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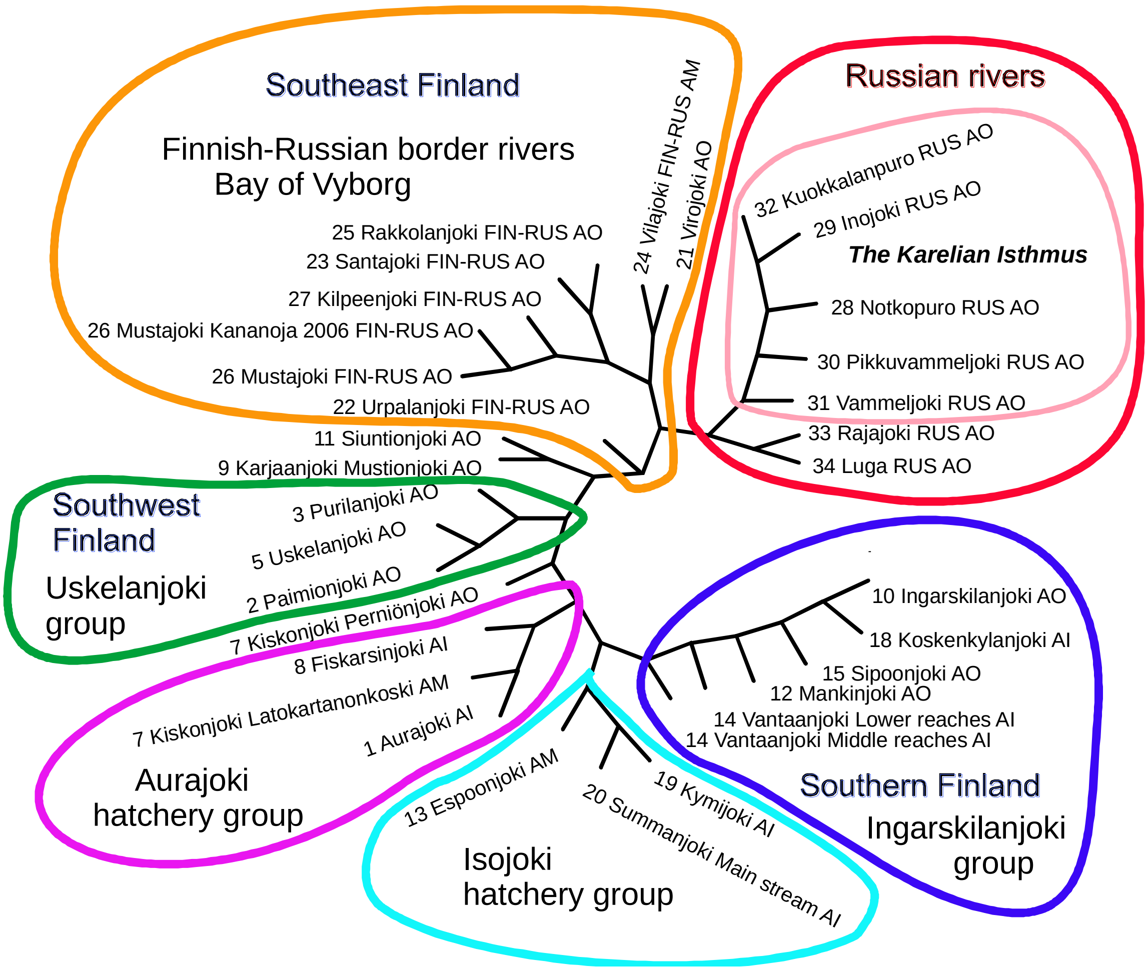
Genetic structure of Finnish and Russian sea trout populations in the Gulf of Finland area

Marja-Liisa Koljonen, Aki Janatuinen, Ari Saura and Jarmo Koskiniemi



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Authors
Marja-Liisa Koljonen, Aki Janatuinen, Ari Saura and Jarmo Koskiniemi

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Abstract
In order to create a management strategy for the sea trout in the Gulf of Finland area, all potential brown trout populations in the area were analysed together with Russian populations from the neighbouring area. In all, 3430 individual brown trout samples from 70 locations and from 34 river systems were analysed from Finnish and Russian rivers. The analysis was based on variation in 16 DNA microsatellite gene loci in these samples.

From all samples, the overall diversity, mean allelic richness and effective population size, as well as the number of full-sib families and mean relatedness was assessed. Genetic differentiation was first analysed within rivers systems and in several stages over all the data. The anadromous and resident populations were also analysed separately. A subpopulation structure was observed in seven river systems (Kiskonjoki, Karjaanjoki, Siuntionjoki, Espoonjoki, Vantaanjoki, Summanjoki and Virojoki). In general, diversity differences were very large. No statistically significant differences could be detected between the river sample pairs Aurajoki – Fiskarsinjoki, Ingarskilanjoki – Koskenkylänjoki, Vantaanjoki, Palojoki – Koskenkylänjoki or Isojoki – Kymijoki. In all cases, similarity was a result of hatchery releases of known origin. In general, the genetic distances between the anadromous stocks followed the geographical distances between the river mouths and the form of the coastline. Anadromous populations could be grouped into six main groups: 1) the Uskelanjoki group, 2) Aurajoki group, 3) Isojoki group, 4) Ingarskilanjoki group, 5) Bay of Vyborg group and 6) the group of Russian rivers, mainly the Karelian Isthmus rivers. Two of the groups were influenced by stocked fish: the Aurajoki and Isojoki groups. The releases of these hatchery stocks should be limited to agreed rivers and for sea ranching purposes. Local genetic material for three coastal areas was still available. For southwest Finland, or Varsinais-Suomi, the diversity levels were lower than in other areas, but local genetic material is still left in the Uskelanjoki group rivers (Uskelanjoki, Paimionjoki and Purilanjoki). For the Uusimaa area, the most diverse and valuable populations are in the Ingarskilanjoki group (Ingarskilanjoki, Koskenkylänjoki, Sipoonjoki, Mankinjoki and Vantaanjoki). For the southeastern part of the coast, local genetic material is still available in the border rivers draining into the Bay of Vyborg, and especially in the River Mustajoki population, from which a broodstock has already been founded. Other rivers for that area are Rakkolanjoki, Santajoki, Kilpeenjoki, and Urpalanjoki and Finnish Virojoki, with Saarasjärvenoja belonging to the same group. Recommendations for the management of brown trout populations of the whole Finnish coastal area and also of individual rivers were provided.

Keywords
Sea trout, Salmo trutta, DNA microsatellites, genetic diversity, management

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Contact
Marja-Liisa Koljonen, marja-liisa.koljonen@rktl.fi

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Tiivistelmä Suomenlahden alueen meritaimenkantojen hoitostrategian luomiseksi selvitettiin sekä suomalaisten että venäläisten Suomenlahteen laskevien jokien taimenkantojen geneettinen rakenne. Kaikkiaan tutkittiin 3 430 yksittäistä taimennäytettä, 70 populaatiosta ja 34 vesistöstä. Analyysi perustuu 16 DNA mikrosatelliittigeeni-lokuksen muunteluun. Kaikista näytteistä analysoitiin kokonaisdiversiteetti, alleelirikkaus, geneettisesti tehollinen populaatiokoko, täyssisarperheiden määrä ja keskimääräinen sukulaisuusaste. Perinnöllinen erilaistuminen ana lysoitiin ensin saman vesistön eri populaatoiden välillä. Vaeltavat ja paikalliset populaatiot analysoitiin myös erik seen. Seitsemässä vesistössä havaittiin populaatioiden välistä erilaistumista eri jokihaarojen tai koskien popu laatioiden välillä. Nämä vesistöt olivat Kiskonjoki, Karjaanjoki, Siuntionjoki, Espoonjoki, Vantaanjoki, Summan joki ja Virojoki. Koko aineistossa geneettisen diversiteetin määrän erot olivat jopa kolminkertaiset vähiten ja eniten muuntelevien populaatioiden välillä. Tilastollisesti merkittävää eroa ei voitu havaita viiden jokinäyteparin välillä: Aurajoki – Fiskarsinjoki, Ingarskilanjoki – Koskenkylänjoki, Vantaanjoki, Palojoki - Koskenkylänjoki, ja Isojoki – Kymijoki. Kaikissa tapauksissa samankaltaisuuden selittivät tunnetut poikasistutukset. Runsaista istutuksista huolimatta meritaimenkantojen perinnölliset etäisyydet vastasivat edelleen varsin hyvin niiden maantieteellisiä etäisyyksiä ja rannikon rakennetta. Meritaimenkannat ryhmittyivät kuuteen pääryhmään: 1) Uskelanjoki, 2) Aurajoki, 3) Isojoki, 4) Ingarskilanjoki, 5) Viipurinlahti ja 6) Venäläiset joet (Karjalan kannas). Näistä ryhmistä kaksi oli sellaisia, joissa oli selvää istutuskantojen vakutusta: Aurajoki ja Isojoki. Näiden laitostaimenkantojen siirtäminen ja istuttaminen tulisi rajoittaa sovittuihin jokiin ja merialueen istutuksiin. Paikallista perinnöllistä aineista oli olemassa edelleen kolmelle alueelle. Varsinais-Suomen alueen alkuperäisimmät meritaimenkannat ovat Uskelan-joen, Paimionjoen ja Purilanjoen taimenet. Tämän alueen kantojen geneettinen diversiteetti oli alhaisempi kuin muiden alueiden, pienten populaatiokokojen vuoksi. Uudenmaan alueen taimenkantojen arvokkain, alkuperäinen geneettinen materiaali on parhaiten säilynyt Ingarskilajoen taimenen lisäksi Koskenkylänjoen, Sipoonjoen, Man kinjoen ja Vantaanjoen taimenpopulaatioissa. Kaakkois-Suomen alueen taimenkantojen geneettinen mate riaali on säilynyt Viipurinlahteen laskevien rajajokien populaatioissa. Näistä tärkein on Mustajoki, josta on jo perustettu emokalasto. Muita rajajokia ovat Urpalanjoki, Rakkolanjoki, Santajoki ja Kilpeenjoki. Myös kokonaan Suomen puo lella oleva Virojoen Saarasjärvenoja kuuluu geneettisesti tähän ryhmään. Hoitosuositukset on annettu paitsi koko Suomen rannikolle, myös kaikille taimenkannoille erikseen.			
Asiasanat Meritaimen, DNA mikrosatelliitti, perinnöllinen monimuotoisuus, hoitostrategia			
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Yhteydenotot Marja-Liisa Koljonen, marja-liisa.koljonen@rktl.fi			
Muita tietoja Tämä työ on osa Central Baltic INTERRED IV A - ohjelmaan kuuluvaa HEALFISH-projektia (2010-2013)			

Contents

1. Introduction

The EU and international organizations (UN, FAO, IUCN, ICES, NASCO, and HELCOM) all recognize the crucial need to conserve genetic diversity as a fundamental part of biodiversity, which is rapidly being depleted due to human activities. The loss of genetic diversity reduces the level of local adaptation and the ability of species to adapt to continued changes in the environment, and results in an irreversible loss of genetic resources and a reduction in the overall evolutionary potential of species.

Because the financial resources and the means to preserve genetic resources are limited, efficient strategies are needed to maximize the overall maintenance of genetic diversity in each situation. A key question is thus the definition of management units for each management activity and geographical level. The valuation, choice and priorisation of populations according to their genetic characteristics are also essential for conservation strategies.

With genetic markers, it is possible to measure diversity levels and the amount of genetic differentiation, estimate current gene flow levels between populations, as well as to analyse the similarity between hatchery stocks and natural stocks as an indication of the influence of hatchery-released fish. Genetic markers also allow estimates of genetically effective population sizes, and levels of inbreeding or mixing of populations. With this information, it is possible to define population borders and hierarchical population structures, and as a conclusion define management units of different levels (Koljonen 2001).

There are currently about 101 rivers or brooks draining into the Gulf of Finland from Finland, Russia or Estonia in which there is an anadromous trout population (*Salmo trutta* L.). From these populations, 85 can be regarded as native wild stocks (ICES 2013). The remaining populations have been supported by hatchery releases. For about one-third of the anadromous trout populations, the conservation status is very poor, as for 29 populations the current smolt production level is less than 5% of the potential smolt production level of the river. In addition, the conservation status is weak and uncertain for another 30 populations.

According to a threat factor analysis for the whole Gulf of Finland, including Russian and Estonian rivers, the most common threat to the sea trout stock was overexploitation (for 47 river populations), followed by habitat degradation (for 45 populations), while for 27 populations the threat was pollution, and for 15 cases its was dam construction (ICES 2013).

In the Finnish Red Data Book, the anadromous trout is listed as Critically Endangered, because natural reproduction is unstable in most Finnish Baltic Sea populations due to intensive fishing, which also targets immature fish, migration obstructions and highly alternating water flow levels in rivers (Kaukoranta et al. 2000, Kallio-Nyberg et al. 2001, Heinimaa et al. 2007, Urho et al. 2010). In Russia, a declaration of trout preservation is in force so that no legal trout fishing should occur. However, despite many of the rivers being situated in the border zone, poaching is a threat. In Finland, the legal minimum catch size of sea trout has been 50 cm, but will be increased to 60 cm at the beginning of 2014. In addition, in 2013, the legal minimum catch size of sea trout was increased in the Finnish governmentally ruled offshore sea area of the Gulf of Finland from 50 cm to 65 cm.

In Finland, dam construction has been especially active and several sea trout stocks have been destroyed (Kallio-Nyberg et al. 2001). Depending on the distance of the first dam from the river mouth, different types of more or less artificially isolated populations have remained in the river systems (Kallio-Nyberg et al. 2010). In the current HEALFISH project, restoration plans exist for five Finnish rivers (Hitolanjoki, Ingarskilanjoki, Vantaanjoki, Koskenkylänjoki and Vaalimaanjoki).

In order to compensate for the decreased population abundance and production levels, artificial reproduction in hatcheries and the release of reared fish or eggs into rivers with the aim of re-establishing extinct or enhancing weak populations are commonly practiced. In addition, hatchery releases to improve sea trout catches have also been widely used along the coastal area. However, this may have resulted in irreversible changes in the genetic composition of local, native populations due to the direct effects of releases or indirect impacts of hatchery fish ascending from the sea to spawn in native rivers.

Even if the released hatchery fish originate from the same river, non-natural selective pressures in hatcheries, termed the domestication effect, or the loss of genetic variation through genetic drift and inbreeding due to the restricted population sizes in hatcheries may compromise local adaptations and decrease the overall diversity of the native populations. These may also pose a threat to the maintenance of genetic diversity. The potential genetic changes may reduce the conservation value of the trout stocks.

In all, 293 000 smolts were released into the Gulf of Finland in 2012. The majority (74%, i.e., 216 000 smolts) were from Finnish releases, 22% (64 000 smolts) from Russia and 4% (13 000 smolts) were from Estonian releases (ICES 2013). Estonia has announced an end to its trout releases in 2013. The profitability of hatchery releases for fishing purposes has been low. The recapture rate of Carlin-tagged, released sea trout has followed a continuously decreasing trend for more than 20 years in the Gulf of Finland (ICES 2013).

Some mixing of anadromous trouts in the sea is known to occur, as tagging experiments have shown in general about 5–10% of the trout tagged in Finland to be returned from the Estonian coast and some also from Russia. Correspondingly, sea trout tagged in Estonia have partly been recaptured in Finnish coastal waters. The coastal sea trout catch in 2012 in Estonia was 13 300 kg, and in Finland 15 900 kg. In addition, Finland announced a total catch of 3 800 kg from rivers (ICES 2013).

In Russia, wild sea trout populations are found in at least 40 rivers or streams. The majority are situated in the northern coast of the Gulf of Finland, but the rivers with the highest smolt production are in the southern area. Average densities are in general below ten 0+ parr per 100 m^2. The total smolt production of Russian rivers has been estimated to be at least 10 000–15 000 smolts. Smolt trap experiments indicate that between 2000 and 8000 sea trout smolts of natural origin annually migrate to the sea from the Luga, the largest Russian trout river. Six Russian rivers, in addition to border rivers, were included in the current analyses to enable a comparison with native wild stocks and describe the level of differentiation in general. Part of the earlier analyzed data on Russian populations (EU Interreg IIIA project ISKALT 2003–2007) was updated for 16 DNA microsatellite loci and used for the analysis of pooled data sets.

Watershed-based analyses of the genetic structure of Finnish brown trout populations have also previously been conducted (Koljonen 1989, Marttinen and Koljonen 1989, Koljonen et al. 1992, Koljonen and Saura 1992, Koskiniemi 2005, Koskiniemi 2007, Koskiniemi 2008, Koskiniemi 2009a,b,c, Aaltonen 2009, Koskiniemi 2010, Aaltonen 2011, Koskiniemi 2012, Nuotio and Koskiniemi 1995, Saura 2005b), but this was the first analysis covering the whole southern coastal area. In addition, research teams from other Baltic Sea countries have studied some restricted areas or river systems of Baltic Sea drainage basin by using allozyme, mtDNA and microsatellite markers (Ryman 1983, Hansen and Mensberg 1998, Hindar et al. 1991, Luczynski et al. 1997, Laikre et al. 2002, Was and Wenne 2002, Wlodarczyk and Wenne 2001, Lehtonen et al. 2009, Samuiloviene et al. 2009).

The aim of this study was to describe the genetic structure and measure the level of genetic differentiation and diversity levels of brown trout stocks in watersheds draining into the Gulf of Finland and Archipelago Sea from Finland and Russia to create a management plan for Finnish sea trout stocks. The plan should utilize all the available genetic resources and potential breeding areas.

The goals of this research have been:

1. To reveal the intraspecific genetic population structure of southern Finnish and Russian brown trout populations in the Gulf of Finland area;
2. To measure the levels of genetic diversity, differentiation and relatedness between and within all populations;
3. To estimate the effective population sizes of the river populations;
4. To assess the impact of hatchery releases and small population sizes on the population genetic structure of Finnish anadromous brown trout stocks;
5. To compare Finnish sea trout stocks with native Russian stocks;
6. To study the formation of the population genetic structure in re-established and/or enhanced sea trout populations;
7. To prepare proposals for conservation and management for individual Finnish seat trout rivers.

In this report, the main goal is to describe the fine-level population structure of Finnish trout populations in the coastal river systems, as this information is especially valuable in management decision making at the local level. In practice, each sample was intially analysed separately to examine how the overall picture has been built and to check whether any clear distinction occurs among samples from separate tributaries. This might indicate a subpopulation structure resulting from isolation caused by migration barriers, natural differences in migration behaviour or the genetic effects of hatchery releases. The pooling of samples for the final calculations was carried out according to this preliminary analysis and it is also reported here. This work was financed by EU Interreg IV A Programme and project HEALFISH (Healthy fish stocks – indicators of successful river basin management) (2010–2013).

2. Material and Methods

2.1. DNA methods

Total genomic DNA was extracted from scale or tissue samples in 95% alcohol using the DNeasy Blood & Tissue Kit method (Qiagen). From each sample, 400 µl of liquid DNA was obtained. Variation was determined at 16 microsatellite loci (Table 1). For each sample, two multiplex PCR reactions were performed using the Qiagen Type-it Microsatellite kit in a 10 µl reaction volume with 3 µl of extracted DNA, 5 µl of kit master mix and primers with concentrations and dyes as presented in Table 1. PCR reactions were carried out PTC200 Thermal Cyclers (MJ Research), and the temperature profile of the PCR program was suggested in the Type-it Microsatellite kit manual. The annealing temperature was 56 °C.

Microsatellite genotypes were detected with an Applied Biosystems ABI 3130 automated DNA sequencer and analysed with GENEMAPPER Analysis Software version 4.0, with the size standard of Applied Biosystems GeneScan 500LIZ. Automatic outputs were manually checked.

Table 1. Microsatellite loci used for brown trout analysis. References, multiplexes, dyes and primer concentrations are also indicated.

	Locus	Reference	Multiplex plate	Dye	Primer concentration
1	BS131	Estoup et al., 1998	MP 1	VIC	0.03 µM
2	*OneU9*	Schribner et al., 1996	MP 2	VIC	0.03 µM
3	*SSa197*	O'Reilly et al., 1996	MP 1	NED	0.02 µM
4	*SSa289*	McConnell et al., 1995	MP 1	PET	0.30 µM
5	*Ssa407*	Cairney et al., 2000	MP 1	NED	0.15 µM
6	*SSa85*	McConnell et al., 1995	MP 2	VIC	0.02 µM
7	*Ssosl311*	Slettan et al., 1995	MP 2	NED	0.07 µM
8	*SSosl417*	Slettan et al., 1995	MP 1	PET	0.04 µM
9	*SSosl438*	Slettan et al., 1996	MP 2	VIC	0.07 µM
10	*SSsp1605*	Patterson et al., 2004	MP 2	NED	0.04 µM
11	*SSsp2201*	Patterson et al., 2004	MP 1	6-FAM	0.03 µM
12	*Str15INRA*	Estoup et al., 1993	MP 1	6-FAM	0.05 µM
13	*Str60INRA*	Estoup et al., 1993	MP 2	PET	0.04 µM
14	*Str73INRA*	Estoup et al., 1993	MP 1	VIC	0.04 µM
15	*Str85INRA*	Presa & Guyomard 1996	MP 2	6-FAM	0.40 µM
16	*Strutt58*	Poteaux 1995	MP 2	6-FAM	0.30 µM

2.2. Statistical analyses

The allele frequencies, genotype distributions and pairwise FST values (Weir and Cockerham 1984) were calculated with Genepop software, version 4.0.7 (Raymond and Rousset 1995, Rousset 2008) (http://kimura.univ-montp2.fr/~rousset/Genepop.htm). The diversity measures, i.e. the number of alleles, allelic richness, mean diversities and FIS values, were calculated with FSTAT version 2.9.3.2. (Feb. 2002) (Goudet 1995, Goudet 2001) (http://www2.unil.ch/popgen/softwares/fstat.htm). Analysis of the differences between samples was based on allele frequency differences, and was tested with FSTAT, which includes Bonferroni correction for multiple tests. Genetic diversity and allelic richness were compared between the stock groups with the two-sided randomization test of FSTAT.

Genetic distances between samples were calculated using Nei's DA distances (Nei et al. 1983). Phylogenetic trees were constructed using a neighbour-joining (NJ) algorithm (Saitou and Nei 1987, Takezaki 1998) with Populations 1.2.32 sofware (http://bioinformatics.org/~tryphon/populations/). Bootstrapping with 1 000 replicates was used to test the statistical strength of the branches. The trees were drawn with TreeView version 1.6.1 (Page 2000) (http://taxonomy.zoology.gla.ac.uk/rod/treeview.html).

The effective population size (Ne), and the number of fullsib families were calculated with COLONY software (version 2, May 2008) (Wang 2004, Wang and Santure 2009). The average pairwise relatedness was calculated with COANCESTRY software (version 1.0, December 1, 2008) (Wang 2007).

2.3. Brown trout samples

In all, 39 watersheds and 3430 individuals were analysed in the current work (Figure 1, Table 2). The samples included both anadromous and resident populations of each watershed to more closely examine the substructure within each river system and to invesitigate the potential isolation level between resident and anadromous parts of the populations. In some cases, isolation had been artificially created by dams, but in other cases it had occurred naturally and was a cause of differentiating evolution.

Most of the river systems (21) were on the Finnish coast. Six of the rivers crossed the border with Russia, such that the upper reaches of the rivers were located in Finland and the lower parts in Russia. Seven rivers were relatively native rivers on the Russian side. In addition, five hatchery stocks were analysed. These have either been used or are suspected to have been used in hatchery releases in the area, and might thus have caused gene flow into the local stocks (Table 2). The Russian samples were collected in the Interreg projects ISKALT and ISKALT II (Saulamo et al. 2007), as well as some previous Finnish samples, and this part of the data was updated here for 16 DNA microsatellite loci, from the previous 10 loci data sets. The Finnish population samples were obtained from rivers discharging into either the nearby Archipelago Sea or into the Gulf of Finland.

The sampled river basins in Finland are located in the Varsinais-Suomi, Uusimaa, Kymenlaakso or Etelä-Karjala, which represent three Centres for Economic Development, Transport and the Environment (ELY Centres): 1. ELY Centre for Southwest Finland (Varsinais-Suomi), 2. ELY Centre for Uusimaa (Uusimaa) and 3) ELY Centre for Southeast Finland (Kymenlaakso and Etelä-Karjala). Some extensive river systems were located in two ELY Centre areas.

The rivers are listed and numbered from west to east along the coast (Table 2). The data also include current information on migratory behaviour, and the populations have been classified as either anadromous or resident. In addition, the preliminary information has been used to classify the populations according to their level of originality as original (native), mixed by stockings or introduced, depending on their stocking history. The most interesting and valuable populations from the management point of view are those that are genetically diverse, anadromous and original. The size of the river systems varies considerably, and thus they were all initially treated separately to support river system-based management and to allow substructure analysis within each river system. Samples were then pooled according to the differentiation level within the river systems. For part of the analysis, only anadromous populations were included.

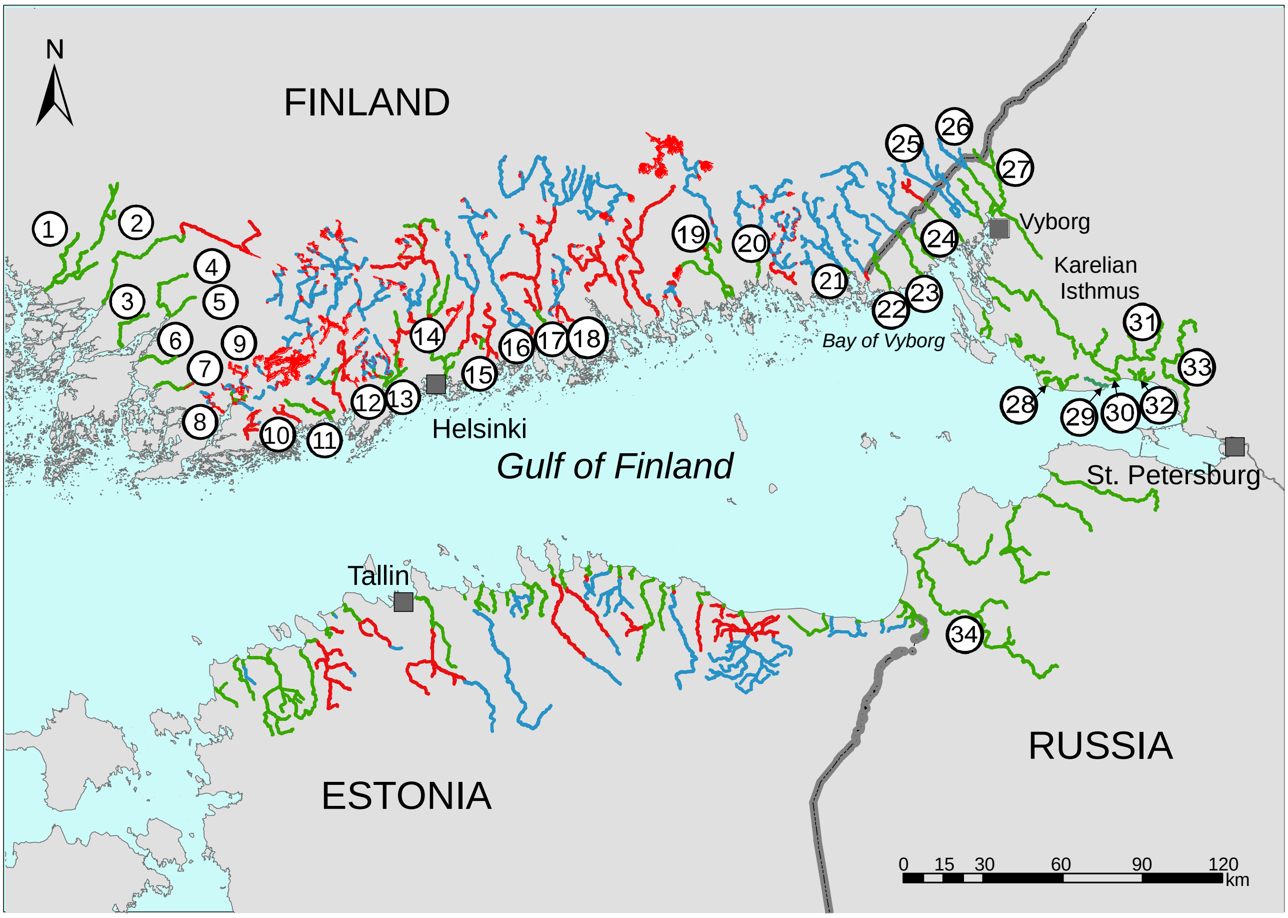

Figure 1. The sampled brown trout rivers in Finland and Russia. The colour of the river indicates its quality as a spawning site and potential environment for brown trout. Red: river is closed; blue: irregular reproduction occurs; and green: open river with regular natural production of brown trout populations. The following names and numbering of the rivers is the same as in Table 2: 1) Aurajoki, 2) Paimionjoki, 3) Purilanjoki, 4) Halikonjoki, 5) Uskelanjoki, 6) Punassuon Lohioja, 7) Kiskonjoki, 8) Fiskarsinjoki, 9) Karjaanjoki, 10) Ingarskilanjoki, 11) Siuntionjoki, 12) Mankinjoki, 13) Espoonjoki, 14) Vantaanjoki, 15) Sipoonjoki, 16) Mustijoki, 17) Porvoonjoki, 18) Koskenkylänjoki, 19) Kymijoki, 20) Summanjoki, 21) Virojoki, 22) Urpalanjoki, 23) Santajoki, 24) Vilajoki, 25) Rakkolanjoki, 26) Mustajoki, 27) Kilpeenjoki, 28) Notkopuro, 29) Inojoki, 30) Pikkuvammeljoki, 31) Vammeljoki, 32) Kuokkalanpuro, 33) Rajajoki (Siestarjoki) and 34) Luga.

Table 2. Analyzed brown trout samples from Finland and Russia. The brown trout juvenile samples, sampled river, tributary or area, country of origin, origin of samples and number of samples used for microsatellite analysis are presented. The migration behaviour, either anadromous or resident (freshwater), and the known stocking history are also indicated.

No	River	Country	Tributary	Year	N	Migr.	Originality
ELY Centre for Southwest Finland							
1	Aurajoki	FIN		2006	37	Anad.	Introduced
2	Paimionjoki	FIN	Vähäjoki, Karhunoja	2004, 2008	22	Anad.	Original
3	Purilanjoki	FIN		2011	15	Anad.	Original
4	Halikonjoki	FIN	Main stream, Kuusjoki, Somer-oja	2008	30	Anad./Resid.	Original
5	Uskelanjoki	FIN	Pitkäkoski, Kaukolankoski, Haukkalankoski	2007	19	Anad.	Original, Introduced
	Uskelanjoki		Hitolanjoki, Myllykoski	2007	15	Anad.	Original, Introduced
	Uskelanjoki		Hitolanjoki, Satakoski	2007	16	Resid.	Original, Introduced
	Uskelanjoki		Terttilänjoki	2007	7	Anad.	Original, Introduced
6	Punassuon Lohioja	FIN		2011	16	Resid.	Original
7	Kiskonjoki	FIN	Latokartanonkoski	2010	29	Anad.	Mixed
	Kiskonjoki		Myllyjoki	2010	15	Resid.	Mixed
	Kiskonjoki		Aneriojoki, Varesjoki-Huhdanoja, Koorlan Lohioja	2010	42	Resid.	Original
	Kiskonjoki-Perniönjoki		Juottimenoja-Piilioja, Pakapyölin Lohioja	2008	50	Anad.	Original
	Kiskonjoki-Perniönjoki		Kylmässuonoja-Metsänoja	2008	25	Resid.	Original

Table 2 continues on the next page.

Table 2. Continued.

No	River	Country	Tributary	Year	N	Migr.	Originality
ELY Centre for Uusimaa							
8	Fiskarsinjoki	FIN	Main branch	2010	50	Anad.	Introduced
			Risslaån	2010	20	Resid.	Introduced
9	Karjaanjoki	FIN	Mustionjoki; Mossabäcken	2001	23	(Anad.)	Original
	Karjaanjoki		Nummenjoki, Pitkiönjoki; Myllykoski, Santsillanoja, Pajasillanoja, Kivanoja	2001	59	Resid.	Original, Mixed
	Karjaanjoki		Nummenjoki, Pusulanjoki, Räpsänjoki	2003	26	Resid.	Original, Mixed
	Karjaanjoki		Nuijajoki; Käyräkoski, Jyrkänkoski, Porraskoski, Korkeakoski	2003	63	Resid.	Mixed, Introduced
	Karjaanjoki		Karjaanjoki, Saavajoki	2003	57	Resid.	Mixed, Introduced
	Karjaanjoki		Vihtijoki	2004	58	Resid.	Original, Mixed
	Karjaanjoki		Vihtijoki, Hiiskula	2006	50	Resid.	Original, Mixed
	Karjaanjoki		Vihtijoki, Tammerkoskenoja	2009, 2010	55	Resid.	Original, Mixed
10	Ingarskilanjoki	FIN	Main stream,Pärthyvelbäcken, Krämars	2005	192	Anad.	Original
11	Siuntionjoki	FIN	Kirkkojoki, Lempansån	2010	54	Anad. Resid.	Original
	Siuntionjoki		Passilankoski	2010	16	Anad.	Original
12	Mankinjoki	FIN	Espoonkartanonkoski	2008, 2010	24	Anad.	Original
	Mankinjoki		Gumbölenjoki; Mynttilänkoski	2005, 2010, 2011	70	Anad.	Original
	Mankinjoki		Gumbölenjoki; Myllykoski, Karhusuonpuro (2 ind.)	2008	39	Anad.	Original
	Espoonjoki	FIN	Glomsinjoki, Espoontienkoski, Kehä III, Myllykoski	2008, 2010	66	Anad.	Original
	Espoonjoki		Ryssänniitunoja	2008	21	Resid.	Original
	Espoonjoki		Glimsinjoki, Espoonjoki main stream (3 ind.)	2008	9	Anad.	Original

Table 2 continues on the next page.

No	River	Country	Tributary	Year	N	Migr.	Originality
14	Vantaanjoki, lower reaches	FIN	Vantaankoski, Pitkäkoski, Ruutinkoski	2010	62	Anad.	Mixed, Introduced
	Vantaanjoki, middle reaches		Nukarinkoski	2010	88	Anad.	Mixed, Introduced
	Vantaanjoki, upper reaches		Toromäenkoski, Käräjäkoski	2010	101	Resid. (Anad.)	Original
	Vantaanjoki, tributary 1		Longinoja	2010	57	Anad.	Introduced
	Vantaanjoki, tributary 2		Palojoki/Rannikonmäki	2010	53	Anad.	Introduced
	Vantaanjoki, tributary 2		Palojoki, Juvankoski	2011	54	Anad.	Introduced
	Vantaanjoki, tributary 3		Lepsämänjoki/ Myllypuro	2011	55	Resid.	Original, Introduced
	Vantaanjoki, tributary 4		Luhtajoki, Matkunoja	2011	14	Resid.	Original
	Vantaanjoki, tributary 5		Epranoja	2001	38	Resid.	Original
15	Sipoonjoki	FIN	Ritobäcken, Byabäcken	2010	46	Anad.	Original
16	Mustijoki	FIN	Kalkinoja	2011	31	(Anad.) Resid.	Original
17	Porvoonjoki	FIN	Vähäjoki, Ylösjoki	2010	51	Resid.	Original
18	Koskenkylänjoki	FIN	Hammarfors, Kvarnfors, Käkikoski, Sahakoski, Seppäläishuopinkoski	2010	31	Anad.	Introduced
ELY Centre for Southeast Finland							
19	Kymijoki	FIN	Kyminkartanonkoski, Kokonkoski, Pykinkoski, Koivukoski, Kotokoski, Martinkoski	2006, 2010	26	Anad.	Mixed
20	Summanjoki	FIN	Mainstream	2008	22	Anad.	Introduced
	Summanjoki		Kelkanjoki	2010	73	Resid.	Introduced
	Summanjoki		Sippolanjoki	2004	50	Resid.	Introduced
21	Virojoki	FIN	Saarasjärvenoja	2004, 2005, 2008	80	Anad. Resid.	Original
	Virojoki	FIN	Virojärvi, upper reaches	2008	61	Resid.	Introduced
	Border rivers						
22	Urpalanjoki	FIN/RUS		2006, 2010	40	Anad.	Original
23	Santajoki	FIN/RUS		2006	19	Anad.	Original
24	Vilajoki	FIN/RUS	Käpylänkoski, Pappilankoski	2006, 2010	63	Resid.	Introduced, Mixed
25	Rakkolanjoki	FIN/RUS		2006	13	Anad.	Original
26	Mustajoki	FIN/RUS		2006, 2007, 2008	336	Anad.	Original
	Mustajoki Kananoja	FIN/RUS		2006	50	Anad.	Original
27	Kilpeenjoki	FIN/RUS		2006	11	Anad.	Original

No	River	Country	Tributary	Year	N	Migr.	Originality
Russian rivers							
28	Notkopuro	RUS		2006	51	Anad.	Original
29	Inojoki	RUS		2006	25	Anad.	Original
30	Pikkuvammeljoki	RUS		2006	50	Anad.	Original
31	Vammeljoki	RUS		2006	39	Anad.	Original
32	Kuokkalanpuro	RUS		2006	23	Anad.	Original
33	Rajajoki	RUS		2006	21	Anad.	Original
34	Luga	RUS		2006	64	Anad.	Original
Hatchery stocks							
1	Lapväärtin-Isojoki	FIN	Laukaa hatchery	2006–2008	98	Anad.	Hatchery
2	Rautalamminreitti	FIN	Laukaa hatchery	2006	98	Resid.	Hatchery
3	Luutajoki	FIN	Laukaa hatchery	2004	40	Resid.	Hatchery
4	Gotland	SWE	Själsöån, Lummelundaån, Åland hatchery	2004–2005	60	Anad.	Hatchery
5	Denmark	DAN	Kolding hatchery	2011	46	Anad.	Hatchery
	Total				3430		

3. Results

3.1. Genetic diversity within populations

The number of actually observed alleles in the brown trout samples varied considerably from 27 in Purilanjoki to 182 in the Danish hatchery population (Table 3). As the number of observed alleles depends on the sample size, which varied greatly from 11 for Kilpeenjoki to 336 for Mustajoki, the sample-size-standardized allelic richness was used to create comparable numbers for allelic diversity. When all populations were included, allele richness was standardized for 11 individuals, and it then varied from 1.67 to 7.43. For larger samples, a measure for 30 individuals was calculated to increase the range of variation (2.62–10.30). The maximum value of allele richness was recorded for the Danish population from the Kolding hatchery (7.43 for 11 individuals and 10.30 for 30 individuals). It has been suspected that this type of trout was released into Finnish rivers in the 1960s, and because of this it has been included as a reference sample.

