

Association between environmental factors, smolt size and the survival of wild and reared Atlantic salmon from the Simojoki River in the Baltic Sea

I. KALLIO-NYBERG*†, E. JUTILA‡, I. SALONIEMI§
AND E. JOKIKOKKO¶

*Finnish Game and Fisheries Institute, Quark Fisheries Research Station, Korsholmanpuistikko 16, FI-65100 Vaasa, Finland, †Finnish Game and Fisheries Institute, P. O. Box 6, FI-00721 Helsinki, Finland, §Department of Biology, Section of Ecology, University of Turku, FI-20014 Turku, Finland and ¶Finnish Game and Fisheries Institute, Bothnian Bay Fisheries Research Station, Jenessintie 2, FI-95200 Simo, Finland

(Received 11 July 2003, Accepted 26 March 2004)

The survival of Atlantic salmon *Salmo salar* in the Baltic Sea was examined in relation to smolt traits (length and origin) and annual environmental factors [sea surface temperature (SST) and seasonal North Atlantic Oscillation (NAO) index], and prey fish abundance (herring *Clupea harengus* and sprat *Sprattus sprattus*) in the main basin and the southern Gulf of Bothnia. The study was based on recapture data for Carlin-tagged hatchery-reared and wild smolts from the Simojoki, a river flowing into the northern Gulf of Bothnia. The survival of the wild and reared groups was analysed using an ANOVA model and a stepwise regression model, with the arcsin-transformed proportion of recaptured fish as the response variable. The results demonstrated a combined influence of smolt traits and environmental factors on survival. For the reared Atlantic salmon released in 1986–1998 (28 groups), the increasing annual mean SST in July in the southern Gulf of Bothnia and increasing mean smolt size improved survival. If the SST in July was excluded from the model, the NAO index in May to July also had a positive effect on survival ($P < 0.10$). The \log_{10} -transformed abundance of 0+ year herring in the southern Gulf of Bothnia entered the model ($P < 0.15$) if the SST and NAO index were excluded. For the wild Atlantic salmon released in 1972–1993 (21 groups), only the increasing SST in July showed a significant association with improved survival ($P = 0.004$). Prey fish abundance in the main basin of the Baltic Sea had no influence on the survival of reared or wild smolt groups. The interaction between smolt size and the SST in July was not significant. The origin was a better, but not a significant, predictor of marine survival compared to the smolt size or the SST in July. The mean recapture rate of the wild groups was twice that of the reared groups in the whole data. The results suggest that cold summers in the Gulf of Bothnia reduce the survival of young Atlantic salmon in both wild and reared groups. The larger smolt size of the reared groups compared with the wild groups to some extent compensated for their lower ability to live in the wild.

© 2004 The Fisheries Society of the British Isles

Key words: Atlantic salmon; NAO index; prey fish abundance; sea surface temperature; smolt size; survival.

†Author to whom correspondence should be addressed. Tel.: +358 205 751 678; fax: +358 205 751 679; email: irma.kallio-nyberg@rktl.fi

INTRODUCTION

Atlantic salmon *Salmo salar* L. show long-term fluctuations in survival, sea age at sexual maturity and in size at age in the Atlantic Ocean (Friedland *et al.*, 2000) and in the Baltic Sea (Alm, 1934; Lindroth *et al.*, 1982; McKinnell & Karlström, 1999). The survival of Atlantic salmon in nature is linked with annual environmental factors (Salminen *et al.*, 1995; Friedland *et al.*, 1998) and with adaptive genetic variation (Jonsson *et al.*, 1991; Fleming *et al.*, 2000). Atlantic salmon mortality is highest in the post-smolt period during the first few months at sea (Salminen *et al.*, 1995). In this phase, young fish are sensitive to variable environmental factors such as sea surface temperature, the North Atlantic Oscillation (NAO) and to food availability (Friedland *et al.*, 1993, 2000; Salminen *et al.*, 1995; Holm *et al.*, 2000). Oceanographic and ecological changes in the Baltic Sea are affected or controlled by climatic factors in the Atlantic (Hänninen *et al.*, 2000).

Many rivers draining into the Baltic Sea still support their native stocks of Atlantic salmon, although much fewer than before the 20th century. These stocks have adapted to the prevailing environmental conditions and to the brackish water of the Baltic Sea (Lindroth *et al.*, 1982). All these Atlantic salmon stocks, of both wild and reared origin, migrate to common feeding areas (Christensen & Larsson, 1979; Koljonen & McKinnell, 1996), and are affected by the same climatic factors and food abundance (Kallio-Nyberg *et al.*, 1999). Two prey fish species in the main basin of the Baltic Sea, sprat *Sprattus sprattus* (L.) and herring *Clupea harengus* L., and herring in the Gulf of Bothnia dominate in the diet of Baltic *S. salar* (Karlsson *et al.*, 1999; Salminen *et al.*, 2001). Reared Atlantic salmon released as smolts have been found to have a lower sea survival than wild fish (Österdahl, 1969; Jonsson *et al.*, 1991; Jonsson, 1997).

