From the river to the open sea – a critical life phase of young Atlantic salmon migrating from the Simojoki river

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Academic dissertation

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Contents

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. Jutila, E., Jokikokko, E. & Julkunen, M. 2005. The smolt run and post-smolt survival of Atlantic salmon, *Salmo salar* L., in relation to early summer water temperatures in the northern Baltic Sea. Ecology of Freshwater Fish 14: 69–78.

II. Jutila, E., Jokikokko, E. & Julkunen, M. 2006. Long-term changes in the smolt size and age of Atlantic salmon, *Salmo salar* L., in a northern Baltic river related to parr density, growth opportunity and postsmolt survival. Ecology of Freshwater Fish 15: 321–330.

III. Jutila, E. & Jokikokko, E. 2008. Seasonal differences in smolt traits and in postsmolt survival of wild Atlantic salmon, *Salmo salar*, migrating from a northern boreal river. Fisheries Management and Ecology 15:1–9.

IV. Jutila, E., Jokikokko, E. & Ikonen, E. Postsmolt migration of Atlantic salmon, *Salmo salar* L., from the Simojoki river in the Baltic Sea. Journal of Applied Ichtyology (Accepted).

V. Kallio-Nyberg, I., Jutila, E., Saloniemi, I. & Jokikokko, E. 2004. Association between environmental factors, smolt size and the survival of wild and reared Atlantic salmon from the Simojoki river in the Baltic Sea. Journal of Fish Biology 65: 122–134.

Abstract

Long-term monitoring data were used in studying the relationships between smolt size and age, smolt and postsmolt migration, environmental conditions, prey abundance and postsmolt survival of the wild Atlantic salmon (*Salmo salar* L.) stock of the Simojoki river, northern Finland. Data on approximately 43 000 wild smolts were collected by annual trapping of sea-running smolts at the river mouth from 1972–2005, and a total of about 24 000 of them were Carlin-tagged during this period. The data also included tag recoveries obtained along the migration routes of salmon.

The onset of the smolt run was significantly ($P < 0.001$) dependent on the rising water temperature in the river during the spring, a rise above 10 °C being the main proximate environmental triggering factor. There was also a significant ($P = 0.035$) correlation between the onset of the smolt migration and decreasing river discharge before it. The duration of the main run was significantly ($P < 0.001$) shorter in years when the onset of the smolt run was delayed.

The annual mean smolt size was found to negatively depend on the density of wild >1 yr parr in the previous autumn (smolt length $P = 0.009$, smolt weight $P = 0.018$), but not significantly on the mean smolt age. The density of hatchery-reared parr released into the river or the growth opportunity, based on the day length and air temperature during the preceding summers, did not significantly affect the size of wild smolts.

The mean length of smolts migrating early in the season was commonly significantly larger and the mean age always significantly higher than among smolts migrating later, while differences in weight were mostly insignificant. Many of the smolts migrating early in the season and almost all smolts migrating later had started their new growth in spring in the river before their sea entry. This suggests that not all presmolts need to attain the smolt size by the end of the autumn preceding smolt migration.

Among postsmolts, the time required for emigration from the estuary was significantly ($P = 0.004$) dependent on the sea surface temperature (SST) off the river, being shorter in years with warm than cold sea temperatures. Outside the estuary, the postsmolts migrated southwards along the eastern coast of the northern Gulf of Bothnia (the Bothnian Bay), the geographical distribution of the tag recoveries coinciding with the warm thermal zone in the coastal area. After arriving in the southern Gulf of Bothnia (the Bothnian Sea) in late summer the postsmolts mostly migrated near the western coast, reaching the Baltic Main Basin in late autumn.

Until the early 1990s there was only a weak positive association between smolt length and postsmolt survival. However, following a subsequent decrease in the mean smolt size, the reported recapture rate of tagged salmon was found to significantly ($P < 0.01$) depend on the smolt size, suggesting better survival for large than for small smolts. The differences in recapture rates between smolts tagged during the first and second half of the annual migration season were insignificant, which indicates that the seasonal variation in smolt size and age and in marine conditions, such as thermal circumstances and food availability, seem to be too small to affect survival.

Among the climatic factors examined, the sea surface temperature (SST) in summer in the Gulf of Bothnia was most clearly related to the survival of wild postsmolts. Postsmolt survival appeared to be highest in years when the SST in June in the Bothnian Bay varied between 9 and 12 °C. In addition, the survival of wild postsmolts showed a significant ($P = 0.004$) positive dependence on the SST in July in the Bothnian Sea, a nonsignificant positive dependence on the prey fish (0+ herring, *Clupea harengus* L.) abundance in the Bothnian Sea, but no dependence on 0+ herring and sprat (*Sprattus sprattus* L.) abundance in the Baltic Main Basin.

1. Introduction

The Atlantic salmon (*Salmo salar* L.) is an anadromous fish species living in the northern Atlantic Ocean and the Baltic Sea area. Salmon spawn in rivers in the autumn, the juveniles live their first years in the river as parr and migrate as smolts to the sea. It is commonly accepted that salmon migrate to the sea to find better feeding resources than their natal streams can provide (Hoar 1976). Before leaving the river, juvenile salmon undergo smoltification, which includes physiological, morphological and behavioural changes enabling them to survive at sea (Virtanen 1988, McCormick *et al.* 1998). After leaving the river in spring the smolts are generally, and also in this thesis, referred to as postsmolts until end of the year of their sea entry, after which in the Baltic Sea area they normally recruit to the salmon sea fishery. Juvenile salmon feed at sea for 1–4 years before returning as maturing adults to their natal river to spawn (Alm 1934, Järvi 1938, 1948, Karlsson & Karlström 1994).

The transition of smolts from the river to the marine environment is one of the most critical phases in the life cycle of Atlantic salmon. Correct timing of the smolt run is essential for the later survival of the smolts after sea entry. However, the environmental conditions may vary considerably between rivers and sea areas and also annually within the same area. Annual variations in postsmolt survival are indicated by variations in the catch and the recapture rate of tagged fish (McKinnell & Karlström 1999). The reasons for the high mortality occurring during the postsmolt migration have been widely studied but are still not properly known (see e.g. reviews by Christensen & Larsson 1979, Hansen & Quinn 1998).

Most studies on the smolt and postsmolt migration and on factors affecting postsmolt survival have been carried out in Atlantic rivers. In the Baltic Sea, the environmental conditions differ from those in the Atlantic Ocean. The greatest differences are related to its brackish water, the winter ice-cover in the northern parts as well as the abundance and diversity of predatory fish stocks and food available at sea. The size and age of smolts may vary between rivers, annually within each river and even during the annual migration season. All these differences may affect the later migration patterns and survival of postsmolts in the sea by affecting, for example, the vulnerability of postsmolts to the predators (Larsson 1985) or the availability of food (Mitans 1970, Salminen *et al*. 2001).

