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Differences in sea migration between wild and reared Atlantic salmon (*Salmo salar* L.) in the Baltic Sea

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Abstract

The effect of origin, smolt size and year of release on the sea migration pattern of Atlantic salmon (*Salmo salar* L.) in the Baltic Sea was examined by tagging experiments conducted in 1991–1993 on wild and reared smolts of the Simojoki river salmon stock. The tag recovery data analysed by log-linear models revealed significant differences in both spatial and temporal sea migrations between the wild and reared salmon; the variation was attributed to the year of release and to the origin of the fish. Grilse accounted for the majority of reared returners (76%) but for a smaller proportion (46%) of the wild fish. The effect of smolt size could be studied only in the smolt groups tagged in 1991. Wild fish were more frequently (71%) caught in the Baltic Main Basin than were reared fish (51%) during their second sea year, and the size variation between wild and reared smolts did not explain the recovery site. No such differences in spatial distribution were found during the third sea year. The tagging place (hatchery/trap) of the reared fish did not affect their later sea migration. The differences in sea migration patterns suggest that the wild salmon are more vulnerable to the intensive salmon fishery in the Baltic Main Basin than are reared fish.

Keywords: Salmon; Migration; Smolt; Reared; Wild

1. Introduction

Comparative studies of hatchery-reared and wild smolts of Atlantic salmon have shown that reared and natural fish do not necessarily have similar life-history traits in the sea (Jonsson et al., 1991; Einum and Fleming, 2001). In the Baltic Sea, for example, the smolt size of salmon released into the northern Gulf of Bothnia was found to have an effect on migration distance in the sea (Salminen et al., 1994; Kallio-Nyberg et al., 1999). The number of breeding generations of sea-ranched salmon has been demonstrated to increase the growth rate and the proportion of grilse in the spawning population (Kallio-Nyberg and Koljonen, 1997). Also the timing of the spawning migration is affected by breeding and age at maturity (Ikonen and Kallio-Nyberg, 1993; Karlsson et al., 1999). Reared salmon return to the northern Baltic Sea later than wild spawners (McKinnell et al., 1994; Karlsson et al., 1999).

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Each salmon stock has stock-specific and genetically determined spatial and temporal marine distributions (Brannon, 1984; Kallio-Nyberg et al., 2000). The effect of domestication has been demonstrated in many components of the behaviour of salmon (Jonsson et al., 1990; Fleming et al., 1997), but the influence of breeding on spatial marine distribution or migration distance has been only scantily studied. The simultaneous production of wild and reared smolts of a common stock, and the extensive fishing and high recovery rate of tagged fish within the Baltic Sea have enabled us to study the effect of different smolt features on the sea migration behaviour and also on the duration of the sea migration of adult salmon.

A great majority (about 90%) of the Atlantic salmon smolts entering the Baltic Sea are hatchery-reared fish, because large-scale compensatory and enhancement stockings of smolts and parr are carried out annually. The natural salmon stocks are endangered due to the decline in the number of returning spawners in rivers as a result of the intensive mixed-stock salmon fishery in the Baltic Sea (Eriksson and Eriksson, 1993; McKinnell, 1997; Anon., 2000). The aim of this work was to study the variation in sea migration and, especially, the effect of the different smolt features arising from origin (wild/reared) on sea migration behaviour. A comparison was also made between the wild and reared salmon in their age at sexual maturity. The variation in sea migration was measured by the spatial and temporal distribution of tag recoveries from caught fish. Because the reared smolts were larger than the wild ones, the effect of smolt size on migration behaviour was also included in the analyses. Our null hypothesis was that origin, whether wild or reared, and smolt size have no influence on the spatial and temporal sea distributions of catch sized fish (>60 cm TL) in the sea. Temporal sea distribution was described both by the duration of the migration (year) in the Baltic Sea and by the catch time (year) of returners in the northern Gulf of Bothnia, Bothnian Bay.

2. Material and methods

2.1. Salmon stock

The salmon used in this study originated from the Simojoki (25°E, 65.5°N), a river running into the northernmost part of the Gulf of Bothnia (Fig. 1). The Simojoki supports a small and endangered natural salmon stock (Jutila and Pruuki, 1988). In order to maintain this genetically unique stock (Koljonen, 1989, 1995) and to prevent it from dying out, the river has been stocked with reared smolts and parr with a view to increase its smolt production (Jutila, 1992).

