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Sea migration patterns in the Atlantic salmon: a comparative study of two stocks and their hybrids

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The sea migration patterns of the Atlantic salmon in the Baltic Sea was examined in a crossing and transplantation experiments. Two genetically different salmon stocks originating from rivers Neva and Iijoki and their hybrids were released as smolts (6 561, 485 and 993 smolts, respectively) into the estuary of the Kymijoki, in the Gulf of Finland. The spatial and temporal marine distributions of the experimental groups were analysed from tag recovery data received during $3^1/_2$ years (42 months) after release. The recovery rate was 6.5%–17.5%. Multi-way contingency analysis showed that the spatial distributions of the stocks differed in the sea. The feeding migration distance of the hybrids was longer than that of the parental Neva stock, and the male line affected the spatial marine distribution of the hybrids more than did the female line. Genetically different parental stocks showed no significant difference in migratory behaviour in this experiment. No differences were recorded in the temporal distributions of the stocks in the sea. The observed differences confirm that the sea migration pattern is a stock-specific, inherited trait. The longer migration pattern of hybrid stocks than that of parental stocks may be due to coadaptive gene combinations that break down in crossing or to a high phenotypic variation in parents within the stocks.

Introduction

Atlantic salmon (*Salmo salar* L.)migrate from their home rivers to the sea to exploit food resources of the sea and to increase their growth and reproductive output (Northcote 1984). The sea migration can be divided into three phases: post-smolt migration from the river to feeding grounds, feeding migration of immature salmon, and spawning migration of maturing salmon to the natal stream. Post-smolts and feeding salmon are generally thought to follow an innately directed pattern of movement in space and time, and homing salmon to orientate by cues acquired during

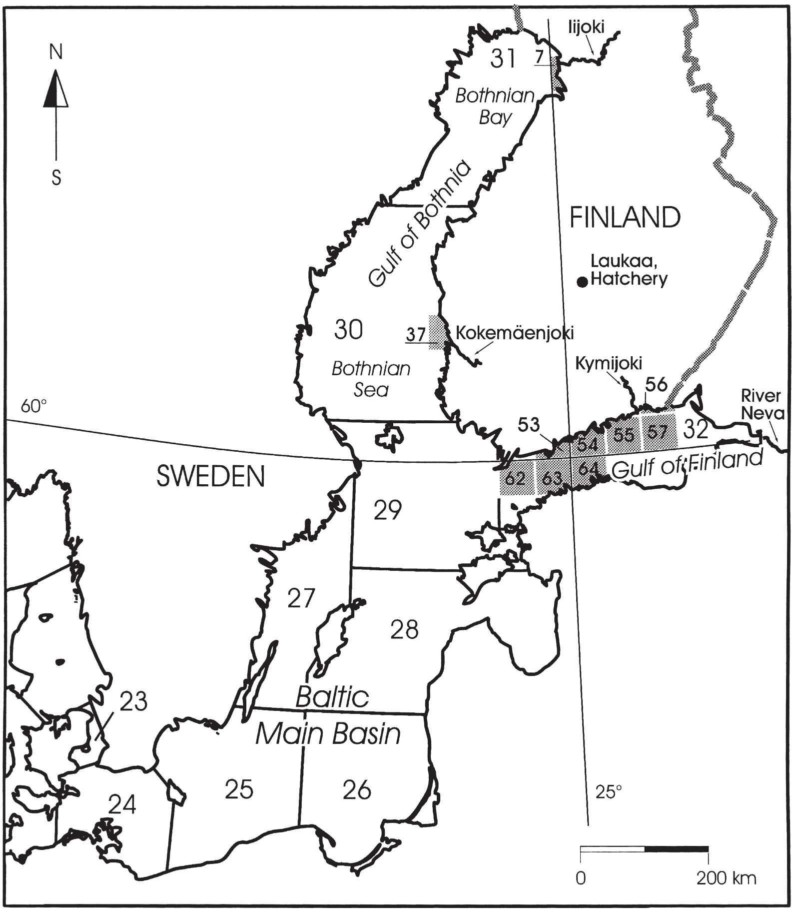

Fig. 1. Map of the Baltic Sea showing sea areas: the Baltic's southern main basin (Sub-divisions 23–26), the Baltic's northern main basin (27–29), the Gulf of Finland (32), the Bothnian Sea (30) and the Bothnian Bay (31). Some small (statistical) squares are numbered 53–57, 62–64, 37 and 7. The Kymijoki drains into the Gulf of Finland (square 55), Kokemäenjoki into the Bothnian Sea (square 37), and Iijoki into the Bothnian Bay (square 7). The location of Laukaa Fisheries Research and Aquaculture hatchery station is shown.

emigration (Brannon 1984, Healey and Groot 1987). Transplantation experiments show that salmon usually return to their site of release (Hansen and Jonsson 1994), although they stray more commonly than locally adapted salmon (Quinn 1993, Pascual and Quinn 1994). The homing ability of salmon has been associated with the frequency of inherited local gene combinations (Bams 1976, McIsaac and Quinn 1988). Components of migration behaviour, e.g. the sea migration pattern, timing of migration, straying rate and homing rate of a salmon stock, are thus inherited traits (Hansen and Jonsson 1991, Pascual and Quinn 1994), although environmental factors also affect the migration behaviour of adult salmon (Groot and Quinn 1987, Quinn and Leggett 1987, Reddin and Shearer 1987, Kallio-Nyberg *et al.* 1999).

