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GENETIC COMPARISON OF SALMON *(SALMO SALAR* L.) FROM THE WHITE SEA AND THE ATLANTIC OCEAN

by

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ABSTRACT

Samples of salmon (*Salmo salar*) from River Kachkovka and R. Nilma in northern Russia were analysed by starch gel electrophoresis and compared to three Norwegian stocks, R. Neiden in northern Norway and R. Øyre and R. Hop on the west-coast.The aim of the study is to calibrate population genetic methods in Norwegian and Russian laboratories. The initial step in this process is to compare starch gel electrophoresis and polyacrylamide gel electrophoresis of salmon stocks, to facilitate comparison of data sets obtained by laboratories in Russia and Western Europe thereby increasing the knowledge about the genetic relationship between salmon populations from the East-Atlantic and the Kola peninsula and the White Sea. The comparison includes the following polymorphic loci: *AAT-4*, IDDH-2*. IDHP-3*, MDH-3,4*, MEP-2*, ESTD** as well as the newly discovered polymorphic loci *FBALD-3** and *TPI-3**. Samples were run side by side on gels, and the results show that the alleles found in the Russian stocks are the same as those found in the Norwegian stocks, although the two electrophoretic methods lead to differences in designations of alleles. A polymorphism in *ESTD** which involves a **94* allele was observed in salmon from the two Russian stocks and in R. Neiden. This allele was absent in the two other Norwegian stocks and in a major brood stock of farmed salmon in Norway. The *IDHP-3*116* allele was found in unusual high frequencies in the Russian stocks and in R. Neiden. Thus, the variability observed at these two loci gives some promise for the possibility in the future to distinguish salmon stocks from the northern part of Norway and Russia from stocks further south along the Norwegian coast.

INTRODUCTION

The Atlantic salmon is distributed on the western and eastern sides of the North Atlantic Ocean, in the Baltic Sea, and in the Ladoga and Onega lakes. Numerous large and small populations are distributed along the coast of Kola peninsula, in the White Sea and along the coast of Barents Sea east to the Kara gate. Due to the natural distribution of salmon and the decline in wild stocks in many regions, Norway and Russia now have the management responsibility for the vast majority of the remaining populations. Norway has a particular management responsibility as a leading producer of farmed salmon, with an annual production close to 300.000 tonnes. Over the years a significant amount of data on Norwegian and Russian salmon stocks has been collected. However, in contrast to the extensive collaboration on some of the marine species, little effort has been put into comparison and exchange of information about scientific methods and population biology and genetic results on salmon. Such exchange is of particular importance when a commercially important species is distributed over geographical areas shared by several nations, and thus harvested and monitored by several parties.

Population genetic studies on Atlantic salmon have revealed major genetic branching points between salmon populations from the West-Atlantic, the East-Atlantic and the Baltic regions. In addition numerous significant differences in allelic frequencies have been found among populations within regions, indicating a genetic differenciation between populations also within regions (Ståhl 1987, Galwin et al. 1993). Among the various isozyme loci studied, *AAT-4**, *MDH-3,4** and *IDDH-2** have been found to have the strongest discriminative power between salmon from the West-Atlantic and East-Atlantic regions. While at *AAT-4** the **100* and **50* allele predominates in European populations, a **25* allele predominates in North-American populations. At *MDH-3,4** the **100* allele predominates along with a rare **85* allele in European stocks, while a **125* allele has been found to predominate in North-American populations. Population genetic studies based on polyacrylamide gel electrophoresis have shown a genetic branching point between salmon populations from Baltic and Arctic regions. ESTD* is polymorphic in White Sea populations but monomorphic in Baltic salmon (Kazakov and Titov 1993; Semyonova and Slynko 1988; 1991).

However, it is a general problem in population genetic research that slightly different experimental conditions may influence the results, and when several laboratories are investigating the population genetic structure of a species, it is therefore important to calibrate electrophoretic methods by analyzing and comparing known samples. Furthermore, as occurrence and frequency of alleles may vary considerably among regions, and the common allele in one region may be rare or absent in another region, populations from different regions must be compared to known controlles, to make sure that results are standardized. Until the present study, no direct comparison of detected allelic variants between White Sea salmon and salmon from the Atlantic has been carried out, and thus little could be said about the relationship between salmon from these two regions.

The aims of this study are, firstly to compare different electrophoretic methods used in Russian and European population genetic studies on salmonid fish species to facilitate comparison of data from previous investigations, and secondly to investigate the genetic variability in salmon stocks from the Arctic Ocean, and compare it to salmon stocks from the Atlantic area.

