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ENDEMIC KARELIAN STRAINS OF BROWN TROUT, *SALMO TRUTTA* L.: A PRELIMINARY ANALYSIS BY MITOCHONDRIAL DNA

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By using polymerase chain reaction and restriction fragment length polymorphism of mitochondrial DNA, we studied the maternal lineages of brown trout populations in Eastern Fennoscandia, in the Baltic Sea, White Sea and Barents Sea basins. The distribution of haplotypes reflects the glacial and postglacial history of fish fauna. The hypothetical postglacial contact zone in Kovda river system in Kuusamo-Paanajärvi area was studied in detail. There, one maternal lineage arrived during the high phase of White Sea Ice Lake (9500 BP). Lacustrine population in Paanajärvi, and several relict brook trout stocks >170 m above the present sea level represent the earliest period, which is marked by a unique mitochondrial haplotype, endemic for lacustrine populations in Russian Karelia. Western upwaters of the Kovda river system were colonized during the high Ancylus lake phase of the Baltic Sea. The lake Kitkajärvi was formed on the edge of retreating ice 9400-9500 BP, and it was colonized from the Baltic basin. About 8400 BP, due to the land uplift, the lake tilted eastwards and became isolated from the Baltic basin. Fish immigration from Paanajärvi was prevented by a seven meter waterfall. The lacustrine trout stock of the Lake Kitka *descends* to the river Kitka for spawning above the waterfall, but the Baltic mitochondrial haplotypes have not colonized Lake Paanajärvi. The anadromous trout populations in the Kola Peninsula differ clearly from the Karelian lacustrine populations, due to colonization from other refugium. The Lake Onega and Lake Ladoga trouts share haplotype frequencies related but not identical with Northern Baltic landlocked populations, supporting the hypothesis that they represent the first colonization wave in the Baltic Basin. The trout phylogeography further emphasize the importance of White Sea – Baltic Sea watershed as a major divide of aquatic fauna, confirmed earlier by the community of grayling, salmon, and the parasite *Gyrodactylus salaris.*

ЯАККО ЛУММЕ[1)], ТИНА АСПЛУНД[2)], ЮССИ КУУСЕЛА[1)], АЛЕКСЕЙ ВЕСЕЛОВ[3)], ИГОРЬ БАХМЕТ[3)], АЛЕКСАНДР ПОТУТКИН[4)], КРЭЙГ ПРИММЕР[5)] КАРЕЛЬСКИЕ ЭНДЕМИЧНЫЕ РАСЫ КУМЖИ, *SALMO TRUTTA* L.: ПРЕДВАРИТЕЛЬНЫЙ АНАЛИЗ МИТОХОНДРИАЛЬНОЙ ДНК

На основании цепной реакции полимеразы и полиморфизма длины рестриктов митохондриальной ДНК изучены материнские линии популяций кумжи Восточной Фенноскандии, бассейнов Балтийского, Белого и Баренцева морей. Распределение гаплотипов отражает историю развития ихтиофауны в ледниковый и послеледниковый периоды. Подробно изучена предполагаемая послеледниковая контактная зона в системе реки Ковда, в районе Куусамо-Паанаярви. Одна материнская линия проникла в этот район в период трансгрессии беломорского озерно-ледникового водоема (9500 л.н.). Популяция озерной форели озера Паанаярви и несколько реликтовых стад ручьевой форели из водоемов, расположенных выше 170 м современного уровня моря, представляют самый ранний период, отмеченный уникальным митохондриальным гаплотипом, встречающимся только в озерных популяциях Республики Карелия. Западная часть верховий системы реки Ковда заселялась во время трансгрессии Анцилового озера на месте части нынешнего Балтийского моря. Озеро Китка образовалось на границе отступающего ледника 9400-9500 л.н. и заселялось из бассейна Балтийского моря. Из-за поднятия земной коры около 8400 л.н., озеро приобрело уклон к востоку и отделилось от бассейна Балтийского моря. Проникновению рыб из Паанаярви мешал семиметровый водопад. Озерная форель из Озера Китка спускается на нерест в реку Китка выше водопада, но колонизации оз. Паанаярви балтийскими митохондриальными гаплотипами не произошло. Анадромные популяции кумжи Кольского полуострова имеют явные отличия от озерных популяций Карелии, так как заселялись из другого рефугиума. У кумжи Онежского и Ладожского озер одни частоты гаплотипов, связанные, но не идентичные пресноводным популяциям северной Балтики, что также подтверждает гипотезу о том, что они возникли в ходе первой волны колонизации в бассейне Балтийского моря. Филогеографические особенности кумжи еще раз показывают значение водосбора Белого и Балтийского морей в качестве основного барьера для водной фауны, о чем свидетельствуют и более ранние исследования сообщества хариуса, лосося и паразита *Gyrodactylus salaris.*