We examined stock-specific sea migration patterns by comparing the spatial and temporal marine distributions of tag recoveries of two genetically different Atlantic salmon stocks and their hybrids. The parental stocks were Neva and Iijoki salmon, two strains whose feeding migration tendencies had been reported to differ (Kallio-Nyberg and Ikonen 1992). The Neva salmon released into the Kymijoki or into their home river, the Neva, both of which drain into the Gulf of Finland, (Fig. 1; square 55), migrate into both the gulf and the Baltic's main basin to feed (Kazakov 1985, Salminen *et al.* 1995). The Iijoki stock, when released into its northern home river, migrates far south into the feeding areas of the Baltic's main basin (Kallio-Nyberg and Ikonen 1992). When these same two strains were released into a river (Kokemäenjoki) on the west coast of Finland in an earlier experiment, their migration patterns differed markedly. The bulk of the Neva salmon

(95%) remained near the release site in the Bothnian Sea area (the southern Gulf of Bothnia; *see* Fig. 1), only 4% of them being captured farther south, in the Baltic's main basin. In contrast, most of the Iijoki salmon (61%) were captured to the south of the Bothnian Sea, and only 39% of them being captured in the Bothnian Sea (Kallio-Nyberg and Ikonen 1992). The Iijoki stock was, thus, expected to have a tendency to migrate farther south than the Neva salmon.

The distribution of tag recoveries depends partly on the fishery (Potter and Russell 1994). However, when fishing is similar for all stocks, and the stocks have the same relative catch rate, the relative stock proportions can be estimated. If the stocks are produced in the same way, are released at the same place and time and are equally catchable and if no genetic differences exist in their migration pattern, they should show similar recovery distributions. To study the spatial and temporal sea migration patterns and the inheritance of the sea migration pattern, we analysed tag recovery data with a multi-way contingency technique. First, we investigated the relationship between three variables: stock, recovery site and recovery time. Then we examined the relationship between three variables; female line, male line and recovery site.

Material and methods

Salmon stocks

The two pure salmon stocks used in this study, the Neva and Iijoki stocks, were hatchery-reared and sea-ranched, but differed markedly in allozyme analysis (Koljonen 1995). The Neva stock originates from the Neva River, which drains from Lake Ladoga in Russia into the Gulf of Finland (Fig. 1). Neva salmon are maintained in Finland with broodstocks and with the collection of spawners in estuaries. They are released into the Gulf of Finland and the Bothnian Sea in the estuaries of rivers in which the original wild salmon stocks have become extinct. The other salmon stock originates from the Iijoki, a northern river draining into the Bothnian Bay. The Iijoki was closed by a hydroelectric dam in the 1960s, and the stock has since been maintained mainly with broodstocks in hatcheries.

The straying rate of the released fish has been low. Only 1.2% of the Neva salmon migrants released into the Kymijoki estuary were observed in a foreign sea area, that is, the Gulf of Bothnia, during the spawning migration (Ikonen and Auvinen 1984). In our study, only one tag of each release group (Neva/1yr, Neva/2yr, Iijoki and hybrid) was recaptured in the Bothnian Sea area. These fish were not included in the analysis.

Mating and rearing

The sea migration patterns of the Neva and Iijoki salmon and their hybrids was studied in a crossing and tagging experiment, the aim being to analyse the sea distribution of the tag recoveries of two genetically different salmon stocks and their hybrids when released in the same place. The spawners were obtained from broodstocks kept at the hatchery station of Laukaa Fisheries Research and Aquaculture in central Finland (Fig. 1). The parental Iijoki and Neva groups (released as 2-year-olds) were mated in 1986 and the hybrid groups (released as 1-year-olds) in 1987. All juvenile groups were reared at the Laukaa hatchery station under standard conditions. The Neva salmon usually reach the smolt stage as 1-year-olds due to their rapid growth rate. The Iijoki salmon, which originate from a more northerly river, need two years to reach the smolt stage.

To create hybrids, eggs of Neva salmon were fertilised with milt of the Iijoki salmon, and eggs of Iijoki salmon fertilised with milt of Neva salmon. The eggs of each female were fertilised with milt of several, usually three, males. The fishes used as parents in the hybrid and pure groups were not the same individuals, because the experimental groups were established partly in different years. The released smolts were one or two years old. Juveniles of each group were pooled after incubation and the families of each group were reared together. The smolts were marked with indivudual Carlin tags before being released into the sea. About 500 smolts were tagged in each hybrid group and the parental Iijoki stock. Four groups of about 500 smolts per group of the 1-year-old Neva salmon, and seven groups of about 500 smolts per group of the 2-year-old Neva salmon were tagged (Table 1). All the fish were released into the Kymijoki estuary, in the Gulf of Finland, in May 1989 (Fig. 1; sub-division 32; square 55).

