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The survival of semi-wild, wild and hatchery-reared Atlantic salmon smolts of the Simojoki River in the Baltic Sea

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The recapture rate and survival of hatchery-reared Atlantic salmon *Salmo salar* stocked as 1 year-old parr (semi-wild) with that of hatchery-reared Atlantic salmon stocked as 2 year-old smolts and wild smolts of Atlantic salmon in the northern Baltic Sea were compared. This was done through tagging experiments carried out in 1986–1988 and 1992. The recapture rate of the semi-wild groups varied from 1·0 to 13·1%, being similar in 3 tagging years and lower in 1 year than that of the wild groups (1·7–17·0%). The recapture rate of the semi-wild groups was similar (in 2 years) or higher (in 2 years) than that of the hatchery-reared groups stocked as smolts (1·3–6·3%). The survival of semi-wild smolts during the sea migration was as high as that of wild Atlantic salmon of an equal size and two to three times higher than hatchery-reared Atlantic salmon stocked as smolts. The survival rate was positively associated with smolt size. The suitability of hatchery-reared parr and smolts in the management of reduced Atlantic salmon stocks is compared.

Key words: parr; *Salmo salar*; smolt; stocking; survival.

INTRODUCTION

Previous studies have shown the survival of wild Atlantic salmon *Salmo salar* L. in nature to be superior to that of reared fish (Jonsson *et al*., 1991, 2003; Kallio-Nyberg *et al*., 2004; Saloniemi *et al*., 2004). Furthermore, captive breeding commonly reduces the spawning success of reared Atlantic salmon and the adaptation of their offspring to natural environments due to domestication. Under rearing conditions, Atlantic salmon adapt genetically, morphologically and behaviourally to aquaculture and simultaneously maladapt to the wild (Hindar *et al*., 1991; Cross, 1998). Increased pre-adult aggregation and a

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decreased response to predators are induced by the rearing conditions (Olla *et al*., 1998; Einum & Fleming, 2001).

The effect of domestication on fitness-related traits accumulates over an increasing number of culture generations and over the prolonged rearing period of an individual (Fleming *et al*., 1994, 1996). The risk of adverse changes in natural stocks due to breeding has been reported (Waples, 1990; McGinnity *et al*., 2003), and artificial propagation has, therefore, been regarded as only a temporary solution in the management of natural stocks (Jonsson *et al*., 1999; Levin *et al*., 2001). Increasing fishing pressure due to large-scale smolt releases is also considered a threat to wild populations (Eriksson & Eriksson, 1993).

Despite their recorded or potential negative effects, however, Atlantic salmon are commonly stocked in Atlantic rivers to compensate for the reduced production of wild smolts, mostly caused by the regulation and damming of rivers for hydropower purposes (Einum & Fleming, 2001; Fjellheim & Johnsen, 2001). In the Baltic Sea, a great majority of hatchery-reared Atlantic salmon smolts are released in compensation for the damming of the rivers, but also partially for enhancement purposes (Eriksson & Eriksson, 1993). For the latter reason, Atlantic salmon parr have also been stocked in considerable numbers in some rivers (Jutila & Pruuki, 1988; Jokikokko & Jutila, 1998, 2004). Although comparisons between the survival of hatchery-reared smolts in relation to wild smolts exist (Jonsson *et al*., 1991, 2003; Kallio-Nyberg *et al*., 2004; Saloniemi *et al*., 2004), smolts stocked as parr have not been studied to such an extent.

The natural Atlantic salmon stock in the Simojoki River, a northern Finnish Baltic river, was in danger of dying out in the 1980s and 1990s due to the overexploitation of Atlantic salmon at sea (Eriksson & Eriksson, 1993; Romakkaniemi *et al*., 2003). This stock has been enhanced by releasing smolts and stocking parr in empty or sparsely inhabited nursery areas and thus partially compensating for reduced natural reproduction. To improve knowledge on the effectiveness of different stocking methods, the results of enhancement releases carried out in the Simojoki River since the late 1980s were analysed. The survival of three Carlin-tagged smolt groups that had spent different times in the river during their juvenile period was compared. Wild smolts had spent their whole life in the river exposed to natural selection. Two hatchery-reared smolt groups, stocked as parr or smolts, were subjected to artificial hatchery selection for 1 or 2 years before stocking, respectively. Smolts stocked as parr (here semi-wild smolts) lived ≥ 1 year in the stream before their sea migration, but hatchery-reared smolts left the river mostly in the spring of their release (Jutila & Pruuki, 1988; Jokikokko & Jutila, 1998). All three groups migrated to the sea at about the same time. Their survival was compared and the effect of smolt total length (L_T) on the survival was also analysed.