The highest allele richnesses in Finnish populations (over 6.0 alleles for 11 individuals) were measured in mixed populations, such as Fiskarsinjoki, the middle and upper reaches of the River Vantaanjoki and the upper reaches of Summanjoki. Into the next category (over 5.0 alleles for 11 individuals) belonged populations from the rivers Aurajoki, Kiskonjoki-Latokartanonkoski, Kiskonjoki-Perniönjoki, Karjaanjoki-Nummenjoki branch, Mankinjoki, the lower reaches of Vantaanjoki, Kymijoki, and the main branch of Summanjoki in Finland. Four out of seven native Russian populations belonged to this relatively high diversity class: Notkopuro, Inojoki, Vammeljoki and Kuokkalanpuro. The hatchery reference samples from the Isojoki and Rautalamminreitti populations, as well as the Swedish population from Gotland additionally belonged to this category.

The lowest allelic richness values were measured for two populations in the rivers of Varsinais-Suomi: Purilanjoki (1.67, minimum) and Punasuon Lohioja. Low values were also observed for populations in the rivers Mustijoki and Virojoki-Saarasjärvenoja. These all are small populations that only occur at restricted sites.

The mean diversity (heterozygosity) within populations varied from 0.22 to 0.72, with a mean of 0.62. This is also a very marked range, being more than three times greater for the most diverse populations than for the least diverse ones. The diversity levels correlated well with the allelic richness estimates and were highest for the same populations. Further pooling of samples from the same river systems would probably increase the values for some cases. The presented pooling of samples was based on information migration obstacles and on river system analysis described below.

When the diversity levels for the population groups classified as anadromous or resident were compared, no differences in their diversity levels could be seen. The hatchery stocks were excluded from this analysis. The mean diversity for both groups was 0.61, and the allelic richness estimates were 4.6 (for 11 individuals) and 6.0 (for 30 individuals) for the anadromous and 4.5 (for 11 individuals) and 5.9 (for 30 individuals) for the resident group.

When the five geographical river groups were compared, there was a tendency of increasing genetic diversity towards the east. However, the only statistically significant differences were between group 1 (ELY Centre for Southwest Finland, Varsinais-Suomi) and the two other groups. Group 1 had on average a lower genetic diversity (0.56) than group 2 (0.65, ELY Centre for Uusimaa, P-value 0.0003), and group 5 (0.65, Russian rivers, P-value 0.02). Group 1 mainly consisted of small native populations, most of which were also geographically isolated.

In general, the sampled populations were not always in Hardy-Weinberg equilibrium for known reasons, which was seen as FIS deviations (Table 3). Population borders in the water systems were not known, and fish from different breeding populations might therefore have been pooled in sampling, presumably causing a deficiency of heterozygosity. Stocking and mixing of populations in the wild temporarily causes an excess of heterozygosity and thus an excess of heterozygotes when compared to the equilibrium situation. Therefore, in the testing of population differentiation, a Hardy-Weinberg equilibrium was not assumed, but the test was conducted by randomizing genotype distributions. Interestingly, there were fewer deviations from the H-W equilibrium in the native Russian populations.

Table 3. Diversity within sampled Finnish and Russian brown trout populations. The number in front of the river name denotes the watershed number. The mean number of individuals analysed over 16 DNA microsatellite loci, number of observed alleles (N), allelic richness for 11 and 30 individuals, mean diversity (DIV), FIS, and its significance are presented.

Population	Mean N/ locus	N all	All Rich for 11 ind.	All Rich for 30 ind.	Mean DIV	FIS
1AurajokiA	36.8	121	5.9	7.3	0.68	0.025
2Paimionjo	18.8	79	4.3	-	0.59	-0.097**
3Purilanjo	14.9	27	1.7	-	0.22	-0.166*
4Halikonjo	29.8	88	4.6	-	0.63	0.028
5Uskelanjo	55.6	109	4.3	5.8	0.50	0.068***
6Punassuon	16.0	39	2.4	-	0.39	0.001
7KiskoLato	28.8	98	5.0	-	0.65	0.019
7KiskoMyll	14.8	67	4.0	-	0.61	0.023
7KiskoKooR	38.1	65	3.4	4.0	0.51	0.138***
7KiskoPern	49.4	99	4.3	5.6	0.56	0.132***
7KiskPerMe	24.6	106	5.7	-	0.71	-0.001
Mean Southwest	*29.8*	*81.6*	*4.1*	*5.7*	*0.55*	
8FiskarsAI	66.6	139	6.0	7.7	0.70	0.040**
9KarjaMust	23.0	53	3.0	-	0.52	-0.159***
9KarNumRO	84.7	131	5.6	7.1	0.69	0.068***
9KarNuiRM	63.0	114	4.9	6.2	0.64	0.032*
9KarjaSaav	56.7	108	4.9	6.1	0.61	0.090***
9KarjaViht	157.3	98	4.3	5.1	0.61	0.099***
10Ingarski	186.4	97	4.5	5.2	0.64	0.043***
11SiuntKir	53.6	82	4.2	4.8	0.66	-0.041*
11SiuntPas	14.9	79	4.7	-	0.68	0.068*
12Mankinjo	129.9	121	5.2	6.4	0.69	0.018
13Espoonjo	72.0	95	4.8	5.6	0.64	-0.009*
12EspooRys	24.0	57	3.1	-	0.48	-0.001
14LoVantaa	117.8	156	5.9	7.7	0.71	0.061***
14MiVantaa	87.5	144	6.0	7.6	0.72	0.019
14UpVantaa	207.0	147	6.3	7.9	0.73	0.145***
14PaVantaa	106.8	97	4.5	5.4	0.63	0.034*
15SipooAO	45.9	59	3.0	3.5	0.55	-0.274***
16Mustijok	31.0	42	2.4	2.6	0.39	-0.303***
17Porvoonj	51.0	93	4.4	5.4	0.64	-0.033
18Koskenky	30.9	80	4.2	5.0	0.62	-0.005
Mean Uusimaa	*80.5*	*99.6*	*4.6*	*5.8*	*0.63*	

Table3. Continued.

Population	Mean N/ locus	N all	All Rich for 11 ind.	All Rich for 30 ind.	Mean DIV	FIS
19Kymijoki	25.9	121	5.9	-	0.70	0.038
20SummaMai	43.0	110	5.3	6.6	0.68	0.056***
20SummUppb	99.0	147	6.1	7.8	0.72	0.051***
21Virojoki	80.0	62	2.9	3.4	0.48	-0.046*
21ViroUppR	61.0	81	4.3	4.9	0.63	-0.071***
Mean Southeast	*61.8*	*104.2*	*4.9*	*5.7*	*0.64*	
22UrpalaFI	39.8	134	6.2	7.9	0.73	0.001
23Santajok	19.0	76	4.4	-	0.62	-0.063*
24Vilajoki	62.6	93	4.3	5.3	0.64	-0.028
25Rakkolan	13.0	54	3.3	-	0.52	-0.107*
26Mustajoki	375.9	127	4.7	5.7	0.63	0.009
27Kilpeenjoki	11.0	58	3.6	-	0.50	-0.265***
Mean Border rivers	*86.9*	*90.3*	*4.4*	*6.3*	*0.61*	
28Notkopuro	50.5	121	5.6	7.0	0.67	0.016
29InojokiR	24.9	109	5.7	-	0.68	-0.018
30Pikkuvam	49.2	109	4.9	6.3	0.60	0.038*
31Vammeljo	38.9	116	5.4	6.9	0.66	0.000
32Kuokkala	22.8	106	5.5	-	0.67	0.036
33Rajajoki	20.2	82	4.5	-	0.64	0.072*
34LugaRUSA	58.8	112	4.9	6.2	0.65	0.051**
Mean Russia	*37.9*	*107.9*	*5.2*	*6.6*	*0.65*	
ISOJOKIANA	97.9	143	5.8	7.6	0.68	0.061***
LUUTAJOKIR	40.0	81	4.1	4.9	0.58	0.017
DENMARK	46.0	182	7.4	10.3	0.77	0.019
RAUTALAMMI	97.9	157	5.5	7.4	0.64	0.023*
GOTLANDSWE	59.9	128	5.6	7.1	0.70	-0.027
All over	*62.5*	*100.0*	*4.7*	*6.2*	*0.62*	
Min	11.0	27	1.7	2.6	0.22	
Max	375.9	182	7.4	10.3	0.77	

3.2. Effective population size and the relatedness within populations

The genetically effective population sizes of the populations understandably varied because of the varying sample sizes, but were rarely over 50, which is the recommended minimum size for individual populations in hatchery breeding. Effective sizes over 50 were only observed for populations of the rivers Vantaanjoki (lower section), Kymijoki, Summanjoki (upper section), Mustajoki and Russian Notkopuro (Table 4).

The sample size independent Ne/N ratio was used as an indirect measure of the relatedness within populations. It is commonly known to be usually less than one in wild populations, often being roughly about half of the actual size, and it can be increased with organized mating or mixing of populations. It can be maximally two, when the effective size is twice the true size. Low Ne/N values of less than 0.4 indicated high relatedness in populations of the rivers Purilanjoki, Karjaanjoki-Mustijoki, Karjaanjoki-Vihtijoki, Ingarskilanjoki, Mankinjoki, Espoonjoki, Upper Vantaanjoki, Vantaanjoki-Palojoki, Sipoonjoki, Mustijoki, Porvoonjoki, Virojoki-Saarasjärvenoja, Vilajoki and Mustajoki.

For the Russian populations, the Ne/N ratio was always above 0.4 and even as high as 1.15 on average. Among these populations, the Luga River was an exception, as its Ne/N ratio was only 0.41. For ordinary hatchery stocks the ratio was also close to 1 as result of organized mating, except for the trout population from Gotland, for which the founder number has probably been small.

The estimated number of full-sib families in the samples can also be used to assess the width of the genetic background in the population. In cases where sampling has been representative, the number of families gives an idea of the true situation in the river. The number of families was often less than 20, and in some cases even less than ten (Purilanjoki, Karjaanjoki-Mustionjoki, Rakkolanjoki and Kilpeenjoki). For Purilanjoki and Mustionjoki, the Ne/N ratio was also low, so there were hardly more families involved in the population. For the Russian rivers Rakkolanjoki and Kilpeenjoki, the Ne/N ratio was relatively high so the small family number was probably explained by the small sample sizes, which were both under 15 fish. The newly founded Mustajoki broodstock had as many as 258 families, although the Ne/N ratio was only 0.35. For Finnish rivers, sampling was more likely to be representative for the whole population, whereas for Russian rivers, sampling was more random and the sampled fish may represent only a fraction of the spawning stock.

The mean relatedness is 0.5 for full-sibs, 0.25 for half-sibs, 0.125 (1/8) for first cousins and 0.031 (1/128) for second cousins. The relatedness of two populations exceeded that of the first cousin level (Purilanjoki, Espoonjoki-Ryssänniitunoja). Values over 0.10 were, however, also observed for four other populations: Karjaanjoki-Mustionjoki, Kiskojoki-Perniönjoki branch, Mustijoki and the Russian Vilajoki. Almost equally high relatedness was also observed in samples from the rivers Halikonjoki, Virojoki-Saarasjärvenoja and Kilpeenjoki. For the native Russian populations, the mean relatedness was 0.045, with the River Luga population having the highest value of 0.062. Excluding the River Luga, the mean was only 0.042, which indicates the level in the wild state for these relatively small rivers.

Table 4. The actual sample size (N) and effective size (Ne) with its 95% confidence interval (95% CI), the Ne/N ratio and the number of full-sib families in the brown trout samples from Finnish and Russian rivers draining into the Gulf of Finland and Archipelago Sea.

Population	N sample	Ne	95% CI	Ne/N	N Fam	Mean Relatedness %
1Aurajoki	37	34	22–58	0.92	28	4.1
2Paimionjoki	22	11	6–27	0.50	12	7.4
3Purilanjoki	15	5	2–20	0.33	6	16.7
4Halikonjoki	30	14	8–31	0.47	14	9.8
5Uskelanjoki	57	39	23–61	0.68	47	6.3
6Punassuon	16	19	10–43	1.19	14	8.7
7KiskoLatok	29	16	8–35	0.55	16	6.9
7KiskoMylly	15	21	10–48	1.40	15	6.2
7KiskoKooR	42	23	13–43	0.55	33	8.3
7KiskoPerniö	50	21	12–39	0.42	32	12.4
7KiskPerMet	25	15	8–34	0.60	17	2.2
Mean Southwest		*16.0*		0.69	*21.3*	*8.1*

Table 4 continues.

Population	N sample	Ne	95% CI	Ne/N	N Fam	Mean Relatedness %
8Fiskarsinjoki	68	45	30–72	0.66	47	4.3
9KarjaMust	23	6	3–20	0.26	8	10.5
9KarjaNumRO	85	35	22–56	0.41	45	5.8
9KarjaNuiRM	63	44	29–70	0.70	45	5.6
9KarjaSaava	57	23	13–42	0.40	28	6.6
9KarjaVihtij	163	40	27–62	0.25	105	7.6
10Ingarskilan	192	45	31–69	0.23	86	5.7
11SiuntioKirk	54	28	17–50	0.52	38	7.4
11SiuntioPas	16	15	7–37	0.94	15	6.3
12Mankinjoki	133	33	21–55	0.25	60	5.8
13Espoonjoki	72	12	7–26	0.17	22	7.4
12EspoonRyssä	24	13	7–30	0.54	15	14.1
14LowVantaa	119	86	62–119	0.72	91	4.4
14MiddleVantaa	88	50	34–77	0.57	67	4.3
14UppVantaa	208	33	22–55	0.16	89	6.6
14PaloVantaa	107	32	21–53	0.30	48	6.8
15Sipoonjoki	46	11	6–26	0.24	17	6.3
16Mustijoki	31	6	2–20	0.19	12	10.7
17Porvoonjoki	51	19	11–38	0.37	24	7.6
18Koskenkylänjoki	31	28	16–51	0.90	26	4.8
Mean		*27.1*		*0.44*	*44.4*	*6.9*
19Kymijoki	26	52	29–107	2.00	23	2.47
20SummajokiMain	43	28	17–50	0.65	27	5.06
20SummUppb	99	61	43–9	0.62	76	4.42
21Virojoki	80	25	15–44	0.31	47	9.51
21ViroUppR	61	40	27–65	0.66	53	5.97
Mean		*41.2*		*0.85*	*45.2*	*5.5*
22Urpalanjoki	40	35	22–61	0.88	33	4.1
23Santajoki	19	14	7–34	0.74	13	7.7
24Vilajoki	63	11	6–28	0.17	23	10.4
25Rakkolanjoki	13	13	6–40	1.00	9	7.2
26Mustajoki	382	133	107–169	0.35	258	5.1
27Kilpeenjoki	11	8	4–26	0.73	5	8.9
Mean		*35.7*		*0.64*	*56.8*	*7.2*
28Notkopuro	51	61	41–92	1.20	45	3.6
29Inojoki	25	24	13–49	0.96	17	4.3
30Pikkuvammeljoki	50	28	17–49	0.56	36	5.3
31Vammeljoki	39	48	30–80	1.23	33	4.4
32Kuokkalanpuro	23	44	26–99	1.91	20	3.2
33Rajajoki	21	37	21–76	1.76	18	4.7
34Luga	64	26	16–46	0.41	38	6.2
Mean		*38.3*		*1.15*	*29.6*	*4.5*

Table 4.Continued.

Population	N sample	Ne	95% CI	Ne/N	N Fam	Mean Relatedness %
ISOJOKI	98	88	63–121	0.90	82	3.8
LUUTAJOKI	40	36	27–61	0.90	36	5.7
DENMARK	46	88	57–136	1.91	46	2.5
RAUTALAMMINR.	98	102	72–137	1.04	89	3.5
GOTLAND SWE	60	19	11–38	0.32	37	5.3
Mean		*66.6*		*1.01*	*58.0*	*4.2*

3.3. Genetic differentiation among populations

Genetic differentiation in allele frequencies among the listed populations (Table 5) was always significant and often highly significant. After strict Bonferroni correction for multiple tests for the genotype differentiation, a non-significant difference was only recorded for four pairs of stocks:

Aurajoki – Fiskarsinjoki (FST 0.01),
Ingarskilanjoki – Koskenkylänjoki (FST 0.01),
Vantaanjoki_Palojoki – Koskenkylänjoki (FST 0.01) and
Isojoki – Kymijoki (FST 0.01)

The difference was only significant at the 5% nominal level for three other stock pairs,
Paimionjoki – Siuntionjoki (FST 0.11),
Kymijoki – Summanjoki (FST 0.02) and
Inojoki – Kuokkalanpuro (FST 0.02).

In addition, differences were not always significant within river systems. These analyses are reported in regional results. Despite the frequently significant differences between populations, there were several stock pairs for which the FST value was low, and even below 0.05 (Table 5). Most of these were cases in which clear genetic effects of hatchery releases could be assumed (Table 5), as known hatchery releases were carried out in just these rivers. The Aurajoki trout has been released into the River Fiskarsinjoki, Koskenkylänjoki has been enhanced with Ingarsilanjoki trout, which explains their identity, and Ingarskilanjoki trout have also been released into Vantaanjoki, and especially into Palojoki. Isojoki trout have regularly been released into the River Kymijoki, and they have additionally been released into Summanjoki. The Russian population pair of the rivers Inojoki and Kuokkalanpuro was the only native brown trout population pair for which no statistically significant difference could be observed. Thus, they were similar for natural reasons, either because of common historical reasons or more likely as a result of currently high gene flow levels.

From the released populations, Ingarskilanjoki had very high similarity with Mankinjoki, the lower parts of Vantaanjoki, the Vantaanjoki Palojoki tributary and Koskenkylänjoki. Ingarskilanjoki trout are known to have been released into other rivers, in addition to Mankinjoki (Table 5). Between Mankinjoki and Ingarskilanjoki, the similarity may simply be a result of a common local history. Isojoki trout had a high degree of similarity with populations from Fiskarsinjoki, Karjaanjoki-Nummenjoki, Espoonjoki, the lower and middle reaches of Vantaanjoki, Kymijoki and the mainstream population of Summanjoki. The Luutajoki hatchery stock had only some similarity with the population in the upper reaches of Summanjoki (FST = 0.08). The Danish trout did not have a very strong similarity with any of the Finnish populations, but nevertheless some similarity with many of them. Some of these were rivers into which the Danish trout have certainly not been released, so no final conclusions could be made on the basis of this analysis. Some more detailed analytical methods, such as the STRUCTURE program (Pritchard and Wen 2004), might offer some insight into the case, if actual traces could any longer be found so many generations after the releases. The previous releases of Danish trout currently have no effect on the management plan or valuation of Finnish trout populations. The Finnish Rautalamminreitti trout did not show very strong similarities with the natural stocks, either. The closest was the population inhabiting the upper reaches of Summanjoki (FST = 0.06). This population also appeared similar to the Swedish trout from the island of Gotland, but this must be a random event. Ingarskilanjoki and Isojoki are known to be the most commonly released stocks in southern Finland, so the similarities found with these stocks are to be expected.

Table 5. Pairwise FST estimates between brown trout samples. FST values from 0.01 to 0.04 are highlighted in red and from 0.05 to 0.08 in yellow.

Pop	1Aurajok	2Paimion	3Purilan	4Halikon	5Uskelan	6Punassu	7KiskoLa	7KiskoMy	7KiskoKo	7KiskoPe	7KiskPer	8Fiskars	9KarjaMu	9KarNumR	9KarNuiR	9KarjaSa	9KarjaVi	10Ingars	11SiuntK	11SiuntP	12Mankin	13Espoon	12EspooR	14LoVant	14MiVant	14UpVant	14PaVant	15SipooA	16Mustij
2Paimion	0.08																												
3Purilan	0.33	0.31																											
4Halikon	0.10	0.18	0.40																										
5Uskelan	0.16	0.17	0.38	0.23																									
6Punassu	0.27	0.33	0.58	0.31	0.34																								
7KiskoLa	0.03	0.13	0.38	0.12	0.23	0.30																							
7KiskoMy	0.13	0.17	0.42	0.20	0.31	0.38	0.15																						
7KiskoKo	0.18	0.18	0.32	0.23	0.10	0.35	0.23	0.27																					
7KiskoPe	0.12	0.14	0.34	0.24	0.26	0.33	0.16	0.21	0.25																				
7KiskPer	0.05	0.07	0.28	0.12	0.16	0.25	0.07	0.13	0.15	0.10																			
8Fiskars	0.01	0.09	0.31	0.11	0.17	0.25	0.03	0.13	0.19	0.12	0.04																		
9KarjaMu	0.24	0.28	0.47	0.30	0.36	0.40	0.28	0.28	0.34	0.27	0.22	0.20																	
9KarNumR	0.07	0.10	0.32	0.15	0.22	0.31	0.09	0.12	0.22	0.16	0.08	0.07	0.23																
9KarNuiR	0.07	0.11	0.32	0.14	0.20	0.32	0.08	0.14	0.20	0.18	0.07	0.06	0.26	0.09															
9KarjaSa	0.08	0.13	0.35	0.13	0.13	0.31	0.13	0.21	0.16	0.20	0.10	0.09	0.29	0.14	0.12														
9KarjaVi	0.13	0.14	0.30	0.16	0.09	0.28	0.17	0.23	0.08	0.21	0.11	0.14	0.30	0.19	0.15	0.11													
10Ingars	0.13	0.13	0.28	0.18	0.23	0.30	0.12	0.19	0.23	0.17	0.08	0.11	0.27	0.15	0.14	0.19	0.20												
11SiuntK	0.16	0.18	0.34	0.18	0.22	0.31	0.18	0.22	0.22	0.23	0.14	0.15	0.25	0.15	0.19	0.16	0.18	0.20											
11SiuntP	0.09	0.11	0.31	0.12	0.20	0.30	0.10	0.17	0.17	0.15	0.04	0.08	0.26	0.12	0.12	0.12	0.13	0.07	0.16										
12Mankin	0.09	0.10	0.24	0.14	0.20	0.28	0.09	0.15	0.19	0.13	0.05	0.07	0.20	0.09	0.10	0.14	0.16	0.04	0.15	0.05									
13Espoon	0.07	0.10	0.33	0.15	0.24	0.31	0.07	0.14	0.25	0.14	0.07	0.06	0.24	0.07	0.08	0.15	0.20	0.11	0.18	0.11	0.07								
12EspooR	0.15	0.16	0.46	0.25	0.31	0.43	0.20	0.21	0.33	0.22	0.17	0.14	0.33	0.16	0.16	0.22	0.25	0.22	0.25	0.21	0.16	0.12							
14LoVant	0.05	0.07	0.25	0.11	0.18	0.25	0.06	0.11	0.18	0.11	0.03	0.04	0.20	0.07	0.08	0.12	0.15	0.03	0.15	0.04	0.02	0.04	0.14						
14MiVant	0.06	0.07	0.24	0.12	0.18	0.26	0.06	0.09	0.16	0.11	0.03	0.05	0.19	0.06	0.07	0.10	0.13	0.05	0.14	0.04	0.03	0.06	0.15	0.02					
14UpVant	0.06	0.09	0.25	0.11	0.14	0.23	0.08	0.13	0.13	0.13	0.05	0.06	0.21	0.08	0.07	0.09	0.10	0.11	0.11	0.07	0.07	0.09	0.16	0.06	0.05				
14PaVant	0.15	0.14	0.28	0.20	0.23	0.31	0.15	0.20	0.23	0.18	0.09	0.13	0.27	0.16	0.16	0.19	0.19	0.02	0.20	0.07	0.05	0.13	0.22	0.04	0.06	0.12			
15SipooA	0.18	0.19	0.40	0.23	0.33	0.38	0.17	0.21	0.31	0.25	0.15	0.16	0.30	0.13	0.19	0.24	0.26	0.12	0.22	0.17	0.12	0.14	0.28	0.10	0.10	0.14	0.14		
16Mustij	0.32	0.35	0.50	0.40	0.40	0.54	0.36	0.30	0.36	0.39	0.32	0.30	0.42	0.28	0.31	0.30	0.30	0.34	0.33	0.36	0.29	0.33	0.42	0.28	0.23	0.25	0.32	0.37	
17Porvoo	0.15	0.20	0.37	0.19	0.26	0.33	0.17	0.19	0.25	0.22	0.13	0.13	0.23	0.15	0.15	0.19	0.20	0.19	0.19	0.17	0.14	0.17	0.27	0.13	0.12	0.12	0.20	0.21	0.32

Table 5. Continued.

Pop	1Aurajok	2Paimion	3Purilan	4Halikon	5Uskelan	6Punassu	7KiskoLa	7KiskoMy	7KiskoKo	7KiskoPe	7KiskPer	8Fiskars	9KarjaMu	9KarNumR	9KarNuiR	9KarjaSa	9KarjaVi	10Ingars	11SiuntK	11SiuntP	12Mankin	13Espoon	12EspooR	14LoVant	14MiVant	14UpVant	14PaVant	15SipooA	16Mustij
18Kosken	0.15	0.15	0.33	0.19	0.24	0.34	0.14	0.22	0.23	0.20	0.08	0.13	0.30	0.15	0.15	0.19	0.20	0.01	0.20	0.07	0.05	0.13	0.26	0.04	0.06	0.10	0.01	0.13	0.37
19Kymijo	0.06	0.10	0.32	0.13	0.22	0.32	0.09	0.09	0.21	0.14	0.07	0.06	0.21	0.05	0.08	0.14	0.17	0.13	0.15	0.11	0.06	0.05	0.14	0.05	0.05	0.08	0.14	0.16	0.32
20SumaM	0.06	0.10	0.31	0.14	0.22	0.30	0.09	0.10	0.23	0.15	0.07	0.06	0.23	0.06	0.08	0.13	0.17	0.13	0.15	0.11	0.08	0.06	0.14	0.06	0.05	0.08	0.15	0.15	0.31
20SumUp	0.04	0.08	0.26	0.10	0.16	0.24	0.06	0.08	0.15	0.12	0.05	0.04	0.20	0.05	0.07	0.09	0.12	0.12	0.13	0.07	0.07	0.07	0.15	0.05	0.03	0.04	0.13	0.14	0.24
21Virojo	0.26	0.29	0.45	0.30	0.41	0.43	0.28	0.29	0.36	0.31	0.24	0.24	0.36	0.22	0.22	0.31	0.30	0.26	0.29	0.28	0.23	0.24	0.33	0.21	0.20	0.19	0.29	0.30	0.44
21ViroUp	0.13	0.18	0.31	0.18	0.21	0.31	0.15	0.19	0.16	0.21	0.12	0.13	0.27	0.15	0.13	0.14	0.14	0.19	0.19	0.15	0.15	0.18	0.26	0.13	0.10	0.08	0.19	0.22	0.29
22Urpala	0.06	0.08	0.25	0.10	0.17	0.25	0.07	0.10	0.14	0.11	0.03	0.05	0.20	0.08	0.08	0.10	0.11	0.10	0.12	0.05	0.05	0.08	0.16	0.04	0.04	0.04	0.10	0.15	0.29
23Santaj	0.11	0.14	0.28	0.18	0.23	0.34	0.15	0.18	0.16	0.16	0.09	0.11	0.24	0.15	0.14	0.16	0.15	0.16	0.18	0.11	0.11	0.16	0.25	0.10	0.10	0.07	0.17	0.23	0.36
24Vilajo	0.13	0.17	0.34	0.18	0.27	0.33	0.15	0.16	0.22	0.18	0.13	0.13	0.25	0.12	0.15	0.16	0.20	0.20	0.18	0.17	0.15	0.15	0.25	0.13	0.11	0.08	0.21	0.21	0.30
25Rakkol	0.18	0.24	0.45	0.23	0.33	0.42	0.19	0.24	0.27	0.22	0.16	0.17	0.32	0.20	0.19	0.25	0.22	0.23	0.26	0.18	0.18	0.21	0.32	0.16	0.16	0.13	0.24	0.29	0.46
26Mustaj	0.13	0.17	0.29	0.14	0.21	0.28	0.15	0.18	0.16	0.19	0.11	0.13	0.25	0.16	0.15	0.15	0.14	0.18	0.18	0.11	0.13	0.17	0.21	0.12	0.12	0.09	0.19	0.23	0.32
27Kilpee	0.20	0.24	0.43	0.24	0.29	0.39	0.23	0.25	0.23	0.24	0.16	0.19	0.31	0.21	0.22	0.22	0.18	0.25	0.21	0.19	0.18	0.23	0.32	0.18	0.17	0.12	0.24	0.31	0.44
28Notkop	0.07	0.10	0.27	0.13	0.16	0.27	0.11	0.14	0.13	0.12	0.07	0.09	0.23	0.11	0.11	0.11	0.10	0.15	0.15	0.09	0.10	0.13	0.16	0.08	0.07	0.07	0.15	0.20	0.30
29Inojok	0.07	0.11	0.30	0.12	0.15	0.28	0.12	0.13	0.13	0.14	0.06	0.08	0.24	0.11	0.10	0.11	0.10	0.15	0.15	0.09	0.10	0.14	0.19	0.09	0.08	0.06	0.16	0.21	0.32
30Pikkuv	0.11	0.13	0.30	0.19	0.22	0.35	0.16	0.15	0.17	0.15	0.10	0.12	0.23	0.13	0.13	0.15	0.15	0.17	0.19	0.13	0.11	0.14	0.19	0.10	0.10	0.09	0.18	0.22	0.32
31Vammel	0.09	0.12	0.29	0.13	0.18	0.27	0.11	0.14	0.14	0.14	0.06	0.09	0.23	0.12	0.11	0.11	0.10	0.16	0.15	0.08	0.10	0.13	0.19	0.09	0.08	0.05	0.16	0.20	0.32
32Kuokka	0.09	0.11	0.32	0.14	0.16	0.30	0.13	0.17	0.13	0.13	0.08	0.09	0.22	0.12	0.11	0.11	0.11	0.16	0.15	0.10	0.10	0.14	0.18	0.09	0.09	0.06	0.15	0.22	0.32
33Rajajo	0.09	0.16	0.40	0.15	0.20	0.31	0.13	0.19	0.21	0.20	0.11	0.11	0.29	0.13	0.14	0.14	0.15	0.19	0.17	0.14	0.14	0.15	0.24	0.12	0.11	0.09	0.19	0.22	0.37
34LugaRU	0.10	0.14	0.33	0.15	0.19	0.27	0.13	0.18	0.17	0.15	0.10	0.10	0.27	0.13	0.14	0.14	0.14	0.17	0.16	0.14	0.13	0.15	0.21	0.11	0.11	0.09	0.17	0.21	0.33
ISOJOKIA	0.05	0.08	0.28	0.14	0.20	0.29	0.07	0.10	0.21	0.12	0.06	0.04	0.21	0.04	0.07	0.12	0.17	0.12	0.15	0.10	0.06	0.03	0.11	0.04	0.04	0.08	0.13	0.14	0.28
LUUTAJOK	0.13	0.16	0.35	0.20	0.24	0.34	0.15	0.16	0.21	0.20	0.11	0.13	0.27	0.15	0.14	0.14	0.15	0.20	0.21	0.14	0.15	0.18	0.26	0.14	0.09	0.11	0.21	0.24	0.29
DENMARK	0.05	0.10	0.30	0.10	0.18	0.23	0.08	0.13	0.18	0.14	0.05	0.05	0.20	0.07	0.09	0.08	0.14	0.13	0.09	0.08	0.08	0.08	0.16	0.06	0.06	0.05	0.14	0.16	0.27
RAUTALAM	0.07	0.14	0.35	0.13	0.24	0.31	0.10	0.15	0.24	0.18	0.10	0.08	0.26	0.07	0.09	0.12	0.20	0.15	0.19	0.14	0.12	0.09	0.20	0.08	0.08	0.08	0.17	0.16	0.33
GOTLANDS	0.05	0.12	0.33	0.11	0.20	0.27	0.07	0.13	0.19	0.14	0.07	0.06	0.23	0.07	0.08	0.11	0.15	0.15	0.15	0.09	0.10	0.09	0.17	0.07	0.06	0.07	0.16	0.16	0.30

Table **5.** Continued.

Pop	17Porvoo	18Kosken	19Kymijo	20SummaM	20SummUp	21Virojo	21ViroUp	22Urpala	23Santaj	24Vilajo	25Rakkol	26Mustaj	27Kilpee	28Notkop	29Inojok	30Pikkuv	31Vammel	32Kuokka	33Rajajo	34LugaRU	ISOJOKIA	LUUTAJOK	DENMARK	RAUTALAM
18Kosken	0.19																							
19Kymijo	0.13	0.14																						
20SummaM	0.14	0.15	0.02																					
20SummUp	0.12	0.12	0.05	0.05																				
21Virojo	0.25	0.29	0.25	0.23	0.18																			
21ViroUp	0.19	0.18	0.16	0.17	0.08	0.26																		
22Urpala	0.12	0.09	0.05	0.06	0.04	0.20	0.09																	
23Santaj	0.16	0.16	0.13	0.14	0.09	0.22	0.11	0.04																
24Vilajo	0.18	0.21	0.13	0.14	0.08	0.23	0.12	0.08	0.12															
25Rakkol	0.25	0.24	0.20	0.21	0.14	0.29	0.18	0.10	0.11	0.17														
26Mustaj	0.17	0.18	0.14	0.14	0.10	0.17	0.14	0.06	0.07	0.14	0.11													
27Kilpee	0.22	0.26	0.19	0.18	0.15	0.32	0.20	0.11	0.17	0.18	0.21	0.11												
28Notkop	0.16	0.15	0.10	0.10	0.06	0.21	0.12	0.04	0.06	0.12	0.14	0.05	0.12											
29Inojok	0.15	0.15	0.09	0.10	0.06	0.23	0.11	0.04	0.07	0.12	0.14	0.07	0.13	0.02										
30Pikkuv	0.18	0.18	0.10	0.13	0.09	0.26	0.14	0.07	0.10	0.14	0.17	0.11	0.16	0.06	0.06									
31Vammel	0.15	0.16	0.09	0.10	0.06	0.22	0.11	0.03	0.07	0.11	0.13	0.05	0.09	0.03	0.03	0.06								
32Kuokka	0.15	0.16	0.10	0.12	0.07	0.23	0.12	0.05	0.09	0.12	0.16	0.09	0.14	0.03	0.02	0.07	0.04							
33Rajajo	0.16	0.19	0.13	0.12	0.10	0.28	0.16	0.09	0.14	0.16	0.21	0.11	0.20	0.09	0.09	0.15	0.10	0.09						
34LugaRU	0.19	0.18	0.14	0.14	0.09	0.26	0.14	0.09	0.13	0.14	0.20	0.15	0.20	0.08	0.08	0.13	0.09	0.07	0.13					
ISOJOKIA	0.15	0.13	0.01	0.02	0.05	0.22	0.16	0.06	0.13	0.14	0.19	0.14	0.19	0.09	0.09	0.11	0.10	0.11	0.12	0.13				
LUUTAJOK	0.18	0.21	0.15	0.16	0.08	0.30	0.11	0.10	0.15	0.15	0.22	0.16	0.20	0.12	0.12	0.16	0.10	0.14	0.20	0.17	0.15			
DENMARK	0.11	0.14	0.06	0.07	0.06	0.23	0.13	0.05	0.11	0.10	0.17	0.12	0.16	0.08	0.08	0.11	0.08	0.08	0.09	0.10	0.06	0.13		
RAUTALAM	0.17	0.17	0.10	0.10	0.06	0.24	0.13	0.09	0.16	0.11	0.20	0.17	0.24	0.13	0.13	0.14	0.13	0.14	0.16	0.14	0.09	0.16	0.08	
GOTLANDS	0.14	0.15	0.08	0.08	0.04	0.20	0.12	0.06	0.12	0.11	0.15	0.11	0.17	0.08	0.08	0.12	0.08	0.09	0.10	0.12	0.07	0.13	0.07	0.08

3.4. Genetic distances among populations

Individual samples were pooled according to the river system-based analyses described below in the regional results. For the overall analysis, only the most original and anadromous populations were initially included to gain an insight into the historically oldest observable structure behind the genetic distances, and for anadromous trout, along the whole Finnish–Russian coast. Hatchery releases tend to blur the historically probably relatively stable structure, and small isolated populations in freshwater environments have often experienced strong random changes because of genetic drift. They therefore no longer reflect the historical pattern.

