

Phylogeographic lineages and differentiation pattern of Atlantic salmon (*Salmo salar*) in the Baltic Sea with management implications

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Abstract: The genetic structure and isolation pattern of the Atlantic salmon (*Salmo salar*) throughout its range in the Baltic Sea were examined as a starting point for a conservation strategy for the species in this area. The allozyme variation in seven polymorphic loci was studied in 5125 salmon from 24 rivers in four countries. A clear dichotomy was observed between stock groups from southeastern (Russia, Estonia, Latvia, southern Sweden) and northwestern (northern Finland, northern Sweden) drainage regions, corresponding to the postglacial colonisation of the Baltic Sea by two phylogeographic lineages, one from the east (the Ice Lake lineage) and one from the west (the Atlantic lineage). The geographical and genetic distances between stocks fit the one-dimensional "isolation-by-distance" model ($p < 0.001$). The estimated gene flow ranged from 0 to 10 migrants per generation. The total diversity of hatchery stocks was 72% of that of the wild stocks. Genetically similar stock groups, phylogeographic lineages, and drainage regions are recommended for use as genetic management units in addition to stock level.

Résumé : On a examiné la structure génétique et le profil d'isolement du saumon atlantique (*Salmo salar* L.) dans toute son aire de répartition dans la mer Baltique en vue d'établir une stratégie de conservation de l'espèce dans cette région. On a étudié la variation des allozymes de sept loci polymorphes chez 5125 saumons prélevés dans 24 rivières de quatre pays. On a observé une nette dichotomie entre les groupes de stocks des bassins hydrographiques du sud-est (Russie, Estonie, Lettonie, sud de la Suède) et des bassins du nord-ouest (nord de la Finlande, nord de la Suède), qui s'explique par la colonisation postglaciaire de la mer Baltique par deux lignées phylogéographiques, l'une de l'est (lignée du lac glaciaire) et l'une de l'ouest (lignée de l'Atlantique). Les distances géographiques et génétiques entre les stocks s'accordent avec le modèle unidimensionnel d'isolement en fonction de la distance ($p < 0,001$). Le flux génétique estimé variait de 0 à 10 migrants par génération. La diversité totale des stocks d'écloserie était de 72 % de celle des stocks sauvages. En plus de la taille des stocks, on recommande de prendre en considération dans les unités génétiques de gestion les groupes de stocks génétiquement similaires, les lignées phylogéographiques et les bassins versants.

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Introduction

A hierarchical structure of population differentiation is evident among Atlantic salmon (*Salmo salar*) populations throughout the range of the species. Baltic salmon constitute one of the three major groups of the species, the others being the west and east Atlantic groups (Ståhl 1987) or races (Cross et al. 1998). Nowadays, Baltic salmon as a whole

form one effectively isolated evolutionary unit of Atlantic salmon and differ clearly from Atlantic salmon of the rivers draining into the Atlantic Ocean and Barents Sea (Ståhl 1987; Koljonen 1989; Kazakov and Titov 1993). A study on Baltic and North Sea populations showed that more than half of the total between-population component (57.5%) derived from a major branching between Atlantic and Baltic areas (Ryman 1983).

The status of natural populations in the Baltic Sea is threatened and their preservation for the future can only be assured by fishing regulation and other conservation measures. The primary reason for loss of the bulk of Baltic salmon stocks is destruction of their reproduction habitats by powerplant construction. Further threats are posed by overfishing in relation to the natural production level and, since 1992, by the highly increased incidence of yolk-sac mortality due to the M-74 syndrome. The majority of smolts (90%) are currently produced in hatcheries. Baltic salmon stocks mix offshore during their feeding and spawning migration and are a target of the intensive international mixed-stock fishery. It is therefore important to include all salmon stocks throughout the Baltic region in analyses. Only then can we

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gain insight into the total evolutionary structure and the reasons for it and thus gain the basic information needed for creating a management and conservation strategy.

The primary factors in the genetic structure of Baltic salmon are related to glaciation history, to the formation of the Baltic Sea, and to the colonisation sources and directions of the salmon stocks. When the front of the ice sheet advanced from the northwest and covered all of Scandinavia, the preglacial (actually interglacial) salmon populations were forced to move southwards and into glacial ice-marginal lakes and catchments draining southwards. Glacial relicts of several species of freshwater crustaceans are thought to have immigrated into Scandinavian lakes from eastern glacial lakes rather than from a western marine Atlantic direction (Segerstråle 1976). The Atlantic salmon rivers of the Baltic Sea basin could thus also have been colonised either from the east, by refugial glacial lake populations, or from the west, by Atlantic populations in the North Sea and to the south of it, or from both sources. Since the formation of present catchments, the role of gene flow has been essential in determining the possibilities for both neutral and adaptive differentiation among salmon stocks. The most recent changes in the genetic structure of Baltic salmon have been caused by human activity.

Preserving genetic diversity implies conserving the genetic discreteness of certain defined genetic units: populations, river stocks, similarity groups, or phylogeographic lineages. The goal here has been to identify these units among Baltic salmon stocks and to show how they might serve as the building blocks of a management strategy. To clarify the reasons behind the genetic structure, the present distribution of genetic diversity in Baltic salmon stocks is attributed to three different aspects: (i) glacial differentiation, (ii) gene flow patterns in the present Baltic Sea, and (iii) the human impact on genetic structure. The observed differentiation pattern is evaluated in relation to the three alternative hypotheses of postglacial colonisation directions (Ice Lake, Atlantic, or both), and allele frequencies are compared with data on potential source populations outside the recent Baltic Sea. The differentiation pattern between populations is tested by the "isolation-by-distance" model, and the level of gene flow between populations is estimated. The diversity patterns of natural and hatchery stock groups and natural and hatchery strains of the Tornionjoki stock are compared. Finally, conclusions are drawn from the results for the formulation of a management and conservation strategy for Baltic salmon. This is the first time that data on eastern and western stocks have been analysed in a comparable way.

Material and methods

Stock samples

The allozyme variation of 5125 Atlantic salmon from 24 rivers or tributaries in the five countries Sweden, Finland, Russia, Estonia, and Latvia that make a major contribution to salmon production in the Baltic Sea was analysed (Table 1; Fig. 1). The stocks were divided into five groups by geographical drainage region according to the corresponding sea areas used by the International Council for the Exploration of the Sea (ICES): Bothnian Bay (31), Bothnian Sea (30), Gulf of Finland (32), Eastern Main Basin (28), and Southern Main Basin (25) (Table 1; Fig. 1). The sampled stocks constituted an overwhelming majority of wild and hatchery production, unsampled stocks accounting for only about 2%. Ac-

ording to an ICES report (Anonymous 1996), the total smolt production of rivers draining into the Baltic Sea was about 5 571 000 individuals in 1995, of which 5.5%, or 299 000, were naturally reproduced. Our estimate (4 862 000 smolts) is somewhat smaller than that and is based only on relatively well-known data (Table 2).

Some of the samples from Finnish and Swedish stocks have been used previously, in conjunction with mixed-stock fishing analyses (Koljonen and McKinnell 1996; Koljonen and Pella 1997) (see Table 1). New data were available for this study from four Swedish (Kalixälven, Byskeälven, Ljungan, Mörrumsån), two Finnish (Iijoki, Oulujoki), four Estonian (Kunda, Loobu, Keila, Vasalemma), and two Latvian rivers (Daugava, Venta) (Table 1). Because one of the samples, Lögdeälven, was from the published data of Ståhl (1983), and these data did not include locus *IDDH-1**, the allele frequencies of the most similar stock, Dalälven, were used instead in this locus, as was also done in an earlier study (Koljonen and Pella 1997).

The 1993 Tornionjoki hatchery sample consisted of offspring from three different broodstocks. Their proportions in the sample were weighted with the smolt production proportions in 1993. In that year-class, 50% ($n = 147$) of the smolts came from the Taivalkoski hatchery and 27% ($n = 80$) from the Lautiosaari hatchery; 23% ($n = 69$) were reared from wild spawners caught in the Kukkola rapids (total $n = 296$). The hatchery sample of 1992 was from the Taivalkoski hatchery.

Published data were used to compare the genetic distances with those of the potential source population outside the present Baltic Sea range. The eastern, refugial direction was represented by data from the Russian landlocked populations from Lakes Ladoga (Kazakov and Titov 1993) and Onega (Koljonen 1989). For these populations, the allele frequency of the most similar, Neva, stock (0.925) was used for the information lacking on the *IDDH-1** locus. The western, Atlantic direction was represented by data from a Norwegian stock from the Numedalslågen, a river draining into the North Sea (Bourke et al. 1997). Published data on the Emån, a Swedish river draining into the Western Main Basin, were also added (Ståhl 1987) (Fig. 1). For this stock, the mean of the Mörrumsån (0.991) and Dalälven (0.987) stocks was used for the information lacking on the *IDDH-1** locus. Two hatchery stocks, Finnish Oulujoki and Swedish Luleälven, were omitted from this comparison because their allele frequencies had been changed markedly by mixing of stocks.

