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Sea migration pattern of two sea trout (*Salmo trutta*) stocks released into the Gulf of Finland

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The sea migration of two sea trout stocks was examined in a tagging and transplantation experiment. The two different stocks, which originated from the rivers Isojoki (Gulf of Bothnia) and Ingarskilanjoki (Gulf of Finland), were released in 1994–1996 as smolts (3991 and 3996 smolts) at two nearby sites in the Gulf of Finland. The tag recovery data received 5–19 months after release (Sep.–Nov.) from the Gulf of Finland were analysed. The recovery rate was about 8%. Multi-way contingency analysis showed that the origin of the stock affected the spatial and temporal sea distribution. The majority (63%) of the Ingarskilanjoki sea trout, but a smaller proportion (49%) of the Isojoki sea trout, were caught in coastal waters, near the release site. The stock-specific spatial sea distributions were not affected by the gear types used. The genetic threats of stocking are discussed.

Introduction

The brown trout (*Salmo trutta* L.) shows variation in its tendency to migrate. Both migratory and resident populations, genetically different from each other, can coexist in the same water system, or both sympatric forms, but with different migratory behaviours, can belong to the same population (Jonsson 1982, 1985, Jonsson & Jonsson 1993, Hindar *et al*. 1991, Skaala & Neavdal 1989). Sea trout (*Salmo trutta* m. *trutta*) is anadromous, that is, it migrates to salt water environment to feed and returns to streaming freshwater to spawn (L'Abee-Lund *et al*. 1989). The sea trout is caught mainly in coastal home waters, although some individuals may have travelled in the open sea 100–600 km away from their home river (Skrochowska 1969, Toivonen & Ikonen 1978, Berg & Berg 1987, Pratten & Shearer 1983). Both immature and mature brown trout tend to migrate annually between sea and river (Jonsson 1985, Sturlaugsson & Johannsson 1996). Sea trout leave the river for the first time as 2–7-year-old smolts (Jonsson 1985, Johannsson & Einarsson 1993). They migrate and grow, on average, for 1–4 summers in the sea before maturing (L'Abee-Lund *et al*. 1989). The straying rate of sea trout varies depending on the stock traits (Berg and Berg 1987, Pratten & Shearer 1983, Johannsson & Einarsson 1993). Tagging and transplantation experiments show that the components of sea migration — distance and direction — are stock-specific traits of sea trout (Svärdson & Fagerström 1982, Jonsson *et al*. 1994). The migration patterns of brown trout are also largely controlled by environmental factors (Bohlin *et al*. 1993).

Two sea trout stocks, those of the Isojoki and the Ingarskilanjoki, are used in stockings in the Gulf of Finland. We examined stock-specific sea migration patterns by comparing the spatial and temporal marine distributions of tag recoveries of these stocks. Other traits of these stocks, e.g., growth rate, are compared in the work of A. Saura and P. Ahlfors (unpubl.). The Isojoki stock, which originates from the Gulf of Bothnia, was also largely used in the Gulf of Finland, in the 1980s and 1990s. The Ingarskilanjoki stock is a new breeding stock that originates from the Gulf of Finland.

The use of a domesticated stock in stockings in large sea areas increases the risk of loss of genetic variation; and moreover transplantation poses a threat to original stocks (Hansen & Loescheke 1994). There are numerous weak natural stocks in the rivers of the Gulf of Finland (Marttinen & Koljonen 1989, Saura 1998). The risk posed to natural stocks by introductions depends, among other things, on the release site and genetic variation of the hatchery fish. Different traits are required of stocks introduced into coastal waters for sea-ranching or into rivers for enhancement purposes. The aim of this work is to compare the sea migration behaviour of these stocks and to discuss on these stocks with management in view.

The tagged experimental smolt groups of both stocks were released at two sites near the estuary of the Vantaanjoki in 1994–1996. We examined the effect of stock origin and release site on the spatial and temporal sea distribution. We tested the null hypothesis that spatial or temporal sea distribution is independent of stock and release site. If phenotypic variation occurred in the sea migration pattern between stocks, the variation must be genetic and stock-specific, because the prevailing conditions were the same for both experimental groups before the release. The migration pattern deduced from the tag recovery data depends on the distribution of the fishery and gear types used. Consequently, we also examined the interrelationships between stocks, recovery sites or times and the gear types used in trout fishery. The tag recovery data of the experimental groups were analysed by log-linear models.

Material and methods

Sea trout stocks

The sea trout stocks used in the experiment originated from two rivers, the Isojoki, which discharges into the Gulf of Bothnia, and the Ingarskilanjoki, which flows into the Gulf of Finland. The sea trout in the Ingarskilanjoki (Degerby å; Hurme 1970) can ascend the river for 13 km to the Myllypato dam, which has closed the upper parts of the river to anadromous trout since the 1930s (Hurme 1970, Marttinen & Koljonen 1989) (Fig. 1). Since 1998 there has been a fish way in the dam that functions when there is enough water in the river (A. Saura, unpubl.). In the lower part of the river, there are 11 rapids (area 890 m^2), five of which provide major habitats for juvenile trout (Marttinen & Koljonen 1989). In status, the Ingarskilanjoki natural sea trout stock is vulnerable (Koljonen & Kallio-Nyberg 1991). Despite stocking with reared parr and smolts, natural production has been very weak since flood prevention work was done in the river in 1989 (Saura 1998).

The Isojoki is 75 km long and has a total area of rapids in the main river and tributaries of 27 hectares. Characteristic of this river system are the number of small streams and brooks in it. Both sea trout and resident trout are present (Ahvonen *et al*. 1993). The natural sea trout stock of the Isojoki is endangered (Koljonen & Kallio-Nyberg 1991).

The breeding history of the Ingarskilanjoki trout is short. The first wild juveniles were caught in the river for rearing in 1987 and 1988 (Saura 1998). The parr were reared as brood fish in a hatchery. The offspring of these fish were kept as brood fish of the second generation, which started to produce eggs for stocking purposes in 1997. Currently, all stocked Ingarskilanjoki sea trout are offspring of these second-generation brood fish. The stock has not been renewed with natural spawners. The Ingarskilanjoki trout differs genetically from other trout stocks living in Finnish river systems entering the Gulf of Finland (Koljonen 1989).