MATERIALS AND METHODS

STUDY AREA AND SALMON STOCK

The Simojoki River (65° 38′ N; 25° 00′ E) empties into the northern part of the Gulf of Bothnia (Fig. 1). The water quality has been rated good enough for Atlantic salmon reproduction, even though forest drainage, peat mining and agriculture cause some

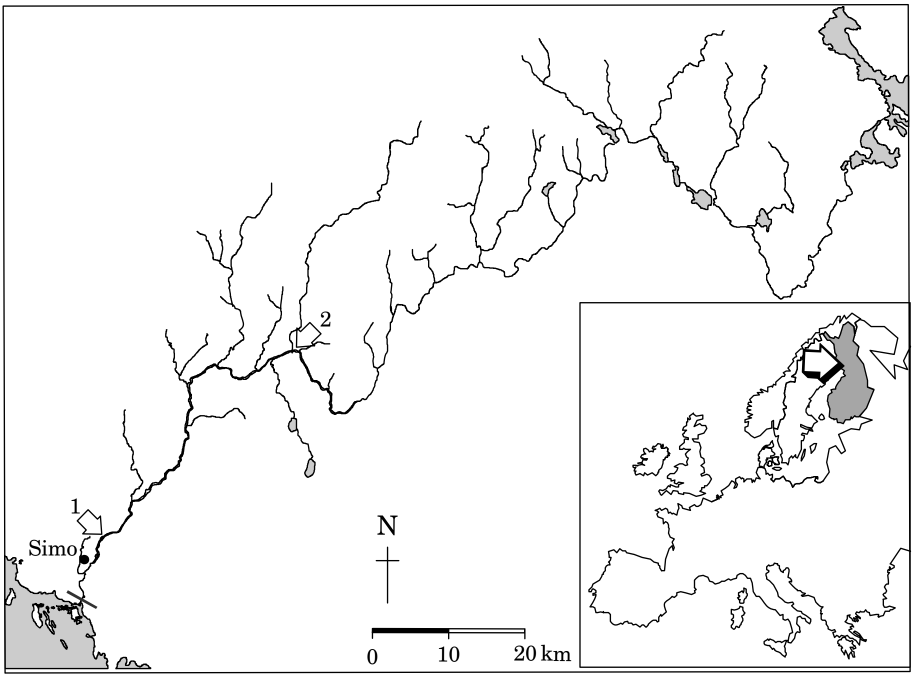

FIG. 1. The Simojoki River and the location of the rapids used in smolt stocking (1, Isopetäjä Rapids; 2, Isotaini Rapids). Diagonal bar, the site of the smolt trap at the river mouth.

nutrient loading into the river. Atlantic salmon normally ascend the river up to 110 km from the sea (Jokikokko & Jutila, 1998). The natural smolt production of Simojoki Atlantic salmon stock has been low since the 1970s, initially due to heavy sea fishing (Romakkaniemi *et al.*, 2003) and later also because of the M74 syndrome, a reproductive disorder of Atlantic salmon (Vuorinen *et al.*, 1997). In recent years, the natural stock has strengthened, mostly in response to decreased fishing pressure at sea (Romakkaniemi *et al.*, 2003), but also due to supportive stocking (Jutila *et al.*, 2003).

All the smolt groups in this study originated from the same Simojoki Atlantic salmon population. Enhancement releases of Simojoki Atlantic salmon started in the mid-1980s when the hatchery facilities for parr and smolts were only provisional. The smolts stocked in 1986 and 1987 and parr stocked in 1986 were stripped from broodfish that were caught as smolts from the Simojoki River in the late 1970s and raised to adults in the Guttorp hatchery in south-western Finland in the early part of 1980s. The smolts released in 1988 and 1992 and parr stocked in 1987, 1988 and 1992 were raised in a new hatchery on the Simojoki River. The smolts were the progeny of returning spawners caught at the river mouth 3 years earlier. The adipose and one of the pelvic fins were removed from the parr before stocking in order to distinguish them from wild and other reared Atlantic salmon. The classification of fish as smolts in the hatchery in the tagging phase was based on their silvering.