The observed correlation in the tag recovery rate between different Atlantic salmon stocks in the Baltic Sea (McKinnell & Karlström, 1999) suggests that common factors affect their survival rates in the critical post-smolt phase. After entering the sea, Atlantic salmon post-smolts feed on surface fauna, mainly consisting of terrestrial insects. These also comprise their main food items during the early summer when they move along the Finnish coast against the main sea current into the southern Gulf of Bothnia (E. Jutila, pers. comm.). From late summer onwards, herring is the most important fish prey for post-smolts and for older Atlantic salmon remaining to feed in the southern Gulf of Bothnia (Salminen *et al.*, 1995, 2001). The Atlantic salmon stocks of rivers entering the northern Gulf of Bothnia undergo a long migration to their primary feeding areas in the southern and central Baltic main basin. The marine feeding migration of Atlantic salmon normally lasts 1–4 years before they return to their home river to spawn. A variable, but relatively small, proportion of Atlantic salmon remain to feed in the southern Gulf of Bothnia, (Bothnian Sea) (Salminen *et al.*, 1994).

The results of Atlantic salmon stocking in the Baltic Sea have been found to vary considerably from year to year with a high spatial and temporal covariation in the abundance among the populations (McKinnell & Karlström, 1999; McKinnell & Lundqvist, 2000). This indicates that several common factors such

as environmental conditions affect the survival of the fish stocks migrating within the same sea area. This all supports the suggestion that long-term data from a single Atlantic salmon stock might be used as an index to describe the success and the population fluctuations of the Atlantic salmon stocks on a larger scale (McKinnell & Karlström, 1999). In the northern Baltic Sea, such data are available from the wild and reared Simojoki *S. salar* smolts tagged in 1972–1998. The survival of fish was studied in relation to environmental factors (the annual sea surface temperature, seasonal NAO), prey fish abundance and smolt traits (smolt size and origin). Furthermore, the focus was on establishing whether there is any interactive effect of smolt size and environmental factors on the survival of stocked smolts. The dependences were analysed both separately for the reared and wild Atlantic salmon groups and for both groups combined in the tagging years when both groups were represented.

MATERIALS AND METHODS

BALTIC SALMON STOCK

The River Simojoki (25°00' E; 65°38' N) flows into the Gulf of Bothnia in the northernmost part of the Baltic Sea (Fig. 1). This river supports a native and genetically differentiated Atlantic salmon stock (Koljonen, 1989). Since the late 1970s, however, the natural stock of Simojoki fish has become endangered because of decreased spawning stock and natural smolt production due to the intensive mixed-stock Atlantic salmon fishing carried out in the Baltic Sea. In addition, the extensive dredging of rapids for floating logs in the 1950s and 1960s reduced the quantity and quality of Atlantic salmon spawning areas. The effects of dredging on the river have later been mitigated with restoration works. In efforts to protect the natural stock from extinction, the river has been stocked with reared smolts and parr to increase smolt production (Jutila & Pruuki,

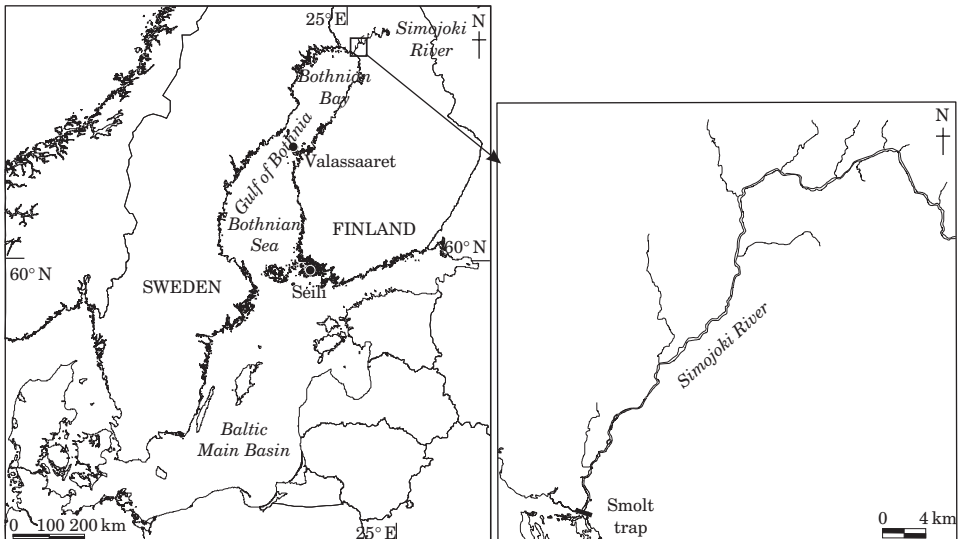


FIG. 1. Map of the Baltic Sea showing the location of the Simojoki River and the site of the smolt trap. The locations of the Valassaaret and Seili stations are also indicated. The northern Gulf of Bothnia = Bothnian Bay; the southern Gulf of Bothnia = Bothnian Sea.

1988). The released reared juveniles have been offspring of the natural stock, and no genetic differences have been found between the reared and wild smolts (Koljonen, 1995).

TAGGING EXPERIMENTS

The wild and hatchery-reared Atlantic salmon groups that were compared originated from a common stock but had a different juvenile life history. The wild groups had spent their whole juvenile period in the natural river environment. They were sampled in spring during their smolt migration by means of a smolt trap installed at the river mouth (Fig. 1). The smolts were carefully removed from the trap and then measured (total length, L_T) and Carlin-tagged under anaesthesia (MS-222 or benzocaine). After keeping them in a recovery cage, they were released on the following day to continue their migration towards the sea. The reared smolts were mainly raised in hatcheries situated on the Simojoki or neighbouring rivers. After hatching, the fingerlings were normally reared for the first summer in fibreglass tanks in a rearing hall and thereafter outdoors in concrete tanks until stocking as 2 year-old smolts. The fish were fed pelleted dry feed at the ambient water temperature and photoperiod (65°38' N).