The Isojoki trout stock used in stockings originates from hatchery-reared brood stocks maintained in hatcheries for many fish generations (Kallio 1986). It was the most widely used Baltic sea trout stock on the Finnish coast of the Gulf of Bothnia and in the Gulf of Finland in the 1980s and 1990s (Anon. 1992). Large anadromous sea trout spawners were favoured when the new brood stock was established with natural eggs. In the wild, local trout may spawn with migratory ones (Jonsson 1985), and in the Isojoki river system, too, non-migratory and migratory trout live partly in the same areas (Jutila *et al*. 1998). The Isojoki trout differs genetically from stocks living in Finnish rivers flowing into the Gulf of Finland (Koljonen 1989). There are genetically different trout subpopulations in the Isojoki river system, and there are also clear genetic differences between the hatchery-reared brood stock and the natural parr sampled in the river (Ahvonen *et al*. 1993)

Experimental groups

The experimental groups were established with the offspring of spawners from the brood stock kept at the Laukaa hatchery station in central Finland. The groups released in 1994 were reared at this station, whereas those released in 1995 and 1996 were reared at the Savon Taimen hatchery station in the same region. All groups compared were raised separately under standard hatchery conditions for 2 years. The fish were held at Laukaa in plastic (first year) and concrete (second year) tanks at ambient water temperature and were fed during daylight hours on commercial pelleted fish food. The rearing conditions were similar for both stocks.

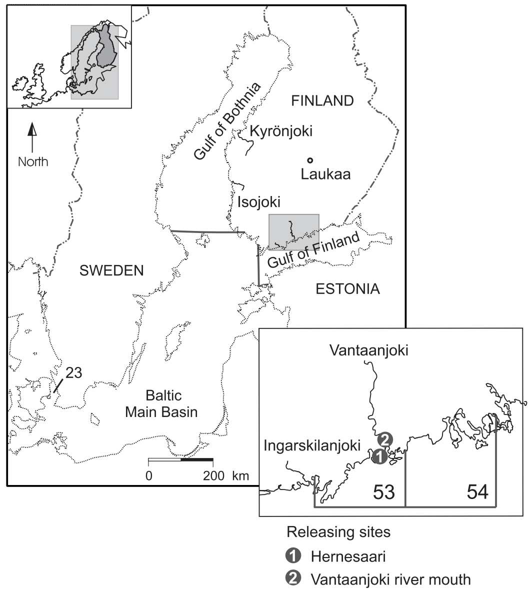

Fig. 1. The Baltic Sea. The estuaries of the rivers Ingarskilanjoki, Vantaanjoki, Isojoki and Kyrönjoki are shown. Sea areas: Gulf of Finland, Gulf of Bothnia, Baltic main basin. Statistical squares 53 and 54 in the Gulf of Finland are drawn. The side of a square is about 55 km long.

One to six months before release, two-year-old pre-smolts 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 of the fish. The weight of the tag (0.15 g) was 0.15% of that of the juvenile (100 g). The tagging was conducted in cold water (2–4 °C) in early spring, because the infection risk is then low and the fish has time to recover from the handling before release. Mortality during tagging was very low (under 0.5%). A total of 4000 juveniles of both stocks were tagged (Table 1). During tagging the total length (mm) of each fish was recorded; this was the length used as the smolt length of the group among recaptured fish.

The sea migration patterns of the two stocks were examined by comparing the tagged groups released in 1994–1996 at two sites near the estuary of the Vantaanjoki in the Gulf of Finland (Table 1). One release site was the mouth of the

Vantaanjoki river and the other was the shore of Hernesaari island. The distance between these two sites is about 8 km (Fig. 1). The groups compared were released every year at the same time in spring (April–May), when the water temperature is under 5 °C and the natural smolts also migrate into the sea.

Recovery data and fishery

The distribution of recoveries collected was affected not only by the migration of trout but also by the distribution of fishing, the catchability of fish and the gear types used in trout fishery. Trout were mainly caught as the by-catch of whitefish (*Coregonus* spp.) and pikeperch (*Stizostedion lucioperca*) in the Gulf of Finland (Saura 1998). The distribution of recoveries therefore depends on the site and time of release. In salmon, the age and size of smolts also have an influence on migration behaviour (Hansen & Jonsson 1991a, Kallio-Nyberg *et al*. 1999).

Marking with external Carlin tags is a useful method in migration studies when comparing groups released at the same site or at the same time, assuming that the same variation exists between the groups in variables such as smolt size, which affect the behaviour of fish and their catchability (Berg & Berg 1987, Hansen *et al.* 1993, Hansen & Jonsson 1991a, 1991b). The visible tag is an important source of information on catch site and time. Many fishermen also provide details of length, weight, sex and scale of fish and on the gear used in fishing. There is some evidence that Carlin tagging has an

Table 1. Tagged experimental groups of Isojoki and Ingarskilanjoki stocks. Release year and site and number of fish tagged are shown.

Stock	Year	Release site	No. of fish tagged
Ingarskilanjoki	1994	Vantaanjoki estuary	998
Isojoki	1994	Vantaanjoki estuary	992
Isojoki	1995	Vantaanjoki estuary	1000
Ingarskilanjoki	1995	Vantaanjoki estuary	999
Ingarskilanjoki	1995	Hernesaari	999
Isojoki	1995	Hernesaari	999
Isojoki	1996	Hernesaari	1000
Ingarskilanjoki	1996	Hernesaari	1000

Table 2. Number of tag recoveries and tag recovery rate (%) of experimental groups of Isojoki and Ingarskilanjoki trout stocks. Period: 1 = May–Aug. in release year, 2 = Sep.–Nov., in release year, 3 = Dec.–Aug. from first to second year, 4 = Sep.–Nov. in second year, 5 = Dec.–Aug. from second to third year, 6 = Sep.–Nov. in third year, 7 = Dec.–Aug. from third to fourth year, 8 = Sep.–Nov. in fourth year, 9 = Dec.–Aug. from fourth to fifth year. Annual spawning migration of trout takes place in September–November. Release site: estuary of the Vantaanjoki (Va) and shore of Hernesaari (He).

