

# Effects of stock-specific and environmental factors on the feeding migration of Atlantic salmon (*Salmo salar*) in the Baltic Sea

Irma Kallio-Nyberg, Heikki Peltonen, and Hannu Rita

**Abstract:** Atlantic salmon (*Salmo salar* L.) stocks in the Baltic Sea are mainly exploited during their sea migration. The offshore fishery in the feeding grounds of these salmon permitted us to analyse the migrations of certain stocks on the basis of tag recovery data. Four salmon stocks from rivers draining into Bothnian Bay (25°E, 65.5°N) were selected for study. During 1984–1991, about 135 000 2-year-old hatchery-reared smolts were tagged and released. We applied logit models, with the site of recovery as a multcategory response variable, to analyse the distribution of tag recoveries in the Baltic Sea feeding grounds. The results showed the combined influence of stock, prey abundance, and smolt size on the spatial marine distribution of the salmon. Although stock-specific sea migration patterns were apparent, annual environmental factors had a stronger influence on the sea migration route of salmon than did the stock factor. The salmon released as small smolts (total length  $\leq 17.0$  cm) were more frequently caught farther from the release site than were those released as larger smolts ( $>17$  cm). The abundance of suitable prey (age 0+ herring) in the year of smolt release was found to be a key factor influencing the migration distance. The salmon released in the years of strong herring recruitment in the Gulf of Bothnia had a higher probability to stay in the Bothnian Sea for feeding and not to migrate farther south.

**Résumé :** Les stocks de saumon atlantique (*Salmo salar* L.) de la mer Baltique sont surtout exploités durant leur migration en mer. La pêche hauturière dans les aires d'alimentation de ces saumons nous a permis d'analyser les migrations de certains stocks grâce aux données de récupération de marques. Nous avons choisi quatre stocks de saumon de rivières qui se jettent dans le golfe de Botnie (25°E, 65,5°N). De 1984 à 1991, environ 135 000 smolts de 2 ans élevés en éclosure ont été marqués et lâchés. Nous avons appliqué des modèles logit, avec le site de recapture comme variable de réponse multicatégorique, pour analyser la distribution des récupérations de marques dans les aires d'alimentation de la Baltique. Les résultats ont révélé l'existence d'une influence combinée du stock, de l'abondance des proies et de la taille des smolts sur la distribution spatiale des saumons en mer. Bien que des profils de migration propres aux différents stocks aient pu être observés, les facteurs environnementaux annuels ont eu une influence plus marquée sur les voies migratoires du saumon en mer que le facteur stock. Les saumons qui étaient de petits smolts (longueur totale  $\leq 17,0$  cm) quand ils ont été lâchés ont été plus fréquemment recapturés à de plus grandes distances du site de lâcher que ceux qui étaient des smolts de plus grande taille ( $>17$  cm) quand ils ont été lâchés. Nous avons observé que l'abondance des proies de choix (hareng d'âge 0+) dans l'année du lâcher des smolts était un facteur clé qui déterminait la distance de migration. Il y avait une plus grande probabilité que les saumons lâchés dans les années de fort recrutement du hareng dans le golfe de Botnie demeurent dans la mer de Botnie pour s'alimenter et ne migrent pas plus au sud.

[Traduit par la Rédaction]

## Introduction

Migratory behaviour is an important adaptation in salmonids (Quinn and Dittman 1990) and is considered to improve foraging success, growth, and reproductive output (Northcote 1984). Variability in the migration behaviour of salmon has both a genetic and an environmental source. Genetic fac-

tors have been shown to control marine distribution and migration distance (Brannon and Setter 1989; Kallio-Nyberg and Ikonen 1992), homing and straying (Bams 1976; Pascual and Quinn 1994), homing accuracy (McIsaac and Quinn 1988), direction of immigration (Hansen et al. 1993), and timing of spawning migration (Hansen and Jonsson 1991). The marine migration of salmon is also affected by

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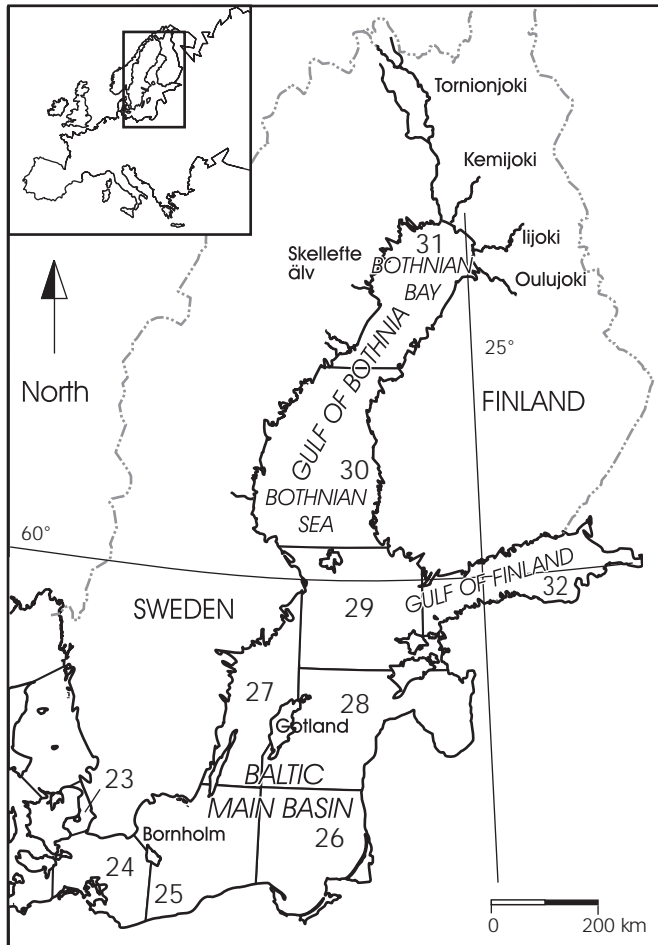
**I. Kallio-Nyberg.**<sup>1</sup> Finnish Game and Fisheries Research Institute, Quark Fisheries Research Station, Korsholmanpuistikko 16, FIN-65100 Vaasa, Finland.