Electrophoresis

Muscle, liver, and, occasionally, eye tissue of salmon was assayed by horizontal starch gel electrophoresis. Six enzymes coded by a total of 18 loci were analysed. Seven of the loci were variable: *sAAT-4** (aspartate aminotransferase (AAT), EC 2.6.1.1), *IDDH-1** and *IDDH-2** (L-iditol dehydrogenase (IDDH), EC 1.1.1.14), *IDHP-3** (isocitrate dehydrogenase (IDHP), EC 1.1.1.42), *sMDH-3,4** (malate dehydrogenase (MDH), EC 1.1.1.37), *mMEP-2** (malic enzyme (ME), EC 1.1.1.40), and *PGM-1** (phosphoglucosmutase (PGM), EC 5.4.2.2). Electrophoresis of IDHP, MDH, MEP, and PGM was conducted with the modified buffer system (pH from 6.6 to 6.8) of Clayton and Tretiak (1972), that of AAT with the same buffer or the system of Varvio-Aho and Pamilo (1980), and that of IDDH with the buffer system of Varvio-Aho and Pamilo (1980). Staining methods were as in Koljonen and Pella (1997).

Data analysis

Several samples of each river stock were pooled in the data analyses. Heterogeneity among samples of wild and hatchery origin was observed in the Tornionjoki stock but not in the groups of the Simojoki stock, and partly for that reason, these groups were treated separately for the Tornionjoki stock, which increased the

Table 1. Composition of Atlantic salmon stock samples.

No.	Subdivision of sea	Stock	Country	Origin	Class of stock	Year	Sample <i>n</i>	Total <i>n</i>
1	31	Tornionjoki	Finland, Sweden	Wild	W	1988 ^a	19	1202
				Wild		1988 ^a	100	
				Wild		1989 ^a	245	
				Wild		1989 ^a	46	
				Wild		1993 ^b	236	
				Hatchery		1992 ^b	260	
2	31	Simojoki	Finland	Hatchery	W	1992 ^b	689	749
				Hatchery		1993 ^b	30	
				Wild		1993 ^b	30	
3	31	Iijoki	Finland	Hatchery	H	1990 ^b	180	393
				Hatchery		1993 ^b	153	
				Hatchery		1997	60	
4	31	Oulujoki	Finland	Hatchery	H	1992 ^b	180	240
				Hatchery		1997	60	
5	31	Kalixälven	Sweden	Wild	W	1987	45	774
				Wild		1988	146	
				Wild		1989	583	
6	31	Luleälven	Sweden	Hatchery	H	1993 ^b		60
7	31	Byskeälven	Sweden	Wild	W	1994		30
8	31	Skellefteälven	Sweden	Hatchery	H	1993 ^b		84
9	31	Vindelälven	Sweden	Wild	W	1989 ^a	50	100
				Wild		1990 ^a	50	
10	31	Umeälven	Sweden	Hatchery	H	1989 ^a	48	98
				Hatchery		1990 ^a	50	
11	31	Lögdeälven	Sweden	Wild	W	1979 ^c		69
12	30	Ångermanälven	Sweden	Hatchery	H	1993 ^b		100
13	30	Indalsälven	Sweden	Hatchery	H	1993 ^b		90
14	30	Ljungan	Sweden	Wild	W	1996		52
15	30	Ljusnan	Sweden	Hatchery	H	1993 ^b		50
16	30	Dalälven	Sweden	Hatchery	H	1988 ^b		200
17	32	Neva	Russia (Finland)	Hatchery	W	1990 ^b	149	320
				Hatchery		1993 ^b	171	
18	32	Kunda Estonia		Wild	W	1994	25	59
				Wild		1995	34	
19	32	Loobu	Estonia	Wild	W	1994	15	50
				Wild		1995	35	
20	32	Keila	Estonia	Wild	W	1994	30	63
				Wild		1995	33	
21	32	Vasalemma	Estonia	Wild	W	1994	7	43
				Wild		1995	36	
22	28	Daugava	Latvia	Hatchery	H	1996	100	125
				Hatchery		1996	25	
23	28	Venta	Latvia	Wild	W	1996		107
24	25	Mörrumsån	Sweden	Wild	W	1994		67
Total								5125

Note: The classification of each river stock is indicated by W for stocks with wild production and H for stocks with only hatchery production.

^aData from Koljonen and Pella (1997).

^bData from Koljonen and McKinnell (1996).

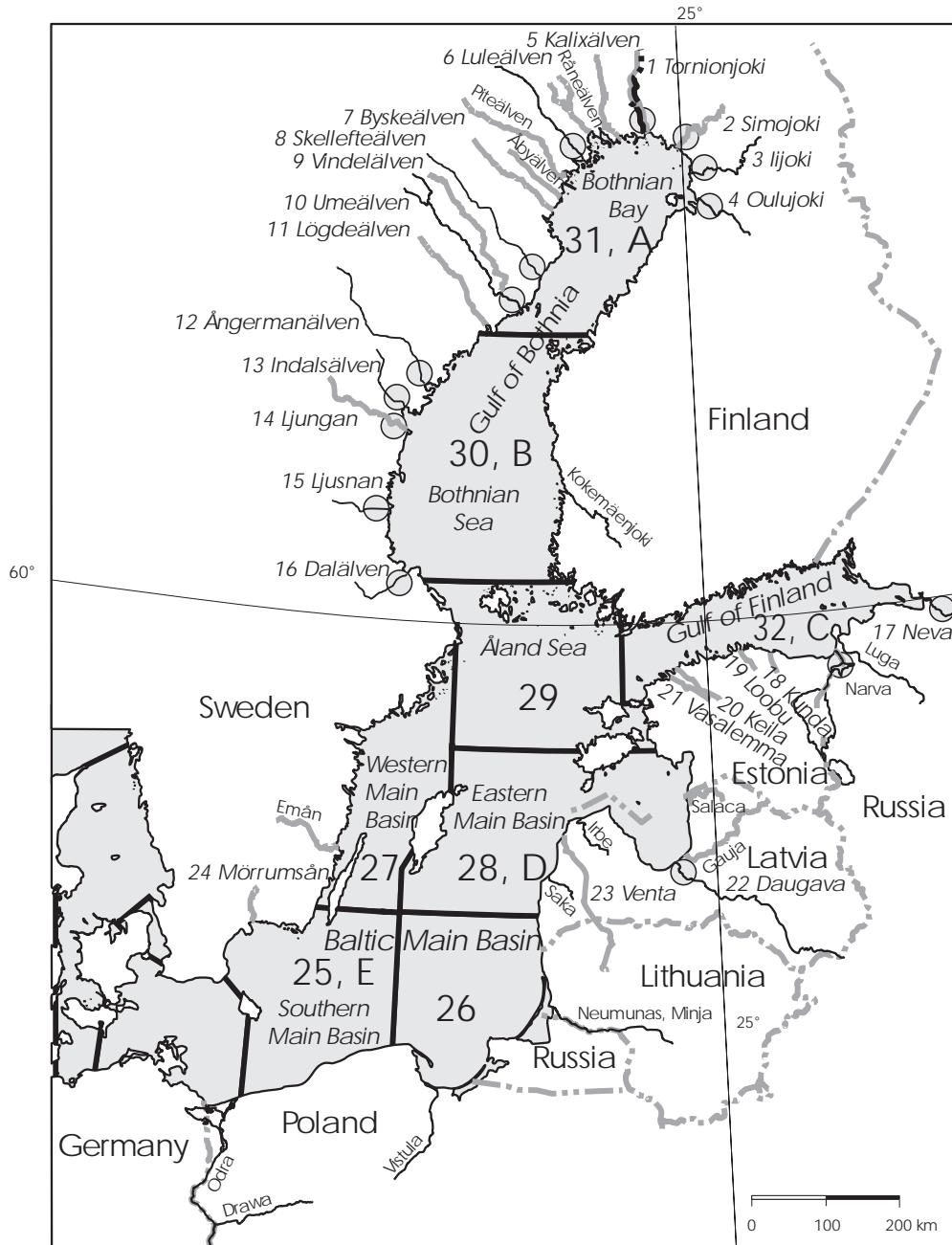
^cData from Ståhl (1983).

number of stocks studied to 25. Whenever the Hardy–Weinberg disequilibrium was observed in a river stock, each sample was submitted to further analyses.

The BIOSYS-1 program (Swofford and Selander 1981) was used to calculate allele frequencies, mean numbers of alleles per locus, and mean heterozygosities and to test the conformance of genotype

frequencies with the Hardy–Weinberg equilibrium. The effect of multiple tests for the Hardy–Weinberg equilibrium was corrected with the Bonferroni procedure. The population differentiation in separate loci within different sea areas and the difference between wild and hatchery strains of the Tornionjoki stocks were tested with the exact probability test (Raymond and Rousset 1995a) of

Fig. 1. Map of the Baltic Sea showing ICES subdivisions 25–32. Rivers with natural Atlantic salmon production are marked in bold, and hatchery production is designated with circles at river mouths. The sea areas into which the rivers studied drain are shaded and marked with the letters A–E.



the STRUC program in the GENEPOP software package (Raymond and Rousset 1995b). Differentiation probabilities across loci were combined with Fisher’s method. Pairwise tests for population differentiation were done by using contingency χ^2 tests.