Earlier, almost all northern rivers had their own genetically distinct salmon populations. However, most of the rivers in the Baltic Sea area have lost their natural salmon stocks because of damming, deterioration of water quality or degradation of freshwater habitats, or due to the extensive sea fishery for salmon (Romakkaniemi *et al*. 2003). In Finland, there are now only two remaining self-reproducing Baltic salmon rivers, Tornionjoki and Simojoki, that support their own natural populations of Atlantic salmon. Both of these empty into the northern part of the Gulf of Bothnia, the Bothnian Bay. The Tornionjoki river is a border river between Finland and Sweden, and the Simojoki river is the only Finnish salmon river entirely situated within the Finnish territory.

Finnish Game and Fisheries Institute started to monitor the status of the wild Simojoki salmon stock in 1972 by electric fishing for parr in the rapids and by trapping and Carlin-tagging smolts at the river mouth. This monitoring of parr density has been carried out annually since then. In addition, some environmental data collected mainly by environmental authorities and research institutes on the riverine and marine conditions are also available from the same period. Such long-term data are valuable in studying the critical characteristics of the wild smolts and postsmolts as well as the effects of environmental variables on the migration patterns and postsmolt survival in a salmon stock. Monitoring of changes in the characteristics of smolts and their environment has also been important because salmon catches and postsmolt survival in the Baltic Sea area have considerably decreased since the 1990s, while the reasons for these trends are largely unknown (Michielsens *et al.* 2006, ICES 2007).

This thesis is focused on two critical phases in the life cycle of young salmon, their migration as smolts from the river and their postsmolt phase in the sea. Based on the long-term data collected on wild Simojoki salmon, this thesis aims at analyzing which factors affect the timing of the smolt migration (Paper I), changes in smolt size and age (Papers II and III), and the migration patterns of postsmolts (Paper IV). An additional aim of the thesis is to examine the effects of smolt size, climatic factors and prey abundance on postsmolt survival (Papers I–III and Paper V) (Fig. 1).

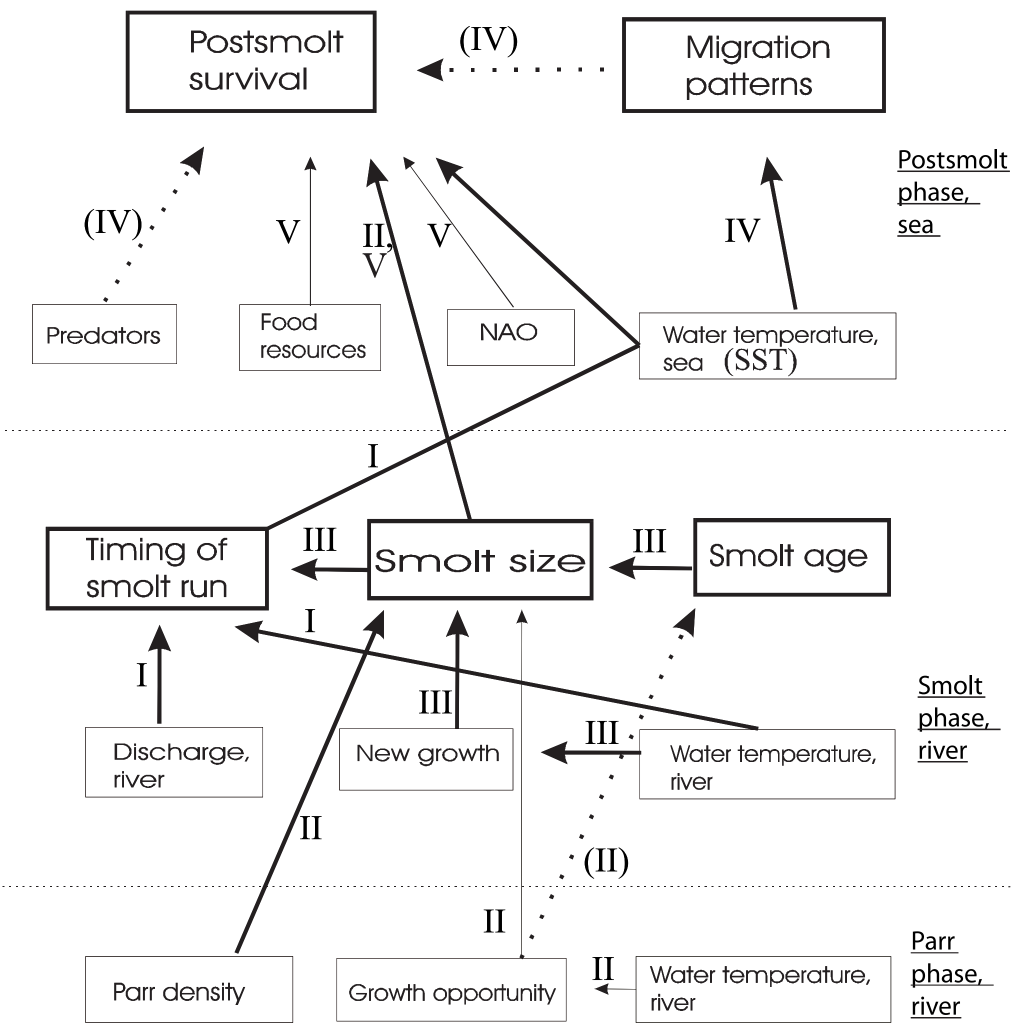

Fig. 1. Schematic diagram of the causal relationships discussed in this thesis. Solid arrows indicate relationships between the variables studied in this thesis and dotted arrows those shown by other studies and discussed here. For causalities studied in the original papers, the respective papers are indicated by Roman numerals (I–V).

2. Material and methods

2.1 Study area

The boreal river Simojoki, northern Finland, runs from the Lake Simojärvi at 176 m above sea level. The length of the river is about 175 km and its mean discharge is 38 $m^3 s^{-1}$. The discharge is at its highest (over 400 $m^3 s^{-1}$) after the ice break up in May, but it falls to about one-tenth of this by late July. The water level in the river also peaks in spring, rising to about 2 m higher than in late summer and in winter. The river empties into the Gulf of Bothnia in the northernmost part of the Baltic Sea (65º38'N, 25º00'E). The estuary is a shallow brackish water area extending about 10 km from the river mouth, and the water depth in adjacent sea areas varies between 10 and 40 m (Fig. 2).