Recovery data

The place of capture was recorded according to ICES (International Council for the Exploration of the Sea) sub-divisions (23–32) and squares (53–64) within the sub-divisions (Fig. 1). The migration area, determined by tag recoveries, was divided into two (the Baltic's main basin and the Gulf of Finland) or three (the Baltic's northern and southern main basin and the Gulf of Finland) parts for the analyses. The Baltic's main basin (MB) consisted of sub-divisions 23–29, and the Gulf of Finland (GF) of sub-division 32. The Baltic's northern main basin (NMB) and southern main basin (SMB) consisted of sub-divisions 23–26 and 27–29, respectively (Fig. 1).

The distribution of salmon in the sea was examined for periods of 6 and 12 months after release. The periods were:

1– 6 months = May–October 1989, first summer.
7–12 months = November–April 1989–1990, first winter.
13–18 months = May–October 1990, second summer.
19–24 months = November–April 1990–1991; second winter.
25–30 months = May–October 1991, third summer.
31–36 months = November–April 1991–1992, third winter.
37–42 months = May–October 1992, fourth summer.
7–18 months = November–October 1989–1990, first winter and second summer.
19–30 months = November–October 1990–1991, second winter and third summer.
31–42 months = November–October 1991–1992, third winter and fourth summer.

Sea migration was analysed separately for summer and winter months, because in summer (13–18 months or 25–30 months in the sea) the mature 1-sea-winter and 2-sea-winter salmon return to their release site. The period from November to April is the main feeding migration season for salmon (Lindroth *et al*. 1982); at least salmon caught in the Baltic's main basin during this period are on their feeding migration. Here, the spawning, migrating and feeding-migrating salmon could not be separated, but the effect of maturation on the sea migration was taken into account by including recovery time in the analysis.

The average total recovery rate of the fish released as 2-year-olds was 14.5% for the Neva stock and 17.5% for the Iijoki stock. The recovery rate of the fish released as 1-year-olds was 12.3% for the Neva stock and 9.0% for the hybrid stocks (Table 1).

Fishery

Owing to the intensity and wide distribution of offshore salmon fishing and the relatively high recapture rate in the Baltic Sea, migration research based on tag recovery data is feasible. The spatial pattern of tag recoveries is, however, a result not only of the migration pattern but also of the fishery distribution. Still, if the groups have the same growth rate, and also the same catch rate, the relative stock proportions can be compared. Moreo-

Table 1. Number of tagged and released smolts (*n*) and the recovery rate of the Neva, Iijoki and hybrid salmon in the experiment. The smolts were released into the Gulf of Finland in 1989. Annual and total numbers of recovered salmon and recovery rate (%) per stock are shown.

Stock/smolt age	*n*	Tag recovery rate					
		1989	1990	1991	1992	Total	%
Neva/1	1 994	9	128	80	27	247	12.3
Neva/2	4 617	74	288	254	45	672	14.5
Iijoki × Neva/1	493	0	14	12	6	32	6.5
Neva × Iijoki/1	500	0	26	27	5	58	11.6
Iijoki/2	485	4	44	33	3	85	17.5

ver, if the fish are of the same size when being fished, and if they migrate in the sea at the same time they are equally catchable with all gear types being used.

In the 1980s and 1990s, the majority of salmon in the Baltic Sea were caught with driftnets and longlines (Anonymous 1996). Driftnets were used offshore in the Baltic's main basin, where thw˙bulk of the catch consisted of feeding salmon. In the Gulf of Finland, most salmon were caught with longlines offshore and with trapnets in coastal areas (Salminen *et al*. 1995). In this area, salmon released in 1980–1991 were mainly caught offshore and with longlines as 0-sea-winter- and 1-sea-winter-olds (Salminen *et al*. 1995). The tag returns in this study were not analysed by gear type, because sufficient information was not available. The smolt groups compared were released in the same year, and the fishery was thus as similar as possible for all groups.

Statistical analysis

Stock-specific differences in the migration patterns were first examined by comparing the spatial distributions of tag recoveries in different periods with the χ^2 test. Recovery data were analysed with multi-way contingency tables (SAS: The CATMOD procedure) (Anonymous 1989). The independence of variables was analysed by log-linear models. The variables were stock, smolt age, female stock (maternal line), male stock (paternal line), recovery site and recovery time. The goal of the analyses was to find the simplest accepable model that would fit the data (parsimony principle). The significance of the nested models was tested with the value of the likelihood ratio (G^2) and the selected risk level (0.05) as the criteria. The difference in the likelihood ratios (G^2) nearly follows a χ^2 distribution.

Three log-linear analyses were conducted. In the first analysis, we examined the effect of the smolt age by studying the independence of the following three variables: the recovery site, recovery time and smolt age, because the data included Neva salmon groups released as both 1- and 2-year-old smolts. For the analyses the tag recoveries were divided into three sea areas and into three periods. Neva salmon groups released as 1- and 2-year-old smolts were included (Table 2).