The genetic differentiation between stocks was measured with Nei et al.’s (1983) D_A distance, which had performed well in creating the topology of the phylogenetic tree in simulation studies (Nei and Takezaki 1994; Takezaki and Nei 1996). The neighbour-joining method (Saitou and Nei 1987) was used to construct a dendrogram. The bootstrap test over loci was performed for the neighbour-joining tree by recalculating the distance for all loci 1000 times with the DISPAN package (Ota 1993).

Geographical distances between stock pairs were compared with their genetic distances to analyse the fit of the isolation-by-distance

model (Wright 1943; Kimura and Weiss 1964). The significance of the fit was tested by the Mantel test of the ISOLDE program in the GENEPOP software package (version 3.1a, August 1997) (Raymond and Rousset 1995b) using 10 000 bootstraps. To analyse the dimensions of the isolation model, semimatrixes of weighted pairwise F_{ST} values ($F_{ST}/(1 - F_{ST})$, Weir and Cockerham 1984) and geographical distances (both distance and ln distance) between river mouths of the stocks were compared (Rousset 1997). Geographical distances were measured as straight lines over the sea between river mouths. The relationship of these two distances was plotted as $\log(M)$ against $\log(\text{geographical distance})$ according to Slatkin (1993), where M is the estimated level of gene flow counted from the F_{ST} values (M , migrants for weighted F_{ST} values, $M = (1 - F_{ST})/(2F_{ST})$). If the data fit the isolation-by-distance model, a clear

Table 2. Estimated smolt production of natural and hatchery stocks of Atlantic salmon in the Baltic Sea in 1995 and production of each river as a proportion of the total.

Sample	Sub-division	Stock	Country	Production × 1000 fish			% of total production
				Natural	Hatchery	Total	
1	31	Tornionjoki	Finland, Sweden	75	262	337	6.9
2	31	Simojoki	Finland	1.4	154	155	3.2
3	31	Iijoki	Finland		792	792	16.3
4	31	Oulujoki	Finland		218	218	4.5
5	31	Kalixälven	Sweden	44		44	0.9
	31	Råneälven	Sweden	1.2		1.2	0.0
	31	Piteälven	Sweden	3		3	0.1
	31	Åbyälven	Sweden	1.2		1.2	0.0
6	31	Luleälven	Sweden		541	541	11.1
7	31	Byskeälven	Sweden	8.7		8.7	0.2
8	31	Skellefteälven	Sweden		122	122	2.5
9	31	Vindelälven	Sweden	15		15	0.3
10	31	Umeälven	Sweden		130	130	2.7
	31	Öreälven	Sweden	0.9		0.9	0.0
11	31	Lögdeälven	Sweden	0.9		0.9	0.0
12	30	Ångermanälven	Sweden		351	351	7.2
13	30	Indalsälven	Sweden		256	256	5.3
14	30	Ljungan	Sweden	4	30	34	0.7
15	30	Ljusnan	Sweden		231	231	4.7
16	30	Dalälven	Sweden		162	162	3.3
17	32	Neva	Russia, Finland	20	478	498	10.2
	32	Luga	Russia	10	20	30	0.6
	32	Narva	Estonia, Russia		10	10	0.2
18	32	Kunda	Estonia	1.8		1.8	0.0
19	32	Loobu	Estonia	1.8		1.8	0.0
20	32	Keila	Estonia	1.8		1.8	0.0
21	32	Vasalemma	Estonia	1.8		1.8	0.0
	28	Pärnu	Estonia	8		8	0.2
	28	Salaca	Latvia	15	94	109	2.2
	28	Gauja	Latvia	13	163	176	3.6
22	28	Daugava	Latvia	5	550	555	11.4
23	28	Venta	Latvia	15	19	34	0.7
	27	Emån	Sweden	4		4	0.1
24	25	Mörrumsån	Sweden	30		30	0.6
	26	Neumunas	Lithuania	5		5	0.1
Total				288	4583	4870.3	100.0

Note: Estonian, Finnish, and Swedish wild productions are from the ICES report (Anonymous 1996). Russian data are according to Anatsky and Dirin (1997), Latvian production data according to Oleg Vasin, and Lithuanian data according to Antanas Kontautas. Hatchery production data of Finland are from Finnish Game and Fisheries Research Institute (unpublished data), of Sweden are from Salmon Research Institute, and of Estonia according to Tiit Paaver.

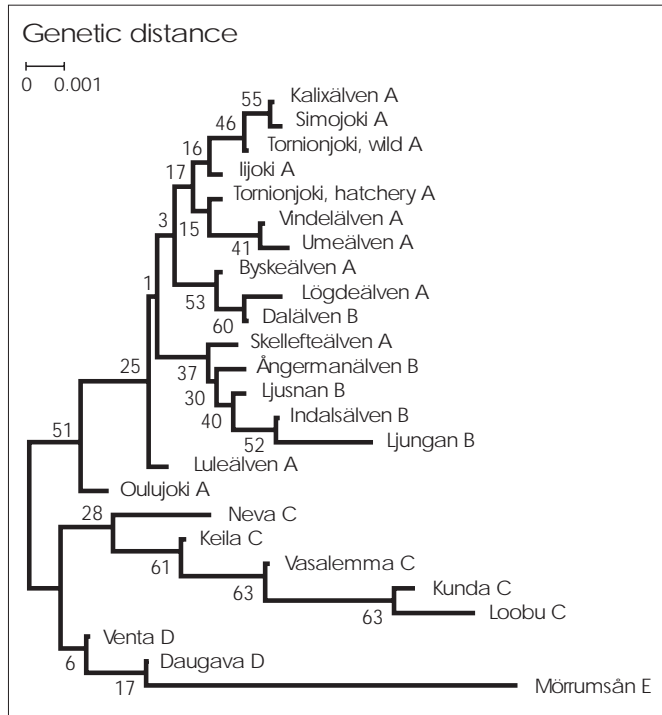
linear negative regression would be expected, and some kind of balance between gene flow and genetic drift would exist. These analyses were based on data from 22 populations. Data from those of Kalixälven, Ljungan, and Lögde were excluded because the individual genotype data needed for GENEPOP analyses were not available for these stocks.

Unbiased expected mean heterozygosities (for all 18 loci) and their standard errors were estimated according to Nei (1978). To examine the source of the variation in diversity estimates, standard errors for average diversities were calculated separately for the total variation and for the intralocus variation component (Nei 1987). In general, the mean heterozygosities of populations were compared by the *t* test for paired observations because allele frequencies and heterozygosities of conspecific populations are historically correlated (Nei 1987). For some samples, the test for individual loci according to Nei (1987) was also conducted. In the

case of the Tornionjoki stock, in which only one generation separates the wild and hatchery populations compared, the historical evolutionary differences can be excluded, and the test could therefore be restricted to the particular set of loci studied and the normal deviate test (Nei 1987) could be used.

The distribution of the genetic diversity of salmon stocks was examined with the hierarchical diversity analysis of Nei (1977). To attain consistency with the assumption of equal weights for populations, the average over groups was determined with weights proportional to the number of stocks in the group (Chakraborty and Leimar 1987). The stocks of the rivers where salmon have access to spawning grounds and can reproduce naturally were classified as wild stocks, even though supportive fish releases have been carried out in some of the rivers (Table 1). The material for supportive releases was derived from either local returning spawners or hatchery broodstocks created from local spawners.

Fig. 2. Genetic distances of Baltic Atlantic salmon stocks. The letters A–E correspond to the sea areas from which the stocks originate (see Fig. 1).



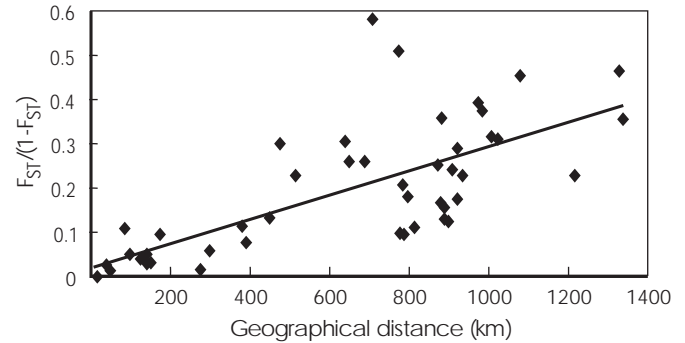
Results

Geographical distribution of genetic differentiation

The genetic distances between populations from geographically different areas were substantial, and a dichotomy was seen between stocks from the east and those from the west (Fig. 2). This dichotomy was largely due to variation in the *IDDH-2** locus. The frequency of the allele *IDDH-2*72* was markedly higher (0.70–0.83) in the three southeastern areas (Gulf of Finland, Eastern Main Basin, Southern Main Basin) than in the northwestern areas (0.18–0.51) (Bothnian Sea, Bothnian Bay) (Table 3). At other loci, Mörrumsån (Southern Main Basin) had an exceptionally high frequency of allele **116* in *IDHP-3** (0.49). In Estonian stocks, the frequencies of *mMEP-2*125* (0.28–0.70) were higher than in Baltic Sea stocks in general (0.01–0.18) (Table 3). Thus, of the three alternative hypotheses of colonisation, genetic distance between stocks was the most consistent with the hypothesis of the colonisation of the Baltic Sea region by two different phylogeographic lineages. The eastern lineage covered stocks of the Main Basin and Gulf of Finland and the western lineage those of the Gulf of Bothnia.