Tagging was performed in cold water (<4°C) in the hatchery during the winter preceding the release. The fish were tagged with individually numbered Carlin tags. In spring, the reared smolts were released in the river in late May to early June, during the migration season of wild smolts. The reared smolts were transported to the river by lorry in aerated tanks and usually released into two or three rapids c. 50 and 100 km from the river mouth. Exceptionally, one group of reared smolts was also tagged in 1991 and 1993 at the trap after a short downstream migration from the release site.

Analysis was performed on the tag recovery data reported by fishermen. Both wild and reared Simojoki fish migrate in the same sea areas (Juttila *et al.*, 2003a). Neither offshore nor coastal fisheries select Atlantic salmon in relation to their origin (Koljonen & McKinnell, 1996). Therefore, the returned tags represent an unselected sample of the adult fish that survived to fishing size.

STATISTICAL METHODS

The Simojoki Atlantic salmon included in this study were tagged as smolts during 1972–1998 and comprised 21 groups of wild and 28 groups of reared fish (Fig. 2). Most of the wild groups (15 out of 21) were tagged in different years from the reared

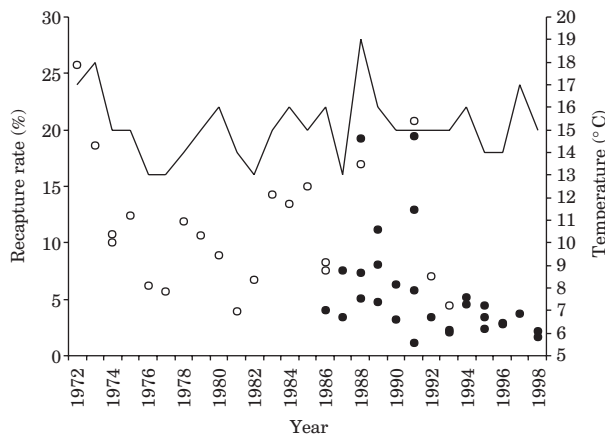


FIG. 2. The recapture rates of tagged and released wild (○; $n=21$) and reared (●; $n=28$) Simojoki Atlantic salmon groups in 1972–1998. The mean sea surface temperature in July in the Bothnian Sea (—) is also given.

counterparts. The association between Atlantic salmon survival and annual environmental factors was examined separately for the wild and reared groups and together for both origin groups (Fig. 2). In addition, the wild groups tagged in 1980–1993 (12 groups) were analysed both separately and together with the wild groups tagged in the 1970s (12 + 9 groups), because the wild smolts were tagged in the 1970s and both reared and wild ones in 1980s and 1990s. There were only 5 years (1986, 1988, 1991, 1992 and 1993) in which both origin groups were released. Using the six wild and 11 reared groups released in these years, the effect of origin on marine survival was also studied.

The proportion of recaptured fish in each group was assumed to indicate the survival of the group. This is correct if natural mortality mainly occurs during the first sea year, before the fish are subject to fishing mortality. In Atlantic salmon, natural mortality at sea is highest, >80%, in the first sea year (Lindroth *et al.*, 1982). The tags recovered and returned by fishermen thus reflect the success of the groups after natural mortality. In addition, the sea fishing of Atlantic salmon unselectively takes wild and reared fish as well as different stocks (Koljonen & McKinnell, 1996). In the Baltic Sea Atlantic salmon fishery, offshore fishing with driftnets and longlines has been dominant 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 Atlantic salmon fishing have mainly been gradual, but the considerable interannual spatial covariation in the abundance of Atlantic salmon populations indicates the importance of post-smolt survival as one of the major factors affecting these fluctuations (Karlsson & Karlström, 1994; McKinnell & Karlström, 1999).

Analysis was performed on the tagging groups, with the proportion of tag recoveries in each group being used as a response variable. These proportions were normalized using an arcsin-transformation. The data were analysed with the SAS statistical package (SAS, 1999) using the GLM and stepwise REG procedures. The mean smolt L_T of the group, sea surface temperature (SST), seasonal NAO index and prey fish abundances were used as explanatory variables. All variables left in the final model were significant at the 0.150 level. When the best explanatory variable was excluded, a new variable could now meet the 0.150 significance level and enter into the model.

Simojoki fish, like other Atlantic salmon stocks originating from the northern Gulf of Bothnia, migrate southwards as post-smolts, reaching the central parts of the Gulf of Bothnia in June and the southern parts in August (Salminen *et al.*, 1994). The annual sea surface temperature is likely to affect Atlantic salmon survival during the period of southwards migration and arrival of post-smolts in the southern Gulf of Bothnia (Fig. 3). Favourable temperatures for feeding and growth of Atlantic salmon in their

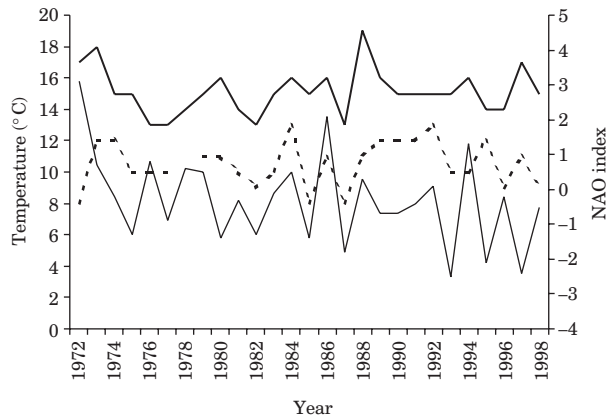


FIG. 3. Sea surface temperature (SST) in June (---) and July (—) in the Bothnian Sea and seasonal NAO index in May to July (NAOMJJ; —) in 1972–1998.

marine phase are in the range of 4–12°C (Saunders, 1993). The sea surface temperature was measured at a depth of 1 m by the Finnish Institute of Marine Research at two field stations in Seili and Valassaaret (Fig. 1). The monthly mean SSTs at these two stations were significantly correlated (Spearman correlation, $P < 0.002$ in June and $P < 0.004$ in July). One SST mean for June or July from these two sites was used in the analyses.