**H. Peltonen.** Department of Limnology and Environmental Protection, Viikki, P.O. Box 27, FIN-00014, University of Helsinki, Finland.

**Hannu Rita.** Department of Forest Resources Management, Statistics, P.O. Box 24, FIN-00014, University of Helsinki, Finland.

<sup>1</sup>Author to whom all correspondence should be addressed. e-mail: irma.kallio-nyberg@rktl.fi

**Fig. 1.** The Baltic Sea. Estuaries of the rivers Tornionjoki, Kemijoki, Iijoki, and Oulujoki are shown. Sea areas: Southern Main Basin (ICES subdivisions 23–26), Northern Main Basin (27–29), and Gulf of Finland (32). The Gulf of Bothnia (30–31) consists of the Bothnian Sea (30) and Bothnian Bay (31).



interannual variations in water currents, sea temperature, and food availability (Reddin and Shearer 1987; Groot and Quinn 1987; Thomson et al. 1992). The genetic component in migratory behaviour can change from generation to generation, but phenotypic manifestation can vary from season to season and without genetic changes. Salmon can adapt behaviourally to unpredictable short-term changes in environmental conditions, and migratory behaviour linked with environmental signals can mitigate the potentially harmful impact of environmental variability on reproductive success (Leggett 1985).

The Baltic Sea (Fig. 1) is a closed system with respect to the feeding migrations of Atlantic salmon, *Salmo salar* L. (Christensen and Larsson 1979). There are, however, differences in the sea migration patterns of the various Atlantic salmon stocks in the Baltic Sea (Carlin 1969; Kallio-Nyberg and Ikonen 1992). The main feeding grounds for salmon from rivers draining into Bothnian Bay extend to the Main Basin, 1600 km farther south. Most smolts released into this bay migrate through the Bothnian Sea in August and September of the releasing year (Salminen et al. 1994). Some post-smolts, however, stay in the Bothnian Sea for feeding,

migrating only 400–500 km from their home stream (Salminen et al. 1994). Extended residence in the Bothnian Sea was connected with smolt size; adult fish recaptured in the Bothnian Sea and Main Basin in the 2nd sea-year or thereafter showed that salmon stocked as large smolts had a higher probability of remaining in the Gulf of Bothnia (Salminen et al. 1994).

Atlantic salmon in the Baltic Sea are exploited in mixed stock fisheries both in their feeding grounds and during their spawning migration (Karlsson and Karlström 1994). Baltic salmon stocks have declined in recent decades owing to the construction of hydroelectric dams, which prevent upstream migration, the occurrence of the M74 syndrome, which causes high mortality of fry, and overexploitation (Karlsson and Karlström 1994; Anonymous 1996b). Moreover, intensive fishing has an adverse effect on the state of small wild stocks (Eriksson and Eriksson 1993). Several original salmon stocks have been lost, and many existing stocks are now maintained by hatchery rearing. During the 1990s, about 5 million reared smolts were released into the Baltic every year, and annual natural production was 0.4 million smolts (Karlsson and Karlström 1994).

Information on the factors that determine the feeding migration of salmon is needed for both fisheries management and salmon conservation. Our objectives in this study were to examine the effects of stock, spatial abundance of prey, and smolt length on the distribution of salmon during their feeding migration. We analysed sea distribution from recoveries during 18–23 months after release, in the 2nd sea-winter of the salmon. From 1984 to 1991, four salmon stocks were tagged and released as smolts into the four rivers draining into Bothnian Bay within a coast line of 120 km. The four stocks, those of the Tornionjoki, Kemijoki, Iijoki, and Oulujoki, were genetically different (Koljonen 1995). Because of the design of the study and the difference in release sites, the stock effect included both the genetic effect and the river effect. In light of earlier observations (Carlin 1969; Koljonen 1995), we expected the spatial sea distribution of Bothnian Bay salmon to be influenced by the stock factor. Smolt length was included in the analysis because it is a factor of interest in sea ranching of salmon and has been reported to have an effect on feeding migration distance (Salminen et al. 1994). In the first model, we analysed the joint effects of three explanatory factors, stock, year, and smolt length, on the sea distribution of salmon to establish whether sea migration is regulated mainly by stock-specific (partly genetic) factors or by annual environmental factors. In the second model, we analysed the effects of two factors, stock and herring abundance, to determine whether yearly variation could be due to the yearly changes in abundance of suitable prey fish along the migration route. Food abundance was the abundance of age 0+ herring in the release year in Bothnian Sea (the nearest feeding area of the Bothnian Bay salmon) (Anonymous 1996a).