MATERIALS AND METHODS

Populations studied

Samples of Russian salmon were collected from River Nilma draining into the western side of the White Sea in the Kandalaksha bay, and River Kachkovka located on the eastern side of Kola peninsula (Fig. 1). R. Nilma is a small, lake fed river. The sample consists of parr, smolt and dwarf males. The distance available for ascending spawners is about 4.2 km. Kachkovka, on the other hand, is a large river with a stretch of about 50 km available for anadromous salmon and trout. In addition to the main stream, salmon also spawn in two large tributaries. The samples which were collected by electrofishing and gill netting in the main stream and one tributary, consist of spawners and parr. Samples of Norwegian salmon were collected from River Øyreselv, R. Hopselv and R. Neiden. The samples were collected by electrofishing, and consist of parr and dwarf males. R. Øyre and Hop are short and small in terms of available spawning habitat for salmon and sea trout, as the available distance for ascending spawners is less then 1.5 km in both rivers. The number of wild searun salmon spawners in R. Øyre recorded by trapping and diving was 16 (1993) and 13 (1994), and the number in R. Hopselv is probably similar or smaller. R. Neiden drains Norwegian and Finnish catchments and flows into the Neidenfjord on the east side of the Varanger peninsula in the county of Finmark. The spawning run consist of over thousand individuals, and the largest fishery is on the 27 km long Norwegian part of the river.

Enzymes and electrophoresis

The following enzymes were stained for: aspartate aminotransferase (AAT, E.C 2.6.1.1); alcohol dehydrogenase (ADH, E.C. 1.1.1.1); adenylate kinase (AK, E.C. 2.7.4.3); creatine kinase (CK, E.C. 2.7.3.2); esterase-D (ESTD, E.C. 3.1.-); glycerol-3-phosphate dehydrogenase (G3PDH, E.C. 1.1.1.8); isocitrate dehydrogenase (IDHP, E.C. 1.1.1.42); iditol dehydrogenase (IDDH, E.C. 1.1.1.14); lactate dehydrogenase (LDH, E.C. 1.1.1.27); malate dehydrogenase (MDH, E.C. 1.1.1.37); malic enzyme (MEP, E.C. 1.1.1.40); glucose-6-phosphate isomerase (GPI, E.C. 5.3.1.9); phosphoglucomutase (PGM, E.C. 5.4.2.2), triose phosphate isomerase (TPI, E.C. 5.3.1.1), and fructose biphosphate aldolase (FBALD, E.C. 4.1.2.13) coded by putatively 35 loci.

For starch gel electrophoresis five buffer systems were tested: I) HIS, Histidine gel buffer: 0.0045M histidin adjusted to pH 7.0 with NaOH; electrode buffer: 0.41M Tri-Na-Citrate2hydrate, adjusted to pH 7.0 with citric acid. II) TCB, tris-citrate-borate gel buffer: 0.015M Tris, 0.001M citric acid, 0.003M boric acid, and 0.001M LiOH; electrode buffer: 0.3M boric acid and 0.1M LiOH; both buffers were adjusted to pH 8.6. III) AM, Citric acid gel buffer: 0.002M citric acid, electrode buffer: 0.04M citric acid, both adjusted to pH 6.1 with aminopropylmorpholine. IV) GLY, Glycine gel buffer: 0.0248M Tris, 0.189M Glycine adjusted to pH 8.5; electrode buffer: 0.0743M Tris, 0.189M glycine, adjusted to pH 8.7. V) CAME (modified from Clayton and Tretiak 1972, with EDTA added): 0.0365M Citric acid, 0.00099M EDTA, adjusted to pH 6.8 with N-(3-aminopropyl)-morpholine. Dilute one part in 20 parts H_20 for gels. For staining, a 0.2M Tris buffer with pH 8.0 was used, apart from in IDDH where pH was raised to 8.5, and for AAT where pH was raised to 9.5. Of these five buffer systems histidin pH 7.0, and TCB pH 8.6 proved superior for the majority of polymorphic loci, and were thus chosen for routine analyses. The CAME buffer, however, proved superior for the *FBALD-3**, and work well also for most of the enzymes run on the HIS gel.

Gels were made with 11% starch in a frame made of plexiglass with dimensions 0.7 x 18 x 26 cm, and slized in 5-6 sheets for staining of individual enzymes. For staining of additional enzymes on the HIS gel, the thickness of the gel can be increased to 1.0 cm without loosing technical quality. In TCB and GLY gels 60 samples were applied in one line on the gel, while in HIS and AM gels samples were applied in two parallell lines thus allowing 120 samples to be analysed in each gel. A prerun of duration 5 minutes with cooling only underneath the gel was used, after which filter papers were removed and electrophoresis continued for the appropriate length of time with cooling on top as well as underneath the gel. Polyacrylamide gel electrophoresis was conducted in 7.5% polyacrylamide gel with a tris-EDTA-borate gel buffer (Peacock et al. 1965): 0.089M Tris, 0.013M Boric acid, 0.0028M EDTA, and the electrode buffer diluted 1:1.7.

As the activity of an enzyme and the resolution of the genotypes at a polymorphic locus varies considerably according to the electrophoretic conditions, the migration of observed variants was measured to denote each variant. Furthermore, samples of Russian and Norwegian salmon were run side by side on the gel for a direct comparison of mobility, and finally Russian samples already analysed by polyacrylamide electrophoresis were reanalysed on starch gel. The data were processed by the BIOSYS-1 PC programme package of Swofford and Selander (1989). A locus was considered polymorphic if more than one allele was detected.