Introduction

Brown trout (*Salmo trutta* L.) is one of the most "structured" fish species studied (Hynes *et al.* 1996). It has very variable and adaptive ecology. Many stocks are anadromous, feeding on open seas and spawning in rivers, usually not very far from the river mouths. The dispersal capacity of this form is large. Other stocks are lacustrine, ascending or sometimes descending to the spawning rapids. Main evolutionary force is adaptation and genetic drift in isolated lakes. Still other stocks don't migrate at all, but are sedentary residents of small creeks and brooks, and commonly dwarfed. All the different forms are most generally considered as a single species, *Salmo trutta*, but numerous local races and geographic and ecological forms can be identified. However, "splitters" working in different geographic areas have described up to 50 different trout *species* since Linnaeus (Hynes et al. 1996; Delling, 2003).

Bernatchez (2001) recently compiled a comprehensive global description of the Eurasian Brown trouts. There are five ancient geographically distinct main clades: Danubian, Mediterranean, Adriatic, Atlantic, and *marmoratus*. The most divergent lineages could indeed deserve a rank of species. In Bernatchez's comprehensive analysis, the Atlantic trout populations of Barents and White Seas were still underrepresented, for good reasons. First, the molecular marker, the mitochondrial control segment or D-loop reveals enormous amount of variability among the southern forms, but less within the Atlantic group of the northern populations. The second reason is that collecting population samples in Russian North needs very specific effort. Thus, the 16 fish from 5 misplaced localities in Barents and White Sea basins hardly are the final word from this area (Bernatchez and Osinov, 1995; Bernatchez, 2001). Makhrov et al. (2002) studied a large sample of trouts from eastern Fennoscandia by allozymes . Since we share many samples with that study, we may compare our mtDNA results with the nuclear marker.

Hansen and Loeschke (1996) and Hansen and Mensberg (1998) studied the mitochondrial DNA variation of the genes ND1, ND3/4 and ND 5/6 among Danish trout populations, which belong to the Atlantic clade, and found them to be very variable. We have used ND1 and flanking sequences as a marker to study the Atlantic, Baltic, White Sea and Barents Sea salmon (Nilsson *et al.* 2001, Asplund et al. 2004, Tonteri et al., 2005), and we therefore decided to use the same DNA segment also for brown trout, to obtain comparable results.

In this paper, we present a preliminary cartographic analysis of the mitochondrial DNA variation among trout populations collected from Eastern Fennoscandia and Northern Russia. The results are discussed with respect to the geological history of the area. We focus specifically to possible contact zones of Baltic and White Sea basins. In the north, the upwaters of the Kovda river system cross the border between Finland and Russia. The system also cross the ancient postglacial divide between the Baltic and White seas, thus representing a case of "upwater sluicing", which occurred 8400 years before present. Another important divide is between the Lake Onega and the White Sea in Russian Karelia. The dramatic case of *Gyrodactylus salaris* epidemic in the river Keret, due to Lake Onega strain of the parasite, is an example of the practical importance of this divide (Meinilä et al., 2003; Kuusela et al., 2005; Kuusela et al., this volume).

Material and Methods

Fish material

Some of the Finnish samples are from the hatcheries of Finnish Game and Fisheries Research Institute (FGFRI). The history of the stocks is carefully documented in the Institute's stock register (Makkonen *et al.*, 2000). All the fish samples from the Russian side of the border were electrofished during several expeditions to the area and represent wild populations.

