. Although the smolt size achieved by the present rearing practices compensates to some extent for the lower survival of reared smolts, indisputable evidence is lacking that endangered wild salmon populations can be effectively enhanced by simply stocking greater numbers of bigger fish.

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