The seasonal NAO index in May to July was included as a factor to explain the survival of Atlantic salmon (index available at: <http://www.cgd.ucar.edu/~jhurrell/nao.html>). The NAO is a climate pattern associated with changes in the strength of surface westerly winds passing across the North Atlantic over Europe. Since 1865, the NAO index has been based on the difference in the normalized sea level pressure (SLP) between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland (Hurrell, 1995). The seasonal NAO index in May, June and July (NAOMJJ) used in this study describes the spring climate in Europe (Fig. 3). A positive seasonal NAO index in May to July means that westerly winds and a mild marine climate are dominant, while a negative seasonal NAO index in May to July means that a continental climate dominates. The SST (Valassaaret and Seili stations) in June or July and the NAO index in May to July were not significantly correlated (Spearman correlation, $P = 0.419$ June and $P = 0.230$ July) (Fig. 3).

The recruitment of suitable prey fishes, herring and sprat, in the Gulf of Bothnia and in the main basin may be important for Atlantic salmon post-smolt survival (Karlsson *et al.*, 1999; Salminen *et al.*, 2001). The abundance of 0+ year herring or sprat at the end of the year was included as an explanatory variable (Fig. 4). The recruitment of 0+ year herring in the southern Gulf of Bothnia correlated with the SST in June or July in the southern Gulf of Bothnia (Spearman correlation, $P = 0.044$ and $P = 0.023$ respectively). The estimations of 0+ year herring and sprat abundances presented in an ICES (2000) report were used in analysis of the survival of reared and wild groups released in 1980–1998 (12 wild groups tagged in 1980–1993, 28 reared groups tagged in 1986–1998). In addition, when the tagging of wild smolts carried out in the 1970s was also included, the most recent estimations of herring abundance in the southern Gulf of Bothnia were used in the analysis of wild Atlantic salmon survival (21 groups altogether in 1972–1993) (E. Aro, pers. comm.) (Fig. 4). The herring and sprat abundance estimates were \log_{10} -transformed for the analysis.

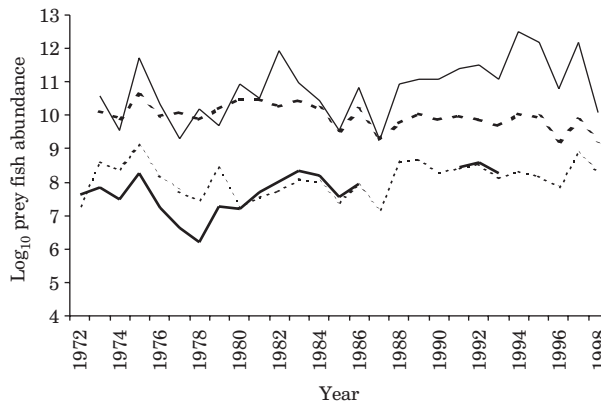


FIG. 4. Estimated abundance of 0+ year sprat (—) and herring (--) in the Baltic Sea main basin and two separate estimations of abundance of 0+ year herring in the Bothnian Sea (southern Gulf of Bothnia) (..., ICES 2000; —, E. Aro, pers. comm.). Prey fish abundance (million individuals) was \log_{10} -transformed.

RESULTS

RECAPTURE RATE

The mean recapture rate for the wild groups (12 groups) was about twice that of the reared groups (28 groups) (tagging experiments 1980–1998) (Table I). Tagged fish were mainly recaptured during the second and third year after release. Wild Atlantic salmon were recaptured later than reared fish (χ^2 test, $P < 0.001$) (Table I). The effect of the different tagging years on the duration of the sea migration was not, however, taken in account. Both origin groups were mainly recaptured in the main basin, but the wild Atlantic salmon were more frequently caught in the main basin than reared fish stocked as smolts (Table II). The reared and released smolts (17.5 ± 1.6 cm mean \pm s.d. L_T) were larger than wild smolts (15.5 ± 0.45 cm) (Kruskall–Wallis test, $P < 0.01$).

The mean recapture rate of the wild Atlantic smolt groups ($n = 9$) tagged in the 1970s was 10% (Table I). The mean smolt L_T of these groups was the same as that of the wild groups tagged in 1980–1993 (15.5 ± 0.43 cm).

The recapture rate of the wild Atlantic salmon groups ($n = 12$) showed no decreasing or increasing trend from 1980–1993 (regression analysis, $b = 0.18$, $P = 0.646$). Among reared Atlantic salmon groups the recapture rate followed a decreasing trend from 1986–1998 ($b = -0.55$, $P = 0.027$) (Fig. 2).

