



Effect of maternal and paternal line on spatial and temporal marine distribution in Atlantic salmon

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We examined the inheritance of the sea migration pattern of Atlantic salmon, *Salmo salar*, in a crossing and tagging experiment in the Baltic Sea. Individuals from the parental stocks, Neva and Iijoki, and their reciprocal hybrids were released as 2-year-old smolts, into the same estuary of the Bothnian Sea in 1994. Two thousand smolts from each of the four groups were marked with Carlin tags. The recapture rate of the tags was nearly 10%. We used log-linear models to analyse the marine distribution of the salmon groups from the tag recovery data. The pure stocks and their pooled hybrid groups all showed statistically significant differences between each other in spatial and temporal sea distribution. The Iijoki salmon were more frequently (9%) caught outside the Bothnian Sea than were the Neva salmon (2%). The majority of the Iijoki salmon (55%), but fewer Neva salmon (40%), were caught in the second sea year. In spatial distribution, the hybrids seemed to be intermediate between the parental stocks, with no differences between reciprocal female and male lines. In duration of sea migration and age at maturity, however, the hybrids were very similar to their maternal line, the effect of which was thus clearly stronger than that of the paternal line.

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Both genetic and environmental factors influence the migration behaviour of salmonids (Quinn & Dittman 1990); each stock has adapted uniquely to the particular environment it has experienced during its life history. Adaptation to the home river and sea is a result of the selection of behavioural traits closely associated with the fitness of the individual. Examples of these traits are the seasonal timing of the return migration in Atlantic salmon, *Salmo salar* (Hansen & Jonsson 1991), the accuracy of homing in Pacific salmon, *Oncorhynchus tshawytscha* (McIsaac & Quinn 1988) and the balance between homing and straying in salmonid species, *Oncorhynchus* spp. and *Salmo* spp. (Altukhov & Salmenkova 1994; Thorpe 1994).

As well as differences in behavioural and life history traits between salmon stocks (Pascual & Quinn 1994), there are differences in life history characters such as age and size at maturity, breeding cost and survival between males and females (Randall et al. 1986; Jonsson et al.

1991a; Fleming 1996). In Atlantic salmon the two sexes may show different migratory behaviours in river (Jonsson et al. 1990; Fleming 1996) and in sea (Schaffer 1979; McKinnell et al. 1994) environments. Usually these differences are linked to differences in the roles of the sexes in reproduction; genetic differences are not thought to be involved. However, because of maternal effects females may have a stronger influence than males on the phenotypic expression of many traits of the offspring. These maternal effects may be due to the mother's nuclear and extranuclear genes and her environmental factors (Falconer & Mackay 1996; Heath & Blouw 1998).

Sea migrations of salmon are wide ranging and long lasting (Carlin 1969; Hansen & Quinn 1998). The feeding migration of Atlantic salmon stocks in the Baltic can take the fish 500–1500 km away from their home river within this brackish-water basin (Carlin 1969; Lindroth et al. 1982; Kallio-Nyberg & Ikonen 1992). Atlantic salmon then usually leave the sea feeding areas after 1–4 years (Jonsson et al. 1991b). In the Baltic Sea, 4-sea-year-old salmon are rare. The homing migration to the natal river or release site is an active and rapid event, but the migration speed declines when fish approach the home river (Hansen et al. 1993). Atlantic salmon in the Baltic Sea, Baltic salmon, are heavily exploited during their feeding migration (Salminen et al. 1995).

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We compared the marine migratory behaviour of two pure stocks of Atlantic salmon and their reciprocal hybrid stocks in a crossing experiment. Our aim was to test whether the stocks showed genetic differences in spatial or temporal marine feeding distributions. The spatial distribution of fish recovered from the sea was assumed to reflect the spatial sea distribution of the stock. We calculated the temporal distribution of the fish from the date of capture of the tagged fish. The tag recovery data of experimental groups were analysed with log-linear models.

The two pure salmon stocks used, Neva and Iijoki, tend to migrate for different distances (Kallio-Nyberg & Ikonen 1992). We expected the phenotypic difference in the sea migration pattern between the groups to be due to genetic factors, because the conditions of the experimental groups were similar before their release. First, we analysed the differences in recovery site and recovery time between the pure and the hybrid stocks. Our null hypothesis was that the stocks did not differ in their spatial or temporal sea distribution. If differences did occur, they might have been a result of either genetic or environmental variance, or both. When the environmental variation was nullified, the observed differences must have been caused by genetic factors. We eliminated environmental variation by treating the fish groups similarly in similar environments and by releasing them at the same time and in the same place. We also tested the hypothesis that the two reciprocal hybrid groups (Iijoki_{females} × Neva_{males} and Neva_{females} × Iijoki_{males}) show similar sea migration patterns, that is, that female and male lines have similar effects on the spatial and temporal marine distributions.