The salmon stocks in the northern Gulf of Bothnia are far migrating, their main feeding area being in the central and southern Baltic Main Basin (Christensen and Larsson, 1979). A minor, but variable, proportion of them feed in the southern Gulf of Bothnia, the Bothnian Sea (Salminen et al., 1994). Feeding salmon remain in the sea for 1–4 years before returning to their native river. Maturing salmon leave the southern Baltic Main Basin in April–June and ascend the rivers in June–September. Thus all adult salmon caught in the northern Gulf of Bothnia during the summer are spawners returning to their home rivers (Ikonen and Kallio-Nyberg, 1993; Karlsson and Karlström, 1994).

Here, all the reared smolts were offspring of returning spawners caught at the river mouth in the summers of 1988–1990. It was assumed that the origin of the caught salmon was similar to that of the salmon spawned in the river. The salmon caught at the river mouth were transported to the Finnish Game and Fisheries Research Institute's Simojoki hatchery (Groups 2a and 2b, Table 1), which is located by the river, about 10 km from the sea, and kept there until they were stripped (Fig. 1). The fertilised eggs were

Table 1
The origin, numbers and length (mm) of salmon smolts tagged in the Simojoki in 1991–1993[a]

Year	Origin/group	Tagging site	Number tagged	Mean length	S.D.
1991	Wild	Trap	999	161	±13
1991	Reared/1	Hatchery (HT)	997	181	±17
1991	Reared/1	Trap (TT)	998	191	±16
1991	Reared/2a	Hatchery (HT)	981	176	±18
1992	Wild	Trap	574	154	±10
1992	Reared/2b	Hatchery (HT)	999	184	±18
1993	Wild	Trap	979	152	±9
1993	Reared/2b	Hatchery (HT)	996	190	±19
1993	Reared/2b	Trap (TT)	768	195	±17

[a] Group 1—Vesiviljely Ky hatchery, smolts released in Tainikoski rapids, Group 2a—Simojoki hatchery, smolts released in Isopetäjäkoski rapids, Group 2b—Simojoki hatchery, smolts released in Tainikoski rapids.