Table 1. Electrophoretic key parameters for isoenzymes included in the starch gel study

Enzyme	Locus	Buffer; time	Power	Tissue
Aspartate aminotransferase	*AAT-4**	I,V; 2h	11V/cm	liver
Esterase-D	*ESTD**	I,V; 2h	11V/cm	liver
Fructose-biphosphate-aldolase	*FBALD-3**	IV; 3h	11V/cm	eye
Glycerol3phosphate dehydrogenase	*G3PDH-2**	I,V; 2h	11V/cm	muscle
Glucosephosphate isomerase	*GPI-1,2**	II; 3h	14V/cm	muscle
Isocitrate dehydrogenase	*IDHP-3**	I,V; 2h	11V/cm	liver
Iditol dehydrogenase	*IDDH-2**	II; 2.30h	13V/cm	liver
Malate dehydrogenase	*MDH-3,4**	I,V; 2h	11V/cm	muscle
Malic enzyme	*MEP-2**	I,V; 2h	11V/cm	muscle
Phosphoglucomutase	*PGM-1**	II; 3h	14V/cm	muscle
Triose phosphate isomerase	*TPI-3**	II; 2.30h	18V/cm	eye

RESULTS

The following polymorphisms and variant alleles were detected: *AAT-4* (75), EST-D*(94), FBALD-3*(91), IDDH-2*(-100, 50), IDHP-3*(117), MDH-3/4*(90, 110), MEP-2*(135)* and *TPI-3*(109)*. Furthermore, *CK-1*, CK-2*, GPDH-2*, GPI-1,2*, GPI-3*, IDHP-2*, LDH-1*, LDH-2*, LDH-3*, LDH-5*, MDH-1*, MDH-2*, MEP-1*, MEP-3*, PGM-1** and *PGM-2** were all monomorphic.

Due to differences in experimental conditions, allelic nomenclature varies somewhat among laboratories. Thus allelic designations based on polyacrylamide electrophoresis differ from designations based on starch gel electrophoresis. Furthermore, there are also considerable differences among laboratories using starch gel electrophoresis (Table 2), and even within laboratories over time. This observation underlines the need for exchange of samples among laboratories.

Table 2. Allelic designations in starch gel electrophoresis and polyacrylamide gels observed in the present study and possible synonyms published in other studies.

Locus	Allelic designations		Possible synonyms and references
	Starch gel	PAG	
*AAT-4**	*55	-	*25[1,7], *57[2], *50[3], *22[5]
*AAT-4**	*75	*87	*50[1,7], *76[2], *80[3], *44[5]
*ESTD**	*94	*92	*89[2]
*FBALD-3**	*91	-	-
*IDDH-2**	*-100	-	*-50[1]; *-72[6,7],
*IDDH-2**	*50	-	*75[4], *10[3], *28[7]
*IDHP-3**	*117	~*100	*130[4], 116[6,7]
*MDH-3,4**	*110	*120	*115[1], 120[7]
*MDH-3,4**	*90	-	*85[1]; 80[6,7]
*MEP-2**	*135	*90	*125[1,7], *88[2]; *115[6]
*TPI-3**	*109	-	*103[6]

1: Stål -87; 2: Kazakov & Titov -93; 3: Koljonen -93; 4: Ståhl & Hindar -88; 5: Crozier -93; 6: Galvin et al. -94; 7:Verspoor et al. -91.

Although the activity in starch gels was good in general, the resolution of the banding patterns in *AAT-4** was found to depend on quality of samples. Furthermore, reducing voltage down to 11 V/cm gel reduced streaking. Increasing pH in staining solution to 9.5 improved the activity considerably. Due to weak resolution in some of the Russian samples, it is not possible to state with certainty the occurrence of more than one slow allele. The mobility of this was identical to that commonly found in the Norwegian samples.

*ESTD** which is diagnostic for separation of brown trout and Atlantic salmon, and which is also polymorphic in Atlantic salmon, showed initially only little activity in TCB, AM and HIS starch gels. However, by soaking a filter paper in the staining solution and placing this directly on top of the gel slice, the ESTD activity was excellent in samples run on HIS gels. *ESTD**, known to be monomorphic in salmon from the Baltic and the East-Atlantic revealed variability in the Russian populations and in R. Neiden. This is in agreement with Kazakov and Titov (1993) who found a slow allele in salmon from Kola peninsula and the White sea, and with other studies on salmon from the East-Atlantic where populations have been monomorphic or a slow allele has been found only rarely and at very low frequencies (Kjetil Hindar, NINA, pers. comm.).

Fructosebiphosphate aldolase activity was good and typing easy although resolution of individual bands in the heterozygotes was poor. The slow variant allele was found in all populations.

The activity of IDDH was initially weak. However, for this enzyme we found the distance between the point of application and the wick from the cathode to be critical. By reducing this distance migration and activity improved. Furthermore, we found it useful to increase pH of

the staining buffer to 8.5, reduce voltage down to 11-12 V/cm, add NAD to the gel and include both NBT and MTT in the staining solution. Also, increasing the thickness from 1 to 2 mm improved the activity of the IDDH bands. Two variant alleles were found, *-100 and *50, according to the observed distance of migration. The *-100 allele was found in all populations, while the *50 allele was absent in R. Neiden and R. Kachkovka, possibly due to small sample size in the latter. The interpretation of the observed variability in IDDH varies among laboratories and over time (Cross and Ward 1980; Ståhl 1987; Verspoor et al. 1991; Youngson et al. 1991; Elo et al. 1994), and we feel that further studies are required to draw firm conclusions about the number of polymorphic loci in this enzyme system, and which alleles belong to the various loci.

