

Wild Estonian and Russian sea trout (*Salmo trutta*) in Finnish coastal sea trout catches: results of genetic mixed-stock analysis

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For responsible fisheries management of threatened species, it is essential to know the composition of catches and the extent to which fisheries exploit weak wild populations. The threatened Estonian, Finnish and Russian sea trout populations in the Gulf of Finland are targets of mixed-stock fisheries. The fish may originate from rivers with varying production capacities, from different countries, and they may also have either a wild or hatchery origin. In order to resolve the composition of Finnish coastal sea trout catches, we created a standardized baseline dataset of 15 DNA microsatellite loci for 59 sea trout populations around the Gulf of Finland and tested its resolution for mixed-stock analysis of 1372 captured fish. The baseline dataset provided sufficient resolution for reliable mixture analysis at regional group level, and also for most of the individual rivers stocks. The majority (76–80%) of the total catch originated from Finnish sea trout populations, 6–9% came from Russian and 12–15% from Estonian populations. Nearly all Finnish trout in the catch were of hatchery origin, while the Russian and Estonian trout were mostly of wild origin. The proportion of fish in the Finnish catches that originated from rivers with natural production was at least one fifth (22%, 19–23%). Two different spotting patterns were observed among the captured trout, with a small and sparsely spotted form being markedly more common among individuals of Russian (28%) and Estonian origin (22%) than among fish assigned to a Finnish origin (0.7%).

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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.). Of 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.

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 that 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 order to increase the escapement of sea trout from the fishery, the legal minimum catch size of sea trout was increased at the beginning of 2014 from 50 cm to 60 cm. In addition, in 2013, the legal minimum catch size of sea trout was increased in the Finnish governmentally con-

trolled offshore sea area of the Gulf of Finland from 50 cm to 65 cm for adipose fin-clipped trout, all others are completely protected from fishery and should be released if caught. 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 does occur. In the Estonian Red List of Threatened Species, the sea trout is listed as Near Threatened (RED DATA BOOK OF ESTONIA 2008).

In Finland, dam construction has been especially active and several sea trout stocks have been destroyed (KALLIO-NYBERG et al. 2001). 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 are commonly practiced with the aim of re-establishing extinct or enhancing weak populations. In addition, hatchery releases to improve sea trout catches have also been widely used along the coastal area.

In all, 293 000 sea trout smolts were released into the Gulf of Finland in 2012. The majority of these (74%, i.e. 216 000 smolts, mainly of Isojoki and Ingarskilanjoki origin) were from Finnish releases, 22% (64 000 smolts, only sea trout from the River Luga) came from Russia and the

remaining 4% (13 000 smolts, mainly of Pudasoo origin) were from Estonian releases (ICES 2013). This also reflects the approximate levels of recent years. Estonia has announced its aim to end sea trout releases.

The mixed-stock fisheries in the Gulf of Finland not only target fish of rivers with varying production capacities or separate national origins, but also a mixture of wild and hatchery fish. This in many respects resembles the situation with Atlantic salmon in the Baltic Sea (KOLJONEN 2006, ICES 2013), although the trout fishery is more restricted to coastal areas.

Some mixing of anadromous trout from different countries is known to occur, as tagging experiments have generally shown 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 to some extent been recaptured in Finnish coastal waters. The coastal sea trout catch in 2012 was 13 300 kg in Estonia and 15 900 kg in Finland. In addition, Finland

announced a total catch of 3800 kg from rivers (ICES 2013).

In Russia, wild sea trout populations are found in at least 40 rivers or streams. The majority are situated along the northeastern coast of the Gulf of Finland, but the rivers with the most abundant smolt production are in the southern River Luga area (Fig. 1). 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 into the sea from the Luga, the largest Russian trout river (TITOV and SENDEK 2008). In Russia, sea trout releases are only carried out into the River Luga and comprise fish of its own river system. In 2014, a total of 48 500 one-summer-old and 43 500 two-summer-old juveniles were released.

In Estonia, sea trout populations are found in 45 rivers and brooks in the Gulf of Finland region, of which 38 have wild populations (ICES 2013). Rivers with higher

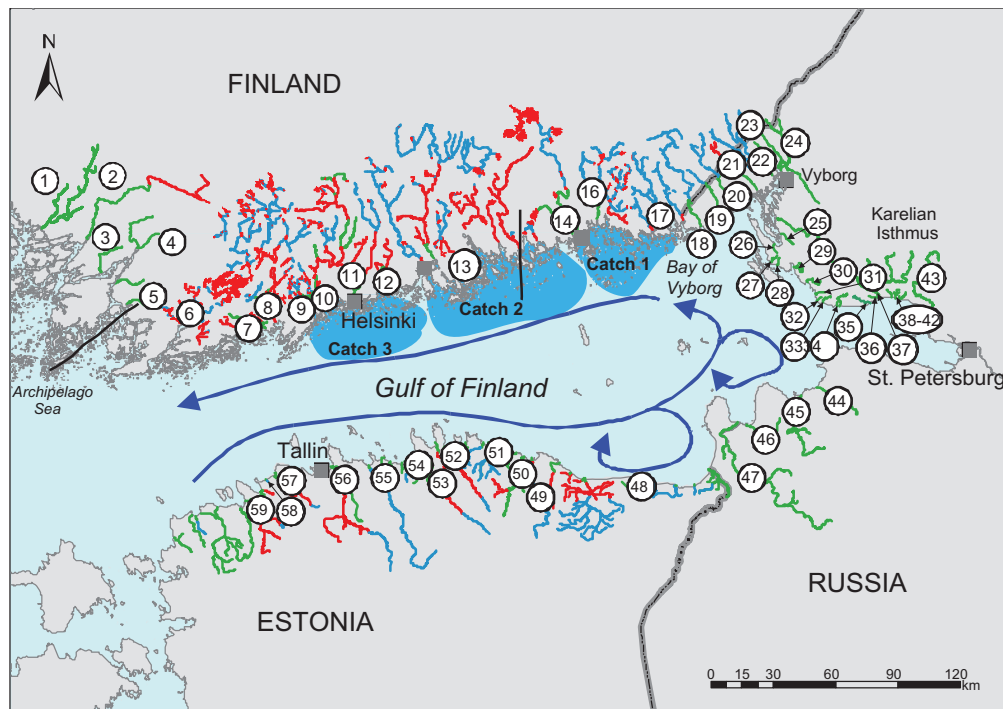


Fig. 1. The sampled brown trout rivers in Finland, Russia and Estonia. The colour of the river indicates its quality as a spawning site and potential environment for brown trout. Red: river is closed; blue: irregular reproduction occurs; and green: open river with regular natural production of brown trout populations. The names and numbering of the rivers are the following: 1) Aurajoki, 2) Paimionjoki, 3) Purilanjoki, 4) Uskelanjoki, 5) Kiskonjoki, 6) Fiskarsinjoki, 7) Ingarskilanjoki, 8) Siuntionjoki, 9) Mankinjoki, 10) Espoonjoki, 11) Vantaanjoki, 12) Sipoonjoki, 13) Koskenkylänjoki, 14) Kymijoki, 15) Isojoki (hatchery stock, not in the map), 16) Summanjoki, 17) Virojoki, 18) Urpalanjoki, 19) Santajoki, 20) Vilajoki, 21) Tervajoki, 22) Rakkolanjoki, 23) Mustajoki, 24) Kilpeenjoki, 25) Römpötinpuro, 26) Myllyoja, 27) Koivistonpuro, 28) Penttilänoja, 29) Kello-oja, 30) Lohijoki, 31) Papinoja, 32) Toivolanpuro, 33) Notkopuro, 34) Jukkolanpuro, 35) Inojoki, 36) Pikkuvammeljoki, 37) Vammeljoki, 38) Tyrisevänoja, 39) Hurrinoja, 40) Terijoki, 41) Huumosenoja, 42) Kuokkalanpuro, 43) Rajajoki, 44) Voronka, 45) Sista, 46) Havlonka, 47) Luga, 48) Pühajõgi, 49) Kunda, 50) Toolse, 51) Selja, 52) Loobu, 53) Valgejõgi, 54) Pudasoo, 55) Mustoja, 56) Pirita, 57) Vääna, 58) Keila, 59) Vasalemma. The borders of Finnish administrative ELY Centres on the coast are indicated by black lines. Approximate sea trout catch areas are shown as dark blue shaded areas along the Finnish coast. The blue arrows indicate the prevalent water currents in the Gulf of Finland.

smolt production are situated in the central part of the north Estonian coast (Fig. 1).

Watershed-based analyses of the genetic structure of Finnish brown trout populations have also previously been conducted for national purposes with both allozymes and DNA microsatellites (KOLJONEN 1989, MARTTINEN and KOLJONEN 1989, KOLJONEN et al. 1992, KOLJONEN and SAURA 1992, NUOTIO and KOSKINIEMI 1995, SAURA 2005, AALTONEN 2009, 2011). In addition, research teams from other Baltic Sea countries have investigated some restricted areas or river systems of the Baltic Sea drainage basin by using microsatellite markers (WAS and WENNE 2002, HANSEN et al. 2006, LEHTONEN et al. 2009, SAMUILOVIENE et al. 2009). However, this study is the first to cover the whole Gulf of Finland coast.