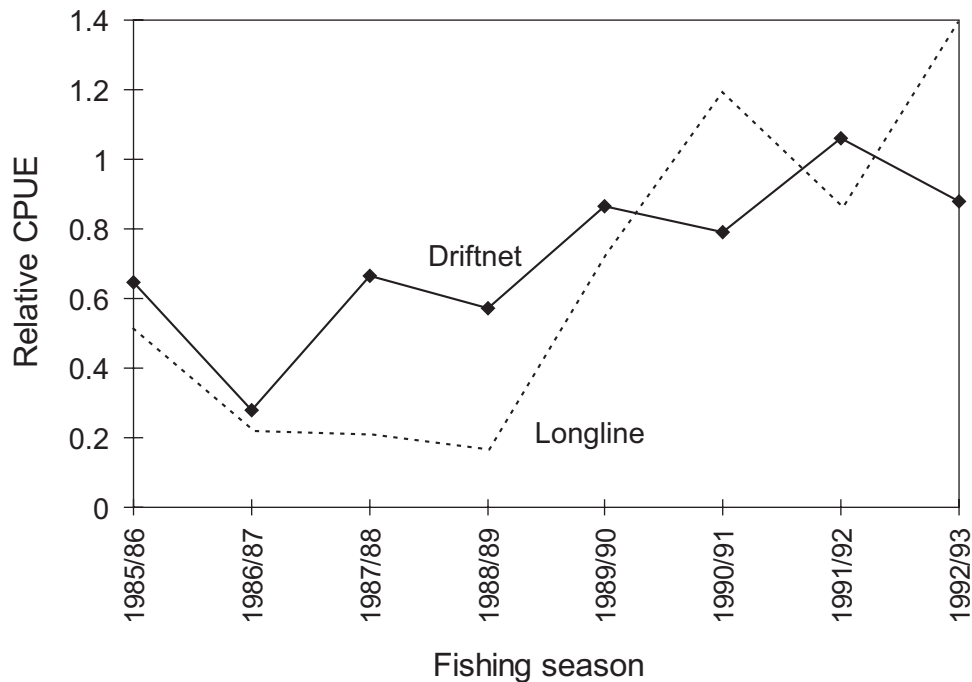
## Material and methods

### Salmon stocks

We analysed the sea migration patterns of Atlantic salmon released as smolts into the estuaries of the Oulujoki, Iijoki, Kemijoki, and Tornionjoki. These rivers drain into Bothnian Bay, which

**Table 1.** Number of tagged salmon of the Tornionjoki, Kemijoki, Iijoki, and Oulujoki stocks released as 2-year-old smolts in 1984–1991.

Stock	Year								Total
	1984	1985	1986	1987	1988	1989	1990	1991	
Tornionjoki	991	6 943	940	3 990	991	994	2 980	1996	19 825
Kemijoki	983	4 968	10 972	6 986	11 315	3 944	1 956	995	42 119
Iijoki	8 869	6 754	8 000	4 803	3 981	2 924	2 893	2 984	41 208
Oulujoki	3 984	3 960	3 993	3 994	3 961	3 946	3 986	3 988	31 812
Total	14 827	22 625	23 905	19 773	20 248	11 808	11 815	9 963	134 964

**Fig. 2.** Relative catches per unit effort (CPUE) by Finnish longline and driftnet fisheries in 1984–1993 (Anonymous 1996b). The values are CPUE in the Gulf of Bothnia divided by CPUE in the Baltic Main Basin.

is located in the northernmost part of the Baltic Sea (Fig. 1). Salmon do not reproduce naturally in the Oulujoki, Iijoki, and Kemijoki rivers, which are regulated for hydroelectric power generation. Only the Tornionjoki has a naturally reproducing salmon stock, although even this is supported by stocking (Juttila and Pruuki 1988). The original Oulujoki stock is extinct, and the present hatchery-reared salmon constitute a genetically unique hybrid stock containing genes from the original Oulujoki stock, the Tornionjoki stock, the Iijoki stock, and the Skellefteälv stock and possibly from other stocks, too (Koljonen 1989). The Iijoki salmon stock is also genetically unique (Koljonen 1989). It has been maintained in hatcheries since the 1960s, when hydroelectric power plants preventing spawning migration were constructed on the river. The original Kemijoki stock is likewise extinct; the present one is a mixed stock (hybrid and pure salmon) originating mainly from the Tornionjoki and Iijoki stocks, which have been released into the Kemijoki estuary. Smolts of the Kemijoki stock are raised from the eggs of spawners captured in the Kemijoki estuary (Kallio-Nyberg and Koljonen 1997).

There are statistically significant allele frequency differences between the Tornionjoki, Iijoki, Kemijoki, and Oulujoki salmon stocks, but quantitatively the differences are small (Koljonen 1995). Genetically, the most similar stocks are those of the Tornionjoki and Iijoki. The Kemijoki stock is genetically more closely related to the Iijoki than to the Oulujoki stock. If allele frequency

differences are considered to predict behavioural differences, then the Oulujoki stock could be assumed to differ most markedly from the Tornionjoki or Iijoki stocks in sea migration behaviour.