*IDHP-3** which resolves weakly in the commonly used citric acid gel buffer of pH 6.1, turned out with excellent activity and resolution in the HIS buffer with pH 7.0. In this locus a fast allele usually termed *IDHP-3*116* has been reported in many studies. We assume that this is synonymous to the *IDHP-3*130* reported by other authors (Ståhl and Hindar 1988). In our study an appropriate designation of the fast allele would be *IDHP-3*117* (Fig 2). *IDHP-3*100* is generally found in frequencies close to fixation in salmon populations from the East and West Atlantic, as well as in the Baltic Sea, while a fast allele has been found in low frequencies in populations from all major regions (Verspoor 1989; Ståhl & Hindar 1988; Koljonen 1993; Galvin et al 1994). However, in both of the included Russian populations the fast allele was found in unusually high frequencies, in particularly in River Nilma (0.708). The relatively high frequency of *IDHP-3*117* observed in Nilma (0.708) and Kachovka (0.273) is to some extent in agreement with Ofitserov et al. (1989) and Kazakov and Titov (1993), who found a fast allele in frequencies up to 0.25 in some other populations from the Kola peninsula and the White Sea.The highest frequency of this allele was found in R. Khlebnaya and Umba on the south coast of Kola peninsula and with the shortest distance to R. Nilma. Nevertheless, the very high frequency of the fast allele in Nilma in the Kandalaksha bay is significantly higher than any other population we know of.

The malate dehydrogenase resolves excellently with a good activity in four loci in HIS buffer. At *MDH-3,4** the *90 allele detected in Atlantic populations was not found in the Russian stocks in our study. However, this may be a result of the low sample size of the Russian populations. Kazakov and Titov (1993) did not publish any results on these loci, so at present the absence of the *90 allele in the Russian stocks must be treated with some caution.

The resolution and activity of the *MEP-2** is also excellent in the HIS buffer. A fast allele, with mobility identical to the fast allele (*135) in Norwegian salmon was found at intermediate frequencies in the Russian stocks.

Triose phosphate isomerase, with a recently detected polymorphism at *TPI-3** was originally recommended to be analysed in a Tris-glycine buffer with pH 8.5 (Galvin et al. 1994; Wilson et al. 1995). In our study, very good migration and activity was obtained in both liver and eye tissue on the TCB buffer system, while the resolution of genotypes at the polymorphic locus was better in eye tissue. The fast allele was denoted *109 according to its mobility relative to the *100 allele, but most likely this is synonymous to the *103 allele reported by Galvin et al (1994). The fast allele was found at intermediate frequencies at all loci. In Baltic salmon populations a slow allele (*90) is also common (Håkan Jansson, Laxforskningsinstitutet, Älvkarleby pers. comm. and Skaala unublished data). Thus, all alleles

detected in the two Russian salmon stocks corresponded in mobility to the alleles found in Norwegian salmon. We found no variant alleles at *TPI-1** and *TPI-2** in the populations included in the study. Again, in Baltic populations a rare slow allele is found at *TPI-2** (Håkan Jansson, pers. comm. and Skaala unpublished data).

Fst values ranged from 0.010 for *MDH-3,4** to 0.386 for *IDHP-3** (Table 4). The test on genetic heterogeneity among the studied populations shows significant heterogeneity for all loci apart from *MDH-3,4** (Table 5).

DISCUSSION

The occurrence of *ESTD*94* and *IDHP-3*117* in comparatively high frequencies in the two Russian samples and in R. Neiden in our study is in accordance with Kazakov and Titov (1993), and gives some promise for the possibility in the future to distinguish salmon stocks from the northern part of Norway and Russia from stocks further south along the Norwegian coast.

A genetic heterogeneity is demonstrated in the pooled material, indicating restrictions in the exchange of genetic material among the various populations. However, due to small sample size, and low number of individuals in some of the classes, particularly in R. Kachkovka, some of the probaility values (Table 5) should be treated with reservation.

Occasionally salmon tagged on the Norwegian coast have been recovered in Russian rivers, and a small number of salmon from Russian populations have been found in the Norwegian Sea and Norwegian home waters. In one tagging experiment with smolt from the River Porja which discharges into the Kandalaksha bay at the northwestern side of the White Sea, six individuals were caught in Norwegian home waters and another two in the Norwegian sea. Another five tags were recovered on salmon caught in the White Sea, and 13 tagged salmon returned to the R. Porja (Yakovenko 1987). Thus, salmon from the White Sea have migration patterns reaching far outside the White Sea region into the Norwegian Sea. Furthermore, the migration route is located near the Norwegian coast (Yakovenko 1987). Also a number of tagging experiments with salmon from R. Pechora reveals that the migration pattern of this stock extends west to the Norwegian Sea. Between 1970 and 1972, a number of adult salmon ranging from 2.0 to 15.0 kg in weight were marked in the Norwegian Sea, 27 of which were recaptured in R. Pechora (Yakovenko 1987). This demonstrates that to some degree there is overlapping migration routes for some of the Russian and Norwegian salmon stocks.