Stock	Year/site	Number of tag recoveries by periods									Total number	Recov. rate
		1	2	3	4	5	6	7	8	9		
Ing.	94/Va	16	8	16	14	6	0	1	0	0	61	6.1
Iso.	94/Va	13	10	26	8	11	0	0	0	1	69	6.9
Iso.	95/Va	20	6	14	4	9	1	0	1	0	55	5.5
Ing.	95/Va	14	6	18	22	8	1	1	0	0	70	7.0
Ing.	95/He	2	16	39	64	17	5	2	1	0	146	14.6
Iso.	95/He	5	10	28	12	24	7	7	1	1	95	9.5
Iso.	96/He	3	23	36	10	7	3	0	0	0	82	8.2
Ing.	96/He	2	21	19	19	8	0	0	0	0	69	6.9

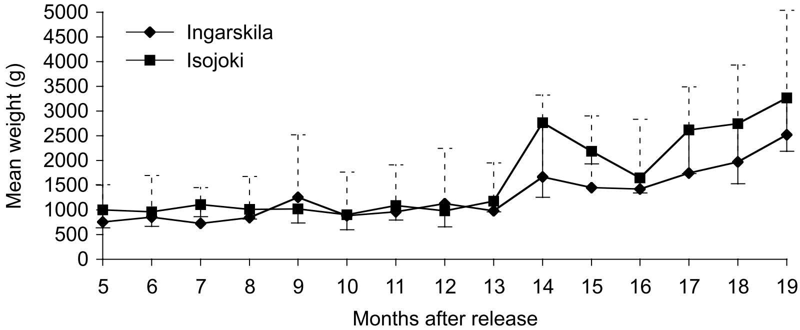

Fig. 2. Mean fish weight (± SD) in Ingarskilanjoki and Isojoki sea trout 5–19 months after release.

adverse effect on the survival of tagged fish in the sea (Hansen 1988). The effect of tagging on the sea migration of fish is unknown, but comparative studies similar to the present one suggest that the differences in migration behaviour between groups are significant (Svärdson & Fagerström 1982). Carlin tagging is the only method able to give information on the migration of individual fish.

In our analysis we deal with the Gulf of Finland, because 89% of the Isojoki sea trout and 93% of the Ingarskilanjoki sea trout were caught there. Within the Gulf of Finland the majority of the Isojoki and Ingarskilanjoki sea trout, 51% and 61%, respectively, were caught in coastal waters. These coastal waters were in statistical squares 53 and 54, which are located on the northern coast of the Gulf of Finland, near the release sites (Fig. 1).

The recovery time was divided into nine periods according to seasonal migration (Table 2). In the first months, 1–4 months after release, the post-smolts were not completely recruited to the fishery. The second period was the first spawning migration (5–7 months after release); the third period was the feeding migration (8–16 months in the sea) and the fourth period was the second spawning migration (17–19 months in the sea). In order to establish whether there was any difference in migration pattern between these two stocks, only recoveries made during 5–19 months in the sea were included in the analysis. Most of the fish were captured during these periods (Table 2).

In salmon (*Salmo salar* L.), the initial smolt size has an impact on migration pattern (Salminen *et al.* 1994, Kallio-Nyberg *et al.* 1999) and on catchability and fishing mortality (Salminen *et al.* 1995). In our data, during the period 5–19 months after release there was no significant difference in mean fish weight between these two stocks. The Isojoki sea trout showed, however, a faster increase in weight than did the Ingarskilanjoki sea trout in the second sea year (Fig. 2). In addition, no differences in mean smolt length were found between the stocks compared (*t*-test: $t = 1.91$, $P = 0.056$; Isojoki stock: 22.6 ± 2.08 cm, $N = 301$ and Ingarskilanjoki stock: 22.3 ± 1.94 cm, $N = 347$). The smolt lengths of sea trout were similar in the two experimental groups in both 1994 and 1996 (Table 3), as calculated from recovered fish. In 1995, however, the mean smolt length of the Isojoki sea trout released on the shore of Hernesaari was greater than that of the Ingarskilanjoki trout in the same year (*t*-test: $N = 95$, $N = 69$, $t = -3.43$, $P < 0.001$) (Table 3). The variation in smolt size within a year and between years was not included in the analysis, because the groups compared did not show any differences.

Table 3. Mean smolt size of experimental groups released in 1994–1996.

Stock	Year/site	Smolt length, (cm)		*N*
		Mean	SD	
Ing.	94/Va	23.3	2.07	61
Iso.	94/Va	23.4	1.99	68
Iso.	95/Va	20.3	1.79	56
Ing.	95/Va	20.7	1.44	70
Ing.	95/He	22.6	1.71	147
Iso.	95/He	23.4	1.74	95
Iso.	96/He	22.8	1.46	82
Ing.	96/He	22.6	1.71	69

The mean lengths of the Isojoki and Ingarskilanjoki sea trout were the same when calculated from fish captured during the first sea winter (Dec.–Mar., from the first to the second year) in the Gulf of Finland (Isojoki: 43.3 ± 5.93 cm, $N = 47$; Ingarskilanjoki: 41.7 ± 4.71 cm, $N = 30$; $t = 1.22$, df = 75, $P = 0.225$). However, after two growth periods in the second sea winter, the Isojoki trout were longer than the Ingarskilanjoki trout in the Gulf of Finland (Isojoki: 63.0 ± 6.07 cm, $N = 17$; Ingarskilanjoki: 53.8 ± 7.36 cm, $N = 8$; $t = 3.30$, df = 23, $P = 0.003$). The corresponding differences in mean length between stocks were shown by fish caught in the Baltic Sea, including all recoveries in the first or second sea winters.

The interactions between gear type and stock or between gear type and recovery site or recovery time were examined. However, not all the recovery reports included information on gear. Such information was available in 453 cases. A total of 25 gear types were used in trout fishery. These were classified into six groups: (1) floating gill net, (2) drift net, (3) trap net, (4) long line, (5) rods and (6) others. The first class included all kinds of bottom gill nets, and bar lengths varied from 27 to 65 mm. In the second class the bar length was 80 mm, which is the smallest bar size allowed for floating gill nets in the Gulf of Finland.