#### Recovery data and fishery

A total of 134 964 2-year-old smolts from each of the four stocks, raised under standard hatchery conditions, were released into the estuary of the respective river in late May from 1984 to 1991 (Table 1). The smolts were marked with individually numbered Carlin tags (Carlin 1969) in early spring and the total length of each fish was recorded. The tag recovery data were acquired from the Finnish Game and Fisheries Research Institute and included recoveries by all national fleets participating in the fishery. Most of the tag recoveries were obtained from commercial offshore driftnet and longline fisheries; in the Bothnian Sea, salmon were caught by both offshore and coastal fisheries. Recoveries from feeding grounds were included in this study. The analysis was restricted to recoveries made between the beginning of October and the end of March. Active spawning migration may start as early as April in the Gulf of Bothnia and typically ends by September (Ikonen and Kallio-Nyberg 1993). The largest fishes of an age-class leave the feeding areas and start their spawning migration in the Main Basin in April (Lindroth et al. 1982). We based our analysis on recoveries in the 2nd sea-winter (sea-ages from 18 to 23 months) and excluded recoveries in the 1st sea-winter because

**Fig. 3.** Estimates (produced with a logit model) of the yearly stock-specific percentages of tag recoveries as a function of smolt length from the three areas of the Baltic Sea: Southern Main Basin (white), Northern Main Basin (grey), and Gulf of Bothnia (black) (a). The length-frequency distributions of the tagged smolts in the recovery data. (b) The distributions are given for the Iijoki, Oulujoki, Kemijoki, and Tornionjoki stocks.

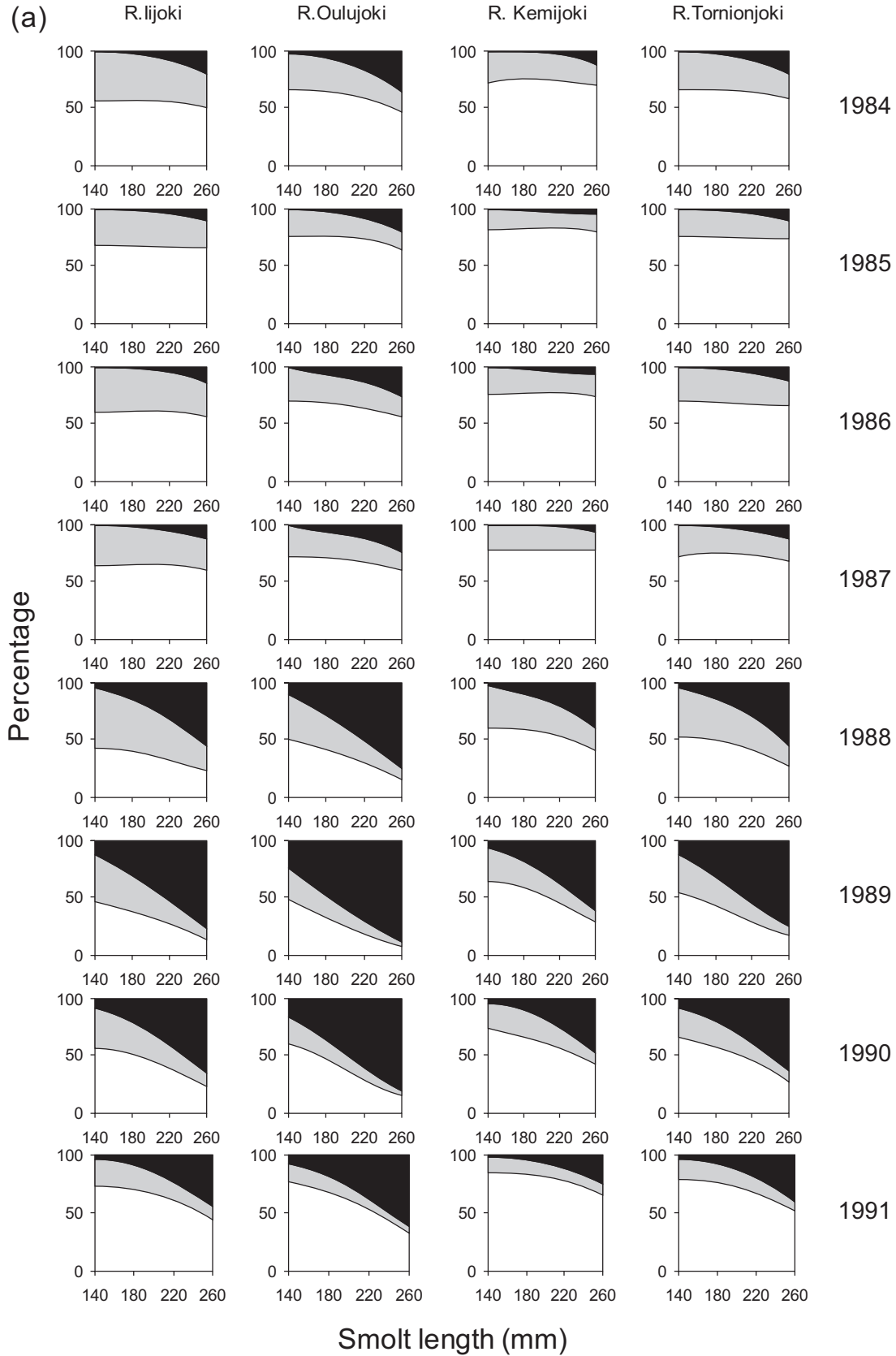
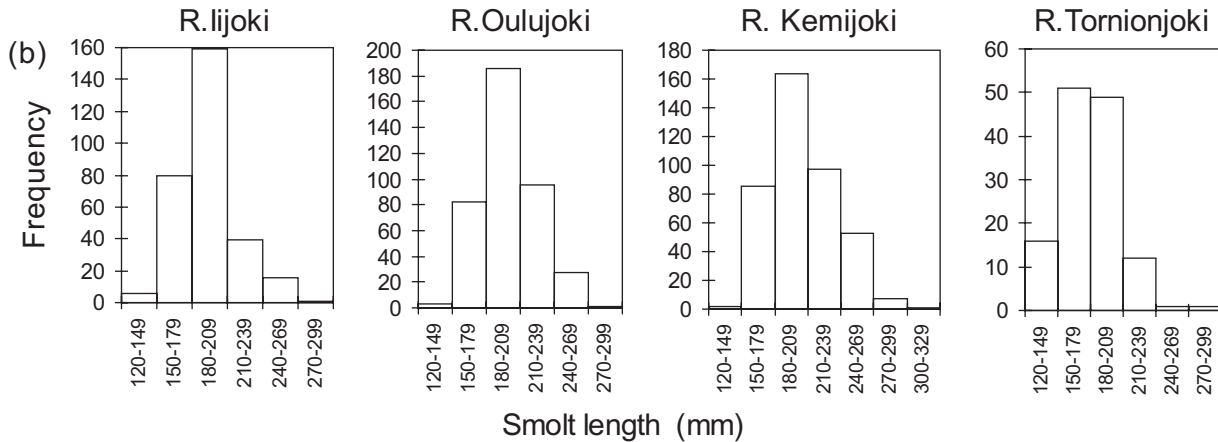