The catchment area of the Simojoki river is 3 160 km^2, with bogs and forests forming typical features of the river basin. Forest drainage, agriculture and peat mining cause the majority of the nutrient load in the river. The water especially in the lower reaches of the river is polyhumic (100–140 mg Pt L^{-1}) due to extensive bogs, and peat harvesting has increased this further. The water quality in the river has been assessed as good according to the general water quality classification used in Finland (Perkkiö *et al*. 1995).

The whole river is accessible to ascending salmon, but they normally spawn only within 110 km from the river mouth. There are about 255 ha of rapids in the river. Until the 1950s, before major human impact, the potential smolt production was estimated at 75 000 smolts per year (Jutila & Pruuki 1988). The natural salmon stock has, however, decreased due to the intensive dredging of rapids carried out in the 1950s and 1960s to facilitate log driving. The dredging reduced and considerably degraded the available spawning and nursery areas for salmon. Log driving ceased in 1964 just after the dredging had been completed.

Three restoration projects have been carried out in the dredged rapids. The first restoration carried out in the 1970s strove to open gaps in the stony deflector walls, the second in the 1980s included partial restoration of the rapids, and the third project in the 2000s completed the restoration of the nursery areas and restored dredged spawning grounds. The results of the restoration on smolt production were at first poor due to the simultaneous reduction of the spawning stock (Jutila 1987). The effects of the restoration have only become apparent following the increase in the spawning stock in the Simojoki river since the late 1990s (Jutila *et al*. 2003*a*), but the results of studies on the effects of the latest restoration measures on smolt production are not yet available.

A second major threat to the wild salmon stock was the intensive mixed-stock sea fishery for salmon in their main feeding areas in the Baltic Sea, and the coastal fishing of the returning spawners in the Gulf of Bothnia. The extensive sea fishing of salmon began in the 1950s (Karlström & Karlsson 1994), but for Simojoki salmon its negative effects were first observed in the late 1970s as a severe reduction in parr densities and in smolt production (Jutila *et al.* 2003*a*). To avoid the extinction of the natural stock, hatchery-reared juveniles (parr and/or smolts) originating from river's own salmon stock have been annually released as adipose fin-clipped fish into the river since 1984.

During the early 1990s, wild smolt production was affected by the M74 syndrome, which reduced the survival of newly-hatched fry (Keinänen *et al*. 2008). Smolt production was at its lowest only some thousands of smolts in the mid-1990s, but since then has rapidly increased, especially due to the strict regulations placed on salmon fishing on the Finnish coast of the Gulf of Bothnia and supportive stocking of reared salmon in the river (Jutila *et al.* 2003*a*, Jokikokko 2006). Estimates of the annual smolt output from the Simojoki river, based on the mark-recapture method, are available since 1987 (ICES 2007) (Fig. 3).

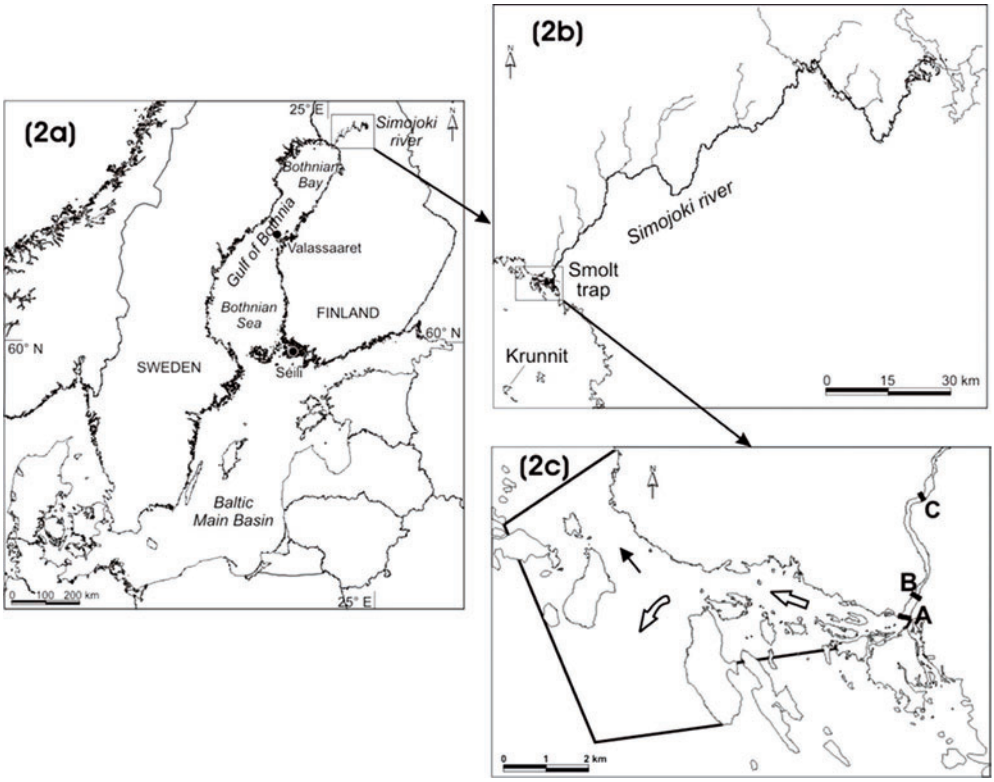

Fig. 2. Map of the Simojoki river, estuary area and the Baltic Sea. The sites of the smolt trap and the measuring sites of SST at the islands of Krunnit, Valassaret and Seili are indicated. 2a) The Baltic Sea, 2b) the Simojoki river, 2c) the estuary area within 10 km distance from the river mouth. Fig. 2c, A = river mouth, B = the smolt trap in 1972–2003, C = the smolt trap in 2004–2005. The black lines show the border of the estuary area within 10 km from the river mouth, the open arrows the direction of the major current and the black arrow the direction of the minor current.

2.2 Data from the river phase

Altogether, 43 000 wild smolts were sampled by annual trapping of downstream-migrating smolts in spring 1972–2005 using a smolt trap placed at first below the lowest rapids in the Simojoki river, 0.4 km from the sea. From 2003 onwards the trapping site was moved 2.7 km upstream (Fig. 2). In total, about 24 000 of the sampled smolts were individually tagged with external Carlin tags (see Carlin 1955) at the trap during the period 1972–2005, apart from those years when only a low number (< 100) of fish were caught (Fig. 4). Trapping began after the break up of ice as soon as the water level was low enough to install the trap. Observations from smolt trapping in springs with various flow conditions indicated that smolt migration during the spring flood was likely to be minimal when the river water was cold (< 5 ^{o}C). The trapping period usually lasted about one month from late May to early July and covered the main annual smolt run (I–V).