Statistical analysis

The recovery data are presented in multi-way contingency tables and were analysed by log-linear models (McCullagh & Nelder 1989) using the CATMOD procedure of the SAS statistical package (Anon. 1989). This method is well suited for analysing frequency data with several dimensions. The dependence of stock, release site, recovery site and time on both gear types was analysed by three-dimensional log-linear models. In the first analyses, we tested the interrelationships between stock, recovery site and recovery time. The details of the analyses of migration pattern by log-linear models have been given by Kallio-Nyberg *et al.* (2000).

Results

Interrelationships between stock and recovery site and time

The majority of the sea trout migrated to the sea to feed near the release site and stayed there during four sea years. Eighty-nine per cent ($N_{all} = 268$) of the Isojoki and 83% ($N_{all} = 314$) of the Ingarskilanjoki sea trout were recovered within the Gulf of Finland and only 11% and 7%, respectively, outside the Gulf, in the Baltic main basin or in the Gulf of Bothnia. About half of the Isojoki (51%, $N_{all} = 259$) sea trout were recovered east of the release site (25°E). Correspondingly, 54% of the Ingarskilanjoki trout were caught in the eastern part of the Gulf of Finland and 46% ($N_{all} = 306$) elsewhere in the Baltic Sea during three sea years (December in the third sea year).

Within the Gulf of Finland about half (49%) of the Isojoki sea trout and the majority (63%)

Table 4. Number of recoveries in three-dimensional contingency table. Variables: stock, recovery site and recovery time. Coastal squares = squares 53 and 54 in Gulf of Finland. Sea = Gulf of Finland, except squares 53 and 54, near the release site.

Recovery site	Recovery time (months after release)							
	Isojoki stock				Ingarskilanjoki stock			
	5–7	8–16	17–19	%	5–7	8–16	17–19	%
Coastal squares	24	38	12	49	28	43	68	63
Sea	13	51	12	51	13	39	31	37
Percentage	25	59	16		18	37	45	

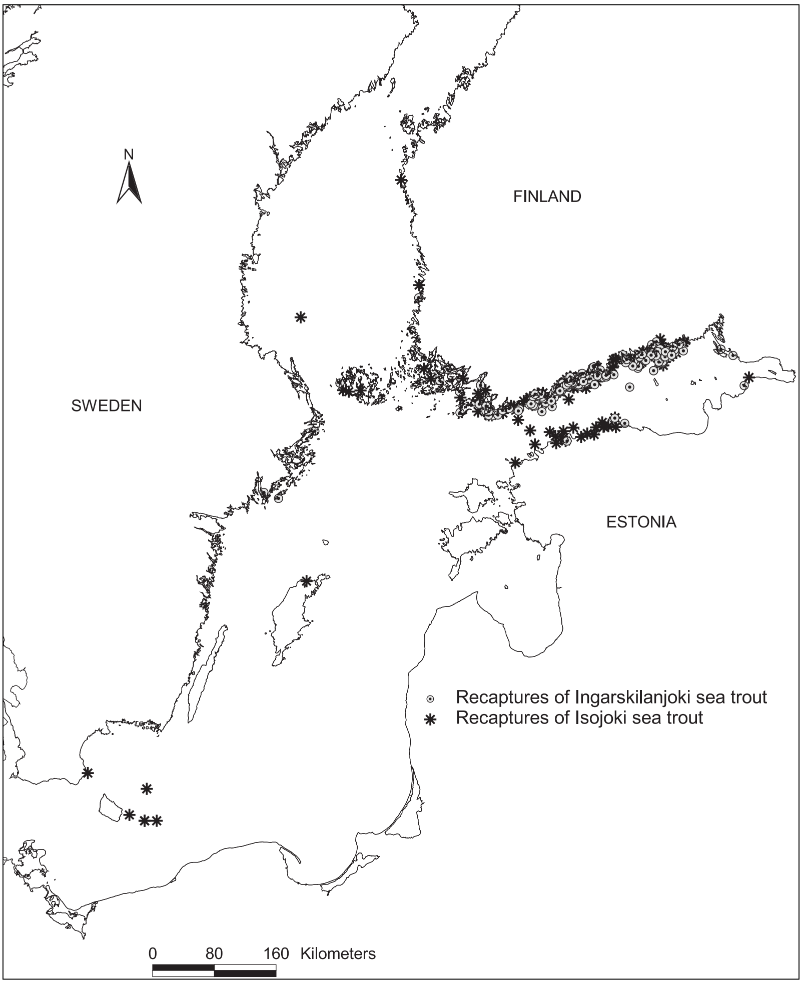

Fig. 3. All recoveries of Isojoki and Ingarskilanjoki sea trout released into the estuary of the Vantaanjoki in 1994–1996.

of the Ingarskilanjoki sea trout were caught in coastal waters within 5–19 months of their release (Table 4). There was some seasonal migration between coastal and offshore waters. In autumn (Sep.–Nov.: here 5–7 and 17–19 months after release) the trout migrated most frequently in coastal waters. From 68% to 69% of the Ingarskilanjoki trout and from 65% to 50% of the Isojoki trout were caught in these autumn months in coastal waters near the release site. During their feeding migration, 8–16 months after release, the Isojoki sea trout in particular migrated in the open sea and also in the coastal waters of Estonia. Of the Ingarskilanjoki trout 2.5%, and of the Isojoki trout over 6%, were caught more than 200 km from the release site. The most distant recaptures of the Isojoki trout occurred more than 800 km from the release site, near Bornholm, an island in the southern Baltic Sea (Fig. 3).

The Isojoki and Ingarskilanjoki trout were recovered during different sea periods. The majority (59%, 89/150) of the Isojoki sea trout, but a smaller proportion (37%, 82/222) of the Ingarskilanjoki fish, were caught in winter and summer (Dec.–Aug.) during their feeding migration, 8–16 months after release (Table 4). The Ingarskilanjoki trout were caught mainly in autumn during the spawning migration (Sep.–Nov.).