Fig. 3 (concluded).



only a small fraction of the one-sea-winter salmon had been recruited into the fishery. The Atlantic salmon have a minimum legal size of 60 cm (total length). Because of heavy exploitation, few salmon survive into their 3rd sea-winter. The tagging experiments revealed that the feeding area of Bothnian Bay salmon is determined in the release year (Salminen et al. 1994). The feeders of the 2nd year are therefore assumed to remain in the areas where they spent their first winter.

About 96% ( $n = 776$ ) of the tag recoveries from releases in 1984–1987 came from the fishery in the Main Basin of the Baltic Sea. However, the proportion of tag recoveries from the Gulf of Bothnia (30%) was markedly higher for releases in 1988–1991 than for previous years. There was also an increase in catches and a simultaneous increase in catches per unit effort (CPUE) in the Gulf of Bothnia compared with that in the Main Basin for releases in 1988–1991 (Fig. 2; Anonymous 1996b).

### Statistical analysis

We analysed the tag recovery data with logit models, as these are suitable for analysing data presented in proportions. The logit model

$$(1) \quad \ln(\pi(x)/(1 - \pi(x))) = \alpha + \beta x$$

gives the probability that an observation falls into a definite category as a function  $\pi(x)$  of a number of explanatory variables. The vector  $x$  consists of the values of explanatory variables, and the vectors  $\alpha$  and  $\beta$  include the parameter estimates. The response variable is usually binary in a logit model (eq. 1), but here the model has been generalised as a multicategory response case (Hosmer and Lemeshow 1989; Collett 1991). The analysis was performed with the BMDP program, Polychotomous Logistic Regression (Moran et al. 1990).

The explanatory variables in the model can be continuous or discrete. The goodness-of-fit of the model was analysed with the log-likelihood ratio statistic (deviance). Continuous explanatory variables were made discrete to facilitate analysis of the fit of the model.

We tested the significance of the explanatory variables by difference of deviances. A variable in a multicategory logit model has several parameters (one less than the number of categories). The significance of these parameter components was analysed with Wald's test, which is based on the confidence limits of the odds ratio (odds ratio =  $e^{\text{parameter estimate}}$ ). An odds ratio equal to 1.0 indicates no effect. If the odds ratio  $> 1$  ( $< 1$ ), the proportion of the corresponding response variable class increases (decreases) compared with the reference class proportion. The response variable classes were formed on the basis of tag returns from different sea areas. We divided the migration area (Baltic Main Basin and Gulf

of Bothnia) into three parts based on the statistical subdivision borders of the International Council for the Exploration of the Sea (Fig. 1): the Southern Main Basin (subdivisions 23–26), the Northern Main Basin (subdivisions 27–29), and the Gulf of Bothnia (subdivisions 30–31). The proportion of recoveries from the Southern Main Basin ( $\pi_{\text{SMB}}$ ) is therefore given by

$$(2) \quad \ln(\pi_{\text{SMB}}/\pi_{\text{GB}}) = \alpha_1 + \beta_1 x$$

and the proportion from the Northern Main Basin ( $\pi_{\text{NMB}}$ ) by

$$(3) \quad \ln(\pi_{\text{NMB}}/\pi_{\text{GB}}) = \alpha_2 + \beta_2 x$$

The symbols are as described in eq. 1. The proportion of recoveries from the Gulf of Bothnia ( $\pi_{\text{GB}}$ ) was used as the reference.

