OULU 2006
A 472

ACTA UNIVERSITATIS OULUENSIS

A
SCIENTIAE RERUM NATURALIUM

Erkki Jokikokko

ATLANTIC SALMON (*SALMO SALAR* L.) STOCKING IN THE SIMOJOKI RIVER AS A MANAGEMENT PRACTICE

FACULTY OF SCIENCE,
DEPARTMENT OF BIOLOGY,
UNIVERSITY OF OULU

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Academic dissertation to be presented, with the assent of the Faculty of Science of the University of Oulu, for public defence in Raahensali (Auditorium L10), Linnanmaa, on November 24th, 2006, at 12 noon

OULUN YLIOPISTO, OULU 2006

Acta Univ. Oul. A 472, 2006

Supervised by
Professor Jaakko Erkinaro

Reviewed by
Professor Hans Lundqvist
Doctor Timo Marjomäki

ISBN 951-42-8223-X (Paperback)
ISBN 951-42-8224-8 (PDF) http://herkules.oulu.fi/isbn9514282248/
ISSN 0355-3191 (Printed)
ISSN 1796-220X (Online) http://herkules.oulu.fi/issn03553191/

Cover design
Raimo Ahonen

OULU UNIVERSITY PRESS
OULU 2006

Jokikokko, Erkki, Atlantic salmon (*Salmo salar* L.) stocking in the Simojoki river as a management practice
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Acta Univ. Oul. A 472, 2006
Oulu, Finland

Abstract

Long-term monitoring of the wild salmon (*Salmo salar* L.) stock of the Simojoki river and the stocked hatchery-reared salmon parr and smolts has provided a considerable amount of information on the development of the stock and factors affecting it. Data on the relationships between wild and reared salmon were collected by tagging and trapping both smolts and adult salmon having either a wild or reared background. The tag recapture rate of wild smolts was about twice as high as that of smolts stocked as two-year-olds and slightly greater than for smolts stocked as parr. When survival was measured in relation to the smolt size, the difference between the wild and reared smolts was even greater, and it seemed to be emphasized in years with a low survival rate.

The difference observed between the wild and reared salmon in the smolt phase generally disappeared in the adult phase. When adult salmon returned to the river to spawn the difference in the timing of the ascent depended more on the age or sex of the salmon, and less on their origin. Similarly, the survival of adult salmon in the river before or after spawning and later after returning to the sea depended on the sex and age of the fish. The origin of fish affected their behaviour, the reared salmon wandering more than wild adults before settling down into spawning areas. When the yield of wild and reared smolts as returning adults was compared, the wild smolts gave the best results, although the survival from smolt to adult was low in all smolt groups, probably due to the high fishing pressure in the sea. The smolts stocked as parr and those stocked as two-year-old fish were similar in this respect. The former group gave better results if the yield was measured as the number of returning multi-sea-winter adults, while the latter group gave better results if one-sea-winter grilse were also included in the yield.

The low yield of adult salmon from stocking and the generally low survival of smolt groups irrespective of their origin emphasises the importance of fishing regulations as a tool in the maintenance or enhancement of naturally reproducing salmon stocks. However, despite the low profitability of stocking, it probably safeguarded the existence of the wild Simojoki salmon stock during its critical phase in the early 1990s. At that time the fishing regulations were not strict enough to prevent the alarming decrease in the salmon stock, and the adult spawners produced by stocking of young salmon may have had a relatively higher value than their number suggests.

Keywords: ascending spawner, parr, Salmo salar, smolt, stocking, survival, tagging

Acknowledgements

This work was carried out at the Finnish Game and Fisheries Research Institute's Bothnian Bay Fisheries Research Station, a field station at Simo. I am especially grateful to Professor Petri Suuronen and Eero Aro for giving me the opportunity to carry out my work independently at the field station. I wish to honour the memory of the late Osmo Simola, the head of the previous Central Fish Culture Station for Northern Finland at Ohtaoja, Taivalkoski, who introduced me as a young student to the life, methods and traditions of fish farmers, scientists and fishermen in northern Finland, especially in the coastal area of the Bothnian Bay.

Daily work and discussions with my co-author and a good friend Eero Jutila have been very fruitful and encouraging, not forgetting his humour and stimulation. Moreover, not to forget life outside work, we have made many enjoyable skiing trips to Lapland together with our trusty pal and colleague Alpo Huhmarniemi, when the focus was on relaxing, not on salmon. My co-authors, Irma Kallio-Nyberg, Irma Saloniemi and Pentti Pasanen, have done excellent work during the writing process, from early drafts to accepted publications.

The skilled staff of the research station at Simo, Kari Hietanen, Tuula Malinen and Markus Ylikärppä, have been the main forces and vitally important in the field work, not forgetting Hanna Iivari. Together with a large group of assistants, including Jukka-Pekka Tikkala, Tapio Kotila, Heikki Leskinen and Väinö Wahlberg, to name a few, they have been responsible for the trapping of smolts and ascending salmon, and the tagging and handling of the sampled fish. The assistance and co-operation of Juhani Rytilahti and Esa-Pekka Juntunen, first at the Simojoki hatchery and later at the Lautiosaari hatchery, has been indispensable in catching and tagging the ascending brood salmon at the mouth of the Simojoki river. Irmeli Torvi interpreted the ages of adult salmon, giving a reliable view of the age structure of the Simojoki salmon brood stock. I greatly appreciate the help given by the Institute's tagging office in collecting the Carlin-tag data and allowing its use. Dr. Roy Siddall kindly checked the language of the thesis.

Finally, I especially want to mention Atso Romakkaniemi, my former colleague at Simo, an inspiring sparring partner, whose high professionalism kept me going. My colleagues in the Institute, such as Ari Leskelä and Outi Heikinheimo, have in their part borne my load in whitefish studies and allowed me to concentrate on my research. Erkki

Ikonen, Tapani Pakarinen and Vesa Niemitalo, good friends and knowledgeable researchers, have always been very helpful, and discussions with them either at my home or abroad have been refreshing and motivating.