TAGGING EXPERIMENT

In 1986–1988 and 1992, a total of 5467 Carlin-tagged smolts (semi-wild, hatchery-reared and wild smolts) were released into the Simojoki River (Table I). The semi-wild and wild smolts were caught by means of a trap net and were tagged at the trap. Tagging was carried out during approximately the whole smolt migration period. The trap net was

TABLE I. Tagged Atlantic salmon smolt releases in 1986–1988 and 1992 and the number of recaptures. The Isopetäjä Rapids are 11 km and the Isotaini Rapids 47 km above the smolt trap. Origin: Wild, wild smolt; Reared, hatchery-reared fish, stocked as smolts; Semi-wild, stocked as parr, tagged during migration at the smolt trap

Origin	Tagging site	Site of release	Date of release	Number released	Number recaptured	Recapature rate (%)
Wild	Smolt trap	Trap	6–19 June 1986	374	30	8·0
Reared	Hatchery	Isopetäjä	10 June 1986	300	12	4·0
Semi-wild	Smolt trap	Trap	6–19 June 1986	556	17	3·1
Wild	Smolt trap	Trap	7–11 June 1987	179	3	1·7
Reared	Hatchery	Isopetäjä	3 June 1987	298	4	1·3
Semi-wild	Smolt trap	Trap	7–11 June 1987	286	3	1·0
Wild	Smolt trap	Trap	8–15 June 1988	188	32	17·0
Reared	Hatchery	Isopetäjä	1 June 1988	984	62	6·3
Semi-wild	Smolt trap	Trap	1–7 June 1988	496	65	13·1
Wild	Smolt trap	Trap	28 May to 11 June 1992	574	40	7·0
Reared	Hatchery	Isotaini	26 May to 1 June 1992	999	34	3·4
Semi-wild	Smolt trap	Trap	28 May to 12 June 1992	233	14	6·0

located at the river mouth below the lowest rapids (Fig. 1). The hatchery-reared smolts were tagged in the hatchery and released during the natural smolt run in May to June either into the Isotaini Rapids, *c.* 47 km from the sea, or the Isopetäjä Rapids, *c.* 11 km from the sea. This difference in migration distance was not expected to have any major effects on the results, because Jokikokko & Mäntyniemi (2003) found the distance-dependent losses to be almost non-existent in the Simojoki smolt migration. The hatchery-reared smolts were released into the river after the smolt trap had been installed and the migration of wild smolts had started. The hatchery smolts were usually released in several batches of *c.* $\geq$100 fish over some days.

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 mainly 15–16° C at the end. The trap net was equipped with a codend of 8 mm mesh net (bar length) and wings of 30 mm mesh net. The length of the codend was *c.* 4 m and the diameter *c.* 1·8 m. The trap net closed about one-third of the river, which was 160–170 m wide at the trapping site. The trap net was normally inspected at 0800 hours, and on the days of peak migration for a second time in the afternoon. All smolts were carefully removed from the codend with a dip-net, anaesthetized (MS-222), their origin checked, L_T (mm) measured and tagged as described in Carlin (1955). The smolts were then moved to recover in fresh water in perforated plywood cages, where no mortality of tagged fish was observed. On the following day, they were released to continue their migration towards the sea.

All the hatchery-reared smolts in this study were 2 years old, as were 80–90% of the semi-wild smolts, the rest of which were 3 years old, based on scale samples (Jokikokko & Jutila, 1998). The wild smolts were mostly 2 or 3 years old. The proportion of 2 year-old wild smolts was *c.* $\leq$40% in 1986–1988 and *c.* 90% in 1992 (Jokikokko & Jutila, 1998). Recaptured fish were mainly caught during their sea migration by commercial offshore and coastal fishing in the second or third year after their release, being *c.* $\geq$60 cm L_T (Salminen *et al.*, 1994; Jutila *et al.*, 2003; Kallio-Nyberg *et al.*, 2004). Recapture data were acquired from the Finnish Game and Fisheries Research Institute, and the recoveries from all Baltic Sea countries were included.