The smolt trap consisted of a fyke net with a mesh size of 8 mm (bar length) in the codend and side arms directed across the river, which is 160–170 m in width at the trapping sites. The trap was attended daily at 8 AM during the trapping season. When removed from the trap, the

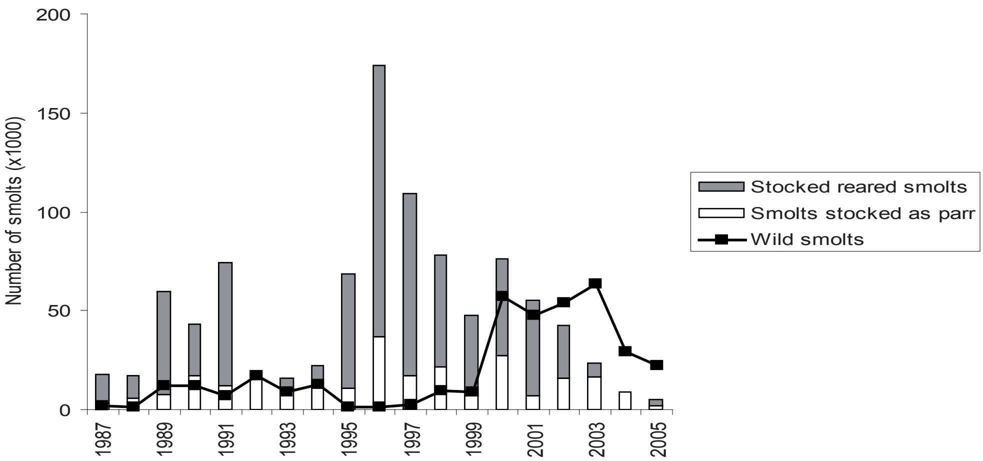

Fig. 3. The annual numbers of wild and hatchery-reared smolts migrating from the Simojoki river in 1987–2005 (ICES 2007).

smolts were anaesthetized (MS-222 or benzocaine), divided into different groups on the basis of the fin clippings, counted and measured (L_T in mm). Weighing of all smolts was difficult in field conditions and thus only a selection of them was weighed in grams. Depending on the number of the smolts captured, about 300–1 000 wild smolts were Carlin-tagged in most years. During the study period, the same experienced tagging team and mainly the same persons performed the tagging using the procedures described by Naarminen (1985). Scale samples for age determination were taken rather variably, ranging from 42 individuals in 1987 up to 1 308 smolts in 2004, with no scale samples in 1981–1982 and 1984–1985. Finally, the smolts were moved to a recovery cage and kept there until the following day, when they were released into the river to continue their migration to the sea (I).

In addition to the wild smolts, a total of about 52 000 hatchery-reared smolts were released as Carlin-tagged fish into the river during the period 1986–2005. The tagging of hatchery-reared smolts was normally performed in the hatchery in winter or in spring prior the release. Semi-wild smolts originating from hatchery-reared parr and groups of hatchery-reared smolts were in some years also tagged at the trap.

During the smolt run the water temperature in the river was measured daily at 8 AM at the smolt trap. Additional data on river water temperatures in spring and summer 1985–2002 were also obtained from the Finnish Game and Fisheries Research Institute's Simojoki hatchery (I).

The density of salmon parr (ind. 100 m^{-2}) was monitored annually at 10–30 permanent sites in the rapids of the Simojoki river using electric fishing according to the methods presented by Bohlin *et al.* (1989). The reared parr were fin-clipped before release into the river by removing the adipose fin and either the right or left pelvic fin to enable their discrimination from the wild parr. The wild >1yr parr were aged from scale samples, and the densities of wild and reared >1 yr parr were estimated separately (II).

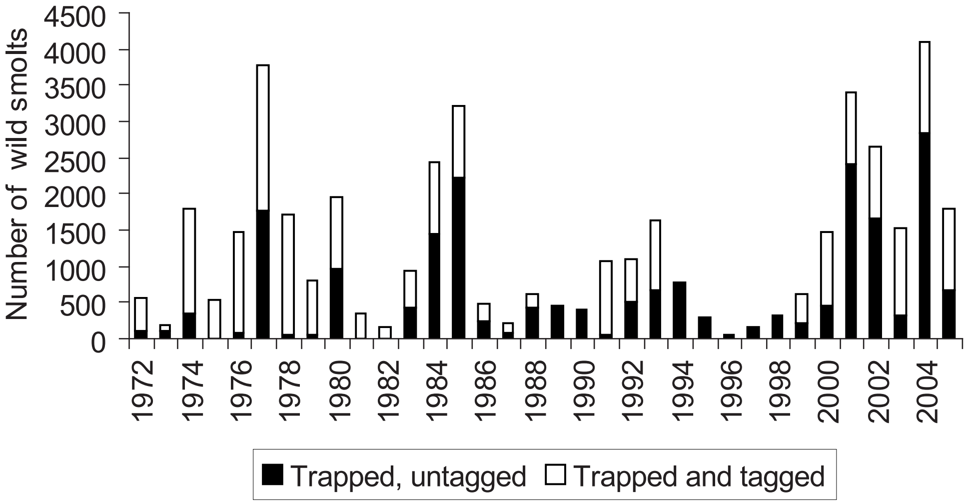

Fig. 4. The annual number of trapped and tagged wild smolts in the Simojoki river in 1972–2005.

Based on the method presented by Metcalfe & Thorpe (1990), an index of annual growth opportunity (*G*) for each year was calculated as:

$$G = \Sigma\, T_i * D_i$$

where T_i is the daily mean air temperature in excess of 5.5 °C in month *i*, and D_i is the hours of daylight in month *i*. Air temperatures measured at the neighbouring Kemi airport, obtained from the Finnish Meteorological Institute, and the daily hours of daylight in each month, obtained from the U.S. Naval Observatory (http://aa.usno.navy.mil/), were used in calculating the annual growth opportunity (II). As the mean age of salmon smolts in the Simojoki river commonly varies between two and three years, the growth opportunity for the smolt year-classes migrating from the river was calculated as a sum of two annual indices of growth opportunity preceding the year of the smolt migration.

2.3 Data from the sea phase

The annual recovery rate and migration patterns of the postsmolts were analysed on the basis of tag recaptures of Carlin-tagged salmon reported by fishermen along the migration routes of salmon in the Baltic Sea and in the river. Data on tag recoveries were compiled by the Finnish Game and Fisheries Research Institute's tagging office (I–V).