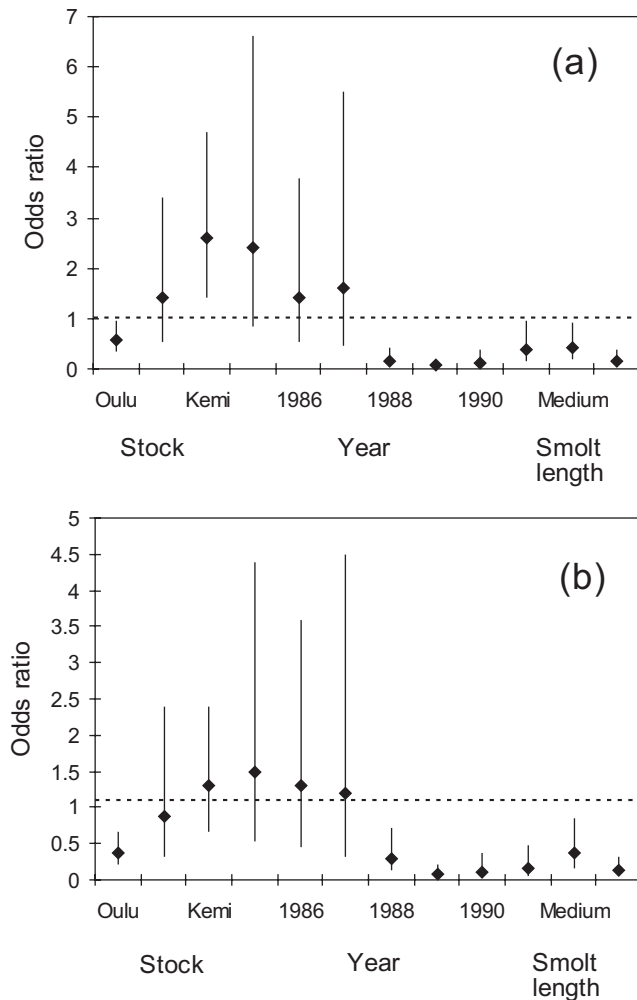
The total number of tags recovered was 1234 in all categories. Of these, 777 were from the Southern Main Basin, 298 from the Northern Main Basin, and 159 from the Gulf of Bothnia. There were 301 recoveries of the Iijoki, 394 of the Oulujoki, 130 of the Tornionjoki, and 409 of the Kemijoki stock. The yearly number of recoveries ranged from 47 to 293. The majority of recoveries (95%) from the northernmost area were from the Bothnian Sea, subdivision 30. Tag recoveries in the Gulf of Finland (subdivision 32) were omitted because Bothnian Bay salmon are rarely caught there (Carlin 1969; Salminen et al. 1994).

Fishing effort varies in the three migration areas. The observed proportions of recoveries from the different sea areas do not therefore necessarily indicate the proportions of tagged salmon migrating to these areas; for example, migration areas with a high fishing intensity are overestimated. The sampling scheme is a generalisation of the classical case-control study favoured in epidemiology. The advantage of logistic models in studies such as ours is that the effects of the explanatory variables on these proportions can be estimated (Collett 1991), despite the inability to give proportions of salmon migrating into different areas.

The explanatory variables in the first model were stock (Oulujoki, Iijoki, Kemijoki, or Tornionjoki), year-class, and smolt length. The model was also fitted with smolt length as a continuous variable. However, to analyse the fit of the model, we grouped the smolts into three length-classes, with total lengths  $\leq 17.0$  cm, 17.1–20.0 cm, and  $> 20.0$  cm. Here, the number of categories is a compromise between accuracy and a sufficient number of observations in each category.

In the second model, we analysed whether the year effect could be due to the abundance of suitable prey fish in the Bothnian Sea at the time that the salmon post-smolts migrate to this area. We assumed that the salmon post-smolts would not migrate farther south if enough suitable prey fish were available in the Bothnian Sea. Age 0+ herring (*Clupea harengus* L.) are important for post-smolts

**Fig. 4.** Odds ratios ( $e^{\text{parameter estimate}}$ ) and respective 95% confidence interval of the logit model, with stock, year, and smolt length as explanatory factors. Smolt length was classified as small (<170 mm), medium (170–200 mm), or large (>200 mm). The Gulf of Bothnia was the reference area, which was compared with (a) Southern Main Basin and (b) Northern Main Basin. The other stocks were compared with the Iijoki stock and the other size categories with the smallest one. A parameter is significant ( $p < 0.05$ ) if the vertical line indicating the 95% confidence interval does not intersect the dashed line (i.e., value one is not included in the interval).



starting to feed on fish (e.g., Salminen et al. 1994). The explanatory variables in the second model were stock and the abundance of young-of-the-year herring in the Bothnian Sea. The abundance of age 0+ herring at the end of the year (Anonymous 1996a) was assumed to indicate the abundance of the same cohort during their first year of life. To enable us to study the fit of the model, we grouped the years into two classes based on the abundance of age 0+ herring in the Bothnian Sea (Anonymous 1996a). The first class consisted of the years 1984–1987 and 1990 (low herring recruitment, <6000 million individuals) and the second class consisted of the years 1988, 1989, and 1991 (high herring recruitment, >6000 million individuals).

## Results

The distribution of tag recoveries was not independent of

stock, year, or smolt length (likelihood ratio test). The test statistics values (difference of deviances) were 47.45 (df = 6,  $p < 0.000$ ), 33.22 (df = 4,  $p < 0.000$ ), and 186.61 (df = 14,  $p < 0.000$ ) for stock, smolt length, and year, respectively. The log-likelihood value, 136.47 (df = 138,  $p = 0.521$ ), indicated a good fit of the model with the data. The estimates of odds ratios indicated that the proportion of Oulujoki stock recoveries was smaller in both the Southern and the Northern Main Basin than was that of Iijoki stock recoveries (Fig. 3). The distribution of Tornionjoki and Iijoki stocks was not significantly different. The proportion of recoveries from the Southern Main Basin was larger for the Kemijoki than the Iijoki stock (Fig. 4). There was also a greater difference in migration patterns between the Oulujoki and Kemijoki stocks than between either of these stocks and the Iijoki stock. The proportion of recoveries from the Southern and the Northern Main Basin was significantly smaller (Fig. 4) for the year-classes 1988–1991 than for the reference year-class 1984. The odds ratios were significant for large smolts in both the Southern and the Northern Main Basin (Fig. 4). Salmon released as small smolts were more frequently caught in the Main Basin than were those released as large smolts (Fig. 3).