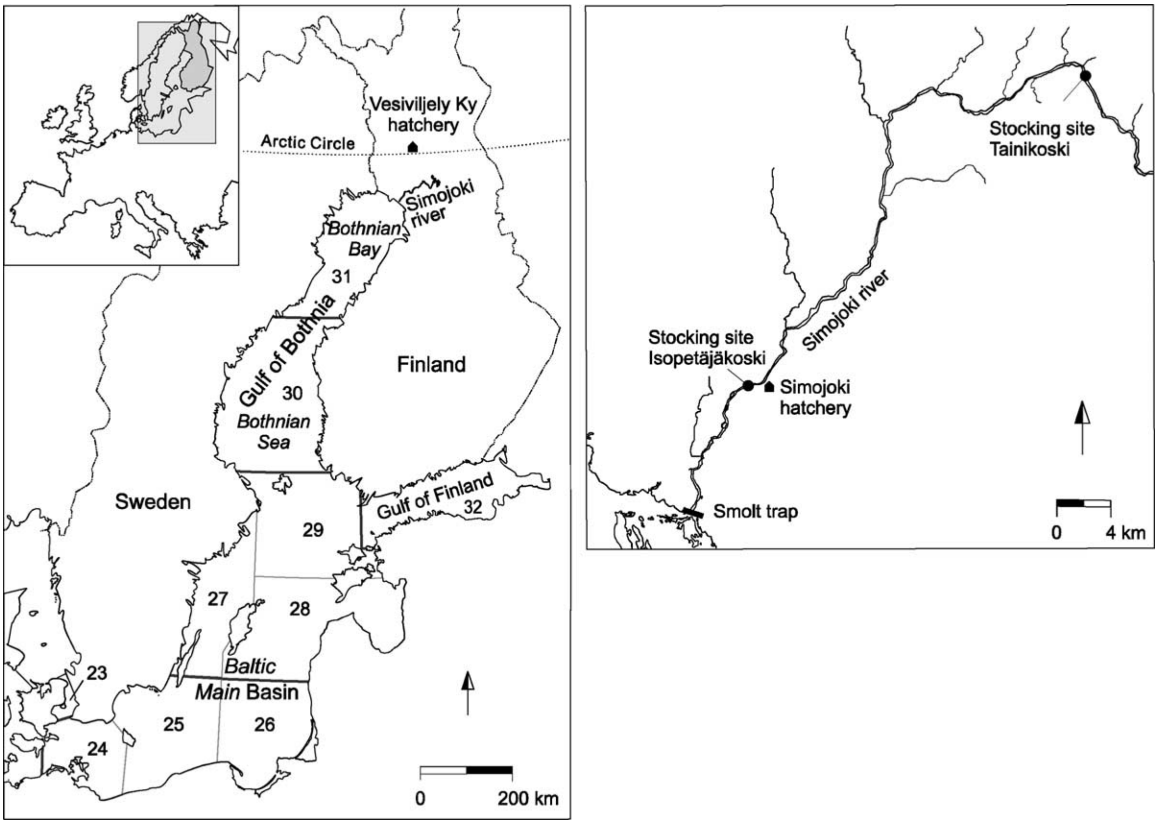

Fig. 1. Map of the Simojoki and the Baltic Sea showing the location of the hatcheries, stocking sites and smolt trap, the main parts of the Baltic Sea and the ICES subdivisions.

incubated and raised at the hatchery as fingerlings before being released in the river as 2-year-old smolts. In spring 1991, however, over half of the smolts released were reared about 100 km north of the Simojoki, at the Vesiviljely Ky hatchery (Group 1), to which they had been transferred as eyed ova. At the hatchery, the fingerlings were reared in their first summer in 4 m^2 fibreglass tanks in a rearing hall and thereafter outdoors in concrete tanks. The fish were fed pelleted dry feed at ambient water temperature and in the natural photoperiod.

2.2. Tagging and trapping

The data for this study were derived from 8291 reared and wild salmon smolts from the Simojoki river that were tagged with external Carlin tags (Table 1). In 1991–1993, four groups of reared smolts (3973 fish) were tagged under anaesthesia (MS-222) at the hatchery from 1 to 3 weeks before the stocking, but in 1992 only 1 day before stocking. During the previous winter, the adipose fin had been removed from all the reared smolts to permit them to be distinguished later from the wild smolts. Before the tagging, the total length (mm) of each tagged smolt was measured. As recoveries of very small smolts had been very poor in earlier tagging experiments (Finnish Game and Fisheries Research Institute, unpublished), only smolts with a minimum size of 140 mm were accepted for tagging. The reared smolts were released in the river during the migration season of wild smolts. The reared hatchery-tagged smolts (=HT) were released in two rapids, Tainikoski (Group 2a only) and Isopetäjäkoski, located 47 and 11 km, respectively, above the river mouth.

The wild smolts (2552 together) were sampled and tagged at a smolt trap placed in the river mouth. The trapping and tagging period covered the main smolt run from late May to the end of June, lasting for about 2 weeks in 1991 and 1992 and 6 weeks in 1993. In 1991 and 1993, several thousand untagged reared smolts were released together with the HT smolts, and 1766 of them were tagged and measured at the trap (trap-tagged = TT). After tagging, all TT and wild smolts were put into a cage to recover from stress before release on the following day.

The majority of the wild smolts were 2- or 3-year-old in different years (Jokikokko and Jutila, 1998), whereas all the reared smolts were 2-year-old. The annual mean length of the wild smolts was lower than that of the reared smolts (Table 1) (Kolmogorov–Smirnov two-sample test, $P < 0.001$).

2.3. Recapture and fishing

It was presumed that the tagging and fishing affected wild and reared salmon similarly. The tagging was expected to have an equal effect on both fish groups because they were tagged by the same persons and released in the same river, the recaptures were from the same years, and the fishing was extensive covering the whole migration area of Simojoki salmon in the Baltic Sea. Fishermen returned the tags with information on the place and time of recapture but they did not know the origin of the tagged fish until the information was sent from the tagging office.