For responsible fisheries management of threatened species, it is essential to know the composition of catches and the extent to which fisheries exploit weak wild production. Mixed-stock analysis based on genetic data has been used for decades in analysing the composition of Pacific salmon catches in North America (SHAKLEE et al. 1999, BEACHAM et al. 2001, 2008) and the Atlantic salmon fishery in West Greenland (REDDIN and FRIEDLAND 1999). It has also been used to reveal the composition of Atlantic salmon catches in the Baltic Sea since 2000 (KOLJONEN 2006, ICES 2013). A genetic baseline database for mixed-stock analysis has additionally been created for Atlantic salmon for the whole European range (GRIFFITHS et al. 2010). Furthermore, catch composition analysis has been utilized to analyse stock proportions in brown trout catches in the large, northern, Finnish Lake Inari (SWATDIPONG et al. 2013).

The aim of this study was to test the possibilities of using microsatellite data for mixed-stock analysis of sea trout catches in the Gulf of Finland. The goals were to: 1) collect international baseline data from all sea trout stocks around the Gulf of Finland; 2) test the resolution of this baseline data set with simulations to analyse stock and stock group proportions, and also the usefulness for individual assignments of captured fish; 3) analyse the national contributions of trout production in the studied Finnish catches; 4) analyse the proportions of wild and hatchery-produced fish in the sea trout catch; and 5) compare the results obtained with Bayesian and maximum likelihood estimation methods

MATERIAL AND METHODS

Fish sampling from rivers to create the baseline dataset

Altogether, 4224 sea trout individuals from 59 watersheds were sampled in the current study to create the baseline

dataset for analysing the origin of Finnish sea trout catches in the coastal waters of the eastern Gulf of Finland. The rivers are numbered from west to east clockwise round the gulf so as the river numbers are showing the geographical proximity of the rivers (Fig. 1, Appendix 1 Table A1). Seventeen of the river systems were entirely on the Finnish side of the coast. Seven of the rivers cross the Russian border, so that the upper reaches of the rivers are located in Finland and the lower parts drain into the sea in Russia. In addition, 23 sea trout populations from relatively native rivers on the Russian coast and also from 12 rivers from the Estonian coast were included in the baseline data (Fig. 1).

The Finnish sea trout population samples were obtained from rivers discharging into either the nearby western area, the Archipelago Sea or into the Gulf of Finland. In addition to the border rivers (the northern coast of the Bay of Vyborg), the Russian samples covered the southern coast of the Bay of Vyborg, the Karelian Isthmus, the northern coast of the Bay of St. Petersburg and part of the southern coast of the Gulf of Finland. Estonian rivers were located on the southwestern coast of the Gulf.

The type and size of the rivers markedly vary among the studied countries and areas. In Finland, the watersheds are typically large and the rivers are often outlets of large lake and river systems. In Russia and Estonia, the rivers are often small and shallow, with the exception of the River Luga system.

The status of the river environment in all countries is classified into three categories, which are shown in Fig. 1. Open rivers are indicated in green, partly open in blue and river stretches above migration obstacles are shown in red. Preliminary information has also been used to classify the populations according to their level of originality as original (native), mixed through stocking or introduced, depending on their stocking history. The most interesting and valuable populations from the management point of view are those that are anadromous, viable, original and still genetically diverse. A substructure analysis within each Finnish river system, in cases where several samples were taken, was performed in KOLJONEN et al. (2013), and only anadromous populations were included in the present study. All 12 Estonian baseline populations and most, 16 out of 23, Russian samples were new to this study.

The Finnish coast is divided into three governmental administrative sectors according to the Centres for Economic Development, Transport and the Environment (ELY Centres). These Centres are responsible for the regional implementation and development tasks of the government. The rivers are listed separately for each ELY Centre (Appendix 1 Table A1; borders are also shown in Fig. 1).

Sea trout sampling from fishery catches

For the catch analysis, a total of 1373 trout were caught by fishermen, mostly using bottom gill nets (70%), but also by rod (17%) or fyke net (13%). Samples were collected from both professional and recreational fishery. The catch sites were divided into three sectors according to the nearest coastal municipality (Table 1, Fig. 1). These catch sectors are not the same as the ELY Centre borders. All catch samples mostly came from the eastern part of the Gulf of Finland, between the city of Helsinki and the Russian border, and relatively close to the Finnish coast. No catch samples were available from the westernmost part of the coast from the area of the ELY Centre for southwest Finland. Fishery sampling was more efficient in the easternmost area (Table 1). The samples were collected over the years from 1996 to 2012 and they do not thus represent any particular time period, but rather provide an overview of the situation in recent years, when hatchery population releases have been quite intensive in Finland. Most samples were collected between years 2006–2012, and only samples less than 50 individuals in previous years. (Table 1).

Fishermen also visually inspected fish in their catch and reported adipose fin-clipped fish, and also fish that somehow deviated in their appearance. Some fish were reported to look more like salmon, being slender and having fewer and smaller spots than fishermen were used to have seen. These fish were identified from the individual assignment database and also analysed separately.

DNA methods

Total genomic DNA was extracted from scale or tissue samples in 95% alcohol using the DNeasy Blood & Tissue Kit (Qiagen) or according to the simplified method of LAIRD et al. (1991). Variation was determined at 16 microsatellite loci (Appendix 1 Table A2). However, locus SSa289 was omitted from the statistical analysis, as it was not included in the Estonian baseline data. For each sample, two multiplex PCR reactions were performed using the Qiagen Type-it Microsatellite kit in a 10- μ l reaction

Table 1. Numbers, sampling sites and main sampling years (> 50 fish year⁻¹) of the analysed Finnish sea trout catch samples.

Area	Municipality	Location	n	Main years
1	Virolahti, Hamina, Kotka	East	656	2006–2012
2	Pyhtää, Ruotsinpyhtää, Loviisa, Pernaja	Middle	492	2009–2012
3	Porvoo, Sipoo, Helsinki, Espoo, Kirkkonummi	West	224	2010–2011
Total			1372	

volume with 3 μ l of extracted DNA, 5 μ l of kit master mix and primers with concentrations and dyes as presented in the Appendix 1 Table A2. PCR reactions were carried out in 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.

The amplification products were separated by capillary electrophoresis on AB3130 (in Finland) and AB3500 (in Estonia) Genetic Analyzers (Applied Biosystems, Foster City, CA), and the sizes of the microsatellite alleles were determined using Genemapper ver. 4.0 and ver. 4.1 software, respectively (Applied Biosystems, Foster City, CA), and manually checked. Cross-laboratory calibration and standardisation of allele sizes for all loci was conducted between laboratories from the University of Helsinki, Department of Agricultural Sciences and the Estonian University of Life Sciences, Institute of Veterinary Medicine and Animal Sciences, Department of Aquaculture. This allowed the pooling of genotype data to establish a joint baseline dataset, and enables the future analysis of all catch samples in both laboratories.

Statistical analysis

Pairwise F_{st} values were calculated with FSTAT ver. 2.9.3.2. (February 2002) (GOUDET 1995, 2001) (<www2.unil.ch/popgen/softwares/fstat.htm>). Analysis of the differences between populations was based on genotype frequencies and was also tested with FSTAT, which includes Bonferroni correction for multiple tests.

Genetic distances between sea trout populations were calculated using Nei's D_A 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 software (LANGELLA 1999) (<<http://bioinformatics.org/~tryphon/populations/>>). Bootstrapping with 1000 replicates was used to test the statistical strength of the branches. The genetic distance tree was drawn with TreeView ver. 1.6.6. (PAGE 1996) (<<http://taxonomy.zoology.gla.ac.uk/rod/treeview.html>>).

The catch composition was analysed with the Bayesian estimation method for mixed-stock analysis using the BAYES program (PELLA and MASUDA 2001). Genetic information on 59 sea trout populations around the Gulf of Finland and Archipelago Sea from Finland, Russia and Estonia was available as baseline population data. Ten iteration chains were calculated for each catch estimate. The prior of each potential baseline population had a maximum proportion of 71.0% in turn, and the others evenly 0.005%. The convergence of the chains to the posterior probability distribution was tested for each catch sample with convergence statistics (GELMAN and RUBIN 1992), included in the BAYES software package. The last 1000

MCMC iterations of each 6000-iteration chain were combined and used to describe the posterior probability distributions of the proportions of each baseline population, and the eight population groups (formed based on the genetic distances among baseline populations), as well as for the individual assignments. The Bayesian estimation was chosen for the estimation of the final results, as it has been shown in previous studies to out-perform the maximum likelihood-based methods ONCOR and SPAM, e.g. in tests where mixed samples of known origin were available (GRIFFITHS et al. 2010, MORAN et al. 2014).

For comparison, the maximum likelihood estimates of the same catches were assessed with ONCOR software (<www.montana.edu/kalinowski/Software/ONCOR.htm>) (KALINOWSKI et al. 2007, ANDERSON et al. 2008).

The analysed sea trout baseline dataset for the Gulf of Finland was very large, including several similar sets of populations. It consisted of nearly 60 sea trout populations, and they originated from a geographically relatively small area for some locations, which sets challenges for the estimation method. For example, when analysing a baseline data set of 57 Atlantic salmon river populations in the southern part of the European range, clear difficulties were met regarding the estimation accuracy because of the genetic similarity of the populations, but possibly also because of the small baseline sample sizes (GRIFFITHS et al. 2010). Thus, the capacity of the estimation method in general to separate so many individual trout populations and groups was first assessed by the simulation options included in the ONCOR software.

The population proportion estimation of individual river populations was evaluated with so-called 100% simulation, in which each baseline population in turn contributed 100% of the analysed mixture. The baseline samples were the same as in the empirical baseline. The mixture sample size was set to 200 and 1300, which were approximately the smallest and largest catch sizes used here (224, 492, 656 and 1372, Table 1), and simulations were repeated 100 times for both individual populations and the eight population groups used here as reporting groups.