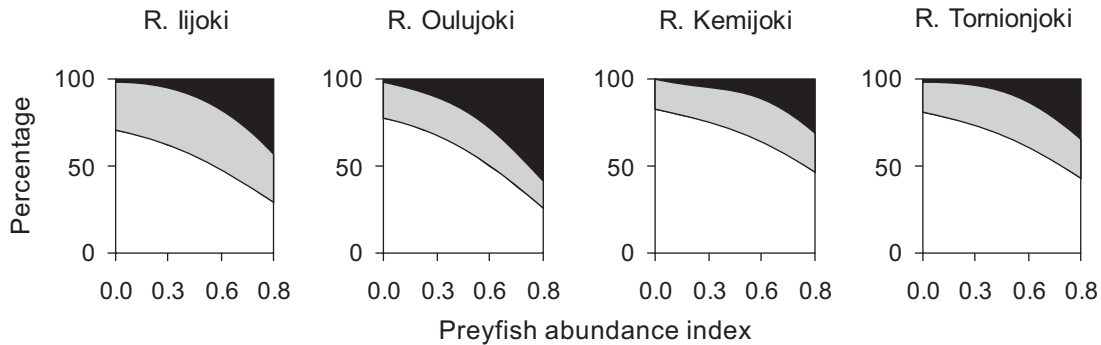
Analysis of the second model showed that the migration pattern was not independent of stock and age 0+ herring abundance (likelihood ratio test, Fig. 5). The test statistic values were 42.06 (df = 6,  $p < 0.000$ ) and 139.70 (df = 2,  $p < 0.000$ ) for stock and herring abundance, respectively. The fit of the logit model, with stock and prey abundance as explanatory variables, was satisfactory with the log-likelihood value 3.241 (df = 6,  $p = 0.778$ ). We also analysed the effect of smolt length in this model but it did not improve the fit well enough to be included in the final model. The factor year in the first model could be replaced by herring recruitment in the Bothnian Sea in the second model. A larger proportion of the salmon released in the years with abundant age 0+ herring in the Bothnian Sea were caught in the Bothnian Sea than of those released in the years with poor herring recruitment (Fig. 5). This was indicated by the significance of the parameters for herring recruitment (Fig. 6).

Both models produced consistent results for stock-specific migration patterns. The parameter estimates of the model with stock and herring abundance as explanatory variables showed a smaller proportion of recoveries of Oulujoki than of Iijoki stock from the Northern Main Basin (Fig. 6). The marine distribution of Iijoki and Tornionjoki stocks was not significantly different. Recoveries of the Kemijoki stock were more frequent in the Southern Main Basin than were those of the Iijoki stock. The findings suggest that the Kemijoki and Tornionjoki salmon migrated into the Main Basin more frequently than did the other two stocks and that the Oulujoki salmon stock had, on average, the shortest migrations.

## Discussion

The results showed that the feeding migration pattern of salmon was influenced by the stock effect, abundance of herring, and smolt size. Interannual environmental factors, that is, food abundance and the year effect, had a stronger

**Fig. 5.** Estimates (produced with a logit model) of the stock-specific percentages of tag recoveries as a function of the prey fish abundance index (abundance of 0-year-old herring at the end of the year) in the three sea-areas of the Baltic Sea. Recoveries from the Southern Main Basin (white), Northern Main Basin (grey), and Gulf of Bothnia (black).



impact on the spatial sea distribution of salmon than did the stock effect. The observed stock-specific differences were parallel from year to year, suggesting that they were not random annual variations. Because of the difference in release sites, the stock effect included the release site effect. Therefore, we could not indicate whether or not the stock-specific differences were solely genetic. The information on different spatial sea distributions of the Bothnian Bay salmon stocks is nonetheless important for management. Although the present analysis indicates the significance of differences between stocks, it does not give estimates of the proportions of each stock that have migrated to a definite area. This is because the spatial pattern of recoveries is due not only to differences in migration patterns but also to yearly differences in natural and fishing mortality among areas.

The stock-specific differences in the spatial distribution followed the genetic clustering of the stocks quite well although they were due not only to genetic factors but also to environmental factors (Koljonen 1995). The small difference in the spatial marine distributions of the Iijoki and Tornionjoki stocks may reflect the small difference in the allele frequencies between these stocks. In addition, the spatial sea distribution of the Iijoki stock differed from the distributions of the Kemijoki and Oulujoki stocks. The genetic distances between these stocks (Iijoki to Kemijoki and Iijoki to Oulujoki) were larger than those between the Iijoki and Tornionjoki stocks, which did not show statistically significant differences. The Oulujoki stock had the shortest migration and the Kemijoki stock the longest migration of these Bothnian Bay stocks.

The feeding migrations of the Oulujoki stock were restricted to the Bothnian Sea more clearly than were those of the other stocks. Genetic stock identification of salmon catches showed that the Oulujoki stock was abundant in the Bothnian Sea in January–February (Koljonen and McKinnell 1996). The short feeding migration of the Oulujoki stock may be a trait inherited from either the Skellefteälv or the original Oulujoki stock.