In the field, fin clips were stored in 70 % ethanol. Samples from hatchery stocks were obtained in different situations, for example, during infection experiments by pearl mussel (*Margaritana margaritifera*) conducted in Western Finland's Environmental Centre's laboratory in Kokkola. Then the liver samples of the *post mortem* fish were used for mtDNA analysis.

Many of the trout population samples are small and from small populations, and therefore, we have pooled them to geographical groups, to be more representative, and also to detect a "phylogeographic" signal behind the noise made by local genetic drift. All the sampling localities are mapped in Figure 1. Total number of haplotyped fish is 1498.

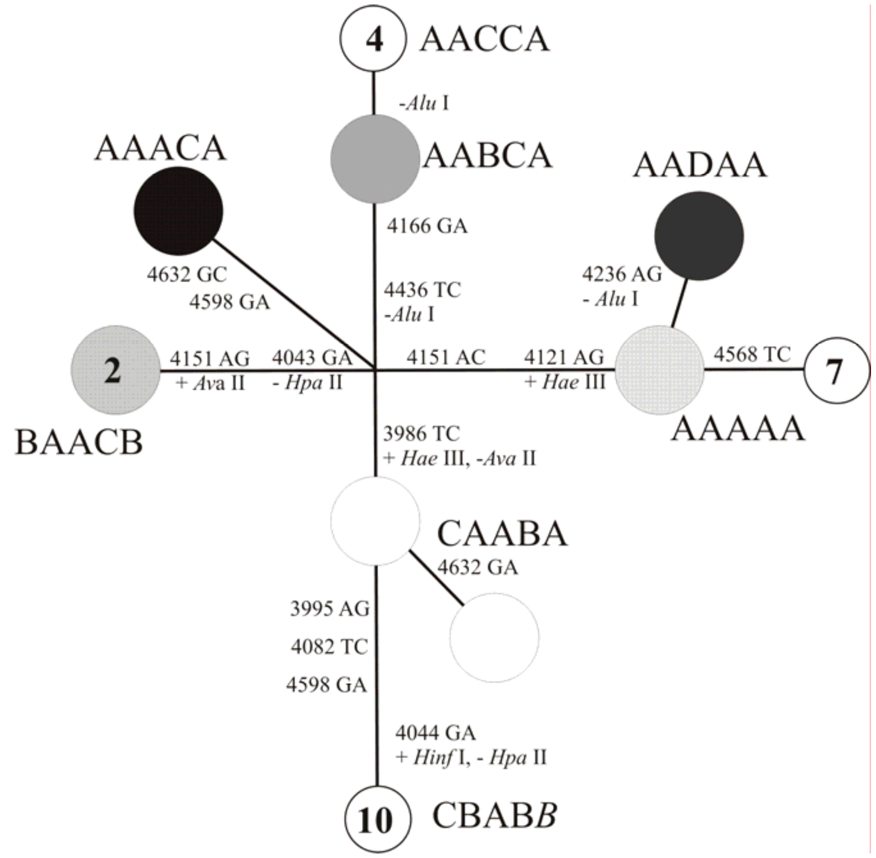

Fig. 1. Minimum spanning tree of *Salmo trutta* haplotypes, based on the sequence of ~1200 nucleotides of ND1 gene and flanking 16SrDNA and two tRNAs. The restriction enzyme cutting site additions and deletions, counted from the midpoint are marked. The non-alphabetic order of enzymes used in naming the haplotypes is *Ava* II, *Hinf* I, *Alu* I, *Hae* III, *Hpa* II. Numbering of the nucleotide positions is based on *Salmo salar* mtDNA sequence of Hurst et al. (unpublished, GenBank accession #U12143). The four numbered balls represent Danish Gudenaa haplotypes (Hansen and Mensberg, 1998; GenBank accession numbers Type 2: AF117716, Type 4: AF117719, Type 7: AF117718, Type 10: AF117717). Uncolored balls are haplotypes found in Denmark but not in our data. Color code refers to the Figures 2 and 3 as well. Italicized letter *B* in haplotype CBAB*B* indicates that –*Hpa* II is caused by substitution 4044 GA, not by 4043 GA like in BAACB

The following geographical groups are formed for mapping approach (see the Map in Fig 3.) The name of the sample indicates the original sampling location. The number of fish analyzed, and the status of population is indicated as wild (W), stocked population (S) and hatchery stock in farm (F).