STATISTICAL METHODS

The survival of the tagged groups was compared by considering a returned tag to indicate the survival of fish. Generalized linear models (GLM) (McCullagh & Nelder, 1989) were applied with survival as a response variable (either 0 or 1), as used by Saloniemi *et al*. (2004). The use of proportions led to a binomial distribution, where the response variable was the number of recaptured fish divided by the number of tagged fish. The most common choice of link function for binomial data, the logit link, was used. This means that the value predicted by the linear model, $\eta = \alpha + \beta_1 x_1 + \beta_2 x_2$, must be transformed by $\eta = \ln [\pi(1 - \pi)^{-1}]$, where π is the predicted proportion of recaptured Atlantic salmon. Model parameters α, β_1 and β_2 are estimated from the data. The logit, or log odds, link has several advantages over other link functions. When using the logit link, model parameters can be interpreted directly (McCullagh & Nelder, 1989). For example, when smolt L_T (*e.g.* x_2) increases by 1 mm, the log odds increase by the coefficient of length given by the model (*e.g.* β_2), assuming that other variables do not change. In many cases, interpretation is easier by transforming log odds to odds: $(\eta) = \pi(1 - \pi)^{-1}$. Length was ln-transformed, since the residuals showed that the effect of fish size was non-linear.

The data were analysed with the SAS statistical package (SAS 8.10) by using the Genmod procedure with binary distribution, logit link and type 3 tests. The data from 1986 to 1988 and 1992 were treated separately in survival analysis. Other SAS procedures for the *t*- and χ^2-tests were also used (SAS, 1999).

RESULTS

RECAPTURE RATE

In 1986 a significantly larger proportion of wild than semi-wild Atlantic salmon were recaptured (Tables I and II). In the other years, the mean recapture rate of wild Atlantic salmon was also higher than that of semi-wild Atlantic salmon, but not significantly (Table II). In general, the wild smolts were recaptured proportionally more frequently than hatchery-reared smolts in all 4 years, and the difference was significant in 3 years (Table II). The recapture rate of semi-wild smolts was significantly greater than that of hatchery-reared smolts in 1988 and 1992, while in the other 2 years it was lower but not significantly different (Table II). In all years the hatchery-reared smolts were significantly larger than wild or semi-wild ones, and the semi-wild smolts were smaller than wild ones (pair-wise *t*-tests) (Fig. 2).

TABLE II. Probability values from pair-wise comparisons of the recapture rates of different smolt groups released in 1986–1988 and 1992 (χ^2-test). Recapture rates are shown in Table I

Compared groups	1986	1987	1988	1992
Wild and semi-wild	0·001	0·560	0·261	0·710
Semi-wild and reared	0·566	0·745	<0·001	0·021
Wild and reared	0·032	0·769	<0·001	<0·001

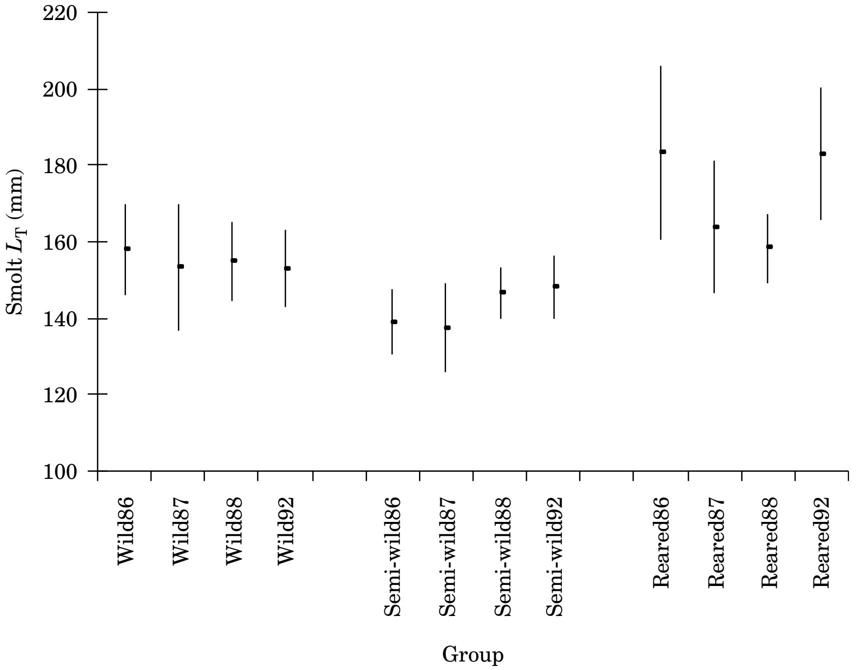

FIG. 2. Mean ± S.D. total length (L_T) of smolt groups released in the Simojoki River in 1986–1988 and 1992. (Sample sizes are given in Table I).