METHODS

Salmon Stocks

We used Iijoki and Neva salmon stocks and their reciprocal hybrids. Experimental groups were released at the same time and at the same site in the estuary of the river Kokemäenjoki (Fig. 1). The Iijoki stock originated from the river of the same name, which discharges into Bothnian Bay (subarea 31) in northern Finland (Fig. 1). The Neva stock originated from the river Neva, which drains into the Gulf of Finland (subarea 32) in Russia (Fig. 1). Both stocks have been reared in hatcheries for several generations, the Iijoki salmon since the 1960s and the Neva salmon since the 1970s. The average feeding migration distance of the Iijoki salmon is longer than the sea migration distance of the Neva salmon when released into the Bothnian Sea (Kallio-Nyberg & Ikonen 1992). Transplantation experiments have shown that Neva salmon tend to remain (95%) in this sea area, only 4 and 1% of them being caught further south, in the Main Basin (subareas 24–29) and Gulf of Finland, respectively. In contrast, less than half (49%) of the Iijoki salmon remain in the Bothnian Sea (Kallio-Nyberg & Ikonen 1992). The majority feed in the Main Basin, in the southern Baltic Sea, although some remain in the Bothnian Sea to feed (Salminen et al. 1994; Koljonen & McKinnell 1996). When Neva salmon were released into their original sea

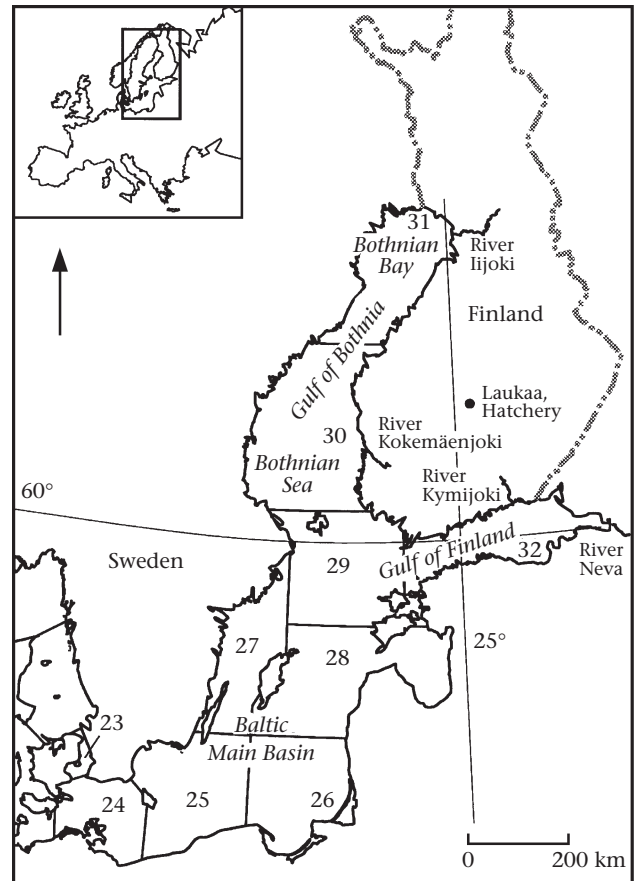


Figure 1. Map of the Baltic Sea showing sea areas: Bothnian Bay (31), Bothnian Sea (30), Gulf of Finland (32) and Baltic Main Basin (24–29). The estuaries of the Kokemäenjoki, Iijoki, Neva and Kymijoki and the hatchery station at Laukaa are marked.

area, the Gulf of Finland, they fed both in the Gulf of Finland and in the Baltic Main Basin (Kazakov 1985; Salminen et al. 1995).

Crossing Experiment

We studied the inherited nature of marine migration by establishing groups of fish that differed from each other only genetically. The same hatchery-reared parental fish, 20 of each sex, from the Neva and Iijoki stocks were used to create reciprocal hybrid and pure groups in 1991. We stripped 2 cm³ of eggs from each female and used half (1 cm³) to establish a pure group and half a hybrid group. The eggs of each female were fertilized by one male selected at random from the mating group. Spawners were taken from broodstocks kept at the Laukaa hatchery of the Finnish Game and Fisheries Research Institute, where the crossing experiment was conducted and the fish were reared (Fig. 1). After the mating, the eggs of each group were pooled. The four groups were reared separately under standard hatchery conditions (from 1991 to 1994). The fish were reared in plastic (first year) and concrete (second year) tanks under ambient water temperature and natural light conditions. They were fed

Table 1. Tag recoveries of Iijoki and Neva stocks and their hybrids ($Ne_{females} \times li_{males}$ and $li_{females} \times Ne_{males}$) in the Baltic Sea in 1994–1997

Stock	Annual recoveries, number of returned tags									
	1994		1995			1996			1997	
	Total	MB	BS	O	Total	MB	BS	O	Total	Total
Iijoki	12	8	96	0	104	8	76	3	87	1
Neva	17	1	57	0	58	2	85	2	89	0
$Ne_f \times li_m$	18	1	54	3	58	4	76	0	80	2
$li_f \times Ne_m$	13	1	80	3	84	5	67	1	73	1

Total: all recoveries per year in the Baltic Sea. Recoveries from the Main Basin (MB) and Bothnian Sea (BS) are shown separately. Recoveries from the Gulf of Finland and Bothnian Bay are pooled (O). Year 1995 from January to December was the second sea year for the salmon. We tagged 2000 smolts per stock.

during daylight hours with commercial pelleted fish food dispersed by automatic feeders that adjusted the amount of food as the fish grew and the water temperature changed. The rearing conditions were kept similar for the experimental groups. We tagged 2000 smolts from each of the four groups. The groups were released into the estuary of the Kokemäenjoki in May 1994 (water temperature 10.2°C; Fig. 1). We recorded the total smolt length (mm) of each fish during tagging and used this initial length as smolt length in analyses.