SURVIVAL OF REARED SMOLT GROUPS

Among the reared Atlantic salmon groups ($n = 28$), survival (the proportion of recaptured fish) was dependent on smolt length (ANOVA, $P < 0.01$) and sea surface temperature (SST) in July ($P < 0.01$) in the Bothnian Sea, the nearest feeding migration area. The model explained 36% of the variation in survival. The interaction between smolt size and SST in July was not significant. The model showed that the larger smolts tended to have higher survival rate. In addition, the higher sea surface temperature in the migration area of the young fish in July increased the survival of the reared Atlantic salmon.

When the survival of reared Atlantic salmon groups ($n = 28$) was analysed by stepwise regression, smolt L_T ($P = 0.007$, $r^2 = 0.24$) and the SST in July

TABLE I. Temporal distribution (n and %) of recoveries in origin groups (G) tagged in 1980–1998 and 1972–1979. Recovery rates (percentage) for the wild and reared Atlantic salmon groups are presented

Origin	G	n	Years after release						Tags (n)	Recovery rate (%)
			1	2	3	4	5	6		
Wild	n	12	28	240	419	102	12	21	7112	11.6
1980–93	%		3	29	51	12	2	3		
Reared	n	28	66	520	561	16	20	25	23439	5.5
1986–98	%		5	40	43	8	2	2		
Wild	n	9	61	164	453	109	14	21	8270	9.9
1972–79	%		7	20	55	13	2	3		

TABLE II. Spatial distribution of recoveries in the Baltic Sea in the second and third sea years in origin groups (G) tagged in 1980–1998. The number (n) of recoveries in two sea areas and the proportion (percentage) of recoveries in the main basin are presented. Differences in spatial sea distribution between origin groups in the second and third sea years were tested by the χ^2 -test

Origin	Year n	G n	Main basin n	Gulf of Bothnia n	Main basin %	P (χ^2 -test)
Wild	2	12	199	56	78	<0.001
Reared	2	28	294	227	56	
Wild	3	12	340	96	78	<0.05
Reared	3	28	369	152	71	

($P=0.042$, $r^2=0.36$) were accepted into the model, leaving the other explanatory factors, the SST in June, the seasonal NAO index, 0+ year herring and sprat abundance in the main basin and 0+ year herring abundance in the southern Gulf of Bothnia unused. The NAO index in May to July ($P=0.089$, $r^2=0.33$) entered into the model if the SST in July was excluded. The recruitment of 0+ year herring entered into the stepwise regression model ($P=0.107$, $r^2=0.32$) if all climate predictors were excluded.

SURVIVAL OF THE WILD GROUPS

No predictor was found to significantly influence the survival of the wild groups tagged in 1980–1993 (12 groups) when all factors were included, *i.e.* smolt L_T , the SST in June and in July, the NAO index in May to July and 0+ year herring and sprat abundance. Of all the predictors considered, only the SST in July was accepted into the stepwise regression model ($F_{1,10}$, $P=0.126$, $r^2=0.22$). Smolt L_T was accepted into the model when the SST in July was excluded ($F_{1,10}$, $P=0.146$).

In the wild groups ($9+12=21$) tagged in 1972–1993, the SST in July significantly explained their survival ($F_{1,17}$, $P=0.004$, $r^2=0.38$), but no other factor (SST in June, NAO index in May to June, age 0+ year herring or sprat abundance) was accepted into the stepwise regression model. When the SST in July was excluded from the model, the abundance of 0+ year herring in the southern Gulf of Bothnia ($P=0.105$, $r^2=0.16$) and smolt length ($P=0.148$, $r^2=0.26$) were accepted into the model ($F_{2,16}$, $P=0.087$). No other variable met the 0.150 significance level of entering into the model. The abundance of 0+ year herring in the southern Gulf of Bothnia was based on an estimation presented by ICES (2000) (see Fig. 4).

In the second stepwise model, in which 0+ year herring abundance in the southern Gulf of Bothnia was based on the most recent estimations (see Fig. 4) (E. Aro, pers. comm.), the results did not change. Only the SST in July significantly explained survival among the wild groups (21) ($F_{1,17}$, $P<0.004$).

The survival (proportion of recaptured Atlantic salmon) was significantly dependent on the SST in July, but not on the mean smolt L_T (GLM procedure: ANOVA). The interaction between smolt size and the SST in July was not significant in the model.

SURVIVAL IN RELATION TO ORIGIN

The origin of the smolt groups (wild $n=6$, and reared $n=11$) explained the survival better, but not significantly, ($r^2=0.09$) than the SST in July ($r^2=0.08$) or the mean smolt L_T ($r^2=0.01$), when the common five release years (Fig. 2) were included in the regression model and the explanatory factors were tested separately. No factor met the 0.150 significance level for entering into the stepwise model. The mean recapture rate was 33% for the wild and 26% for the reared groups in these years.

DISCUSSION

SURVIVAL IN RELATION TO CLIMATIC FACTORS AND PREY FISH ABUNDANCE

The survival of Atlantic salmon smolt groups was influenced by the July sea surface temperature in the southern Gulf of Bothnia ($P < 0.01$) in the year of release. This was earlier observed with reared Neva fish in the same sea area (Salminen *et al.*, 1995), and with wild Atlantic salmon stocks in the North Sea (Friedland *et al.*, 2000). A weak positive association was found between prey fish abundance (0+ year herring) in the southern Gulf of Bothnia and the survival of reared and wild Simojoki fish, as has earlier been reported for reared Neva fish (Salminen *et al.*, 1995).