The dendrogram also matched the present geographical form of the Baltic Sea. The populations were clustered into three branches corresponding to the three main parts of the sea from which they originated: Gulf of Bothnia (Bothnian Bay (A), Bothnian Sea (B)), Gulf of Finland (C), and Main Basin (Eastern Main Basin (D), Southern Main Basin (E)) (Fig. 2). Within the Gulf of Bothnia group, the stocks from its two parts Bothnian Bay and Bothnian Sea grouped partly together, yet with some differentiation between them. Within

Fig. 3. Relationship of pairwise genetic distances and geographical distances of Baltic Atlantic salmon stocks to the one-dimensional dispersal pattern.



the Main Basin, the Mörrumsån stock clearly deviated from the Latvian salmon stocks of the Eastern Main Basin.

Allele frequency differences were highly significant for all loci throughout the Baltic Sea. Population differentiation was also highly significant ($p < 0.001$) within the Gulf of Bothnia, Bothnian Sea, and Gulf of Finland and significant ($p < 0.05$) within the Eastern Main Basin. The great majority of all pairwise tests for contingency between stocks were highly significant. In only nine out of 625 tested pairs could a statistically significant difference not be observed, at least at the 5% level.

Most of the populations studied were in Hardy–Weinberg equilibrium. After Bonferroni correction for several loci per population, statistically significant deviations were seen in four (all hatchery samples) out of 152 of the tests: an excess of heterozygotes in the Tornionjoki 1993 sample (*IDDH-2**, $p = 0.024$) and a deficiency of heterozygotes in Neva 1990 (*IDDH-1**, $p < 0.001$), Skellefteälven (*IDDH-2**, $p = 0.025$), and Ångermanälven (*IDDH-2**, $p = 0.025$). At stock level, when the probabilities of different loci were joint with Fisher’s method, the only statistically significant deviations were in samples from hatchery stocks of Skellefteälven ($p = 0.03$) and Neva 1990 ($p < 0.001$).

The geographical and genetic distances of Baltic salmon stock pairs fitted the isolation-by-distance model. According to the Mantel test, the correspondence was highly significant ($p < 0.001$) for all stocks studied and for wild stocks; there was, however, no correspondence ($p = 0.14$) if only hatchery stocks were considered. The observed genetic distances also fitted the isolation-by-distance pattern when the two lineages were treated separately. For the eastern lineage the correlation was highly significant ($p < 0.001$) and for the western lineage was significant ($p = 0.027$). The data on wild stocks had a better fit with the regression model in which $F_{ST}/(1 - F_{ST})$ values were plotted directly against geographical distance (regression coefficient 0.70, Fig. 3) rather than on its natural logarithm (regression coefficient 0.66), indicating that the dispersal of salmon stocks bears a closer resemblance to the one- than to the two-dimensional pattern (Slatkin 1993).

The apparent pattern of isolation-by-distance among Baltic salmon populations could also be seen when the F_{ST} values were transformed into estimates of gene flow as number of migrants by plotting the $\log(\text{migrants})$ on $\log(\text{geographical distance})$ from all population pairs of wild and hatchery populations (Fig. 4a). The linear regression line was then

Table 3. Allele frequencies in variable loci in Baltic salmon stock samples.

Stock	<i>sAAT4*</i>				<i>IDDH-1*</i>			<i>IDDH-2*</i>		
	<i>n</i>	100	25	50	<i>n</i>	100	28	<i>n</i>	100	72
31. Bothnian Bay										
1a. Tornionjoki W	641	0.732	0.265	0.003	645	0.998	0.002	643	0.658	0.342
1b. Tornionjoki H	579	0.904	0.096	0	556	1	0	512	0.673	0.327
2. Simojoki	653	0.643	0.353	0.004	700	1	0	643	0.632	0.368
3. Iijoki	284	0.794	0.206	0	374	0.995	0.005	351	0.620	0.380
4. Oulujoki	230	0.770	0.215	0.015	239	0.969	0.031	230	0.596	0.404
5. Kalix	719	0.677	0.323	0	764	1	0	764	0.673	0.327
6. Luleälven	60	0.825	0.133	0.042	60	0.975	0.025	60	0.650	0.350
7. Byskeälven	29	0.931	0.069	0	26	0.981	0.019	30	0.583	0.417
8. Skellefteälven	84	0.893	0.101	0.006	84	0.946	0.054	84	0.494	0.506
9. Vindelälven	100	0.850	0.150	0	100	1	0	100	0.760	0.240
10. Umeälven	98	0.893	0.107	0	89	0.995	0.005	97	0.820	0.180
11. Lögdeälven ^a	69	0.986	0.014	0	69	0.987	0.013	69	0.552	0.448
30. Bothnian Sea										
12. Ångermanälven	100	0.930	0.070	0	100	0.940	0.060	100	0.510	0.490
13. Indalsälven	89	0.949	0.051	0	88	0.892	0.108	88	0.733	0.267
14. Ljungan	51	0.804	0.196	0	52	0.750	0.250	52	0.788	0.212
15. Ljusnan	50	0.840	0.160	0	50	0.900	0.100	50	0.560	0.440
16. Dalälven	200	0.960	0.040	0	200	0.987	0.013	196	0.561	0.439
32. Gulf of Finland										
17. Neva	170	0.691	0.229	0.080	320	0.925	0.075	320	0.166	0.834
18. Kunda	40	0.587	0.413	0	25	0.980	0.020	42	0.250	0.750
19. Loobu	35	0.772	0.214	0.014	15	1	0	33	0.303	0.697
20. Keila	40	0.625	0.325	0.050	22	0.977	0.023	40	0.300	0.700
21. Vasalemma	30	0.750	0.233	0.017	7	1	0	30	0.283	0.717
28. Eastern Main Basin										
22. Daugava	125	0.804	0.196	0	88	1	0	125	0.232	0.768
23. Venta	107	0.678	0.322	0	94	1	0	107	0.299	0.701
25. Southern Main Basin										
24. Mörrumsån	67	0.746	0.254	0	57	0.991	0.009	67	0.231	0.769
Total	4650				4824			4833		

^aData are from Ståhl (1983).

$\log(\text{migrants}) = 2.96 - 0.68 \log(\text{distance (km)})$. The regression explained 69% of the variation in the data. When only the 11 wild stocks were included, the regression line was very similar, $\log(\text{migrants}) = 2.82 - 0.82 \log(\text{distance})$, whereas the coefficient of determination was as high as 82% of the observed variation (Fig. 4b). For the hatchery stock group, the isolation-by-distance model did not fit the data. Hatchery production also caused increased scattering of the data points, as seen in the figure for joint hatchery and wild production (Fig. 4a).

The population distances studied covered the range from over 100 migrants to zero. Most of the population pairs were separated by distances of between 100 and 1000 km. At this range, the estimated number of migrants decreased from about 10 to near zero (Fig. 4a). The migration rate between several population pairs from distances of over 600 km (2.6 in log scale) was already very low, near the one individual per generation level (0 in log scale) (Fig. 4).

Mean diversities of populations and groups

In the diversity analyses the hierarchical levels used were total, lineage, area, and stock. Within the whole Baltic Sea, the proportion of the between-stock diversity component was

a substantial 15% ($G_{ST} = 0.147$) (Table 4). As much as half of this was a consequence of differentiation between the two proposed phylogeographic lineages ($G_{LT} = 7.5\%$), but differences between sea areas within lineages were also apparent ($G_{AL} = 2.9\%$). Together, these upper hierarchical levels constituted two thirds of the between-stock component.

The total diversity was almost 30% higher for the wild group ($H_T = 0.076$) than for the hatchery group ($H_T = 0.054$) (Table 4). This was explained partly by the dissimilar distributions of wild and hatchery stocks among sea areas and partly by the historically different levels of diversity within these areas. This could also be seen in the substantially higher G_{ST} estimate ($G_{ST} = 0.161$) for diversity between wild stocks than between hatchery stocks ($G_{ST} = 0.063$). Within Bothnian Bay alone, where historically more similar genotype structures could be expected, the level was the same. For this area, H_T for the six wild stocks was 0.057 and for the six hatchery stocks was 0.055.

Diversities within populations, measured as mean expected heterozygosities for 18 loci, varied from 3 to 8.2% (Table 5). The average mean heterozygosity was somewhat higher for the wild stocks (6.3%) than for the hatchery stocks (5.1%), but the difference was not significant ($t = 1.536$, $df = 6$, one-tailed $p < 0.10$). When the mean heterozygosities of popula-

Table 3 (concluded).