We analysed the interrelationships between stock, recovery site and recovery time by log-linear models. The simplest log-linear model with $P > 0.05$ featured two interactions between stock and recovery time and recovery time and site (Model, H_0: S, T, P, S × T, T × P: $G^2 = 4.60$, $P = 0.20$; *see* Table 5). The model with three interactions was not significantly better than this model with two interactions ($G^2_{\mathrm{ST,\,TP}} - G^2_{\mathrm{ST,\,TP,\,SP}} = 3.67$, df = 3 – 2 = 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 temporal sea distribution between the two stocks. As pointed out above, the Isojoki sea trout were caught mainly in winter–summer and the Ingarskilanjoki trout in autumn. The interaction between recovery time and recovery site shows that either trout move seasonally between coastal waters and the open sea or that fishing activity varies seasonally between sea areas. The majority (51%) of the Isojoki trout, but a smaller proportion (37%) of the Ingarskilanjoki trout, were caught in the open sea in the Gulf of Finland. This difference in spatial sea distribution between stocks was not, however, statistically significant. The effect of release site was not included in our analysis.

Table 5. Effect of stock on spatial and temporal sea distribution in the Gulf of Finland. Log-linear models and test of independence between classified variables: stock, S (Isojoki and Ingarskilanjoki trout), recovery site; P (statistical squares 53 and 54 = coastal and other waters of the Gulf of Finland), recovery time, T (5–7, 8–16, 17–19 months in the sea). The contingency table with sample sizes is shown in Table 4. Variables are expected to be independent when separated by a comma and to interact when there is no comma. Model, null hypothesis; df = degrees of freedom; G^2 = likelihood ratio; °*P*-values indicate the discrepancy between the model and the data; *f** shows the models with the best fit ($P > 0.05$).

Model	df	G^2	°*P*
S, T, P	7	52.9	0.000
S, T, P, S × P	6	46.4	0.000
S, T, P, S × T	5	17.3	0.003
S, T, P, P × T	5	40.1	0.000
S, T, P, S × P, S × T	4	10.9	0.029
S, T, P, S × P, T × P	4	33.7	0.000
S, T, P, S × T, T × xP	3	4.6	0.204*f**
S, T, P, S × P, S × T, T × P	2	0.9	0.626*f**

Stock, release site and recovery site

The genetic characteristics of the stock, but not the release site, had an effect on the spatial sea distribution of fish. The one-interaction model with the interaction between stock and recovery site was compatible with our data (H_0: S, R, P, S × P: $P = 0.5$), and was significantly better than the model without the interaction ($G^2_{\mathrm{S,\,R,\,P}} - G^2_{\mathrm{S,\,R,\,P,\,S\times P}} = 8.80 - 2.36 = 6.44$; df = 4 – 3 = 1; $\chi^2_{0.05} = 3.84$) (Table 6). The more complex model, with interactions between stock and recovery site and between release and recovery site, was even more compatible with the data ($P = 0.551$), but it was not significantly better than the one-interaction model ($G^2_{\mathrm{S,\,R,\,P,\,S\times P}} - G^2_{\mathrm{S,\,R,\,P,\,S\times P,\,S\times R}} = 1.17$, df = 3 – 2 =1; $\chi^2_{0.05} = 3.84$). The release site was an independent variable in the model used. The model that included the release site showed the effect of origin of stock on the spatial sea distribution. Forty-nine per cent ($N_{\mathrm{all}} = 150$) of the Isojoki trout and 63% ($N_{\mathrm{all}} = 222$) of the Ingarskilanjoki trout were caught in the coastal squares (Fig. 4).

Table 6. Effect of stock and release site on spatial sea distribution in the Gulf of Finland. Log-linear models and test of independence between classified variables: stock, S (Isojoki and Ingarskilanjoki trout), release site, R (estuary of the Vantaanjoki and coastal waters of Hernesaari island) recovery site, P (statistical squares 53 and 54 = coastal and other waters of the Gulf of Finland). Sample sizes are shown in Fig. 4. Variables are expected to be independent when separated by a comma and to interact when there is no comma. Model, null hypothesis; df = degrees of freedom; G^2 = likelihood ratio; °*P*-values indicate the discrepancy between the model and the data; *f** shows the models with the best fit ($P > 0.05$).

Model	df	G^2	°*P*
S, R, P	4	8.80	0.066
S, R, P, S × P	3	2.36	0.500*f**
S, R, P, R × P	3	7.63	0.054
S, R, P, S × R	3	7.64	0.054
S, R, P, S × P, R × P	2	1.19	0.551*f**
S, R, P, S × P, S × R	2	1.20	0.550
S, R, P, R × P, S × R	2	6.46	0.039
S, R, P, S × P, R × P, S × R	1	0.30	0.586

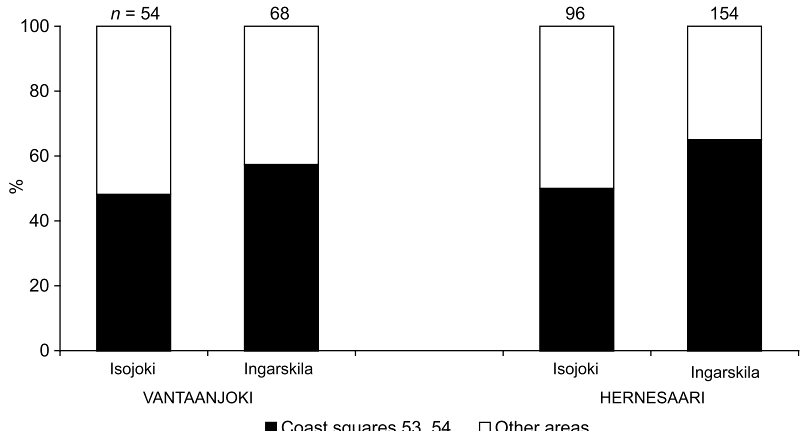

Fig. 4. Spatial sea distribution of recoveries in the Gulf of Finland. Recovery site (two classes): Other areas (= Gulf of Finland, except squares 53 and 54, near the release site) and coastal squares (= squares 53 and 54). The release sites (estuary of the Vantaanjoki and shore of Hernesaari island) are located in square 53. Recoveries 5–19 months after release are included.