The accuracy of individual assignment was tested with the leave-one-out procedure and results were obtained similarly for individual populations and reporting groups. In addition, the accuracy of the estimation was assessed by a simulation option called 'Realistic fishery simulation', with simulated mixtures of 200 individuals so that each of the baseline populations in a set of 20 populations contributed 5% to the simulated catch. The results of these simulations are combined into one table. In addition, the option 'Three way error decomposition: Fishery, Loci, Baseline', was used to analyse the source of observed uncertainty for each baseline population by setting the number of individuals in each population to be 5, 7 and

10, with the corresponding mixture sample sizes of 295, 413 and 590.

RESULTS

Genetic differentiation and distances between baseline populations

The level of differentiation (as estimated by F_{st}) between pairs of baseline populations varied from 0.002 to 0.437. Most of the baseline populations were significantly differentiated from each other, and statistically non-significant differences in genotype frequencies (after Bonferroni correction for multiple tests) were only observed for two Finnish population pairs and one Estonian population pair (F_{st} values for these pairs are presented in red in Table 2): Aurajoki – Fiskarsinjoki (F_{st} 0.009), Ingarskilanjoki – Koskenkylänjoki (F_{st} 0.013) and Pudisoo – Pühajõgi (F_{st} 0.002). The genotype frequencies of these population pairs were thus identical to each other, and fish transfers or releases are known to have occurred in all of them. The difference was also only significant at the 5% nominal level for two very similar population pairs of rivers, Paimionjoki (2) – Siuntionjoki (8) in Finland and Hurinoja (40) – Kuokkalanpuro (42) (Fig. 1) on the Karelian Isthmus in Russia. The latter pair of rivers should have contained native populations, but are geographically very close to each other (Fig. 1). All rivers numbered from 38 to 42 almost discharge into the same location.

In addition to the already mentioned very similar population pairs, F_{st} values smaller than 0.02 were observed between thirteen Estonian population pairs, and also between occasional population pairs in some other geographically close rivers from other areas (all shown shaded in Table 2). All F_{st} values less than 0.02 were, however, observed between population pairs of the same geographical area. Separating these very similar populations on the basis of genetic data could be assumed to be difficult, and these populations are unlikely to be distinguished as individual populations in mixed-stock analysis, and were thus of special interest in the simulation analysis.

In most of the cases with a very high similarity between populations, genetic effects of hatchery releases of known sources could be assumed according to the history of hatchery fish releases. Among the Finnish populations, Aurajoki trout have been released into the River Fiskarsinjoki and Koskenkylänjoki has been restocked using Ingarskilanjoki trout, which explains their identity, while Isojoki trout have also regularly been released into the Rivers Kymijoki and Summanjoki, which can be seen in the high similarity between them. In Estonia, Pudisoo and Pühajõgi trout have at least also been mixed, in addition to some others, but the geographical proximity there is also high. In Russia, mixing of populations is not known to

Table 2. Genetic differentiation of the most similar baseline populations when measured as pairwise F_{st} values. Values less than 0.01 were statistically non-significant and are highlighted in red, and all observed values less than 0.02 are highlighted in orange. Only columns and rows with values less than 0.02 are shown.

Pop	1	7	14	31	33	35	39	44	48	49	51	52	56	57	58
	Aurajoki	Ingarskilanjoki	Kymijoki	Papinoja	Notkopuro	Inojoki	Hurrinoja	Voronka	Pühajögi	Kunda	Selja	Loobu	Pirita	Vääna	Keila
6 Fiskarsinjoki	0.009														
13 Koskenkylänjoki	0.150	0.013													
15 ISOJOKI	0.046	0.116	0.010												
32 Toivolampuro	0.107	0.171	0.138	0.020											
35 Inojoki	0.068	0.152	0.101	0.039	0.015										
37 Vammeljoki	0.086	0.153	0.099	0.061	0.032	0.017									
39 Hurrinoja	0.070	0.147	0.105	0.029	0.019	0.014									
41 Huumosenoja	0.070	0.160	0.112	0.063	0.032	0.020	0.016								
42 Kuokkalanpuro	0.094	0.165	0.119	0.029	0.027	0.024	0.012								
45 Sistajoki	0.065	0.125	0.090	0.074	0.041	0.042	0.046	0.017							
46 Havlonka	0.057	0.145	0.093	0.077	0.046	0.036	0.045	0.020							
51 Selja	0.047	0.125	0.086	0.075	0.053	0.045	0.045	0.049	0.025	0.017					
52 Loobu	0.071	0.142	0.107	0.082	0.057	0.058	0.064	0.067	0.034	0.011	0.020				
54 Pudasoo	0.056	0.153	0.097	0.085	0.067	0.058	0.061	0.071	0.002	0.032	0.028	0.033			
56 Pirita	0.064	0.128	0.096	0.086	0.055	0.052	0.051	0.054	0.041	0.032	0.019	0.036			
57 Vääna	0.051	0.125	0.096	0.073	0.052	0.045	0.042	0.052	0.025	0.024	0.015	0.027	0.031		
58 Keila	0.057	0.133	0.098	0.064	0.041	0.035	0.042	0.047	0.024	0.014	0.012	0.017	0.028	0.015	
59 Vasalenna	0.045	0.124	0.081	0.058	0.043	0.034	0.036	0.040	0.023	0.013	0.011	0.017	0.018	0.014	0.010

have occurred, although some River Luga trout have been released back into the Luga itself.

When a phylogenetic tree was constructed based on the genetic distances between all populations, a clear and logical grouping could be seen in the baseline data, which followed surprisingly well the geographical distances between the populations and the form of the coastline (Fig. 2), despite the long history of releasing hatchery populations into the area. The exceptions to the geographical order along the coastline came from the already known hatchery releases of Isojoki and Aurajoki hatchery populations. In addition, the release history explains the similarity of the Ingarskilanjoki trout with the Koskenkylänjoki and Vantaanjoki populations, into which it has been released. The similarity of the Ingarskilanjoki and

the relatively native Mankinjoki, Espoonjoki and Sipoonjoki populations from the nearby area could at least partly be assumed to be a result of their common evolutionary history.

The four westernmost river populations formed the Uskelanjoki group, and these rivers mostly drain into the Archipelago Sea. The Russian populations grouped very precisely according to their geographical distances. The Bay of Vyborg populations formed a tight group, and within it even the subgroups from the northern and southern coast of the bay could be separated, as two populations, Myllyoja (number 25) and Römpötinpuro (26) from the southern coast, formed a small subgroup of its own (Fig. 2).

All the Russian populations from the Karelian Isthmus grouped together, but with some distinction from popula-

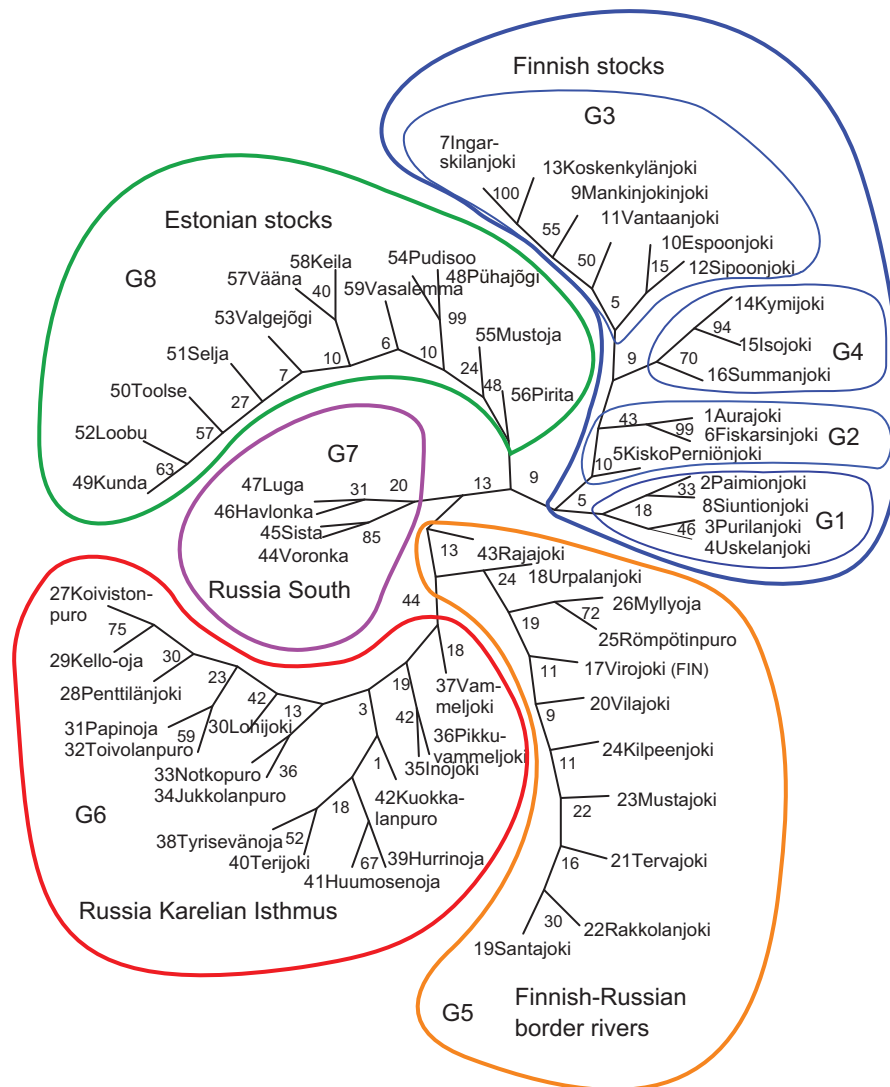


Fig. 2. Genetic distances (Nei's D_A distance, neighbour-joining unrooted tree) among Finnish, Russian and Estonian anadromous brown trout stocks in the Gulf of Finland. Watersheds are numbered from west to east clockwise around the gulf and watershed numbers are presented together with the river names. Bootstrap numbers for the branches are shown as a percentage from 1000 repeats.

tions north and south of the Inojoki (35). The Inojoki population belonged to the southern group, which mainly includes rivers draining into the Bay of St. Petersburg. The Russian Rivers Papinoja (31) – Toivolanpuro (32) and Notkopuro (33) – Jukkolanpuro (34) formed geographically close pairs. In addition, a very tight group of five small rivers (38–42) was also found on the northern coast of the Bay of St. Petersburg, all of which were difficult to distinguish from each other. The Rivers Hurrinoja (39) – Huumosenoja (41) and also Tyrisevänoja (38) – Terijoki (40) formed close pairs, with Kuokkalanpuro (42) belonging to the same group with all of them (Fig. 1, 2).