The positive effect of both climatic environmental factors and prey fish abundance on the survival of Atlantic salmon was expected, because these factors are directly or indirectly associated. The NAO phase affects not only climatic but also oceanographic conditions in the Baltic Sea, such as salinity. The appearance of saline pulses could be more probable during a low NAO index phase (Hänninen *et al.*, 2000). The salinity is known to influence the biota in the Baltic. For example, the decreasing salinity in the 1980s has brought a change in zooplankton species composition and abundance, and the food composition of herring has simultaneously changed (Flinkman *et al.*, 1998). Herring has suffered from the decreased abundance of its main food, the large neritic copepods. The association between the Atlantic salmon survival and the decrease in the mean mass-at-age of Baltic herring in the 1980s (Flinkman *et al.*, 1998), however, was not analysed here.

Interannual variability in the spring and summer abundance of a small zooplankton species (small copepods) that is food for herring has been reported to be linked with climate variability (NAO and SST) during the winter (Dippner *et al.*, 2001). In this study, the SST and 0+ year herring abundance in the southern Gulf of Bothnia were also correlated. In the Baltic Sea, the SST, averaged from December to February, and the NAO index correlated positively in 1960–1992 (Dippner *et al.*, 2001). The positive phase of the NAO affects the Barents Sea through an increasing influx of warm water from the south-west and increasing cloud cover and air temperature, all leading to an increase in water temperature. This, in turn, influences fish growth and survival directly or indirectly (Ottersen & Stenseth, 2001; Stenseth *et al.*, 2002). Both a positive

NAO index and a high SST increased the survival of the reared and wild groups, but only SST had a significant effect.

The dependence of Atlantic salmon survival on prey fish abundance in the southern Gulf of Bothnia, where only herring dominates in the diet of piscivorous Atlantic salmon, was expected (Salminen *et al.*, 1994, 2001). In the main basin, however, where two prey fish (sprat and herring) dominate (*c.* 95%) in the diet of Atlantic salmon >60 cm L_T (Karlsson *et al.*, 1999), no positive association was found between Atlantic salmon survival and sprat or herring abundance. This suggests that the mortality of Atlantic salmon after their first sea year is not dependent on prey fish abundance (sprat or herring) in the feeding area of the main basin. In contrast, the present results and an earlier study (Salminen *et al.*, 1994) suggest that food abundance in the first summer and year in the southern Gulf of Bothnia, in the nearest feeding area, is important for the success of the Atlantic salmon stocks originating from the northern Gulf of Bothnia. The sprat and herring biomass in the main basin in a particular year, however, was found to explain the mass of the 2 year-old Atlantic salmon spawners in that year (Karlsson *et al.*, 1999).

A corresponding association between the sea temperature and post-smolt survival to that observed in this study has also been recorded in the North Sea, where the marine survival of post-smolts correlated positively with a warm (8–10°C) thermal seawater habitat in front of the rivers (Friedland *et al.*, 1998). In contrast to the North Sea, the post-smolts of the Finnish Bothnian Bay rivers appear to initially migrate along the eastern coast of the bay, and thus swim against the main current (E. Jutila, pers. comm.) to reach a favourable thermal habitat. In the Baltic Sea, however, the prevailing sea currents are much weaker than in the northern Atlantic Ocean, thus allowing this type of adaptation.

Lindroth (1965) has suggested that stock fluctuations occur simultaneously in adjacent Baltic Atlantic salmon rivers. The fluctuation timing, however, differs between the Baltic and Atlantic stocks, although no exact reasons for this could be determined (Lindroth 1965). McKinnell & Karlström (1999) showed that recapture rates of tagged Atlantic salmon released from different hatcheries along the Gulf of Bothnia were all positively correlated, suggesting a substantial degree of synchrony in post-smolt survival. Thus, the relationship between the survival of Simojoki fish and the prevailing environmental factors, abundance of potential prey and smolt traits could also indicate more extensively the factors affecting the survival of the northern Baltic Atlantic salmon stocks.

SURVIVAL AND SMOLT TRAITS

This study demonstrated that the success of wild and reared smolt groups was related in the same way to the 0+ year herring abundance in the southern Gulf of Bothnia, although the spatial distribution of the groups differed. The relationship between smolt L_T and survival differed between wild and reared fish. There was a significant positive association between smolt L_T and survival among reared Atlantic salmon, but not among wild ones. In addition, the recapture rate of the wild groups was twice that of the reared groups and the origin explained survival better than other smolt traits or climatic factors. A higher marine recapture rate of wild Atlantic salmon smolts compared with

reared fish has also earlier been reported for both Baltic (Österdahl, 1969; Jutila *et al.*, 2003b) and Atlantic salmon (Jonsson *et al.*, 1991).

Higher recapture rates of larger smolts have been observed several times among reared Atlantic salmon (Vehanen *et al.*, 1993; Kallio-Nyberg *et al.*, 1999). In reared Neva fish in the southern Gulf of Bothnia, the recapture rates increased gradually with an increase in smolt L_T (Salminen *et al.*, 1995). The differences in post-smolt survival between size classes were mainly attributed to their different abilities to withstand unfavourable environmental conditions (Salminen *et al.*, 1995). A large smolt size has also been suggested to decrease the risk of size-dependent predation (Skilbrei *et al.*, 1994). A large size might therefore be more important for reared smolts than for wild Atlantic salmon in reducing predation pressure. Wild fish are better able to avoid predators than reared ones (Jonsson & Abrahams, 1991). The result suggests that the larger smolt size of reared Atlantic salmon compensated to some extent for their poorer ability to live in the wild, for example by decreasing the predation risk. In contrast, among wild fish, smolt size displayed little variation and was not associated with their success at sea.