Dahl and Sømme (1938) who caught and tagged a number of salmon returning to the coastal waters in southern and northern Norway in order to study migration routes, found that salmon caught near Sørøya off the coast of Finmark northern Norway in 1937, had a marked eastern trend. That year, close to 6% of the tagged individuals, and about 20% of the recaptures were reported from Russian areas, while the following year, there were no reports from Russian areas.

These observations open some questions concerning migration pattern of postsmolt and adults from Russian and North-Norwegian salmon stocks in relation to ocean currents. While juvenile salmon from stocks in southern and mid-Norway will follow the direction of the coastal

current up to the feeding areas in the Norwegian Sea, Russian salmon and salmon from Northern-Norway entering the same feeding areas will have to migrate against the direction of the current. In some Pacific salmonids, the response by juveniles to current has been found to be inherited and also stock specific (Raleigh and Chapman1971; Brannon 1972). This may indicate that salmon stocks from different regions feeding in the Norwegian Sea have different or even opposit responses to the direction of the sea current.

Alternatively, salmon from Northern-Norway and Russia follow an eastern route as post smolts along the current and then turnes north and west in the Barents sea, and then east again to hit the coast of Finmark and Kola on their spawning migration (Novikov and Kuzischin 1990; Kjell Moen, Finmark county, pers. comm.). Although there is no sampling for salmon in the Barents Sea, and thus little information about salmon in this area to support the hypothesis, individual salmon is occationally represented as bycatch on research cruises in the Barents Sea (Knut Jørstad, unpublished observation; Sigbjøn Mehl, Institute of Marine Research, pers. comm.).

However, there is a general lack of information about salmon during the marine phase, including migration routes of various stocks. Also little is known about the relative importance and fluctuation in the various suspected causes of mortality. Fortunately, there is a potential to gain increased knowledge about salmon in the sea from by-catches of salmon in some of the herring cruises conducted by the Norwegian Institute of Marine Research, and from the joint salmon research cruises between different Norwegian institutions and in particular from the planned joint research cruise between Norway and Russia in the Barents Sea and White Sea.

The occurrence of a low number of specimens from Russian and Norwegian salmon populations in the same feeding area does not imply that the main feeding area of Russian stocks is overlapping completely with that of the Norwegian stocks, and it does not give any information about the separation of spawning populations or the genetic differentiation between the two groups. Such information can only be extracted from a genetic comparison of a larger number of Arctic and Atlantic stocks or from a larger number of genetic loci.

Until recently, population genetic research on Atlantic salmon has suffered from a low number of polymorphic isozyme loci that could be used for population screening to resolve the natural level of genetic exchange among populations, and thus the genetic population structure of the species. Furthermore, at least one locus, *MEP-2** has been suspected to be influenced by some sort of natural selection, thus causing some uncertainty about its value in population genetic studies (Jordan et al. 1990; Jordan and Youngson 1991). At another locus, *IDDH-2** various laboratories have interpreted the observed variation somewhat differently, stressing the importance of collaboration between laboratories.

Lately, the number of scorable polymorphic isozyme loci has been increased, improving the resolution power of starch gel electrophoresis in population studies on salmon. Furthermore, several new methods based on analyses of DNA are now beeing developed (Taggart and Ferguson 1990; Prodöhl 1993; Ferguson 1995; Taggart et al 1995; Wright and Bentzen 1995). The technical development now proceeds at a speed that necessitates close collaboration to ensure that methods and nomenclature are standardized in such a way that data sets from different laboratories can be compared. Moreover, a correct methodological approach must be used in future research of genetic variability of Atlantic salmon. This approach require a

long-term study at all levels of intraspecific differentiation, similarly to those carried out on Pacific salmons (Altukhov 1990).

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REFERENCES

Altukhov, Yu.P. 1990. Population genetics. Diversity and Stability. Harwood Academic Publishers. london. 352p.

Bakshtansky, E.L., M. Ya. Yakovenko, L.F. Zaguraeva and V.D. Nesterov. 1974. Results of the Atlantic salmon tagging in the Soviet Union. ICES/ CM (M:17), 12p.

Brannon, E.L. (1972). Mechanisms controlling migration of sockeye salmon fry. Internat. Pacific Salmon Fisheries Commission Bulletin XXI.

Clayton, J.W. and D.N. Tretiak.1972. Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Board Can. 29, 1169-1172.

Cross, T. and R.D. Ward. 1980. Protein variation and duplicate loci in the Atlantic salmon, *Salmo salar* L.Genet. Res., Camb. 36, 147-165.

Crozier, W.W. and I.J.J. Moffett. 1990. Inheritance of allozymes in Atlantic salmon (Salmo salar L.). Aquaculture 88, 253-262.