The interannual variability in food abundance was found to influence sea migration. The increase in salmon CPUE in the Gulf of Bothnia compared with the CPUE in the Main Basin in 1984–1993 (Anonymous 1996b) also supports observations that salmon stocked in years with abundant prey fish remained in the Bothnian Sea more often than did those stocked in years with fewer age 0+ herring. Our present

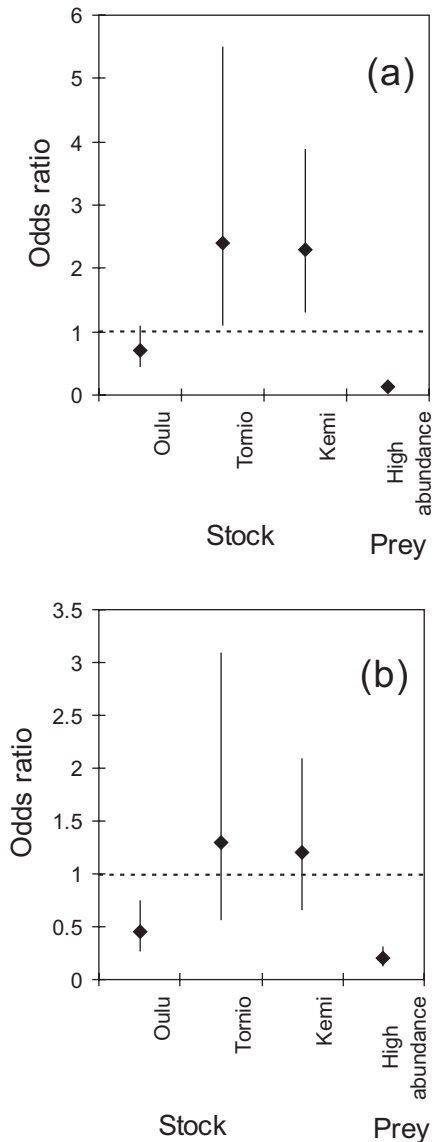
findings support a strong effect of the spatial abundance of prey fish on the feeding migration pattern of salmon. The spatial distribution of stock-specific tag recoveries in 1990 resembles those in 1988, 1989, and 1991 (Fig. 3). In the model including prey abundance, the prey fish abundance in 1990 was the highest of those in the lower prey fish abundance category. Although the fit of the model was satisfactory, it might have been better if the year 1990 had been placed in the high prey abundance class. The determination of the class limits is not a critical point in the model. However, the class limits have to be selected before the analysis has been conducted (e.g., Sokal and Rohlf 1995). Selecting new class limits based on analysis results is not statistically appropriate.

Abundant herring year-classes seem to stimulate salmon to make their feeding migrations in the Bothnian Sea, whereas feeding in the Gulf of Bothnia was also connected with smolt length at release. As in the present study, Salminen et al. (1994) found that salmon beginning their migrations as large smolts completed their feeding migration within the Gulf of Bothnia more frequently than did small smolts. The large post-smolts are assumed to stay in the Bothnian Sea at the beginning of their migration because they are able to change their diet from invertebrates to fish (Salminen et al. 1994).

Other reasons may also exist for the observed effect of smolt size on migration distance. Salmon stocked as large smolts mature earlier than those stocked as small ones and so have less time to spend in the rich feeding grounds of the southern Baltic Sea than have salmon stocked as small smolts. The net energy gain of a far-reaching feeding migration may not be high enough to compensate for the energetic costs. In light of the short migration distance of delayed-release smolts, Eriksson (1988) suggested that the distance travelled in the sea was a result of active migration according to a biological clock rather than orientation to a definite goal.

The persistent year-to-year differences between stocks suggest that the sea migration pattern of salmon is also affected by stock-specific, genetic factors. However, salmon were able to react to the interannual spatial variation in food abundance by changing their migration patterns. Most likely, they are also able to adapt their migration to enable them to return to their spawning sites or locations of release, irrespective of the variability in their feeding migrations.

**Fig. 6.** Odds ratios ( $e^{\text{parameter estimate}}$ ) and the respective 95% confidence interval of the logit model, with stock and prey fish abundance as explanatory factors. Prey fish abundance was classified as low or high (see text). The Gulf of Bothnia served as the reference area, which was compared with (a) Southern Main Basin and (b) Northern Main Basin. The other stocks were compared with the Iijoki stock. A parameter is significant ( $p < 0.05$ , Wald's test) if the vertical line indicating the 95% confidence interval does not intersect the dashed line (i.e., number one is not included in the interval).



The sea migration patterns of the original wild stocks are not known. Unintentional domestication of stocks farmed for many generations, e.g., the Iijoki stock, may have changed the genetic variability and thereby also the migration pattern. Artificial breeding has also been shown to affect the seasonal timing of spawning migration and migratory behaviour (Jonsson et al. 1990; Økland et al. 1995). In the present study, the 2-year-old smolts of the farmed and ranches stocks were, on average, larger than those of the less domesticated Tornionjoki salmon stock. The faster growth rate of the farmed salmon stocks has been attributed to domestica-

tion selection and adaptation to hatchery conditions (Kallio-Nyberg and Koljonen 1997). The increase in the level of domestication has been shown to increase the growth rate in the sea and to decrease the sea age, but there are no observations of changes in spatial marine distributions (Kallio-Nyberg and Koljonen 1997).

The spatial sea distribution of the less domesticated Tornionjoki salmon stock in the Main Basin differed from that of the sea-ranched Oulujoki stock, although the distributions largely overlapped. Stock-specific exploitation in feeding grounds is not possible because other wild and sea-ranched stocks migrate in the same feeding areas and there may be annual shifts in stock-specific distributions. The Bothnian Bay salmon stocks are, however, genetically different (Koljonen 1995) and the existing genetic variation is the basis for future adaptation of the Baltic salmon.

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