In Baltic *S. Salar*, the growth rate and sexual maturation as parr are linked (Lundqvist & Fridberg, 1982). Precocious fish are smaller than immature smolts of the same age (Lundqvist *et al.*, 1988) and they are also less well adapted to salt water (Berglund *et al.*, 1992). The observed low survival of small smolts may partly be due to the high proportion of precociously mature fish in this group.

The recapture rate decreased from 1980–1998 in the reared groups but not from 1972–1993 in the wild groups. The declining trend could be the result of declining survival of the reared smolts. McKinnell & Karlström (1999) have also reported a long-term declining trend in recapture rates in most hatchery stocks in the Baltic from the 1950s to the 1990s. The results for wild smolts did not, however, extend until the late 1990s, when the decreasing trend was most obvious (McKinnell & Karlström, 1999).

This study was carried out at the Finnish Game and Fisheries Research Institute. The first tagging of wild and reared smolts was performed by J. Toivonen and A. Tuikkala. Since the early 1980s, K. Hietanen and his assistants have organized and carried out the tagging. The staff of the tagging office in Helsinki organized the collection of the tags. K. Westman, P. Pasanen and J. Ryttilahti and the staff of the Aquaculture Unit were responsible for the production and tagging of the reared smolts. E. Aro and R. Parmanne kindly provided the prey fish recruitment data. M. Salminen offered valuable comments and criticism of the manuscript. The Swedish Meteorological and Hydrological Institute and the Finnish Institute of Marine Research collected the sea surface temperature data. R. Siddall checked the language and J. Stigzelius prepared the figures. The authors are very grateful to all these people for their valuable help. The comments of two anonymous referees improved the paper considerably.

References

- Alm, G. (1934). Salmon in the Baltic Precincts. *Conseil Permanent International pour l'Exploration de la Mer. Rapports et Procès-Verbaux des Réunions* **XCII**, 1–63.
- Berglund, I., Schmitz, M. & Lundqvist, H. (1992). Sea water adaptability in the Baltic salmon (*Salmo salar* L.): a bimodal smoltification pattern in previously mature males. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1097–1106.
- Christensen, O. & Larsson, P-O. (1979). Review of Baltic salmon research. *ICES Cooperative Research Report* **89**.

- Dippner, J. W., Hänninen, J., Kuosa, H. & Vuorinen, I. (2001). The influence of climate variability on zooplankton abundance in the Northern Baltic Archipelago Sea (SW Finland). *ICES Journal of Marine Science* **58**, 569–578. doi: 10.1006/jmsc.2001.1048.
- Fleming, I. A., Hindar, K., Mjølnerad, B., Jonsson, B., Balstad, T. & Lamberg, A. (2000). Lifetime success and interactions of farm salmon invading a native population. *Proceedings of the Royal Society London B* **267**, 1517–1523. doi: 10.1098/rspb.2000.1173.
- Flinkman, J., Aro, E., Vuorinen, I. & Viitasalo, M. (1998). Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s: top-down and bottom-up processes at work. *Marine Ecology Progress Series* **165**, 127–136.
- Friedland, K. D., Reddin, D. G. & Kocik, J. F. (1993). Marine survival of North American and European Atlantic salmon: effects of growth and environment. *ICES Journal of Marine Science* **50**, 481–492. doi: 10.1006/jmsc.1993.1051.
- Friedland, K. D., Hansen, L. P. & Dunkley, D. A. (1998). Marine temperature experienced by post-smolts and survival of Atlantic salmon, *Salmo salar* L., in the North Sea area. *Fisheries Oceanography* **7**, 22–34. doi: 10.1046/j.1365-2419.1998.0047.x.
- Friedland, K. D., Hansen, L. P., Dunkley, D. A. & MacLean, J. C. (2000). Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES Journal of Marine Science* **57**, 419–429. doi: 10.1006/jmsc.1999.0639.
- Hänninen, J., Vuorinen, I. & Hjelt, P. (2000). Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnology and Oceanography* **45**, 703–710.
- Holm, M., Holst, J. C. & Hansen, L. P. (2000). Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. *ICES Journal of Marine Science* **57**, 955–964. doi: 10.1006/jmsc.2000.0700.
- ICES (2000). Report of the ICES Advisory Committee on Fishery Management, 2000. *ICES Cooperative Research Report* **242**, 670–798.
- Johnsson, J. I. & Abrahams, M. V. (1991). Interbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 243–247.
- Jonsson, B. (1997). A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. *ICES Journal of Marine Science* **54**, 1031–1039. doi: 10.1016/S1054-3139(97)80007-0.
- Jonsson, B., Jonsson, N. & Hansen, L. P. (1991). Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. *Aquaculture* **98**, 69–78.
- Jutila, E. & Pruuki, V. (1988). The enhancement of the salmon stocks in the Simojoki and Tornionjoki rivers by stocking parr in the rapids. *Aqua Fennica* **18**, 93–99.
- Jutila, E., Jokikokko, E., Kallio-Nyberg, I., Saloniemi, I. & Pasanen, P. (2003a). Differences in sea migration between wild and reared Atlantic salmon (*Salmo salar* L.) in the Baltic Sea. *Fisheries Research* **60**, 333–343. doi: 10.1016/S0165-7836(02)000169-8.
- Jutila, E., Jokikokko, E. & Julkunen, M. (2003b). Management of Atlantic salmon in the Simojoki river, northern Gulf of Bothnia: effects of stocking and fishing regulation. *Fisheries Research* **64**, 5–17. doi: 10.1016/S0165-7836(03)00107-3.
- Kallio-Nyberg, I., Peltonen, H. & Rita, H. (1999). Effects of stock-specific and environmental factors on the feeding migration of Atlantic salmon (*Salmo salar*) in the Baltic Sea. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 853–861.
- Karlsson, L. & Karlström, Ö. (1994). The Baltic salmon (*Salmo salar* L.): its history, present situation and future. *Dana* **10**, 61–85.
- Karlsson, L., Ikonen, E., Mitans, A. & Hansson, S. (1999). The diet of salmon (*Salmo salar*) in the Baltic Sea and connections with the M74 syndrome. *Ambio* **28**, 37–42.
- Koljonen, M.-L. (1989). Electrophoretically detectable genetic variation in natural and hatchery stocks of Atlantic salmon in Finland. *Hereditas* **110**, 23–35.
- Koljonen, M.-L. (1995). Distinguishing between resident and migrating Atlantic salmon (*Salmo salar*) stocks by genetic stock composition analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 665–674.