The River Rajajoki (River Siestarjoki) formed an intermediary type to the southern coastal Russian group, in which the River Luga has the largest smolt production. The four rivers on the southern coast drain into two small gulfs, two into each, and their genetic similarity also reflected this pattern. The Rivers Voronka (44) and Sista (45) formed a pair, as well as the Rivers Havlonka (47) and Luga (48). Interestingly, the Estonian trout populations clearly differed from this Luga type of trout, and were very similar to each other. Some effects of hatchery fish releases could be seen, as Pudisoo and Pühajõgi were genetically very similar, and Pudisoo trout is known to have been released into the Pühajõgi river. Along the

Estonian coast, a slight subgrouping could additionally be seen, and populations from the Rivers Keila and Vääna were also very similar.

In all, five major groups could be formed based on their genetic distances: Finnish populations (groups 1–4), border river populations (group 5), eastern Russian populations (group 6), southern Russian populations (group 7) and Estonian populations (group 8) (Fig. 2, 3). Deviating from this, the Finnish River Virojoki, located next to the border rivers, grouped with them according to its genetic similarity. Consequently, the Bay of Vyborg group actually includes border rivers and the River Virojoki from Finland near the border. The Finnish populations, in turn, could be further divided into four groups: Archipelago Sea area populations (1), Aurajoki hatchery type populations (2), Ingarskilanjoki type populations (3) and Isojoki hatchery type populations (4). As most of the captured fish originated from Finnish populations, finer-scale grouping was necessary in order to gain more detailed information on the catch composition. These eight population groups were used as reporting groups in the catch analysis (Fig. 2), and this served as the first output level of the origin information (Table 3).

The locations of the rivers in the reporting groups are indicated in Fig. 3. Four of the groups (G1 to G4) are

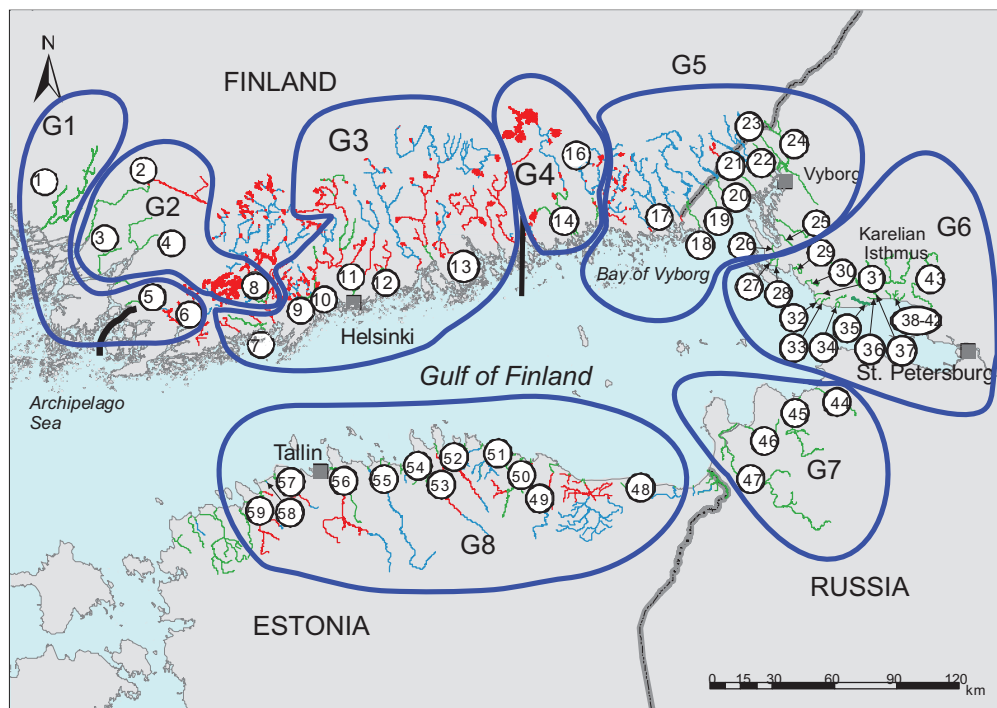


Fig. 3. The location of the eight genetic catch analysis reporting groups of the Finnish, Russian and Estonian sea trout stocks in the Gulf of Finland. The river numbering is the same as in Fig. 1. Administrative ELY Centre borders on the Finnish coast are indicated by black lines.

Table 3. Sea trout river populations included in the reporting groups of the catch analysis. The mean F_{st} value over stock pairs within each group is also presented.

Group	River populations	Country	Mean F_{st}
1 Aurajoki	Aurajoki, Kiskonjoki, Fiskarsinjoki	FIN	0.079
2 Uskelanjoki	Paimionjoki, Purilanjoki, Uskelanjoki, Siuntionjoki	FIN	0.239
3 Ingarskilanjoki	Ingarskilanjoki, Mankinjoki, Espoonjoki, Vantaanjoki, Sipoonjoki, Koskenkylänjoki	FIN	0.078
4 Isojoki	Kymijoki, Isojoki, Summanjoki	FIN	0.029
5 Bay of Vyborg	Virojoki (FIN), Urpalanjoki, Santajoki, Vilajoki, Tervajoki, Rakkolanjoki, Mustajoki, Kilpeenjoki, Römpötinpuro, Myllyoja	FIN/RUS	0.066
6 Karelian Isthmus	Koivistonpuro, Penttilänjoki, Kello-oja, Lohijoki, Papinoja, Toivolanpuro, Notkopuro, Jukkolanpuro, Inojoki, Pikkuvammeljoki, Vammeljoki, Tyrisevänoja, Hurrinoja, Terijoki, Hurrinoja, Kuokkalanpuro, Rajajoki	RUS	0.055
7 Russia south coast	Voronka, Sista, Havlonka, Luga	RUS	0.032
8 Estonia	Pühajõgi, Pudisoo, Mustoja, Pirita, Kunda, Toolse, Selja, Loobu, Valgejõgi, Vääna, Keila, Vasalemma	EST	0.028

completely on the Finnish coast, one group (G5) crosses the Finnish–Russian border, two groups are located in Russia (G6 and G7) and one group in Estonia (G8).

Resolution of the baseline dataset

When the so-called 100% simulation of each baseline population was conducted, the results showed that a likelihood of correct proportion estimation below 90% occurred in the most similar and hatchery rearing-influenced Finnish populations (Aurajoki, Fiskarsinjoki, Koskenkylänjoki, Kymijoki), for which the stocking history was known (Table 4). In addition, low values were also obtained for four native Russian populations on the Karelian Isthmus, belonging to the tight population group Vammeljoki (37), Tyrisevänoja (38), Hurrinoja (39), Huumosenoja (41), Kuokkalanpuro (42), Voronka (44, mixing with Sista, 45) and Havlonka (46, mixing with 47 Luga) on the Russian southern coast, and several Estonian populations (Valgejõgi, Pudisoo, Mustoja, Pirita, Vääna, Keila and Vasalemma). The value for the Pudisoo population was especially poor, being only 0.09. Clear uncertainty is thus evident in the individual population estimates for some of these populations, and at least the most similar populations should be grouped in all potential grouping options to obtain reliable estimates, especially for small catch sample analysis. However, for all individual river populations, the likelihood of being correctly assigned to its reporting group was at least 0.97 (Table 4.). If the mixture sample size was increased to the maximum used for the total catch of about 1300 fish, it did not essentially affect the result.

There was considerably more uncertainty in the individual assignments of the fish than for the population or

population group proportion estimates. When the accuracy of individual assignment was assessed with the leave-one-out procedure, the likelihood of correct assignment was over 90% for only 7 out of the 59 baseline populations. For 20 river populations it was over 80%, while for 26 populations the likelihood of correct assignment was still over 75%. For four Estonian populations (Keila, Kunda, Vääna and Pudisoo) it was less than 50%, again indicating a very high degree of similarity among some of them. In particular, the Pudisoo population had a very low likelihood of being correctly assigned, and it was more often assigned to Pühajõgi than to its own river, which indicates that it possibly does not even deserve the status of a separate population. However, when the likelihood of correct assignment of the individuals to their own reporting group was estimated, on average up to 93% of the individuals were assigned to the correct population group. For as many as 45 river populations out of 59 (76%), the percentage of correct assignments was over 90%. All individual assignments at the group level were correct, at least at the 77% level. The highest uncertainty occurred between some Finnish hatchery populations.