Stock, release site and recovery time

The origin of the stock, but not the release site, affected the recovery time. The one-interaction model between stock and recovery time was significantly better than the model without the interaction ($G^2_{\mathrm{S, R, T}} - G^2_{\mathrm{S, R, T, S \times T}} = 47.09 - 3.64 = 43.09$; df = 7 – 5 = 2; $\chi^2_{0.01} = 9.21$) (Table 7). The two-interaction model between stock and recovery time and between release site and recovery time was more compatible with our data ($P = 0.902$), but it was not statistically significantly better than the one-interaction model ($G^2_{\mathrm{S, R, T, S \times T}} - G^2_{\mathrm{S, R, T, S \times T, R \times T}} = 3.64 - 0.57 = 3.24$; df = 5 – 3 = 2; $\chi^2_{0.05} = 5.99$). Fifty-seven per cent of the Isojoki trout ($N_{\mathrm{all}} = 169$) and 34% ($N_{\mathrm{all}} = 248$) of the Ingarskilanjoki trout were caught in the feeding period (Dec.–Aug.) (Fig. 5).

Stock, gear type and recovery site

The model with two interactions, between stock and recovery site and between gear type and recovery site, was compatible with our data ($P = 0.412$). It was significantly better than the model with one interaction, between gear type and recovery site ($G^2_{\mathrm{S, G, P G \times P}} - G^2_{\mathrm{S, G, P, S \times P, G \times P}} = 13.39 - 8.22 = 5.17$; df = 9 – 8 = 1; $\chi^2_{0.05} = 3.84$) (Table 8). Adding the interaction between stock and gear type did not improve the model signifi-

Table 7. Effect of stock and release site on temporal sea distribution in the Gulf of Finland. Log-linear models and test of independence between classified variables: stock, S (Isojoki and Ingarskilanjoki trout), release site, R (estuary of the Vantaanjoki and shore of Hernesaari island) recovery time, T (5–7, 8–16, 17–19 months in the sea). The sample sizes are shown in Fig. 5. Variables are expected to be independent when separated by a comma and to interact when there is no comma. Model, null hypothesis; df = degrees of freedom; G^2 = likelihood ratio; °*P*-values indicate the discrepancy between the model and the data; *f** shows the models with the best fit ($P > 0.05$).

Model	df	G^2	°*P*
S, R, T	7	47.09	0.000
S, R, T, S × T	5	3.64	0.603*f**
S, R, T, R × T	5	44.03	0.000
S, R, T, S × R	6	46.32	0.000
S, R, T, S × T, R × T	3	0.57	0.902*f**
S, R, T, S × T, S × R	4	2.87	0.579
S, R, T, R × T, S × R	4	43.26	0.000
S, R, T, S × T, R × T, S × R	2	0.31	0.854

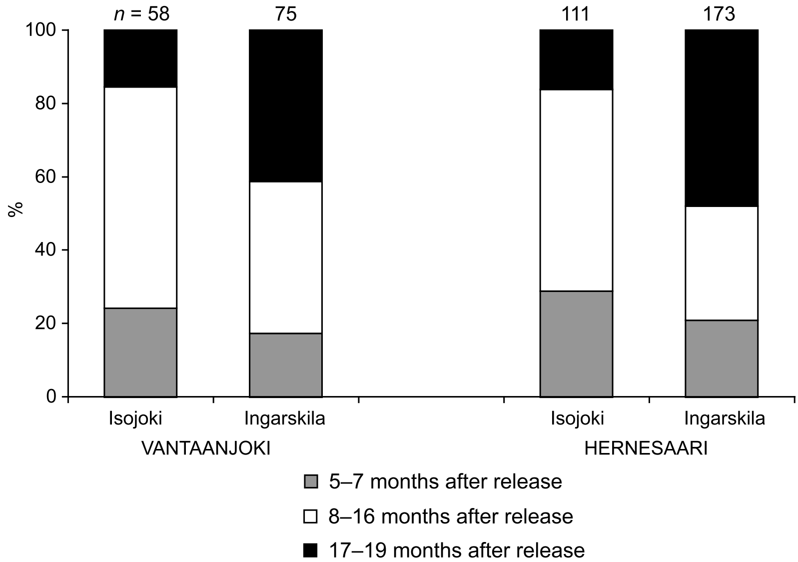

Fig. 5. Temporal sea distribution of recoveries in the Gulf of Finland. The release sites (estuary of the Vantaanjoki and shore of Hernesaari island) are located in square 53. Recovery time: (three classes): 5–7, 8–16 and 17–19 months after release.

Table 8. Interrelationships between stock, gear type and release site in the Gulf of Finland. Log-linear models and test of independence between classified variables: stock, S (Isojoki and Ingarskilanjoki trout), gear type, G (classes 1–5: bottom gill net, floating gill net, trap net, long lines, rods) recovery site, P (statistical squares 53 and 54 = coastal and other waters of the Gulf of Finland. Recoveries 5–19 months after release are included. The contingency table with sample sizes is shown. Variables are expected to be independent when separated by a comma and to interact when there is no comma. Model, null hypothesis; df = degrees of freedom; G^2 = likelihood ratio; °*P*-values indicate the discrepancy between the model and the data; f^* shows the models with the best fit ($P > 0.05$).