In the second analysis, we examined the difference between pure and hybrid groups in the sea migration behaviour by analysing the independence of the following three variables: the stock, recovery site and recovery time (Table 3). The stocks were: Neva, Iijoki, Hybrid. The Neva groups released as 1- or 2-year olds were pooled. The reciprocal hybrid groups were also pooled in this analysis. The classes of the recovery site were the Baltic's main basin and the Gulf of Finland. The classes of the recovery time were 7–18, 19–30 and 31–42 months in the sea.

In the third analysis, we examined the independence of the following three variables: the female stock (maternal line), male stock (paternal line) and recovery site. The classes for the paternal and maternal lines were the same, the Neva and Iijoki stocks. The classes of the recovery site were the Gulf of Finland and the Baltic's main basin. The Neva fish released as 1- and 2-year-old smolts were pooled. Recoveries for the period 7–42 months in the sea were included (Table 4).

The growth rate of the salmon stocks was studied for the salmon caught in the release square (55) in the summer periods, when the spawning migrants returned after 13–18 (second summer) or 25–30 (third summer) months at sea. The sample sizes in the winter were too small for growth analysis. The sea growth rate was estimated as

Table 2. Number of recoveries in three-dimensional contingency table. Variables: smolt age (1, 2), recovery time (7–18, 19–30, 31–42 months in sea) and recovery site.

Recovery site: sea area	Smolt age 1: Neva/1 Recovery time			Smolt age 2: Neva/2 Revovery time		
	7–18	19–30	31–42	7–18	19–30	31–42
Baltic's southern main basin	1	6	3	5	6	1
Baltic's northern main basin	18	5	4	43	16	6
Gulf of Finland	102	48	15	223	176	30

the increment of length (length of caught fish–total smolt length).

Results

All the stocks were caught in the Gulf of Finland and the Baltic's main basin areas (Fig. 2). In winter months during their feeding migration, salmon were captured 0–400 km from the release site in the Gulf of Finland, and 400–1 000 km from the release site in the Baltic's main basin (Fig. 2). In the summer months, salmon were caught mainly in the Gulf of Finland (Fig. 3). Only one fish of each group (I/2yr, H/1yr, N/1yr, N/2yr) was observed to have strayed in the Gulf of Bothnia area (Fig. 1).

Effect of smolt age on recovery site and time

The independence of the smolt age (A: 1, 2; Neva salmon) of recovery site and recovery time was first tested. The model, in which time (year, T: 3 classes) and recovery site (P: SMB, NMB, GF) were independent of smolt age, fitted the data (H_0: A, PT: $G^2 = 15.11$, df = 8, $p = 0.057$; Table 5). This model, with an interaction between recovery site and recovery time, was significantly better than the model without the interaction ($G^2_{A,P,T} - G^2_{A,PT} = 16.1$, df = 12 – 8 = 4; the critical value of χ^2 disribution at the 0.05 significance level was 9.48). In the comparison, the models with one and two interactions showed that the addition of an interaction between smolt age and recovery time (year in the sea) increased the goodness of fit of the model ($G^2_{A,PT} - G^2_{PT,AT} = 7.3$, df = 8 – 6 = 2; $\chi^2 = 5.99$; Table 5). Thus, the smolt age affected recovery year, but not the recovery site. The interaction between the recovery time and recovery site meant that fish were caught at the different sites in the different periods regardless of smolt age. The interaction between the recovery time and smolt age meant that fish released as 1- or 2-year-olds were caught in different years. Because the effect of the smolt age on the recovery site was not significant, the spatial distribution of the Neva, Iijoki and hybrid groups could be compared despite the differences in the smolt age. In contrast, the possible stock-specific differences in the temporal sea distribution could also be due to the smolt age variation in the pooled data.

Table 3. Number of recoveries in three-dimensional contingency table. Variables: stock (Iijoki, Neva, Hybrid), recovery site (Baltic's main basin = MB and Gulf of Finland = GF) and recovery time (7–18, 19–30, 31–42 months in sea). The proportion of recoveries (%) in MB and GF per stock are also shown.

Stock	Recovery site	Recovery time (months in the sea)			
		7–18	19–30	31–42	%
Iijoki	MB	10	4	1	21
Iijoki	GF	30	25	2	79
Neva	MB	67	33	14	16
Neva	GF	325	224	45	84
Hybrid	MB	13	6	1	31
Hybrid	GF	24	11	9	69

Table 4. Number of recoveries in three-dimensional contingency table. Variables: female stock (maternal line) (Neva, Iijoki), male stock (paternal line) (Neva, Iijoki), recovery site (Gulf of Finland, Baltic's main basin).