<i>IDHP-3*</i>			<i>sMDH-3,4*</i>				<i>mMEP-2*</i>			<i>PGM-I*</i>		
<i>n</i>	<i>100</i>	<i>116</i>	<i>n</i>	<i>100</i>	<i>80</i>	<i>115</i>	<i>n</i>	<i>100</i>	<i>125</i>	<i>n</i>	<i>100</i>	<i>75</i>
645	0.997	0.003	645	0.992	0.003	0.005	645	0.898	0.102	646	0.980	0.020
502	0.996	0.004	555	0.988	0.009	0.003	571	0.901	0.099	555	0.990	0.010
706	0.999	0.001	749	0.998	0.002	0	747	0.886	0.114	747	0.991	0.009
365	1	0	393	0.982	0.018	0	382	0.853	0.147	393	1	0
208	0.887	0.113	240	0.998	0.002	0	238	0.847	0.153	240	0.998	0.002
773	1	0	773	0.995	0.005	0	745	0.917	0.083	756	0.988	0.012
60	0.992	0.008	59	0.992	0	0.008	59	0.907	0.093	60	1	0
30	1	0	30	1	0	0	30	0.817	0.183	30	0.983	0.017
84	1	0	84	0.994	0.006	0	84	0.988	0.012	84	1	0
100	1	0	100	1	0	0	100	0.950	0.050	100	1	0
98	1	0	98	1	0	0	98	0.980	0.020	98	1	0
69	1	0	69	1	0	0	69	0.819	0.181	69	1	0
100	0.955	0.045	100	1	0	0	100	0.980	0.020	100	1	0
89	0.994	0.006	89	1	0	0	89	0.972	0.028	89	1	0
52	1	0	52	1	0	0	52	0.962	0.038	52	1	0
50	0.980	0.020	50	1	0	0	50	0.980	0.020	50	1	0
200	1	0	200	1	0	0	200	0.880	0.120	200	1	0
316	0.979	0.021	320	0.997	0.003	0	319	0.878	0.122	320	1	0
40	1	0	59	1	0	0	58	0.431	0.569	59	1	0
36	1	0	50	1	0	0	50	0.300	0.700	50	1	0
39	1	0	63	1	0	0	63	0.714	0.286	63	1	0
30	1	0	43	1	0	0	43	0.616	0.384	43	1	0
125	0.964	0.036	125	1	0	0	125	0.904	0.096	125	0.996	0.004
103	0.981	0.019	107	1	0	0	107	0.902	0.098	107	1	0
65	0.515	0.485	67	1	0	0	67	0.881	0.119	67	1	0
4885			5120				5091			5103		

tion pairs were compared at the total genome level by the pairwise *t* test, which includes the between-loci variation component, no statistically significant differences ($p > 95\%$) were found between any of the population pairs, not even between Mörrumsån (8.2%) and Umeälven (3.0%) ($t = 2.17$, for five variable loci, $df = 4$, two-tailed $p < 0.10$). Differences were, however, statistically significant between these stocks at the locus level in four out of five individual loci at $p < 0.001$: *IDDH-1**, *IDDH-2**, *IDHP-3**, and *mMEP-2**. Similarly, several other stock pairs displayed significant differences at the locus level but not at the total genome level, although allele frequency differences between population pairs were statistically significant in most cases. The variation in standard errors was mainly due to the variation between loci (Table 5).

The mean heterozygosity of the Tornionjoki hatchery strain was lower (0.47) than, but not significantly different from, that of the wild strain (0.61) ($t = 1.640$, $df = 6$, one-tailed $p < 0.10$) for the total genome level. The heterozygosity of three individual loci was, however, significantly lower in the Tornionjoki hatchery strain than in the wild stock sample (*sAAT-4**, $p < 0.001$; *PGM-I**, $p < 0.05$; *IDDH-1**, $p < 0.001$). When only the set of the variable loci studied was included, and only intralocus variances were used, the normal deviate test showed that the Tornionjoki

hatchery strain had a lower mean heterozygosity at $p < 0.001$ in these loci. In addition, allele frequency differences between the two Tornionjoki strains were highly significant in four out of seven loci (*sAAT-4**, $p = 0.000$; *IDDH-2**, $p = 0.000$; *sMDH-3,4**, $p = 0.0017$; *PGM-I**, $p = 0.0012$).

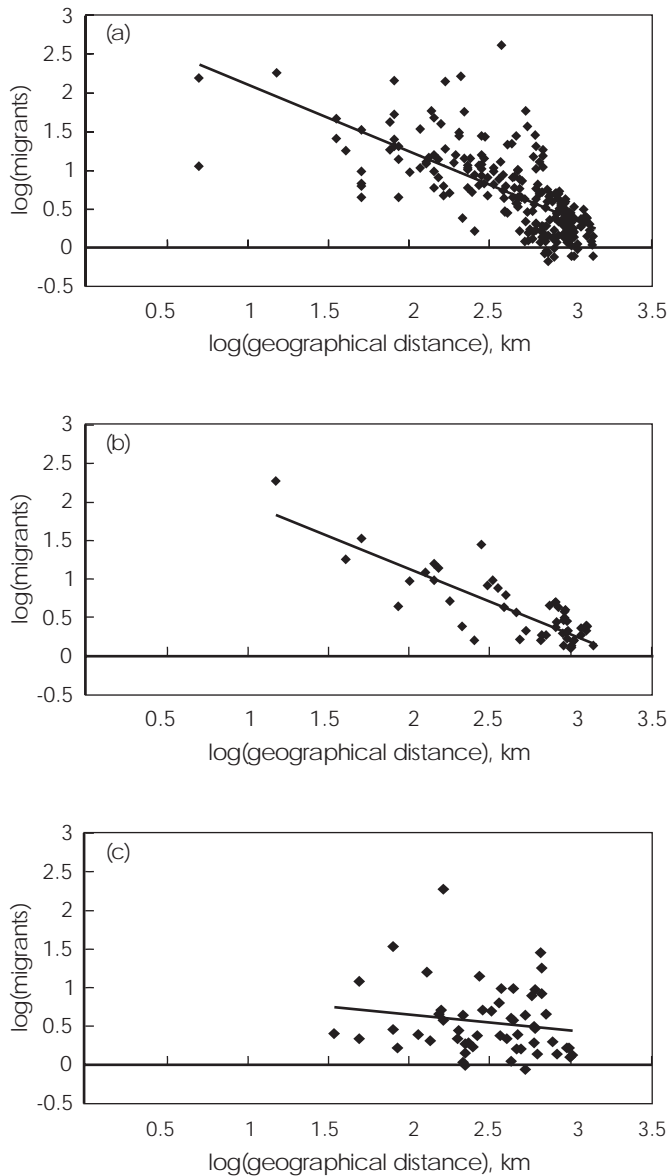
When the genetic variability was measured as the number of different alleles, a somewhat different picture emerged. For example, small Estonian stocks had quite high levels of heterozygosity but a low number of alleles. Hatchery stocks had, on average, even slightly higher values than wild stocks (Table 5). The Tornionjoki wild stock, however, was the only one having all observed potential 16 alleles (average 2.3) in the seven polymorphic loci. The highest number of alleles was in stocks of the Bothnian Bay area.

Discussion

Pattern of genetic differentiation of populations

The genetic distances of stocks within the Baltic Sea showed a dichotomy between northwestern and southeastern stocks (Fig. 2) that was consistent with the hypothesis of two distinct postglacial colonisation lineages. When the allele frequencies of the potential source populations outside the Baltic Sea were compared with those of the corresponding

Fig. 4. Relationship of gene flow (log (migrants)) to geographical distance (log (geographical distance (km))) for (a) wild and hatchery Atlantic salmon stocks, (b) wild stocks alone, and (c) hatchery stocks alone.



lineages within the Baltic Sea, the results gave further support to this hypothesis of colonisation from both east and west. In our data, within the Baltic Sea, the frequency of the allele *IDDH-2**-72 was clearly higher in the eastern lineage (0.70–0.83) than in the western lineage (0.18–0.50). The frequency of this same allele was, however, still higher in the eastern landlocked populations: 1.00 in Lake Onega (Koljonen 1989) and 0.92 in Lake Ladoga (Kazakov and Titov 1993) (Fig. 1). The similarity between these Russian landlocked populations and the southeastern lineage within the Baltic Sea was evident.