SURVIVAL OF SMOLT GROUPS

There were statistically significant differences in the survival of smolt groups of different origin (wild, semi-wild and hatchery-reared smolts) released in 1986–1988 (Table III). The pair-wise comparison of odds ratios (OR) for each of the origin groups (model 1, Table III) showed that the survival of the semi-wild group was similar to that of the wild groups and twice that of the hatchery-reared group for a given smolt size (Table IV). Within all groups the longer smolts tended to have a higher survival rate (χ^2-test d.f. = 1, $P < 0{\cdot}001$). The model demonstrated, for example, that the survival of a 164 mm wild smolt was equal to that of a 167 mm semi-wild smolt and a 217 mm reared smolt (Fig. 3).

TABLE III. The effect of origin (wild, hatchery-reared and semi-wild) and smolt total length (ln-transformed) on the survival of tagged smolts in the experiments conducted in 1986–1988 (model 1) and 1992 (model 2)

Model	Origin χ^2	Origin d.f.	ln l_T χ^2	Scale	Deviance χ^2	Deviance d.f.	Log likelihood P
1	19·35***	2	11·58***	1·04	217·76	201	−789·00
2	13·84**	2	2·72^0	0·97	156·58	166	−364·39

^{0} $P < 0{\cdot}10$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$.

TABLE IV. Comparison of odds ratios (OR) (95% CL in parentheses) for survival in different smolt groups (wild, hatchery-reared and semi-wild). The table gives the OR of the vertical groups when compared with the horizontally listed groups. The values are based on models 1 and 2 presented in Table III

	OR when compared to	
	Reared	Semi-wild
Wild/86–88, model 1	2·1 (1·5–3·1)***	1·0 (0·7–1·5)
Semi-wild/86–88	2·1 (1·4–3·1)***	
Wild/92, model 2	3·5 (1·8–7·0)***	1·0 (0·6–1·9)
Semi-wild/92	3·4 (1·4–8·2)**	

** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$.

Similarly to 1986–1988, the survival of Atlantic salmon was dependent on their origin in the smolt groups tagged in 1992 (Table III; χ^2-test, d.f. = 2, $P < 0{\cdot}01$), but smolt L_T had no significant effect on survival in this year (χ^2-test, d.f. = 1, $P = 0{\cdot}099$). The odds of tag recovery (1·0) were similar for semi-wild and wild Atlantic salmon, but the semi-wild and wild groups had, respectively, 3·4 and 3·5 times better odds of returning than the hatchery-reared Atlantic salmon (Table IV).