Gear types	Isojoki stock			Ingarskilanjoki stock		
	Recovery site		Total (%)	Recovery site		Total (%)
	Coast	Other areas		Coast	Other areas	
Bottom gill net	50	37	67	77	46	59
Floating gill net	4	1	4	19	1	10
Trap net	2	12	11	7	11	9
Long line	1	1	2	1	1	1
Rods	8	13	16	27	18	21

Model	df	G^2	°*P*
S, G, P	13	40.96	0.000
S, G, P, S × P	12	35.79	0.000
S, G, P, G × P	9	13.39	0.145
S, G, P, S × G	9	34.39	0.000
S, G, P, S × P, G × P	8	8.22	0.412f^*
S, G, P, S × P, S × G	8	29.91	0.000
S, G, P, G × P, S × G	5	6.81	0.235
S, G, P, S × P, G × P, S × G	4	2.98	0.561

cantly ($G^2_{\text{S, G, P, S} \times \text{P, G} \times \text{P}} - G^2_{\text{S, G, P, S} \times \text{P, G} \times \text{P, S} \times \text{G}} = 8.22 - 2.98 = 5.24$; df = 8 – 4 = 4; $\chi^2_{0.05} = 9.48$). Thus the origin of the stock had an effect on the spatial sea distribution in the two different sea areas where different gear types were used. The analysis also showed that stocks were not caught with different gear types. The stock-specific migration patterns were not due to the different gear types used. The majority of the Isojoki (67%) and Ingarskilanjoki (59%) sea trout were caught with gill nets (Table 8).

Stock, gear types and recovery time

The model with two interactions, between stock and recovery time and between gear type and recovery time, was most compatible with the data ($P = 0.555$) (Table 9) and was significantly better than the model with one interaction ($G^2_{\text{S, G, P, S} \times \text{T}} - G^2_{\text{S, G, P, S} \times \text{T, G} \times \text{T}} = 26.73$; df = 10 – 6 = 4; $\chi^2_{0.001} = 18.46$ and $G^2_{\text{S, G, P, G} \times \text{T}} - G^2_{\text{S, G, P, S} \times \text{T, G} \times \text{T}} = 24.34$; df = 8 – 6 = 2; $\chi^2_{0.001} = 13.81$). This implies that the recovery time depended on the stock and that different gear types were used seasonally. The analysis also shows that both the Isojoki and the Ingarskilanjoki trout were caught equally frequently with these three gear types. The majority of fish, 72% of Isojoki and 66% of Ingarskilanjoki trout, were caught with bottom gill nets, when three gear types were included in the analyses (Table 9). The bottom gill net catch was overwhelmingly dominant in the feeding period, December–August.

Discussion

Stock-specific sea migration

The two sea trout (*Salmo trutta*) stocks compared here differed significantly from each other

Table 9. Interrelationships between stock, gear type and release time in the Gulf of Finland. Log-linear models and test of independence between classified variables: stock, S (Isojoki and Ingarskilanjoki trout), gear type, G (classes 1, 3, 5: bottom gill net, trap net, rods) recovery time, P (5–7, 8–16, 17–19 months after release. Recoveries from the Gulf of Finland are included. The contingency table with sample sizes is shown. Variables are expected to be independent when separated by a comma and to interact when there is no comma. Model, null hypothesis; df = degrees of freedom; G^2 = likelihood ratio; °*P*-values indicate the discrepancy between the model and the data; *f** shows the models with the best fit ($P > 0.05$).

	Isojoki stock				Ingarskilanjoki stock			
	Recovery time			Recovery (%)	Recovery time			Recovery (%)
Gear types	5–7	8–16	17–19		5–7	8–16	7–19	
Bottom gill net	26	58	6	72	31	60	43	67
Trap net	2	6	6	11	1	9	13	11
Rods	7	8	6	17	11	11	23	22

Model	df	G^2	°*P*
S, G, T	12	55.98	0.000
S, G, T, S × T	10	31.64	0.000
S, G, T, S × G	10	54.44	0.000
S, G, T, G × T	8	29.25	0.000
S, G, T, S × T, S × G	8	30.10	0.000
S, G, T, S × T, G × T	6	4.91	0.555*f**
S, G, T, G × T, S × G	6	27.72	0.000
S, G, T, S × T, S × G, G × T	4	4.19	0.384

in spatial and temporal sea distributions. The Ingarskilanjoki trout migrated more frequently to feed in coastal waters, in the archipelago area, near the release site than did the Isojoki trout. The null hypothesis, that spatial sea distribution is independent of stock, was thus rejected. The stock-specific differences were expected, because the salmon stocks originated from different parts of the Baltic Sea. The Gulf of Bothnia, which is the natural migration area for the Isojoki sea trout, and the Gulf of Finland, which is the home area of the Ingarskilanjoki sea trout, have different food resources for salmon (Salminen *et al*. 1995). The stocked Neva salmon, which migrates only a short distance, grows more slowly in the Gulf of Bothnia than in the Gulf of Finland. Moreover, most of the salmon originating from the Gulf of Bothnia migrated to feed outside the gulf (Kallio-Nyberg *et al*. 1999). This may be the reason why the Isojoki trout need a wider feeding area. In both salmon and sea trout, stock-specific tendencies to migrate are maintained in foreign release sites and habitats (Hansen & Jonsson 1990, Kallio-Nyberg & Ikonen 1992, Svärdson & Fagerström 1982).

The phenotypic differences in spatial sea distribution observed between stocks could be largely genetic, because the environmental variation between groups was minimized in the experiment. Moreover, the sea trout stocks studied have been shown to be genetically different (Koljonen 1989). Stock-specific differences in some other components of the migration behaviour of trout have been shown to have a genetic basis. For example, the genetic and stock-specific direction of smolt migration (Huusko *et al*. 1990, Koljonen & Huusko 1993) and the inherited response to the direction of the river current in the smolts of brown trout (*Salmo trutta*) (Jonsson *et al*. 1994) have been demonstrated.

The temporal sea distribution was stock dependent. The null hypothesis was thus rejected. The trout stocks were caught at different times (stock-recovery time interaction), as fishing activity varied seasonally between different sea areas or the stocks migrated seasonally between coastal and offshore waters (recovery site and recovery time interaction). The seasonal move between freshwater and the sea one or more years before maturation is typical of the behaviour of migratory trout (Jonsson 1985). In winter, the Isojoki trout were mainly caught offshore. At that time, ice covers the coastal waters, where the Ingarskilanjoki trout migrate to feed. The results do not tell us how long the trout spend in the sea. Most of them were probably caught before the first spawning migration.