The tag recovery rate was 20.8% for the wild fish and 12.7% for the reared fish tagged in 1991, but remained very low in the groups tagged in 1992 and 1993 (Table 2). Both the wild and the reared salmon were caught mainly in the Gulf of Bothnia (ICES subdivisions 30–31) or in the Baltic Main Basin (subdivisions 24–29). To permit a more detailed analysis of the distribution of tag recoveries, the Baltic Main Basin was divided into the Northern Main Basin (subdivisions 27–29) and the Southern Main Basin (subdivisions 24–26). A few recoveries were made outside this area, in the Gulf of Finland (subdivision 32) and in the river, but they were excluded from the analysis of sea migration (Table 3). Most recoveries of adult salmon (91% of reared and 88% of wild salmon) were from the second and third sea years.

The annual variation in the spatial and temporal sea distributions of recoveries was analysed. The relationships between origin, year of release and recovery site or time were studied in the groups tagged in 1991–1993. The number of recoveries was so low for the groups tagged in 1992 and 1993 that the effect of smolt size on sea migration behaviour could be studied only in smolts tagged in 1991. The effect

Table 3
Spatial distribution of recoveries in numbers within sea areas[a]

Tagging year/origin	Sea area			
	GB	NMB	SMB	GF
1991/wild	61	41	93	1
1991/all reared HT	142	64	139	7
1991/reared TT	70	36	70	3
1992/wild	16	7	16	3
1992/reared HT	9	1	16	0
1993/wild	7	11	22	0
1993/all reared HT, TT	10	8	18	1

[a] Gulf of Bothnia (GB), Northern Main Basin (NMB), Southern Main Basin (SMB), Gulf of Finland (GF). One wild and two reared fish were recovered in the river after the release year. In 1991, all reared hatchery-tagged smolts (HT) and in 1993 all reared smolts, whether hatchery- or trap-tagged (HT/TT) are pooled.

Table 2
Number of tag recoveries and the recovery rate (%) in groups tagged in 1991–1993[a]

Tagging year/origin	Annual recoveries					Total	Recovery %
	1st	2nd	3rd	4th	5th–6th		
1991/wild	1	78	104	19	6	208	20.8
1991/all reared HT	5	203	144	25	2	379	12.7
1991/reared TT	1	110	75	8	1	195	19.5
1992/wild	4	15	19	1	1	40	6.0
1992/reared HT	1	14	14	0	2	31	3.1
1993/wild	2	8	24	8	3	45	4.5
1993/all reared HT, TT	2	7	22	2	6	39	2.2

[a] In 1991, all reared hatchery-tagged smolts (HT) and in 1993 all reared smolts, whether hatchery- or trap-tagged (HT/TT) are pooled.

of smolt size was first compared between wild and reared smolts, and then to eliminate the effect of the different tagging/releasing places, between TT reared and wild smolts only.

2.4. Statistical methods

The recovery data were presented in multiway contingency tables and analysed by log-linear methods (McCullagh and Nelder, 1989; Everitt, 1992) using the CATMOD procedure of the SAS statistical package (Version 8e). Log-linear methods are designed for categorical data such as the numbers of recovered tags in our study. The method endeavours to explain the effects of single variables or their combinations (interactions) on recoveries. We included four effect variables (origin, smolt size, recovery site and recovery time) in our three-dimensional log-linear models. The variable origin referred to either wild smolts or reared smolts. The analysis of sea migration by log-linear models is described by Kallio-Nyberg et al. (2000). Non-parametric methods were used to compare smolt sizes and catch dates between wild and reared salmon.