Crozier, W.W. 1993. Evidence of genetic interaction between escaped farmed salmon and wild Atlantic salmon (*Salmo salar* L.) in a Northern Irish river. Aquaculture 113, 19-29.

Dahl, K. and S. Sømme. 1938. Salmon markings in Norway 1937. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. I. Mat.-Naturv. Klasse. 1938. No. 2.

Dahl, K. and S. Sømme. 1942. Salmon markings in Norway 1938, 1939 and 1940. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. I. Mat.-Naturv. Klasse. 1941. No. 10.

Ferguson, A. 1995. Molecular genetics in fisheries: current and future perspectives. P. 111-115. In: Molecular genetics in Fisheries. G.R. Carvalho and T.J. Pitcher (eds.). Chapman and Hall, London.

Galvin, P., T. Cross and A. Ferguson. 1994. Genetic differentiation and gene flow in Atlantic salmon, Salmo salar L.: a case study of the River Shannon system in Ireland. Aquaculture and Fisheries Management 25 (Supplement 2), 131-145.

ICES, 1993. Extract of the Report of the Advisory Committee on Fishery Management to the North Atlantic Salmon Conservation Organization. May. 40pp.

Jordan, W.C., A.F. Youngson and J.H. Webb. 1990. Genetic variation at the malic enzyme-2 locus and age at maturity in sea-run Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 47, 1672-1677.

Jordan, W.C. and A.F. Youngson. 1991. Genetic protein variation in natural selection in

atlantic salmon (*Salmo salar*, L.) parr. Journal of Fish Biology 39 (Supplement A), 185-192.

Jordan, W.C., A.F. Youngson, D.W. Hay and A. Ferguson. 1992. Genetic proten variation in natural populations of Atlantic salmon (Salmo salar) in Scotland: temporal and spatial variation. Canadian Journal of Fisheries and Aquatic Sciences 49, 1863-1872.

Kazakov, R.V. and S.F. Titov. 1993. Population genetics of salmon, Salmo salar L., in northern Russia. Aquaculture and Fisheries Management 24, 495-506.

Novikov. G.G. and Kuzischin, K.V. 1990. To the problem of ocean migrations of Atlantic salmon. In: Atlantic salmon symposium proceedings. Syktyvkar. p 48 (in Russian).

Ofitserov, M.V., T.S. Golovanova, L.V. Vitvitskaya and S.I. Nikonorov. 1989. Effects of hatchery cultivation on the genetic variability of Atlantic salmon, Salmo salar. Journal of ichthyology 29, 132-135.

Peacock, A.C., Bunting S.L., Queen K.G. 1965. Serum protein electrophoresis in acrylamide gel: patterns from normal human subjects. Science 147, 1451-1452.

Prodöhl, P. 1993. Multi locus and single locus minisatellite DNA polymorphism in brown trout (*Salmo trutta* L.) populations. PhD thesis, The Queens University of Belfast. 273pp.

Raleigh, R.F. and D.W. Chapman. 1971. Genetic control in lakeward migrations of cutthroat trout fry. Trans. Am. Fish. Soc. 100, 33-40.

Reddin, D.G. 1988. Ocean life of Atlantic salmon in the Northwest Atlantic. P 483-511. In Atlantic Salmon: planning for the future. Mills D. and Piggins D. eds. The Proceedings of the Third International atlantic Salmon Symposium, Biarritz, France 21 - 23 Oct. 1986.

Semyonova, S.K. and V.I. Slynko. 1988. Polymorphisms in populations of Atlantic salmon (Salmo salar L.), brown trout (S. trutta L.) and their hybrids. Genetica 24, 548-555. (in Russian).

Semyonova, S.K. and V.I. Slynko. 1991. Genetic differentiation in Atlantic salmon populations in north-west region of the USSR. Symposium on Biochemical Genetics and Taxonomy of Fish. Queen`s University, Belfast, 22-26 July 1991. Abstracts p.2.

Skaala, Ø. and K.E. Jørstad. 1994. Genetic markers in Atlantic salmon, Salmo salar L., their potential for experimental studies of gene flow and adaptation. Aquaculture and Fisheries Management 25 (Supplement 2), 121-129.

Ståhl, G. (1987). Genetic population structure of Atlantic salmon. In: Population genetics and Fishery Management, N. Ryman and F. Utter (eds.), University of Washington Press, Seattle, USA.

Ståhl, G. og K. Hindar. 1988. Genetisk struktur hos norsk laks: status og perspektiver. Rapport fra fiskeforskingen No. 1.

Swofford, D.L. and R.B. Selander. 1989. BIOSYS-1. A PC program for the analysis of allelic variations in genetics. Release 1. July 1989.

Taggart, J.B. and A. Ferguson. 1990. Minisatellite DNA fingerprints of salmonid fishes. Animal Genetics 21, 377-389.

Taggart, J.B., P.A. Prodöhl and A. Ferguson. 1995. Genetic markers for atlantic salmon (Salmo salar L.): single locus inheritance and joint segregation analysis of minisatellite (VNTR) DNA loci. Animal Genetics 26, 13-20.

Verspoor, E., N.H.C. Fraser and A.F. Youngson. 1991. Protein polymorphism in Atlantic salmon within a Scottish river: evidence for selection and estimates of gene flow between tributaries. Aquaculture 98, 217-230.