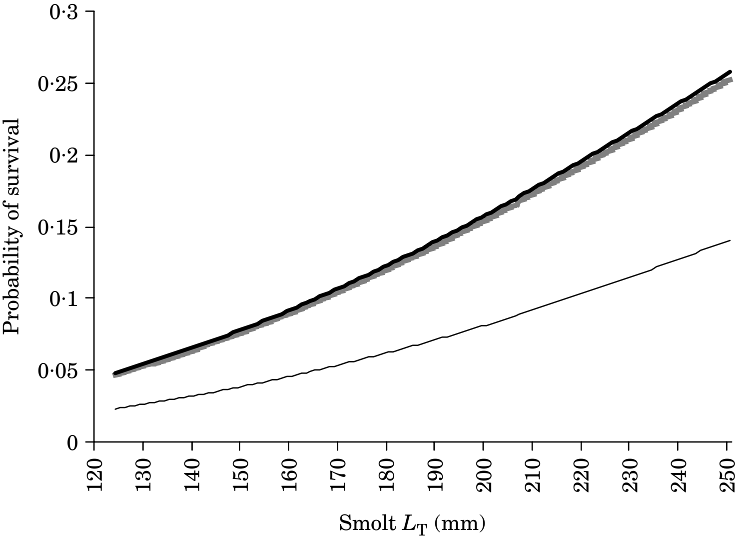

FIG. 3. Probability of survival as a function of smolt size according to model 1 (tagging years 1986–1988) presented in Table III. Survival curves are shown separately for: (wild ━━), $y = 1 + 11280000e^{-2{\cdot}749 \ln x}$; semi-wild (—), $y = 1 + 11560000e^{-2{\cdot}749 \ln x}$; reared (—), $y = 1 + 23890000e^{-2{\cdot}749 \ln x}$ smolts.

DISCUSSION

SIMILARITIES BETWEEN SEMI-WILD AND WILD SMOLTS

The present study demonstrated that hatchery-rearing of Atlantic salmon parr followed by a 1 or 2 year period in the wild before smoltification produces smolts that are similar to their wild counterparts with regard to survival during their sea migration. Atlantic salmon stocked as parr are exposed to the natural environment, resulting in very close to natural selection (Fjellheim & Johnsen, 2001). This generally similar juvenile phase may explain why Atlantic salmon stocked as parr had a similar survival rate to wild fish; they had adapted early in their life to the natural conditions (Jonsson *et al.*, 1991; Fleming *et al.*, 2000; Johnsson *et al.*, 2001). The similarity of semi-wild and wild Atlantic salmon extends further to the adult phase, as they are known, for instance, to ascend their natal river at the same time (Jokikokko *et al.*, 2004). Competition with wild parr, however, may decrease the growth and survival of stocked parr in the river phase, which is also indicated by their smaller smolt size (Jokikokko & Jutila, 2004). Although having a similar survival to wild fish of an equal size, the observed smaller size of semi-wild smolts probably leads to higher mortality in the sea (Salminen *et al.*, 1994; Saloniemi *et al.*, 2004).

DIFFERENCES BETWEEN SEMI-WILD AND HATCHERY-REARED SMOLTS

Atlantic salmon stocked as parr had a significantly higher survival rate than Atlantic salmon stocked as smolts. Both groups had a similar genetic background, but the most important reason for the survival difference during the marine phase was probably that the reared smolts had lived under sheltered hatchery conditions before tagging and release. Their survival to the smolt stage may be *c.* 40% compared with the usual 1–2% for wild fish (Jonsson & Fleming, 1993). The situation changes drastically when cultured fish are released into the wild due to, among other factors, their poorer ability to recognize and escape predators than wild fish (Olla *et al.*, 1998; Dieperink *et al.*, 2002). Wild fish may also be better able to respond to changing and sub-optimal natural conditions (Saloniemi *et al.*, 2004).

The adaptation of stocked parr to life in the wild may have great importance concerning their later behaviour in relation to predators and prey (Johnsson *et al.*, 2001), which correlates with survival under natural conditions. Jonsson *et al.* (1991) concluded that juvenile experience appears to explain differences in behaviour observed between hatchery-reared and wild Atlantic salmon. Before tagging and release the semi-wild fish, but not the hatchery-reared smolts, were subjected to natural selection for 1 or 2 years before smolting. Thus, the low recapture rate of hatchery-reared smolts reflects their lower adaptation to natural conditions than the other groups before recruiting to the fishery. The fishery also may affect the survival of the groups in various ways due to the different migration patterns and growth rates of wild and reared Atlantic salmon (Jonsson *et al.*, 2003; Jutila *et al.*, 2003).

The different tagging sites and handling of reared smolts should be taken into account, when interpreting the results. Considerable stress during handling, transport and stocking (Schreck *et al.*, 1989; Iversen *et al.*, 1998), which no longer affected semi-wild smolts in the tagging phase, may have increased the mortality of hatchery-reared smolt groups soon after stocking, thus lowering their recapture rate. For example, Iversen *et al.* (1998, 2004) suspected that handling and transport prior to release partly caused a low recapture rate and survival of hatchery-reared Atlantic salmon smolts. A considerable difference in mortality between wild and reared smolts, however, may exist although they are handled and tagged similarly (Saloniemi *et al.*, 2004). Carlin tags and handling during tagging are known to increase mortality, especially in small smolts (Isaksson & Bergman, 1978; Hansen, 1988). This means that semi-wild smolts were likely to suffer more due to the tag, so their higher recovery rate compared to the hatchery-reared fish indicates an even greater difference in survival between them. The potential harmful effects on parr of removing their pelvic fin before stocking probably no longer affect the survived semi-wild fish in the smolt migration phase.