The proportion of recaptured salmon was considered to indicate the survival of the tagged fish. This is correct if natural mortality largely occurs during the first sea year. In the Baltic Sea, postsmolt mortality is highest, commonly > 80%, during the first few months at sea before the young fish are recruited in late autumn to the salmon fishery (Christensen & Larsson 1979, Salminen *et al.* 1995, Kallio-Nyberg *et al.* 2006). Thus, the tags recovered and returned by fishermen reflect the success of the tagged fish after natural mortality. In the salmon fishery in the Baltic Sea, offshore fishing with driftnets and longlines predominated during the second half of the 20th century, but its effort and proportion of the total catch has gradually decreased. At the same time, the importance of coastal and river fishing has increased. The changes in salmon fishing have been gradual, but the considerable interannual and spatial covariation in the abundance of salmon populations indicates the importance of postsmolt survival as one of the major factors affecting these fluctuations (Karlsson & Karlström 1994, McKinnel & Karlström 1999) (V).

The changes in fishing and catches have affected the wild salmon stocks in the northern Gulf of Bothnia and possibly also their reported recapture rates (see Jutila *et al*. 2003*a*, Romakkaniemi *et al*. 2003). However, based on the data on salmon fishing in the Baltic Main Basin and in the Gulf of Bothnia, no significant relationship was found between the recovery rate of tagged Simojoki salmon and the cumulative catch of salmon in three consecutive years after the year of their sea entry in 1972–2004 ($P = 0.057$) or between the recovery rate and the cumulative total effort of the salmon fishery in three consecutive years after the year of their sea entry ($P = 0.235$) (II).

Data on the sea surface temperature (SST) prevailing off the Simojoki river during the main smolt run season in June measured at the Islands of Krunnit (I, III*)* and later in July in the southern Gulf of Bothnia at the islands of Valassaaret and Seili were provided by the Finnish Institute of Marine Research (V). A map illustrating the distribution of sea surface temperatures in the Gulf of Bothnia in June 2005 was obtained from the websites of the Swedish Meteorological and Hydrological Institute (IV).

The estimations made by ICES of 0+ herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) abundances in the Bothnian Sea were used in analysis of the survival of wild and reared tagged groups of salmon (ICES 2000, E. Aro, Finnish Game and Fisheries Research Institute, pers. comm. 2003) and were log-transformed before analysis. In addition, the seasonal North Atlantic Oscillation (NAO) index in May-July was included in the analysis (http://www.cgd.ucar.edu/~jhurrell/nao.html) (V).

3. Results and discussion

3.1 Timing of the smolt migration

Experimental evidence suggests that among juvenile salmon the timing of the seaward migration is seasonal and governed by an endogenous, circannual rhythm (Eriksson & Lundqvist 1982, Lundqvist & Eriksson 1985). The photoperiod is considered to be the most important environmental factor synchronizing annual patterns of physiology and behaviour of salmonids (Eriksson *et al*. 1982). Changing day length thus probably functions as an ultimate trigger and the environmental conditions such as water temperature, discharge and turbidity serve as proximate triggers controlling the smolt run in different rivers (Jonsson 1991, McCormick *et al*. 1998, Whalen *et al*. 1999). However, as the increase in day length occurs equally from year to year it cannot cause the annual variations in smolt run timing (I).

In the Simojoki river, the onset of the smolt run was significantly positively correlated with the rising river water temperature ($P < 0.001$), a rise above 10 °C being the main proximate environmental triggering factor (I). The warming of river water in the spring is probably the most sensitive ecological cue to guide the smolt migration and to synchronize it with tolerable environmental conditions in the sea. These results are very similar to those recorded in the Swedish Rickleå and Umeå rivers, the central Gulf of Bothnia, where the smolt run also started when the river water temperature rose above 10 °C (Österdahl 1969, Lundqvist & Eriksson 1985, Fängstam *et al*. 1993). Studies in Atlantic rivers have also shown that water temperature commonly triggers the onset of smolt emigration, although the temperature at which migration occurs may vary between rivers (Solomon 1978, Jonsson & Ruud-Hansen 1985, Jonsson 1991, Hvidsten *et al*. 1998, Veselov *et al*. 1998, Erkinaro *et al*. 1998).

There was also a significant positive correlation (P = 0.035) between the decreasing river discharge in the spring and the onset of the smolt migration (I). Although the discharge in the Simojoki river declines considerably during the spring, it did not correlate with smolt migration as clearly as temperature. This may be because the discharge decreases gradually with no exact threshold value that could be associated with, for instance, a distinct survival advantage due to decreased predation. Although not studied in this connection, the turbidity of the river water is also highest during the spring flood, gradually declining with decreasing discharge, but without any rapid change that could explain the onset of the migration.

The duration of the main smolt run was significantly (P < 0.001) shorter in years when the onset of the run was delayed (I). A similar compression of the smolt run in springs with a late water warming was also observed in the Varzuga river (Veselov *et al*. 1998). This may be connected with the smoltification process, which continues through the spring (Virtanen 1987). The later the run is postponed, the greater is the proportion of smolts that are ready to migrate. This phenomenon also results in an arrival time in the sea that is annually less variable than the onset of the smolt run in the river.

McCormick *et al*. (1998) have stated that smolt survival is affected by a limited period of readiness (a physiological “smolt window”) and by the timing of seawater entry controlled by environmental conditions such as temperature, food and predators (an ecological “smolt window”). In terms of the physiological “smolt window”, the smoltification process takes place in spring in the river. The ecological “smolt window” also first opens in the river, allowing smolt migration, and in the Simojoki river it seems to largely be controlled by the thermal conditions in the river (I). The results of Simojoki salmon concur with the conclusions of Hansen & Jonsson (1989) and Hvidsten *et al*. (1998), who noted that smolts leave the river when the marine conditions are optimal or at least tolerable to begin the feeding migration in the sea, and the timing of the smolt migration in salmon rivers may be adapted through natural selection to the prevailing environmental conditions in each area. The optimal timing of the smolt run could also be related to the avoidance of predators in the river or at the river mouth (Lindroth 1955, Larsson 1985, Hansen & Jonsson 1989).

3.2 Changes in smolt size and age

3.2.1 Interannual changes

In 1972–2004, the annual mean smolt size was found to negatively depend on the density of wild >1 yr parr in the previous autumn (smolt length P = 0.009, smolt weight P = 0.018). Even though smolt length was also negatively dependent (P = 0.003) on the combined density of >1 yr wild and hatchery-reared parr, the density of reared parr released in the river did not alone considerably affect the smolt size in the following spring. Moreover, neither the growth opportunity, based on the day length and air temperature during the two previous summers, nor the annual mean smolt age significantly affected the size of wild smolts (II).