Two months before release, the 2-year-old presmolts were individually marked with external Carlin tags under MS 222 anaesthesia (Carlin 1969). The tag was attached by a double-steel wire through the dorsal musculature. The Carlin tag is a plastic tab (18 × 4 × 0.5 mm) and weighs 0.15 g (a tagged fish weighs about 120 g). Carlin tagging has been classified as an animal experiment without pain by the committee of animal experimentation of the Game and Fisheries Research Institute and also by the Provincial State Office based on the Act of Animal Protection. The licence for this study was given by the Game and Fisheries Research Institute. The tagging was conducted in cold water (1.0°C) in early spring, when the infection risk is low and the fish have time to recover from the handling before they are released. Mortality during tagging is very low, under 0.001% (M. Naarminen, tagging chief, personal communication).

External Carlin tags have been used in migration studies to compare groups released at the same time or in the same place (Jonsson et al. 1990; Hansen & Jonsson 1991). There is some evidence that the use of Carlin tags on salmon smolts has adverse effects on survival in the sea (Isaksson & Bergman 1978; Hansen 1988), but this depends on the size of the tagged fish and the handling and physiological condition of the fish (Isaksson & Bergman 1978; Soivio & Virtanen 1985). Tagging has had no effect on the mortality of larger (over 24 cm) sea trout, *Salmo trutta* (Berg & Berg 1987). In our experiment, the smolts were relatively large (mean 23 cm). Carlin tagging was the only method available to provide information on individually tagged fish, which the fishermen could detect and collect from offshore and coastal catches. Adipose fin clipping could only have been used to distinguish reared fish from wild fish as a group in the total

catch, not to get information on individual growth or migration. Tagging can be expected to have an equal effect on the fish groups studied.

Recovery Time and Site

The recovery data were based on tagged fish caught by fishermen (Table 1), who returned the tags with information on the date of capture, and the catch site and size of the fish. The recovery sites were classified into two categories according to the ICES subdivisions of the Baltic Sea (Anonymous 1996), that is, the Baltic Main Basin (MB; subareas 24–29) and the Bothnian Sea (BS; subarea 30; Fig. 1). Two subareas, the Gulf of Finland (32) and Bothnian Bay (31), were excluded because of the small number of recoveries from them. The majority (over 80%) of recoveries were made in the Bothnian Sea and in the second (1995) and third (1996) sea years. Our analyses were based on fish of those year classes only. These fish could have been on either the feeding or homing migration. The total number of salmon recovered in the four groups was 763, that is, 218 Iijoki fish, 177 Neva fish, 183 $Neva_{female} \times Iijoki_{male}$ hybrids and 185 $Iijoki_{female} \times Neva_{male}$ hybrids, including all recoveries in the sea and river and recoveries without information on catch time and site (see Table 1). The recapture rate was ca. 10%.

As salmon are known to return to their release site when they mature (e.g. McKinnell et al. 1994), we could use their return to estimate the age at maturity. The sea age at sexual maturity for each of the four groups was determined separately only for those adult salmon that had returned to the release square at the mouth of the river Kokemäenjoki in 1995 and 1996. There were 381 such fish, which accounted for half (49.9%) of all returned tags.

Recapture and Fishery

Baltic salmon are caught mainly in the open sea, only 3% of the total catch being taken in rivers (Karlsson & Karlström 1994). Salmon are heavily exploited in both the Main Basin and the Gulf of Bothnia (Anonymous

Table 2. Mean smolt length at tagging and growth as increment of length in the sea

Stock	N	Smolt length (cm)*	Increment of length (cm)†			
			N	Second sea year	N	Third sea year
Iijoki	218	22.7±1.89	45	37.2±8.59	48	75.5±7.17
Neva	177	22.6±1.67	31	34.3±11.76	45	78.1±6.73
Ne _f ×Ii _m	183	22.9±1.74	31	37.4±8.61	40	76.8±7.32
Ii _f ×Ne _m	185	22.5±1.34	45	36.5±5.97	46	75.5±7.64

*Mean smolt length±SD of captured fish measured at tagging.

†Mean length at capture minus smolt length at tagging±SD.