When all anadromous and original brown trout stocks were included in the analyses, roughly two groups were formed: stocks west of Virojoki and stocks east of Virojoki, with Virojoki included in the eastern group (Figure 2). In all, six main groups could be identified.

The three most western populations, Purilanjoki, Paimionjoki and Uskelanjoki, formed one group (A). The second group was represented the most typical anadromous trout of the Uusimaa area, including stocks similar to Ingarskilanjoki (B). Groups C and D were mostly comprised of the border rivers draining into the Bay of Vyborg, with Finnish Virojoki belonging to this group. Group E was formed of stocks located in the Karelian Isthmus in Russia, and the last group, G, was formed of the two most distant rivers, Rajajoki (Siestarjoki) and Luga, from the more distant part of the coast.

The genetic structure thus relatively closely followed the geographical distances between rivers and also the structure of the coast.

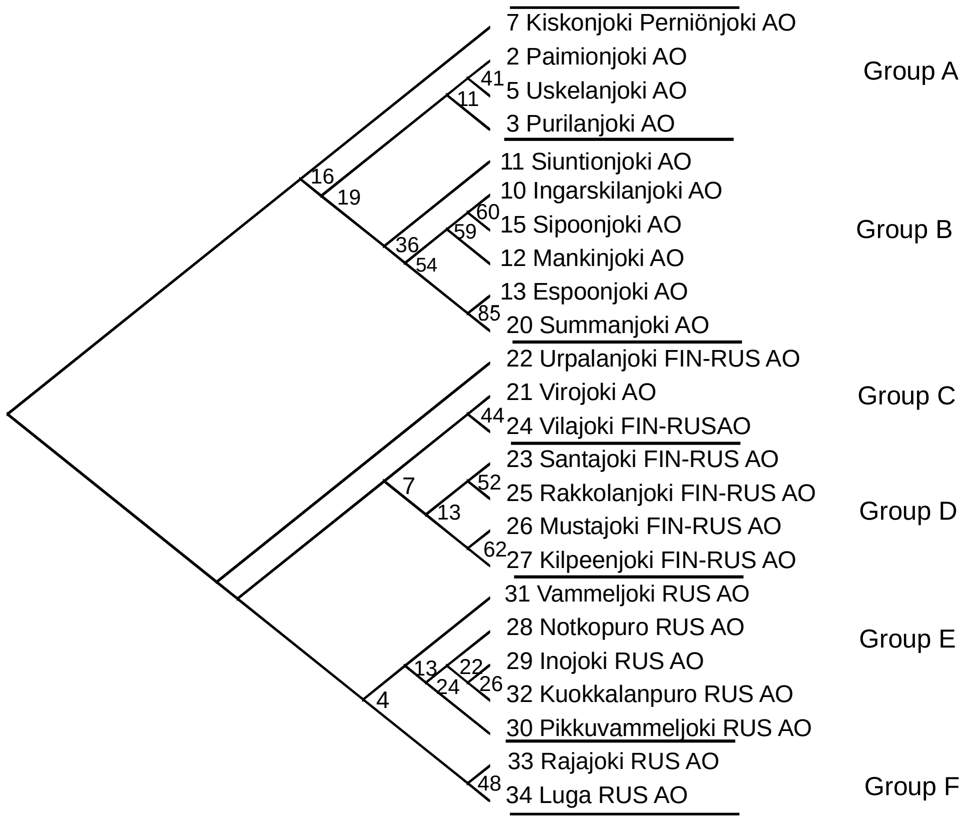

Figure 2. Genetic distances (Nei's DA distance, neighbour-joining tree) among Finnish (FIN), Russian (RUS) and cross-border (FIN-RUS) anadromous brown trout stocks, which are regarded as both anadromous (A) and the most original (O) ones. The river systems are numbered from west to east around the gulf and the numbers are presented with the river names. Bootstrap numbers for the branches are shown as a percentage from 1000 repeats. A stands for anadromous and O for original populations.

When the introduced and mixed anadromous stocks were also included in the analysis, the main structure remained the same (Figure 3). The same six original groups could be found and the introduced populations were placed into the tree according to their genetic history. For many populations, the history was known and the placement in the tree was thus understandable, although not exactly according to their geographical location.

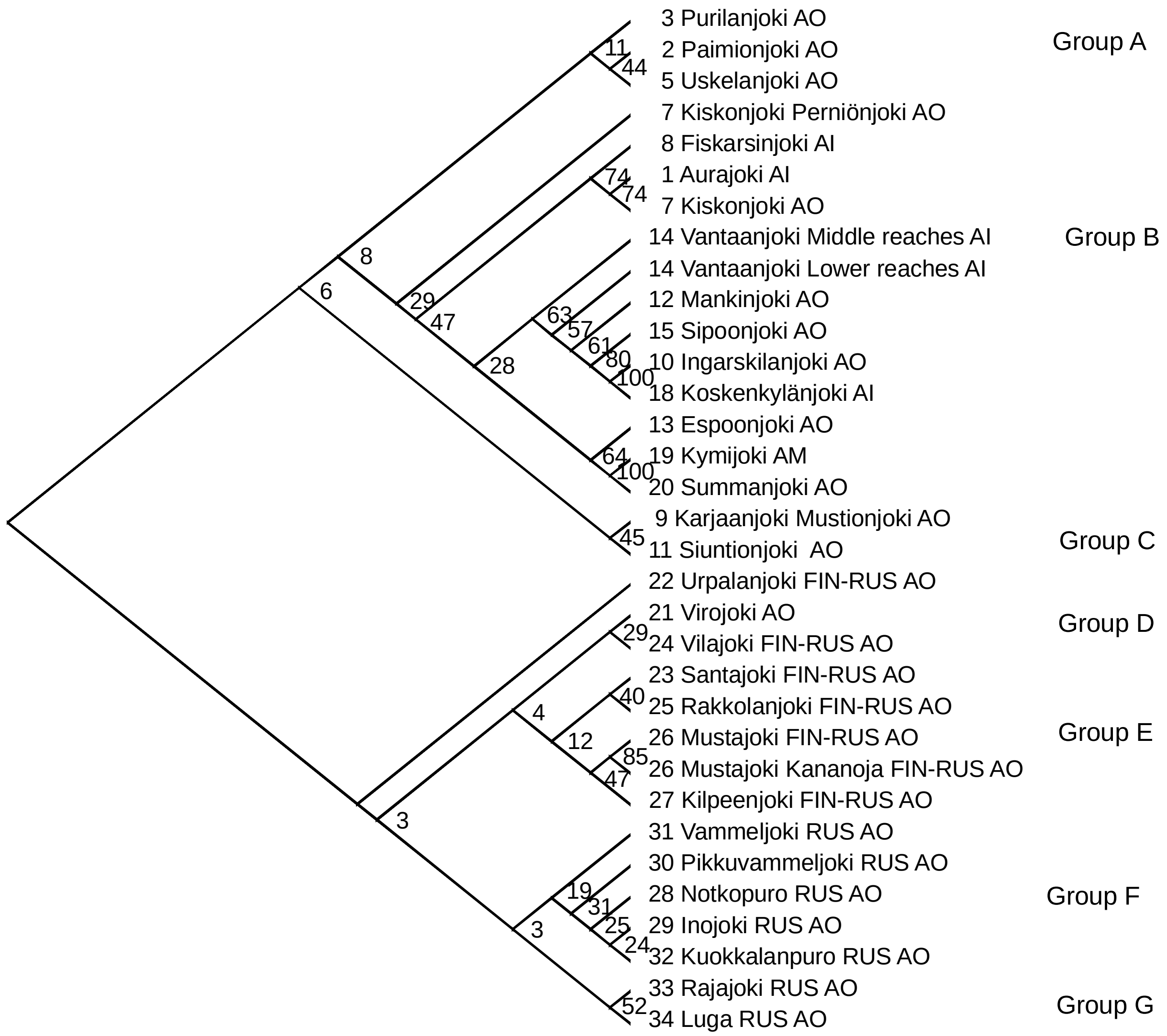

Figure 3. Genetic distances (Nei's DA distance, neighbour-joining tree) among Finnish and Russian anadromous brown trout populations. The river systems are numbered from west to east and the numbers are presented with the river names. Bootstrap numbers for the branches are shown as a percentage from 1000 repeats. A stands for anadromous, O for original, I for introduced and M for mixed populations. Cross-border rivers are indicated as FIN-RUS.

When the resident stocks were included in the distance tree some, changes occurred (Figure 4). Often, but not always, anadromous and resident samples from the same river system pooled into the same branch or near to each other. From Kiskonjoki, the resident Myllyjoki sample grouped together with small western populations Paimionjoki and Purilanjoki. The two samples from the Perniönjoki tributary grouped together as one distinct unit, and Latokartanonkoski grouped together with the Aurajoki trout. Thus, three stock groups were observed within the Kiskonjoki tributary. The Fiskarsinjoki samples grouped together.

From the Vantaanjoki tributary, the lower and middle reaches grouped together, and the Palojoki tributary was also placed relatively close to them. However, the populations from the upper reaches grouped together with the Siuntionjoki samples.

From the Karjaanjoki river system, tributaries from Nummenjoki and Nuijajoki were similar and placed into the group with an Isojoki influence. Saavajoki and Vihtijoki were more similar to Uskelanjoki and Kiskonjoki. In addition, Karjaanjoki Mustionjoki grouped with Porvoonjoki and Punassuon Lohioja, so three units also occurred within the Karjaanjoki river system.

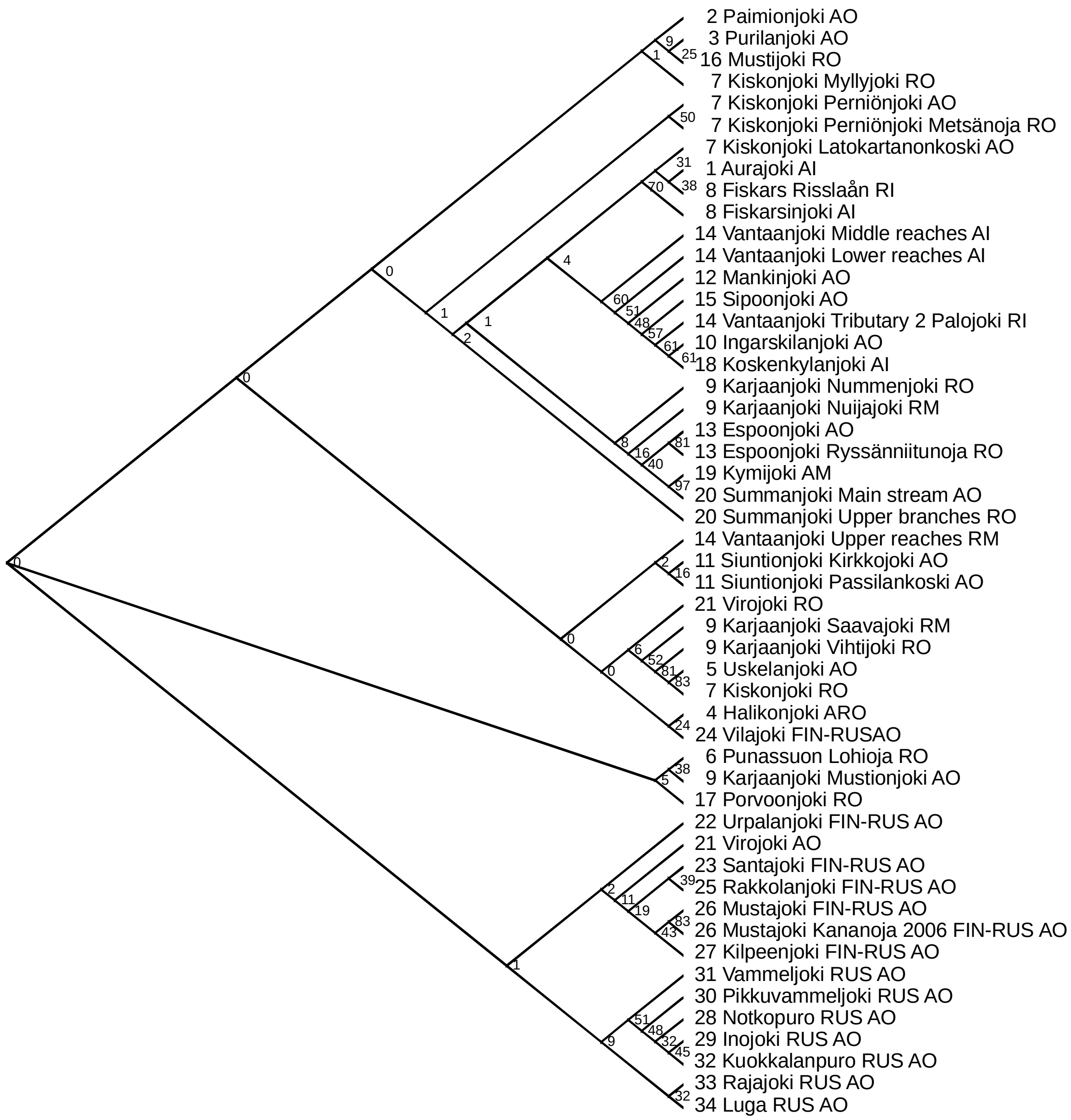

Figure 4. Genetic distances (Nei's DA distance, neighbour-joining tree) among Finnish and Russian anadromous and resident brown trout stocks. Watersheds are numbered from west to east and watershed numbers are presented with the river names. Bootstrap numbers for the branches are shown as a percentage from 1000 repeats. A stands for anadromous, R for resident, O for original, I for introduced and M for mixed populations.

Espoonjoki, Summanjoki and Siuntionjoki river systems were all represented by two samples, which grouped together with their sample from the same river.

In an unrooted tree, it can be seen that, in all, six main groups could be formed (Figure 5): the Uskelanjoki group, Aurajoki group, Ingarskilanjoki group, Isojoki group, Bay of Vyborg group and Russian rivers.

The Uskelanjoki group is obviously relatively native for the southwestern part of the coast. Its diversity is no longer very high, but presumably sufficient for its independent existence. Some of the smallest rivers were possibly too small by themselves to be able to maintain diversity in the long term. The Aurajoki group is of hatchery origin, but justified by its nature as a new enhancement stock for the Archipelago sea area.

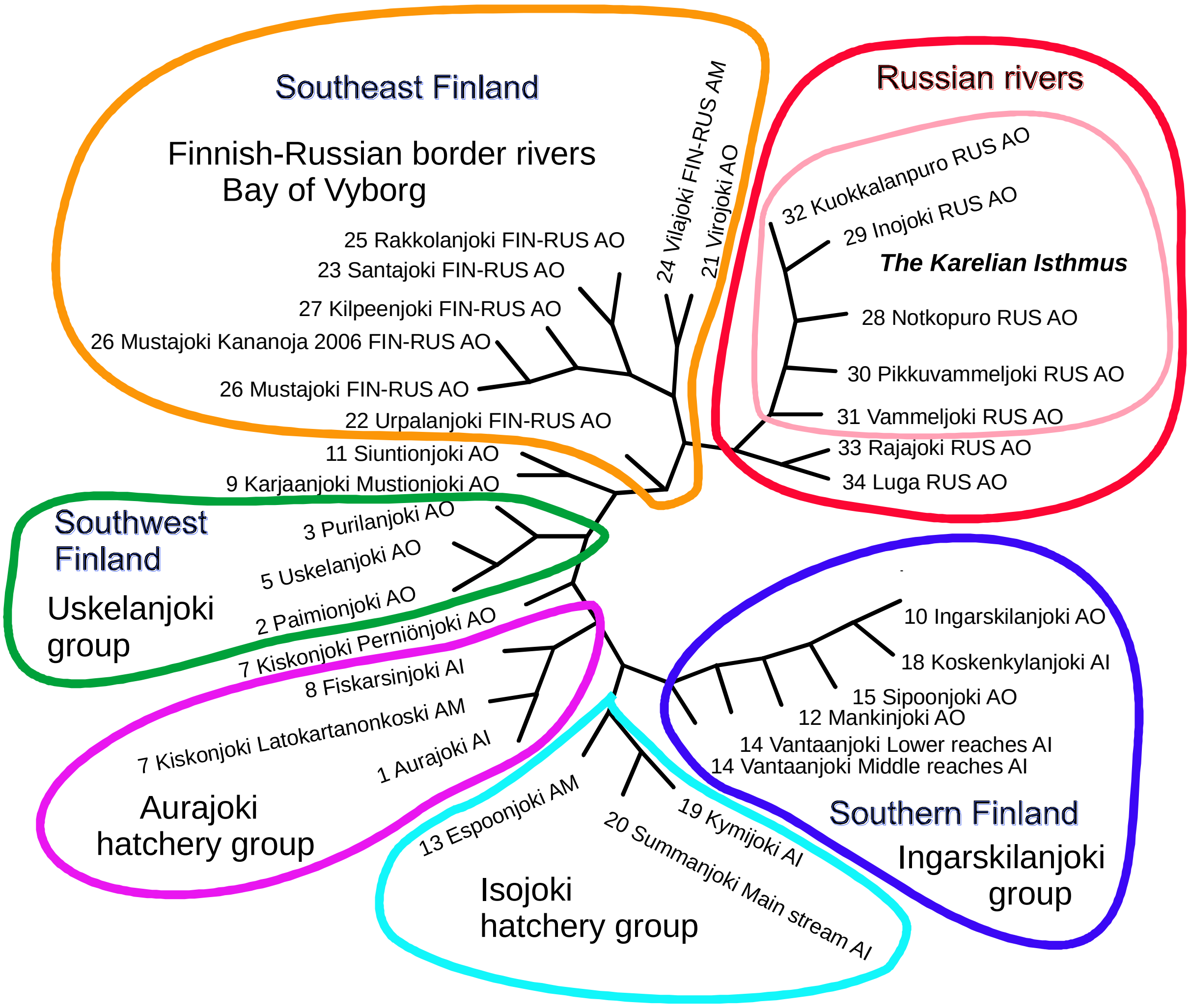

Figure 5. Unrooted tree of anadromous Finnish and Russian brown trout populations from the Gulf of Finland area, showing five similarity groups.

The Ingarskilanjoki group consists of the most typical Finnish southern brown trout stocks. It includes stocks that have been supported by Ingarskilanjoki trout releases and also stocks that belong to that area.

The Isojoki group is composed of stocks that are influenced by Isojoki hatchery releases. For the Espoonjoki, the source of influence is not so clear, and mainly results from the small Ryssänniitunoja sample. Some other release stock could be recommended if releases for those rivers are needed. In Kymijoki and Summanjoki, the Isojoki releases could be changed to some other eastern stock, possibly Mustajoki trout.

The populations of the Bay of Vyborg form their own unit (Figure 5), which should be saved as such. If enhancement releases are necessary, Mustajoki trout can be used at least after some years. The native state of Russian trout populations is recommended to be saved, and their smolt production levels to be increased.

4. Regional results and management recommendations

4.1. ELY Centre for Southwest Finland

In the next section, we present the results and genetic differentiation for each river system and for each of the five geographical areas.

4.1.1. Aurajoki

The River Aurajoki drains into the Archipelago Sea in the middle of the City of Turku (Figure 6). The Aurajoki drainage area covers 874 km^2, and 0.25% of its surface area consists of lakes (Ekholm 1993).

The spawning migration possibilities have been relatively poor for brown trout in Aurajoki since the early Middle Ages, as a mill dam had already then been built in the lowest rapid, Halistenkoski. The river was fully closed in 1922 at the latest, when the dam of Turku waterworks was completed at Halistenkoski, about 6 km above the river mouth (Kääriä et al. 1992).

Before the dam construction, sea trout and possible salmon catches were notable. After the dam closed the river, sea trout catches dropped, and after the 1930s trout became very rare. In the 1960s, only occasional sea trout are known to have been caught below the dam (Hurme 1962, 1967).

A fish ladder was constructed in 1995 at the Halistenkoski rapids, and the lowest part of the river was again open. From 1996 to 2008, the number of ascending sea trout varied between 34 and 322. Sea trout can nowadays migrate in the main branch upstream to Lieto, where the next dam is located in Nautelankoski rapids (Figure 6) (Tolonen 2012).

As the original Aurajoki sea trout population has been lost, the current stock has been created by hatchery releases, which are assumed to be mainly of Isojoki hatchery origin, but may also include Swedish Dalälven trout. Smolts of anadromous trout have been released into Aurajoki since the 1980s, and releases into the Archipelago Sea were already started much earlier (Kääriä et al. 1992). Since 1990, broodfish from the river's own enhanced stock have been in used for the rearing and stocking of juveniles into Aurajoki and the Archipelago Sea (Tolonen 2012).

Currently, spawners are caught from the river and offspring are reared in Trollböle hatchery (Trollböle fiskkläckeri) at Raasepori. The spawners are examined for diseases, and the roe are transported to Trollböle to be grown as broodstock. Released fish are thus second-generation hatchery fish. The samples in this study were from the hatchery offspring. These are also commonly used in releases in the nearby area, the Archipelago Sea and western part of the Gulf of Finland. In the Archipelago Sea, stocked smolts originating from the Aurajoki stock have given better catch yields than the Isojoki stock releases (Mäntynen & Saura 2002).

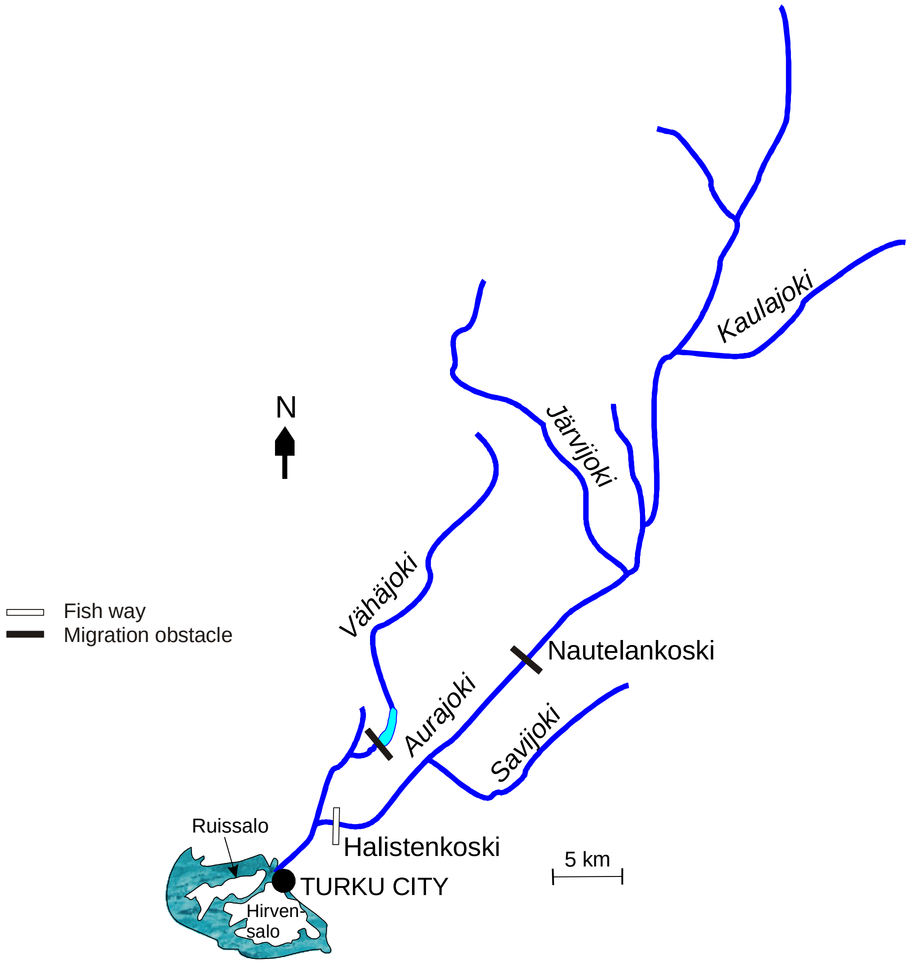

Figure 6. The River Aurajoki watershed. River names are written in italics.

The diversity measures for the Aurajoki sample were above the average for both allelic richness and mean diversity, so the population appears not to have suffered from a loss of genetic diversity as a result of hatchery rearing (Table 3). The high diversity levels may also be a result of mixing of the stocks. The ratio of the genetically effective size to the true size (Ne/N) was also relatively high (0.92), and the mean relatedness was low (4.1%), which implies successful hatchery practices.

Genetically, the Aurajoki sample does not group together with the other more local stocks from the Varsinais-Suomi area, but it is very closely related to the Fiskarsinjoki trout from the Uusimaa area. No statistically significant difference could be observed between these two samples. In addition, the Aurajoki sample shows similarity with Kiskonjoki-Latokartanonkoski. Aurajoki trout have been released into both of these rivers, and the results indicate that these releases have been successful.

From the management point of view, the Aurajoki trout is a useful and obviously viable anadromous stock, but it does not have any special genetic conservation value, other than its current diversity. It has been chosen as the stock for enhancing natural reproduction in the otherwise empty River Aurajoki, and these supportive releases will continue. The Aurajoki stock is also used for sea-ranching purposes in the Archipelago Sea area. In addition to Aurajoki, Latokartanonkoski rapids in Kiskonjoki and Fiskarsinjoki, this hatchery stock has been released into some other nearby rivers.

The Aurajoki trout is recommended to be used in sea-ranching programmes and Aurajoki enhancement projects, and possibly in releases to areas and spawning sites that have no other more native local genetic material. It is, however, not recommended to continue Aurajoki trout releases into the Kiskonjoki, as several viable trout populations also live in this river system.

The fish ladder at the Halistenkoski rapids now works, but flow management is still required to provide a more favourable and constant water flow, enabling the fish to enter the river for spawning, and to ensure natural reproduction. The building of fishways at other dams is recommended, as well as the improvement of spawning sites, especially in tributaries (Tolonen 2012).

4.1.2. Paimionjoki

River Paimionjoki drains into the Archipelago Sea (Figure 7). The drainage area is 1 088 km^2, and 1.58% of the area is formed of lakes (Ekholm 1993). There are three hydropower dams in Paimionjoki, which have a fall height of between 12 and 15 metres. The uppermost, Juvankoski, was built in 1916, the middle one, Juntolankoski, in 1919 and the lowest, Askalankoski, in 1936 (Figure 7). Before the construction of these dams, salmon and sea trout migrated up the river a long way upstream, even though smaller mill dams were also already present. Since the 1930s, migration has only been possible up to Askalankoski dam, which is located some 10 km upstream from the river mouth (Hurme 1967).

In 1962 there were still both salmon and sea trout in the river (Hurme 1962, Hurme 1967). In the small, 3-km-long Lohioja tributary draining into Paimionjoki, 1 km above the river mouth, anadromous trout weighing 3–4 kg have regularly been caught. The largest trout have weighed up to 6 kg. Trout still occurred in Lohioja in the late 1970s and early 1980s, but lately the tributary has lost its significance because of water intake, damming and pollution (Hurme 1962, Koskiniemi and Nuotio 1995).

From the River Paimionjoki, only 22 fishes were analysed and classified as anadromous. There are three power plants in the Paimionjoki main stream, and their total fall height is over 40 m. In addition to the dams, the river is also heavily regulated. Therefore, in the River Paimionjoki itself in its current state, there are no possibilities for river spawning fish to live. Although Paimionjoki belongs into the Natura 2000 network, water flow is in practice occasionally non-existent. Brown trout, however, occur in the lowest tributary, Vähäjoki, and in its branch, Karhunoja, which are both located below the lowest dam. There is an open route to these tributaries from the sea.

According to Aaltonen (2008), trout are only found in the lower parts of Vähäjoki and in the Karhunoja brook, probably because of problems with water quality. The reproduction of this population has continuously been very weak, and also in the Karhunoja tributary, because of habitat loss, the low minimum water flow level and high sediment load. The trout population in Paimionjoki is clearly under constant risk of extinction.

The Karhunoja trout have already previously been subjected to allozyme analysis (Nuotio and Koskiniemi 1995), and a few fish have more recently undergone microsatellite analysis (Koskiniemi 2005)

The Paimionjoki sample was quite small and it is obviously quite a small population. Its diversity was, however, not very low and the sample showed an excess of heterozygosity, indicating mixing of populations. It also did not differ from the Siuntionjoki trout at all, possibly because of the small sample size. The effective size of the sample was only 11 fish and 12 families. The Ne/N ratio was at the average level, and somewhat elevated relatedness could be observed in the sample.

Despite there being very few spawning grounds, relatively little potential for stock improvement and several dams in the river system, the trout population is regarded as native and original. It is also regarded as a typical representative of the southwestern coast, as it grouped tightly together with the Uskelanjoki trout. Despite the low family number, it is not recommended to release foreign stocks in the river. In case some support is needed, the Uskelanjoki trout is the genetically most similar population. River restoration programmes are recommended to improve the state of nursery areas and to increase their size. Fishways through the dams would markedly improve the situation of trout in the river, but most of the new suitable production areas are in the upper reaches, which are located behind all three hydropower dams. Net fishing in the river mouth and river itself should be restricted at the spawning migration time to enable the few spawners to enter the river. Diurnal regulation of water flow prevents the successful natural reproduction of the trout population, and also that of salmon and whitefish in the rapids below the Askala dam. The water level in the rapids should not become too low for the trout, and a minimum sustainable flow should be established for the river in order to make spawning and juvenile production again possible in the main stream.

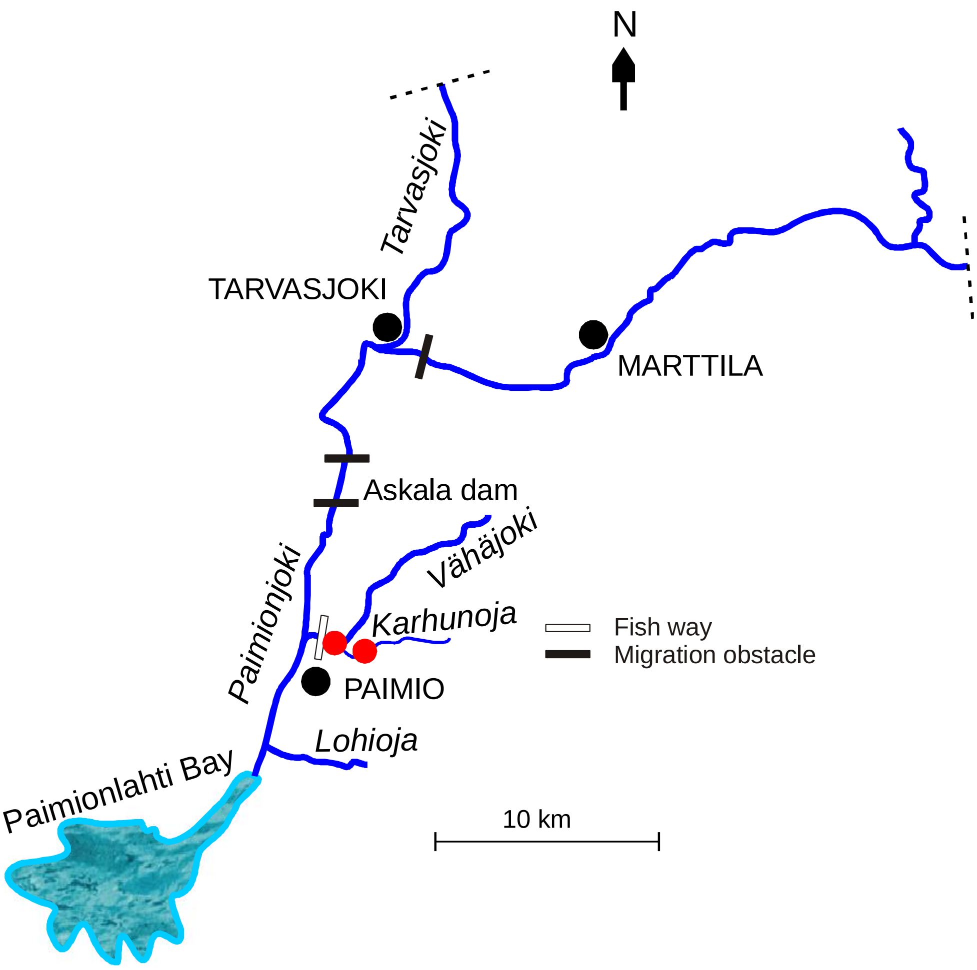

Figure 7. The River Paimionjoki watershed. River names are written in italics. Sampling sites are shown as red dots.

4.1.3. Purilanjoki

The River Purilanjoki drains into the Archipelago Sea, and the drainage area is only 82 km^2, of which 0.13% is composed of lakes (Ekholm 1993) (Figure 8). Purilanjoki is located west of Halikonjoki and east of the River Sauvonjoki. Both of these are known to be historical sea trout rivers, but the trout population in Sauvonjoki has become extinct during the last few decades (Tolonen 2013a,b,c). According to local people, there have always been trout in the River Purilanjoki. Trout are known to have occurred in the river at the time of the Winter War (1939–1940). According to Tolonen (2013d), local people fished trout from the river in the 1960s, but trout have also been observed in the river in more recent decades, so the population is assumed to be a native, anadromous stock and not a result of hatchery releases. There are some migration hindrances in the River Purilanjoki.

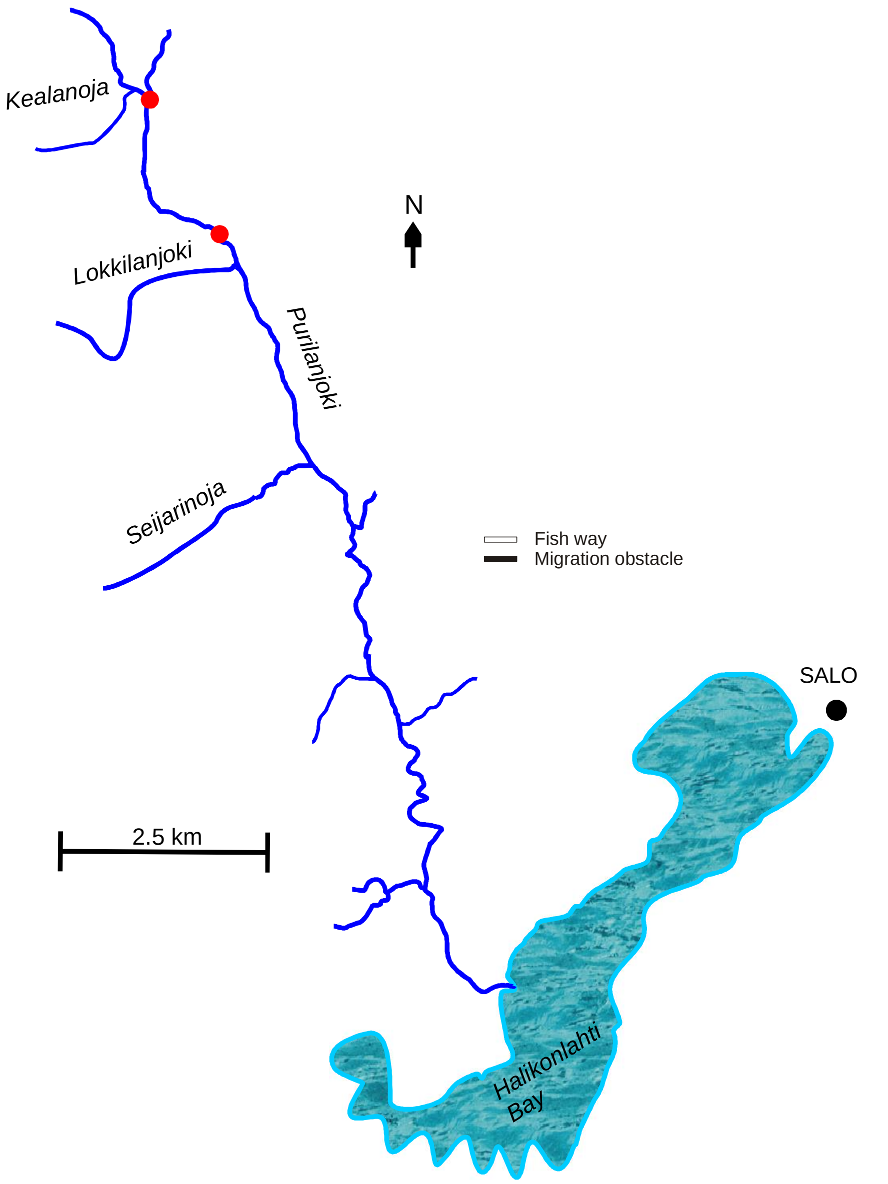

Figure 8. The Purilanjoki river system. River names are written in italics. Sampling sites are shown as red dots.

Only 15 samples were available from the Purilanjoki trout. All sampled fish were juveniles of the summer and they were only sampled from two sites.

The Purilanjoki trout showed the lowest diversity level (allelic richness 1.67) of all samples and very little similarity with any other stock, but grouped into the local Uskelanjoki group. The stock thus appears not have been strongly affected by releases, but possibly suffers from a very small population size or isolation, or sampling has not been successful. The effective population size of the sample was only five fish, and only six families were involved in their production. The Ne/N ratio was also below 0.5, indicating a high proportion of siblings in the sample. From the management point of view, the diversity level appears very low if sampling can be assumed to be representative.

The population seems quite unique, but more samples are needed before final recommendations can be made. The population size is probably larger than the samplings indicate. Research and spawning ground inventories are needed. The trout stock appears native and there have been no known releases in the area. There is a need for an improvement inventory in the area, and no fishing should be permitted in the river.