The above-named people and all the others contributing to this work are warmly thanked. Last but not least, I thank Professor Jaakko Erkinaro and Aki Mäki-Petäys, my immediate superiors, who gave me free hands for writing and never questioned my work, allowing me to complete the thesis in a pleasant atmosphere.

Oulu, Septermber 2006 Erkki Jokikokko

List of original papers

The thesis is based on the following original papers, which are referred to in the text by their Roman numerals:

I Saloniemi, I., Jokikokko, E., Kallio-Nyberg, I., Jutila, E. & Pasanen, P. 2004. Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. ICES Journal of Marine Science 61, 782–787.

II Jokikokko, E., Kallio-Nyberg, I., Saloniemi, I. & Jutila, E. 2006. The survival of semi-wild, wild and hatchery-reared Atlantic salmon smolts of the Simojoki River in the Baltic Sea. Journal of Fish Biology 68, 430–442.

III Jokikokko, E., Kallio-Nyberg, I. & Jutila, E. 2004. The timing, sex and age composition of the wild and reared Atlantic salmon ascending the Simojoki River, northern Finland. Journal of Applied Ichthyology 20, 37–42.

IV Jokikokko, E. 2002. Migration of wild and reared Atlantic salmon (*Salmo salar* L.) in the Simojoki river, northern Finland. Fisheries Research 58, 15–23.

V Jokikokko, E., Kallio-Nyberg, I., Jutila, E. & Saloniemi, I. 2006. Effect of origin, sex and sea age of Atlantic salmon on their recapture rate after river ascent. Journal of Applied Ichthyology, in print.

VI Jokikokko, E. & Jutila, E. Numbers of ascending wild and reared Atlantic salmon adults in relation to smolt output of the Simojoki river in the northern Baltic Sea. MS

Contents

1 Introduction

The natural stocks of Atlantic salmon (*Salmo salar* L.) are commonly supported by stocking programmes. The most important reason for stocking has been the decline of stocks and catches. For example, the global catches of wild Atlantic salmon fell by more than 80% from 1970 to 2000 (Young 2001). The main reasons for such a negative development have been the elimination or reduction of the natural reproduction of salmon due to factors such as acidification of the freshwater habitats (Hesthagen & Hansen 1991) or the damming and regulation of rivers for hydropower purposes, which has caused a more than 90% decline in the Baltic salmon populations (Ackefors *et al.* 1991). Recently, over-fishing has also considerably taxed the remaining wild stocks in the Baltic (e.g. Romakkaniemi *et al.* 2003). Because of the unwanted consequences of hydropower production, the hydropower companies were obliged to compensate for the losses to natural reproduction through extensive releases of reared salmon into the dammed rivers. The remaining wild stocks, which suffered from over-exploitation, were supported in Finland by common releases funded from the state budget. Large-scale stocking programmes were started, although their enhancement effects have often been quite low (Fjellheim & Johnsen 2001) or even negative (Saltveit 1998, Einum & Fleming 2001, Levin *et al.* 2001).

Due to the stocking, the proportion of reared salmon was exceptionally high in the Baltic Sea area in the 1990s, when over 90% of the annual smolt production was of reared origin (ICES 2004). The intensive mixed-stock salmon fishing in the Baltic Sea during that period also worsened the decline in the existing natural stocks in rivers accessible for salmon ascent and spawning (Jutila 1992, Karlsson & Karlström 1994). Since the early 1990s, the pathological syndrome M74 has also killed salmon alevins in the remaining salmon rivers of the northern Baltic Sea (Keinänen *et al.* 2000, Karlsson & Karlström 1994). Following the long critical period from the late 1970s to the early 1990s, natural salmon production has, however, recovered as a consequence of fishing regulation (Romakkaniemi *et al.* 2003), and the proportion of wild salmon in the Baltic Sea has considerably increased (ICES 2004).

There are only two remaining salmon rivers on the Finnish coast of the Baltic Sea, the Simojoki and Tornionjoki rivers. Their salmon stocks have primarily been managed by national regulation of salmon fishing and, since the early 1980s, by annual releases of reared parr and smolts into the river. The post-release marine survival of hatchery-reared smolts is known to be lower and more variable during the sea phase than that of wild smolts (Jonsson *et al*. 1991, Crozier & Kennedy 1993, Jonsson & Fleming 1993, I, II). Survival has been observed to be better for larger smolts (Eriksson 1989, Virtanen *et al.* 1991, Salminen *et al.* 1995, Kallio-Nyberg *et al.* 1999, I, II), which is probably due to lower predation. The adaptation of stocked fish in the wild may affect their behaviour as predators or prey (Johnsson *et al.* 2001), also affecting their later survival under natural conditions. Poorly developed predator avoidance behaviour is considered to be one important reason for this difference (e.g. Olla & Davis 1989), and training has been observed to improve the ability of fish to react to predators (Järvi & Uglem 1993, Hirvonen *et al*. 2000, Vilhunen & Hirvonen 2003, Vilhunen 2005a).

Jonsson *et al.* (1991) concluded that the differing experiences as juveniles appear to explain the differences in behaviour between reared and wild fish. Therefore, stocking with parr instead of, or in addition to, smolts could be justified if stocking is used as a general salmon stock management practice. Parr have a similar juvenile phase to wild fish and are obviously better able to survive in the wild than salmon stocked as two-year-old smolts. Most stocking in the Simojoki river has been carried out with one-summer- and one-year-old parr (Jokikokko & Jutila 2004), which live in rapids for one or more years before smolt migration to the sea. Parr released in the autumn as one-summer-olds live a longer time in the river than one-year-old parr released in the spring. These parr groups are thus exposed to differing mortality before smolting. This may be important in selecting the optimal stocking strategy for each river. The production of one-summer-old parr is cheaper than that of one-year-old parr, but due to the possible higher mortality of younger parr during their first winter in the river the stocking of one-year-old parr may be preferable. In northern latitudes, the winter is long and the rivers are ice covered for at least six months. Harsh winter conditions affect the feeding and metabolism of stream fish (Cunjak & Power 1987) and, as a consequence, reduce their overwinter survival. In the Simojoki river the one-year-old parr have produced proportionally more smolts than one-summer-old parr (Jokikokko & Jutila 2004).