1996). In the Main Basin of the Baltic Sea, the majority of tag recoveries were made offshore by commercial drift-net and long-line fisheries. In the Bothnian Sea, salmon were caught by both offshore and coastal fisheries. The scarcity of data ($N=30$, see Table 4 in the Results) from the Main Basin was due not to the low fishing effort but to the lack of interest by fishermen in returning tags. Of the total number of tag recoveries ($N=763$), 8.6% were returned without information on the recovery site or time. The tagging experiment did not therefore convey a full picture of the migration routes and the contribution of the different feeding areas. We can nevertheless compare fish groups with equal catchability, that is, with similar age-specific length and the same release time and place. There may be variation in the tag return rate between different sea areas, but this is not important in a comparative study such as ours, in which all the groups compared use the same feeding areas, in this study the Main Basin and the Bothnian Sea (Table 1).

Smolt size is reported to affect the marine feeding migration pattern of salmon (Salminen et al. 1994; Kallio-Nyberg et al. 1999). Both the initial smolt size of the fish and their growth have an effect on catchability and fishing mortality (Salminen et al. 1995). We did not include smolt length in our analysis, because we could not find any differences in smolt sizes between the stocks; all groups had the same smolt length (23 cm, $N=763$; $F_{3,759}=2.28$, $P=0.078$; Table 2). In addition, no differences were found in growth rates (length at capture minus smolt length at tagging) between the pure and hybrid stocks in either year (second year: $F_{3,148}=0.85$, $P=0.468$; third year: $F_{3,175}=0.95$, $P=0.415$; Table 2). We therefore assume that the groups had a similar fishing mortality in relation to the time they spent in the sea and the gear used.

Statistical Methods

The recovery data were presented in multiway contingency tables and analysed by log-linear methods (McCullagh & Nelder 1989; Everitt 1992) using the CATMOD procedure of the SAS statistical package (SAS Institute 1989). Log-linear methods are designed for categorical data such as the numbers of recovered tags in our study. The method aims to explain the effects of single variables or their combinations (interactions) on the recoveries. We included three effect

variables (stock, recovery site and recovery time) in our three-dimensional log-linear models. The stock variable was either pure stocks and hybrids or maternal and paternal lines.

The models were analysed in a hierarchical way by first introducing single variables into the model, and then adding interactions one by one until all possible interactions were covered. At each step, the fit of the model was checked by a likelihood ratio (G^2) test. When a model did not differ significantly from the data ($P>0.05$), we checked whether a model with more interactions gave a statistically better fit to the data. In likelihood ratio tests, this can be done by calculating the difference in G^2 values. The differences have approximately the same distribution as a χ^2 distribution with the degrees of freedom of the test equal to the difference in degrees of freedom of the models that are compared. When the P value of the difference was above 0.05 (i.e. the more complex model did not fit significantly better than the simpler one), we accepted the simpler model. We continued the testing until the new terms no longer improved the fit of the accepted model.

RESULTS

Effect of Stock on Marine Distribution

The majority of salmon (85%) of all groups were caught in the Bothnian Sea (subarea 30) in their second and third sea years in 1995 and 1996 (Table 1, Fig. 1). The Iijoki stock was caught more frequently outside the Bothnian Sea than was the Neva stock. In 1995 and 1996, 8.5% of the Iijoki salmon, but only 2.1% of the Neva salmon and 3.8% of the hybrids (Neva_{female} × Iijoki_{male} 3.7% and Iijoki_{female} × Neva_{male} 3.9%), on average, were caught in the Baltic Main Basin in both sea years, excluding the few recoveries from the Gulf of Finland or Bothnian Bay (Table 1). The duration of sea migration differed between the parental stocks, the Iijoki salmon being caught somewhat earlier (55% in the second sea year) than the Neva salmon (40% in the second sea year). Of the hybrid salmon (pooled stocks), 47% were caught in the second sea year (Table 1).

We analysed the interrelationships between stock, recovery site and recovery time by log-linear models. The simplest log-linear model with $P>0.05$ included two interactions: with stock (S) and recovery site (P), and with

Table 3. Effect of stock on spatial and temporal marine distribution

Model	<i>df</i>	G^2	<i>P</i>
S,P,T	7	20.61	0.004
T,SP	5	12.33	0.030
P,ST	5	12.76	0.025
S,PT	6	18.97	0.004
SP,ST	3	4.48	0.214f
SP,PT	4	10.69	0.030
ST,PT	4	11.12	0.024
SP,ST,PT	2	1.86	0.394f

Log-linear models and test of independence between classified variables: stock (S): Neva, Iijoki, hybrids (pooled); recovery site (P): Bothnian Sea, Main Basin; recovery time (T): 8–19 months, 20–31 months in sea. Model: variables are expected to be independent when separated by a comma and to interact when there is no comma. G^2 =likelihood ratio, test value. *P* values indicate discrepancy between model and data. f shows models with best fit ($P>0.05$).

stock and recovery time (T) (Table 3). The model with three interactions was not significantly better than this model ($G_{SP,ST}^2 - G_{SP,ST,PT}^2 = 2.62$, $df=1$; the critical value of the χ^2 distribution with $df=1$ and at the risk level 0.05 is 3.84). This shows a statistically significant difference in the spatial and temporal sea distribution of these three groups. As pointed out above, the Iijoki salmon were caught earlier than the Neva salmon (second versus third sea year) and the majority of the salmon caught further away from the release site, in the Main Basin, belonged to the Iijoki stock. The spatial and temporal sea distributions of the pooled hybrid group were intermediate between those of the parental stocks. The analyses also showed that there was no interaction between recovery site and recovery time. Thus the spatial distribution of the groups was independent of the duration of sea migration.