1. North Atlantic basin: Inarinjärvi (8W/S), Juutuanjoki (3W/S), Kaitamo (1W) Kevojoki (7W) Kvaenangsbotn (5W), Utsjoki (3W)

2. Kola Peninsula (all wild): Kolvica (5), Pis'em (41), Babya (3), Danilovka (18, Elovoje (36), Kachkovka (2), Lihodeevka (1), Ponoy (8), Pulonga/Kola (2), Runda (27), Salniza (26), Titovka (1), Varzina (46), Varzuga (24), Kurbych Ozero (48W)

3. Bothnian Bay drainages: Heinjoki (56W), Isojoki (27F) Lylyjoki (9S), Miekak (5W), Ohtaoja (50F), Ounasjoki (50F), Piehinki (50F), Rostojaur (1W), Vaarainjoki (31F), Kirintö (49F), Kitka above Jyrävä (81F)

4a. Paanajärvi: Asterva (40W), Oulanka (5W/S), Kuusinki (47F), Paanajärvi (1W/S), Lohilampi creek (27W), Oleksei's pond creek (13W), Pihlajajärvi (2W). The hatchery stocks Kitka below Jyrävä (20F) and Kuusinki (47F) have been reportedly mixed (Makkonen et al., 2000) and are not used in Map in Fig. 3, but are drawn in Fig. 2.

4b. Pjaozero: Palojoki (41W), Kitijoki (17W), Pjaozero (1W), Olanga (3W)

4c. White Sea Basin (Karelia): Vincha (61W), Nilma (4W), Vilavatoje Ozero (19W)

5. Lake Onega: Spawning rivers Andoma (4 W specimen), Arzema (30W), Gornaja (9W), Lizhma (1W), Lukdozhma (41W), Orzega (22W), Shoksha (19W) Tchobinka (18W), Tuba (5W)

6. Lake Ladoga: Spawning rivers Einojoki (36W), Hiitola (1W), Jänisjoki (16W), Paasujoki (11W), Soskuanjoki (11W), Syskynjoki (11W)

7. Southern Baltic drainages: Lake Saimaa (50F), Luutajoki (50F), Laajaoja (54W), Asikkala (21S)

8. Lake Pielinen: Lieksanjoki (8W), Pusonjoki (10W), Vinapuro (33W)

9. Archangelsk oblast: Malaya (24W), Megra (2W), Zolotiza (6W)

RFLP analyses of mitochondrial DNA

DNA was extracted from fin or liver tissue stored in ethanol according to the protocol of Taggart *et al.* (1992). The 2009 bp long mitochondrial region, extending from 16SRNA over tRNA^{leu} and ND-1 coding region to tRNA^{ile} was amplified by PCR using the primers described by Nielsen *et al.* (1998). The PCR conditions were identical to those described by Nielsen *et al.* (1996). The segment was cut by restriction endonucleases *Ava*II, *Hinf*I, *Alu*I, *Hae*III and *Hpa*II, as described by Nielsen *et al.* (1998). Fragments were visualized by 2 % agarose electrophoresis and photographed.

A subsample of the RFLP haplotypes was sequenced, to identify the variable restriction sites, and the compare the haplotypes with the four published Danish haplotype sequences (AF117716-19). We made an attempt to name the restriction haplotypes in accordance with Hansen and Loeschke (1996) and Hansen and Mensberg (1998), but finally decided to use an independent system, because our fish material probably differs too much from the Danish to be put in uniform system without a large scale DNA sequencing.

In this preliminary report, we use only cartographic data analysis, placing the haplotypes (Fig. 1) on a map (Figs. 2 and 3). This method works while the data contain some qualitative geographical signals, for example the unique Karelian haplotype AAACA, which has a restricted distribution.