An Atlantic salmon stock from the Atlantic, Numedalslågen, had a frequency of 0.36 of allele *-72 (Bourke et al. 1997), which is identical to the mean of our data from the stocks in the Gulf of Bothnia area. In their dendrogram, this Norwegian salmon stock also groups together with the salmon stocks

from the Gulf of Bothnia (Tornionjoki, Simojoki, Dalälven, Luleälven; Bourke et al. 1997). In the nearest Atlantic populations, i.e., those of Ireland and Scotland, the frequency of this allele was very similar to that of the Gulf of Bothnia (0.38; Bourke et al. 1997). As a result, the allele frequencies of the stocks from the southeastern part of the Baltic Sea (Russia, Estonia, Latvia, southern Sweden) were closer to those of the eastern, landlocked stocks (Lakes Onega and Ladoga) than to those of the northwestern Baltic salmon stocks around the Gulf of Bothnia (northern Finland, northern Sweden), which in turn bore a closer resemblance to the stocks from rivers draining into the North Sea and eastern Atlantic (Fig. 5). The hypothesis was also supported by the finding that genetic distances for variable allozyme loci among stocks from the coast of continental Europe and the northern Baltic were under 0.03 (Bourke et al. 1997) but that the average distance within the Baltic Sea between the northwestern group and Neva stocks was 0.045.

That the present dispersal areas of the western and eastern lineages correspond to the extent of the Baltic Sea stages in which dispersal could have been possible during glaciation provides further support for the hypothesis that dispersal occurred in two directions and at different times. The range of the stocks of the eastern lineage is compatible with the extent of the first stage of the Baltic Sea, the Baltic Ice Lake, which formed at about 12 200 – 12 000 years BP, when the ice-dammed lakes in the eastern Gulf of Finland were joined with the rest of the Baltic basin (Donner 1995). Until the end of the Baltic Ice Lake stage, the Baltic Sea was a lake and the ice sheet had not yet retreated from Finland and northern Sweden (Fig. 6a). Even on the south coast of Sweden, the Rivers Emån (0.65; Ståhl 1987; Fig. 1) and Mörrumsån have high frequencies of the eastern allele (*-72) and thus seem to come within the range of influence of the eastern lineage.

Lake Ladoga was at that time part of the Baltic Ice Lake, which explains the similarity between salmon from Lake Ladoga and the stocks of the eastern lineage. Lake Onega was isolated from the preceding River Onega Ice Lake before the Baltic Ice Lake stage (12 500 – 11 500 BP) (Saarnisto et al. 1995) and drained into Lake Ladoga. The existence of landlocked salmon in Lake Onega indicates that they had survived in glacial lakes. The exceptional allele frequency (0.49) of allele *IDHP-3**116 in the Mörrumsån stock could not be explained by gene flow from the North Sea, as high frequencies were not observed there, the range being from 0.00 to 0.20 (Bourke et al. 1997). This exception is therefore attributed to genetic drift in an isolated population. The eastern lineage of the Baltic Sea stocks together with the present landlocked stocks from Lakes Ladoga and Onega is here called the Ice Lake lineage.

The initial provenance of the eastern lineage was most likely glacial ice lakes in present-day Russia. Segerstråle (1976) proposed that the Ice Lake of the River Onega basin (Fig. 6) and glacial lakes along the edge of the continental ice sheet served as refugia for glacial relicts of the Baltic Sea area, e.g., the fourhorn sculpin (*Myoxocephalus quadricornis*), a fish that had colonised Finland via this eastern route. The outer margin of the ice sheet was less than 80 km southeast of Lake Onega (Saarnisto et al. 1995). From this refugium area, salmon were able to colonise both Lakes

Table 4. Hierarchical diversity analysis of Baltic Atlantic salmon stocks.

Stock group	K	H_T	H_L	H_A	H_S	G_{ST}	G_{SL}	G_{SA}	G_{AL}	G_{AT}	G_{LT}
Whole Baltic Sea	25	0.067	0.062	0.060	0.058	0.147	0.075	0.042	0.029	0.105	0.075
Lineage											
Atlantic	17		0.055	0.055	0.053		0.047	0.040	0.007		
Ice Lake	8		0.077	0.072	0.063		0.108	0.040	0.069		
Sea area											
31. Bothnian Bay	12			0.056	0.054			0.039			
30. Bothnian Sea	5			0.053	0.051			0.044			
32. Gulf of Finland	5			0.076	0.072			0.064			
28. Eastern Main Basin	2			0.056	0.056			0.006			
25. Mörrumsån	1			0.081	0.081						
Wild stocks	14	0.076			0.063	0.161					
Hatchery stocks	11	0.054			0.051	0.063					

Note: Distribution of total diversity was also examined separately for wild and hatchery stock groups. K , number of stocks within each grouping (relative weight of group in analysis); H_T , total diversity; H_L , diversity for lineages; H_A , diversity for sea areas; H_S , diversity for samples. Estimates of G are the proportions of between-stock diversity components between corresponding hierarchical levels: G_{ST} , in the whole data; G_{SL} , between stocks within lineages; G_{SA} , between stocks within areas; G_{AL} , between sea areas within lineages; G_{AT} , between sea areas; G_{LT} , between lineages.

Onega and Ladoga and also the southeastern Baltic Sea rivers. The homing behaviour of salmon has played a role in maintaining the patterns of this first colonisation.

Salmon stocks of the Gulf of Bothnia from north of central Sweden formed the western lineage, the range of which corresponded to the geographical region that was liberated from ice after the Baltic Ice Lake stage, i.e., at the Yoldia Sea stage. This stage began when a wide sound opened across central Sweden over the large basins of Lakes Vänern and Vättern, via the Närke strait, and the first great ingress of seawater turned the water of the Baltic Sea brackish (Fig. 6b). This period lasted from about 10 300 to 9000 BP (Donner 1995), i.e., until the sea connection was closed and a second, shorter lake period, the Ancylus Lake, began. During the Yoldia Sea stage the northern Baltic Sea coasts could have been colonised by salmon from the North Sea. At that time, Finland and most of the present Swedish coast were already free of ice, and spawning habitats were available in rivers (Fig. 6b). The western lineage is suggested to have colonised along this route and is called the Atlantic lineage. At the Yoldia Sea stage, other marine fauna, also, such as molluscs and crustaceans, colonised the Baltic Sea area (Donner 1995). This route was probably also used by the ringed seal (*Phoca hispida*) (the subspecies in the Baltic Sea is *Phoca hispida botnica*) to invade the Baltic Sea (Forstén and Alhonen 1975). It is possible that some salmon of the Atlantic lineage entered the Baltic Sea later, during the Littorina Sea stage, via the sounds between Sweden and Denmark (about 9000 BP; Donner 1995), and afterwards.

The Finnish salmon of Lake Saimaa are closer to the stocks of the Atlantic Lineage (the frequency of the *-72 allele was 0.27; M.-L. Koljonen, unpublished) and, moreover, the western colonisation route was also possible for this population. The Lake Saimaa area was covered by ice at the time of the Baltic Ice Lake (Fig. 6a) and its first outlet, at about 8000 years BP, was northwestwards into the Gulf of Bothnia. The secondary outlet, into Lake Ladoga, did not form until about 5000 years BP (Saarnisto 1970). Thus, this landlocked population derived originally from an ancient salmon population in the Gulf of Bothnia area. Lake Saimaa also hosts a landlocked ringed seal (*Phoca hispida saimensis*) pop-

ulation, which is assumed to be of western origin (Forstén and Alhonen 1975).

The hypothesis of two phylogeographic colonisation lineages was supported by three factors: (i) possible donor populations and colonisation routes existed for both lineages, (ii) the lineages in the Baltic Sea were genetically more similar to their postulated donor stocks outside the present Baltic Sea than to each other, and the genetic distance between these lineages was considerable, and (iii) the ranges of the suggested lineages within the Baltic Sea were compatible with the glaciation stages at which colonisation is expected to have occurred.

In light of the above colonisation history, the oldest and more rare genetic material for this area is currently to be found in the present salmon stocks of Estonia, Latvia, Lithuania, Russia, and southern Sweden in the Ice Lake lineage. The freshwater period was markedly longer, over 60 000 years, in the evolution of this lineage than in that of the Atlantic lineage of northern Finland and northern Sweden. The risk of the Ice Lake lineage becoming extinct is greater than is that of the Atlantic lineage within the Baltic Sea, as indicated by current wild smolt production levels (Table 2). The genetic adaptation of all Baltic salmon to a freshwater (brackish) environment is demonstrated by their genetic resistance to *Gyrodactylus salaris* (Bakke et al. 1990), a fatal freshwater ectoparasite that is responsible for the death of several Atlantic salmon stocks in Norway. This parasite was introduced into Norway accidentally in the course of a stock transfer from the Baltic region. A vital proportion of the genetic diversity (with likely adaptive differences in, say, migration behaviour) within the Baltic salmon lies between these two lineages. They have evolved relatively independently until now and their existence should be taken into account in efforts to conserve the genetic diversity of the Baltic salmon.

The genetic differentiation between sea areas, within the phylogeographic lineages, is due partly to the longer geographical distances and partly to the more recent differences in the form and environment of the Baltic Sea; thus, it represents a different aspect of genetic differentiation from that caused by ancient glacial isolation and old colonisation routes.

Table 5. Mean number of alleles for seven loci and standard errors and mean heterozygosities for 18 loci and their standard errors (SE total, including variation both between and within loci; SE sample, excluding variation between loci).