However, the number of ascending adult salmon rather than smolt production ultimately describes the success of management stocking. A significantly higher wild/reared ratio was found among the multi-sea-winter (MSW) spawners returning to the Simojoki river than among the smolts at their sea entry (Jutila *et al.* 2003a), and the stocked smolts also produced significantly fewer MSW spawners returning to the river than wild smolts, clearly due to a lower survival rate of stocked smolts at sea (Jutila *et al.* 2003a, I, II). Due to the reasons above, many authors have preferred the regulation of fishing and restoration of freshwater nursery habitats to stocking as a management strategy for salmonids (Jonsson & Fleming 1993, Einum & Fleming 2001, Levin *et al.* 2001). The recovery of the salmon stocks in the Baltic Sea has consequently increased fishing pressure in the rivers (e.g. Jutila *et al.* 2003a). This may have considerable effects on the spawning stock, because the recapture rate of ascended salmon may be high in rivers due to the popularity of sport fishing (Erkinaro *et al.* 1999). Therefore, it is uncertain whether more efficient restrictions should also be implemented in rivers and not only at sea. As the present fishing regulations are based on differences in timing between wild and reared fish during the sea migration, it is also important to determine whether these differences also exist in the river entry phase.

In the research reported in this thesis I evaluated the consequences of salmon stocking in the Simojoki river for the smolt and adult phases, and the effects of the origin of salmon, i.e. wild or reared, on the observed results. As the economic investment in stocking in the Simojoki river has been high, having varied between € 54 000 and € 217 000 annually in 1994–2002 (P. Heinimaa, pers. comm.), it is understandable that an overview of the results is needed. This investigation focused on the effects of the size and origin of salmon on their survival in the post-smolt phase and as adults. The survival calculations were based on differences in the recapture rate of tagged fish. My study on the effect of different factors on survival and on fish behaviour covered the life-cycle beginning from the smolt migration and through the entire adult phase. The main purpose of the investigation was to improve our knowledge and understanding of the mechanisms affecting the stocking results in the Simojoki river, and of how to benefit from the acquired information in future enhancement activities.

2 Material and methods

2.1 Study area

The study was carried out in the boreal Simojoki river (65°38'N, 25°00'E), which drains into the northernmost part of the Gulf of Bothnia in northern Finland (Fig. 1). The river begins from lake Simojärvi (98 km²), and is 175 km in length with a drop of 176 m (Perkkiö *et al.* 1995). The mean discharge is 38 $m^3 s^{-1}$ and the discharge is highest (over 400 $m^3\ s^{-1}$) after the break-up of the winter ice, usually at the beginning of May, falling to about one-tenth of this by late July. Water quality in the river has deteriorated slightly during recent decades and is now classified as good according to the general Finnish water quality classification scheme (Perkkiö *et al.* 1995). About one-third of the area of the river basin is swamp, resulting in polyhumic water in the stream, and peat mining has increased this further. The greatest nutrient loading into the river comes from forest drainage and agriculture. According to Perkkiö *et al.* (1995), the pH is about neutral or in spring slightly below it. The water colour in the lower part of the river is 100–140 mg Pt l^{-1}, COD_{Mn} 10–15 mg $O_2\ l^{-1}$ and alkalinity 0.1–0.3 mmol l^{-1}. The corresponding figures in the upper part of the river are 20–40 mg Pt l^{-1}, 6–7 mg $O_2\ l^{-1}$ and 0.08–0.1 mmol l^{-1}, showing a deterioration in water quality from the upper reaches to the river mouth. The high iron content is typical of the watercourse; in the main stem it may exceed 1 mg Fe l^{-1} and in some tributaries it can be 3–4 mg Fe l^{-1}.

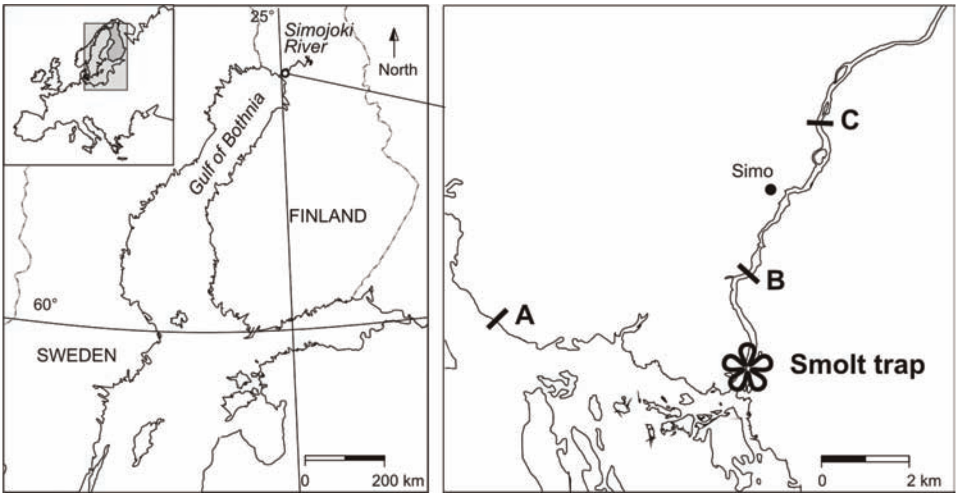

Fig. 1. The location of the Simojoki river and the smolt trap, the brood fish trap (A) and the traps for ascending adults (B in 1996 and 1997, C in 1998).