When simulated mixtures with the same proportions of each population were analysed, variation in estimation bias could be compared. Biases with a nominal value of over 1% for a 5% proportion occurred for 16 out of 59 baseline populations (Table 5). The uncertainty was highest among the Estonian populations. In Finnish populations, the proportion of Koskenkylänjoki trout was underestimated in favour of the Ingarskilanjoki trout, from which it originates. On the Karelian Isthmus, the sample from the river Inojoki (baseline sample size $n = 98$) population seemed to represent well the trout of the area, as its proportion was overestimated at the cost of some of the

Table 4. Results of the 100% baseline simulations for the sea trout baseline dataset covering the Gulf of Finland, with true baseline sampling sizes and with the minimum used mixture sample size of 200. An estimate of the percentage of correct estimates and its 95% maximum likelihood intervals is presented for individual river stocks, and also the proportions of individual stocks correctly assigned to their reporting group together with 95% likelihood intervals. Values below 90% are shaded.

Stock	Correct stock	95%	Interval	Correct group	95%	Interval
1 Aurajoki	82	76	88	99	98	100
2 Paimionjoki	99	98	100	99	98	100
3 Purilanjoki	100	100	100	100	100	100
4 Uskelanjoki	100	100	100	100	100	100
5 Kiskonjoki	100	100	100	100	100	100
6 Fiskarsinjoki	81	74	88	96	91	99
7 Ingarskilanjoki	99	95	100	100	100	100
8 Siuntionjoki	99	97	100	99	97	100
9 Mankinjoki	100	98	100	100	100	100
10 Espoonjoki	100	99	100	100	100	100
11 Vantaanjoki	99	97	100	100	98	100
12 Sipoonjoki	100	100	100	100	100	100
13 Koskenkylänjoki	53	44	62	100	100	100
14 Kymijoki	85	79	91	100	99	100
15 Isojoki	93	86	97	99	98	100
16 Summanjoki	94	89	98	100	99	100
17 Virojoki	100	100	100	100	100	100
18 Urpalanjoki	98	96	100	99	97	100
19 Santajoki	98	94	100	100	99	100
20 Vilajoki	97	94	99	100	99	100
21 Tervajoki	99	97	100	100	100	100
22 Rakkolanjoki	100	98	100	100	100	100
23 Mustajoki	100	99	100	100	100	100
24 Kilpeenjoki	99	97	100	100	100	100
25 Römpötinpuro	99	98	100	100	99	100
26 Myllyoja	100	99	100	100	99	100
27 Koivistonpuro	100	99	100	100	100	100
28 Penttilänjoki	92	88	96	100	99	100
29 Kello-oja	98	94	100	100	100	100
30 Lohijoki	95	91	98	100	99	100
31 Papinoja	91	86	96	100	99	100
32 Toivolanpuro	94	88	98	100	99	100
33 Notkopuro	93	88	97	99	98	100
34 Jukkolanpuro	99	97	100	100	99	100
35 Inojoki	94	91	98	100	98	100
36 Pikkuvammeljoki	98	96	100	100	100	100
37 Vammeljoki	88	82	92	97	95	99
38 Tyrisevänoja	88	82	93	100	98	100
39 Hurrinoja	89	82	94	100	99	100
40 Terijoki	93	87	97	100	99	100
41 Huuosenoja	87	82	93	100	99	100
42 Kuokkalanpuro	56	47	64	100	98	100
43 Rajajoki	100	99	100	100	100	100
44 Voronka	61	52	67	98	96	99
45 Sista	95	92	99	98	96	100
46 Havlonka	78	71	83	90	84	93
47 Luga	98	96	100	99	97	100

(Continued)

Table 4. (Continued)

Stock	Correct stock	95%	Interval	Correct group	95%	Interval
48 Pühajogi	96	92	99	100	99	100
49 Kunda	87	81	93	100	100	100
50 Toolse	91	86	97	100	99	100
51 Selja	94	90	98	100	99	100
52 Loobu	97	93	99	100	99	100
53 Valgejõgi	79	72	84	100	98	100
54 Pudisoo	9	4	15	100	99	100
55 Mustoja	88	82	94	99	98	100
56 Pirita	87	82	92	99	98	100
57 Vääna	68	60	76	98	96	100
58 Keila	79	72	86	100	99	100
59 Vasalemma	88	81	93	99	99	100
Mean	90	86	93	99	98	100
Min	9	4	15	90	84	93
Max	100	100	100	100	100	100

populations from the neighbouring rivers. The population from the River Kuokkalanpuro, in contrast (baseline sample size $n = 23$), was clearly underestimated in the analysis. In Estonian samples, the Pühajõgi ($n = 176$) estimate included Pudisoo ($n = 22$) fish, while Pudisoo fish were hardly found at all. The estimate for the Vasalemma populations ($n = 99$) also tended to additionally include fish from the nearby rivers. More even baseline sampling sizes would possibly even the biases as well for some cases.

When the simulation results were analysed for the eight reporting groups, a 5% unit range in the 95% confidence interval was observed for the Russian south coast and Estonian group (Table 6). For others, the variation was less than this. The biases were very small in relation to the estimated proportions in this reporting group analysis. The estimated proportions can be regarded as very reliable for reporting groups when the mixture sample size was at least 200 individuals.

When the observed error was divided into its components with the 'error decomposition' simulation option, all of the uncertainty was related to either similarity in the baseline structure or the baseline sample size, as the proportion of fishery sampling was 0% if the mixture sample size was at least 100 individuals.

The error caused by the baseline was divided differently for the baseline populations, depending on the baseline sample size and its genetic similarity with other populations. When the baseline sample size was small, most of the error resulted from this, especially if the population was easily distinguishable and had a clearly different genetic profile from neighbouring populations. However, if the similarity with other populations was high, not even large baseline sample sizes could increase the resolution of the population. The mean decomposition percentages were 0% for fisheries for a sample size of 100

Table 5. Results of an accuracy simulation in which each baseline stock was set to contribute 10 individuals and 5% of the actual catch. The mixture sample size was 200. The true proportion, estimated proportion, its 95% confidence interval, and the bias of the estimation for each baseline stock are presented, when the nominal value of the bias was over 0.2.

Population	Country	True %	Obs. %	95 %	Interval	Bias %
1 Aurajoki	FIN	5.0	4.6	2.3	6.8	-0.4
7 Ingarskilanjoki	FIN	5.0	7.7	5.5	10.2	2.7
8 Siuntionjoki	FIN	5.0	4.7	3.6	5.3	-0.3
13 Koskenkylänjoki	FIN	5.0	2.3	0.0	4.6	-2.7
15 Isojoki	FIN	5.0	5.7	2.8	7.9	0.7
16 Summanjoki	FIN	5.0	4.2	2.7	5.2	-0.8
20 Vilajoki	FIN/ RUS	5.0	4.6	3.6	5.5	-0.4
23 Mustajoki	FIN/ RUS	5.0	5.4	3.8	6.5	0.4
24 Kilpeenjoki	RUS	5.0	4.6	3.7	5.1	-0.4
32 Toivolanpuro	RUS	5.0	4.7	2.1	7.1	-0.3
33 Notkopuro	RUS	5.0	4.7	2.7	7.4	-0.3
34 Jukkolanpuro	RUS	5.0	5.3	4.1	6.7	0.3
35 Inojoki	RUS	5.0	6.6	3.1	9.4	1.6
36 Pikkuvammeljoki	RUS	5.0	4.6	3.4	5.6	-0.5
37 Vammeljoki	RUS	5.0	4.2	1.8	6.1	-0.8
38 Tyrisevänoja	RUS	5.0	4.3	1.4	6.0	-0.8
40 Terijoki	RUS	5.0	4.7	3.2	6.2	-0.3
41 Huumosenoja	RUS	5.0	4.2	2.1	6.5	-0.8
42 Kuokkalanpuro	RUS	5.0	2.4	0.2	4.3	-2.6
44 Voronka	RUS	5.0	3.1	1.0	5.1	-1.9
45 Sista	RUS	5.0	6.1	3.9	8.7	1.1
46 Havlonka	RUS	5.0	3.6	1.3	5.9	-1.4
47 Luga	RUS	5.0	5.8	4.2	7.4	0.8
48 Pühajõgi	EST	5.0	9.8	7.4	11.8	4.8
50 Toolse	EST	5.0	3.9	2.2	5.8	-1.1
51 Selja	EST	5.0	6.7	4.5	9.5	1.7
52 Loobu	EST	5.0	6.2	3.9	8.9	1.2
53 Valgejõgi	EST	5.0	3.4	0.8	6.2	-1.6
54 Pudisoo	EST	5.0	0.6	0.0	2.9	-4.4
55 Mustoja	EST	5.0	3.8	1.7	5.7	-1.2
56 Pirita	EST	5.0	3.7	1.6	5.6	-1.4
58 Keila	EST	5.0	4.8	1.5	8.3	-0.3
59 Vasalemma	EST	5.0	8.5	4.1	12.5	3.5

fish, 37% for the genetic resolution and 63% for the baseline sample size. The minimum error percentage for the baseline sample size was 35% when the size was 148 individuals.

In general, if the baseline sample size was less than 50, the proportion of the error resulting from baseline sample size tended to be over 60% and varied between 60% and 100% (Fig. 4). When the sample size was less than 25 individuals, the error arising from the baseline sample size was over 70%. A proportion of the error resulting from the baseline sample size varying between 40% and 60%

only resulted for populations with a baseline sample size of at least 50 individuals. An error level of less than 60% arising from baseline sampling size was only observed for baseline populations for which the sample size was at least 50 individuals. Thus, increasing the baseline sample size to at least 50 would possibly increase the estimation accuracy. Wood et al. (1987) have previously estimated that 40 individuals would be a limit value under which uncertainty markedly increases.