Vuorinen, J. and O.K. Berg. 1989. Genetic divergence of anadromous and nonanadromous Atlantic salmon (Salmo salar) in the River Namsen, Norway. Canadian Journal of Fisheries and Aquatic Sciences 46, 406-409.

Wilson, I.F., E.A Bourke and Thomas F. Cross. 1995. A triose-phosphate isomerase polymorphism in the Atlantic salmon Salmo salar L. Biochemical Genetics 33 (1/2), 25-33.

Wright, J.M. and P. Bentzen. 1995. Microsatellites: genetic markers for the future. P. 117-121. In: Molecular genetics in Fisheries. G.R. Carvalho and T.J. Picher (eds.). Chapman and Hall, London.

Yakovenko M. Ja. 1987a. On migrations of Atlantic salmon marked in the Norwegian Sea and in the Porja River. Ecol and Phys. studies of commercially valuable fish species in the North basin, Leningrad, p. 69-75 (in Russian).

Youngson, A., S.A.M. Martin, W.C. Jordan and E. Verspoor. 1991. Genetic protein variation in Atlantic salmon in Scotland: comparison of wild and farmed fish. Aquaculture 98, 231-242.

Table 3. Allelic frequencies at eight polymorphic loci, mean heterozygosity (unbiased estimate), H, with standard error and mean number of alleles per locus, N_{all}, in some Russian and Norwegian salmon populations.

	Population				
Locus	R. Øyre	R. Hop	R. Neiden	R.Kachkovka	R. Nilma
AAT-4*					
(N)	51	33	73	10	36
*75	.176	.015	.068	.050	.153
*100	.824	.985	.932	.950	.847
IDDH-2*					
(N)	106	32	63	9	22
*-100	.495	.250	.437	.500	.136
*50	.033	.188	.000	.000	.068
*100	.472	.563	.563	.500	.795
IDHP-3*					
(N)	114	34	76	11	48
*100	.952	1.000	.908	.727	.292
*117	.048	.000	.092	.273	.708
MDH-3,4*					
(N)	115	121	86	28	49
*90	.017	.000	.006	.000	.000
*100	.983	1.000	.994	1.000	1.000
MEP-2*					
(N)	109	121	84	28	49
*100	.317	.607	.464	.554	.429
*135	.683	.393	.536	.446	.571
TPI-3*					
(N)	115	58	86	12	22
*100	.704	.647	.634	.500	.500
*109	.296	.353	.366	.500	.500
FBALD-3*					
(N)	111	60	78	11	19
*91	.153	.092	.237	.136	.342
*100	.847	.908	.763	.864	.658
ESTD*					
(N)	19	11	64	29	16
*94	.000	.000	.188	.241	.031
*100	1.000	1.000	.813	.759	.969
H(SE)	.258(.070)	.217(.090)	.305(.066)	.366(.071)	.320(.069)
N_{all}(SE)	2.00 (.19)	1.75 (.25)	2.00 (.00)	1.88 (.13)	2.00 (.19)

Table 4. Summary of F-statistics at all loci

Locus	F(IS)	F(IT)	F(ST)
AAT-4*	-.018	.063	.045
IDDH-2*	-.082	-.002	.074
IDHP-3*	-.163	.286	.386
MDH-3,4*	-.015	-.005	.010
MEP-2*	.106	.142	.041
TPI-3*	-.040	-.011	.028
FBALD-3*	-.072	-.018	.051
ESTD*	.247	.341	.125
Mean	-.011	.090	.100

Table 5. Contingency chi-square analysis at all loci

Locus	No. of alleles	Chi-square	D.F.	p
AAT-4*	2	16.156	4	.00282
IDDH-2*	3	58.316	8	.00000
IDHP-3*	2	237.718	4	.00000
MDH-3,4*	2	7.075	4	.13199
MEP-2*	2	41.240	4	.00000
TPI-3*	2	9.892	4	.04229
FBALD-3*	2	18.208	4	.00112
ESTD*	2	20.225	4	.00045
(Totals)		408.831	36	.00000