The whole river up to the lake Simojärvi, and even up to tributaries draining into the lake, is accessible to salmon, which naturally reproduce in the river. Most salmon spawning has been observed to take place up to 110 km from the sea (Jokikokko & Jutila 1998). Until the 1950s, before any major human impact, the original smolt production has been estimated at about 75 000 per year (Jutila & Pruuki 1988). Salmon reproduction in the Simojoki river declined considerably in the 1950s and 1960s, when most of the rapids were dredged to facilitate log floating. In the early 1960s the natural annual smolt production was estimated to be 55 000–65 000 smolts (Toivonen & Jutila 1982). This decline prompted the restoration of the dredged rapids, and the densities of salmon parr increased slightly following the partial restoration of the river in 1976–1977 (Jutila 1992). The restoration is still continuing, and new spawning grounds have also been created by adding gravel in suitable places.

2.2 Stocking of salmon

The natural smolt production of the Simojoki salmon stock, which suffered from dredging of the rapids, declined even further due to heavy sea fishing in the 1970s and 1980s (Romakkaniemi *et al.* 2003), and later the yolk-sac-fry mortality (M74) additionally worsened the situation (Vuorinen *et al.* 1997). As the regulation of the salmon fishery in the Baltic Sea in the 1970s and 1980s was insufficient to prevent the rapid decline of this natural salmon stock, enhancement releases of Simojoki salmon started in the mid-1980s (Jutila *et al.* 2003a) when the hatchery facilities for parr and smolts were only provisional. In first years of stocking the parr and smolts were offspring of brood fish that were caught as smolts from the Simojoki river and raised to adults in the Guttorp hatchery in the Åland Islands, south-western Finland. Later, the stocked salmon were raised in a new hatchery beside the Simojoki river over a 10-yr period. Simultaneously with the construction of the Simojoki hatchery, the rearing of the Simojoki brood salmon was also started in the Central Fish Culture Station of the Northern Finland at Taivalkoski, and at Kainuu Fisheries Research and Aquaculture in Paltamo, places not far from the Simojoki river. The fish produced in these facilities were the progeny of the river's own salmon stock. Stocked salmon have been fin-clipped, which is carried out by removing the adipose fin, a pelvic fin, or both, depending on the age of fish at stocking, in order to distinguish them from wild fish when recaptured later in the river or at sea.

The releases of parr have been directed to the whole river, although the main stocking area has been the lowermost 100 km. The main stocking sites of two-year-old smolts have been the Iso Tainikoski rapids, 47 km from the river mouth, and the rapids at the Simojoki hatchery, about 11 km from the sea, until its closure in 1999. The rapids at Raiskio, 98 km from the sea, were selected as a new stocking site, and from 1999 onwards these two rapids have been the permanent sites for smolt releases. The reason for extending the releases further upstream was to imprint the smolts along the whole river, not only in one place (see Heggberget *et al.* 1986, 1988). The total number of stocked one-summer- and one-year-old parr exceeded 300 000 in 1995, which was the peak year of stockings. Their numbers were high during the late 1990s, when an attempt was made to compensate for the poor natural production in mid-1990s with reared fish. After the turn of the millennium the parr stockings were gradually reduced due to the recovery of natural smolt production. Annual smolt stocking started in the latter part of 1980s, at first irregularly. The number of stocked smolts reached 50 000–60 000 at the end of the 1980s and beginning of the 1990s, but decreased to a few thousand in the early 1990s. The releases of reared smolts increased again and were at their highest level of almost 150 000 fish in 1996 and 1997. After that, the annual numbers decreased but were still close to the assumed natural potential. Smolt stockings were practically stopped at the beginning of the millennium.

2.3 Sampling and handling of the study fish

2.3.1 Smolt trapping

Sea running smolts were sampled annually in the Simojoki river by using a smolt trap at the river mouth (Jutila *et al.* 2003a), and the smolt numbers were estimated by the mark-recapture method (Bagenal 1978). The calculations were based on trap recaptures of hatchery-reared Carlin-tagged smolts usually released at two sites about 45 and 100 km upstream from the smolt trap. In some years, the calculations were also based on Panjet-marked smolt groups (Jokikokko & Mäntyniemi 2003). The trapping period generally lasted about one month, from late May onwards. The trap was continuously in the river and was checked every day. Captured smolts were counted and identified according to their fin clips and their length was measured.

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 generally 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 about four metres and the diameter about 1.8 metres. The trap net closed about one-third of the river, which is 160-170 m wide at the trapping site. The trap net was normally inspected at 8.00 a.m. 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 or benzocaine), their origin checked, the total length measured (mm) and tagged according to methods 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.

2.3.2 Trapping and tagging of ascending spawners

The ascending salmon were trapped and tagged in a trap net, which was set in a pool about four kilometres upstream from the river mouth in 1996 and 1997 (Fig. 1). The mesh size of the codend was 30 mm (from knot to knot) and of the wings 43 mm and 60 mm. Because the trap net caused some disturbance and negative reactions among the fishermen (IV), in 1998 it was installed four kilometres upstream from the previous site. In both years the whole river was closed in order to catch all ascending salmon, although this goal could not be completely attained (IV). In 1998 the trapping was delayed due to flooding of the river. The main run of multi-sea-winter (MSW) salmon was missed then, and the catch mainly consisted of one-sea-winter (1SW) grilse (III).

Tagging with radio transmitters and Carlin-tags was carried out in a boat attached along the codend of the trap net (IV). In 1996 salmon were equipped with transmitters in the river trap and in 1998 tagging was carried out in the river mouth while trapping ascending brood fish (Fig. 1). The radio transmitters used were Model 7PN (ATS, Advanced Telemetry Systems, Inc., USA) with dimensions of 60 mm (total length) x 18 mm (width) x 9 mm (height) and a weight of 14–15 g in air. Each transmitter had a different combination of transmitting frequencies (42.431–43.492MHz in 1996 and 42.022–43.592 MHz in 1998 at least 10 kHz apart), which were used for identification. The pulse rate was 55–60 ppm in both years. In 1997 and 1998 all the captured salmon were tagged with Carlin tags, excluding some fish injured in the trap.