4.1.4. Halikonjoki

The River Halikonjoki drains into the Archipelago Sea (Figure 9). The drainage basin is 307 km^2 in area, and only 0.05% of it consists of lakes (Ekholm 1993). Halikonjoki is located west of Uskelanjoki, east of Purilanjoki, and south of Paimionjoki, which all are known as historical sea trout rivers. The River Halikonjoki is known as a spawning river for local anadromous trout and possibly also for Atlantic salmon (Hurme 1962, 1967). The lowest migration obstacle is currently the Häntälä mill dam, which is located about 9 km from the river mouth. From the tributaries of the Halikonjoki river, the River Kuusjoki and especially its tributary, Someroja, were already long ago described as spawning grounds for local trout (Hurme 1967). There are at least two dams in the river system, at Häntälänkoski and Sahakoski.

The Halikonjoki trout population is currently assumed to be mainly resident. However, large trout have sometimes been caught below the Häntälä dam (for example, Tolonen 2013c). Natural, original brown trout offspring production also occurs in the river above the Häntälä dam. In electrofishing inventories, juveniles have been found throughout the river area. The main spawning areas are in the upper reaches, which currently have no sea connection, such as Someroja brook. However, there are also dams in the Someroja.

According to local people, there have also been trout in several other small brooks (Krapuoja, Liedonoja and Kakarinoja) and in the rapids of the main stream. For instance, Krapuoja brook, draining into the lower reaches of Halikonjoki, was well known as a notable brook for fishing (presumably juvenile) trout. Nowadays, trout appear to have become extinct in this brook, possibly mainly due to illegal fishing (Tolonen 2013c).

It appears that the distribution of trout has decreased during the last decade in the Halikonjoki drainage basin. Currently, the population seems quite small and natural reproduction mainly occurs only in the small Someroja brook. There appears to be a high risk of the population becoming extinct (Tolonen 2013c).

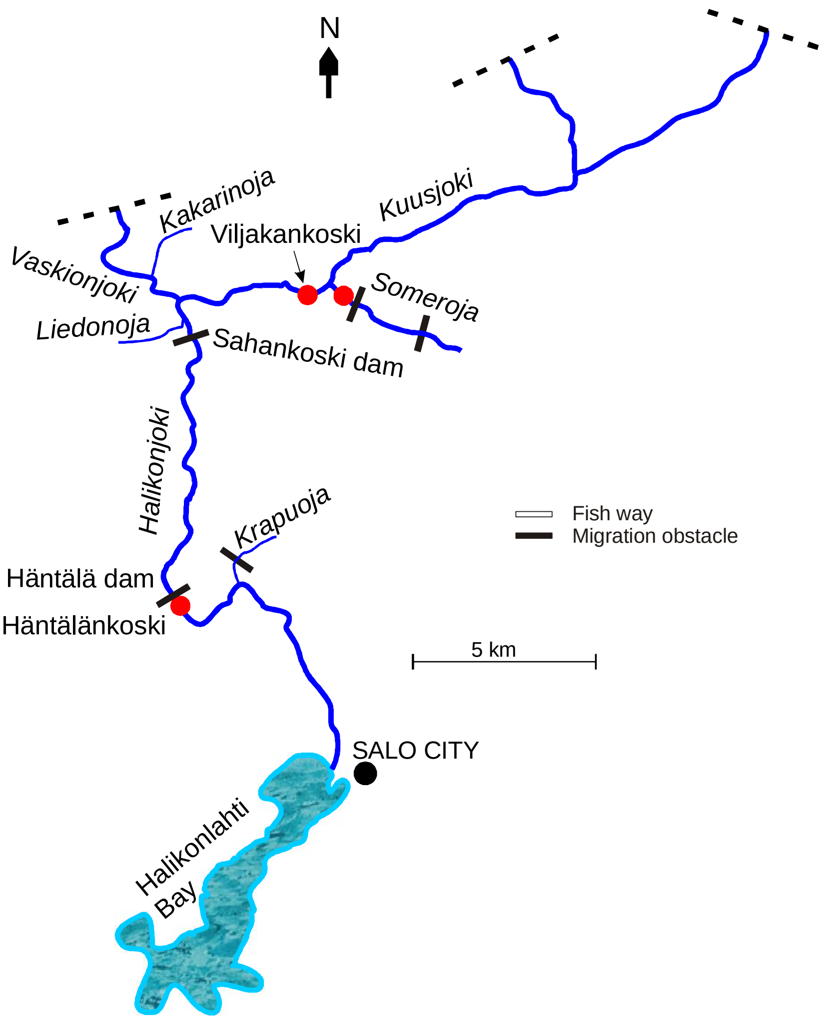

Figure 9. The Halikonjoki river system. River names are written in italics. Sampling sites are shown as red dots.

The diversity of Halikonjoki trout was at the average level, for both allelic richness (4.56) and mean diversity (0.63) (Table 3). No clear signs of gene flow from hatchery stocks could be detected. According to Nuotio and Koskiniemi (1995), there has been a forest fire on the shores of Someroja, which led to a decrease in the trout stock of the brook. Small numbers of Rautalamminreitti trout have possible been released there (Tolonen 2013c).

Halikonjoki trout can clearly be considered as a potential sea trout stock and relatively unique. The effective size of the sample was 14, with 14 families. The Ne/N ratio was 0.47, which is at the average level for a wild population, and the mean relatedness in the sample was relatively high, being 9.8% (Table 4).

There have been no major hatchery releases in the area, and neither are they recommended in the future. The opening of migration hindrances should be clarified as soon as possible. The stock cannot sustain a fishery in the river area. An inventory of the river area and the distribution of trout is needed, and a restoration plan for potential spawning sites should be created. The Halikonjoki population grouped loosely with the local Uskelanjoki group (Figure 4), so in case supportive releases are needed, some material from this group could be considered.

4.1.5. Uskelanjoki

The River Uskelanjoki drains through the city of Salo into the Archipelago Sea (Figure 10). It is a relatively wide river system (567 km^2), and only 0.6% of it consists of lakes (Ekholm 1993). Uskelanjoki is known to have been a trout river for a long time, and it was possibly even a salmon river (Hurme 1962). Salmon, possibly referring to sea trout, have been know to migrate upstream to spawn at least as far as the Yyrö mill in the Yyrönkoski rapids in Pertteli (Hurme 1967).

Hurme (1962, 1967) assumed the trout and salmon stocks to have disappeared in the 1920s. It has also been proposed that the trout stock in the river originates from hatchery releases in the 1960s (Nuotio and Koskiniemi 1995). The potential release stocks at that time were the trout stocks from Rautalamminreitti or Karjaanjoki-Vihtijoki. In the current data, the FST between Uskelanjoki and Rautalamminreitti was 0.24, which is quite high, and that between Uskelanjoki and Karjaanjoki-Vihtijoki was 0.09, which is not very low, although clearly lower than between Uskelanjoki and Rautalamminreitti (Table 5). Consequently, there remains some uncertainty about the origin of the Uskelanjoki population, and it might include some genetic material from Vihtijoki. In addition, approximately 21 000 trout juveniles of Isojoki and Aurajoki origin were released into the Uskelanjoki during 1990–2006. About half of the releases took place near to the river mouth in the Moisionkoski rapids, and the rest in the rapids of Haukkalankoski and Yyrönkoski, below the Pitkäkoski rapids (Aaltonen 2009).

The river has three main branches: the Rivers Rekijoki, Terttilänjoki and Hitolanjoki (Figure 10). Hitolanjoki, in particular, is a known spawning site for trout. The Satakoskenoja tributary and its rapids, Satakoski, are located in the upper part of Hitolanjoki, and this is assumed to be one the most important spawning areas for the trout population. The water quality is good, as part of the water comes from wells. The source of the Satakoskenoja tributary is the Kultalähde spring. In the lower reaches of the Hitolanjoki there is, however, a steep waterfall above the Myllykoski rapid, so that spawners from the sea can mostly only proceed as far as Myllykoski and its rapids. In 2011, the lower migration hindrance was removed and the construction of a fishway for the upper dam is included in the current HEALFISH project.

Anadromous trout are known to migrate at least to the Myllykoski rapid in the River Hitolanjoki (Figure 10). Several samples were taken from the Uskelanjoki river system to analyse the potential substructure:

1) Haukkalankoski and Kaukolankoski rapids in the main branch;
2) Pitkäkoski rapids (also in the main branch);
3) River Hitolanjoki, Myllykoski rapids;
4) River Hitolanjoki, Satakoski rapids;
5) River Terttilänjoki.

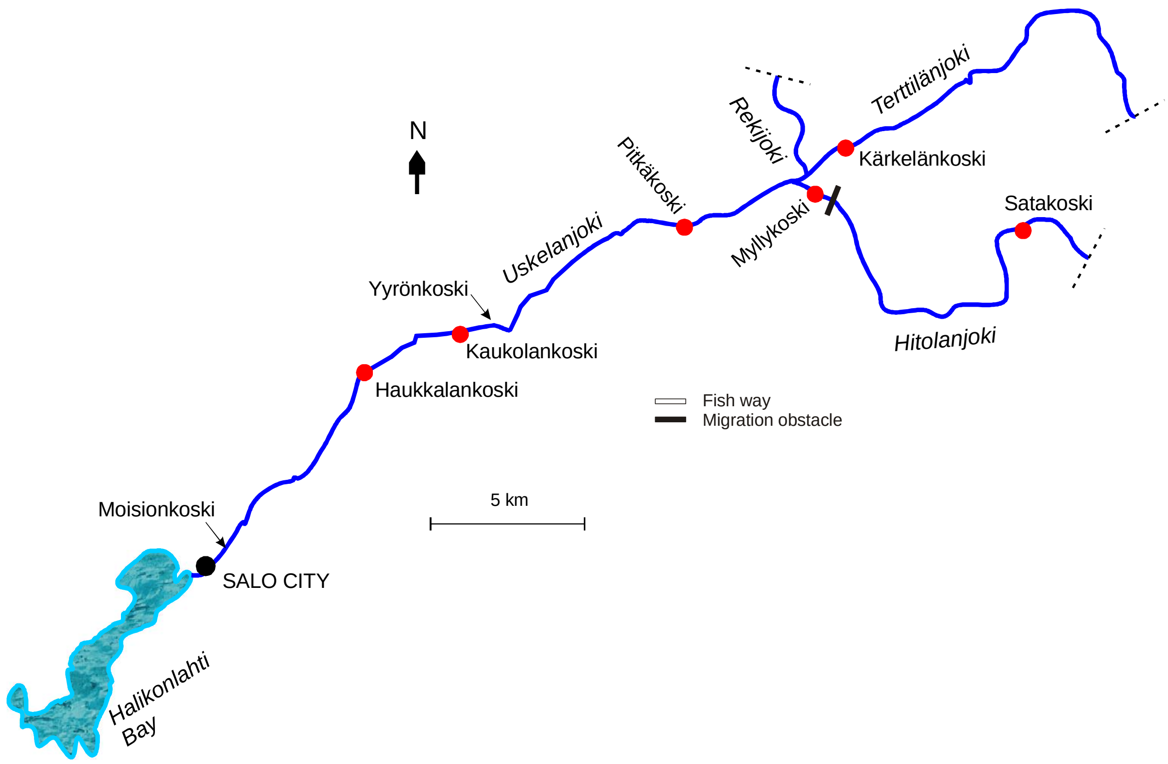

Figure 10. Sampling sites of the Uskelanjoki river system. The sampled rapids are named and sampling sites are shown as red dots.

Figure 11. Genetic distances between all samples from the Uskelanjoki river system.

Genetic distances among samples and tributaries were small (Figure 11). They grouped into three groups, although similarities were high. Samples from the Uskelanjoki and Hitolanjoki did not group separately, but mixed with each other.

Table 6. Statistical significance of genetic differentiation between samples within the Uskelanjoki river system (Usk_) and also between those samples and nearby rivers. Symbols: NS = nonsignificant, * 5%, ** 1% and *** 0.1 % levels of significance.

Sample	2	3	4	5	6	7	8	9	10
1 Aurajoki	***	***	***	*	***	***	***	***	***
2 Paimionjoki		***	***	*	***	***	**	***	***
3 Purilanjoki			***	*	***	***	**	***	***
4 Halikonjoki				**	***	***	***	***	***
5 Usk_Haukkalankoski					NS	NS	NS	NS	**
6 Usk_Pitkäkoski						NS	NS	NS	***
7 Usk_Hitola_Satakoski							NS	NS	***
8 Usk_Terttilänjoki								NS	***
9 Usk_Hitola_Myllykoski									***
10 Punassuon Lohioja									

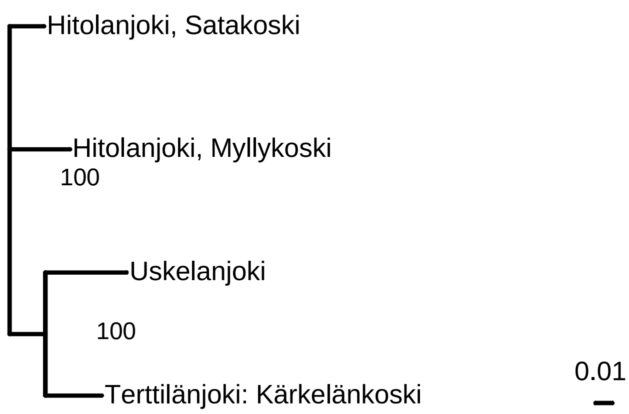

Figure 12. Distance tree of samples from the Uskelanjoki river system, after samples from Uskelanjoki were pooled.

When all three samples from the Uskelanjoki (Kaukolankoski, Haukkalankoski and Pitkäkoski) were pooled, Terttilänjoki was the most similar river to the main branch (Figure 12). Distances were nevertheless very small, and bootstrap values showed 100% pooling of the branches (Figure 12).

The test of genetic differentiation between samples clearly showed that all the differences between the Uskelanjoki tributary samples were statistically nonsignificant. Thus, all samples were pooled to represent the Uskelanjoki watershed and the at least partly anadromous Uskelanjoki trout. No differences in allele frequencies could be detected between any of the other samples of the Uskelanjoki river system (Table 6). A previous genetic analysis of the Uskelanjoki river system also revealed high similarity among samples from different branches (Koskiniemi 2009).

The Haukkalankoski sample was also quite similar to the trout of the nearby rivers Aurajoki, Paimionjoki and Purilanjoki, with only a 5% level of significance for the differentiation.

Reproduction probably mainly occurs in the Hitolanjoki area and its branches. Only older juveniles have been found in the Uskelanjoki main branch. Some releases of Vihtijoki trout have been carried out into Hitolanjoki.

When all samples from Uskelanjoki were pooled, its allelic richness, 4.3, was approximately on the average level, but the mean diversity was slightly less than the overall mean (Table 3). It is relatively unique, and the only similarity was observed with the Karjaanjoki-Vihtijoki sample (FST 0.09), from which some releases are known to have taken place (Table 5). The effective size of the total sample was 39 and the fish came from about 47 families, so when evaluated for the whole Uskelanjoki river system, the population size is not very small. The relatedness among the individuals was somewhat elevated (6.3%) (Table 4). Although Uskelanjoki trout obviously have both anadromous and resident components, no differences could be detected among the samples. The trout within the river system can therefore be treated as one unit, which quite clearly differs from the nearby rivers as well as from the most common hatchery stocks, despite the releases of foreign stocks.

No releases of hatchery stocks are recommended. Possibilities for the further removal of migration barriers should be clarified. The transportation of trout from the spawning sites of the same river system can be used in enhancement programmes. If case fishing is permitted, only restricted sites should be provided for fishermen and only a catch and release fishery should be allowed.

4.1.6. Punassuon Lohioja

The Punassuon Lohioja brook is part of the Lake Sahajärvi watershed, which drains into the Archipelago Sea in Teijonselkä bay (Figure 13). It is only 14 km^2 wide, and 4% of its surface area is composed of lakes (Ekholm 1993). The brook has its sources in the wells of the Punassuo bog and it drains into Lake Sahajärvi.

The brown trout population in Punassuon Lohioja was originally also anadromous, but there are two migration obstacles on the way to the sea, which have existed for decades at least, and possibly even for centuries. The ironworks of Teijo was founded in 1686, and the lower dam was constructed for the second time at the beginning of the 1700s for future use by the ironworks. The ironworks was closed in 1908 (Salokorpi 2007, Museovirasto 2013d).

Currently, the stock can thus be regarded as resident. It also has a long isolation history. The brook is located only two kilometres from the sea, but there is a lake, Lake Sahajärvi, between the river and the sea. Trout may also migrate into the lake. There have been no enhancement activities in the area. Some releases, possibly with the Rautalamminreitti hatchery stock, took place in 1969 and 1970 into the downstream lake. A small bifurcation brook from nearby Lake Hamarijärvi drains into the lake Sahajärvi, although it mostly drains into the sea via its own larger outflow brook. In the 2000s trout of the Aurajoki stock were released in brooks locating both downstram and upstream of Lake Hamarinjärvi (Tolonen 2013b). Restoration of the Punassuo bog in 2006 and 2009 led to significantly lower oxygen concentrations downstream in the Lohioja brook. In 2011, six years after the restoration work, a lack of oxygen was still observed (Sallantaus 2013).

The sample size was only 16 fish, which creates uncertainty in the results. The level of diversity in the population was low, the allelic richness was 2.4, but the population appears quite unique. No high similarities (FST less than 0.09) were found with any other studied stocks. The effective size was 19, but the Ne/N ratio was high, being 1.19, which indicates a possible substructure and mixing of populations in the sample. The number of families involved in the sample was estimated to be 14, and the relatedness among sampled individuals was somewhat elevated (8.7) (Table 4).

The true population size is probably much larger than that observed here. Spawning ground enhancement and the removal of migration obstacles, as well as overall habitat quality improvement and restoration of the brook are recommended. No fishing should be permitted in this brook system.

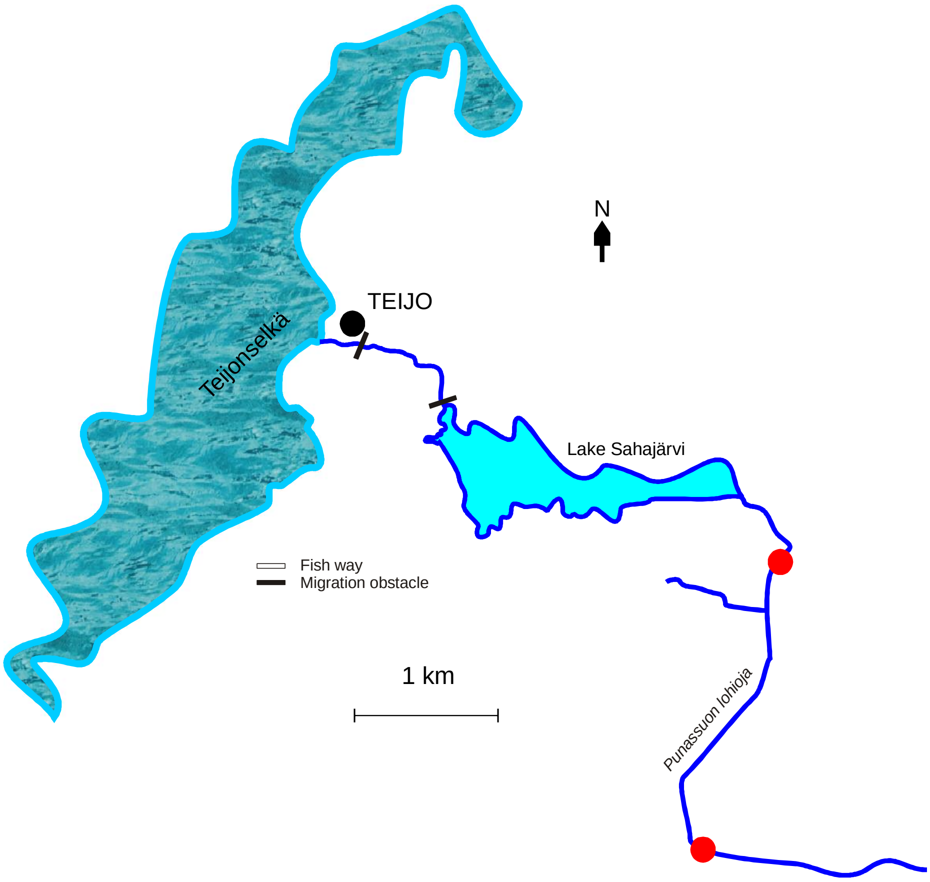

Figure 13. Punassuon Lohioja. Sampling sites are shown as red dots.

4.1.7. Kiskonjoki

The Kiskonjoki-Perniönjoki watershed drains into the Archipelago Sea in Krailanselkä (Figure 14). It is a wide watershed of 1 047 km^2, and lakes comprise 6% of its surface area. The Perniönjoki tributary accounts for 417 km^2 of the total area and 2% of its surface area consists of lakes (Ekholm 1993). Kiskonjoki is an old salmon and sea trout river. In the 1960s, sea trout and also salmon were still quite abundant in the Latokartanonkoski rapids, which are located on the lower reaches of the river (Figure 14) (Hurme 1962, Hurme 1967). There have been freshwater pearl mussels in the Kiskonjoki basin, but the state of the mussel population is nowadays uncertain (Oulasvirta 2010a).

Access of sea trout to the upper parts of Kiskonjoki river and the drainage basin has been restricted for at least a few hundred years. The ironworks of Koski was already founded in 1679, and in 1826, upstream from Koski, a dam and a canal lock was also built in Hålldam. In 1908–1909, the ironworks at Koski was followed by a hydropower plant, mill and sawmill at Koskenkoski rapids (Salokorpi 2007, Museovirasto 2013c). In the lower part of the River Kiskonjoki, at the Latokartanonkoski rapids, another ironworks was founded in 1830 (Museovirasto 2013a).

The genetic structure of Kiskojoki trout has previously been analysed by allozymes (Nuotio and Koskiniemi 1995), and later also with microsatellites (Aaltonen 2011).

In all, nine samples were collected from the Kiskonjoki river system (Table 2) (Figure 14), and in the initial analyses they all were treated separately (Figure 15). Only two individuals were available from Huhdanoja, which was thus omitted from the allelic differentiation test. No statistical differences could be observed between several resident brown trout populations from the upper reaches (Table 7). Trout from the Aneriojoki were similar to populations from Varesjoki and Koorlan Lohioja, so these three populations together with Huhdanoja formed one tight resident group (Figure 15). The Aneriojoki trout was also similar to the resident stock from Myllyjoki of the Kiskonjoki river system, but additionally similar to Paimionjoki trout outside the Kiskonjoki system (Table 7).

Figure 14. The River Kiskonjoki watershed. River names are written in italics. Sampling sites are shown as red dots.

Table 7. Statistical significance of allelic frequency differences among samples from the Kiskonjoki river system and all nearby rivers in the Varsinais-Suomi area.
Symbols: NS = nonsignificant, * 5%, ** 1% and *** 0.1% levels of significance.

Pop	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Aurajoki	***	***	***	***	***	***	***	***	***	***	***	***	***	NS	**
2 Paimionjoki		***	***	***	***	***	***	***	**	NS	***	***	***	***	***
3 Purilanjoki			***	***	***	***	***	***	***	*	***	***	***	***	***
4 Halikonjoki				***	***	***	***	***	***	**	***	***	***	***	***
5 Uskelanjoki					***	***	***	***	**	***	***	***	***	***	***
6 Punassuon Lohioja						***	***	***	***	*	***	***	***	***	***
7 Kisko_Latokartanonkoski							***	***	***	**	***	***	***	***	***
8 Kisko_Myllyjoki								***	**	NS	***	***	***	***	***
9 Kisko_Koorlan Lohioja									*	NS	***	***	***	***	***
10 Kisko_Varesjoki										NS	***	***	**	***	***
11 Kisko_Aneriojoki											*	*	*	**	*
12 Kisko_Perniö_Juottimenoja												***	***	***	***
13 Kisko_Perniö_Pakapyölin Lohioja													***	***	***
14 Kisko_Perniö_Metsänoja														***	***
Fiskars_Main branch															***
Fiskars_Rislaån															-

In a genetic distance tree, the samples from the Kiskonjoki-Perniönjoki watershed were grouped into five groups (Figure 15). From all the samples, four presumably resident populations from the Kiskonjoki area were very similar (Huhdanoja [only two fishes], Varesjoki, Aneriojoki and Koorlan Lohioja). This result is also very logical, as Huhdanoja drains into Varesjoki and Koorlan Lohioja into Aneriojoki. They are all resident populations from the upper reaches of Kiskonjoki, and some gene flow obviously occurs among them. These four resident samples were pooled in the further analysis.

Two samples from the Perniönjoki tributary also resembled each other (Pakapyölin Lohioja and Juottimenoja-Piilioja): they were both assumed to be anadromous, and the samples were relatively small (Juottimenoja 21 individuals and Pakapyölin Lohioja 28 individuals), which might also have caused the difference. All three Perniönjoki samples differed to some extent from the trout populations of the Kiskonjoki river system, which includes an anadromous population at Latokartanonkoski in the lower reaches of the River Kiskonjoki and a resident population in the River Myllyjoki (Figures 15 and 16).

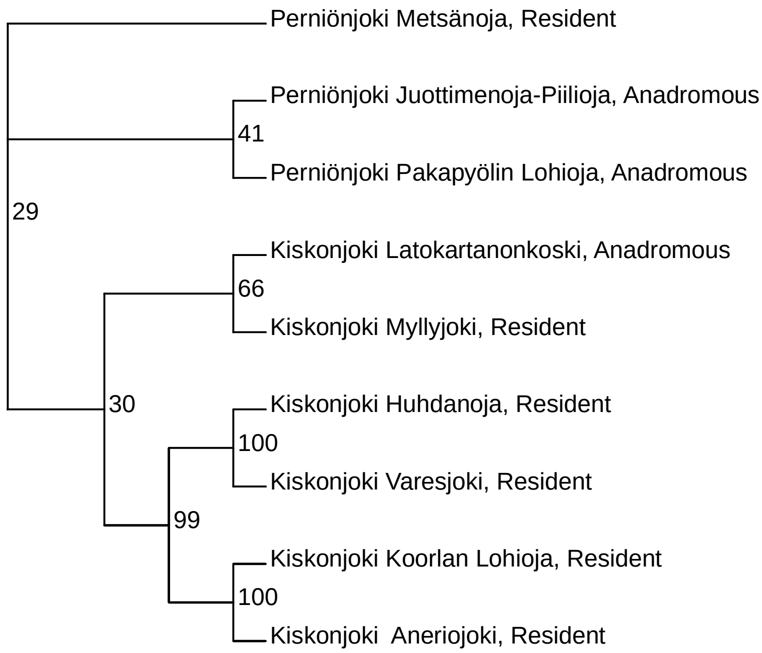

Figure 15. Genetic distances between all samples from the Kiskonjoki-Perniönjoki watershed.

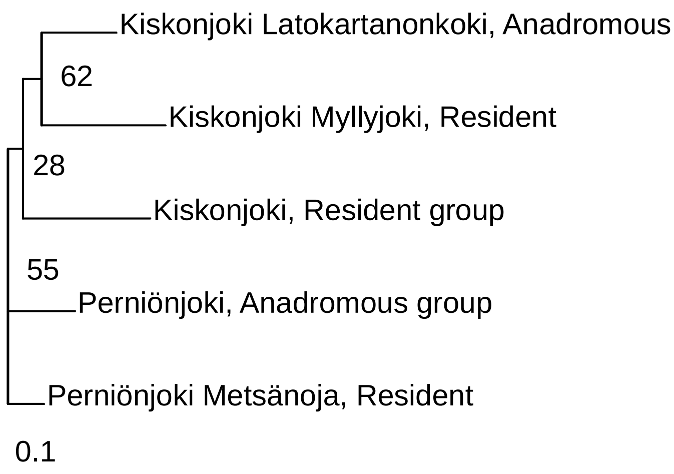

Figure 16. The five groups of brown trout populations in the Kiskonjoki water system after pooling of the most similar populations.

Five groups were used in the total analysis, and two of these were regarded as anadromous: the anadromous population of Perniönjoki and the Latokartanonkoski population (Figure 16). All five groups differed highly significantly from each other in their allele frequencies.

The diversity levels of Kiskonjoki groups varied for allelic richness from 3.45 for the Kiskojoki resident group to 5.65 for the Kiskonjoki-Perniönjoki-Metsänoja sample (Table 3). The Ne/N ratios of the Kiskonjoki samples were mostly at the average level, but the value for Myllyjoki was high, indicating mixing of stocks (Table 4). There was a fish hatchery (Heikurinen) until the 1980s, and since then releases of Rautalmminreitti brown trout have also taken place. According to the FST values, the Metsänoja sample showed somewhat unexpectedly strong similarities with Fiskarsinjoki, Siuntionjoki and Espoonjoki-Ryssänniitunoja, with the lower reaches of Vantaanjoki, and even with Urpalanjoki trout from eastern Finland. This indicates at least mixing with some hatchery stocks, although the stock is classified as resident and original (Table 5). The relatedness among sampled individuals was also especially low, being 2.2%, which indicates mixing of populations (Table 4). There may additionally have been some unknown trout releases into the area, which might explain the values. Further sampling is recommended before final conclusions can be drawn, because some of the samples were taken from below the dam. Straying fish might thus affect this result, and the effect of hatchery releases might result from this.

The anadromous Latokartanonkoski sample in the lower reaches of Kiskonjoki also shows similarity with Fiskarsinjoki trout. The other three Kiskonjoki groups appear to be relatively unique, or at least no strong similarities with other stocks could be detected (Table 5). The most likely anadromous material seems to be in the Perniönjoki tributary. This population might even serve as founder material for a new hatchery stock, if needed, to be used as an enhancement stock in southwestern Finland, or as a sea ranching stock, in addition to Aurajoki trout.

It is recommended not to release foreign stocks into this river system, and to stop releasing Aurajoki or any other stock into the Latokartanonkoski rapids. The transportation of fish from strong donor populations within the river system could instead be considered as an enhancement method, provided that potential spawning grounds are available. The catching of spawners and release of their newly hatched fry would be one cost-effective way to improve juvenile densities in the spawning grounds.

All southwestern populations were also compared with each other and with the Fiskarsinjoki trout from Uusimaa, which is genetically very similar to the Aurajoki and Kiskonjoki-Latokartanonkoski populations (Figure 17). Together with the two Fiskarsinjoki samples, they also formed one group in the tree. Two samples from the River Fiskarsinjoki (Fiskarsinjoki main stream and Risslaån) differed somewhat from each other because of Ingarskilanjoki trout releases into the Risslaån. The local original Fiskarsinjoki trout from the Brunkombäcken has probably already disappeared from the main stream.

Kiskonjoki populations were distributed in several branches of the large tree when other stocks were included. However, the anadromous and resident populations from the Kiskonjoki-Perniönjoki grouped into the same branch (Figure 17).

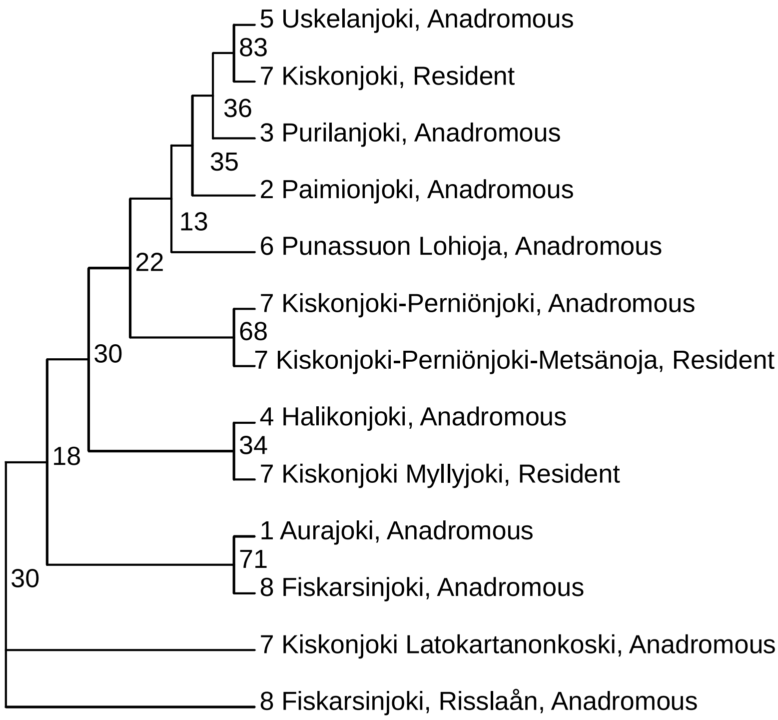

Figure 17. Dendrogram of the populations of river systems numbered 1–8 from the Varsinais-Suomi area and the Fiskarsinjoki population from the Uusimaa area.

Southwest Finland populations

For the whole Varsinais-Suomi area (ELY Centre for Southwest Finland), the genetically most valuable anadromous trout potential is in the rivers Paimionjoki, Halikonjoki, Uskelanjoki and Kiskonjoki-Perniönjoki. In addition, valuable resources occur in Aurajoki and Kiskonjoki-Latokartanonkoski, although they are mixed populations. Clearly very small effective sizes were observed for Purilanjoki and Punassuon Lohioja. The potential for anadromous trout populations might exist in the upper reaches of the Kiskonjoki watershed, if only the migration routes were open and the migration distances were not too long. Nevertheless, valuable resident trout populations currently also occur there.

The two large river systems, Uskelanjoki and Kiskonjoki, clearly differed in their population substructure. No substructure could be observed in the Uskelanjoki system, while a clear substructure and potentially different anadromous and resident groups occurred in the Kiskonjoki river system. Some of the differentiation might be native and caused by migration barriers or differences in migration tendency, but some were evidently caused by the releasing fish of a different origin into different areas of the river. These differences tended to remain, at least up until the time of sampling.

4.2. ELY Centre for Uusimaa

4.2.1. Fiskarsinjoki

River Fiskarsinjoki drains into the Gulf of Finland, and the area of the watershed is 82 km^2, with as much as 18% of this is consisting of lake surface (Ekholm 1993). At the beginning of the 20th century, some Atlantic salmon and anadromous trout were still occasionally caught from the river. The last salmon weighing over 10 kg was caught in 1910 (Hurme 1962). In 2000, yolk sac fry of Ingarskila trout were released into the Fiskarsinjoki tributary, Risslaån (Figure 18).

Trout have previously also been released into the main stream and the Brunkombäcken tributary. Below the lowest dam in the Fiskarsinjoki, newly hatched fry of Isojoki trout were released in 1986 and also in 1987. Newly hatched fry of Dalälven trout from Sweden have also been released into the Brunkombäcken. Further trout releases have been carried out into Lake Degersjö and the tributaries above it, including Myllykylänjoki (Kvarnbyån) and Anskunjoki (Lempinen 2001). The recent releases have been of Aurajoki trout, and most recently, following the sampling for this study, Ingarskilanjoki trout (Janatuinen 2012a).

Two samples for this study represent Fiskarsinjoki trout: one from the main branch and the other from the Risslaån tributary (Figure 18), and they are relatively similar. Trout from the Fiskarsinjoki main branch are no longer assumed to be native, as so many fish of foreign origin have been released there.

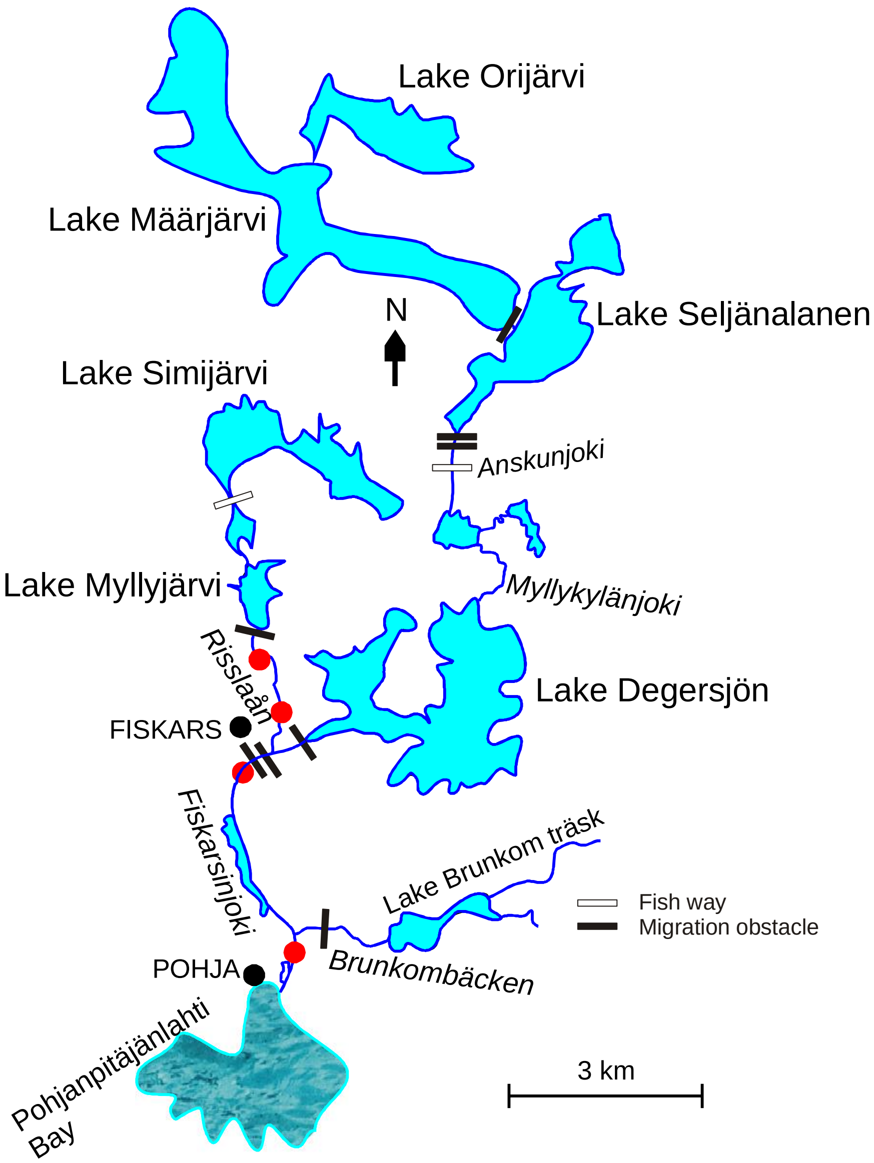

Figure 18. The Fiskarsinjoki river system. Sampling sites shown as red dots.