3. Results

3.1. Annual variation in spatial sea distribution

We analysed interrelationships between the origin (wild/reared smolt), year of release (1991, 1992, 1993) and recovery area (GB, NMB, SMB) of tagged salmon by log-linear models (Table 4). Recovery area was dependent on year of release (AY) but there was an interaction between origin and year of release (OY) ($P > 0.091$). This indicates that the spatial distribution varied from year to year. The proportion of recoveries made in the Gulf of Bothnia varied yearly from 17 to 41% in wild fish and from 27 to 41% in reared fish. The results show that the difference between wild and reared fish also varied, depending on the year of release. Wild fish released in 1991 and 1993 were caught less frequently in the Gulf of Bothnia than were reared fish, but for fish released in 1992 the opposite was true. The number of recoveries was, however, very small in the groups tagged in 1992 and 1993. The three-interaction model was not significantly better than the two-interaction model ($G^2_{\mathrm{OA,OY,AY}} - G^2_{\mathrm{OY,AY}} = 10.91 - 5.78 = 5.13$, d.f. $= 6 - 4 = 2$, $\chi^2_{0.05} = 5.99$) but origin had, however, a slight influence on the spatial distribution of fish ($P > 0.10$). The interannual variation in spatial distribution was thus stronger than the variation due to the origin of the smolt groups.

Table 4
Relationships between origin, year of release and recovery site[a]

Year	Origin					
	Wild smolts			Reared smolts		
	GB	NMB	SMB	GB	NMB	SMB
1991	61	41	93	142	64	139
1992	16	7	16	9	1	16
1993	7	11	22	10	8	18
Models	d.f.	G^2	P			
OA, OY	8	14.8	0.062			
OY, AY	6	10.9	0.091 f			
OA, OY, AY	4	5.8	0.216			

[a] Contingency table and three log-linear models with best fit are shown. Log-linear models and test of independence include the classified variables: origin (O: wild/reared), year of release (Y: 1991/1992/1993) and recovery area (A: Gulf of Bothnia/Northern Main Basin/Southern Main Basin). Model—variables are expected to interact when written together (like OA). G^2 is the likelihood ratio, test value. P values indicate discrepancy between model and data. f shows models with best fit ($P > 0.05$).

3.2. Annual variation in temporal sea distribution

There were significant relationships between origin (wild/reared), year of release (1991, 1992, 1993) and recovery time (second sea year and third to fifth sea years) (Table 5). The three-interaction model was compatible with the data ($P > 0.545$). The interaction “origin–recovery time” (OT) shows that wild and reared fish were caught at different times, the wild fish usually later than the reared ones. The interaction “recovery time–year” (TY) shows the variation in the duration of the sea migration between the groups released in different years. For example, in the smolt groups released in 1993, over 80% of recoveries from both wild and reared salmon were made shortly after the second sea year. In the groups released in 1991 and 1992, the proportion of fish older than two sea years was 61 and 58% in recoveries of wild fish but only 43

Table 5
Relationships between origin, year and recovery time[a]

Year	Origin			
	Wild smolts		Reared smolts	
	2nd	3rd–5th	2nd	3rd–5th
1991	73	115	193	149
1992	14	20	13	12
1993	7	32	6	26
Models	d.f.	G^2	P	
OT, TY	4	15.4	0.004	
OY, TY	3	15.8	0.001	
OY, OT, TY	2	1.2	0.546 *f*	

[a] Contingency table and three log-linear models with best fit are shown. Log-linear models and test of independence include the classified variables: origin (O: wild/reared), year of release (Y: 1991/1992/1993) and recovery time (T: 2nd/3rd–5th sea years). Model—variables are expected to interact when written together (like OT). G^2 is the likelihood ratio, test value. *f* shows models with best fit ($P > 0.05$).

and 48% in those of reared salmon, respectively. The “origin–year” interaction (OY) shows that the relative difference in temporal sea migration between wild and reared fish varied from year to year. In the wild and reared groups released in 1993, the proportions of recaptures made in the second sea year were fairly similar, but in the groups released in 1991 and 1992 wild fish were more frequently recovered after the second sea year. The results indicate that the duration of the sea migration in the groups released in different years should not be analysed together without a year (of release) variable.

3.3. Sea age at sexual maturity

In the tagging groups released in 1991–1993, sea age at maturity was calculated from tag recoveries of fish caught in Bothnian Bay after one sea winter as grilse or later as multi-sea-winter (MSW) salmon after two and three sea winters. The majority (76%) of the reared salmon, but a smaller proportion (46%) of the wild fish, returned as grilse during the 3 years following the release. Most of the wild fish had spent two or three winters on their feeding migration before starting their spawning migration. The proportions of grilse and MSW salmon differed significantly between the reared and the wild salmon ($\chi^2 = 13.6$, d.f. = 2, $P < 0.001$) (Fig. 2). The mean sea age at sexual maturity was 1.27 ± 0.52 years in the reared and 1.67 ± 0.69 years in the wild salmon.