The origin of trout in sea catches

The composition of the sea trout catches in the Gulf of Finland was separately calculated for the total catch and the three coastal catch areas, and also separately for all individual baseline populations, and for the previously defined 8 reporting groups. In addition, the probability of each individual fish originating from any of the baseline populations was calculated. Moreover, the proportions of national contributions and of wild and reared fish were estimated by forming reporting groups on the basis of the country in which the river was located. In this analysis, border rivers were included in the Russian estimate. Their proportion in the catch was nevertheless very small.

The majority of the catch in all studied areas (76–80%) came from Finnish trout populations (Table 7, Fig. 5). The largest group of captured fish came from the Finnish Isojoki hatchery population releases, which alone accounted for about half of the total catch in the eastern (54%) and middle area (53%), and somewhat less in the westernmost area (41%), while the Ingarskilanjoki trout group formed a larger proportion here (36.5%) than in the eastern areas (20% and 23%). The third Finnish group that could be observed was the Aurajoki group. However, this does not refer to the River Aurajoki on the southwestern coast, but rather to trout from the River Fiskarsinjoki, which drains directly into the Gulf of Finland, and also trout releases done with this Aurajoki hatchery population directly into the sea both in the western Gulf of Finland and eastern Archipelago Sea. This population accounted for less than 5% of the total catch. Trout from the southwestern Finnish Archipelago Sea area, from the Uskelanjoki population group, did not occur in these catches, and no catches from that area were available.

Slightly contrary to expectations, the Russian populations were generally rare in Finnish catches, even in the easternmost area of the gulf, although they are geographically closer and are known to still be native. The trout from the Bay of Vyborg population group (5) only occurred in the eastern area (2%), and represented only about 1% of the total catch. The Russian groups from the Karelian Isthmus (6) and Russian south coast (7) were somewhat more common and together represented about 7% (6–9%) of the total catch. The trout from the south

Table 6. Results of accuracy simulation for reporting groups in which each baseline stock was set to contribute 10 individuals and 5% of the actual catch. The mixture sample size was 200. The true proportion, estimated proportion for each reporting group, its 95% confidence interval, and the bias of the estimate are presented.

Reporting group	Country	True%	Estimated%	95%	Interval	Bias
1 Aurajoki	FIN	15.0	14.5	12.9	15.8	-0.5
2 Uskelanjoki	FIN	20.0	19.4	18.4	20.0	-0.6
3 Ingarskilanjoki	FIN	30.0	31.0	29.6	32.9	1.0
4 Isojoki	FIN	15.0	15.0	13.5	16.4	0.0
5 Bay of Vyborg	FIN/RUS	30.0	30.2	29.1	31.4	0.2
6 Karelian Isthmus	RUS	70.0	69.6	67.4	70.9	-0.4
7 Russia South coast	RUS	20.0	18.5	15.8	20.8	-1.49
8 Estonia	EST	60.0	61.2	58.8	63.7	1.23

coast were slightly more abundant in the catch (Table 7) than the populations from the Karelian Isthmus. Their occurrence in the westernmost catch at all was uncertain.

Somewhat surprisingly, the Estonian trout populations (group 8) quite commonly occurred in the Finnish catches, although they are located more distantly along the coast than the Russian rivers. Estonian trout particularly occurred in the western catch sector on the Finnish coast, where they comprised nearly one-fifth of the catch (18%). In all, this group represented about 15% of the total catch.

Nearly all Finnish fish were of hatchery origin, so that altogether about 76–80% of the total catch originated from Finnish hatchery population releases, and were mainly of Isojoki and Ingarskilanjoki origin. The Ingarskilanjoki group is not entirely based on hatchery production, and hatchery and wild production of the same population cannot be distinguished in this type of analysis, so no exact number can be given. However, Finnish wild production is currently not assumed to be very significant, so the proportion of wild fish is probably not much higher than the pooled Estonian and Russian

proportion. In future decades Finnish wild sea trout production is assumed to increase as result of active enhancement work.

The four groups that almost entirely represented the wild sea trout populations (Estonian Group, Russian South Coast Group, Karelian Isthmus Group, Bay of Vyborg Group; Table 7, Fig. 5) contributed about one fifth, i.e. 22% (19–23%), to the total catch. There is also some wild production in Finland, but as this cannot be distinguished and is assumed to form a very small fraction of the total production, the pooled proportion of these foreign fish on the Finnish coast can be regarded as a minimum estimate of wild fish in the catches. One-third of these wild sea trout were from Russia and two-thirds from Estonia.

When the total catch, i.e. 1372 individuals, was analysed for all baseline populations (Table 8), the large majority came from the Finnish Isojoki hatchery population (43%). Ingarskilanjoki and Koskenkylänjoki were the next most abundant populations and represent fish of the same origin, so their mutual proportions are uncertain. From the cross-border rivers of the Bay of Vyborg, Mustajoki and Tervajoki trout populations obviously occur in the sea and occasionally also in Finnish catches. From the Russian eastern populations, Inojoki was most abundant and the others only very rarely present. The southern Voronka, Sista and Luga type trout were slightly more common. The similarity among the Estonian populations was so high that that the individual river population estimates are uncertain, but for some reason, the Vasalemma type trout was common in the studied Finnish catches. Vasalemma was also slightly overestimated in general, and the estimate may thus additionally include fish from the neighbouring rivers.

When the same estimation of reporting group proportions was carried out with the maximum likelihood method of the ONCOR program, the result was the same, and all proportion estimates were within the 95% probability intervals of the Bayesian estimates. The largest difference was 3%, which occurred for the Isojoki estimate in the western area, where the mixture sample size was the

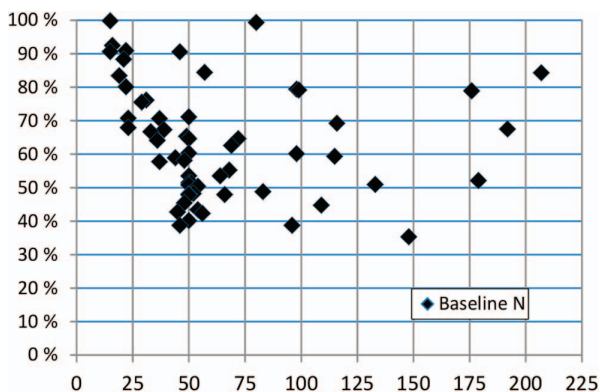


Fig. 4. The relationship between the baseline sample size and the proportion of error caused by the baseline sample size. Results from an error decomposition simulation in which five individuals of each baseline stock contributed to the mixture and the mixture sample size was 295.

Table 7. Medians and 95% probability interval for the Bayesian estimates of sea trout population group proportions (%) in Finnish sea trout catches in the Gulf of Finland from three sea areas numbered from east to west. The stock group proportion and its 95% probability intervals are presented. Proportions that differ statistically significantly from 0 are shaded.

Reporting group	East 1			Middle 2			West 3			Total		
	Prop. %	2.5 %	97.5 %	Prop. %	2.5 %	97.5 %	Prop. %	2.5 %	97.5 %	Prop. %	2.5 %	97.5 %
1 Aurajoki (Fisk.)	2	1	3	4	2	6	2	1	5	4	3	6
2 Uskelanjoki	0	0	0	0	0	0	0	0	0	0	0	0
3 Ingarskilanjoki	23	20	26	20	16	23	37	30	43	24	22	26
4 Isojoki	54	50	58	53	48	57	41	34	48	49	47	52
5 Bay of Vyborg	2	1	4	0	0	0	0	0	2	1	0	2
6 Karelian Isthmus	3	2	5	3	1	4	1	0	4	3	2	4
7 Russia South Coast	4	2	5	5	3	8	1	0	2	4	3	5
8 Estonia	12	9	15	15	12	19	18	13	23	15	12	17
Finnish total	79	76	82	76	72	79	79	75	84	78	76	80
Russian total	9	7	11	8	5	10	2	1	7	7	6	9
Estonian total	12	9	14	15	13	19	18	11	22	15	12	16
Minimum wild	21	18	23	23	20	27	20	15	25	22	19	24

smallest and the proportion of the Isojoki population group quite large. The Bayesian estimate was 41% and the maximum likelihood estimate 38%. The ranges of Bayesian probability intervals and maximum likelihood intervals were very much the same. At most, a 1% difference occurred among the ranges of the same catch samples.

When the individual river population estimates were compared, some differences could be seen in the few most similar populations. Some fish were found to originate from 25 out of 59 baseline populations according to either estimation method, but of these, the Bayesian median estimate was over 1% for only 12 populations. The population proportions were consequently very uneven, which made the comparison difficult for the populations from

which only a few individuals occurred in the catches. In this respect, the simulations provided more information. The pooled estimate for Ingarskilanjoki–Koskenkylänjoki was 23.7% in Bayesian estimation and 23.0% according to maximum likelihood estimation. However, their mutual individual population estimates differed, and similarly for the Isojoki group (Isojoki–Kymijoki–Summanjoki), the pooled Bayesian estimate was 49.3% and the maximum likelihood estimate 50.9%, but within the group the mutual river estimates differed. As the true proportions were not known, no other conclusions can be drawn here. As it is unlikely that any method could correctly resolve the origins of these populations with the same origin, their pooling in the future baseline appears justified.