		Gulf of Finland		Baltic's main basin	
		Male Neva	Male Iijoki	Male Neva	Male Iijoki
Female	Neva	594	27	114	13
Female	Iijoki	17	57	7	15

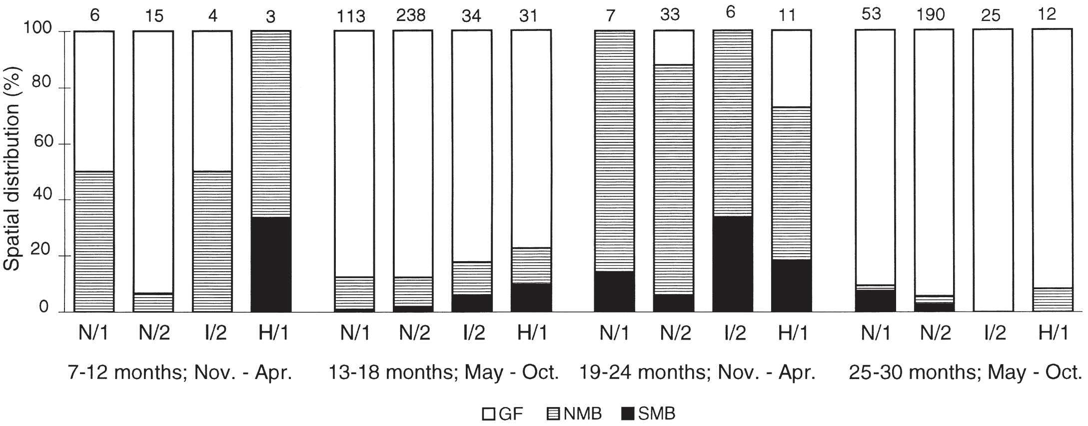

Fig. 2. Spatial distribution of the Neva (N/1, N/2), Iijoki (I/2) and hybrid (H/1, reciprocal hybrid stocks pooled) salmon stocks in 6-month periods (7–12, 13–18, 19–24, 25–30 months) after release into the Baltic Sea. 13–18 = summer months, when 1SW salmon return. 25–30 = summer months, when 2SW salmon return. The Baltic Sea areas: Gulf of Finland (GF), northern main basin (NMB), southern main basin (SMB).

Effect of stock on recovery site and time

Hybrids (reciprocal groups pooled) were caught more frequently (29% and 39% of recoveries) in the Baltic's main basin than were Neva salmon (Neva/1yr and Neva/2yr pooled, 13% and 18%) in the first winter and second summer, and in the second winter and third summer, respectively (Fig. 3). The Neva salmon showed the shortest migration pattern, and were caught more frequently (N/1yr: 86%; N/2yr: 88%) in the Gulf of Finland than were hybrid salmon (71%; χ^2 test: N/1yr & H all: $p = 0.041$ and N/2yr & H all: $p = 0.005$; Fig. 3) during the first winter and second summer. Although the Iijoki salmon tended to migrate farther (7–18 and 19–30 months: 21% and 19%), no significant difference could be found between the Neva (13% and 18%) and Iijoki stocks in any period in this experiment (χ^2 test, I & N/2yr: 7–18 months: $p = 0.116$ and 19-30 months: $p = 0.847$) (Fig. 3).

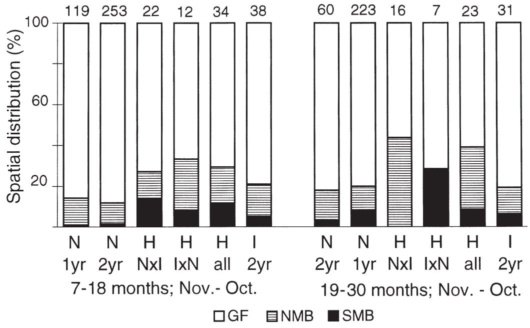

Fig. 3. Stock-specific spatial marine distributions in periods 7–18 (Nov.–Oct. 1989–1990) and 19–30 (Nov.–Oct. 1990–1991) months after release. Stocks: N = Neva, I = Iijoki, H = hybrid, N × I = hybrid with the Neva females and Iijoki males. 1 yr and 2 yr = 1- and 2-year-old smolts at release. Sample sizes are shown over the columns. The Baltic Sea areas: Gulf of Finland (GF), northern main basin (NMB), southern main basin (SMB).

Table 5. Effect of smolt age on spatial and temporal marine distributions in the Gulf of Finland and in the Baltic's main basin. Log-linear models and tests of independence between classified variables: smolt age (A) (Neva: 1, 2), recovery site (P) (SMB, NMB, GF), recovery time (T) (7–18, 19–30, 31–42 months in sea). The contingency table with sample sizes is shown in Table 2. Variables are expected to be independent when separated by a comma and to interact when there is no comma. H_0 = null hypothesis; df = degrees of freedom; G^2 = likelihood ratio; °*p*-values indicate the discrepancy between the model and the data; * shows the models with best fit ($p > 0.05$).

H_0	df	G^2	°*p*
A, P, T	12	31.2	0.001
T, AP	10	28.2	0.001
P, AT	10	24.0	0.007
A, PT	8	15.1	0.057*
AT, AP	8	20.9	0.007
PT, AP	6	12.0	0.060*
PT, AT	6	7.8	0.246*
AT, AP, PT	4	4.5	0.338*

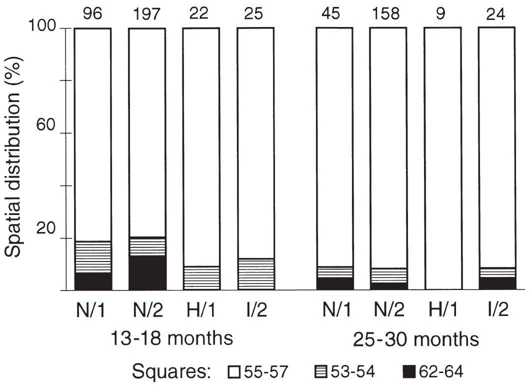

Fig. 4. Spatial marine distribution of Neva (N/1; N/2) and Iijoki (I/2) salmon and hybrid (H/1) salmon in Gulf of Finland 13–18 months (May–October in 1990) and 25–30 months (May–October in 1991) after release. Squares 55–57, 53–54, 62–64 are shown in Fig. 1.