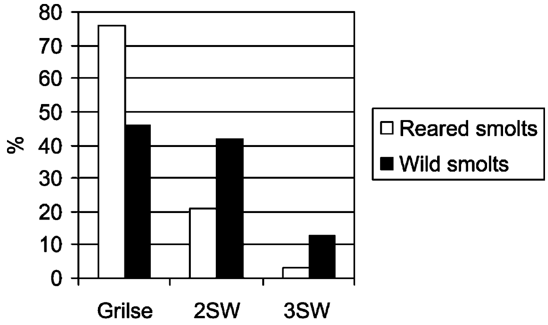

Fig. 2. Grilse (1 sea-winter; SW), 2SW and 3SW salmon (age at sexual maturity) as proportions of wild and reared salmon in spawning migrants recovered in Bothnian Bay, the tagging groups released in the Simojoki in 1991–1993.

3.4. Sea migration in groups tagged in 1991

3.4.1. Effect of origin and smolt size

Most recoveries of all the smolt groups of Simojoki salmon released in 1991 were made in the Baltic Main Basin during the second and third years after release (wild 72%, reared 61%) (Table 6). The recoveries show that salmon in the category of large smolts (170–269 mm) were more likely to stay in the Gulf of Bothnia during their feeding migration (25%) than were salmon in the category of small (131–169 mm) smolts (10%). The majority of the reared salmon caught in the Gulf of Bothnia (90%) were ranked in the category of large smolts, whereas only a minority (36%) of the wild smolts belonged to this category.

To start with, we analysed the effect of origin and smolt size on the spatial distribution of tag recoveries during the second and third sea years. In the second sea year (1992), about half (49%) of the reared fish migrated in the Gulf of Bothnia. In contrast, only 29% of wild fish recoveries were made in that sea area. The majority (71%) of the wild fish were caught in their second sea year in the Main Basin. The spatial sea distributions of the wild and reared fish differed from each other in their second sea year; smolt sizes also differed. The model with two interactions, between

Table 6
Effects of origin and smolt size on recovery site in smolts tagged in 1991[a]

	Smolt size	Wild fish			Reared fish		
		GB	NMB	SMB	GB	NMB	SMB
Recoveries in 2nd sea year	131–169	16	11	22	12	6	3
	170–269	5	5	14	83	23	66
Recoveries in 3rd sea year	131–169	18	15	27	3	3	6
	170–269	9	4	25	26	30	61
Year	Model	d.f.	G^2	P			
2nd	OA, OS	4	7.9	0.095 f			
	OA, OS, AS	2	2.1	0.346			
3rd	OS	6	6.5	0.367 f			
	OA, OS	4	4.9	0.288			

[a] Contingency table with recoveries in the 2nd and 3rd sea years is shown and the annual recoveries are analysed separately. Log-linear models and test of independence include the classified variables: origin (O: wild/reared), smolt size (S: 131–169 mm/170–269 mm) and recovery area (A: Gulf of Bothnia/Northern Main Basin/Southern Main Basin). Model—variables are expected to interact when written together (like OA). G^2 is the likelihood ratio, test value. f shows models with best fit ($P > 0.05$).

origin and recovery site and between origin and smolt size, fitted the data ($P > 0.095$) (Table 6). Adding the interaction between recovery site and smolt size did not improve the model significantly. Thus, origin explained spatial sea distribution but not smolt size. Accordingly, the wild fish were caught more frequently in the feeding areas of the Main Basin than were the reared fish, which preferred to stay in the Gulf of Bothnia during their feeding migration.

We found no differences in spatial sea distribution between the wild and reared fish in their third sea year. The model with an interaction only between origin and smolt size was compatible with the data ($P > 0.367$) (Table 6). Adding the number of interactions did not increase the compatibility with the data, implying that the differences in spatial sea distribution between the wild and reared fish in the second sea year had disappeared in the third sea year.