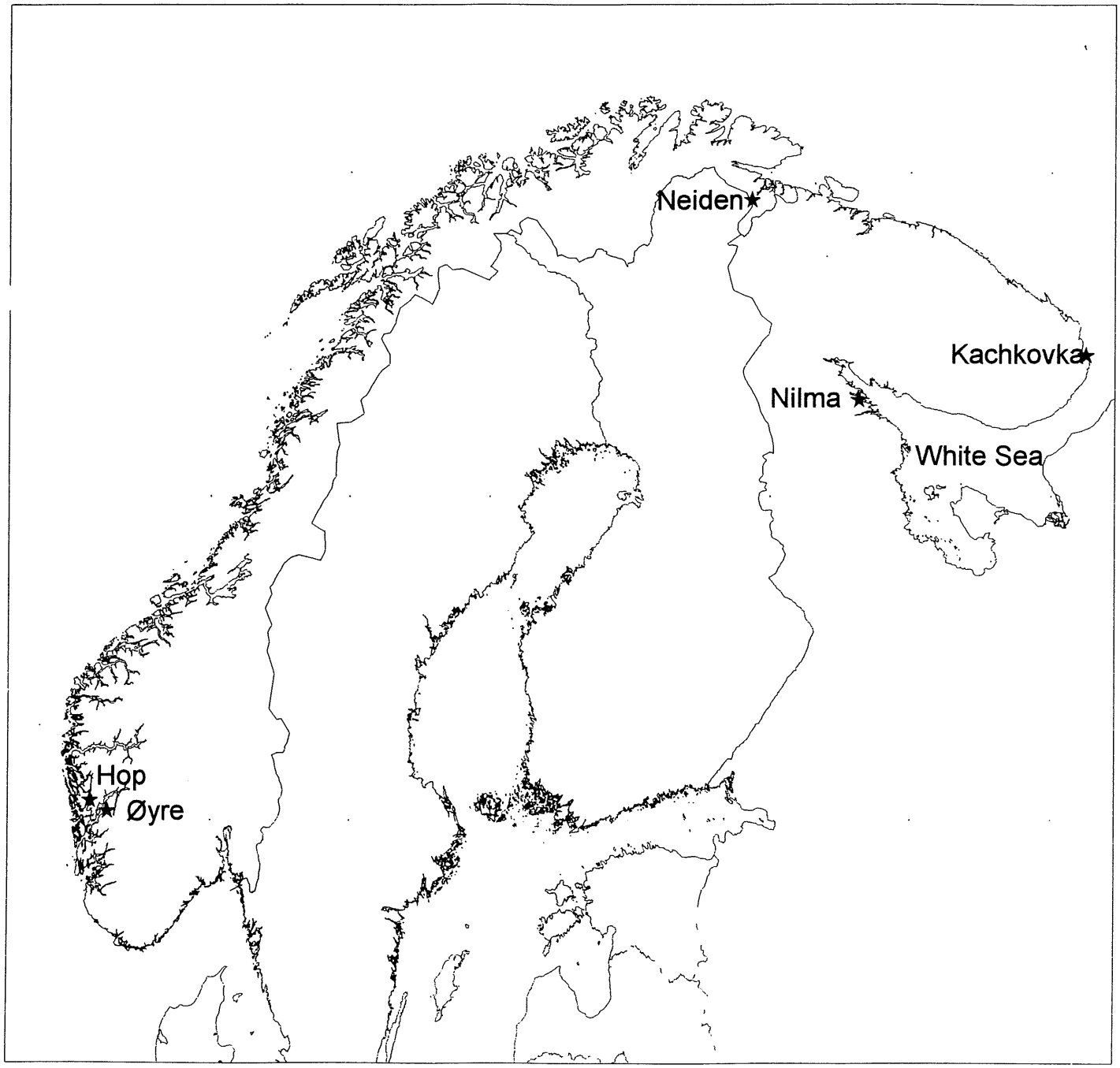

Fig. 1. Map of Norway, Kola peninsula and the White Sea with sampled locations indicated.

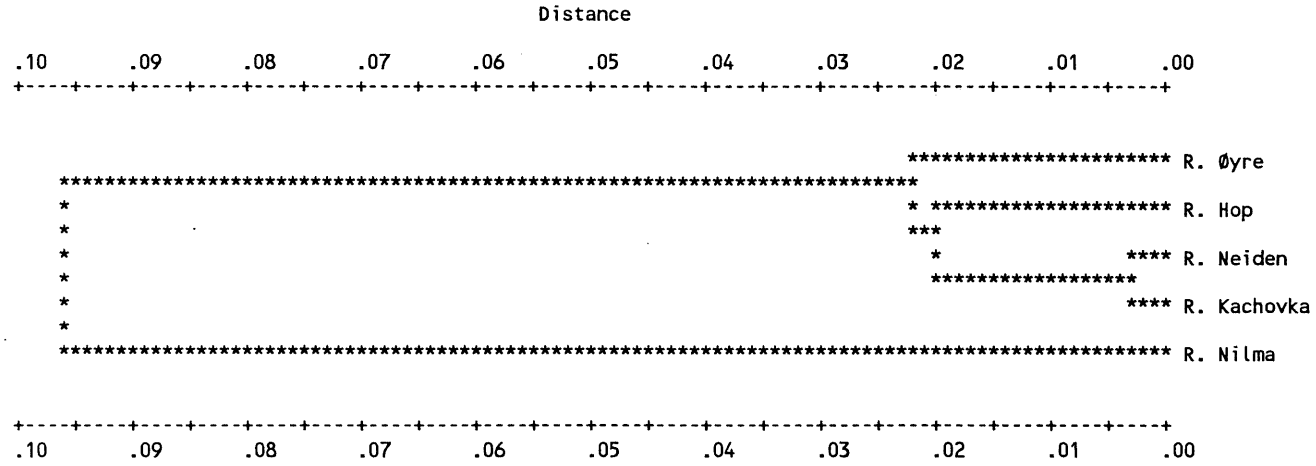

Fig. 2. Dendrogram showing genetic distances between the Russian and Norwegian populations studied