Stock	Origin	Country	Alleles for seven loci	SE	Heterozygosities for 18 loci	SE total	SE sample
31. Bothnian Bay							
1a. Tornionjoki, W	Wild	Finland, Sweden	2.3	0.18	0.061	0.033	0.0020
1b. Tornionjoki, H	Hatchery	Finland	2.0	0.22	0.047	0.027	0.0022
2. Simojoki	Wild	Finland	2.0	0.22	0.064	0.036	0.0016
3. Iijoki	Hatchery	Finland	1.7	0.18	0.061	0.033	0.0027
4. Oulujoki	Hatchery	Finland	2.1	0.14	0.076	0.035	0.0039
5. Kalixälven	Wild	Sweden	1.7	0.18	0.059	0.034	0.0016
6. Luleälven	Hatchery	Sweden	2.0	0.22	0.056	0.030	0.0071
7. Byskeälven	Wild	Sweden	1.7	0.18	0.056	0.031	0.0090
8. Skellefteälven	Hatchery	Sweden	1.9	0.26	0.046	0.029	0.0048
9. Vindelälven	Wild	Sweden	1.4	0.20	0.040	0.024	0.0049
10. Umeälven	Hatchery	Sweden	1.6	0.20	0.030	0.019	0.0048
11. Lögdeälven	Wild	Sweden	1.6	0.20	0.047	0.031	0.0045
Mean			1.8		0.054		
30. Bothnian Sea							
12. Ångermanälven	Hatchery	Sweden	1.7	0.18	0.048	0.029	0.0048
13. Indalsälven	Hatchery	Sweden	1.7	0.18	0.042	0.024	0.0055
14. Ljungan	Wild	Sweden	1.6	0.18	0.062	0.031	0.0077
15. Ljusnan	Hatchery	Sweden	1.7	0.20	0.057	0.031	0.0072
16. Dalälven	Hatchery	Sweden	1.6	0.20	0.045	0.029	0.0030
Mean			1.7		0.051		
32. Gulf of Finland							
17. Neva	Wild	Russia	2.0	0.22	0.064	0.031	0.0039
18. Kunda	Wild	Estonia	1.6	0.20	0.078	0.041	0.0059
19. Loobu	Wild	Estonia	1.6	0.30	0.068	0.037	0.0073
20. Keila	Wild	Estonia	1.7	0.29	0.077	0.041	0.0071
21. Vasalemma	Wild	Estonia	1.6	0.30	0.071	0.039	0.0074
Mean			1.7		0.072		
28. Eastern Main Basin							
22. Daugava	Hatchery	Latvia	1.7	0.18	0.051	0.027	0.0050
23. Venta	Wild	Latvia	1.6	0.20	0.060	0.033	0.0045
Mean			1.7		0.056		
25. Southern Main Basin							
24. Mörrumsån	Wild	Sweden	1.7	0.18	0.082	0.038	0.0064
Total mean			1.75		0.058		
Mean wild			1.7		0.063		
Mean hatchery			1.8		0.051		

It nevertheless made a clear contribution to the total diversity (one fifth of the between-stock component, Table 4).

The differences observed between populations within each sea area, the lowest level in the hierarchy of the genetic structure, were systematically statistically significant, yet not generally very large. The marked deviations between the Oulujoki and Luleälven stocks and the other Gulf of Bothnia stocks are due to mixing of stocks in the rearing process. Thus, this human interference was seen as deviations from the expected differentiation pattern. In Latvia, salmon from the River Venta very likely resemble those of the River Daugava more than historically because both eggs and juveniles have been transferred from the Daugava to the Venta over a long period.

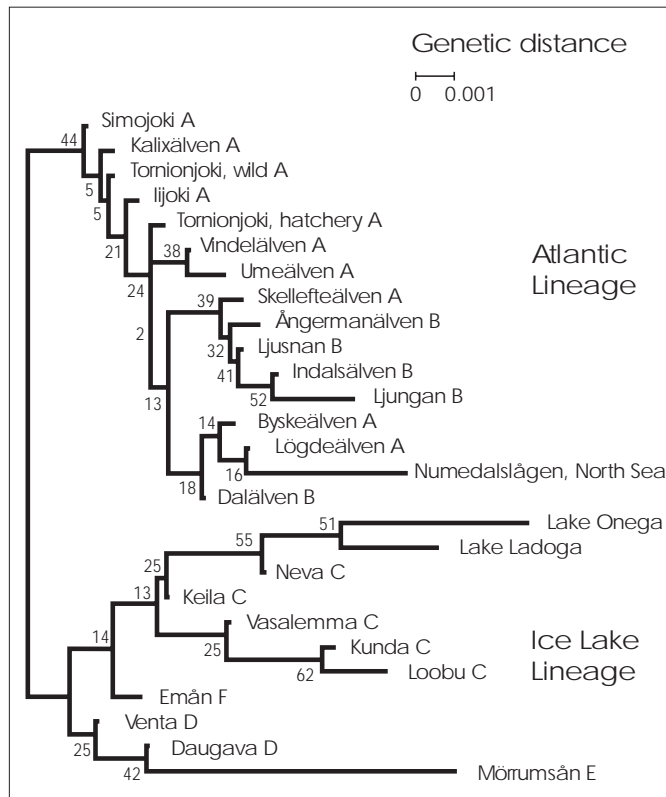
Isolation pattern and rate of gene flow

The pattern of differentiation of Baltic Sea salmon popu-

lations fits the isolation-by-distance model (Wright 1943; Kimura and Weiss 1964). Migrant dispersal was restricted to short distances and was thus most common between geographically adjacent stocks. So, although all stocks feed in the Baltic Main Basin, spawners tend mainly to stray to the neighbouring river along the shore.

The observed differentiation pattern fitted the one-dimensional migration pattern better than the two-dimensional plane pattern. It can be described by the theoretical one-dimensional "stepping stone" model (Kimura 1953), according to which populations are located as "steps" on a line, and in each generation, an individual can migrate a restricted number of "steps" in either direction along the line (Kimura and Weiss 1964). Considerable local differentiation will be more readily expected in the one-dimensional than in the two-dimensional migration pattern, and in this model the correlation between geographical distance and genetic dis-

Fig. 5. Genetic distances between Atlantic salmon stocks when populations outside the present Baltic Sea were added. The letters A–E refer to the sea areas from which the stocks originate.



tance also holds for longer geographical distances than in the two-dimensional model (Kimura and Weiss 1964). Thus, the location of river mouths along the shore, in a line, and over long distances offers relatively good prospects for salmon stocks to develop local adaptations. The occurrence of this pattern indicates the relatively neutral nature of allozyme variation.

The rate of gene flow was very low for distances of over 600 km; since geographical distances between the proposed phylogenetic lineages usually exceeded 550 km, there was very little gene flow between populations from different lineages. The geographical location of stocks corresponds roughly to that of two lines apart from each other. For shorter distances, gene flow had clearly occurred, and although our estimates are rough, they indicate that the role of gene flow has probably been underestimated in maintaining diversity among populations.

The occurrence of the isolation-by-distance pattern has only recently been tested on Atlantic salmon, previous authors having stressed the completely independent evolution of each river stock (e.g., Fontaine et al. 1997). Isolation by distance has been found to occur in salmon populations over long distances in data from west Atlantic populations in eastern Canada (McConnell et al. 1997) and from east Atlantic populations from Norway to Spain (Blanco et al. 1992; Bourke et al. 1997). In addition, isolation was observed over shorter geographical distances in Danish Atlantic salmon stocks from 1913, before human interference changed the population structure (Nielsen et al. 1999).

Before human impact, the population structure of Baltic

Sea salmon most likely corresponded better to the isolation-by-distance pattern than it does today. A balance probably prevailed right up until the 1930s, when damming of the big rivers resulted in the beginning of fish rearing, which tends to mix populations. Thus, despite the many human-induced changes in the genetic structure of salmon populations, isolation by distance can still be recognised in the population differentiation pattern.

Amount of genetic diversity

The total diversity (H_T) of natural stocks in the recent Baltic Sea is still about 30% higher (7.6%) than that of all hatchery stocks together (5.7%). Despite their weak and threatened status, recent natural stocks make a very marked contribution to the genetic biodiversity of Baltic salmon, especially those of the Ice Lake lineage. Recent hatchery stocks cannot completely replace the genetic resources of these stocks. When the hatchery and wild stock groups of the Bothnian Sea alone were compared, the diversity levels were about the same, showing that by using captive breeding in hatcheries, it is possible to maintain genetic variability (number of alleles) at least at a higher level than in the smallest wild stocks.

Population sizes tend to be smaller in ordinary hatchery stocks than in a medium-sized natural salmon stock, which causes loss of genetic variation. An effective size of 1000 individuals is large for a hatchery stock, but big natural stocks can have as many as tens of thousands of spawners. The smallest Estonian wild stocks, however, have fewer than 100 spawners a year. In the Tornionjoki stock case, two out of 16 alleles (12.5%) were lost in broodstock sampling.