The Fiskarsinjoki trout had a level of high diversity, with an allelic richness of 6.0 (Table 3), and it displayed similarity with several other stocks: Isojoki hatchery stocks and also populations from the lower reaches of Vantaanjoki and upper reaches of Summanjoki, where Isojoki trout have been released (Table 5). Because of its strong similarity with the Aurajoki trout, it clustered close to the geographically more western trout stocks. The ratio of effective to actual size (Ne/N) was 0.66 in the sample, which is clearly above 0.5, and indicates a wide genetic background. The mean relatedness was also relatively low (4.3%) (Table 4).

In the River Fiskarsinjoki, no original brown trout genetic material probably remains, and natural production is only occasional. During recent years some offspring have, however, been found. The water quality in the river system is excellent, but the spawning sites, which can be accessed from the sea, are small. Restoration is still needed, as some spawning grounds are unrestored.

The Fiskarsinjoki trout stock has high diversity, but a mixed background. It is not recommended to be distributed further into other watersheds with more native trout populations. Spawning sites should be improved and a long-term decision on the enhancement stock should be made, if enhancement releases are needed. Large dams already exist before Risslaån. At least the two lowest dams should be opened for spawners to ascend to the spawning sites in the Risslaån. In the long term, fishways at dams above Risslaån should also be constructed. The recently renewed hydropower plant has an obligation to allow the building of a fishway and provide its water supply. The power plant is located in the uppermost dam of the River Fiskarsinjoki, and thus above the Risslaån and just below Lake Degersjö.

4.2.2. Karjaanjoki

The River Karjaanjoki watershed is 2 046 km^2 in area, and 12% of this is lake surface (Ekholm 1993). The watershed drains into the Gulf of Finland via the River Mustionjoki (Figure 19). Salmon and sea trout were caught in Mustionjoki as early as in the 14th century. Sea trout previously ascended Mustionjoki to the rivers above the large Lake Lohjanjärvi. The River Mustionjoki was finally closed to fish entrance in 1956, when the dam at the Åminnefors rapids was rebuilt (Jääskeläinen 1944, Marttinen 1990, Marttinen and Vuorinen 2005). The native trout stocks of the Karjaanjoki watershed have previously been subjected to allozyme analysis (Koljonen et al. 1992), and also microsatellite analysis in the Karjaanjoki Life project (Saura 2005a, 2005b).

Eight samples of trout were available from the Karjaanjoki watershed. Above Lake Lohjanjärvi, the watershed is divided in three main river systems: (1) Nummenjoki (Nummenjoki–Pitkiönjoki and Pusulanjoki-Räpsänjoki-Myllypuro), (2) Karjaanjoki (Saavajoki and Nuijajoki) and (3) Vihtijoki, which all have further tributaries. The trout from the upper reaches probably do not generally migrate to the sea. There have also been trout populations in the smaller tributaries, but they have disappeared during the last 10 or 20 years. However, Hongistonpuro, a small tributary that drains into Lake Hiidenvesi, still contains trout.

The history of the trout population in the Vihtijoki tributary is unknown prior to the beginning of the 20th century. A fish hatchery in Hiiskula village, in the upper reaches of the Vihtijoki River, already operated from 1892. Trout were imported from Russia for the hatchery, and released into the Vihtijoki for the first time in 1893 and 1894 (Marttinen 1990, Kettunen 1992a). In addition, Danish trout have later been released into the Sortoja brook, for the first time in 1962. Since then, trout from the Rautalamminreitti stock have mainly been used in lake releases in the area (Kettunen 1992a). On the other hand, there is old information on the harvesting of freshwater pearl mussels from Vihtijoki (Oulasvirta 2010b). This means that already before the stocking there must have also been trout in Vihtijoki, as well as above the lakes Hiidenvesi and Lohjanjärvi.

In the Karjaanjoki (Vanjoki) tributary, trout were already fished with sport fishing equipment in the years following the Winter War (1939). The first known larger scale stocking efforts took place in the 1960s, but more systematic releases started in 1971 (a few thousand juveniles per year). In the 1970s, mostly one-summer-old trout were released into many of the smaller tributaries and brooks in the Karkkila area, waters that eventually flow into the River Karjaanjoki. In the 1980s and 1990s, stocking was conducted by local authorities and water owners, mainly with older juveniles. At the same time, trout were also stocked into lakes on a smaller scale (Jormanainen 1989, Lehtinen 1982). Trout stocking into streams ceased in this area after the early 1990s.

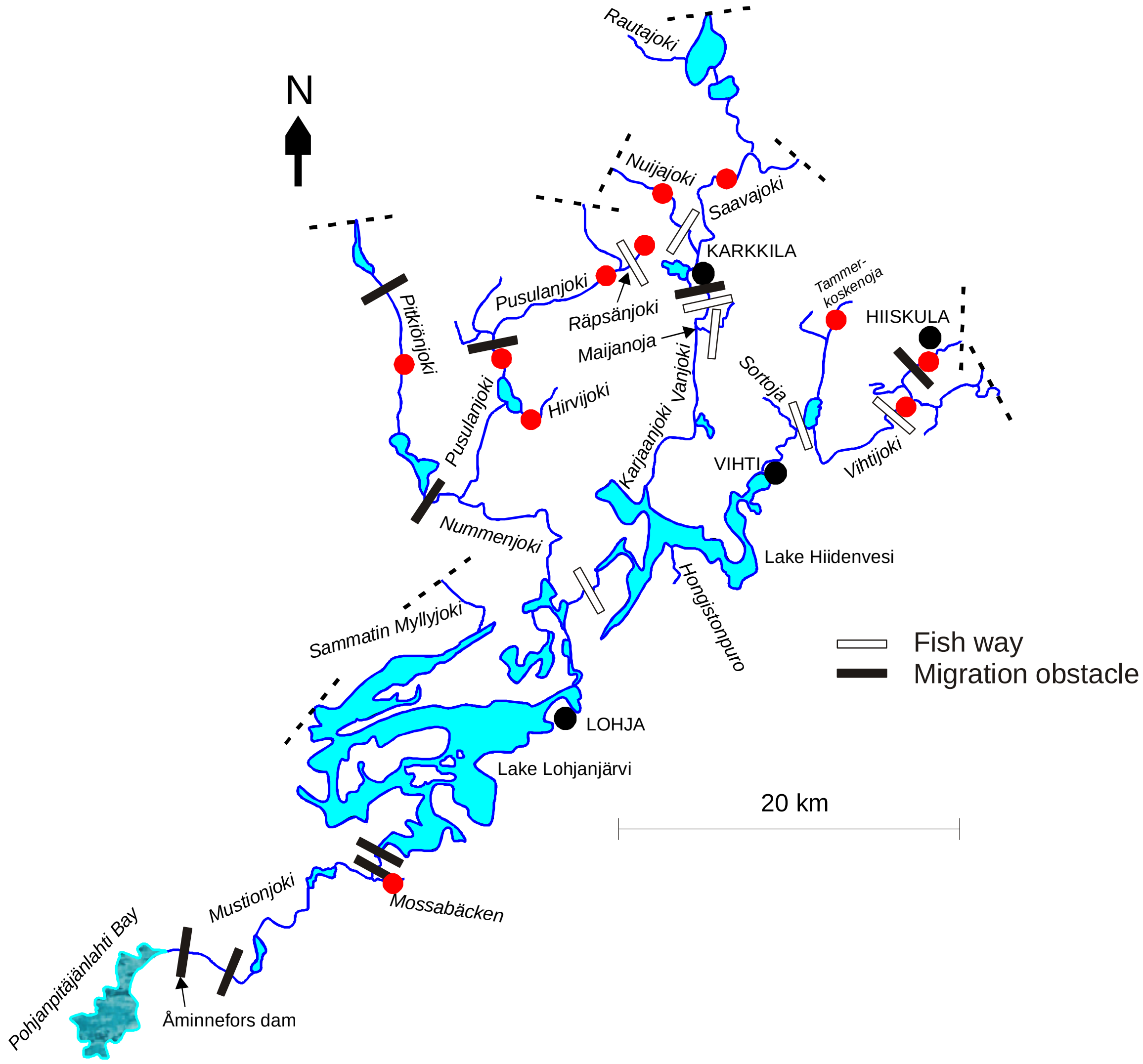

Figure 19. The Karjaanjoki water system. Mustionjoki drains into the sea. Sampling sites are shown as red dots.

Current trout populations use Lake Lohjanjärvi as a feeding migration area, and partly comprise migratory freshwater trout. According to local information, large migratory freshwater trout were already observed in the River Vihtijoki in the 1940s below the lowest dam. Freshwater trout smolts were also caught in the river mouths of Karjaanjoki and Vihtijoki in Lake Hiidenvesi in the 1990s and 2000s.

From the previous analysis of the Karjaanjoki Life project, which only included samples from the Karjaanjoki watershed, it can be seen that several samples from the River Pitkiönjoki form one group and samples from Nuijajoki, Saavajoki and Maijanoja from the Karjaanjoki area form another group (Figure 20). The Mustionjoki, Mossabäcken population differs clearly from the others.

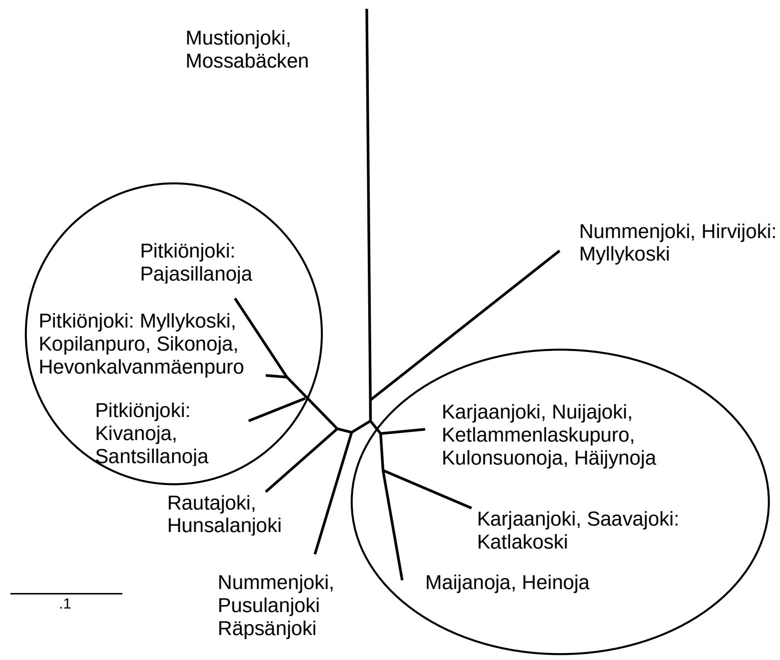

Figure 20. Genetic distances among the previously analysed samples within the Karjaanjoki watershed, in the Karjaanjoki Life project (Saura 2005a, 2005b).

In the current analysis, partly the same samples were used and more loci were genotyped, so that the number of analysed loci was increased from 10 to 16 (Figure 21). In addition, samples from the Vihtijoki tributary were included.

In general, grouping of samples corresponded to the geographical distances between the tributaries. All Vihtijoki samples grouped tightly together, and next to these were Saavajoki and Nuijajoki, which are both tributaries of the River Karjaanjoki (Figure 21). The two samples from the Nummenjoki branch also grouped together with Pitkiönjoki and Pusulanjoki, Räpsänoja. This geographically logical structuring supports the idea that at least some of the populations still retain their original genetic material.

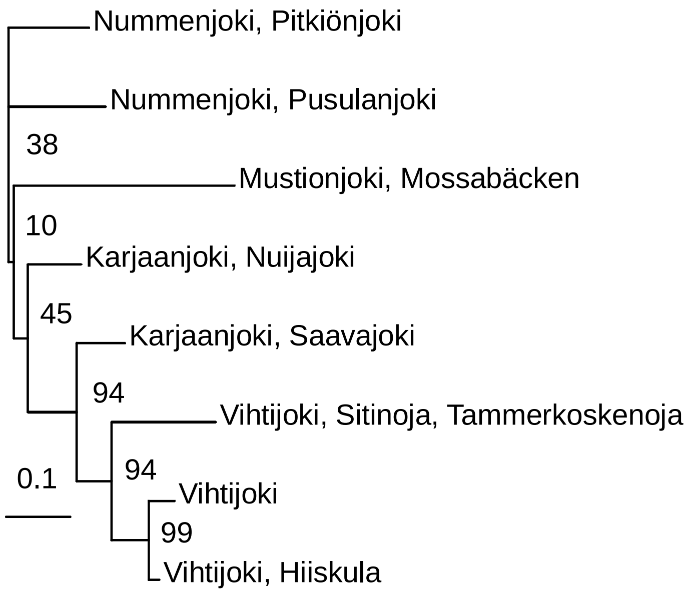

Figure 21. Genetic distances among currently analysed brown trout samples from the Karjaanjoki water system, based on 16 DNA microsatellite loci.

Population differentiation among all population pairs was statistically highly significant. However, differences between differentiation levels occurred, when measured as pairwise FST values (Table 8). Most unique was the Mustionjoki population, and the lowest FST was between Vihtijoki and Vihtijoki Hiiskula samples (FST = 0.04). Differentiation between samples within the rivers Nummenjoki and Karjaanjoki was the same, being 0.12. Mustionjoki is potentially an anadromous population. All other Karjaanjoki populations are assumed to be resident, and the migration distance to the sea is long for them. In the later analysis, all three Vihtijoki samples were pooled, as well as the Nummenjoki samples and Karjaanjoki samples.

Table 8. . Pairwise FST values among brown trout populations in the Karjaanjoki watershed.

	Population	Mustion joki	Num. Pitkiön	Num. Pusula	Kar. Nuija	Kar. Saava	Kar. Vihti	Kar. ViHiis
1	Mustionjoki	-						
2	Nummenjoki Pitkiönjoki	0.26	-					
3	Nummenjoki Pusulanjoki	0.27	0.12	-				
4	Karjaanjoki Nuijajoki	0.26	0.11	0.12	-			
5	Karjaanjoki Saavajoki	0.29	0.17	0.16	0.12	-		
6	Vihtijoki	0.33	0.23	0.22	0.16	0.15	-	
7	Vihtijoki, Hiiskula	0.27	0.19	0.17	0.13	0.11	0.04	-
8	Vihtijoki Tammerkoskenoja	0.44	0.33	0.35	0.28	0.20	0.21	0.19

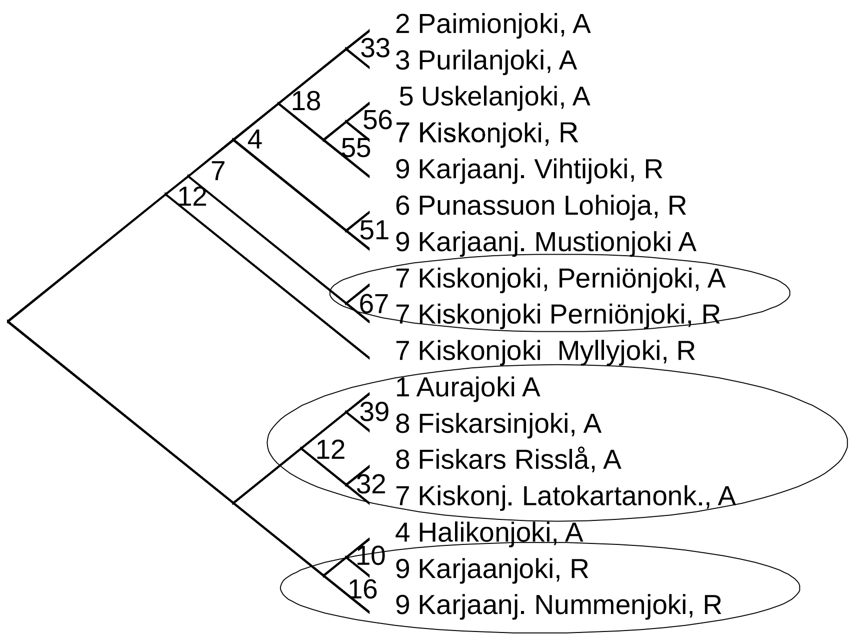

Figure 22. Karjaanjoki samples together with previously analysed brown trout samples. A denotes anadromous and R resident populations. The numbers in front of the rivers names indicate the number of the river system from west to east.

Karjaanjoki samples grouped in the analysis into three different branches in a distance tree with other brown trout stocks from the same area (Figure 22). Karjaanjoki Vihtijoki grouped together with resident Kiskonjoki trout and anadromous Uskelanjoki trout. The Mustionjoki population has similarity with the Punassuon Lohioja population, and Karjaanjoki grouped together with Nummenjoki and Halikonjoki. Both anadromous and resident Perniönjoki populations were placed in the same branch. In addition, as previously, Aurajoki, Fiskarsinjoki and Kiskonjoki Latokartanonkoski grouped together.

The diversity levels in the Karjaanjoki brown trout populations were generally high, with the Mustionjoki population having the lowest level (0.52), and Nummenjoki populations having the highest diversity (0.64, 0.69), being above the average level (0.62) (Table 3).

The sample size (23), and especially the effective size of the Mustionjoki population was very low, being only 6, and all fish could possibly have resulted from 8 pairs. The Ne/N ratio was low, 0.26, indicating a narrow genetic background (Table 4). The relatedness among individuals in the Mustionjoki sample was also very high, being 10.5% (Table 4). In this case, sampling was assumed to have been sufficient, so the state of the population in the Mustionjoki and Mossabäcken brook is obviously very weak, and it can hardly be regarded as a self-sustaining population any longer.

In the upper tributaries the situation seems better, with the Nuijajoki tributary having the highest Ne/N ratio (0.70). In the Vihtijoki tributary, the number of founder families for the sample was the highest, being over 100 families, but the Ne/N ratio was only 0.25 (Table 4). The effective size of the Saavajoki population was probably underestimated, as sampling was not successful.

Different strategies are recommended, at least for the Nummenjoki and Mustionjoki areas. The Karjaanjoki and Vihtijoki populations are more similar, but if the number of individuals in spawning areas seems sufficient for separate strategies, this is recommended. Sitinoja Tammerkoskenoja was clearly a distinct resident population, and the samples were also collected above dams.

Both Nummenjoki populations displayed some similarities with Mankinjoki and Vantaanjoki populations. Other Karjaanjoki populations appeared more unique.

The Mustionjoki population is weak and probably very small. The level of natural production is unknown. It has possibly already disappeared, as the only spawning brook is small, and in recent years no trout have been caught there. The brook is located between hydropower dams. Between the brook and sea there are two dams, and above, between the brook and Lake Lohjanjärvi, are two further dams. The isolation time from the sea has possibly been too long for a trout population to survive after damming of the river. There have also been changes in land use and the water quality of the spawning brook.

The populations above Lohjanjärvi are suspected to not usually migrate to the sea, but rather to undergo a feeding migration in the lake, and are thus migratory freshwater trout. All upper spawning grounds produce fish that enter the lakes, but the returning routes are not always open. The Karjaanjoki water system is a wide and important water system in southern Finland. Although the upper parts of it do not include anadromous trout or even very much potential for such, the brown trout populations are included in the current analysis.

The uniqueness of the Karjaanjoki trout should be maintained, and if enhancement or reintroducing releases are needed, trout from its own river system should be used. Mustionjoki is the only river in the Uusimaa area in which freshwater pearl mussels (*Uniocrassus margaretifera*) are known to still exist. They additionally occur only in the Kiskonjoki watershed and in the Russian Vammeljoki. The River Mustionjoki is also included in the EU Natura 2000 network, and in the new National Fish Way Strategy it is classified as a target of high importance. Other rivers mentioned in this strategy are Kiskonjoki, Siuntionjoki, Kymijoki, Virojoki and Hiitolanjoki.

The small, but aged, population of freshwater pearl mussels in the River Mustionjoki has not reproduced in several decades, but is still capable of reproducing. Their reproduction is dependent on the occurrence of trout or salmon juveniles and a suitable habitat for the smallest mussels (Oulasvirta 2010a, 2010b, Oulasvirta & Syväranta 2011, Vuorinen 2011, 2012).

4.2.3. Ingarskilanjoki

The area of the Ingarskilanjoki river system is 160 km^2 and 0.17% of this consists of lakes (Ekholm 1993). It is an old sea trout river, and the history of the trout has already been described (Marttinen and Koljonen 1989, Saura 2001). The water flow varies strongly and the water level may occasionally be critically low for trout. The contemporary trout stock has sometimes been suspected to originate wholly or partly from possible releases of Danish trout in the 1960s. It is, however, known that trout have existed in the river both before and after possible releases. The Ingarskilanjoki trout population was rescued by taking it into a hatchery in 1987–1988. The population in the river was strongly supported by hatchery releases. The current stock mainly originates from hatchery releases, and the parr density was on average 20.8 (0–82.2) 0+ individuals per 100 m^2 during 2001–2012 (ICES 2013). Ingarskilanjoki and Mustajoki are the only anadromous southern stocks from which a representative broodstock has been created. This broodstock has been widely used in stockings and reintroductions in several rivers of the Uusimaa area.

Two samples of Ingarskilanjoki trout were available: one sample from 2005 simply named Ingarskilanjoki (n = 175), which is partly of hatchery origin, and another sample of wild offspring from 2011 from the Pärthyvelbäcken Krämars brook, which is located in the headwaters of the main branch (n = 17) (Figure 23). The FST between samples was 0.10. However, they grouped tightly together in the distance tree and they were pooled in the later analyses (Figure 24).

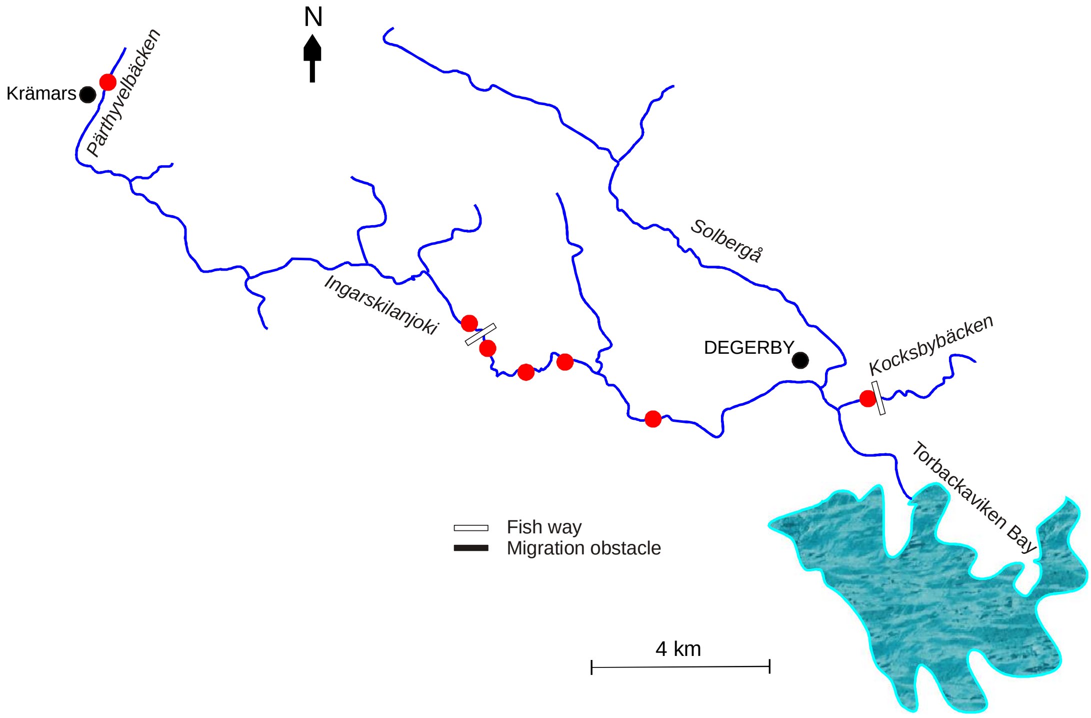

Figure 23. The Ingarskilanjoki river system. Sampling sites are as shown as red dots.

The Ingarskilanjoki trout has a high diversity value of 0.64 (Table 4), and it is relatively unique. It bears close resemblance to many of the sampled populations, as it has been regularly released into several rivers, especially Vantaanjoki (0.02, 0.03, 0.05) and Koskenkylänjoki (0.01). For both of these, the FST values were low (Table 5). The close similarity with Mankinjoki (0.04) and Siuntionjoki (0.07) is more likely a result of the original similarity of the geographically very close populations. The FST value between Ingarskilanjoki and the suspected Danish sea trout sample was 0.13 (Table 5), which is not especially low. However, several other studied populations were more similar to the Danish trout than the Ingarskilanjoki trout. The result does not therefore support the expectation of Danish origin. At least the majority of the population originates from other sources. The FST between Ingarskilanjoki and Isojoki was of approximately the same level, 0.12, as that between Ingarskilanjoki and the Danish trout.

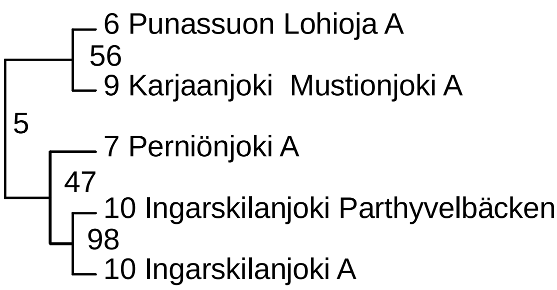

Figure 24. Genetic distance tree of two Ingarskilanjoki brown trout samples and some of the nearby anadromous populations. The numbers between branches showing the bootstrap values for similar clustering from 1000 repeats.

The effective size of the Ingarskilanjoki sample was 45, and it was a result of over 100 full-sib families. However, the Ne/N ratio was quite low, being only 0.23 (Table 4), which is probably a result of hatchery breeding. The mean relatedness was, however, not very high (5.7%) (Table 4).

Ingarskilanjoki is the only anadromous trout stock from which both wild and hatchery components are available. The water quality in the river is sufficient for brown trout and the spawning sites are in quite a good state, but the large variation in water flow has been a problem. Smolt production has increased to such an extent that supportive releases could be reduced. Smolt releases could be carried out into the river mouth. The ending of releases should be set as a goal in the medium term. In its current state, the stock cannot sustain a river fishery, and temporal fishing regulation for the river mouth fishery is in force.

Ingarskilanjoki should be defined as an index river for the natural production of wild smolts for the Finnish side of the Gulf of Finland. Monitoring of both spawners and smolts should be established.

4.2.4. Siuntionjoki

The drainage area of Siuntionjoki is 488 km^2. It drains into the Gulf of Finland via Pikkalanlahti Bay. About 5% of its area consists of lakes (Ekholm 1993). Sea trout in the Siuntionjoki are already historically well known. Their distribution, history and population size fluctuations have also previously been reported (Marttinen and Wessman 1987, Heino 1997). According to Segerstråle (1947a, b), in 1938 to 1940, trout spawners were caught from the Sjundby rapids by the Fiskodlingens Vänner society, and newly hatched fry were released back into the river system. The activity ended later after the war because of difficulties in obtaining spawners from the Sjundby area, which remained in Russian rented territory. In the spring of 1939, a small number of juveniles (about 9000 individuals) of Vantaanjoki (Kylmäoja) origin were also released into the river by the same manager.

The Siuntionjoki trout is regarded as a relatively native, original anadromous trout stock for the Uusimaa area. Two samples were available, one from the main stream of Siuntionjoki, Passilankoski (N = 15), which is regarded as anadromous, and the other from Kirkkojoki Lempanså (N = 54), which is probably nowadays mainly resident (Figure 25). The samples were not very similar to each other, (FST = 0.16), as all grouped into different branches (Figure 26). The sample from the Passilankoski was small, and the difference might be a result of the small samples size. Nevertheless, the two samples were kept separate. The main stream sample somewhat resembles Ingarskilanjoki trout (FST = 0.07) and Mankinjoki (FST = 0.06), and several Vantaanjoki samples, especially the lower and middle reaches of the Vantaanjoki populations, where Ingarskilanjoki trout have been released.

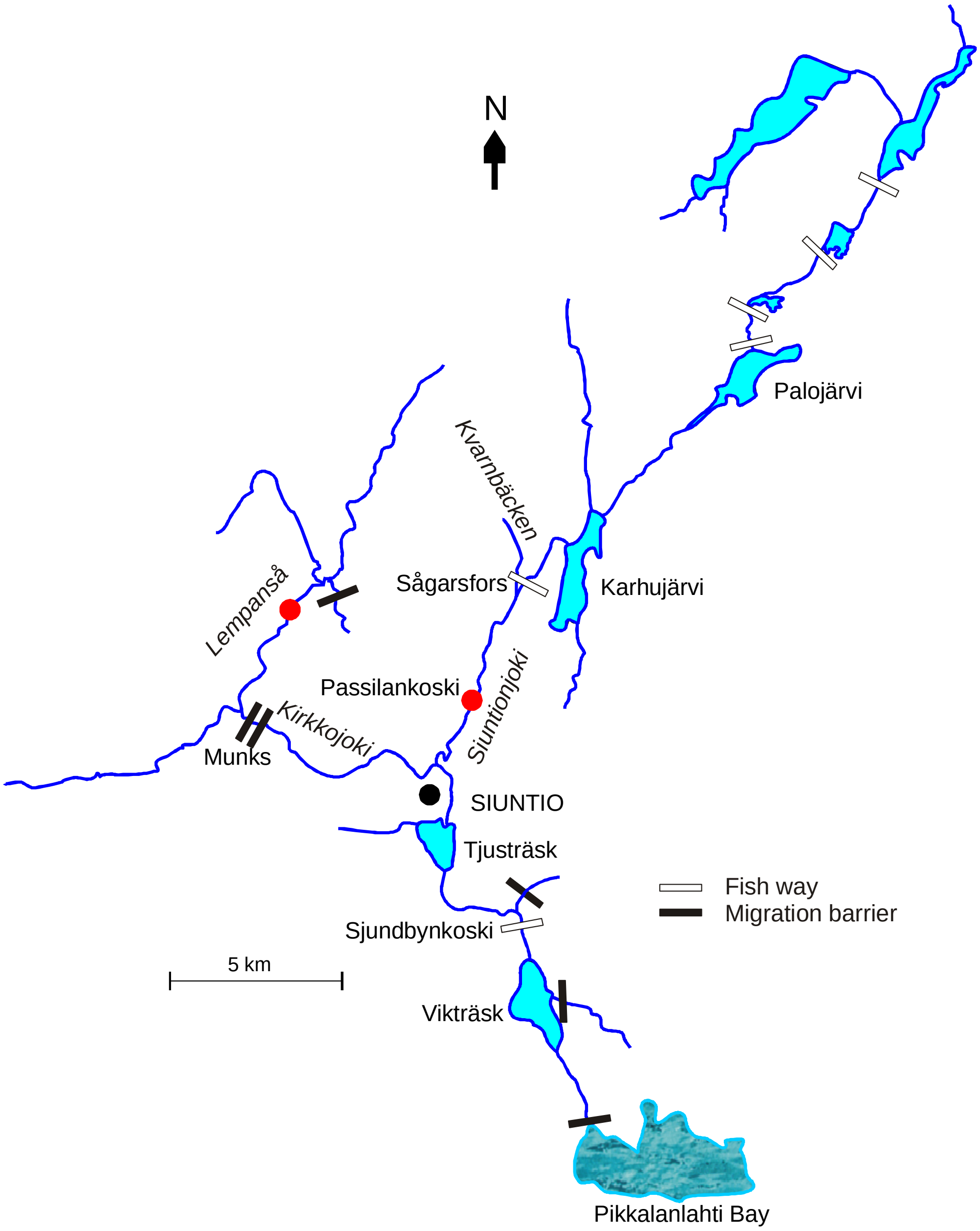

Figure 25. The Siuntionjoki river system. Sampling sites are shown as red dots.

The resident Kirkkojoki sample deviated more from the nearby stocks (FST 0.15–0.27), and did not have any very closely related populations. There should not have been any major releases into the Siuntionjoki, so the similarity with the Ingarskilanjoki and Mankinjoki populations is assumed to be a result of their common colonization history and close geographical connection. Ingarskilanjoki, Siuntionjoki and Mankinjoki represent the same type of Uusimaa sea trout. The diversity in both Siuntionjoki samples was approximately on the average level.

More families represented the Kirkojoki sample (38), than the Passilankoski sample (15) (Table 4). The Ne/N ratio was high for both, and the unrepresentative sampling and small sample size (16) might have caused the exceptionally high value (0.94) for the Passilankoski sample. In both samples, the relatedness within populations was somewhat elevated (Table 4).

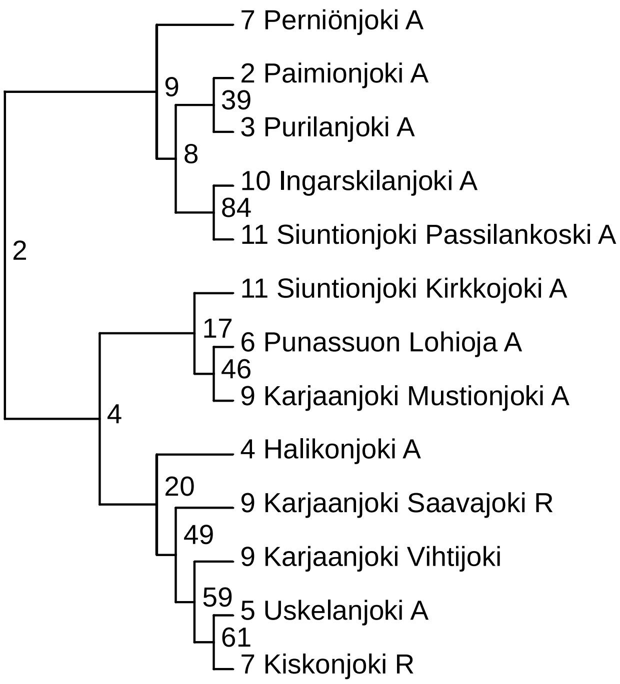

Figure 26. Genetic distance tree for the two Siuntionjoki brown trout samples, Passilankoski and Kirkkojoki, and the genetically most similar populations from rivers of the nearby area.

More samples are needed from the Siuntionjoki brown trout population and especially from the main branch before final conclusions can be drawn. At present, it can be regarded as one management unit. There are some water quality problems in the river and also dams in the tributaries, most notably in the River Kirkkojoki in Munks. A fishway has been planned at the Munks dam. River restoration is recommended. The Kvarnbäcken tributary offers especially good spawning sites. At the beginning of the 1990s it was the main spawning site of the main branch, but is now possibly already empty of trout juveniles. Other important improvement sites include Lappträskbäcken brook in the lower reaches of the main branch and the third upper branches of the Lempansån tributary (including Munkkaanoja, Kivikoskenpuro and Kivikoskiån).

The stock cannot sustain a river fishery at present, and in the future, only a catch and release fishery could probably be permitted. No foreign stocks should be released there. The River Siuntionjoki belongs to the EU Natura 2000 network, partly because of its original sea trout stock.

Siuntionjoki is known to have been an old freshwater pearl mussel river, but the species has become extinct in this watershed (Siuntionjokineuvottelukunta 1989). There is also some old information on freshwater pearl mussel harvesting in either Siuntionjoki or Mankinjoki watersheds (Rudenschöld 1899).

4.2.5. Mankinjoki

The River Mankinjoki watershed is 175 km^2 wide and about 8% of its area consists of lakes (Ekholm 1993). Mankinjoki is a historically well-known sea trout river (Segerstråle 1937, Saura 2001, Janatuinen 2009). In the 1930s, there was a sea trout run along the Gumbölenjoki tributary up to the Gumböle dam. In the Mankinjoki branch, upstream running was only possible as far as the dams of Espoonkartanonkoski (Figure 27).

The River Mankinjoki has considerable potential for sea trout production. Several sectors have unconstructed river stretches. Some dredging has been carried out and wastewaters have been a problem, especially in the past.

It is assumed that the native sea trout stock has remained in the river until the present. A genetic analysis of Mankinjoki and Espoonjoki trout stocks has also previously been conducted. The history and current state of the trout stock was described by Janatuinen (2009).

In the upper branches of the river system, above several dams in the Nuuksion Myllypuro brook, draining into the Nuuksion Pitkäjärvi Lake, a self-sustaining brown trout stock exists, which at least partly originates from releases (Janatuinen 2009). It is located mostly inside the Nuuksio National Park. In some small brooks draining into Lake Pitkäjärvi, some juveniles have also been found in the last decades, obviously of hatchery origin.

Tree samples representing Mankinjoki (Espoonkartanonkoski, Gumbölenjoki Mynttilänkoski and Gumbölenjoki Myllykoski) (Figure 28) were all very similar and grouped near to each other. In particular, the two samples from the Gumbölenjoki tributary were similar. They also grouped near to the geographically close Ingarskilanjoki and Sipoonjoki populations. All Mankinjoki river system samples were pooled for further analysis.