Ascending salmon were handled in a similar way when tagged with either radio transmitters or Carlin tags (III, IV). They were taken from the codend using a dip net and were placed in a container filled with fresh water. Before tagging, the fin clippings were checked, scales sampled and the length of the fish recorded. A radio transmitter or Carlin tag was attached externally below the dorsal fin. Fish were not anaesthetised during tagging. This was due to the possibility that fishermen could catch the fish soon after their release, and we wanted to avoid any potential harmful effects of anaesthetic traces in fish used for human consumption. Despite the absence of anaesthesia the fish were calm during the tagging and when released into the river upstream of the trap. The recapture data from all Carlin-tagged fish were acquired from the Finnish Game and Fisheries Research Institute's tagging office.

3 Results and discussion

3.1 Differences in survival depend on the origin and size of smolts

The mean length was one of the main factors affecting the survival of salmon smolts in the sea. It had a positive effect on the tagging results of both reared and wild fish (I, II). The length was not, however, the only decisive factor, as the origin was also important. Wild smolts, which were usually smaller than reared smolts, survived better than the latter. Wild smolts had on average a 4.5 times better survival rate than reared smolts of an identical size, and the survival varied considerably in different years (I). It is very probable that the conditions in each year affect the survival of stocked fish, as the variation between years is high and the differences between the wild and reared smolts have varied accordingly, sometimes being negligible. The survival difference was especially apparent in an unfavourable release year (I). Semi-wild smolts, stocked as parr in the river, resembled wild smolts. Their recapture rate was clearly higher than that of stocked smolts, despite their smaller size, but the rate also varied more than that of wild smolts (II).

The effect of length on the survival of smolts is well established (Eriksson 1989, Virtanen *et al.* 1991, Lundqvist *et al.* 1994, Salminen *et al.* 1995, Kallio-Nyberg *et al.* 1999, Jonsson & Jonsson 2004), as well as that of origin (Jonsson *et al*. 1991, Kostow 2004). However, in previous studies the length effect has not been compared to such extent as in the present study. Usually, the recovery rate of wild fish is at least two-fold greater than that of reared fish (Jonsson *et al*. 1991), which also seemed to be the case in this investigation (I, II). This relationship is generally applicable to salmon, because current hatchery practices produce smolts that are considerably longer than wild ones, thus compensating for the survival difference to some extent. The survival difference is detectable in the stock composition of many rivers where wild and reared salmon live together. The proportion of wild salmon is higher among ascending spawners than among smolts migrating to the sea, indicating better survival of wild smolts in the sea phase (Crozier & Kennedy 1993, Romakkaniemi *et al.* 2000, Jutila *et al*. 2003a). However, it should be noted that fishing mortality may vary between origin and smolt size groups due to their different migration patterns (Salminen *et al.* 1994, Jutila *et al.* 2003b). It could also be considered whether this may cause variation in the tag return activity in different sea areas and thus partly affect the observed results.

Jonsson *et al.* (1991) concluded that differing experiences in the juvenile phase appear to explain the differences in behaviour between reared and wild fish. This was obvious among the semi-wild salmon (II). Reared fish lack experience of predators, and their response to them differs from that of wild fish (Johnsson *et al.* 2001). Vilhunen *et al.* (2005) examined in the laboratory the demonstrator-observer dynamics necessary for the social learning of predator recognition, and such learning could also happen in nature. The parr stocked in the river are observers, who learn from native demonstrators. It is difficult to determine the extent to which learning, a positive phenomenon, compensates for intra-specific competition and its negative effects. The spatial avoidance of predators suggested by Vilhunen (2005b) may not occur in dense populations of wild parr, because the available territories are scarce and incomers may not be able to compete with the resident fish (Johnsson *et al.* 1999, Harwood *et al.* 2003). Vilhunen & Hirvonen (2003) have shown considerable individual variation in the number and strength of antipredator responses, and this was associated with the differences in survival when exposed to predators (Vilhunen & Hirvonen 2005). We do not know how much the higher survival of semi-wild smolts compared to stocked smolts in paper (II) was due to learned skills, and how much the elimination of the poorest specimens in the parr phase was due to either predation or common weakness. In any case, recently stocked reared fish are vulnerable to predation, and in some northern Baltic rivers about 10–20% of smolts (Kekäläinen 2005) and even up to 50% of them (Larsson 1985) have been found to be predated by pike (*Esox lucius*) and burbot (*Lota lota*) during the migration phase to the sea. Losses following stocking are partly due to stress associated with the rearing practices, transport and release (Olla *et al.* 1994). Thus, predator avoidance behaviour deserves more attention in future stocking programmes (Hirvonen *et al.* 2000, Vilhunen & Hirvonen 2003, Vilhunen 2005a).

3.2 The timing of the ascent is affected by the origin

The proportion of wild and stocked salmon among ascending spawners provides an ultimate measure of the survival of smolts, and the spawning stock composition reflects the stocking results. If we think about the results from the fisherman's point of view, the catch is a clear indicator of the success of stocking. The majority of returning salmon in 1996–1998 originated from reared smolts. They were the predominant group among both male and female ascending salmon (III). Thus, stocking seems to fulfil at least partially the target set by managers, although the yield is not as high as with wild smolts (Jutila *et al.* 2003a). The existence of stocked salmon in the spawning stock does not, however, completely explain the spawning success, which is essential for enhancement activities. This success may vary considerably between salmon of different origin, and the spawning success of reared salmon can be very low (Jonsson *et al.* 1991, Fleming *et al.* 1996, Fleming *et al.* 1997). Studies on steelhead trout (*Oncorhynchus mykiss*) have produced controversial results. According to Chilcote *et al.* (1986), the success of hatchery fish in producing smolt offspring was only 28% of that of wild fish, but in some cases the hatchery stock may produce more smolt offspring per parent than naturally spawning parents (Kostow 2004). In the study of Chilcote *et al.* (1986), the proportion of naturally produced steelhead smolts of hatchery origin was 62%, because the hatchery spawners effectively outnumbered wild spawners. These results demonstrate that hatchery fish, although probably not always as good as their wild counterparts, may be able to produce a considerable number of offspring and thus contribute to natural populations.