3.4.2. *Effect of tagging procedure*

To eliminate the effect of different tagging and releasing procedures, we studied differences in spatial sea distribution between the wild and reared smolts in smolt groups tagged identically at the smolt trap in 1991. In contrast to previous analyses, only TT smolts (reared TT/wild) were compared and the sea area was divided into two parts (Gulf of Bothnia/Main Basin). Here, too, the spatial sea distribution of the wild salmon differed from that of the reared fish during the second sea year. There were interactions between origin and recovery site and between origin and smolt size ($P > 0.555$). The best model was the same as that in Table 6 and it fitted the data even better. Adding the interaction between smolt size and recovery site did not increase compatibility with the data.

The origin of the fish did not effect spatial sea distribution during the third sea year. The model including an interaction between origin and smolt size was compatible with the data ($P > 0.898$). The spatial sea distribution of the reared fish tagged at the trapping site was similar to that of all reared fish. The results show that the different tagging places (HT/TT) of the smolts before their release had no effect on the spatial distribution of the tag recoveries in the Baltic Sea.

4. Discussion

4.1. *Effect of origin*

There was a difference in sea migration behaviour between wild and reared fish. The null hypothesis that there are no differences in sea migration behaviours between wild and reared fish was thus rejected. The reared salmon had a shorter feeding migration distance and they also left the feeding areas at a younger age than did the wild fish. These observations are consistent with the finding that breeding changes the behaviour of salmon during their spawning migration (Jonsson et al., 1990, 1991; McKinnell et al., 1994) and during spawning itself (Fleming et al., 1996, 1997; Jonsson, 1997). The shorter sea migration distance of reared salmon implies that their migration activity is lower than that of wild salmon.

The migration behaviour of salmon is known to be partly genetically controlled (Bams, 1976; McIsaac and Quinn, 1988; Hansen and Jonsson, 1991), and reduced genetic variability has been observed even in the first generation of a hatchery population (Verspoor, 1988). However, no genetic differences between natural and reared salmon have been found in the Simojoki stock (Koljonen et al., 1999). Several studies have demonstrated that the different selection factors prevailing in the wild and in a hatchery may result in differences in the morphology, physiology, behaviour and survival of salmon (Økland et al., 1995; Fleming et al., 1996; Jonsson, 1997; Karlsson et al., 1999). Here, the larger smolt size of the reared than of the wild fish was a consequence of their different growth conditions. Also, the survival of juvenile salmon to the smolt stage may be up to 20 times as high in the hatchery as in the wild (Jonsson and Fleming, 1993). Our study shows, however, that the ability of reared smolts to survive in the sea and to perform a complete sea migration was poorer than that of wild salmon.

4.2. Effect of smolt size

A major difference was also found in smolt size between the wild and reared groups. Earlier studies (Salminen et al., 1994; Kallio-Nyberg et al., 1999) have shown that large smolts stocked in Bothnian Bay are more likely to stay for feeding in the Bothnian Sea, at a distance of about 500 km from their home river, than are small smolts. The small smolts in turn migrate relatively more frequently in the Main Basin, at distances of about 1000–1500 km from their home river. In this study smolt size did not explain significantly the spatial sea distribution. Thus the short migration distance of the reared salmon was not a consequence of their large smolt size. This work provided evidence that the mere origin itself, wild or reared, was sufficient to explain the different spatial distributions of the tagged groups.

The differences in migration distance could be observed in the second sea year, suggesting that the differences in spatial distribution between the wild and reared salmon are most pronounced in the year when the Bothnian Bay salmon have reached their feeding areas. In the Baltic Sea, the best feeding areas for salmon are in the Main Basin (Christensen and Larsson, 1979). The results suggest that the reared salmon did not undertake the long feeding migrations typical of Bothnian Bay salmon to the same extent as did the wild salmon. Thus the reared salmon may not have migrated in optimal areas.