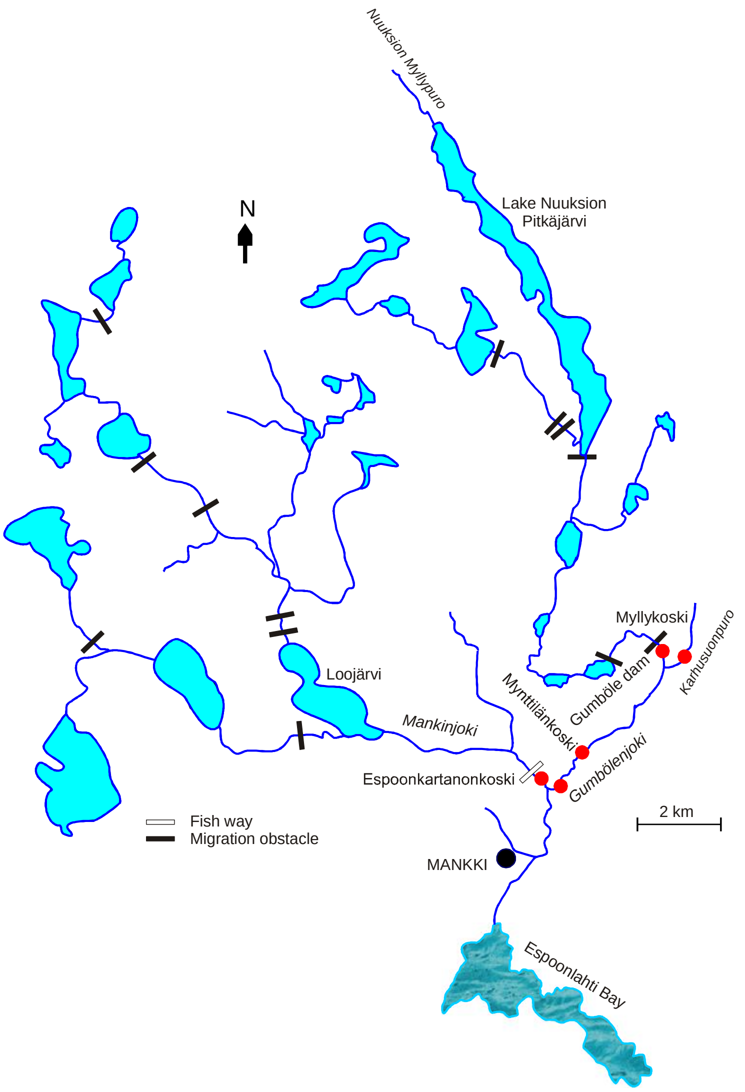

Figure 27. The Mankinjoki river system. Sampling sites are shown as red dots.

Figure 28. Genetic distances between brown trout samples from the rivers Mankinjoki, Siuntionjoki and Ingarskilanjoki.

Table 9. Pairwise FST values between brown trout samples from Ingarskilanjoki, Siuntionjoki, Mankinjoki and Espoonjoki.

	Ingar Parth	Ingar-skilanj.	Siuntio Kirkko	Siuntio Passila	Manki Espoo	MankiG Myntti	MankiG Mylly	Espoo Gloms	Espoo Glims
Ingarskilanj.	0.10								
SiuntioKirkko	0.27	0.20							
SiuntioPassi	0.14	0.07	0.16						
MankiEspoo	0.12	0.06	0.16	0.05					
ManGMyntti	0.14	0.06	0.15	0.06	0.06				
ManGMylly	0.18	0.07	0.19	0.08	0.06	0.05			
EspooGloms	0.17	0.11	0.18	0.11	0.11	0.09	0.09		
EspooGlims	0.23	0.15	0.21	0.15	0.12	0.09	0.09	0.08	
EspooRyssän	0.38	0.25	0.27	0.25	0.24	0.22	0.21	0.14	0.23

All FST values within the Mankinjoki river system were below 0.09 (Table 9). In addition, all of them bore close similarity with Ingarskilanjoki trout and also with the Siuntionjoki Passilankoski sample. The differences compared to the Espoonjoki tributaries Glomsinjoki and Glimsinjoki were also small. The sample from Espoonjoki Ryssänniitunoja was slightly more different. The diversity level of Mankinjoki trout (0.69) was above the average level (0.62) (Table 3). The Mankinjoki trout belongs to the same group as Ingarskilanjoki (FST = 0.04) and Siuntionjoki (FST = 0.05). Some influence of Isojoki trout releases is also possible (FST = 0.04) (Table 5).

The number of families involved in production was quite high, being 60 full-sib families (Table 4). The effective size of the sample was 33, but the Ne/N ratio was only 0.25. Relatedness among individuals as a whole was not very high (5.8%) (Table 4).

The Mankinjoki population is still regarded as relatively native, and the similarity among samples within the river system was so high that the Mankinjoki trout can be regarded as one management unit. Good potential for increasing smolt production exists in this river system. No releases of foreign stocks should be allowed. Restoration of juvenile and spawning habitats is needed, as well as opening of migration barriers. The spawning stock cannot sustain a river fishery. The route of returning spawners cross Espoonlahti Bay, into which the River Mankinjoki (and neighbouring Espoonjoki) drains, should be free of fishing. A fishway from the sea into the river should be opened for the spawners ascending the river mouth.

In the Mankinjoki watershed, freshwater pearl mussels still existed in the River Gumbölenjoki less than fifty years ago, but the species has now become extinct (Laaksonen et al. 2008, Oulasvirta 2010). There is also some old information on freshwater pearl mussel harvesting in either Siuntionjoki or Mankinjoki watersheds (Rudenschöld 1899).

4.2.6. Espoonjoki

The Espoonjoki watershed is 132 km^2 wide and about 6% of the area is formed by lakes (Ekholm 1993). It drains into the Gulf of Finland via the same Espoonlahti Bay as the River Mankinjoki. There were anadromous trout in Espoonjoki in historical times, and the stock is assumed to have run along the River Glimsinjoki as far as Lake Pitkäjärvi (Ovaskainen and Pärnänen 1971, Janatuinen 2009). Some catches were recorded from 1800 century, and it is believed that the stock was quite strong until the 1960s (Kettunen 1992b), but it markedly declined until the 1990s. Beside the current sites of occurrence, brown trout have lived in the Häklänpuro brook draining into Lake Bodomjärvi. The last observations of these trout are from the 1970s (Kettunen 1992b). In 1992, trout of the Rautalamminreitti stock were released once into the brook, but this release did not provide any results. The only other release into the river system has been of 200 one-summer-old juveniles, which were released into the Pikku-Ryssänoja brook, a tributary of Ryssänniitunoja.

Three main sites were sampled in the River Espoonjoki: the tributaries Glomsinjoki, Glimsinjoki and Ryssänniitunoja (Figure 29). Glomsinjoki and Glimsinjoki grouped together (FST = 0.08), and Ryssänniitunoja was slightly different from these (Figure 30). The sample from the Glimsinjoki tributary grouped more closely to the Mankinjoki population, but it included only nine fishes.

According to pairwise FST values (Table 5), the Espoonjoki trout population has some similarity with the Ingarskilanjoki trout, but not as strong as with trout from Mankinjoki. The genetic distance from the neighbouring Mankinjoki was, however, not large. The diversity level of Ryssänniitunoja was low and that of the other pooled sample was above the average value. The Ryssänniitunoja population is regarded as resident and possibly at least partly isolated from the main population, the pooled Glomsinjoki-Glimsinjoki population, which is anadromous. The sample size of the Espoonjoki trout was relatively large (72), but the effective size was small, being only 12, and only 22 full-sib pairs were involved in producing the sampled fish, although sampling occurred in two years (Table 4). In Ryssänniitunoja the Ne/N ratio was 0.54, but the measured relatedness was very high.

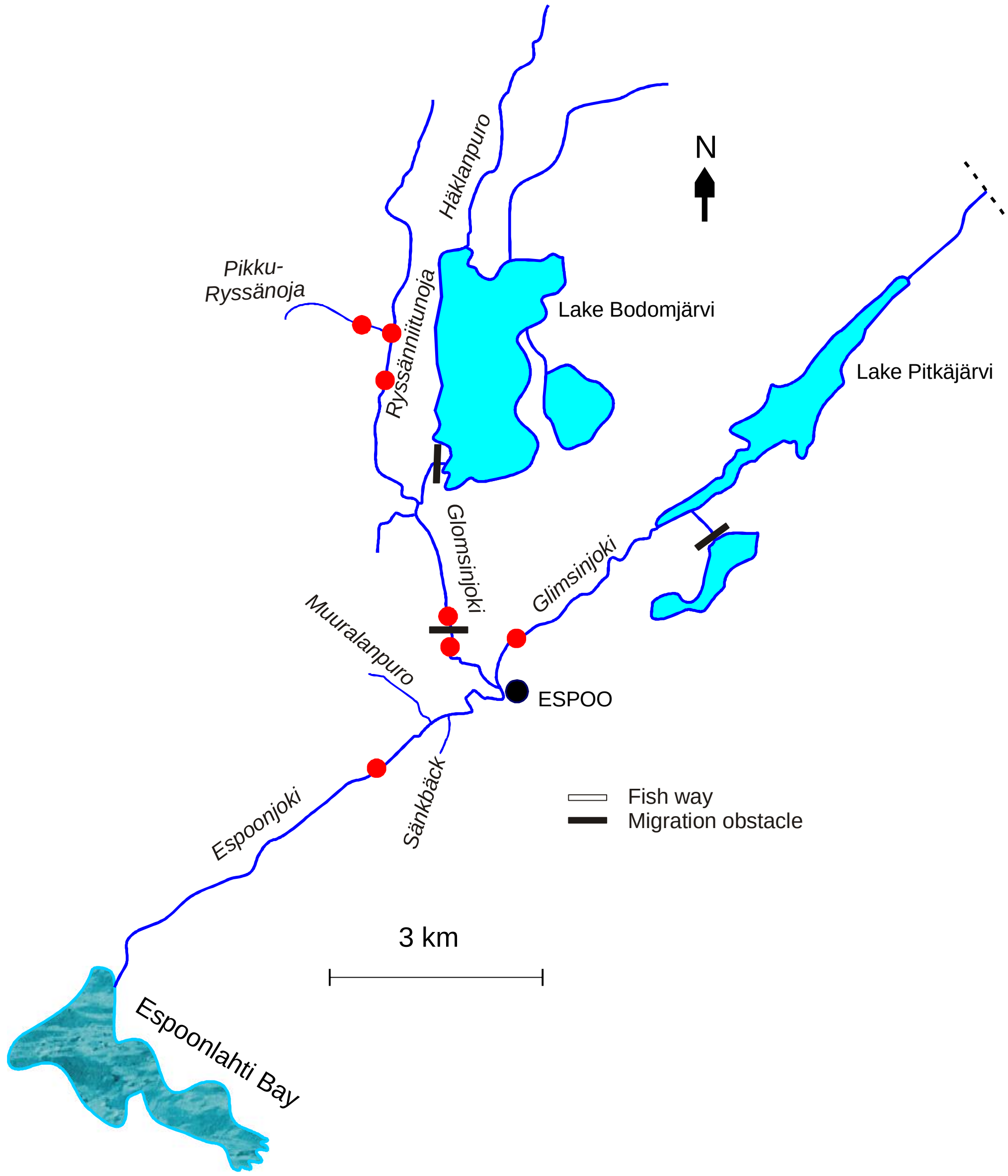

Figure 29. The Espoonjoki river system. Sampling sites are shown as red dots.

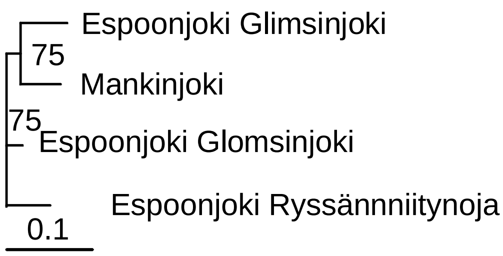

Figure 30. Genetic distances between three brown trout samples from the River Espoonjoki and a pooled sample of brown trout from the nearby River Mankinjoki .

In recent years the Espoonjoki trout population has improved. In addition, it now also regularly reproduces in the Espoonjoki main branch and Glimsinjoki, in which reproduction has previously only been occasional. There have been no releases into Espoonjoki itself.

The situation with Espoonjoki is very similar to that of the River Mankinjoki. No releases of foreign stocks should be permitted. The stock should have sufficient potential to recover if only spawning run is able to succeed. The weak population cannot sustain any river fishery. The opening of a migration route for ascending spawners across the Espoonlahti Bay is also critical to the recovery of Espoonjoki sea trout. A sea connection from the spawning sites of Ryssänniitunoja and the upper parts of Glomsinjoki should be reopened. Water level regulation of Lake Bodomjärvi should be ended and the reproduction areas of the watershed should be improved.

More sampling should be carried out in order to better ensure a representative picture of the genetic structure in the whole current distribution area of Espoonjoki trout. Samples are especially needed from the Espoonjoki main branch and Glimsinjoki, since the currently studied sample was mainly from a short stretch in the lower reaches of the River Glomsinjoki.

Archaeological findings from very near the main stream of Espoonjoki have included shells of freshwater pearl mussels (Hämäläinen 2007). This might indicate that Espoonjoki has also been a historical freshwater pearl mussel river, as has Mankinjoki, which is located next to Espoonjoki.

4.2.7. Vantaanjoki

Vantaanjoki has a very wide watershed, 1 686 km^2 in area, and it drains to the sea through the City of Helsinki (Figure 31). About 2% of the area is composed of lakes (Ekholm 1993). This river would need a whole investigation just in itself.

The last remnants of the local trout have remained as resident populations following the damming of the river mouth (Levander 1927, Segerstråle 1947a, Kettunen 1968, Hurme 1970a, Särömaa 1994, Janatuinen 2012b). Trout production was recorded in the river at least at the beginning of the 1950s, as sea trout of different ages were regularly caught in Vanhankaupunginlahti Bay, into which Vantaanjoki drains. Occasionally, some sea trout also succeeded in passing the dam in previous times (Halme and Hurme 1952, Hurme 1952, Anonymous 1968). The building of the first large dam already began in 1569, with the permission of the Swedish-Finnish king Juhana III. The condition for the permission was that it should not disturb the salmon fishery. The final impedance to migration occurred at the latest in 1872, when a new dam was built. The river was closed until 1986, when a fishway was opened (Janatuinen 2012b).

Reintroductions of the Vantaanjoki sea trout population were started in 1980, with the only available hatchery stock being from the River Isojoki (Ikonen et al. 1987). Since then, many trout of several types have been released into the Vantaanjoki watershed. The majority of the fish have been of Isojoki origin, but Ingarskilanjoki and Aurajoki trout have also subsequently been released into the river. In the middle and upper reaches of the river, other stocks have also been used, especially Luutajoki trout (Ikonen et al. 1987, Mikkola and Saura 1994, Saura 2001, Janatuinen 2012b). For example, during 1993–1996, 10 000 one-summer-old juveniles of Luutajoki origin were annually released into the Nukarinkoski rapids (Saura 2001). According to current results, the best response in terms of increased natural reproduction seems to have resulted from the latest releases of Ingarskilanjoki trout.

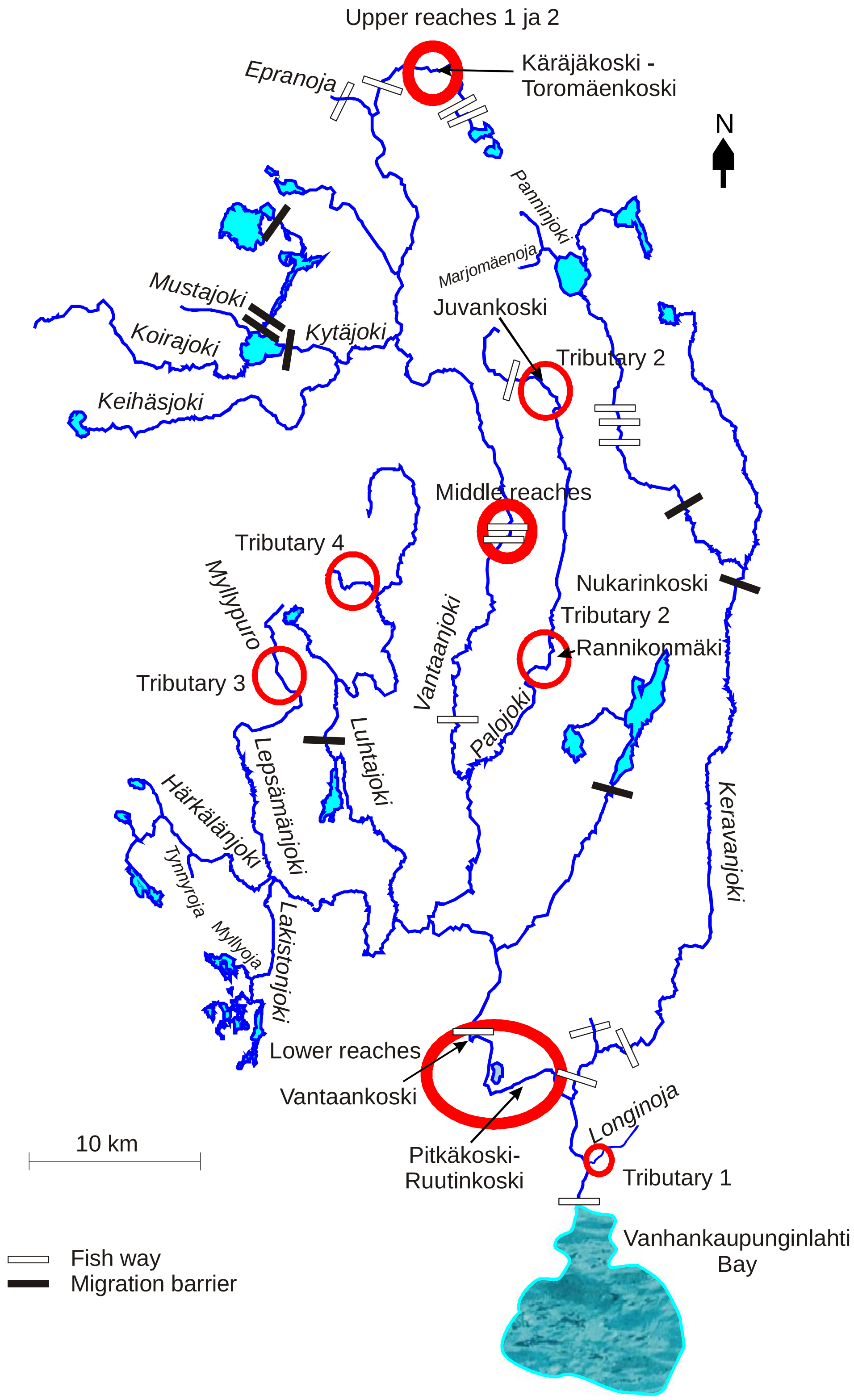

Figure 31. The Vantaanjoki river system. Sampling sites are shown as red circles.

In the years from 1996 to 2008, releases were also carried out using fish reared from spawners caught from the Vantaanjoki river mouth. The goal was to create an individual sea trout stock for the Vantaanjoki river from those fish that had undergone natural selection and had returned from the sea. A roe hatchery was founded for this purpose (Penttinen 2003, Janatuinen 2012b). The work was organized by Virtavesien hoitoyhdistys, the Society for Stream Conservation (http://www.virtavesi.com/).

Native and relatively isolated populations have remained in the upper reaches of the river. These might represent the local original trout. There are several sites where trout might live, such as Lakistonjoki draining into Lepsämänjoki, Myllyoja draining into Lakistonjoki, Tynnyroja draining into Härkälänjoki, and Keihäsjoki, Koirajoki and Mustajoki in the Kytäjoki tributary, in addition to the uppermost reaches of Keravanjoki, Marjomäenoja and Panninjoki. However, no samples were available from these sites.

In this study, 523 samples were taken from the Vantaanjoki watershed, which was divided into several sectors. The main branch of the River Vantaanjoki was divided into three parts: lower (Ala Vantaanjoki; Vantaankoski, Ruutinkoski and Pitkäkoski rapids), middle (Keski-Vantaanjoki; Nukarinkoski rapids) and upper (Ylä-Vantaanjoki) reaches. In addition, samples were taken from five tributaries (Longinoja, Palojoki, Lepsämänjoki, Luhtajoki and Epranoja). At least the lower and middle parts of the river system once maintained anadromous trout.

All samples were first analysed separately for pairwise FST values (Table 10), and a distance tree was constructed (Figure 32) in order to determine the potential substructure.

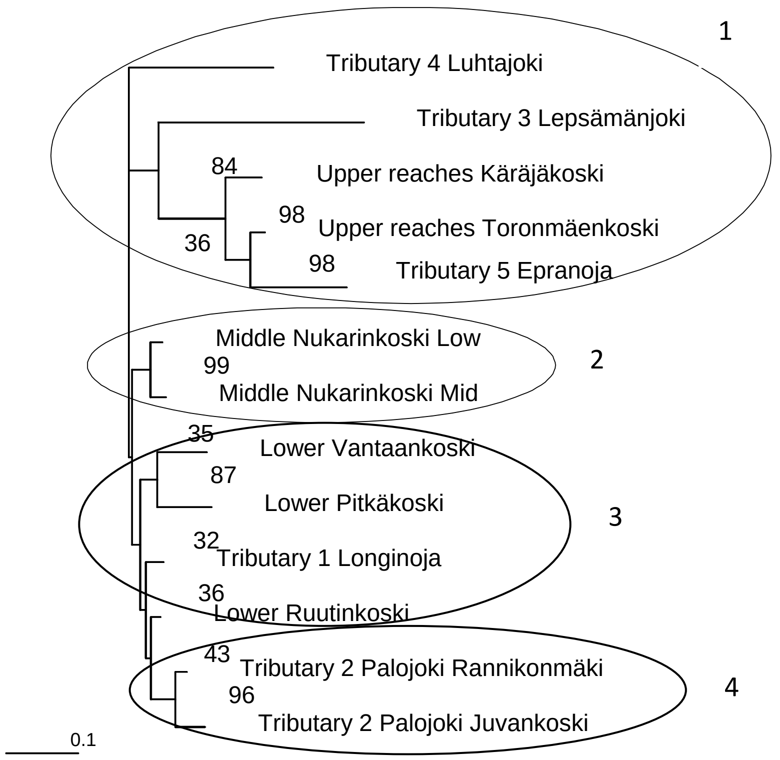

Figure 32. A tree representing the genetic distances among all brown trout samples from the Vantaanjoki river system. The numbers in the branch forks indicate the percentage of similar branching results from 1000 bootstrap runs.

In all, four main groups could be observed in the genetic distance tree (Figure 32): 1) the upper reaches, including samples from Käräjäkoski and Toromäenkoski, as well as tributaries 3 (Lepsämänjoki), 4 (Luhtajoki) and 5 (Epranoja); 2) both samples from the middle reaches of the Nukarinkoski rapids; 3) samples from the rapids of the lower reaches (Vantaankoski, Pitkäkoski and Ruutinkoski) and the Longinoja tributary from the lower part of the river; and 4) samples from the two rapids of the River Palojoki (Figures 32 and 33).

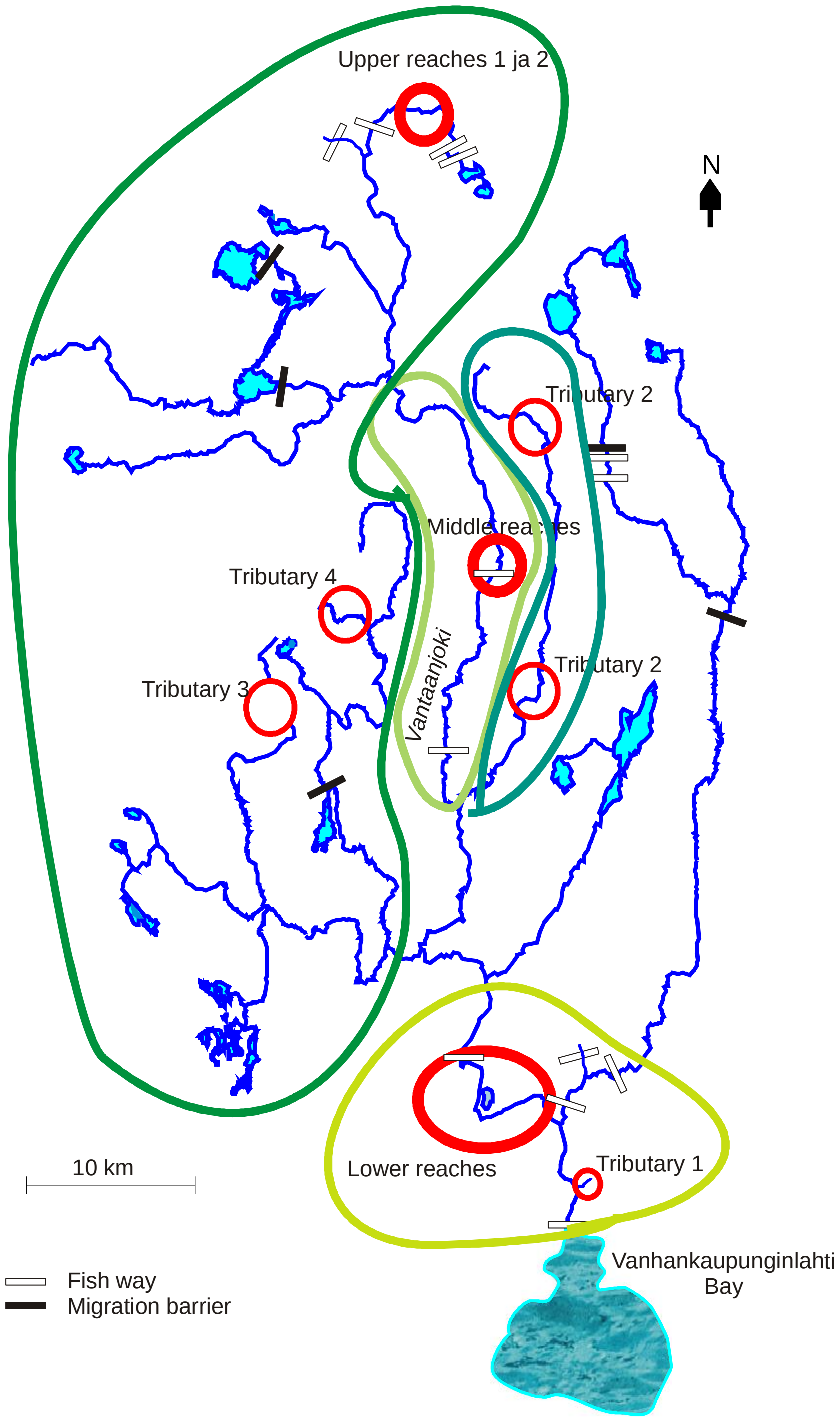

Figure 33. Current structure of the brown trout populations in the Vantaanjoki river system.

Table 10. Pairwise FST values for brown trout samples collected from the Vantaanjoki river system. Values below 0.05 are highlighted in yellow.

Samples	Vantaan-koski	Pitkä-koski	Ruutin-koski	Longin-oja	Nukari Low	Nukari Middle	Toro-mäenk.	Käräjä-koski	Lepsäm	Epran-oja	Luhta-joki	Palojoki Ranniko
Pitkäko	0.02											
Ruutink	0.04	0.01										
Longinoja	0.03	0.01	0.00									
NukLow	0.03	0.01	0.02	0.01								
NukMidd	0.04	0.02	0.03	0.02	0.00							
Toronmä	0.11	0.12	0.11	0.10	0.10	0.10						
Käräjäko	0.09	0.09	0.11	0.09	0.09	0.09	0.04					
Lepsämä	0.24	0.24	0.22	0.20	0.20	0.18	0.26	0.23				
Epranoja	0.14	0.15	0.16	0.14	0.13	0.13	0.08	0.09	0.30			
Luhtajok	0.17	0.14	0.15	0.16	0.14	0.16	0.23	0.22	0.36	0.26		
PaloRann	0.10	0.06	0.02	0.04	0.06	0.06	0.14	0.16	0.24	0.19	0.19	
PaloJuva	0.12	0.10	0.04	0.06	0.08	0.08	0.19	0.20	0.24	0.24	0.22	0.03

The FST values among all samples from the lower (Vantaankoski, Pitkäkoski, Ruutinkoski and Longinoja) and middle reaches (Nukarinkoski lower reaches and Nukarinkoski middle reaches) were very low, being under 0.05 (Table 10). In practice, they represent the same reintroduced brown trout population. As in the tree, both Palojoki samples were also highly similar. They also resembled samples from Ruutinkoski and Longinoja. The Palojoki tributaries Rannikonmäki and Juvankoski both contain reintroduced populations of Ingarskilanjoki origin.

Table 11. Result of pairwise population differentiation test. NS = nonsignificant, * 5% and ** 1% nominal level.

Pop	Pitkä-koski	Ruutin-koski	Longin-oja	Nukari Lower	Nukari Middle	Toron-mäenk.	Käräjä-koski	Lepsäm-oja	Epran-oja	Luhta-joki	Palojoki Rannikon	Palojoki Juvav
Vantaank	NS	*	**	**	**	**	**	**	**	**	**	**
Pitkäkosk		NS	NS	NS	NS	**	**	**	**	**	*	**
Ruutink			NS	**	**	**	**	**	**	**	**	**
Longinoja				**	**	**	**	**	**	**	**	**
NukLow					NS	**	**	**	**	**	**	**
NukMidd						**	**	**	**	**	**	**
Toronm							**	**	**	**	**	**
Käräjäk								**	**	**	**	**
Lepsäm									**	**	**	**
Epranoja										**	**	**
Luhtajoki											**	**
PalojRan												**

When the pairwise differentiation among samples was tested, there were several nonsignificant differences among populations from the lower and middle reaches of the River Vantaanjoki (Table 11). In addition, a difference at only the 5% significance level occurred between Pitkäkoski and Palojoki Rannikonmäki.

The diversity level of Vantaanjoki trout (Table 3) was high, being over 0.7 for all other areas except Palojoki (0.63). It diplayed close similarity (Table 5) to Ingarskilanjoki (min. FST = 0.02) and also to Isojoki (min. FST = 0.04), which are the source stocks for releases, and also to the geographically close Espoonjoki (min. FST = 0.04), Mankinjoki (min. FST = 0.02) and Siuntionjoki (min. FST = 0.04) stocks.

In the lower and middle part of the river, the effective sizes and numbers of families were high (86 and 50, respectively) and the relatedness was low (4.3–4.4%). In the upper parts and tributaries, the Ne/N ratio was low (0.16–0.30) and the relatedness among individuals was also elevated (6.6 – 6.8%) (Table 4).

In conclusion, reintroduction releases with the Ingarskilanjoki stock have earlier been successful, and anadromous trout production has increased, especially in the Palojoki area, which has been empty of trout and suffered from very poor water quality (Vainio 1999, Schönach 2003). The lower and middle parts of the Vantaanjoki spawning areas are inhabited by a relatively homogeneous, viable trout population, but with relatively high diversity.

In the upper reaches, mostly resident populations form one or two groups. The samples from Toromäenkoski and Käräjäkoski were very similar, and the sample from Epranoja belongs to the same group. The Luhtajoki and Lepsämänjoki are somewhat more differentiated. All these resident populations are also regarded as relatively native, and they possibly include the same genetic material as the historical but now in practice extinct anadromous Vantaanjoki trout.

The natural juvenile production of the Vantaanjoki river system is currently so stable that no massive releases are any longer needed in the spawning areas. Supportive releases could be carried out into the river mouth. Adipose fin clipping of released fish is recommended to enable the identification of the wild-born spawners. There are some water quality problems in the spawning areas, but the quality is mostly sufficient for trout. Additional improvement of the spawning grounds would increase the area for offspring production. The goal is to once again create a unique, locally adapted, anadromous trout population in Vantaanjoki. Hundreds of spawners already now return from the sea. The stock could even sustain some river fishing, although a catch and release fishery is recommended, and particularly individuals with an adipose fin should be released after capture.

In the Vantaanjoki river system, a reintroduced salmon stock also exists, originating from releases of Neva salmon. The salmon enhancement programme would also gain from the fishing regulations.

4.2.8. Sipoonjoki

The area of the River Sipoonjoki watershed is 220 km^2, with less than 1% of this comprised of lakes (Ekholm 1993) (Figure 34). According to old information, trout were a target of fishing in the Middle Ages as high as in Paippinen, which is located in the upper reaches of the river (Anonymous 1989). However, little information is available on trout in the Sipoonjoki river from the last hundred years. Neither Segerstråle (1937) nor Hurme (1962) named Sipoonjoki as a sea trout river. Only Niinimäki (1967) mentioned that some sea trout had been caught from the river. Those fish might also have been from releases into the tributaries in the 1960s, or stray fish from other rivers. In 1986, newly hatched fry of Isojoki trout were released into the river (Marttinen and Koljonen 1989).

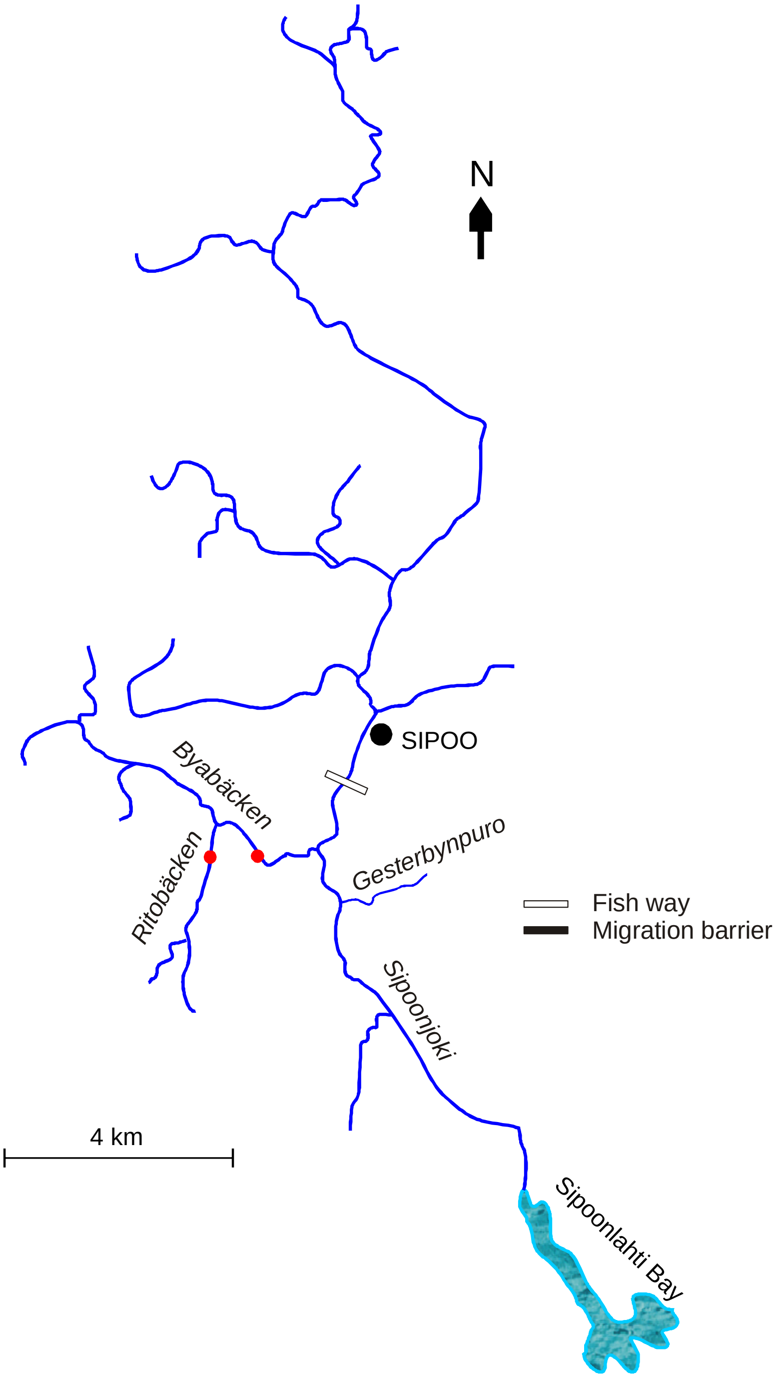

Figure 34. The Sipoonjoki river system. Sampling sites are shown as red dots.

The Sipoonjoki brown trout population has only recently dramatically decreased. At the end of the 1980s there were still large numbers of wild juveniles. The spawning stock is currently probably only tens of fishes. There are quite good spawning grounds, but the water quality is deteriorating.

The population is regarded as still relatively native, and no releases are recommended as long as any spawning seems to be taking place. Very little information is available on the Sipoonjoki trout population, but it is likely that there have been anadromous trout in the river for a very long time. The Sipoonjoki trout sample comprised only 46 fish from two sampling sites, Ritobäcken and Byabäcken, with only four fish available from Byabäcken (Figure 34).

The diversity of Sipoonjoki trout was below the average level, being 0.55 (Table 3), and it displayed no close resemblance to any of the other studied stocks, but instead grouped loosely with other trout stocks of the Uusimaa area. The effective number of the sample was low, only 11, and the Ne/N ratio was only 0.24. The relatedness among sampled individuals was slightly elevated (6.3%) (Table 4).