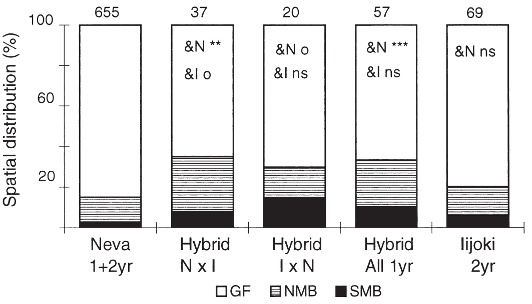

Fig. 5. Stock-specific spatial marine distributions in the Baltic Sea 7–30 months after release. Hybrid groups are shown both separately and pooled (all). Hybrids: N × I = Neva females and Iijoki males; I × N Iijoki females and Neva males. The results of the χ^2 tests are shown in the columns. The Baltic Sea subareas: Gulf of Finland (GF), northern main basin (NMB), southern main basin (SMB).

The genetic characteristics of the stock had an effect on the migration distance but not on the catch time. The one-interaction model with an interaction between the stock and recovery site was compatible with the data (H_0: T, SP: $p = 0.086$) (Table 6), and was significantly better than the model without the interaction ($G^2_{S,P,T} - G^2_{T,SP} = 8.64$; df = 12 – 10 = 2; $\chi^2_{0.05} = 5.99$). The more complicated model, with the interaction between the stock and site, and between the stock and time, was even more highly compatible with the data (H_0: SP, ST: $p = 0.158$; Table 6), but it was not significantly better than the one-interaction model ($G^2_{T,SP} - G^2_{SP,ST} = 7.22$, df = 10 – 6 = 4; $\chi^2_{0.05} = 9.48$). Thus, in accordance with the parsimony principle, the catch site depended on the stock, but the recovery time (year) was independent of the stock.

Table 6. Effect of stock on spatial and temporal marine distributions in the Gulf of Finland and in the Baltic's main basin. Log-linear models and tests of independence between classified variables: stock (S): Iijoki, Neva (N/1 and N/2 pooled), hybrid salmon. Recovery site (P): Baltic's main basin, Gulf of Finland. Recovery time (T): 7–18, 19–30 and 31–42 months after release. The contingency table with number of recoveries is shown in Table 3. Variables are expected to be independent when separated by a comma and to interact when there is no comma. H_0 = null hypothesis; df = degrees of freedom; G^2 = likelihood ratio; °*p* values indicate the discrepancy between the model and the data; * shows the models with best fit ($p > 0.05$).

H_0	df	G^2	°*p*
S, P, T	12	25.13	0.014
T, SP	10	16.49	0.086*
S, TP	10	20.77	0.022
P, ST	8	17.92	0.021
TP, SP	8	12.13	0.145*
SP, ST	6	9.27	0.158*
ST, TP	6	13.56	0.035
SP, ST, TP	4	5.55	0.235*

In the Gulf of Finland, most recoveries were made near the release site (squares 55–57; Figs. 1 and 4). The distributions of the hybrid and Iijoki groups in the sea seemed to be similar, and their 1-year-old fish were caught near the release site. The Neva salmon, in contrast, were more widely distributed in the Gulf of Finland and were even caught in the southern part of the Gulf of Finland (squares 62–64). They were caught in the second summer 200–400 km from the release site, in areas where the Iijoki salmon and hybrids were not observed. However, the spatial marine distributions of the 1-year-old Neva and Iijoki salmon, 13–18 months after release, did not differ significantly in the Gulf of Finland (Fig. 4; χ^2 test: $p > 0.05$).

Effect of paternal and maternal lines on recovery site

The two reciprocal hybrid groups (Neva$_{\text{females}}$ × Iijoki$_{\text{males}}$ and Iijoki$_{\text{females}}$ × Neva$_{\text{males}}$) both showed a long feeding migration pattern but differed to some extent from each other (Figs. 3 and 5). In the pooled data of the whole period of 7–30 months in the sea, the offspring of the hybrid group with the Neva females were caught slightly more frequently in the Baltic's main basin than was the parental Iijoki salmon stock ($\chi^2 = 2.80$, $p = 0.094$) (Fig. 5). The spatial marine distributions of the other hybrid group with the Iijoki females ($\text{Iijoki}_{\text{females}} \times \text{Neva}_{\text{males}}$), and the pooled hybrid group did not differ significantly from the spatial distribution of the Iijoki salmon (Fig. 5; χ^2 test: $p > 0.10$).