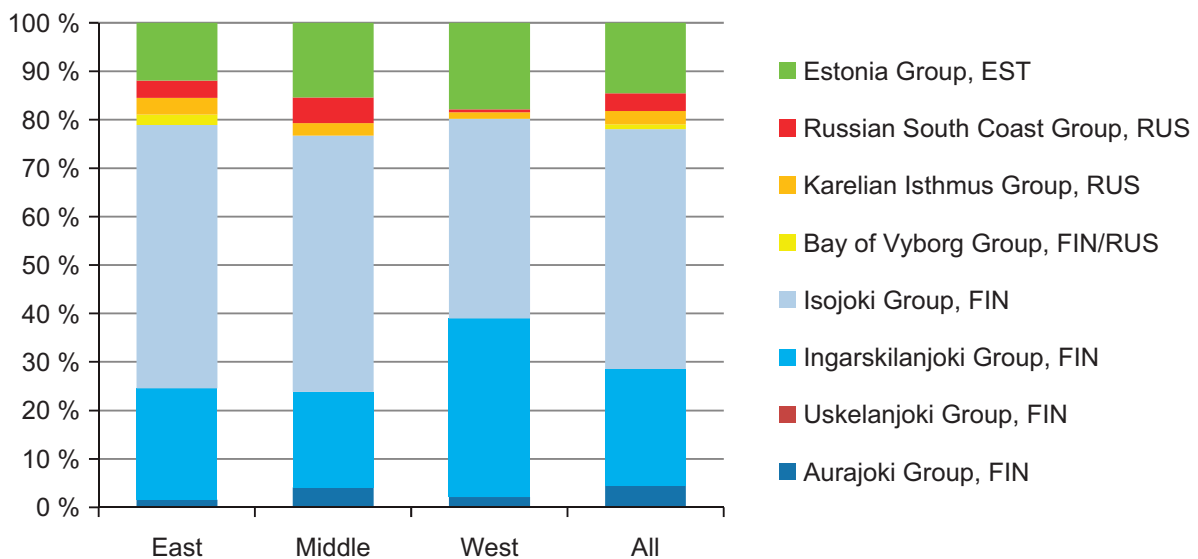


Fig. 5. Stock group proportions in Finnish sea trout catches in the Gulf of Finland for eight reporting groups.

Table 8. Bayesian estimates of sea trout stock proportions (%) of the total Finnish sea trout catch sample in the Gulf of Finland. Only stocks for which the median estimate differed from 0 are included. The median of the stock proportion estimate and its 95% probability intervals are shown. (OR lower limit differs from 0).

Stock	Country	Median	2.5%	97.5%
1 Aurajoki/Fiskarsinjoki	FIN	4.4	1.8	6.0
7 Ingarskilanjoki	FIN	6.8	4.6	9.3
11 Vantaanjoki	FIN	0.4	0	0.9
13 Koskenkylänjoki	FIN	16.9	14.1	19.7
14 Kymijoki	FIN	6.1	4.5	8.1
15 Isojoki	FIN	43.3	40.4	46.1
<i>Total</i>		<i>77.7</i>		
21 Tervajoki	FIN/RUS	0.1	0.02	0.5
23 Mustajoki	FIN/RUS	0.4	0.09	0.9
<i>Total</i>		<i>0.6</i>		
26 Myllyoja	RUS	0.2	0.03	0.5
27 Koivistonpuro	RUS	0.3	0.05	0.7
32 Toivolanpuro	RUS	0.2	0	0.6
35 Inojoki	RUS	1.0	0.4	1.8
38 Tyrisevänoja	RUS	0.3	0.01	0.9
40 Terijoki	RUS	0.3	0	0.9
42 Kuokkalanpuro	RUS	0.3	0	0.9
44 Voronka	RUS	1.8	0.8	3.0
45 Sista	RUS	0.8	0.3	1.6
47 Luga	RUS	0.9	0.3	1.9
<i>Total</i>		<i>6.1</i>		
48 Piihajögi	EST	0.6	0.02	3.0
49 Kunda	EST	1.4	0.6	2.6
51 Selja	EST	2.2	1.2	3.5
54 Pudisoo	EST	0.6	0.2	1.3
57 Vääna	EST	2.1	0.8	3.7
58 Keila	EST	1.0	0	2.3
59 Vasalemma	EST	6.0	4.4	7.7
<i>Total</i>		<i>13.8</i>		

Visual observations

Fishermen also visually inspected fish in their catch and reported adipose fin-clipped fish and also fish that somehow deviated in their appearance. Observation of adipose fin-clipping was systematic, but for the other traits the activation may have varied. Some fish were reported to look more like salmon, being slender and having fewer and smaller spots than fishermen were used to seeing. These 'sparsely spotted' fish were identified from the individual assignment database and also analysed separately.

The adipose fin-clipped fish could be used as independent test for correct assignment, as additional information about their origin was thus available. In all, 67 captured fish were reported to have a clipped adipose fin. All of these fish were assigned to Finnish hatchery populations. Most of them (41) were assigned to the Isojoki popula-

tion, and 26 to the Koskenkylänjoki or Ingarskilanjoki population, so at least for these individuals the origin was very probably correct.

Altogether, 79 fish were reported to look special and to have fewer spots than usual for Finnish sea trout. Most of these were assigned to originate from outside Finnish borders. Over half of them (43) were assigned to originate from Estonia and 29 from Russia populations, and less than 10% of them, only 7 individuals, from Finnish hatchery populations. Thus, especially when compared to the observed proportions of these groups in the catches, these sparsely spotted fish were far more abundant in the Russian and Estonian populations. Up to 25% of fish assigned to Estonian populations and 35% assigned to Russian populations were reported to have less spots than typical Finnish trout. This polymorphism in the spotting pattern is an interesting phenomenon and needs to be further clarified. It very likely is a genetic difference.

DISCUSSION

Baseline resolution

The pattern of observed genetic differentiation and genetic distances between the studied sea trout populations (baseline populations) of the Gulf of Finland correspond well to the known history of population transfers and to the geographical distances between rivers. It was not possible to individually assign all populations with acceptable uncertainty, but the proportion estimates of the eight reporting groups were trustworthy according to the simulations and method comparison. Misassignments of individuals were always to nearby rivers in the same reporting groups, and did not therefore disturb the estimation of reporting group proportions. Some pairs of the most similar populations could be pooled in the baseline of future analysis, such as the Finnish Aurajoki–Fiskarsinkki and Ingarskilanjoki–Koskenkylänjoki populations and the Estonian Pudasoo and Piihajögi populations.

This same baseline data set could also be grouped into some other finer groups in cases where catches from some other area need to be analysed. The strong similarities between some populations sets certain conditions for the groupings, but finer-scale grouping could have been used for some areas. Because the catches in this study were from the Finnish coast, our assumption was that most of the captured fish were of Finnish origin, and our main interest was also in Finnish source populations. The differentiation among Finnish sea trout was also stronger than among those of the other countries, partly because it covered a wider geographical area and hatchery production from different sources.

Several methods, including F_{st} -analysis and simulations, gave signal of the uncertainty of identifying same

population pairs or groups of populations. According to simulations, the mixture sample sizes used here were clearly sufficient for the baseline resolution, although the number of baseline populations was high. However, as not all populations contributed to the catches, the actual number contributing into true catches was lower, as it was only 25 out of 59 populations. In simulations all baseline populations were included in the catches. Ultimately the level of grouping depends on the level of uncertainty accepted.

The baseline resolution could be further improved to some extent by increasing the sample size of certain baseline populations, especially in cases when it numbered less than 50 individuals. In a previous analysis by WOOD et al. (1987), 40 individuals was found to be a limit value for the baseline sample size, and with values under this the uncertainty clearly increased. In our study, the baseline sample size was less than 40 individuals in 15 (25%) out of 59 baseline samples.

The results from the individual assignments were more uncertain, and not all populations could be unambiguously identified. However, as the misassignments were commonly to nearby rivers, the population group or area could be assigned to most individuals with a relatively high degree of certainty, and datasets of this type could be utilized later in more detailed analysis.

Both adipose fin clipping and spotting polymorphism could be used as additional variables in the mixed-stock analysis once their occurrence and stability over time is confirmed. As hatchery and wild fish cannot be distinguished with genetic methods when they originate from the same population, when this information is required, other methods such as adipose fin clipping need to be used. Different spotting patterns have also previously been found and some of them are clearly of genetic origin (APARICIO et al. 2005; SKAALA and JØRSTAD 1988, 2011), but in certain cases the environment, especially salinity and stress, has also been shown to affect the spotting pattern (KOCABAŞ and BAŞÇINAR 2013).

In conclusion, the 15 locus DNA microsatellite dataset provided sufficient resolution for sea trout mixture analysis in the studied Gulf of Finland area, and it provided useful new information on the occurrence of wild Estonian and Russian sea trout in Finnish catches. No essential difference was observed between the maximum likelihood and Bayesian estimate proportions in analysis at the group level.

Catch composition

There was an unexpectedly high proportion of Russian and Estonian wild sea trout in the Finnish coastal sea trout catches. It has not previously been known that sea trout migrate regularly over such long distances in the sea. At

least one-fifth of the total Finnish catch, i.e. 22% (19–23%), was of foreign wild origin, and there must in addition have been some Finnish wild fish, as some wild production also occurs in Finnish coastal waters. However, the percentage is probably quite small compared to hatchery production, and this proportion could not be estimated here because of the high similarity between Finnish wild and hatchery produced trout.

In addition, more of the wild production, totalling about two-thirds, came from Estonian than Russian rivers, although the Russian coast is geographically closer. The types of the rivers and their production levels, as well as the tendency of trout to migrate to the sea, varies between areas. There have been very few tagging experiments in the small Russian rivers, so it is not actually known what proportion of these fish migrate to the sea. Some of the populations may be more resident, even though the rivers are open to the sea, or they may only undergo short-distance coastal migration. In the eastern part of the Gulf of Finland, the Russian rivers often drain into smaller gulfs like the Bay of Vyborg and Bay of St. Petersburg, and the trout may also remain there closer to the coast. One indication of this might also be the fact that the size of the spawners in those rivers is known to be usually only 1–2 kg (SEGERSTRÅLE 1937).