The Sipoonjoki trout is one of the trout stocks that is currently extremely endangered, and no river fishery for this stock should be permitted. Water quality improvement is recommended, as well as spawning ground restoration. The route to the spawning grounds across the Sipoonlahti Gulf is especially difficult, as it is long and easy to fish effectively. River mouth fishing closures should be considered. Despite the poor state of the stock, releases are not recommended before other attempts to enhance the stock with its own genetic material have been carried out. Currently, the most important spawning sites are in the Sipoonkorpi National Park. The whole main branch of Sipoonjoki and eight of the tributaries are protected in the Natura 2000 network.

It is evident that nowadays the only spawning grounds in use are located within the catchment area of the Byabäcken tributary. Trout juveniles are a rare catch in the main branch, but information is available from a few decades ago on trout in the Gesterbynpuro brook, which drains into Sipoonjoki (Juvonen and Vainio 2008, Vainio 2013).

The state of the Sipoonjoki trout population is still critical, even though there have been some efforts to restore the spawning grounds. However, there have been two recent dredging operations just above the only known spawning and nursery sites (Vainio 2013). It seems that at least in Ritobäcken, dredging has not permanently affected the spawning sites, since in 2013 the trout year class was the largest in years.

A decision has recently been made to temporarily close area in the Sipoonlahti Bay, in which all fishing is now forbidden from the beginning of August until mid-October. This restriction is in force until 2015, and will potentially be continued if needed.

4.2.9. Mustijoki

The area of the Mustijoki-Mäntsälänjoki river system is 786 km^2, and lakes comprise 1.5% of this (Ekholm 1993). According to Segerstråle (1939, 1947c), sea trout migrated in the 1930s up to Lahankoski dam, which is situated 22 km from the river mouth (Figure 35). It is not known how far up the river the sea trout used to run before it was dammed. The mean size of the fish has been 3–4 kg, and the catches in the 1930s numbered several tens of fishes, but only some 30 to 70 years before the catches had annually been as high as several hundred sea trout.

The association Fiskodlingens Vänner also caught spawners for hatching and rearing of offspring in 1938–1940. The newly hatched fry were released back into the river (Segerstråle 1947a). The Mustijoki trout has been an important anadromous stock. In the 1960s, a water supply dam was built at Brasas, which closed the river completely, so that only an isolated, resident stock was left.

The Mustijoki trout is currently resident. One sample from Kalkinoja represented Mustijoki trout. It appears very unique and had a low diversity (0.39). The effective versus actual population size was low (0.19), and the relatedness among sampled individuals was very high (10.7%).

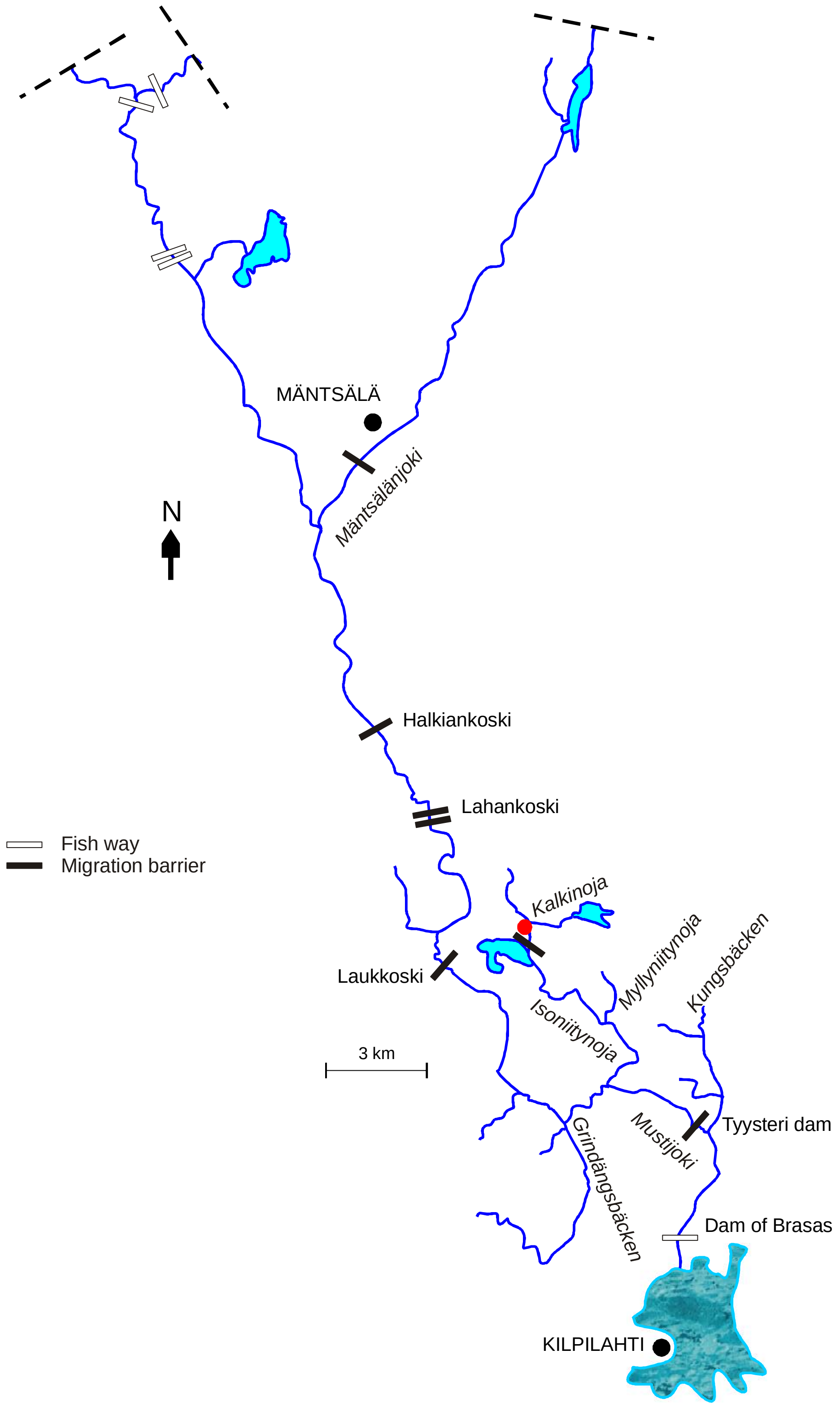

Figure 35. The Mustijoki river system. The sampling site is shown as a red dot.

There is some uncertain information that single trout stockings might have been carried out into the Kalkinoja brook. However, Kalkinoja has been known as a self-sustaining trout population for decades, and there is more reliable information that supports the idea of an original trout population, which is the last one remaining in the Mustijoki watershed (Vainio 2007).

The trout population in Kalkinoja is very threatened, and there is a risk of extinction due to the small size of the population and restricted distribution area. There have been some occasional catches of trout from Lake Kotojärvi, where the trout have migrated downstream from Kalkinoja, but the population nowadays seems to be mostly resident. In the early 2000s, trout were also found in Isoniitynoja brook, flowing from Lake Kotojärvi, and in Myllyniitynoja brook, which drains into Isoniitynoja. Large sea trout migrated up to Isoniitynoja and Myllyniitynoja before the building of Brasas dam in 1965. After the river was closed, the population became resident in Myllyniitynoja and Isoniitynoja, but this lower population has now become extinct (Marttinen and Koljonen 1989, Vainio 2004, 2007, 2013).

Sea trout have also migrated into the Kungsbäcken and Grindängsbäcken brooks, which drain into the lower reaches of Mustijoki near the Isoniitynoja-Myllyniitynoja-Kalkinoja system. The original trout populations of Kungsbäcken and Grindängsbäcken have become extinct. In Kungsbäcken, the trout population still seemed quite strong in the 1960s, when trout also inhabited the smallest headwaters of the brook (Segerstråle 1939, Vainio 2004).

There is also some local information on trout historically inhabiting the upper reaches of Mustijoki (brooks around Halkia area) and its tributary, Mäntsälänjoki (Vainio 2004).

Regular roe releases of the Ingarskilanjoki stock have been carried out in recent years in empty areas within the drainage basin. In the lower reaches, in the Brasas fishway, large spawners have been regularly been seen (Vainio 2013). In practice, however, almost no spawning grounds for anadromous trout are left. Currently, the most important migration barrier is the Tyysteri (Tjusterby) dam. As long as no migration routes are open, the only option is to try to keep the original resident stock alive in the upper tributaries. This can be promoted by transferring fish from inhabited brooks to empty brooks. No fishing should be permitted in the Kalkinoja brook.

Mustijoki has historically been a freshwater pearl mussel river, but the species has become extinct. There is old information about the harvesting of freshwater pearl mussels, at least in the Laukkoski rapids (Rudenschöld 1899).

4.2.10. Porvoonjoki

Porvoonjoki is a relatively large river with a watershed area of 1 273 km^2, lakes forming 1.3% of this (Ekholm 1993). Historically, it is known to have had both anadromous and resident trout populations. According to Hurme (1962, 1970b, 1972), sea trout were even able to reach the highest branches of the tributary before the start of damming of the river (Figure 36). In 1919, a power plant was established in the river mouth at the Strömberginkoski rapids, and trout could not pass it. Trout have, however, run to a tributary, Pikkujoki, which drains below the dam (Segerstråle 1937, 1939). The area suitable for sea trout spawning was only about 6 km. Below the dam, trout were regularly observed until the 1970s (Anttila and Virtanen 1976). In the Pikkujoki tributary and in Paunioja brook, a tributary of Pikkujoki, trout were last recorded in the early 1980s (Marttinen and Koljonen 1989). The original local trout most likely disappeared from the lower reaches by then at the latest. According to Segerståle (1939, 1947a), spawners were caught from the river in 1938–1940, and newly hatched fry were released back by the association Fiskodlingens Vänner.

Currently, only a resident stock lives in the headwaters of the river. The population is assumed to be original, because according to local people trout have always been present in this area (Vainio 2007). The water quality is good in the Vähäjoki tributary, but poor in the River Porvoonjoki itself.

Extensive releases of Ingarskilanjoki trout have been carried out to reintroduce anadromous trout (Vainio 2013). This local trout population is excluded from the Ingarskilanjoki reintroduction programme. Luutajoki trout have previously been released into the lower reaches of the Vähäjoki as obligatory releases (Vainio 2007).

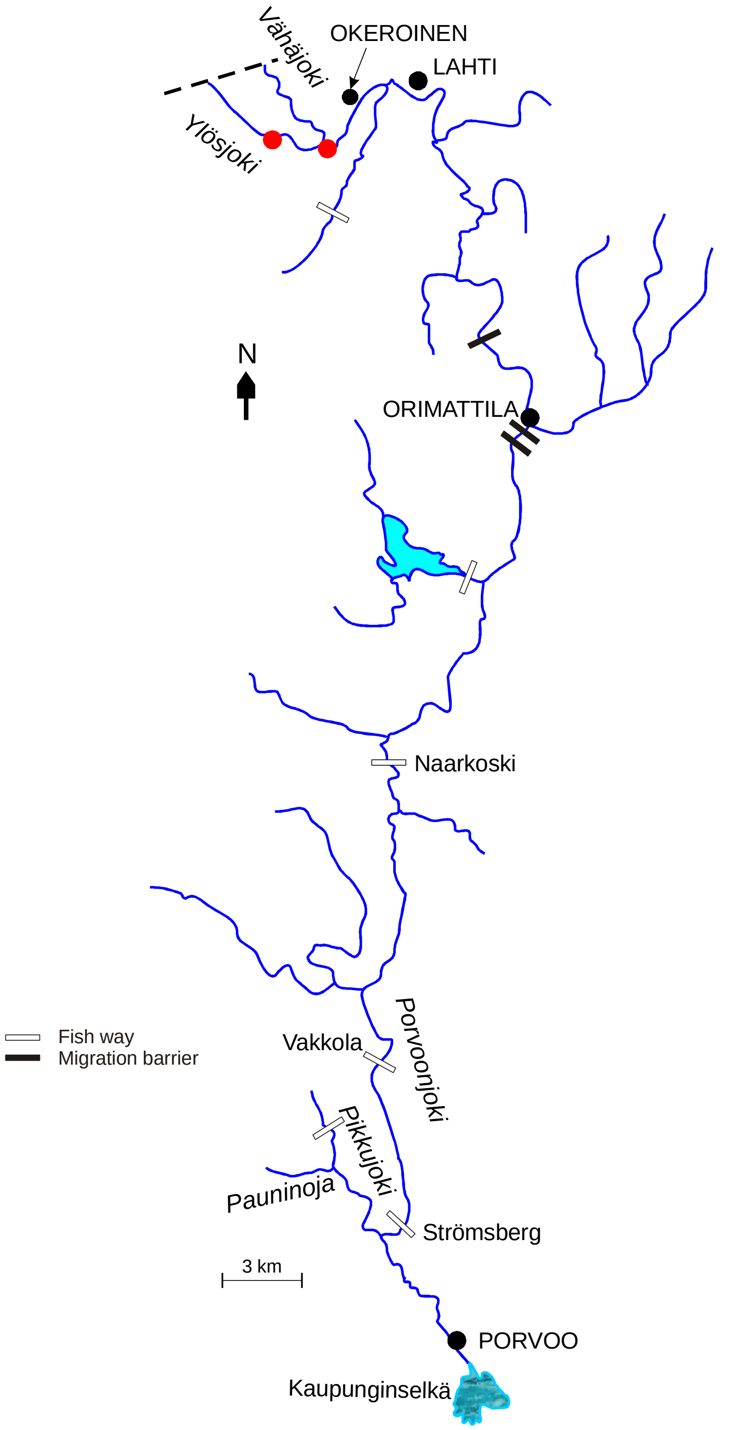

Figure 36. The Porvoonjoki river system. Sampling sites are shown as red dots.

Two sample groups were available from the upper reaches of Porvoonjoki. Both of them were from Vähäjoki: eight fish from Okeroinen and the rest from the River Ylösjoki. They were treated as one group. The population had quite a high diversity and did not closely resemble any other stock. The sampled fish represented 24 full-sib families. The relatedness of the sampled fish was somewhat higher than in an average native population, being 7.6% (Table 4). The local population cannot sustain a river fishery and would gain from restoration efforts, especially from spawning habitat restoration.

Porvoonjoki has historically been a freshwater pearl mussel river, but the species has now disappeared (Oulasvirta 2010).

4.2.11. Koskenkylänjoki

The Koskenkylänjoki watershed is 893 km^2 in area, with lakes forming 4.4% of this (Ekholm 1993). According to Segerstråle (1937, 1939), some occasional sea trout were caught at the river mouth in the 1930s, although the river had already been closed at the lowest rapids at Forsby (Koskenkylä) for several centuries (Figure 37).

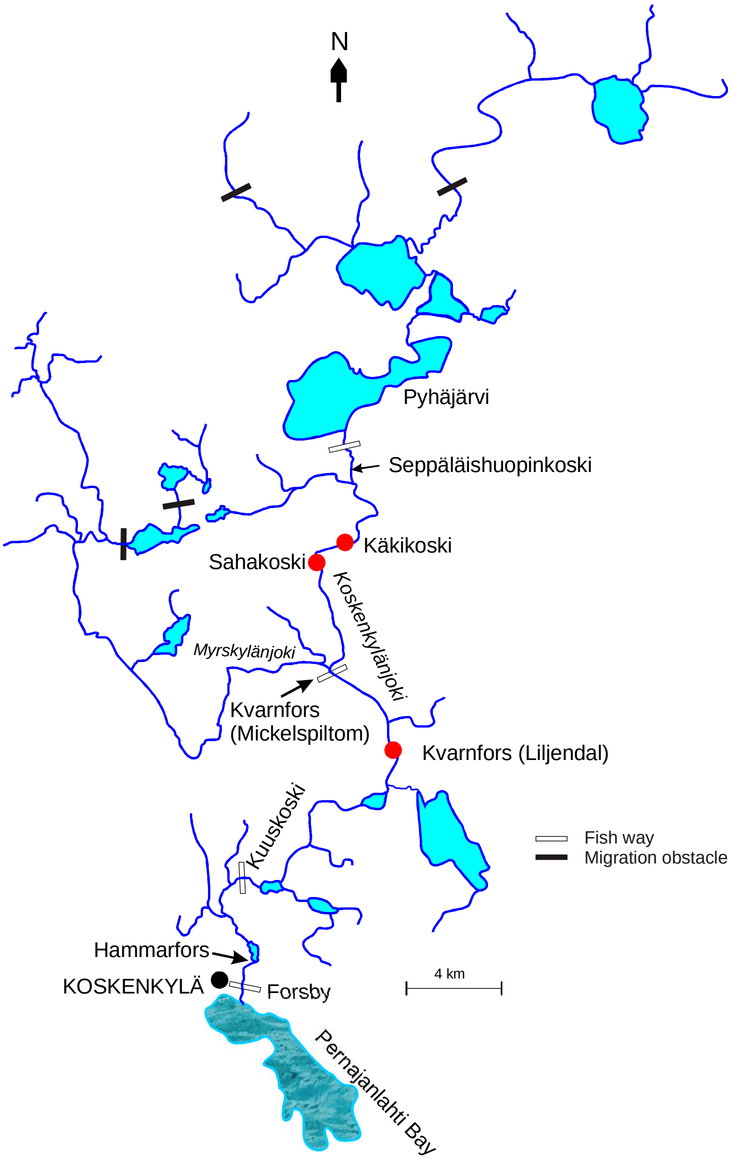

Figure 37. The Koskenkylänjoki river system. Sampling sites are shown as red dots.

The river was already closed in 1682, when the ironworks of Koskenkylä with its dams was built (Hurme 1970a, Salokorpi 2007, Museovirasto 2013b). Hurme also mentions that in the 1970s, some sea trout were caught from the river mouth. The dam at the Forsbynkoski rapids was deconstructed in 1993 (Saura 2001), and since then reintroductions of brown trout, mainly of Ingarskilanjoki origin, have been conducted (Vainio 2013).

There are no remaining native brown trout populations in the River Koskenkylänjoki. In the early 1990s, when the river was reopened, the Ingarskilanjoki trout was selected to be the enhancement stock. Brown trout in the Koskenkylänjoki are thus in practice an introduced stock from Ingarskilanjoki. This is clearly seen in the results. Koskenkylänjoki trout are identical to Ingarskilanjoki trout (FST = 0.01), with an average level of diversity (0.62) (Table 3). The ratio of the effective population size to the actual size was also quite high (0.90), indicating that there were very few siblings in the sample. The relatedness among individuals was also not high (Table 4).

This river has possibly also been a salmon river, and salmon stock reintroduction has been conducted with Neva salmon. Some successful reproduction has been observed (Lempinen 2013). The stock can sustain some river fishing. However, wild-born fish with an adipose fin should be released.

4.3. ELY Centre for Southeast Finland.

4.3.1. Kymijoki

Kymijoki is a very extensive watershed and its area is as much as 37 159 km^2, with large lakes forming 18% of the watershed area (Ekholm 1993). The whole river drains via five river mouth outlets into the Gulf of Finland (Figure 38). Kymijoki, currently a closed river, has obviously originally been a salmon river rather than a sea trout river, and there are few trout juveniles in the open rapids today. It has traditionally been managed by releasing Isojoki trout. Spawners still enter the river from the sea. The practiced water level regulation particularly disturbs trout spawning, as trout usually spawn in shallower water than salmon. If the planned fishway through the Korkeakoski dam is realized, about 40 to 50 hectares of new spawning grounds would become available for trout and salmon.

The sample of Kymijoki trout comprised wild-born juveniles, and they were mainly from the Kotokoski rapids. Only 26 individual fish were caught.

This small sample showed relatively high diversity of 0.7, as the mean value was 0.62 (Table 3). This sample was identical to Isojoki trout (FST = 0.01), as assumed, and also very similar to the population from Summanjoki main stream (FST =0.02), into which Isojoki trout have also been released (Table 5). Some populations from other rivers with Isojoki trout were also similar to the Kymijoki sample. If other trout populations still occur in the river, this could not be detected from this sample. The Ne/N ratio of the sample was very high, being the theoretical maximum for one population, i.e. 2. The within-sample relatedness was also very low (Table 4). This might be a result of the mixing of populations in the sample.

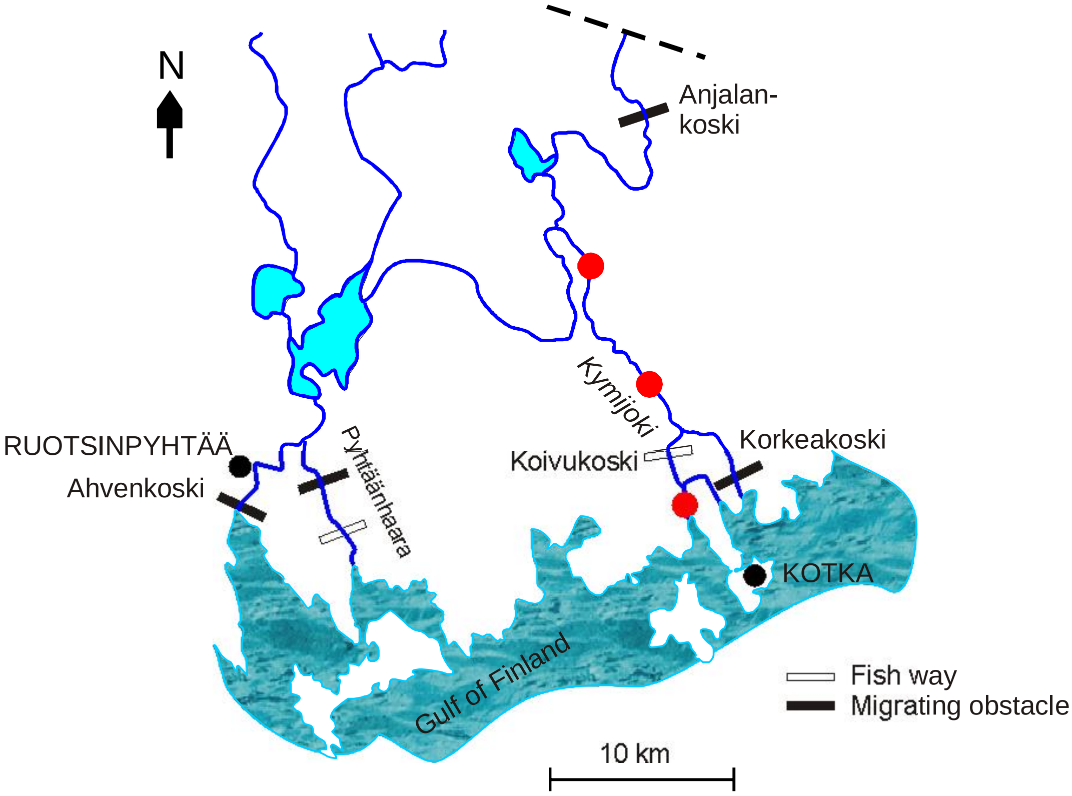

Figure 38. The lower parts of the Kymijoki watershed, and two outlets to the sea.

In this eastern area, the new Mustajoki trout hatchery stock could possibly be one option for a release stock. It could increase the overall diversity among the release stocks and diminish the harm from straying in case released fish enter some nearby wild trout rivers.

Kymijoki has historically been a freshwater pearl mussel river, but the species has become extinct (Oulasvirta 2010).

4.3.2. Summanjoki

The River Summanjoki drains into the sea via the Summanlahti Bay in the city of Hamina (Figure 39). The watershed area is 569 km^2, with few lakes (2.21%) (Ekholm 1993). Summanjoki is a partly open river. The first migration hindrance has been the dam at Sahakoski rapids, in the village of Metsäkylä. The mean size of the spawners has been 2–3 kg. In the Suurioja brook, trout have been caught 10–15 km from the sea. In the 1960s there still was an abundant trout stock in the brook (Hurme 1962). In the Suurioja brook, trout have also recently been found (Lempinen 2001). Trout releases have been carried out since 1983, and the stocks from the Luutajoki, Rautalamminreitti, Isojoki and Vuoksi watershed have been used. In addition, large smolt releases have been carried out into the Summanjoki river mouth.

Three juvenile trout samples were collected from the Summanjoki: from the main stream, Sippolanjoki, and Kelkanjoki in the upper reaches. The similarity was high among samples (Figure 40), and also with the Kymijoki sample (Figure 41). The sample from the main stream was very similar to the Isojoki hatchery sample (FST = 0.02) and the Kymijoki river sample (0.02). Isojoki trout have been released into Summanjoki, so the result confirms that the population in the main stream was mainly of Isojoki origin.

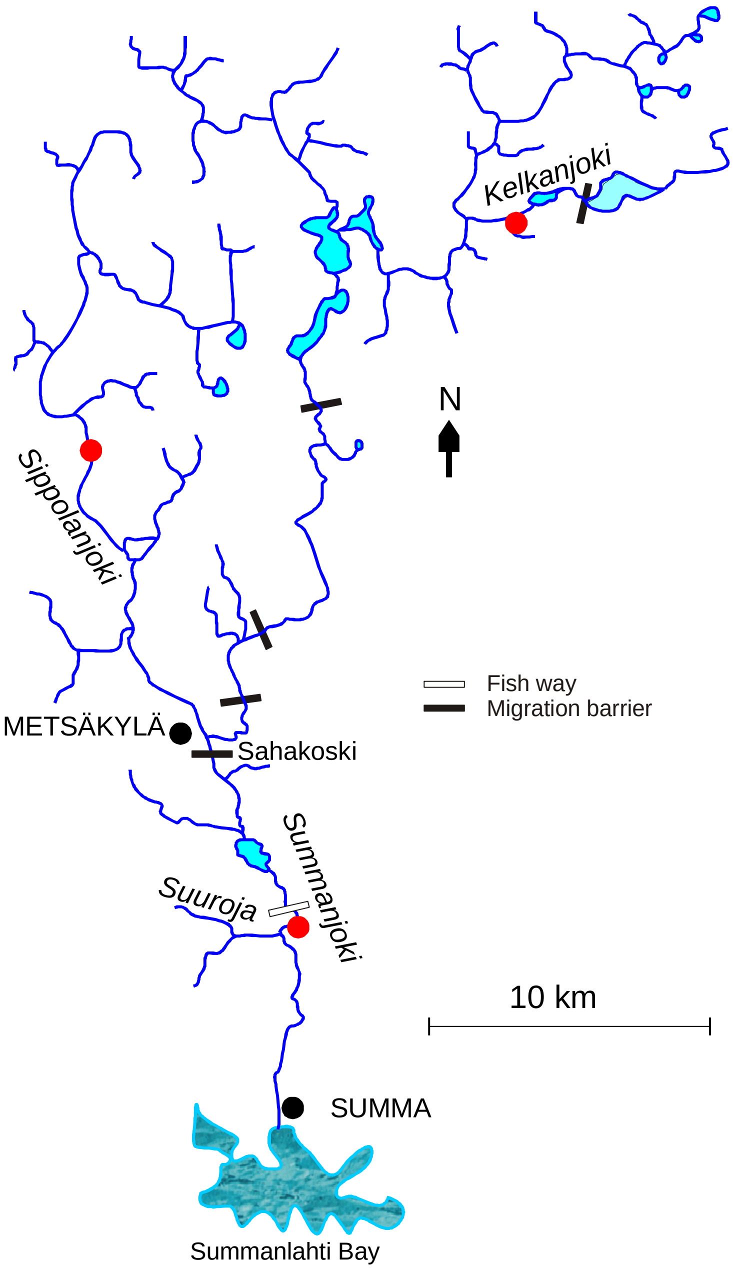

Figure 39. The Summanjoki river system. Sampling sites are shown as red dots.

Although all samples were very similar, the Kelkanjoki sample from the upper reaches did not so closely resemble the Isojoki stock (FST = 0.05) as did the main stream sample (Table 5). It was more similar to the Urpalanjoki trout (FST = 0.04), and for some possibly random reasons with some other stocks such as Fiskarsinjoki and Vantaanjoki, with which it could not have had gene flow. It also resembled some more native eastern stocks such as the upper reaches of Virojoki, Vilajoki and the Russian rivers Notkopuro, Vammeljoki and Kuokkalanpuro.

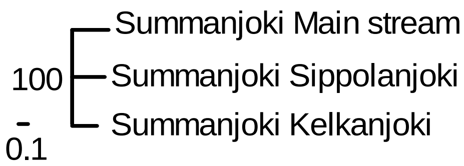

Figure 40. Genetic distances among brown trout samples from the River Summanjoki.

Two groups were left for further analysis. The main stream population is assumed to be anadromous, while trout from Sippolanjoki, Kelkanjoki and other upper branches are assumed to be resident. These two groups were kept separate in subsequent analysis.

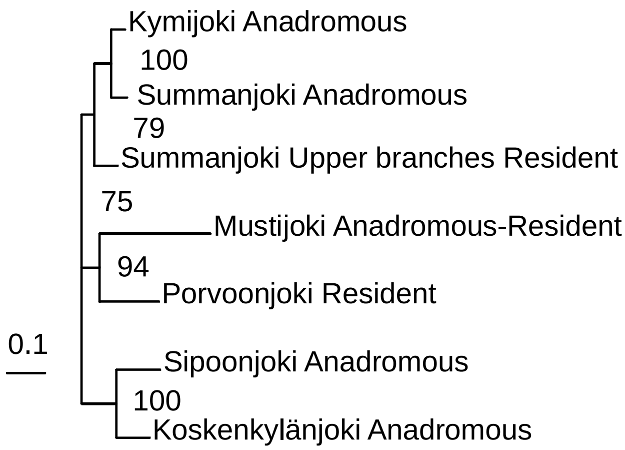

Figure 41. Genetic distances among anadromous and resident groups of the Summanjoki water system and nearby rivers.

The diversity level was above the average in both samples, and the effective size of both populations was also high. The Ne/N ratio was over 0.6 for both samples, and the relatedness was not very high (4.2–5.0) (Table 4). As a recommendation for the management of the river system, it is suggested the migration barriers should be opened, and the release stock could be changed from the Isojoki to the Mustajoki stock, when possible.

4.3.3. Virojoki

The Virojoki watershed is 357 km^2 in area, with lakes forming 4% of this (Ekholm 1993). It is a partly open river. The lowest migration obstacle is the power plant dam at Kantturakoski rapids, built in 1926 (Figure 42). The power plant has an obligation to construct a fishway, but this has not been realized. The dam is located about 3 km from the sea. In the 1960s, the spawning run clearly stopped at a mill dam in Virojoki village, only two kilometres from the sea. Fish ladders exist in both dams, but they have never functioned (Hurme 1962, 1970a).

The Saarasjärvenoja tributary is the main spawning site of the anadromous trout, and this population has been assumed to still be native. Trout with a size of almost 3 kg have previously been caught there (Hurme 1962, 1970a).

The samples from Lake Virojärvi and the upper branches were taken above the dam, where the populations are regarded as resident. Three sites were sampled: the upper reaches of Virojoki, Lake

Virojärvi and Saarasjärvenoja. Two groups were formed from these samples, comprising anadromous Saarasjärvenoja and the upper reaches together with the Lake Virojärvi sample, because the grouping was very clear (Figure 43). Samples from Saarasjärvenoja were available from several years, and the population structure appeared to be temporally stable, as samples from 2004 to 2011 were very similar.

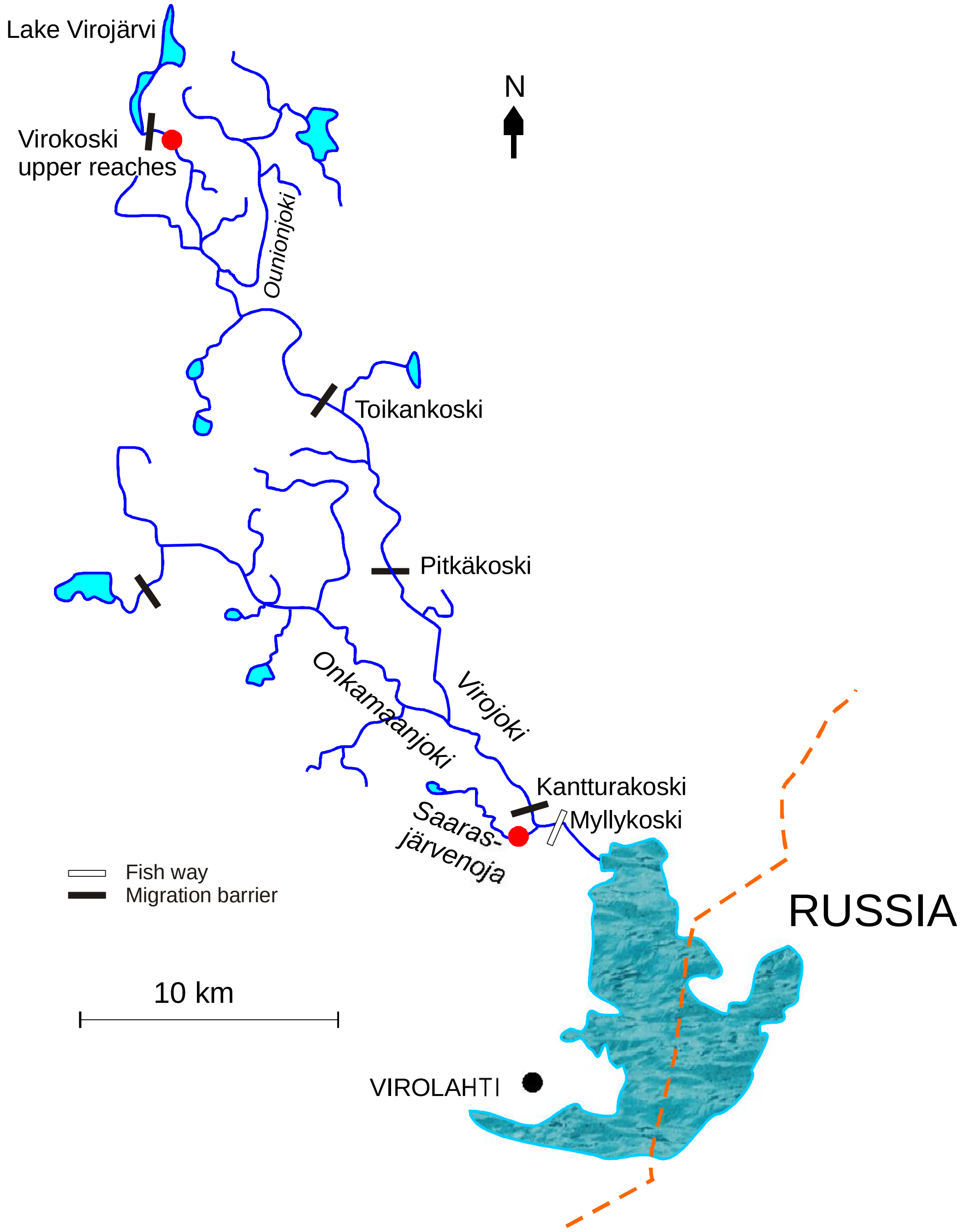

Figure 42. The Virojoki river system. Brown trout sampling sites are shown as red dots.

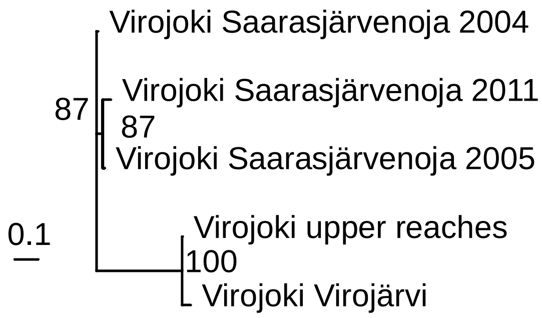

Figure 43. Genetic distances among samples from the River Virojoki water system.

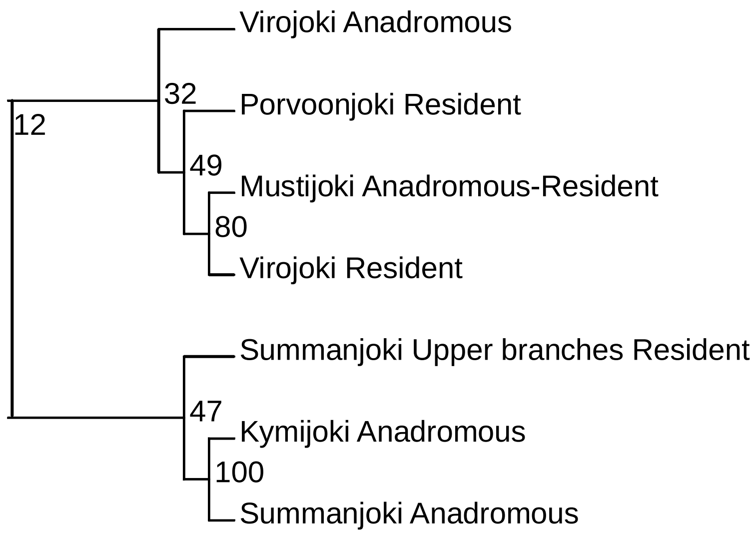

Figure 44. Genetic distances among anadromous and resident groups of the Virojoki water system and the nearby rivers.

When grouped into Virojoki anadromous (Saarasjärvenoja) and Virojoki resident (upper reaches) trout, these two groups remained separate in the large tree, the resident stock having greater similarity with some other resident stocks (Figure 44).

Both samples seem very unique. In particular, the anadromous population does not have any clear similarity with any other stock. The upper reaches have some similarity with upper reaches of Urpalanjoki and Vantaanjoki. The diversity level of the anadromous part was somewhat lower (0.48) than that of the population above the dam (0.63) (Table 3). The sampled individuals in the anadromous sample were related (9.51%) (Table 4), but in the upper reaches the relatedness was lower (5.9%).