The male parent had a stronger effect on the recovery site of the hybrid strain than did the female parent. The two-interaction model, with one interaction between recovery site and paternal line and one between the paternal and maternal lines, fitted the data ($G^2_{\text{FM, MP}} = 4.2$, df = 2, $p = 0.117$; Table 7). This two-interaction model was significantly better than the model with only one interaction between the female and male lines ($G^2_{\text{P, FM}} - G^2_{\text{FM, MP}} = 4.5$, df $= 3 - 2 = 1$; $\chi^2_{0.05} = 3.84$). Thus the model in which the male stock but not the female stock affected the spatial marine distribution of the hybrid groups fitted the data best (Table 7).

Growth rate

The mean lengths of the Neva 2+ smolts and Iijoki 2+ smolts were the same, whereas those of the two hybrid groups differed, the offspring group with the Neva females being somewhat greater (Hybrid: Neva × Iijoki: mean length ± SD: 15.3 ± 1.41 cm, $n = 58$ and Iijoki × Neva: 13.9 ± 0.62 cm, $n = 32$, $t = -6.7$, df = 84.8, $p < 0.001$). Both hybrid smolt groups were smaller than the smolts of the pure parental groups (Table 8). Until the second summer, the growth rate and lengths of the fish in all the groups measured on recapture at the release site (square 55) were very similar. However, in the third summer, the growth rate of the the hybrid offspring was higher than that of the Neva salmon, both caught at the same site. No difference between the hybrid and Iijoki salmon was observed (Table 8). The average difference in the length between the Neva salmon groups released as 1- and 2-year-olds decreased from 5 cm to 2 cm during the period of 0–25 months in the sea.

Table 7. Effect of paternal and maternal lines on spatial marine distributions in the Gulf of Finland and in the Baltic's main basin. Log-linear models and tests of independence between classified variables: recovery site (P) (MB, GF), female stock (maternal line) (F) (Neva, Iijoki), male stock (paternal line) (M) (Neva, Iijoki). The contingency table with number of recoveries is shown in Table 4.

H_0	df	G^2	°*p*
P, F, M	4	249.4	0.000
M, FP	3	247.5	0.000
F, MP	3	245.0	0.000
P, FM	3	8.7	0.033
FP, MP	2	243.1	0.000
FM, MP	2	4.2	0.117*
FM, FP	2	6.7	0.033
FM, FP, MP	1	4.2	0.038

Table 8. Mean smolt length (cm) of captured salmon (measured during tagging) and length increment (cm) during 2 years in the sea (2SW fish). The 2SW fish were caught in the Kymijoki estuary 25–30 months after release. The significance levels (*p*) of the *t*-test between stocks (&) are shown.

Stock	Smolt			2SW fish			
	n	Length ± S.D	*p*	*n*	Increment ± S.D	*p*	Stocks compared
N/1[†]	247	16 ± 1.0	***	36	69 ± 6.0	**	N/1 & H/1
H/1	90	14 ± 1.3	***	7	77 ± 6.0	**	H/1 & N/2
N/2	671	21 ± 3.1	ns	111	66 ± 8.3	*	N/2 & I/2
I/2	86	22 ± 3.1	***	17	71±10.8	ns	I/2 & H/1

[†] Neva salmon/1-year-old smolts at release.

Discussion

Stock-specific migration pattern

Analysis of the recovery data with a multi-way contingency technique showed that the catch site of salmon was not independent of the genetic characteristics. The proportion of the parental Neva salmon caught in the Gulf of Finland, near the release site, was higher than that of the hybrid stocks. The analysis of the spatial distribution with the χ^2 test showed that the hybrid stocks migrated into the Baltic's main basin for feeding more frequently than did the Neva salmon stock. Moreover, no significant difference was observed in the migration behaviour of the parental stocks in this environment. The results obtained here differed in this respect from earlier reports of differences between the Neva and Iijoki stocks (Kallio-Nyberg and Ikonen 1992). In the Gulf of Bothnia, the Iijoki salmon tended to have a far-migratory pattern and the Neva stock a short-migratory pattern (Kallio-Nyberg and Ikonen 1992). The lack of differernce between the parental stocks here, is most likely linked to the ability of the Neva salmon to migrate into the Baltic's main basin from the Gulf of Finland; they did not migrate from the Bothnian Sea. Maybe better food resources in the Gulf of Finland than in the Bothnian Sea also induced the Iijoki salmon to stay for feeding in the gulf. Consequently, both the environmental and genetic traits had an effect on the sea migration pattern.

Stock-specific variations in sea migration behaviour are reported in both Atlantic and Pacific salmon. The transplantation experiments by Pascual and Quinn (1994) on chinook salmon (*Oncorhynchus tshawytscha*) showed that the marine distribution of these salmon was a stock-specific trait. The other components of migration behaviour — seasonal return pattern (Hansen and Jonsson 1991b), straying pattern (Pascual and Quinn 1994) and accuracy of homing (McIsaac and Quinn 1988) — are likewise likely to have a stock-specific component but are also influenced by environmental conditions.