- Koljonen, M.-L. & McKinnell, S. (1996). Assessing seasonal changes in stock composition of Atlantic salmon catches in the Baltic Sea with genetic stock identification. *Journal of Fish Biology* **49**, 998–1018. doi: 10.1006/jfbi.1996.0228.
- Lindroth, A. (1965). The Baltic salmon stock. Its natural and artificial regulation. *Internationale Vereinigung für theoretische und angewandte Limnologie. Mitteilungen* **13**, 163–19.
- Lindroth, A., Larsson, P.-O. & Bertmar, G. (1982). Where does the Baltic salmon go? In *Coastal Research in the Gulf of Bothnia* (Muller, K., ed.), pp. 387–413. The Hague: Dr W. Junk.
- Lundqvist, H. & Fridberg, G. (1982). Sexual maturation versus immaturity: different tactics with adaptive values in Baltic salmon (*Salmo salar* L.) male smolts. *Canadian Journal of Zoology* **60**, 1822–1827.
- Lundqvist, H., Clarke, W. C. & Johansson, H. (1988). The influence of precocious sexual maturation on survival to adulthood of river stocked Baltic salmon, *Salmo salar*, smolts. *Holarctic Ecology* **11**, 60–69.
- McKinnell, S. M. & Karlström, Ö. (1999). Spatial and temporal covariation in the recruitment and abundance of Atlantic salmon populations in the Baltic Sea. *ICES Journal of Marine Science* **56**, 433–443. doi: 10.1006/jmsc.1999.0456.
- McKinnell, S. M. & Lundqvist, H. (2000). Unstable release strategies in the reared Atlantic salmon, *Salmo salar* L. *Fisheries Management and Ecology* **7**, 211–224.
- Österdahl, L. (1969). The smolt run of a small Swedish river. In *Salmon and Trout in Streams* (Northcote, T. G., ed.), pp. 205–215. Vancouver: University of British Columbia.
- Ottersen, G. & Stenseth, N. C. (2001). Atlantic climate governs oceanographic and ecological variability in the Barents Sea. *Limnology and Oceanography* **46**, 1774–1780.
- Salminen, M., Kuikka, S. & Erkamo, E. (1994). Divergence in the feeding migration of Baltic salmon (*Salmo salar* L.); the significance of smolt size. *Nordic Journal of Freshwater Research* **69**, 32–42.
- Salminen, M., Kuikka, S. & Erkamo, E. (1995). Annual variability in survival of sea-ranched Baltic salmon, *Salmo salar* L.: significance of smolt size and marine conditions. *Fisheries Management and Ecology* **2**, 171–184.
- Salminen, M., Erkamo, E. & Salmi, J. (2001). Diet of post-smolt and one-sea-winter Atlantic salmon, in the Bothnian Sea, Northern Baltic. *Journal of Fish Biology* **58**, 16–35. doi: 10.1006/jfbi.2000.1426.
- Saunders, R. L. (1993). The thermal biology of Atlantic salmon: Influence of temperature on salmon culture with particular reference to constraints imposed by low temperature. *Report of the Institute of Freshwater Research Drottningholm* **63**, 68–81.
- Skilbrei, O. T., Holm, M., Jorstad, K. E. & Handeland, S. A. (1994). Migration motivation of cultured Atlantic salmon, *Salmo salar* L., smolts in relation to size, time of release and acclimation period. *Aquaculture and Fisheries Management* **25**, 65–77.
- Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S. & Lima, M. (2002). Ecological effects of climate fluctuations. *Science* **297**, 1292–1296.
- Vehanen, T., Aspi, J. & Pasanen, P. (1993). The effect of size, fin erosion, body silvering and precocious maturation on recaptures in Carlin-tagged Baltic salmon (*Salmo salar* L.). *Annales Zoologici Fennici* **30**, 277–285.

Electronic References

- Hurrell, J. (1995). *NAO Index Data provided by Climate Analysis Section, NCAR, Boulder, USA*. Web page: www.cgd.ucar.edu/~jhurrell/nao.html. Information was retrieved 15 August 2002.
- SAS (1999). *SAS OnlineDoc[®], Version eight*. Cary, NC: SAS Institute Inc. Available online: v8doc.sas.com/sashtml/