Young trout are observed to follow the predominant sea currents on their feeding migration in the sea, which also may explain the occurrence of the trout from different rivers along the coast (DEGERMAN et al. 2012). The water current circulates from the Estonian coast towards the eastern Gulf of Finland, and then turns back along the Finnish coast, as illustrated in Fig. 1. Therefore, Estonian trout following the currents obviously end up on the Finnish coast before returning home. The low abundance of the Karelian Isthmus populations in the catch may, on the other hand, be explained by the current circulating in the opposite direction in the southeasternmost part of the Gulf of Finland, possibly resulting in their feeding migration being directed to the coastal areas of Estonia and Russia in the southeastern part of the Gulf of Finland.

The national contributions of Russian and Finnish sea trout to the catch were also slightly difficult to estimate, as six of the rivers were common border rivers, with the upper parts located in Finland. The total proportion of fish coming from these Bay of Vyborg rivers was, however, so small, only comprising 0–2% of the total catch, that it did not make a marked difference to the national estimates.

Some variation also occurred in catches along the coast. The clearest difference was in the relative proportions of Finnish Isojoki and Ingarskilanjoki trout, with Isojoki trout being more common in the eastern areas. Fish of this population have regularly been released into the Kymi-joki, which explains the observed pattern. The Ingarskilanjoki trout has been released into more western rivers

such as Vantaanjoki, Koskenkylänjoki and Ingarskilanjoki itself. The Isojoki trout originates from a river that does not drain into the Gulf of Finland at all, but further to the north, into the Gulf of Bothnia. The use of this population for trout releases in the Gulf of Finland could be reconsidered in future, as it may well cause some gene flow to the still native rivers. A hatchery broodstock has already founded from the border-river, Mustajoki, population for potential use in releases in the eastern Gulf of Finland (PEUHKURI et al. 2014). The Russian populations were slightly more common in the eastern catches.

The baseline dataset collected in this study is highly valuable and will enable future catch analyses in all areas of the Gulf of Finland with reasonable costs. It thus offers a useful tool for fisheries management and conservation of the still native sea trout populations of the Gulf of Finland area.

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Appendix 1

Table A1. Analysed sea trout river population samples for the baseline data from Finland, Russia and Estonia. The sampled river, country of origin, tributary or area, sampling year, number of individuals and originality of the sampled population are presented.

No	River	Country	Tributary	Year	n	Originality
<i>West coast, ELY Centre for Southwest Finland</i>						
1	Aurajoki	FIN		2006	37	Introduced
2	Paimionjoki	FIN	Vähäjoki, Karhunoja	2004, 2008	22	Original
3	Purilanjoki	FIN		2011	15	Original
4	Uskelanjoki	FIN	Pitkääkoski, Kaukolankoski, Haukkalankoski, Hitolanjoki, Terttilänjoki	2007	57	Original, Introduced
5	Kiskonjoki	FIN	Perniönjoki, Juottimenoja-Piilioja, Pakapyölin Lohioja	2008	50	Original
<i>Middle coast, ELY Centre for Uusimaa</i>						
6	Fiskarsinjoki	FIN	Main stream	2010	50	Introduced
7	Ingarskilanjoki	FIN	Main stream, Pärthyvelbäcken, Krämars	2005	192	Original
8	Siuntionjoki	FIN	Passilankoski	2010	15	Original
9	Mankinjoki	FIN	Espoonkartanonkoski, Gumbölenjoki	2005, 2008, 2010	133	Original
10	Espoonjoki	FIN	Main stream, Glomsinjoki, Glimsinjoki	2008, 2010	72	Original
11	Vantaanjoki	FIN	Vantaankoski, Pitkääkoski, Ruutinkoski, Nukarinkoski, Longinoja	2010	207	Mixed, Introduced
12	Sipoonjoki	FIN	Ritobäcken, Byabäcken	2010	46	Original
13	Koskenkylänjoki	FIN	Hammarfors, Kvarnfors, Käkikoski, Sahakoski	2010	31	Introduced
<i>East coast, ELY Centre for Southeast Finland</i>						
14	Kymijoki	FIN	Main stream	2006, 2010	96	Introduced
15	Isojoki	FIN	Lapväärtin Isojoki, Hatchery stock	2006–2008	98	Hatchery
16	Summanjoki	FIN	Main stream	2003, 2008	19	Mixed
17	Virojoki	FIN	Saarasjärvenoja	2003, 2005, 2011	80	Original
<i>Border rivers</i>						
18	Urpalanjoki	FIN/ RUS	Urpalanjoenpuro (RUS), Main stream (RUS, FIN)	1999, 2005, 2006, 2010, 2012	69	Original
19	Santajoki (Kaltanjoki)	FIN/ RUS	Main stream (RUS)	2005, 2006	50	Original
20	Vilajoki	FIN/ RUS	Main stream (RUS)	2001, 2004, 2005, 2006	33	Original
21	Tervajoki	FIN/ RUS	Tervajoenpuro (RUS)	2004, 2005	48	Original
22	Rakkolanjoki	FIN/ RUS	Main stream (RUS), Hanhijoki (RUS)	2004, 2005, 2006	109	Original
23	Mustajoki	FIN/ RUS	Main stream (FIN, RUS), Kananoja (RUS), Tupakkamylynoja (FIN), Alhonpuro (FIN), Pölkkyoja (FIN)	2004, 2005, 2006, 2007, 2008, 2012	438	Original
24	Kilpeenjoki	FIN/ RUS	Main stream (RUS)	2001, 2006	16	Original
<i>Russian rivers</i>						
25	Römpötinpuro	RUS		2005	50	Original
26	Myllyoja	RUS		2005	44	Original
27	Koivistonpuro	RUS		2005	50	Original
28	Penttilänoja	RUS		2004, 2005	50	Original
29	Kello-oja	RUS		2004, 2005	54	Original
30	Lohijoki	RUS		2004, 2005	56	Original
31	Papinoja	RUS		2004, 2005	46	Original
32	Toivolampuro	RUS		2004, 2005	52	Original
33	Notkopuro	RUS		2006	51	Original
34	Jukkolanpuro	RUS	Three close streams	2004, 2005	148	Original

Continued

Table A1. *Continued.*

No	River	Country	Tributary	Year	n	Originality
35	Inojoki	RUS	Main stream and two tributaries	2004, 2005	98	Original
36	Pikkuvammeljoki	RUS		2006	50	Original
37	Vammeljoki	RUS		2004, 2005, 2006	50	Original
38	Tyrisevänoja	RUS		2004, 2005	48	Original
39	Hurrinoja	RUS		2004, 2005	54	Original
40	Terijoki	RUS		2004, 2005	45	Original
41	Huumosenoja	RUS		2004, 2005	50	Original
42	Kuokkalanpuro	RUS	Two close streams	2006	23	Original
43	Rajajoki	RUS	Main stream, Siesjoki	2006	21	Original
44	Voronka	RUS		2005	23	Original
45	Sista	RUS		2005	64	Original
46	Havlonka	RUS	River Tchernaja	2005	29	Original
47	Luga	RUS	River Solka, R. Lemovzha, Vudoni stream	2005	115	Original
<i>Estonian rivers</i>						
48	Pühajõgi	EST		2010, 2011	176	Mixed
49	Kunda	EST		2009, 2010	83	Original
50	Toolse	EST		2011	49	Original
51	Selja	EST		2010, 2011	116	Mixed
52	Loobu	EST		2010, 2011	179	Original
53	Valgejõgi	EST		2010	39	Mixed
54	Pudisoo	EST		2011	22	Mixed
55	Mustoja	EST		2009	36	Mixed
56	Pirita	EST	Leiva	2010	37	Original
57	Vääna	EST		2011	68	Original
58	Keila	EST		2010, 2011	66	Original
59	Vasalemma	EST		2010, 2011	99	Original
					4224	

Table A2. *Microsatellite loci used for sea trout analysis. References, multiplexes, dyes and primer concentrations are also indicated.*

	Locus	Reference	Multiplex	Dye	Primer concentration
1	<i>BS131</i>	Estoup et al. 1998	MP 1	VIC	0.03 µM
2	<i>OneU9</i>	Schribner et al. 1996	MP 2	VIC	0.03 µM
3	<i>SSa197</i>	O'Reilly et al. 1996	MP 1	NED	0.02 µM
4	<i>SSa289</i>	McConnell et al. 1995	MP 1	PET	0.30 µM
5	<i>Ssa407</i>	Cairney et al. 2000	MP 1	NED	0.15 µM
6	<i>SSa85</i>	McConnell et al. 1995	MP 2	VIC	0.02 µM
7	<i>Ssos1311</i>	Slettan et al. 1995	MP 2	NED	0.07 µM
8	<i>SSos1417</i>	Slettan et al. 1995	MP 1	PET	0.04 µM
9	<i>SSos1438</i>	Slettan et al. 1996	MP 2	VIC	0.07 µM
10	<i>SSsp1605</i>	Patterson et al. 2004	MP 2	NED	0.04 µM
11	<i>SSsp2201</i>	Patterson et al. 2004	MP 1	6-FAM	0.03 µM
12	<i>Str15INRA</i>	Estoup et al. 1993	MP 1	6-FAM	0.05 µM
13	<i>Str60INRA</i>	Estoup et al. 1993	MP 2	PET	0.04 µM
14	<i>Str73INRA</i>	Estoup et al. 1993	MP 1	VIC	0.04 µM
15	<i>Str85INRA</i>	Presa and Guyomard 1996	MP 2	6-FAM	0.40 µM
16	<i>Strutt58</i>	Poteaux 1995	MP 2	6-FAM	0.30 µM