The sea migration of salmon can be regarded as an adaptation to improve foraging success, growth and reproductive output (Northcote 1984). We can therefore expect the inherited spatial marine distribution of salmon stock to be in relation to the location of the feeding grounds and their distance from the home river. Distant migration is very likely an adaptive behavioural trait for the Iijoki salmon, because only scant food is available for post-smolts and adult salmon in the Bothnian Bay (northern Gulf of Bothnia; *see* Fig. 1), near the marine entry of the home river (Salminen *et al*. 1994). The short-migratory pattern of the Neva salmon is also related to their original environment, because there are feeding grounds for salmon in the Gulf of Finland, near the native area of the Neva stock (Salminen *et al*. 1995). Brannon (1984) postulated that when salmon enter the marine environment they have an innate directional preference or sequence of preferences that orientate them into their ancestral feeding range. He also reported that transplantation to another river system changes the sea distribution of recoveries to some extent but that transplantation within the same river system, without changing the entry into the sea, does not change the migration pattern in marine waters. In accordance with his ideas, the Iijoki stock released at a foreign point of marine entry followed the innate long distance migration pattern. In this case, although released into the Gulf of Finland, the Iijoki salmon migrated to the feeding grounds in the Baltic's main basin, to which they also migrate when released in their native northern area. It is possible that they were guided by environmental factors, for example, surface currents in the sea. Despite the long distance between the foreign release site and the location of their home river, the Iijoki salmon seemed to have as precise a homing ability in this foreign environment as had the Neva salmon in their sea area.

Inheritance of migration pattern

The crossing experiment conducted between the two salmon stocks with different spatial marine distributions revealed the inheritance of the migration pattern. The spatial sea distributions of the hybrid offspring differed from those of the pure parental groups released at the same place and time. Moreover, the reciprocal hybrid groups had different sea migration patterns. The male parent had a slightly stronger effect on the spatial distribution of the offspring in the sea than had the female parent.

One assumption is that the marine distribution of salmon is a polygenic trait and its genetic variation is mainly additive. In that case, the hybrids should have an intermediate manifestation to those of the parental stocks. Here, however, both hybrid groups migrated farther than did the parental stocks. Such a change in a phenotypic trait may be due to loss of adapted gene combinations in crossing and non-additive genetic variation. Salmon populations are widely differentiated and adapted to local environments. This adaptation is controlled by a combination of genes, genes in many loci being selected for their joint effect on fitness. Some stock-specific adaptive characters may even appear because of epistatic interactions (Falconer and Mackay 1996). If the stock-specific feeding migration pattern is controlled by several coadapted genes, crossing may break these combinations, and the sea migration of the offspring in the F_1 generation will then differ from that of the parents. The crossing did not, however, increase the straying rate; straying was no more common among the hybrid offspring groups than it was among the parental stocks, at least over long distances.

Another reason for the unexpected, long feeding migration of the hybrids might be the large phenotypic and genetic variation in the parental stocks. The experimental groups were not the best possible because they were partly established in different years. Hence the parents in the hybrid and pure groups were not the same individuals. In addition to the genetic variation between stocks, the genetic variation within a stock could have an effect on the phenotypic variation between the groups. Had the female parents in the parental and hybrid groups been the same individuals, the hybrid offsprings might have resembled their mother stock more partly due to the greater similarity in genotype, but also due to the similarity in maternal effects (Falconer and Mackay 1996).

Smolt age and size and migration pattern

The recovery rate varied among experimental groups, increasing with the mean smolt size of the group. This phenomenon in salmon has been connected with the better survival of large smolts after release than that of small smolts (Salminen *et al.* 1995). The different recovery rate of the experimental groups was thus more likely linked to the different smolt size than to genetic factors.

Smolt age had no significant influence on the catch site, but it did have an effect on the catch time. Other authors (Hansen and Jonsson 1991a, Salminen *et al.* 1994) have noted that the smolt age influences the migration behaviour of the released salmon to some extent. The minor difference we documented was consistent with the findings of the Neva salmon transplantation experiments conducted in Norway, in which a large proportion of the 2+ Neva smolts remained in a fjord in their first sea year, but the 1+ Neva smolts left the fjord soon after release (Hansen and Jonsson 1991a). Our experiments showed a similar slight difference between the 1+ and 2+ Neva salmon groups. In the first winter, the Neva salmon released as 1-year-olds seemed to be caught more frequently in the Baltic's main basin than were the Neva salmon released as 2-year-olds (Fig. 3). If small smolts tend to migrate greater distances, as previously observed in the Iijoki stock (Salminen *et al.* 1994), then the inherent difference in the spatial distribution between the parental Neva (1+ and 2+ smolts) and Iijoki stocks (2+) was even greater than the difference we observed.

Another likely reason for the somewhat larger frequence of the 2+ Neva smolts in the Gulf of Finland is that they were more catchable during the first sea winter. Salminen *et al.* (1995) showed size-selective post-smolt fishing mortality of large smolts in the Gulf of Finland for releases in 1980–1991. The largest smolts started to recruit in the longline fishery in the first sea year in the Gulf of Finland. The rise in the recapture rate of adult salmon levelled off when the smolt size exceeded 22 cm (Salminen *et al.* 1995). In our study, the mean lengths of the 2+ Neva and 2+ Iijoki smolts were 21 and 22 cm, respectively. It is reasonable to suppose, then, that the 2+ smolts were, to some extent, more catchable in the first sea year.

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