This population seems very unique and is very possibly still a native anadromous population, and valuable as such. Such populations are very rare on the Finnish side of the coast. The population above the dam is also valuable and has possibly been previously part of the anadromous stock. No releases with foreign stocks are recommended. The transportation of individuals from the upper parts to the Saarasjärvenoja over the dam could be considered if the effective population size of the anadromous part is very low, and the population size is decreasing.

4.3.4. Urpalanjoki

The area of the Urpalanjoki river system is 467 km^2, 5% of which consists of lakes (Ekholm 1993). Urpalanjoki is the first of the rivers in this study that cross the Finnish–Russian border, and it drains into the Bay of Vyborg (Figure 45). About 84% of the watershed is on Finnish side and the rest in Russia (Saura 2001). The River Urpalanjoki is historically known as a good sea trout river. Trout have previously migrated over 20 km up the river, until reaching Lake Salajärvi. Currently, it is only possible for trout to migrate to the dam at Muurikkala, about 15 km from the sea. The mean weight of fish captured at Muurikkala has been 3–5 kg. Juveniles were regularly observed below the dam until the 1960s (Hurme 1962).

The River Urpalanjoki is relatively native on the Russian side, and the first migration obstacle is about 2 km from the border on the Finnish side. The Finnish side of the river is dredged and no brown trout had been caught there in about 30 years. However, in 2012, one fish was caught with a net and a few juveniles were found below the lowest dam. A few sea trout, the first in several decades, had been caught from the Finnish side of the river some years earlier. Some releases have been carried out with the resident Luutajoki trout into the headwaters Kirkkojoki, leading to a self-sustaining population. Brown trout compensation releases into the river already ended 20 years ago (Vihtonen 2012). On the Russian side there have always been trout, and the environment is suitable for them, with only occasional water quality problems.

On Finnish side there is plan to restore the river and construct fishways through the dams. Some salmon releases have also been carried out into the river. The river is mostly in the border area, and no official fishing is permitted, although poaching occurs. On the Russian side there is a ban on fishing for brown trout.

Most of the samples (38 out of 40) were collected in 2006, and only two fish were sampled in 2010. The trout population is still regarded as native. The mean diversity of the sample was 0.73, which is not low (Table 3). The samples show strong similarities with Vantaanjoki, but also with several native border river populations nearby, such as Santajoki, Vilajoki and Mustajoki, as well as with other Russian rivers such as Notkopuro, Inojoki and Vammeljoki. The effective population size/population size ratio was high (0.88), and the relatedness among individuals was at the level of native wild stocks (Table 4).

The Urpalajoki trout still deserves the status of native anadromous trout. Migration obstacles, such as steel fences in the border zone, should be removed. No releases are recommended or are even currently legal according to the Border Rivers Agreement. Urpalanjoki is also a locally important lamprey river, which indicates the free connection with the sea. In its current state the population cannot sustain a river fishery.

Figure 45. Sampled border rivers and Russian brown trout rivers.

4.3.5. Santajoki

River Santajoki is also called Kaltonjoki. It is 557 km^2 wide, and only 35% of the watershed area is on the Finnish side (Ekholm 1993, Saura 2001) (Figure 45). Historically, it had been quite a good sea trout river (Hurme 1962). It is an open river, but there is only a very short stretch on the Finnish side, with the river mainly running in Russia. Samples were collected from the Finnish side in 2006 and they totalled only 19 trout. The diversity of the population was 0.62 (Table 3), which is about the average level, and the population was very similar to the Urpalanjoki trout (FST = 0.04) (Table 5). The Ne/N ratio was rather high (0.74), but the relatedness in the sample was somewhat elevated (7.7%, Table 4). The river is still free and native and should be conserved as such. Samples from the Russian side would be interesting to study.

4.3.6. Vilajoki

The Vilajoki river system also belongs to the border rivers and drains into the Bay of Vyborg (Figure 45). Its drainage area is 344 km^2 and 73% of it is on Finnish side. About 6% of the whole watershed is formed of lakes (Ekholm 1993, Saura 2001). Vilajoki is a free river that drains into the Bay of Vyborg, as do all the border rivers. Vilajoki was also known as a sea trout river (Hurme 1962).

Samples were collected from the Finnish side of the river, and thus from the upper reaches. The sites were Pappilankoski rapids (n = 46) and Käpylänkoski rapids (n = 6). The trout population is possibly resident there. On the Finnish side, good spawning grounds are available. The mean diversity of the sample was 0.64 (Table 3), and despite possible small-scale releases into the rivers, very little similarity with hatchery stocks could be detected. The FST with upper Vantaanjoki was 0.8 (Table 5), which might indicate hatchery releases. Other similar populations were Summanjoki and Urpalanjoki.

The Ne/N ratio of the Vilajoki sample was low, only 0.17, and the relatedness in the sample was very high (10.4%, Table 4), especially when compared to nearby populations. The number of potential full-sib families was also quite low, being 23. These results indicate a hatchery influence.

4.3.7. Rakkolanjoki

The River Rakkolanjoki is also known as Lautalanjoki, and its tributary has been called Hounijoki or Alajoki. The river system is 621 km^2 wide and about 59% of it is on the Finnish side (Ekholm 1993, Saura 2001) (Figure 45). The first migration obstacle used to be a power plant dam about 5 km from the sea. According to Hurme (1962), there were sea trout in the river at the time when it was part of Finland.

The river has a water quality problem, as wastewaters from the Finnish city of Lappeenranta are released into the river. At Rakkolanjoki there have been several old hydropower dams, but none of them is currently a permanent migration obstacle for sea trout. Four dams remain in the Hounijoki tributary, three of which are on the Russian side of the river. The trout population in Rakkolanjoki is still quite strong. Atlantic salmon releases of the Neva stock have also recently been carried out into the river. Occasional reproduction of salmon has been detected in the lower reaches of the river, even before the stocking efforts started in last few years (Lindgren 2013).

Only 13 trout samples from 2006 were available from Rakkolanjoki. The population is assumed to be anadromous. The diversity of the sample was 0.52 (Table 3), and it appeared very unique, having no clear similarities with any other stocks (Table 5). The Ne/N ratio was good, being 1.00, but a somewhat elevated relatedness could be seen in the sample (Table 4). The sample size was, however, so small that no final conclusions could be drawn. Some plans exist to remove the dams from the main river and tributaries.

4.3.8. Mustajoki (Juustilanjoki)

The Juustilanjoki or Näätälänjoki watershed is usually known by the name of its tributary, Mustajoki. The watershed is 621 km^2 wide, with 60% of it on the Finnish side, and 3.64% of the watershed consists of lakes (Ekholm 1993, Saura 2001) (Figure 45). The River Mustajoki maintains the most viable anadromous brown trout stock of the border rivers. Even wild salmon juveniles have during a couple of recent years been found on the Finnish side in the other tributary, Soskuanjoki. The river is mostly open to the sea, although some obstacles still exist that may influence fish migration. The River Mustajoki drains into the Saimaa Canal, so the river mouth will remain open in the future. According to Hurme (1962), sea trout occurred in the river before Second World War (1939–1945).

Active sampling in the River Mustajoki was carried out from 2006 to 2008, e.g. for the ISKALT project, in both the Finnish and Russian parts of the river and also in its tributary, Kananoja, on the Russian side. All Mustajoki samples grouped together (Figure 46), with short genetic distances, and the overall diversity was rather high, being 0.63 (Table 3). Mustajoki was found to be very unique, and only bears some similarity to Urpalanjoki and Santajoki, other border rivers in the Bay of Vyborg area (Table 5).

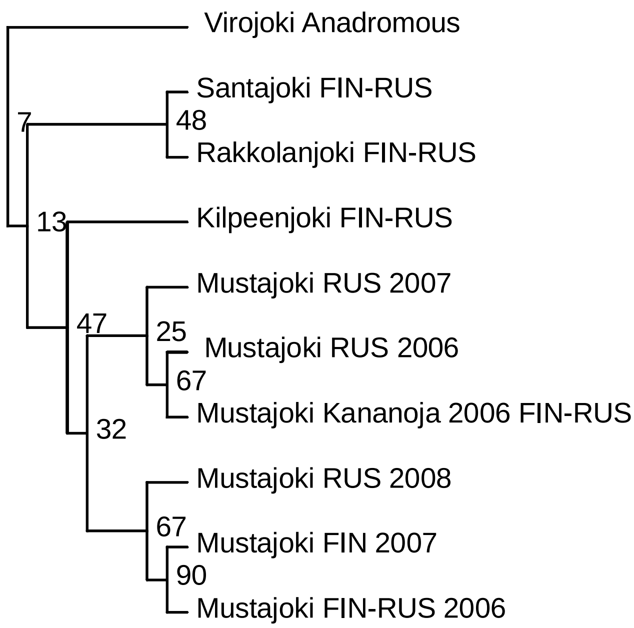

Figure 46. Genetic distances among samples from the Mustajoki river system and the nearby rivers.

The effective size of the sample was 133, and it came from about 258 full-sib families. The Ne/N ratio was quite low (0.35), but the relatedness was not very high (5.1%).

A broodstock has been founded from the anadromous Mustajoki trout. Juveniles have been collected from 2010 to 2013. Currently, 165 fish are growing in the hatchery. The founding of the broodstock is part of the RIFCI project funded by ENPI CBC South-East Finland–Russia Programme 2013–2017 (http://www.rktl.fi/english/fish/exploitation_of_fish/the_recovery_of.html). The plan is to use Mustajoki trout for compensation and enhancement releases in rivers east of the River Kymijoki, instead of Isojoki trout, which have been the most commonly used.

4.3.9. Kilpeenjoki

The River Kilpeenjoki is the last of the Finnish–Russian border rivers draining into the Bay of Vyborg, and only a short stretch of it is on the Finnish side (Figure 45). The whole watershed covers 958 km^2, with 2.2% of it (only 21 km^2) being located on the Finnish side (Ekholm 1993).

Only 11 samples from the Kilpeenjoki River were available. The samples were from the Russian side and most likely of an anadromous stock, which the river is assumed to have. There are also potential spawning areas on the Finnish side, but trout do not currently migrate up to that area. Migration routes should be opened. More samples are, however, needed. The diversity level of the population was low (0.50) (Table 3), probably because of the very small sample size. The Ne/N ratio was good (0.73), but the relatedness was elevated in the sample (Table 4). No similarity with any other stock could be observed (Table 5). Similarly to the River Mustajoki, the River Kilpeenjoki drains into the lower part of the Saimaa Canal, and is thus open to the sea.

4.4. Russian rivers

4.4.1. Notkopuro

Notkopuro is the first of the Russian rivers located on the Karelian Isthmus (Figure 45). In all, 51 samples from the anadromous Notkopuro trout were analysed. It had a good diversity level (0.67), a very good Ne/N ratio above 1 (1.2, Table 4), and very low relatedness (3.6%, Table 4).

4.4.2. Inojoki

It is known that historically the mean size of the trout in Inojoki has been 2–3 kg, and the annual catch about 500–1000 fish (Segerstråle 1937). The diversity level of the contemporary population is still good, 0.68, and the allelic richness was also high (Table 3). The Ne/N ratio was high and the relatedness low (Table 4).

4.4.3. Pikkuvammeljoki

Historically, the annual trout catch from this river was about 200 sea trout, and the mean size was 1.5 kg (Segerstråle 1937) (Figure 45). The diversity level is currently still high, and very little relatedness could be seen in the sample.

4.4.4. Vammeljoki

The size of the river system is 648 km^2 (Figure 45). Vammeljoki, Gladyshevka in Russian, is historically known as both a salmon river and a sea trout river. The mean size of sea trout has been 3–4 kg, and the annual catch 500–1000 fish (Segerstråle 1937, Hurme 1962). The current average density of young brown trout in the sections of the river with rapids is no more than 10 individuals/m^2. The size of the sea trout population is estimated to be only 700–800 individuals of mixed-aged young fish. Clearly, only one or two dozen sea trout enter the river to spawn. Therefore, the current condition of the sea trout population in the river has been defined as unstable and unsatisfactory (Titov & Sendek 2008). Large-scale dredging has been carried out to enable timber rafting.

Vammeljoki, or Gladyshevka, is a relatively small river that belongs to a lake and river system located on the Karelian Isthmus 70 km from St. Petersburg. It flows from Lake Gladyshevskoye, and merges with the River Roshinka, thus forming the River Chornaya flowing into the Gulf of Finland.

The Gladyshevka-Chornaya system is the only river system in the northern part of the Gulf of Finland in the Russian Federation, where used to be a local Atlantic salmon population. This population disappeared from the river by the 1970s, but possibly already in the 1960s. At the end of the 1970s and beginning of the 1980s, attempts were made to re-establish the population of salmon in the river by releasing fish of River Neva origin. After these attempts, stocking efforts continued in the 2000s. During the last seven years, over 80 000 mixed-aged salmon bred at the Narva fish farm have been released at the rapids of the river (Titov and Sendek 2008).

Similarly to the other Russian trout populations, the diversity level was still high and the relatedness within the river very low.

4.4.5. Kuokkalanpuro

In all, 23 trout were analysed from Kuokkalapuro (Figure 45). The diversity was high, the Ne/N ratio was very high (1.91) (Table 4), and the relatedness was the lowest observed in the native stocks, being 3.2%.

4.4.6. Rajajoki, Siestarjoki

The other name for the River Rajajoki is Siestarjoki (Figure 45). Segerstråle (1937) did not mention the River Rajajoki being a sea trout river. However, it very likely to have a native trout population with a high diversity level, although slightly lower than in the other rivers of the Karelian Isthmus.

4.4.7. Laukaanjoki, Luga

The watershed of the River Luga is free and wide, with several tributaries (Figure 45). The river is 359 km long, 400 m wide in the mouth section, and the area of the watershed is 13 600 km^2 (Titov and Sendek 2008). It is eutrophic and has a relatively steep profile. Essentially, the main river is more suitable for Atlantic salmon. According to Titov and Sendek (2008), there are local populations of brown trout in all northeastern tributaries of the Luga where spawning occurs. The total number of trout living in the basin of the Luga and annually entering the river to spawn has been estimated to be several hundred (Titov & Sendek 2008).

A ten-locus DNA microsatellite study of River Luga trout has previously been carried out (Lehtonen et al. 2009). A potential substructure was detected within the river, but further research was recommended before drawing final conclusions.

The diversity of the brown trout population is high. The Ne/N ratio was lower (0.41) than in most of the other Russian populations, and the relatedness was also slightly higher (6.2%, mean for the area 4.5%).

In a previous analysis of the genetic structure of the Russian trout populations in the Gulf of Finland area, a clear distinction could be seen between the stock from the Bay of Vyborg and Karelian Isthmus (Figure 47). In addition, a substructure among the Karelian Isthmus populations was revealed.

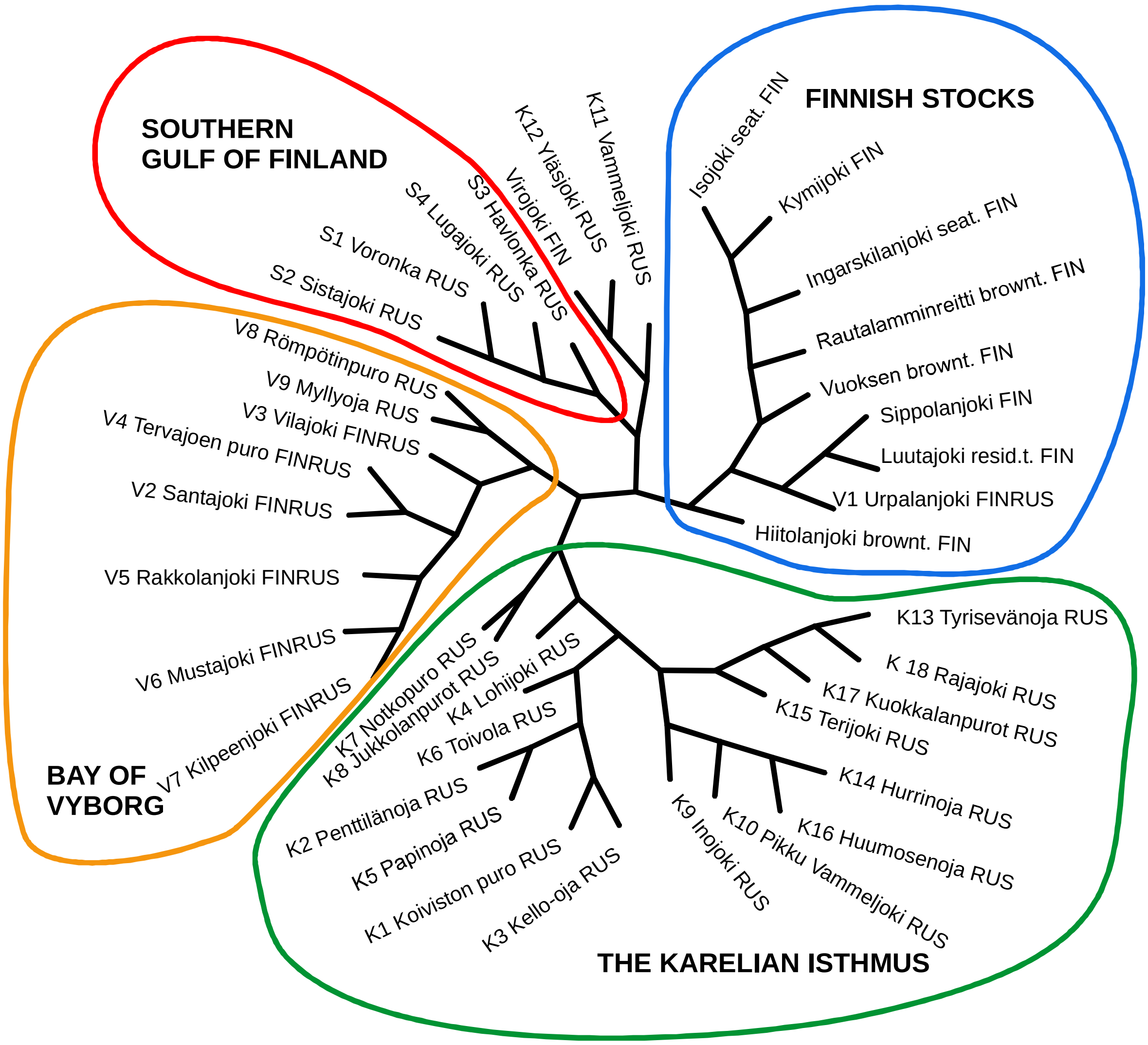

Figure 47. Genetic distances among Finnish and Russian trout populations according to a previous analysis based on 10 DNA microsatellite loci. Symbols before the river name describe the geographical location along the coast, when numbered clockwise for three different coastal areas; V1–V9 for the Bay of Vyborg, K1–K18 for the Karelian Isthmus, and S1–S4 for the southern coast of the Gulf of Finland.

4.5. Hatchery stocks for comparison

4.5.1. Lapväärtin-Isojoki

The River Isojoki drains into the Gulf of Bothnia and does not belong to the study area, but anadromous Isojoki hatchery trout have commonly been released since the 1970s into watersheds in southern Finland. It has therefore been included into the study as a reference stock. It was previously the only anadromous hatchery stock of brown trout. Isojoki has been a famous native sea trout river, from which several reports are available (e.g. Ryhänen 1957, Hurme 1962, Huovinen et al. 2005). The first broodstock was founded in 1967, when the spawners were caught below the Vanhakylä fish hatchery. The Finnish Game and Fisheries Research Institute founded its own broodstock of Isojoki trout in the Laukaa fish hatchery in 1970 by transporting four-summer-old juveniles from the Hatsina fish hatchery. Since 1980, the broodfish have been caught from the wild (Kallio-Nyberg 2002).

The diversity level of the Isojoki trout was high (Table 3), and the relatedness was low. This was a regular pattern for all hatchery stocks, except for the Swedish stock from the Island of Gotland.

4.5.2. Rautalamminreitti

Rautalamminreitti is an extensive watershed (7 312 km^2) in central Finland in the headwaters of the Kymijoki watershed above Lake Päijänne. It has large lakes, and 20% of the watershed area consists of lakes (Ekholm 1993). The migratory, freshwater brown trout from there have commonly been released into several water systems all over in Finland. The watershed is very extensive, draining via the River Kymijoki into the sea. The stock is a heterogeneous group of several broodstocks kept by both governmental and private hatcheries. The sample of this study was from the governmental Laukaa hatchery. Rautalamminreitti trout is no longer a homogeneous stock, as it is reared by both governmental and private hatcheries.

4.5.3. Luutajoki

The Luutajoki trout is a relatively resident trout population from southern Finland. It has been used for releases in small rivers, especially if no open migration routes are available, as it has a tendency to stay and succeeds in reproducing in small brooks.

The Luutajoki trout is assumed to be a complex mixture of several different natural and broodstocks. The current hatchery stock was established in 1976 from Luutajoki, and it has occasionally been renewed with fish from the wild. It is uncertain whether there were trout in Luutajoki before the river was first stocked in 1893 with Russian trout, brought from near St. Petersburgh. Luutajoki has since been stocked with several different stocks.

Besides this Russian stock, an unknown German stock and trout were brought in 1906. Trout from Huopanankoski rapids in central Finland were regularly purchased, starting in 1911. The first spawners were collected from Luutajoki in 1904. Up until 1945, the Evo hatchery also collected spawners from Vihavuodenkoski rapids, which are located some fifty kilometres downstream of Luutajoki in the same Hauho watercourse of the Kokemäenjoki watershed. Later, the Evo hatchery bought trout from Puntarinkoski hatchery in eastern Finland, which had a broodstock of Lake Höytiäinen trout. In the late 1950s and early 1960s, small numbers of unknown trout from Porla hatchery and Danish trout were also brought to the Evo hatchery (Brofeldt 1920, Kirjavainen and Westman 1992).

4.5.4. Sweden, Gotland

As a comparison sample from Sweden, anadromous trout from the Island of Gotland were used. These fish were collected for a broodstock to produce offspring for enhancement releases in the Åland Islands of Finland. On the Island of Gotland lives a form of brown trout having a very short freshwater stage, and it was assumed to also be suitable for stocking in the small, easily drying brooks of the Åland Islands. Enhancement releases have been carried out with this stock, and the corresponding broodstock is kept by the Provincial Government of the Åland Islands. This population originates from roe brought in 2004 and 2005 from Själsöan and Lummelundaån (Härkönen 2012).

4.5.5. Denmark, Kolding

Danish trout were introduced in Finland in the 1960s, and were mainly from only one hatchery located in Kolding. To determine whether any signs of these releases are to be seen, a comparison sample of a hatchery stock from Denmark was analysed.

5. Discussion

5.1. Diversity levels

The diversity level differences in the data were large. Slightly against the common view, hatchery rearing and releasing has not reduced the diversity of trout, when measured as allelic richness or mean heterozygosity. On the contrary, the highest diversity values for Finnish populations were in hatchery stocks such as Aurajoki, and especially in populations in which fish of different origin were mixed in the wild, usually because of releases, such as in the Vantaanjoki river system.

The native Russian populations already had a high diversity in their wild natural state. Finnish wild populations tended to be small and had probably often undergone bottlenecks. Population sizes had partly already been small because of their isolated location above either natural or manmade migration obstacles, but also because of the lack of spawners from the sea. Often, the reasons had been both: on one hand, human-induced changes such as migration obstacles, poor water quality, poor spawning ground quality, and intensive coastal and river fisheries, and on the other hand the already naturally isolated location of the population in the upper branches of the rivers. A network of populations has very likely occurred in the complicated river systems. Thus, there may well have been a metapopulation structure with partial gene flow, especially from upper populations to those nearer to the sea. The spawning migration distance of the spawners from the sea has also varied, and they have occasionally reached the more distant spawning grounds.

No differences in the level of diversity could be seen between Finnish populations classified as either anadromous or resident. However, the reasons for the relatively low diversity level for both of these were probably partly different. For resident populations, isolation has played a more marked role, while for anadromous populations the lack of spawners due to the coastal fishery and damming of the rivers have probably been more important.

In the southwestern Varsinais-Suomi area, the diversity levels were significantly lower than in other areas, but fish releases have not been common in that area, and some possibly still native, very small populations have remained, such as in Paimionjoki and Purilanjoki. In the Uusimaa area, the diversity level of the populations has clearly increased because of extensive releases. In the Russian and border river populations, the diversity levels were still naturally high, as there had seldom been releases into these rivers. There were also relatively few dams in these rivers, although some migration obstacles in the border zone often hampered spawning migration in the border rivers. Despite poaching, the fishing intensity has obviously also been quite low in Russian rivers and the coastal area, which has enabled better maintenance of the brown trout stocks there than in Finland. Because of their relatively good state, these populations offered a good point of comparison for the Finnish brown trout stocks.

The effective sizes of the native brown trout populations have probably always been quite small, the only native population having an Ne value over 50 being the Russian Notkopuro population on the Karelian Isthmus. When founding hatchery populations, the recommended minimum effective size is 50 individuals, which is often translated as 100 true individuals. However, in the wild, several populations seem to have survived with relatively small effective sizes, and this may be a result of gene flow between them.

The estimates of effective population sizes were often based on several samples and several year classes, thus being more reliable than single samples and samples of a single year class. Overlapping of generations increases the overall effective size of the population. The estimated effective sizes also only indicate the true population when sampling has been representative. For most Finnish populations this was probably the case, but for the Russian populations the effective sizes may be larger than estimated here, because of small sample sizes.

The Ne/N ratio was not so dependent on the sample size, and it also seemed to be much more sensitive in revealing hatchery releases than the plain diversity level measures as such. The Ne/N ratio was high for ordinary hatchery stocks when sampled from hatcheries, as organized matings increase it. The Danish population, in particular, had almost the theoretical maximum of 2 (1.91), which indicates effective mixing of families in breeding practice. The governmental Finnish hatchery stocks had a level of about 1 (0.9–1.04), as did the Aurajoki hatchery stock (0.92) (Table 4). The same level was reached on average in the Russian wild populations, and even in border river populations if hatchery rearing was not involved. Interestingly, among the border rivers, the only values below 0.5 were for Vilajoki and Mustajoki. Releases have been carried out into Vilajoki. In the Uusimaa area, Ne/N values below 0.50 occurred for several enhancement rivers, such as Ingarskilanjoki, Mankinjoki, Espoonjoki, Vantaanjoki, Sipoonjoki, Mustijoki and Porvoonjoki, which indicates that the effects of a small founder number and previous bottlenecks in population sizes for these populations are still apparent when compared to populations with a wild undisturbed background.

Relatedness, when measured as the proportion of the same genetic background, was in general somewhat higher than assumed (about 3%) in normal large wild populations. It was also clearly higher in populations with some hatchery background than in the native Russian populations, for which the mean was 4.25%, excluding the River Luga (Table 4). Relatedness of over 10% occurred in six populations, most of which were known to be very small, such as Purilanjoki, Karjaanjoki-Mustionjoki, Espoonjoki-Ryssänniitunoja, Mustijoki and Vilajoki, and related individuals are likely to occur there.

The level of diversity in the Finnish populations usually seemed not to be an issue, but the relatedness tended to increase when hatchery rearing was involved in the enhancement. This might have been partly a result of samplings, if siblings were sampled by chance more frequently than they occur in the river on average. However, high relatedness did not occur in the wild native stocks. It can thus be assumed that relatedness was higher in the enhancement populations, although not in the hatchery broodstocks themselves. This means that either the released fish have been more related or the number of spawners in the enhancement rivers is still often so small that relatedness occurs in the new generation. This may be a transient problem. If releases cease and the number and density of spawners increases, relatedness may decrease.

5.2. Genetic structure

The genetic structure for the anadromous populations seemed to closely follow the geographical distances between populations, and also the form of the coastline. This original structure was still to be seen, even after so many years of mixing and releasing of populations. Most of the deviations from the geographical order could be explained by known transportations of the populations. As with Atlantic salmon stocks, a reasonable assumption for the anadromous brown trout populations is that the geographically closest population is also the genetically most similar in undisturbed circumstances.

Along the Finnish coast there have been three at least partly isolated groups: the first in the southwest, or Varsinais-Suomi, the second in Uusimaa and the third group comprising the Bay of Vyborg rivers. The River Kymijoki has been a large water system, and it is not known which group its original population has belonged to. It is possible that there has once been one more group on the eastern coast before the Bay of Vyborg, into which Summanjoki and Kymijoki and some other nearby river populations have been included. No reliable genetic material from this has, however, remained. It may also have been a continuum from the southern Uusimaa coastal populations.

Genetic material from all these three groups is still left in several rivers. Uskelanjoki and Paimionjoki are the most representative populations of the western group, Ingarskilanjoki, Koskenkylänjoki, Mankinjoki, Sipoonjoki and Vantaanjoki of the second group, and Virojoki, Mustajoki, Rakkolanjoki and Santajoki of the third original Finnish anadromous brown trout group. In addition, two groups with a foreign hatchery influence occurred, most clearly the Aurajoki group, which seems to have deviated from the other populations and to have formed a group of its own with Fiskarsinjoki and Kiskonjoki-Latokartanonkoski populations. In addition, a group was formed of the Espoonjoki, Kymijoki and Summanjoki populations, in which the influence of Isojoki releases of differ stages could be seen. The Kymijoki population is based entirely on Isojoki releases. In Summanjoki, the original stock had also been weak if existing at all when Isojoki stock releases were started. In Espoonjoki, somewhat more native genetic material has been left, but in the dendrogram it groups with these Isojoki-influenced populations, although with a lower bootstrap value (64%) than Kymijoki and Summanjoki together (100%). Kymijoki and Summanjoki are from the same geographical area, and their original genetic material has also been quite similar.

In addition to the at least partly Finnish populations, one group based on entirely Russian stocks was formed. Within that group, the populations from rivers draining from the Karelian Isthmus formed one clear group, and populations from the rivers Rajajoki and Luga formed a small group of their own (Figure 5). In the data from the previous analysis, it could be seen that there was a further distinction into two groups among the Karelian Isthmus populations when more of them were studied (Figure 45). At least one distinction exists along the coast before the River Inojoki, whereby populations after it and including Inojoki belong to the more southern group. In that data set it could be seen that rivers from the southern coast of the Bay of Vyborg (Römpötinpuro and Myllyoja) also belonged to that group, and not to the Karelian Isthmus group. When more populations from the Russian side were also included from the southern coast, the River Luga population and its neighbouring rivers formed a clear group of its own.

Overall, the populations were structured at several levels, and this information can be used for management decisions at the corresponding level. When considering whole river systems, the observed large-scale structure offers information on the current state and can be used when deciding on the optimal treatment for the contemporary population, either conserving it as such, supporting it with releases of a suitable genetic material if too weak, or even gradually changing the population, when more optimal genetic material is available.

The individual river system level analysis revealed clear substructures in seven river systems, in which decisions are needed for their future treatment.

- Kiskonjoki – 5 subpopulations: anadromous Latokartanonkoski, resident Myllyjoki, resident Kiskonjoki-Koorla, anadromous Perniönjoki and resident Perniönjoki – Metsänoja;
- Karjaanjoki – 5 subpopulations: anadromous Mustionjoki, resident Nummenjoki, resident Nuijajoki, resident Vihtijoki, resident Saavajoki;
- Siuntionjoki - 2 subpopulations: resident Kirkkojoki and anadromous Passilankoski;
- Espoonjoki – 2 subpopulations: anadromous main branch and resident Ryssänniitunoja;
- Vantaanjoki – 4 subpopulations: anadromous low, anadromous middle, resident upper reaches and resident Palojoki;
- Summanjoki – 2 subpopulations: anadromous main branch and resident upper reaches (very similar);
- Virojoki - 2 subpopulations: resident upper reaches and anadromous Saarasjärvenoja.

In many of these, the structure within the river system also followed the direction and connections of the waterflow. In the Kiskonjoki river system, samples from the Kiskonjoki branched (Huhdanoja and Varesjoki together, and Koorlan Lohioja and Aneriojoki together), and all together they separately form the Perniöjoki branch (Fig. 14). From the Perniönjoki branch, all populations similarly grouped together. In the Karjaanjoki river system, separate samples from the three branches, Nummenjoki, Karjaanjoki and Vihtijoki, also grouped together within their home tributary, and these branches could also be considered as management units within the river system. Only one population was observed in Uskelanjoki, Mankinjoki and Sipoonjoki. The situation in Siuntionjoki remained partly open, because of the small sample size from the main stem.

5.3. Management

The long-term goal of brown trout management is to maintain maximal adaptive genetic diversity in self-sustaining populations, and also to allow sustainable fishing of brown trout populations whenever possible, without jeopardizing the maintenance of genetic diversity. The necessary prerequisites for this goal are that sufficient and permanent spawning areas are available and that current genetic diversity is maintained in populations of a sufficient effective size.

The 27 Finnish river systems analysed here are in very different stages in relation to this goal. The individually defined goals for the river systems may also vary, depending on the local circumstances for both the availability and quality of the spawning grounds and the current genetic material in the river. The main issue is to develop an overall strategy in which the maintenance of the most valuable genetic material is safeguarded in sufficiently large populations. Some of the river systems or tributaries may well be reserved for more efficient utilization, such as rod fishing, as long as this does not threaten the defined goals. For long-term management, it is essential that the strategies for the rivers are not changed once defined. The enhancement and adaptation of river populations often takes several fish generations before the populations can thrive, and when created they cannot be changed or moved without harming them. Thus, changing of the management plan for a river may risk the work done until then.

In general, more spawning grounds should be established within reach of the anadromous trout populations, and the lack of spawning grounds has been the main reason for the loss of so many anadromous brown trout stocks in Finland. In addition, fishing has for several reasons been much more intensive in Finland than in Russia or Estonia, where more brown trout stocks have remained in their natural state. By building fishways or bypasses at dams or other migration obstacles, several spawning grounds could be returned to their original use. This work has been neglected for a long time, partly because of some unsuccessful attempts, but technologies have improved and new natural types of fishways may in several places offer new options to resolve the fish migration passage problem.

Some mixing of genetic material has occurred as a result of the Finnish policy of fish releases. Foreign stocks have been released into several locations, either directly into the rivers to enhance the weak local populations or to create a population in an empty river. These enhancement projects have also been successful, as naturally reproducing populations have been created in several rivers as result of the releases. For example, the River Koskenkylänjoki was enhanced with Ingarskilanjoki trout, and in the River Vantaanjoki natural reproduction currently occurs in several tributaries. These populations are valuable as such, despite their hatchery origin.

From the observed five genetic groups in which Finnish stocks were found, two were originally of hatchery origin, the Aurajoki group and Isojoki group. The Isojoki population is from a river draining into the Bothnian Bay area, so when possible its genetic material from the Gulf of Finland area is recommended to be replaced by the local genetic material. Previously, local genetic material has not been sufficiently available, but nowadays the Ingarskilanjoki broodstock is producing fish for stocking, and in the future, genetic material of Mustajoki trout from the Bay of Vyborg group will also be available. Releases into the River Summanjoki and possibly also the River Kymijoki could be changed so that Mustajoki trout are released. From the Aurajoki group, releases into Kiskonjoki Latokartanonkoski should be ended. To support natural production, some transfer of fish from the same or a nearby tributary could be carried out.

From the five groups, three were regarded to represent at least to some extent the original genetic material of the trout for the area. On the southwestern coast of Finland, local genetic material is still left in the Uskelanjoki group, especially in the Uskelanjoki river, but obviously also in the Paimionjoki and Purilanjoki rivers and in the Perniönjoki branch of the Kiskonjoki rivers. Currently, some populations are too small, with only a few families left. New local genetic material is needed from somewhere for these. As no broodstock of the local genetic material is available, transfers of fish from one river to another could be considered as a possible tool, as long as the spawning sites are in good condition and fishing does not hamper the enhancement of the naturally reproducing stock. The founding of a broodstock from local material could be considered. The distribution of the Aurajoki stock should be limited only to agreed rivers and for sea ranching purposes, and not into river systems with their own local stocks, such as Kiskonjoki.

In the coastal rivers of Uusimaa, local genetic material is left in several rivers of the Ingarskilanjoki group. In addition to Ingarskilanjoki itself, local genetic material for the Uusimaa area occurred in Koskenkylänjoki, Sipoonjoki, Mankinjoki and Vantaanjoki, and also in Espoonjoki. In several river systems, the enhancement of natural reproduction has succeeded so well that the reduction of enhancement releases could be considered, to allow the populations to recover and further distribute themselves. If releases are needed, Ingarskila trout could be used, but careful evaluation of the need is recommended, as differentiation among river systems should be supported by ending releases when possible. The diversity levels of brown trout populations in the Uusimaa area were usually high and population sizes were sufficient in most cases. The distribution of Aurajoki trout should be restricted only to currently agreed rivers and for sea ranching purposes, and not into river systems with their own local stocks. Isojoki trout should be used only in sea ranching, and if possible, not even for that use at all.

For the southeast coast, local genetic material is still left in the Bay of Vyborg population group, especially in the River Mustajoki population, but also in Rakkolanjoki, Santajoki and Kilpeenjoki. In addition, Urpalanjoki and Virojoki-Saarasjärvenoja belong to this same group. The Mustajoki trout is recommended as an enhancement stock for the area if needed, and possibly for Kymijoki releases as well. The diversity levels of the populations were on average high for the area, and there are still several native self-sustaining stocks left, in contrast to the other two areas. The distribution of Isojoki hatchery stocks should be limited at most to releases for the River Kymijoki.

A recommendation for all three areas is the improvement of spawning and nursery areas, opening of migration routes and regulation of both the sea and river fisheries at a sustainable level. In many cases, the spawning stock sizes are so small that a catch and release fishery in the rivers is recommended if fishing is allowed at all.

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