In the Simojoki river, the growth of salmon parr appears to be density-dependent. During the study period, the density of wild >1 yr parr increased significantly. The mean density of wild salmon parr was until the late 1990s very low, mostly only 1–3 parr 100 m^{-2}, but varied after that between 7 and 17 parr 100 m^{-2}. Before the increase in parr density there was probably only minor intraspecific competition. The strengthening of regulations in the salmon fishery in 1996 resulted in increased numbers of spawners ascending the river, and parr density also rose manyfold (Jutila *et al*. 2003*a*, Romakkaniemi *et al*. 2003). Intraspecific competition became apparent and has been manifested in a reduced size of wild smolts since the late 1990s. These results are consistent with several studies showing density-dependent growth among stream-dwelling salmonids (e. g. Bergheim & Hesthagen 1990, Bohlin *et al.* 2002, Lobón-Cerviá 2005*a*, 2005*b*, Imre *et al*. 2005). In a study by Grant & Imre (2005) based on literature data on 19 populations, 15 of them showed a significant decrease in growth rate with increasing density. Their results also supported the hypothesis that density-dependent growth in stream salmonids primarily occurs at low population densities, as was the case in the Simojoki river. It is also probable that the wild parr may have had the advantage of being prior residents in the river (Harwood *et al.* 2003) and that the stocked parr have mainly been able to occupy only secondary territories.

On the basis of experimental data for maximum growth and food consumption from five Atlantic salmon rivers, Jonsson *et al.* (2001) estimated optimum temperatures for the growth of juvenile salmon to be between 16 and 20 °C. Metcalfe & Thorpe (1990) have suggested that the index of growth opportunity is able to explain differences in mean smolt age between different salmon rivers. In the Simojoki river, however, the annual climatic conditions represented by the index of growth opportunity did not significantly affect the size of the wild smolts. In the River Margaree, Canada, where no one-year-old smolts were produced, Strothotte *et al.* (2005) also found that water temperature differences during the growing season were insufficient to explain the differences in growth rates and size among the sites sampled. It is possible that the index of growth opportunity may lack some important information in monitoring interannual temperatures within a river. In particular, it ignores the growth taking place at low winter temperatures (Koskela *et al*. 1997, Finstad *et al*. 2004) and also the period of rapid growth in early summer when high assimilation is accompanied by low temperatures and maintenance rates (Jones *et al*. 2002). It also possibly misinterprets the period of highest summer temperatures, when the water temperature exceeds the optimal range for growth.

3.2.2 Seasonal changes

Seasonal differences in the smolt traits were investigated among wild smolts caught by smolt trapping in 1991–2004. The annual trapping season was split in two halves based on the median catch date. The mean smolt length was generally significantly larger and the mean smolt age always significantly higher during the first half of the season than during the second half, while differences in weight were mostly insignificant. The higher mean age and length of smolts during the first half of the smolt run, observed in most years of the study, indicates that the largest and oldest presmolts tend to smoltify first (III). This is common among anadromous salmonids. For example, in the Swedish river Rickleån in the Gulf of Bothnia, older salmon smolts migrated earlier during the smolt run than younger ones (Österdahl 1969). Similarly, Dunkley (1986) reported that smolt age in the River North Esk appeared to decrease as the smolt run advanced. In their studies in southern Sweden, Bohlin *et al*. (1996) observed that those sea trout parr that were bigger in early winter tended to migrate earlier in the following season and at larger body size than initially smaller fish. Thus, the length of migrating smolts decreased with time during the migration season. Our results agree with their conclusion that rapidly-growing individuals tend to migrate younger and at a smaller size but later in the season, while more slowly-growing fish migrate at a bigger size and later in life but earlier in the season.

Many smolts migrating during the early season and almost all smolts migrating later had started their new annual growth in the river, which indicates that smolts frequently grow in the spring in the river before sea entry. Particularly the youngest and smallest presmolts had grown in the spring, which may be a precondition for attaining the smolt status (III). In the River

Rickleån in Sweden, Österdahl (1969) also reported that the smolts migrating at the end of the season commonly had wide plus-zones in their scales.

Experimental studies have confirmed that growth of salmon juveniles takes place in low water temperatures (1–6 ^{o}C) among winter-acclimatised fish (Finstad *et al*. 2004), the estimated lower temperature limits for feeding and growth for 1+ Baltic salmon being 0.35 ^{o}C and 0.6 ^{o}C, respectively (Koskela *et al*. 1997). Jones *et al*. (2002) have observed that maximal growth occurs early in the season when high assimilation of food is accompanied by low temperatures and low maintenance rates. A study of wild Atlantic salmon parr in the Girnock Burn, Scotland, by Bacon *et al*. (2005) also revealed that appreciable growth can take place in late winter and early spring before smolts leave the stream. Simpson & Thorpe (1997) suggested that the appetite of Atlantic salmon parr peaks in May with the rising ambient temperature and parallels the numbers of optimally-sized drifting prey. The results observed in the Simojoki river are consistent with the conclusion of Bacon *et al*. (2005) that smolts do not always need to achieve their required growth during the previous summer.

In the River Rickleån, Österdahl (1969) also reported that smolts actively fed during their seaward migration. He stated that evolutionally the smolt migration is a feeding migration, which takes place in spring when there is a great abundance of food in the river offered by hatching insects. Active feeding of migrating smolts has also been recorded in other Baltic and Atlantic rivers in the spring (e.g. Mitans 1970, Garnås & Hvidsten 1985, Heinimaa & Erkinaro 1999). In the Simojoki river, migrating smolts commonly have aquatic insects in their stomachs, especially in late spring (E. Jutila unpubl.), when benthic macroinvertebrates are abundant in Finnish rivers (Haapala & Muotka 1998).

The results observed from the Simojoki river suggest that smolts in the northern Baltic salmon rivers frequently start new growth before their sea entry. The new growth in spring in the river especially enables the youngest smolts to migrate late in the season. The widespread occurrence of this phenomenon suggests that it has an essential role in the annual smoltification process and in the smolt production capacity of salmon rivers.

3.3 Migration patterns of postsmolts

3.3.1 Postmolt migration in the estuary

In 1972–2005, the tag recoveries of wild salmon in the estuary within 10 km from the river mouth (see Fig. 2c) were reported on average 3.5 days after release, the time required for emigration from the estuary being negatively dependent on the SST off the river (P = 0.004) (IV). The results indicate that most of the postsmolts probably do not swim straight out of the estuary or that they are not actively moving all through the day. In Norway, Thorstad *et al*. (2004) observed that postsmolts were actively swimming in the estuary area and not only passively drifting along the current. However, they were moving in random directions in relation to the water current (Økland *et al*. 2006). On average, Simojoki postsmolts remained in the estuary almost three times longer than would have been needed for passive drifting straight through the area.