Results

RFLP variation in Eastern Fennoscandian brown trouts

In Figure 1, we present a sequence supported phylogenetic hypothesis of the relationships of the PCR-RFLP haplotypes observed among the trouts analyzed in this study. We have detected seven haplotypes. There are only four haplotypes sequenced in Danish populations, and only 12 in our data set, so that there remains a lot of unresolved variation. Only one haplotype (BAACB) is common to our sample of seven and Danish four.

To support further research, the restriction fragment lengths are listed in Table 1.

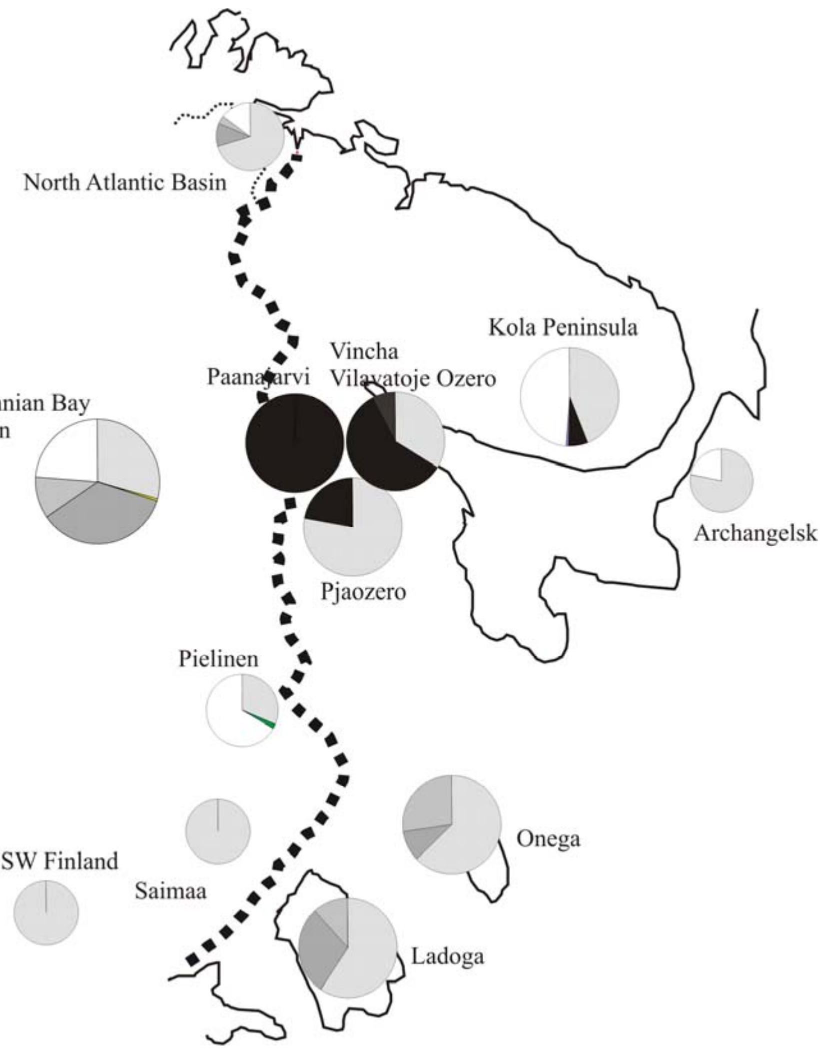

Fig. 2. Distribution of trout mtDNA haplotypes in Eastern Fennoscandia

Shading code is the same as in Figs. 1 and 3, the Karelian types AAACA and AADAAA are the dark sectors