In addition to origin, the sex ratio also has a considerable effect on the reproductive potential of the salmon stock. Females formed the majority of wild adults in 1996 and 1997, but the minority of adults originating from reared salmon released as smolts (III). The semi-wild migrants originating from released parr also had a different sex ratio from fish released as smolts, resembling more the wild salmon. Thus, fish that spent at least part of their juvenile life in the river seem to produce proportionally more returning females than do reared fish released as smolts. Not only the sex but also the age of fish determines their reproductive capacity: the bigger (and usually older) they are, the more gametes they produce. This is especially true for females. Therefore, it is important to be aware that stocking of reared smolts results in a higher proportion of 1-sea-winter (1SW) fish, i.e. grilse, than is observed among wild salmon, or is produced by stocking parr (III).

Most grilse are males, suggesting low productivity, although male grilse have been observed to survive to repeat spawning, thus safeguarding the genetic diversity of the salmon stock (Jokikokko & Jutila 2005). One reason for this is their small size: as only a fraction of grilse attain the minimum legal size of 60 cm during the feeding migration, they suffer from much lower exploitation (McKinnell 1997). Older, bigger salmon, mainly wild females, also ascend the river earlier than their younger counterparts, which are mostly males stocked as smolts (III). This behaviour has been utilized by restricting the coastal fishing during the salmon migration to their spawning rivers, which has resulted in a clear increase in the early-ascending part of the spawning populations (Romakkaniemi *et al.* 2003). They mainly are MSW salmon, independent of their sex or origin (III). The positive effect of smolt length on survival, especially in reared smolts (I, II), seems controversial in the light of Salminen's (1997) finding that the proportion of grilse is linked to the size of reared smolts, with large smolts yielding proportionally more grilse than smaller ones. Probably the best way to resolve the dilemma is to simply accept that male grilse form the majority and take this into account when planning stockings.

3.3 Wild and reared adults behave differently in the river

Although the behaviour of ascended salmon during spawning in the Simojoki river is unknown, some conclusions can be drawn according to the radio-tagging results from ascending spawners in the river (IV). The origin of the salmon affected the observed migration distance so that the reared salmon ascended farther and their migration distance varied more than that of wild salmon. Despite the difference in the maximum distance, the mean distance from the trap to the spawning location was quite similar for both salmon groups, indicating larger overshooting (wandering) for reared fish. The reared salmon also took longer than wild salmon to settle down in the spawning area after river ascent. As suggested by Jonsson *et al.* (1991), reared salmon may not be able to recognize a suitable spawning ground as well as their wild counterparts, and attachment to a particular area of the river fails, causing the wandering behaviour. Intraspecific conflicts probably also force the reared salmon to wander up and down the river more than wild salmon (Jonsson *et al.* 1991, Økland *et al.* 1995).

The short migration distance of spawners in the Simojoki river may be explained by the homing hypothesis. Salmon return to the section of the river they lived in before the smolt phase (Heggberget *et al.* 1986, 1988), and the strength of imprinting can be affected by the release location of smolts (Heggberget *et al.* 1991). Smolts have been stocked in the lowest 50 km of the Simojoki river, probably causing the observed short migration distance. Of course, there could also be other reasons. One possible reason may be the presence of good spawning areas in the lower reach, where most of the rapids are situated in the Simojoki river. This assumption may be valid, as electrofishing surveys have shown that several of the best rapids with high wild parr densities are situated in the lower part of the river. Therefore, even wild salmon seem to have their spawning grounds in the same region, causing the young fish to imprint there after hatching and later return to spawn in the same area. Despite the bigger overshooting of the reared salmon they seem to spawn in the same areas as wild salmon, further indicating the effect of good spawning grounds.

The findings of paper (IV) were applied in subsequent stocking programmes by moving one smolt release site considerably further upstream in 1999. Extending the stocking area was assumed to enhance the imprinting of stocked smolts to the upper part of the Simojoki river, thus giving more space for the ascending salmon to select their spawning grounds and better utilize the river's capacity. A wider distribution of spawners would also decrease the fish density and competition, which appears to especially have a negative effect on the reared salmon (Jonsson *et al.* 1991, Økland *et al.* 1995). The longer migration distance of smolts to the sea has not been observed to cause higher mortality in the river, thus justifying the use of the upper stocking sites (Jokikokko & Mäntyniemi, 2003). Because of the rapid recovery of the natural reproduction and high parr densities in the Simojoki river from the late 1990s (Jutila *et al.* 2003a, Romakkaniemi *et al.* 2003), intraspecific competition between the hatchery and wild fish should be taken seriously (Jonsson *et al.* 1998, Weber & Fausch 2003).

3.4 The fate of adult salmon during and after river ascent depends on their sex but not their origin

The later survival of ascended spawners is not well documented and there have been few studies concerning the tagging of adult Atlantic salmon in order to follow their survival after spawning (N. Jonsson *et al.* 1991). Most salmon survival studies have been based on the tagging of smolts (e.g. I, II). This method is generally only suitable for studying the life history of salmon up to their first spawning, because most salmon are caught during their first feeding migration (Romakkaniemi *et al.* 2003). Only a small proportion of salmon tagged as smolts reach the spawning river, and even fewer of them are caught in the sea during their second feeding migration. It has long been known that salmon may spawn several times under favourable conditions (Alm 1934, Järvi 1938, 1948), and this has been observed even under the high fishing pressure in the Baltic Sea (Romakkaniemi *et al.* 2003, Jokikokko & Jutila 2005). Intensive stocking of the Simojoki river in the mid-1990s, with a high output of reared smolts (Jutila *et al.* 2003a), has been assumed to increase the strength of older MSW age groups and the occurrence of repeat spawners in the catch (Jokikokko & Jutila 2005).