Effect of release site on sea migration

Both the Ingarskilanjoki trout and the Isojoki trout released into two sites on the coastline showed stock-specific spatial distributions independent of release site. At both sites, the Isojoki trout migrated offshore more frequently than did the Ingarskilanjoki trout. The Isojoki sea trout left the waters near the release sites, except for the release site itself, and tended to migrate to feed offshore, too. The Ingarskilanjoki trout stayed near the coastline. Release further out from the estuary, in the waters of Hernesaari, did not stimulate the Ingarskilanjoki sea trout to leave the coastal waters. The results suggest that migration distance is partly genetically and partly environmentally controlled. The attempt to reach suitable feeding areas may guide the sea migration of trout. Salmon originating from Bothnian Bay presumably remain in the Gulf of Bothnia in years with ample food resources (Salminen *et al*. 1994, Kallio-Nyberg *et al*. 1999).

Migration tendency of experimental stocks

Trout show great variation in life history, migration behaviour and activity, and growth rate (Jonsson 1985), and both anadromous and resident life-history forms may exist in the same population (Jonsson 1982). There is not much information on the proportions of migratory and resident forms in the natural stocks in the rivers Isojoki and Ingarskilanjoki. The reared groups at least are anadromous. Allozyme studies showed that the brood stocks of the Isojoki and Ingarskilanjoki have been changed genetically by breeding (Saura 1998, Ahvonen *et al*. 1993). Thus the experimental groups of these stocks may represent only a part of the variation in these stocks. Trout from the two rivers have different breeding histories (Saura 1998, Kallio 1986). The Isojoki trout have been reared through many fish generations, since the 1960s, but the Ingarskilanjoki trout through only two generations, since the 1980s. Breeding with unintentional or intentional selection has probably affected the genetic traits of fish in brood stocks as it has changed the traits of salmon (Fleming *et al*. 1996). Also, the differences in the tendency of trout to migrate have been shown to be affected by environmental selection pressure in the wild (Jonsson 1982). Large anadromous spawners were favoured when the brood stock of the Isojoki trout was established, but the brood stock of the Ingarskilanjoki trout was established with juveniles caught in the stream, without information on life history, sea migration or sea growth rate. The long breeding history and the domesticating selection of the Isojoki trout may partly explain the higher sea growth rate of the Isojoki than of the Ingarskilanjoki trout.

Both experimental stocks were established for stocking purposes. The Isojoki stock is used in its own river for improving the stock there and in other rivers for sea-ranching in the Gulf of Bothnia. Because no reared sea trout stocks originating from the Gulf of Finland existed before the Ingarskilanjoki brood stock, the Isojoki stock has also been used for stockings in the Gulf of Finland. This comparative study showed that both experimental stocks had a tendency to migrate.

On the basis of migration behaviour, both stocks are suitable for stocking in coastal areas of the Gulf of Finland. However, the Ingarskilanjoki trout stock is better for enhancement purposes, at least in its own river and near empty rivers, due to its genetic origin. In enhancement, the goal is to establish a natural stock with long-term natural production. The present Isojoki stock might be more suitable for sea-ranching, because its growth rate was higher than that of the Ingarskilanjoki stock after the first sea year. In the future, the Ingarskilanjoki brood stock may eventually have a higher growth rate after many hatchery generations due to domestication. The Ingarskilanjoki trout stock can also be recommended for sea-ranching in the Gulf of Finland, because it originated from this area and because the strayers of the transplanted stock pose a threat to the genetic structure of the original stock (Hansen & Loescheke 1994). The management of sea trout in the future could be conducted with the aid of natural smolt production and strict fishing regulation in some rivers and artificial production for fishery in some others.

Sea migration and sea area

Both stocks were caught mainly in the coastal waters of the Gulf of Finland. The limited spatial distribution of recoveries observed here was similar to that reported for sea trout in other sea trout stocks (Svärdson & Fagerström 1982, Berg & Berg 1987). There are no earlier observations on the distribution of the Ingarskilanjoki trout in the sea. Tagging experiments in the Gulf of Bothnia show that the Isojoki sea trout is a stationary type in terms of spatial sea migration. It was caught mainly near the release site, in coastal waters, and it migrated mainly northwards in this sea area (Ikonen & Auvinen 1984, Leskelä & Hudd 1997). The Isojoki trout released into the estuary of the Kyrönjoki in the Gulf of Bothnia were caught as adults (over 35 cm) most frequently in Finnish coastal waters, half more than and half less than 50 km from the release site. Only one fish was caught outside the Gulf of Bothnia (N = 318) (Leskelä & Hudd 1997). The Isojoki sea trout released into the estuary of the Kokemäenjoki in the Gulf of Bothnia also showed a tendency to migrate northwards and to remain in coastal waters (Ikonen & Auvinen 1984). Here, when Isojoki sea trout were released into the estuary of the Vantaanjoki, 11% of them left the Gulf of Finland, without showing, however, any clear preference for direction of migration.

Sea migration and fishery

The spatial and temporal distributions of tag recoveries also depend on the distribution of fishery. In a comparative study, it is, however, essential that the method should not affect the differences between groups. There was no statistical indication, that is, no stock-gear interaction, that stocks were caught with different gear types. Therefore, gear types did not influence the stock-specific differences in spatial and temporal sea distributions. Likewise, fish size, and release time, two factors that may affect catchability, were similar for both stocks. However, the difference in the temporal distribution of the two stocks might partly be due to the difference in the spatial distribution of the stocks in the season. The interaction between recovery site and recovery time supported this assumption. Both stocks were caught intensively in coastal waters in winter, but because the Isojoki trout is found more frequently in the open sea, they might be caught more often offshore in winter, when coastal waters are covered with ice. The Isojoki trout may also move seasonally more actively between coastal waters and the open sea.

In the management of fish stocks, it is important to favour measures that promote the conservation of adaptive variation in fish species. Salmon populations living in their own habitat are locally adapted (Quinn 1982). In contrast, a transplanted fish stock has poorer fitness, for example, homing success, than has the local population (Bams 1976). Moreover, in cultivation the reared fish stock has a high probability of losing its genetic variability (Verspoor 1988). Primarily, owing to the genetic threats in particular, the Ingarskilanjoki stock should be favoured in future stockings in the Gulf of Finland.

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