4.3. Interannual variation

Observations on the migration distance of wild salmon originating from natural spawn in the Baltic Sea are scarce (Toivonen, 1977), most tagging experiments having been carried out on reared smolts (Salminen et al., 1994, 1995; Kallio-Nyberg et al., 1999). Reared salmon originating from the Tornionjoki, Iijoki or Oulujoki rivers in the northern Gulf of Bothnia tend to migrate in the Main Basin. Fewer salmon stay in the Bothnian Sea during their feeding migration (Kallio-Nyberg et al., 1999). Baltic salmon stocks show a stock-specific sea migration pattern (Kallio-Nyberg and Ikonen, 1992), but the annual variation in spatial sea distribution due to environmental factors is greater than the variation due to origin. At least, it has been suggested that the variation in food abundance from one year to the next influences the annual marine distribution of salmon (Kallio-Nyberg et al., 1999) and survival correlates positively with sea–surface temperatures (Salminen et al., 1995). Here, too, the year factor was found to have a marked effect on the spatial sea distribution of salmon. The number of recoveries was, however, low in 2 of the 3 years analysed. It is likely that both the reared and the wild salmon react to annual environmental factors, although the activity to migrate far into the southern Baltic Sea may vary between these groups.

4.4. Spawning migrants in the Gulf of Bothnia

The reared salmon returned to Bothnian Bay at a younger age than did the wild ones. Kallio-Nyberg and Koljonen (1997) have shown that the proportion of grilse is higher in a more domesticated than in a less domesticated stock. Better growth early in the growing season, in particular, has been demonstrated to result in a younger smolt age of salmon (Thorpe, 1991). Domesticative selection probably favours individuals able to grow fast due to their genetic traits. In salmon, there is a negative genetic correlation between growth rate and age at sexual maturity (Gjerde and Gjedrem, 1984).

Despite the grilse majority in the reared spawning stock, we do not have any evidence of permanent changes in these traits in stocked Bothnian Bay salmon stocks. The observed lower mean sea age at maturity in the reared than in the wild salmon is most probably due to the higher proportion of males in the reared than in the wild smolts (e.g. Jokikokko and Jutila, 1998). Because the high growth rate of salmon smolts tends to favour maturation as grilse (Skilbrei, 1989; Salminen, 1997), the larger size of the reared smolts may also have caused the differences observed in age at maturity.

4.5. Tagging procedure

The tagging procedure may have different effects on fish, depending on whether it is conducted in the hatchery or, later, at the smolt trap in the river. Catching and transport cause physiological stress that may last for as much as 2 days (Iversen et al., 1998), and smolts have been reported to be sensitive to the size-selective mortality caused by tagging (Berg and Berg, 1987; Hansen, 1988; Hansen and Jonsson, 1988). Despite the differences in tagging occasions between the hatchery and the smolt trap and their potential effects on fish survival, the results indicated that the tagging differences did not affect later sea migration patterns.

4.6. Implications for management

Artificial crossing and juvenile breeding in one fish generation caused behavioural and phenotypic divergence of the hatchery-reared and stocked salmon from the wild fish. Annual variation notwithstanding the wild salmon smolts produced relatively more MSW salmon that tended to migrate in the Baltic Main Basin more frequently than did the reared salmon. Wild salmon are thus exposed to the intensive mixed stock salmon fishery in the Baltic Main Basin for a longer period than are reared salmon. Because over half of the total salmon catches in the Baltic Sea area are taken annually from the Baltic Main Basin (Anon., 2000), small wild salmon stocks, e.g. that of the Simojoki river, are particularly vulnerable to the salmon fishery carried out there.

The reared smolts produced salmon that were mostly caught as grilse. Since the majority of grilse salmon are males, the eggs for the spawn are produced by MSW females, which are thus essential for natural reproduction. As the proportion of males is higher in the reared than in the wild smolts of Simojoki salmon (Jokikokko and Jutila, 1998), and because the sea age at maturity is lower in reared than in wild salmon, reared smolts produce fewer MSW female spawners than do equal numbers of wild smolts. Moreover, the reproduction success of reared spawners may be lower than that of wild salmon (Jonsson et al., 1991; Fleming et al., 1996). Thus, the releases of reared smolts in the Simojoki river have probably enhanced the natural stock less than might be expected directly from their numbers and those of the wild smolts.

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