Most of the tag returns of tagged spawners appear to have come from the Simojoki river, showing the impact of river fishing, despite only rod fishing being allowed (V). Although the proportion undoubtedly varies between rivers, the results indicate that river fishing may have a considerable impact on the spawning stock (see also Erkinaro *et al.* 1999). Most of the river catch originated before the spawning season, which makes the effect on the spawning population even more pronounced. Because the present study (V) revealed no difference in the recapture rate of wild and stocked salmon, and their spawning areas seemed to be about the same (IV), no selective protection method for wild spawners exists. Thus, in the river phase, the adult population cannot be separated into wild and reared components.

The observation that there was no difference between the recapture rates of wild and reared salmon in the adult phase (V) suggests that the possible differences between these groups as smolts have disappeared during the feeding migration, and the specimens that survived to ascend the river appear to be similar. However, as stocking produces a slightly different stock composition (III), it also proportionally affects the recapture rate of tagged fish. The results indicate that male grilse have the potential for repeat spawning, and this was confirmed by examining the age composition of the repeat spawners (Jokikokko & Jutila 2005). The male grilse of stocked origin did not seem to only be surplus fish that could be rejected in all stock evaluations. Although they do not probably affect the number of fish hatching, they increase the effective stock size necessary for a successful survival strategy (Niemelä 2004). What was revealed as important for the salmon stock in paper (V) was the better survival of MSW females compared to MSW males, because the overall number of offspring is dependent on the eggs produced by these females. This was not affected by the origin of the fish, suggesting similarity between wild and reared adults, and thus giving a positive signal for salmon stocking.

Although smolts of reared origin produce adults that survive spawning, thus supporting the salmon stock, their effect is not comparable to that of wild smolts. The ascending adults of wild origin outnumbered their reared counterparts about three-fold in relation to the smolt numbers in the Simojoki river in the years 1996–1998 (VI). This was slightly less than observed by Kostow (2004) with steelhead, where the difference was five- to six-fold. The proportions varied slightly depending on whether the grilse were taken into account, but this effect was not very great. Two-year-old smolts produced more adults if grilse were included in the figures (see also III), whereas semi-wilds were better when considering MSW adults. However, due probably to the high exploitation rate during the feeding migration in the sea, the survival from smolts to adults returning to their spawning river was much lower than given by Jonsson & Jonsson (2004) in their review, where the marine survival appeared in most cases to be about 10%, varying from 2% to 30%.

3.5 Many-fold effects due to releases of young salmon

As revealed in paper (VI), stocking produces considerable numbers of ascending adults, thus enhancing the native stock. This was the original goal of stocking, and the stocking of smolt and parr was justified and necessary especially during the 1990s when the river's wild salmon population was in a critical state (Romakkaniemi *et al.* 2003). Kostow *et al.* (2003), however, caution about concluding that natural spawning and smolt production by hatchery fish is evidence of success, because the return of adult offspring and lack of depression of wild productivity should also be demonstrated. The adult offspring could not be verified in connection with this investigation, but the need to avoid negative effects on the wild stock may favour the stocking of smolts rather than of parr. Because stocking results were approximately equal with both groups (VI), the temptation to stock two-year-old smolts will be high, as the mean number of returning fish will linearly increase with the number of released smolts (Finstad & Jonsson 2001). This is because after stocking the smolts migrate to the sea, where density-independent mortality factors appear to dominate (Jonsson *et al.* 1998). In the river, intra-specific competition with wild fish for food and space affects the survival of released parr, and the population size is limited by the carrying capacity (Jonsson *et al.* 1998).

By stocking smolts instead of parr it is possible to avoid competition. This is known to be an important negative interaction between hatchery and wild salmonids (see review of Weber & Fausch 2003, Kostow *et al.* 2003) that may cause, for instance, a smaller smolt size and therefore poorer subsequent survival in the sea (I, Jokikokko & Jutila 2004). The cost of stocked two-year-old smolts in the Simojoki river has been slightly lower than that of smolts produced by stocking one-year-old parr, and much lower than one-summer-old parr (Jokikokko & Jutila 2004). Although the survival of salmon stocked as parr seems to be better than that of salmon stocked as smolts during the feeding migration (II), the difference is negligible when the adult salmon ascend the river, being even more favourable for salmon of smolt origin (VI). Thus, the expenses and the yield support the stocking of two-year-old smolts.

However, simply increasing the number of stocked smolts is not the solution to enhancing natural salmon reproduction, and the cost is not the only reason to carefully plan the stocking policy. As warned by McGinnity *et al.* (2003), the fitness reduction and potential extinction of wild populations of Atlantic salmon have been observed to follow from the interaction between farmed and wild salmon, as a result of both interbreeding and competition. Reared smolts do not pose a similar threat in the Baltic Sea to farmed escapees in Atlantic rivers, and so far the distinct genetic features of the Simojoki salmon have been found to be preserved despite its use for stocking (Koljonen 1995, Koljonen *et al.* 2005). It could even be assumed that rearing might have safeguarded the diversity of the Simojoki salmon in its critical phase in the mid-1990s due to several brood stocks being kept in hatcheries, although Reisenbichler & Rubin (1999) have found that artificial propagation can rapidly and substantially reduce the reproductive success of reared fish due to genetic changes. Survival is also known to decrease due captive breeding (Kostow 2004), and according to Chilcote *et al.* (1986) the wild and hatchery fish appear to differ in some unknown traits that negatively affect offspring survival.