MANAGEMENT IMPLICATIONS

Due to the effective exploitation of Atlantic salmon in the Baltic Sea fishery, stocking is necessary in many rivers to maintain production, even though it may also involve ecological and genetic risks for wild populations (Fleming *et al.*, 2000; Levin *et al.*, 2001; McGinnity *et al.*, 2003). There is also evidence of domestication without an accompanying loss of natural fitness (Dannewitz *et al.*, 2004). Fjellheim & Johnsen (2001) approved of stocking to restore extinct populations because of quicker recolonization and a better opportunity to control the genetic quality of the fish.

The release of hatchery-reared parr may adversely affect the wild fish living in the stream, because stocked parr live for ≥ 1 years in the same habitats before smolt migration. Competition between hatchery-reared and wild fish for territories and food is clear (Einum & Fleming, 1997, 2001; Jokikokko & Jutila, 2004). This ecological perspective is important if stocking is used in rivers where Atlantic salmon still reproduce naturally. Based on a comprehensive study of salmonid stocking in Norway, Fjellheim & Johnsen (2001) warned against increasing fish densities above the river's carrying capacity, because such attempts will fail. Stocking with smolts avoids such problems, and the number of returning fish will increase as more smolts are released (Finstad & Jonsson, 2001). The size of smolts can also be controlled during hatchery rearing and thus, to some extent, affect their survival, as observed here (Saloniemi *et al.*, 2004). Sea cage rearing of wild smolts is also suggested to have considerable potential as a stock rebuilding tool for Atlantic salmon (Dempson *et al.*, 1999).

Genetic interaction between native and non-native fishes has been suggested to disrupt the local adaptation (Einum & Fleming, 1997). Long-term genetic consequences of stocking non-native fishes have already appeared in Pacific salmon *Oncorhynchus* sp. (Levin *et al.*, 2001) and have also been demonstrated in Atlantic salmon (McGinnity *et al.*, 2003). In all stocking activities there is a risk of disturbing the adaptive structure of the stock, although the native stock of the river is used. The salmonid stock within a river system may also consist of genetically distinct populations adapted to local conditions (Pascual & Quinn, 1994). Koljonen (1995), however, observed no genetic differences between wild and reared Simojoki Atlantic salmon. This indicates that a stocking policy considering the origin of the stocked fishes and stocking native specimens does not necessarily represent a genetic risk to the original population.

The reproductive activity of Atlantic salmon stocked as parr may be higher than those stocked as smolts, because parr have lived in territories and imprinted on their nursery area, unlike Atlantic salmon stocked as smolts (Hansen *et al.*, 1989). The early experience with natal environment has been found to increase the reproductive performance of Atlantic salmon (Fleming *et al.*, 1997). Imprinting before the smolt migration is important for recognition of the home site when salmonids return to spawn (Dittman *et al.*, 1996). The smolt output of stocked parr is distributed over several years (Jokikokko & Jutila, 1998), unlike that of 2 year-old smolts, which mostly migrate to the sea in the year of release. As a result of stocking with parr, more year classes take part in spawning in later years, and this increases the effective population size and decreases the level of inbreeding (Saunders & Schom, 1985).

Variability in the life-history traits of Atlantic salmon has been considered a means to increase the genetic variation of the local spawning population, which may be small and isolated. Even in rivers with a viable Atlantic salmon stock, large variation among smolts and in the sea ages of Atlantic salmon is advantageous for the survival of the Atlantic salmon population, especially if the exploitation rate is high or extreme environmental conditions cause a loss of juvenile production in some years (Niemelä, 2004). Stocking is probably only a temporary solution in safeguarding endangered Atlantic salmon stocks. The role of fisheries management and different biotope protection and improvement techniques should be emphasized instead of stocking (Jonsson & Fleming, 1993; Fjellheim & Johnsen, 2001; Romakkaniemi *et al.*, 2003).

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