Effect of Sexes on Spatial Marine Distribution

The spatial marine distributions of the two reciprocal hybrid stocks were similar and intermediate between the distributions of the parental stocks. Within the Bothnian Sea and Main Basin, during the period 8–31 months in the sea, 9% of the Iijoki, 4% of the hybrid and 2% of the Neva salmon were caught in the Main Basin (Table 4, Fig. 1).

There was an interaction both between maternal line (F) and recovery site (P), and between paternal line (M) and recovery site (Table 4). Thus, there were no differences between males and females in their influence on the spatial distributions of the hybrids. The model with three interactions was not significantly better than this two-interaction model ($G_{FP,MP}^2 - G_{FM,FP,MP}^2 = 2.43$, $df=1$, $\chi_{0.05}^2 = 3.84$). There was, however, a significant difference between the two-interaction model and the nested models with one interaction (e.g. $G_{M,FP}^2 - G_{FP,MP}^2 = 4.22$, $df=1$, $\chi_{0.05}^2 = 3.84$). Both female and male parents had, therefore, a statistically significant influence on the catch site of the hybrids (Table 4).

Table 4. Effects of maternal and paternal lines on spatial marine distribution in the Main Basin and Bothnian Sea

	Recovery site			
	Bothnian Sea		Main Basin	
	Male Iijoki	Male Neva	Male Iijoki	Male Neva
Female Iijoki	172	147	16	6
Female Neva	130	142	5	3
Model	<i>df</i>	G^2	<i>P</i>	
F,M,P	4	11.24	0.024	
P,FM	3	8.29	0.040	
M,FP	3	6.71	0.081	
F,MP	3	7.02	0.071	
FM,FP	2	3.76	0.152	
FM,MP	2	4.07	0.130	
FP,MP	2	2.49	0.288f	
FM,FP,MP	1	0.06	0.801f	

Log-linear models and test of independence between classified variables: female (maternal) line (F; Neva stock, Iijoki stock), male (paternal) line (M; Neva, Iijoki), recovery site (P; two classes: Main Basin and Bothnian Sea). Model: variables are expected to be independent when separated by a comma and to interact when there is no comma. G^2 =likelihood ratio, test value. *P* values indicate discrepancy between model and data. f shows models with best fit ($P>0.05$). The number of recoveries is shown in relation to recovery site, male line and female line.

Effects of Sexes on Temporal Sea Distribution

The duration of migration in years was very similar in hybrid offspring and their mother stocks. Of the two groups with Iijoki salmon as female parents (Iijoki_{female} × Iijoki_{male} and Iijoki_{female} × Neva_{male}), 55 and 53%, respectively, were caught in the second sea year. Correspondingly, about 40% of the two groups with Neva salmon as female parents (Neva_{female} × Neva_{male} and Neva_{female} × Iijoki_{male}) were caught in the second sea year (Table 5, Fig. 2).

The model with an interaction between female line (F) and recovery time (T) showed a reasonable fit with the data (Table 5), whereas the model with an interaction between male line (M) and recovery time was not compatible with the data (Table 5). The first model, with an interaction between female line and time, was significantly better than the model with independent factors ($G_{F,M,T}^2 - G_{M,FT}^2 = 11.94$, $df=1$, $\chi_{0.05}^2 = 3.84$). Adding the interaction of female line and male line did not improve the model significantly ($G_{M,FT}^2 - G_{FM,FT}^2 = 2.95$, $df=1$, $\chi_{0.05}^2 = 3.84$). The model with three interactions was also in good agreement with the data, but the addition of interactions other than that between the female line and time (FT) did not improve the model significantly ($G_{M,FT}^2 - G_{FM,FT,MT}^2 = 3.12$, $df=2$, $\chi_{0.05}^2 = 5.99$). The maternal line alone was thus sufficient to explain the duration of sea migration. This interaction (FT) was due to differences in recovery time between both reciprocal hybrid groups and between pure groups. In the second sea year, the hybrids from the Iijoki maternal line were more common than those from the Neva maternal line. More hybrids

Table 5. Effects of maternal and paternal lines on temporal marine distribution

	Recovery time			
	2 years		3 years	
	Male Iijoki	Male Neva	Male Iijoki	Male Neva
Female Iijoki	104	81	84	72
Female Neva	55	58	80	87
Model	<i>df</i>	G^2	<i>P</i>	
F,M,T	4	15.10	0.004	
T,FM	3	12.15	0.006	
M,FT	3	3.16	0.368f	
F,MT	3	14.69	0.002	
FM,FT	2	0.21	0.901f	
FM,MT	2	11.74	0.002	
FT,MT	2	2.74	0.253	
FM,FT,MT	1	0.04	0.842	

Log-linear models and test of independence between classified variables: female line (F; Neva, Iijoki), male line (M; Neva, Iijoki) and recovery time (T; sea year 2=8–19 months, sea year 3=20–31 months in sea). Recoveries within the Main Basin and Bothnian Sea are included. Model: variables are expected to be independent when separated by a comma and to interact when there is no comma. G^2 =likelihood ratio, test value. *P* values indicate discrepancy between model and data. f shows models with best fit ($P>0.05$). The number of recoveries is shown in relation to recovery time, male line and female line.