Carlin-tagging data with a time resolution of one day were rather scarce in the estuary area, but the study included observations from several years and releases carried out throughout the annual smolt run season. Thus, they probably describe well the general pattern of postsmolt migration within the 10 km of the estuary area, while a pilot study using acoustic transmitters and manual tracking within 3 km from the river mouth showed a much higher speed (1.7 body length s^{-1} or 25.2 km d^{-1}) (see Hyvärinen *et al.* 2006). A similar difference between the seaward movement measured with manual tracking and the recorded emigration from the estuary was observed in the Romdalsfjord system in Norway (Thorstad *et al.* 2007). In studies using ultrasonic transmitters, the mean migration speed of wild postsmolts was 1.2 body length s^{-1} or 15.5 km d^{-1} by manual tracking (Økland *et al.* 2006), while wild salmon postsmolts passed receivers at 9.5 km distance on average 135 h (5.6 days or 1.7 km d^{-1}) after their release (Thorstad *et al.* 2007).

The emigration of postsmolts from the Simojoki estuary was clearly more rapid than the mean migratory speed of 1.6 km d^{-1} in the fjord off the River Imsa, Norway, reported in Carlin-tagging of hatchery-reared smolts (Jonsson *et al*. 1993). Contrary to the non-tidal Baltic Sea, however, the tidal currents in the estuary of Atlantic rivers may affect the migration by delaying or accelerating the emigration to the open sea (Fried *et al*. 1978, Lacroix & McCurdy 1996).

3.3.2 Postsmolt migration in the sea

After leaving the estuary, the postsmolts migrated southwards along the eastern coast of the northern Gulf of Bothnia, the reported tag recoveries coinciding with the warm thermal zone in the SST occurring along the coastal area. When they arrived in the southern Gulf of Bothnia in late summer the postsmolts mostly migrated near the western coast, reaching the Baltic Main Basin in late autumn (IV, Ikonen 2006).

Outside the Simojoki estuary in the Gulf of Bothnia, the warming of the sea surface after ice melting is more rapid near the shores. The central parts of the Bothnian Bay commonly remain cold (< 8 °C) until late June, while clearly separated zones of warm surface water exist along the coast in spring and early summer (Kullenberg 1981). When salmon postsmolts from the northern stocks are migrating southwards they probably utilize the warmer thermal channel along the shores of the Bothnian Bay (IV, Ikonen 2006). In a study by Holm *et al.* (2000) in Norway, all the captures of Atlantic salmon postsmolts also occurred in a relatively restricted water mass, mostly within the temperature interval between about 9 and 11 °C.

The migration patterns of the Simojoki postsmolts were rather similar to those observed by Larsson & Ateskhar (1979) in Swedish tagging experiments on reared salmon smolts in the Gulf of Bothnia. Most tag recoveries of postsmolts occurred along the coasts of the Bothnian Bay and the Bothnian Sea. However, the prevalence of migration in the open sea is uncertain because fishing, which produces most of the recoveries, is concentrated close to the Finnish and Swedish coast of the Gulf of Bothnia. As salmon postsmolts seem to migrate in upper water layers in the sea (Soikkeli 1973, Jutila & Toivonen 1985, Holm *et al*. 2000, 2003), tag recoveries of postsmolts in the offshore areas are unlikely because offshore fishing for herring is commonly performed with bottom trawls and postsmolts are difficult to detect in the catches due to the large catch volumes.

3.4 Factors affecting postsmolt survival

3.4.1 Smolt size

During the period extending from the 1970s until the early 1990s, there was only a weak nonsignificant positive association between the smolt length and survival of wild smolts of Simojoki salmon, while a significant positive dependence of the postsmolt survival on smolt length ($P < 0.01$) was found among hatchery-reared Simojoki salmon (V). After a decrease in the mean smolt size since the early 1990s, a significant positive dependence of the recapture rate on smolt length ($P = 0.004$) and weight ($P = 0.010$) could also be detected among wild smolts of Simojoki salmon (II).

A higher marine recapture rate of wild salmon smolts than that of reared salmon has been reported both for Baltic salmon (e.g. Toivonen 1977, Saloniemi *et al*. 2004, Jokikokko *et al*. 2006) and for North Atlantic salmon (Jonsson *et al*. 1991). Among hatchery-reared salmon in the Bothnian Bay rivers, the recapture rate of large smolts released in the Ume river was higher than that of the small ones (Lundqvist *et al*. 1994), and among Iijoki and Oulujoki (Montta) salmon it gradually increased with increasing smolt length (Kallio-Nyberg *et al*. 2006). The differences in postsmolt survival between size classes are mainly attributed to their different abilities to withstand unfavourable environmental conditions (Salminen *et al*. 1994, 1995). A large smolt size has also been suggested to decrease the risk of size-dependent predation (Skilbrei *et al*. 1994). Wild fish are more likely to avoid predators than reared ones (Johnsson & Abrahams 1991). A large size might therefore be more important for hatchery-reared smolts in reducing predation pressure. However, the results from the Simojoki river (II) indicate that when the size of wild smolts significantly decreased, a positive association between smolt size and survival also appeared to prevail among them.

Differences in recapture rates between smolts tagged during the first and second half of the smolt run seemed to be insignificant. Accordingly, although variations in smolt traits and environmental conditions can produce interannual variation in postsmolt survival, their seasonal differences appear to be too small to have an effect or are masked by other sources of variation (III). It is probable that the increased density of wild >1 yr parr has contributed to the decreased smolt size in the Simojoki river since the late 1990s, and the reduced size of wild smolts could be involved in the simultaneous declining trend in postsmolt survival observed among wild salmon in the Baltic Sea (II).

3.4.2 Climatic factors

The results obtained for the Simojoki salmon suggest that the favourable development of the SST in spring and summer is in many ways essential for the survival of postsmolts in the Gulf of Bothnia. Among postsmolts, the time required for emigration from the estuary was significantly ($P = 0.004$) dependent on the SST off the river, being shorter in years with warm than cold temperatures. In late or cold springs, the seawater remains cold for a long period and postsmolts cannot find warm water layers in the sea (IV). On the Swedish coast of the Bothnian Bay, Larsson (1985) suggested that estuary predation by pike (*Esox lucius* L.) and burbot (*Lota lota* L.) significantly affected the postsmolt survival of salmon in the Lule river. In the Finnish rivers of the Bothnian Bay, the pike is the main predator for salmon smolts (Kekäläinen *et al*. 2008), and its population is also abundant in the estuary of the Simojoki river. The predation risk may thus be higher and a reduced survival of postsmolts may be possible in a cold spring when postsmolts remain several days longer in the estuary than in a warm one.