Chilcote *et al.* (1986) recommend not replacing or supplementing low numbers of wild spawners with hatchery fish in order to achieve a desired smolt production goal, but if stocking is considered necessary they suggest the rigorous use of wild fish as the sole source of brood stock in order to maintain the genetic integrity of wild populations. However, the removal of brood fish from an already limited natural spawning population, such as in the Simojoki river, may be problematic. In the worst case it is even possible that more parental fish would be needed to produce hatchery fish than to produce natural offspring (Saltveit 2006). Increased stocking can also be a double-edged sword by intensifying fishing, and due to the mixed stock fishery in the Baltic Sea the capture of wild specimens cannot be avoided. When the status of wild stocks is weak, every specimen is important for natural reproduction and thus stocking, despite its good intentions, may have negative consequences.

4 Conclusion

The present study demonstrated that stocking produces adult salmon that survive and ascend the river in which they were stocked. Although wild smolts gave better results in every respect, stocking can potentially support the native stock. The survival of wild smolts was twice as high as that of stocked fish, taking into account the size difference between the fish in this study. This relation can be reasonably applied in future studies, because current farming practices produce smolts of a greater size than their wild counterparts. Without the benefit of this size difference, the survival of reared smolts would be even worse than that of the wild ones. Despite their small size, semi-wild smolts stocked as parr closely resembled wild smolts in several respects, including their survival at sea. However, similar proportions of semi-wild salmon and salmon stocked as two-year-old smolts were recorded among adults ascending the river.

Despite the increased fishing pressure and the threats to fitness caused by releasing young fish, stocking in the Simojoki river has produced ascending salmon and thus enhanced the natural reproducing population. Therefore, stocking seems to have responded to the needs that arose in the critical period during the mid-1990s, when the native stock had almost disappeared and the fishing regulations were not strong enough to allow the recovery of natural reproduction. The superiority of wild compared to stocked fish is well known and has been discussed in several contexts. It must be kept in mind, however, that the mortality and losses of young wild fish are also extensive (Jonsson & Fleming 1993, Kostow 2004); only the timing of mortality is different. Reared fish encounter the harsh natural conditions as soon as they have been released, independent of their size or age. Not only novelty and insufficient knowledge to react appropriately in the new environment but also transport and handling stress negatively affect reared fish, increasing their post-stocking mortality, due mainly to predation (Olla *et al.* 1994). Survival calculations based on egg numbers would probably show completely different ratios between wild and reared fish compared to the present practice, where the survival of reared fish groups is often counted from the time of stocking. As shown by Kostow (2004), the egg-to-adult survival of hatchery fish can be higher and they may produce many more offspring per parent than naturally produced fish.

It is still not known how successfully stocked salmon spawn alongside with their wild counterparts, or the extent to which they enhance the offspring numbers. It is reasonable to assume that the adult salmon of reared origin are close to wild spawners in their reproductive ability, because their qualities and behaviour are otherwise quite similar. The most significant difference seems to be the better survival of wild salmon compared to reared ones during the post-smolt phase in the sea. Other differences are apparent in the timing of river ascent, in behaviour before and after spawning and in the proportion of grilse. According to Carlin tagging the fate of adult salmon in the river and later in the sea after spawning shows that the possible differences observed between the wild and reared salmon are more strongly related to sex or age and not to the origin of the fish.

Although the origin of salmon, i.e. wild or reared, is probably not a decisive factor in the adult phase, the current practice of only producing a certain number of fish of a particular size, preferably as big as possible, is no longer acceptable. As demonstrated in this thesis, stocking may be a useful method to produce young salmon to support the weak native stock, but only if its ecological value is sufficiently high. Although the economics of salmon stocking in the Simojoki river were not assessed, it is clear that the input has been much higher than the yield, if the flesh value is used as the indicator. Although it cannot be decisive in the Simojoki river, increasing the effectiveness of stocking is a necessity in the future in other enhancement projects. One of the challenges is to develop ecologically meaningful and widely applicable methods for antipredator training of stocked fish (see Vilhunen 2005b).

However, the solution to the observed problems is not always dependent on the lack of knowledge, as shown by Lichatowich *et al.* (1999), but there is often political reluctance to use measures that the depletion of the resource. Captive rearing can be used as a tool to assist stock restoration, and improvements in fish culture, release strategies and other areas can help to reduce many of the deleterious effects of fish culture, but they cannot be avoided completely (Waples 1999). It is well known that artificial propagation will not lead to the recovery of a stock unless the fundamental problems that caused the population decline are resolved (Jonsson *et al.* 1999). Therefore, due to their effectiveness, fishing restrictions should for the time being be the main method used to regulate the status of the Baltic salmon stocks (Jutila *et al.* 2003a, Romakkaniemi *et al.* 2003).

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Original papers

The thesis is based on the following original papers, which are referred to in the text by their Roman numerals:

I Saloniemi, I., Jokikokko, E., Kallio-Nyberg, I., Jutila, E. & Pasanen, P. 2004. Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. ICES Journal of Marine Science 61, 782–787.

II Jokikokko, E., Kallio-Nyberg, I., Saloniemi, I. & Jutila, E. 2006. The survival of semi-wild, wild and hatchery-reared Atlantic salmon smolts of the Simojoki River in the Baltic Sea. Journal of Fish Biology 68, 430–442.

III Jokikokko, E., Kallio-Nyberg, I. & Jutila, E. 2004. The timing, sex and age composition of the wild and reared Atlantic salmon ascending the Simojoki River, northern Finland. Journal of Applied Ichthyology 20, 37–42.

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V Jokikokko, E., Kallio-Nyberg, I., Jutila, E. & Saloniemi, I. 2006. Effect of origin, sex and sea age of Atlantic salmon on their recapture rate after river ascent. Journal of Applied Ichthyology, in print.

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ISBN 951-42-8223-X (Paperback)
ISBN 951-42-8224-8 (PDF)
ISSN 0355-3191 (Print)
ISSN 1796-220X (Online)