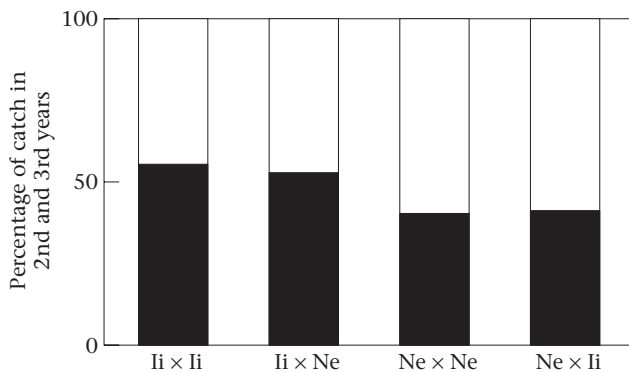


Figure 2. Temporal marine distribution of Iijoki (Ii×Ii), Neva (Ne×Ne) and hybrid stocks (Ii_{female}×Ne_{male} and Ne_{female}×Ii_{male}) of Atlantic salmon within the Baltic Sea. ■: Percentage of catch in second sea year; □: percentage of catch in third sea year. The number of recoveries is shown in Table 5.

from the Neva maternal line were caught in the third sea year than were those from the Iijoki maternal line. No such effect was found in offspring of the paternal line.

The age at sexual maturity as estimated from the fish that had returned to the release square at the mouth of the Kokemäenjoki was lower for the Iijoki salmon than for the Neva salmon. The returning hybrids resembled their mothers more than they did their fathers in a similar way as when analysed from the sea age of the total catch. At the release square, the second sea year or the one sea winter salmon accounted for 57% ($N=124$) of the Iijoki group, 51% ($N=85$) of the hybrids Iijoki_{female} ×

Neva_{male}, 46% ($N=89$) of the hybrids Neva_{female} × Iijoki_{male} and 39% ($N=83$) of the Neva group. The age at maturity, as calculated from fish returning in the release square after one or two sea winters, was 1.42 years for Iijoki salmon, 1.49 years for the maternal Iijoki hybrid group, 1.61 years for Neva salmon and 1.53 years for the maternal Neva hybrid group. Thus the age of salmon caught in the sea and the age at sexual maturity were correlated and both were largely determined by the characters of the female parents.

DISCUSSION

Marine Distribution of Pure Stocks

Our results showed that the sea migration pattern of salmon is a stock-specific and quantitatively inherited trait. All three (Neva, Iijoki, hybrid stock) groups differed significantly from each other in their sea migration pattern. The null hypothesis that there is no difference in sea migration patterns between the pure stocks was thus rejected. The feeding migration distance of the pure Neva stock was shorter than that of the other pure stock, Iijoki, as documented by Kallio-Nyberg & Ikonen (1992). The phenotypic differences in the spatial marine distribution could be expected to have a genetic basis, because growth conditions were similar for both stocks and also because smolt size as well as growth rates were similar for all groups. These findings agree with Hansen et al.'s (1993) observations that the sea migration pattern of Atlantic salmon may be partly genetically determined. In addition to genetic factors, smolt size and the abundance of food are expected to affect the feeding migration pattern (Salminen et al. 1994; Kallio-Nyberg et al. 1999).

The Iijoki stock was more frequently caught in its second sea year than was the Neva stock. Moreover, the frequency of 1-year-old returners, and thus probably mature fish, was higher for Iijoki than for Neva salmon. The heritable variance in age at maturity was documented in Atlantic salmon by Gjerde (1984). Here the Iijoki salmon tended to undergo a longer feeding migration within a shorter time frame (2 years) than did the Neva salmon (3 years). The spatial distribution of sea migration was thus independent of the duration of the migration. It is therefore unlikely that stock-specific differences in spatial sea distribution were due to differences in the parental sea age or age at sexual maturity of the stocks; the stock-specific differences in the duration of the sea migration were, however, very probably stock-specific genetic traits. This suggests that spatial and temporal distribution are under separate genetic control.

Since the lengths of the smolts in all four groups were the same, variation in smolt size could not have caused the observed variation in spatial sea distribution; smolt size was therefore excluded from the analyses. Other experimental releases of salmon smolts into Bothnian Bay have, however, shown that smolt size does have an effect on the spatial sea distribution of offspring. Salmon released into Bothnian Bay as smaller smolts migrate further south than those released as larger smolts (Salminen et al. 1994; Kallio-Nyberg et al. 1999).