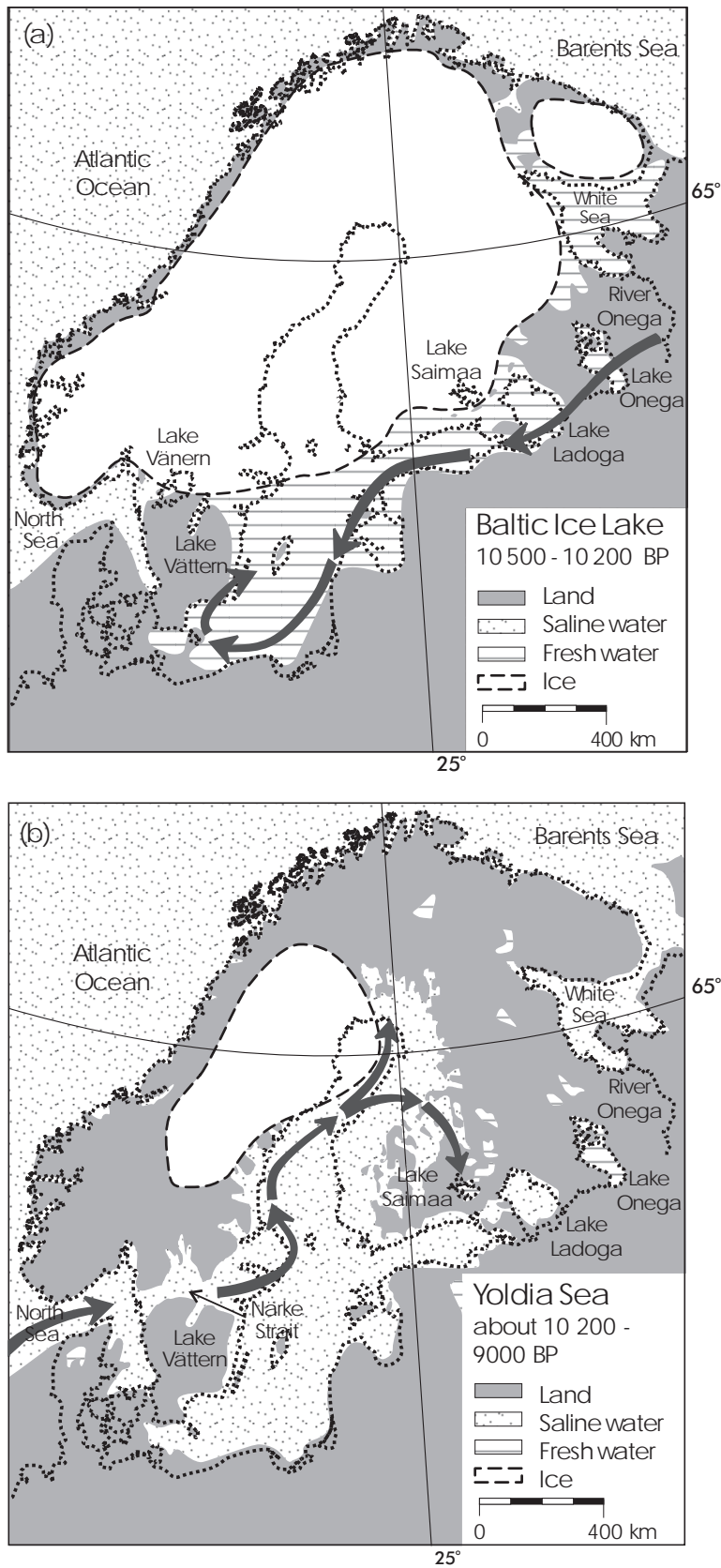
Rare alleles have, however, very likely been lost in the small natural stocks as well, e.g., those of Byskeälven and Lögdeälven. The small Estonian stocks (Kunda, Loobu, Keila, Vasalemma) also seemed to have fewer rare alleles than the Neva stock of the same area (Table 3). The loss of alleles could be expected to be a direct consequence of small population size and to occur in both natural and hatchery populations when they are small and isolated. The small population sizes and isolated status of wild stocks are often a result of human activity, which is thus also responsible for these losses. In the Gulf of Bothnia, only the population sizes of the Tornionjoki stock (75 000 smolts) have succeeded in maintaining all potential (found) alleles. Management strategies should therefore take account of the risk of losing diversity arising from both cases.

Because of the limited number of variable loci available, allozyme studies in general enable only severe bottlenecks to be established as statistically significant changes in mean heterozygosities. To increase the power of the tests for mean heterozygosities, McCommas and Bryant (1990) estimated that for an 80% probability of detecting a bottleneck at 5% significance, 15 loci were needed for a bottleneck size of four reproductive pairs and as many as 46 loci for 16 pairs when 30 individuals per population were analysed. The single-locus tests revealed, however, that changes in particular loci had clearly taken place.

Management implications

The maintenance of genetic diversity is internationally accepted as a common long-term goal for the management of

Fig. 6. (a) Proposed route by which the Ice Lake lineage of Atlantic salmon colonised Baltic Sea rivers at the Baltic Ice Lake stage. The final phase of the Baltic Sea Lake stage before the marine connection to the North Sea. Modified from a map by Eronen and Haila (Alalammi 1992). (b) The proposed route by which the Atlantic lineage of Atlantic salmon colonised Baltic Sea rivers at the Yoldia Sea stage. Modified from maps by Eronen and Haila (Alalammi 1992).



all living natural resources (United Nations 1992). It has also been stated often and unequivocally that the conservation of genetic diversity requires conservation of both levels of diversity, that between and that within stocks (e.g., Waples 1991; Ryman et al. 1995). The conservation strategies of these two components of diversity are, in practice, often opposed to each other, as the first seeks to avoid gene flow and the second loss of variation due to small population sizes, possibly with aid of organized gene flow.

When considering management principles for Baltic salmon, in the longest term, we should ensure that genetic material is preserved throughout the Baltic Sea range with a diversity and viability sufficient to permit the continuous evolution of self-sustaining populations of this isolated, brackish water adapted form of salmon. With the harnessing of reproduction rivers, many salmon stocks and their habitats have been irreversibly lost, and the recent Baltic salmon gene pool is only a fraction of what it was before human impact (only about 25 out of 90 stocks remain). There can be no return to the original state of Baltic salmon stocks; we can only safeguard their continuous evolution from the present state, in an environment with limited potential for natural reproduction. It is therefore crucial that we maintain what remains of the total gene pool after glaciations and human impact to as large an extent as possible. The long-term conservation goal thus gives priority to future evolutionary potential over attained adaptation, should these two come into conflict.

The scope for enhancement projects is limited by the range of potential reproduction areas, making it all the more important to locate them in areas where natural reproduction can still take place at a relatively high level and with considerable population sizes. It would be important to ensure the effective use of (at least) these areas for natural salmon reproduction.

The genetic resources of Baltic salmon derive from both wild and hatchery stock groups, one group complementing the other. The long-term conservation strategy should therefore seek to achieve a match between recent genetic material and potential reproduction areas and to ensure that all genetic material and all potential reproduction habitats are in use. For the genetic resources of hatchery stocks to become a viable component of salmon evolution in the Baltic Sea, they need to be reintroduced into the wild as naturally reproductive stocks.

To be able to retain the upper genetic structure above stock level, upper hierarchical levels need to be considered in conservation strategies. The prioritized goal of conserving viability by using large population sizes, the evidence of lost variability because of small population sizes, and the observed isolation-by-distance pattern all emphasize the need to use larger units or certain stock groups as genetic management units in addition to the usual stock level.

The two goals of the maintenance of genetic diversity, keeping population sizes large and conserving the observed stock structure to the greatest extent possible, can be combined by constructing the conservation strategy from the top of the hierarchy instead of from the individual stock level. The population sizes maintained within units will limit the level to which it is possible to proceed in splitting the structure. As the two phylogeographic lineages still have rela-

tively many stocks and sufficient variability for adaptation, at least these two large genetic management units can be formed. Separate strategies are needed to ensure maintenance of genetic diversity within the lineages; gene flow between them should be avoided. Similarly, if the stocks from the Gulf of Finland and the Eastern Main Basin can be considered to manage by themselves, a further distinction can be made and three management units formed. The establishing of management units depends basically on genetic differentiation, but information is also needed on potential reproduction areas, stock numbers, smolt production levels, geographical location of stocks, survival risks, fishing pressure, and possible differences in quantitative traits such as migration behaviour (Allendorf et al. 1997).

In principle, the same hierarchy as in the genetic structure should regulate the order of gene flow levels in the management strategy. Controlled gene flow should be allowed to maintain diversity between similar stocks. The position of a stock in a stock hierarchy can also be used as a weight value in the assessment of the conservation values for the stocks.

Treating the sea areas (Gulf of Bothnia, Gulf of Finland, Main Basin) separately would also be sensible for fisheries management. Each of the main sea areas has its own problems with its salmon stocks due to differences in reproduction potentials, genetic structure, migration routes, and fishing patterns. Thus, long-term strategies are needed to create solutions for each area separately, taking the local potential for maintaining naturally reproductive stocks into account.

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