The relationship between the survival of Carlin-tagged wild smolts and the SST in June off the river mouth appeared to follow a dome-shaped pattern (I). The survival of postsmolts was significantly ($P = 0.02$) lower in cold early summers (SST < 9 ºC) than in those with an average SST (9–11.9 ºC), and lower again, although not significantly, in warm early summers (SST ≥ 12 ºC). The long-term average SST in June in the northern Gulf of Bothnia (10 °C) is also within this optimal range of 9–12 °C. Given an adequate food supply, the growth of salmonids increases within a given range linearly with water temperature (Brett 1979). Therefore the lower survival in cold water temperatures may be due to the unfavourable temperature for growth, resulting in an increased vulnerability of postsmolts to predation. Friedland *et al*. (2003) concluded that one possible explanation for the poor postsmolt survival associated with a warm spring could be that growth may be slower at higher temperatures if food is limited, because a higher temperature is often associated with increased basic metabolic demands. At higher temperatures postsmolts may also require increased swimming to seek optimal thermal conditions after their sea entry. Water temperatures that are too low and probably also too high in early summer could thus be among the factors affecting fluctuations in the postsmolt survival of salmon in the Baltic Sea.

Later in summer the postsmolts migrate southwards in the Gulf of Bothnia. In the Bothnian Sea, the SST in July significantly ($P = 0.004$) explained the survival of wild salmon postsmolts, which was better in warm than in cold summers (V). A similar positive relationship between SST prevailing in the migration area in summer and postsmolt survival was also observed among hatchery-reared Simojoki salmon (V), among hatchery-reared Neva salmon released in the Bothnian Sea area (Salminen *et al*. 1995), among hatchery-reared salmon released in the estuaries of Oulujoki and Iijoki rivers in the Bothnian Bay (Kallio-Nyberg *et al*. 2006) and among wild Atlantic salmon stocks migrating in the North Sea (Friedland *et al*. 1998). To a lesser extent, a positive NAO index in May to July was also positively related to the survival of hatchery-reared Simojoki salmon, but not to that of the wild ones. If the incidence of extreme thermal conditions were to increase due to climatic changes, it could reduce the postsmolt survival of wild salmon stocks in the Baltic Sea.

3.4.3 Prey abundance

During their migration along the coast of the Bothnian Bay, postsmolt salmon in early summer mainly eat airborne winged insects on the sea surface (Jutila & Toivonen 1985). After leaving the estuary, the postsmolts appear to follow the warm thermal zone in the SST occurring along the coastal area (IV), where the probability of predation on airborne insects is also greatest. In the sea, wild postsmolts probably continue feeding on surface fauna similarly to the way they forage earlier in the river. The low survival rate of wild postsmolts in cold springs may be caused by the limited availability of surface prey in those years. Hatchery-reared smolts are not used to preying on living animals, which may partially explain their lower survival compared to wild smolts. On the other hand, hatchery-reared smolts are larger than the wild ones (hatchery-reared smolts about 200 mm, wild smolts about 150–160 mm in the Simojoki river) and are therefore able to change to piscivory earlier than wild smolts.

The postsmolts reach the Bothnian Sea in July (IV). There, in late summer, they are able to feed on 0+ herring, which are their main food items in the Bothnian Sea (Salminen *et al.* 2001). In years with good herring recruitment a great proportion of the hatchery-reared postsmolts, especially the larger ones, remain to feed in the Bothnian Sea (Salminen *et al*. 1994, Kallio-Nyberg *et al.* 1999), while smaller wild smolts continue their migration, arriving in the Baltic Main Basin in late autumn (Jutila *et al*. 2003*b*). A weak nonsignificant positive association was found between prey fish abundance (0+ herring) in the Bothnian Sea and the survival of wild Simojoki salmon tagged in 1972–1993. Similarly, a weak positive nonsignificant relationship was also detected between the abundance of 0+ herring in the Bothnian Sea and the survival of hatchery-reared smolt groups of Simojoki salmon (V).

The abundance of prey fish (0+ herring and sprat) in the Baltic Main Basin had no influence on the survival of wild or reared smolt groups (V). This may indicate that postsmolt mortality mainly occurs in the Gulf of Bothnia during the first summer before postsmolts reach the Main Basin.

The effects of the SST and prey fish abundance on postsmolt survival are difficult to separate, because in the Bothnian Sea, for example, the SST in summer and the abundance of 0+ herring are positively correlated (V). It is therefore possible that the favourable effects of an increasing SST on the postsmolt survival of salmon are partially mediated by the positive impact of the warm SST on prey fish abundance.

4. Conclusions

Long-term monitoring of fish populations and the aquatic environment is important in assessing the changes and causal links between fish and their environment. The results of this study support the conception that the timing of migration and smolt traits in a salmon river are adapted through natural selection to the prevailing average thermal and feeding conditions at sea (I). The results also indicate that climatic factors, independently or linked with the coastal ecology of salmon and the recruitment of prey organisms, may at least partly regulate the postsmolt survival of the wild stocks of Atlantic salmon in the Gulf of Bothnia (I, V). Therefore, if the incidence of extreme weather conditions were to increase due to climatic changes, it would probably reduce the postsmolt survival of wild salmon populations and thus endanger their maintenance.

The survival of wild postsmolts has since the late 1990s been significantly lower than in earlier years, and the decreasing trend has been even more obvious among hatchery-reared smolts (see Michelsiens *et al*. 2006). Several studies have suggested that the larger size of hatchery-reared smolts partially compensates for their lower survival compared with wild ones. On the other hand, despite the smaller size of wild smolts their survival rate has been at least twice as high as that of their much longer and fatter hatchery-reared counterparts (V). In the Baltic Sea area, predatory fish in the estuary are mainly the same species as wild smolts become used to avoiding in the river. Before sea entry, wild smolts have commonly started to prey on aquatic and surface insects, which are their main food items during the first weeks or months in the sea. Hatchery-reared smolts are larger and fatter than wild smolts, and they are not used to avoiding predators or preying on living animals. In order to improve the performance of hatchery-reared juveniles, it could be useful to examine opportunities to produce hatchery-reared smolts that are more similar to the wild smolts described in this thesis. Some recent studies may provide new perspectives on this question, for example, those on antipredator conditioning (Hirvonen *et al*. 2003, Vilhunen 2006) and exercise programmes for achieving an optimal oxidative swimming capacity in smolts (Anttila *et al*. 2006).

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