Marine Distribution of Hybrid Stocks

The hybrid groups had similar spatial distributions in the sea, and their behaviour was intermediate (3.8% in the Main Basin) between that of the two parental stocks (2.1 and 8.5% in the Main Basin, Table 1), implying that the inherited traits of female and male parents regulate the spatial sea migration behaviour equally. The intermediate expression of the spatial marine distribution indicates that the level of migratory activity can be inherited. Inheritance of spatial sea distribution has not previously been demonstrated in Atlantic salmon, although the population-specific migration patterns observed in Pacific salmon have been considered partly genetically determined (Brannon 1984; Pascual & Quinn 1994). The inheritance of both migration distance and direction have been studied extensively in passerine birds (Berthold & Pulido 1994; Helbig et al. 1994). Crossing experiments have shown that hybrid blackcaps, *Sylvia atricapilla*, whose parent populations migrate for different distances, had an intermediate level of migratory activity (Berthold 1991). The conclusion was that migrant blackcaps were equipped with inherited population-specific programmes that determined the duration of migration (Berthold 1991). It is possible that the sea migration of Atlantic salmon is regulated by a multilocus system similar to that proposed for migratory blackcaps.

Our analyses, which were based on the spatial distribution of recoveries from only two areas, did not reveal stock-specific differences in migration direction; they did, however, show a clear difference in migration distance. The frequency data enable us, in principle, to detect differences in spatial distribution between groups with the same migration distance but a different migration direction. However, the data would have to be subdivided into smaller classes than the limited number of recoveries allowed. We observed differences in spatial distribution by using only two classes for each recovery place. The determination of classes was subjective and was based on the idea that the fish have a choice between the food resources of two basins, the Bothnian Sea and the Main Basin.

In temporal marine distribution, the effect of the maternal line was stronger than that of the paternal line. Both hybrid stocks were caught at the same age as their maternal stock. The difference between the parental stocks in the duration of the sea migration obviously had a direct genetic basis, but the strong effect of the female line on the hybrids indicates that temporal marine distribution is largely subject to maternal effects. In fish, maternal effects can be transmitted through the eggs (Gjerde & Refstie 1984) either as nutritional prenatal and postnatal influences or as extranuclear organelles. In Atlantic salmon, the body weight of fingerlings and adults is thought to be influenced by maternal effects (Gjerde & Refstie 1984). The maternal effects do not necessarily have a direct influence on behavioural traits. Behavioural changes may rather be a secondary consequence of changes in other traits influenced by maternal effects (Heath & Blouw 1998). The strong effect of the maternal line on the duration of marine migration in

adult fish suggests that maternal effects may have a genetic component as well.

The hybrid groups attained maturity at the same year of age as their maternal line, suggesting that maternal effects are more important than direct genetic factors for the age at which offspring mature. Maternal effects have been thought to account, among other things, for the large variation in age at maturity in Atlantic salmon and rainbow trout, *Oncorhynchus mykiss* (Gjerde 1986). Here, the age at maturity was almost invariably linked to the maternal line when the stocks were reared in similar environments. The conclusion is that the age at maturity is controlled by products of the mother's nuclear and extranuclear genes and the maternal environment. The age at maturity controlled the temporal distribution of the fish in the sea and in the catches.

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References

- Altukhov, Y. P. & Salmenkova, E. A. 1994. Straying intensity and genetic differentiation in salmon populations. *Aquaculture and Fisheries Management*, **25**, Supplement 2, 99–120.
- Anonymous 1996. *Report of the Baltic Salmon and Trout Assessment Working Group*. Copenhagen: International Council for the Exploration of the Sea.
- Berg, O. K. & Berg, M. 1987. Effects of Carlin tagging on mortality and growth of sea trout, *Salmo trutta* L. *Fauna Norvegica Series A*, **8**, 15–20.
- Berthold, P. 1991. Genetic control of migratory behaviour in birds. *Trends in Ecology and Evolution*, **6**, 254–257.
- Berthold, P. & Pulido, F. 1994. Heritability of migratory activity in a natural bird population. *Proceedings of the Royal Society of London, Series B*, **257**, 311–315.
- Brannon, E. L. 1984. Influence of stock origin on salmon migratory behaviour. In: *Mechanisms of Migration in Fishes* (Ed. by J. D. McCleave, G. P. Arnold, J. J. Dodson & W. H. Neill), pp. 103–111. New York: Plenum.
- Carlin, B. 1969. The migration of salmon. *Swedish Salmon Research Institute Report Laxforskningsinstitutet Meddelande*, **2–4**, 14–22.
- Everitt, B. S. 1992. *The Analysis of Contingency Tables*. London: Chapman & Hall.
- Falconer, D. S. & Mackay, T. F. C. 1996. *Introduction to Quantitative Genetics*. 4th edn. Harlow: Longman.
- Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Review in Fish Biology and Fisheries*, **6**, 376–416.
- Gjerde, B. 1984. Response to individual selection for age at sexual maturity in Atlantic salmon. *Aquaculture*, **38**, 229–240.
- Gjerde, B. 1986. Growth and reproduction in fish and shellfish. *Aquaculture*, **57**, 37–55.
- Gjerde, B. & Refstie, T. 1984. Complete diallel cross between five strains of Atlantic salmon. *Livestock Production Science*, **11**, 207–226.
- Hansen, L. P. 1988. Effects of Carlin tagging and fin clipping on survival of Atlantic salmon (*Salmo salar* L.) released as smolts. *Aquaculture*, **70**, 391–394.

- Hansen, L. P. & Jonsson, B. 1991. Evidence of a genetic component in the seasonal return pattern of Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology*, **38**, 251–258.
- Hansen, L. P. & Quinn, T. P. 1998. The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **55** (Suppl. 1), 104–118.
- Hansen, L. P., Jonsson, N. & Jonsson, B. 1993. Oceanic migration in homing Atlantic salmon. *Animal Behaviour*, **45**, 927–941.
- Heath, D. D. & Blouw, D. M. 1998. Are maternal effects in fish adaptive or merely physiological side effects? In: *Maternal Effects as Adaptations* (Ed. by T. A. Mousseau & C. W. Fox), pp. 178–201. New York: Oxford University Press.
- Helbig, A. J., Berthold, P., Mohr, G. & Querner, U. 1994. Inheritance of a novel migratory direction in central European blackcaps. *Naturwissenschaften*, **81**, 184–186.
- Isaksson, A. & Bergman, P. K. 1978. An evaluation of two tagging methods and survival rates of different age and treatment groups of hatchery-reared Atlantic salmon smolts. *Journal of Agricultural Research in Iceland*, **10**, 74–99.
- Jonsson, N., Jonsson, B. & Hansen, L. P. 1990. Partial segregation in the timing of migration of Atlantic salmon of different ages. *Animal Behaviour*, **40**, 313–321.
- Jonsson, N., Hansen, L. P. & Jonsson, B. 1991a. Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology*, **39**, 739–744.
- Jonsson, N., Hansen, L. P. & Jonsson, B. 1991b. Variation in age, size and repeat spawning of adult Atlantic salmon in relation of river discharge. *Journal of Animal Ecology*, **60**, 937–947.
- Kallio-Nyberg, I. & Ikonen, E. 1992. Migration pattern of two salmon stocks in the Baltic Sea. *ICES Journal of Marine Science*, **49**, 191–198.
- Kallio-Nyberg, I. & Koljonen, M.-L. 1997. The genetic consequence of hatchery-rearing on life-history traits of the Atlantic salmon (*Salmo salar* L.): a comparative analysis of sea-ranched salmon with wild and reared parents. *Aquaculture*, **153**, 207–224.
- 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.
- Kazakov, R. 1985. Condition of fish stock, yield to fishery and migrations of Atlantic salmon from rivers of the USSR to the Baltic Sea. *Finnish Fisheries Research*, **6**, 43–54.
- 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.
- Lindroth, A., Larsson, P.-O. & Bertmar, G. 1982. Where does the Baltic salmon go? In: *Coastal Research in the Gulf of Bothnia* (Ed. by K. Muller), pp. 387–413. Hague: W. Junk.
- McCullagh, P. & Nelder, J. A. 1989. *Generalized Linear Models*. London: Chapman & Hall.
- McIsaac, D. O. & Quinn, T. P. 1988. Evidence for a hereditary component in homing behaviour of chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 2201–2205.
- McKinnell, S., Lundqvist, H. & Johansson, H. 1994. Biological characteristics of the upstream migration of naturally and hatchery-reared Baltic salmon, *Salmo salar* L. *Aquaculture and Fisheries Management*, **25**, Supplement 2, 45–63.
- Pascual, M. A. & Quinn, T. P. 1994. Geographical patterns of straying of fall chinook salmon *Oncorhynchus tshawytscha* (Walbaum), from Columbia River (USA) hatcheries. *Aquaculture and Fisheries Management*, **25**, Supplement 2, 17–30.
- Quinn, P. & Dittman, A. H. 1990. Pacific salmon migrations and homing: mechanisms and adaptive significance. *Trends in Ecology and Evolution*, **5**, 174–177.
- Randall, R. G., Thorpe, J. E., Gibson, R. J. & Reddin, D. G. 1986. Biological factors affecting age at maturity in Atlantic salmon (*Salmo salar*). In: *Salmonid Age at Maturity* (Ed. by D. J. Meerburg), pp. 90–96. Canadian Special Publication of Fisheries and Aquatic Sciences 89. Ottawa: Minister of Supply and Services Canada.
- 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.
- SAS Institute 1989. *SAS/STAT User's Guide, Vol. 1, Version 6*. 4th edn. Cary, North Carolina: SAS Institute.
- Schaffer, W. M. 1979. The theory of life-history evolution and its application to Atlantic salmon. *Symposia of the Zoological Society of London*, **44**, 307–326.
- Soivio, A. & Virtanen, E. 1985. The quality and condition of reared *Salmo salar* smolts in relation to their adult recapture rate. *Aquaculture*, **45**, 335–343.
- Thorpe, J. E. 1994. Significance of straying in salmonids and implications for ranching. *Aquaculture and Fisheries Management*, **25**, Supplement 2, 183–190.