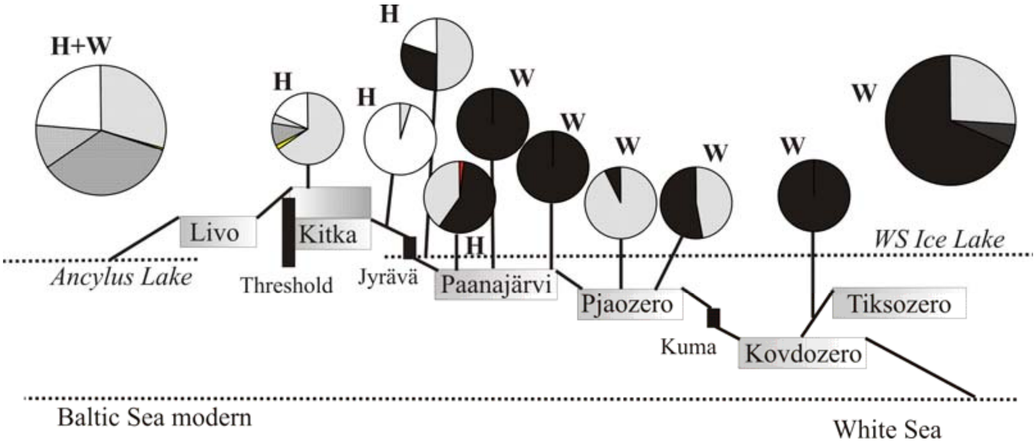

Fig. 3. The Baltic Sea – White sea transect along the Kovda river system. The feeding lakes are named, and the pie diagrams describe the trout haplotype distribution in rivers. The big pies left and right of the figure represent "background frequencies", pooled over larger areas of Baltic (Bothnian Bay) and White Sea basins. Ancient shorelines of Ancylus lake and White Sea Ice lake are drawn schematically, and the position of restrictive waterfalls (Jyrävä, Kuma) is indicated. Karelian haplotypes AAACA and AADAA are the darkest sectors

Table 1. Exact restriction fragment sizes based on nucleotide sequencing of representative specimens. The small fragments (< 100 bp) are not readable from the gels, but inferred from the known sequence

Ava II			*Hinf* I	*Alu* I			*Hae* III			*Hpa* II	
A	B	C	A	A	B	D	A	B	C	A	B
		881	982	599	599	599	604	604	604		702
866			529		458			499	499	492	492
	699		498			414	395			448	
406	406	406		384	384		284	284	284	437	437
304	304	304		281		281	215		215	254	
215	215	215		219	219	219	193	193	193	181	181
	167			177		177		182		119	119
152	152	152		168	168	168	104			57	57
51	51	51		83	83	83	84	84	84	21	21
15	15			30	30		73	73	73		
				23	23	23	49	49	49		
				20	20	20		33			
				16	16	16	8	8	8		
				9	9	9					

Geographic distribution of haplotypes in Eastern Fennoscandia

In Figure 2, a rough map of the distribution of haplotypes is presented. In this scale, some of the missing haplotypes, or haplotypes found only in restricted areas are of interest. For example, the lakes Onega and Ladoga almost shared the haplotype frequencies (N = 149 and N = 86, respectively), and differed clearly from the neighboring populations in southern Finland, which are represented by farm stocks. In the Northern Baltic basin, the samples collected from several isolated stocks are more diverse, containing four haplotypes, including the CAABA (white), which is widespread but definitely missing in the Lakes Ladoga and Onega. Most common the CAABA is in Kola Peninsula. The haplotype AAACA (black) is restricted to the area of former White Sea Ice Lake. The pale gray AAAAA is found in all areas. However, the Danish haplotype #7 differs by one nucleotide from the AAAAA sequenced in our samples, and the real identity of all AAAAAs remains to be studied. The haplotype AABCA (gray) is almost restricted to the Baltic Basin, and missing completely in the White Sea basin.

The contact zone in Kuusamo-Paanajärvi area

In Kuusamo-Paanajärvi area, trout populations are of specieal interest, because the well-known geographical history of the area extends to the first millennia after the deglaciation. Many of the populations, especially in the Russian side of the border are pristine. On the other hand, the populations in the Finnish side are effectively managed, by supportive stocking of juveniles produced in a hatchery.

In Fig. 2, we present tha haplotype distribution along the Baltic-White Sea transect in Kuusamo-Paanajärvi area on the Finnish-Russian border. The presentation also schematically presents the hydrological history of the area (see discussion for details).

In rivers and brooks draining to Paanajärvi, the endemic Karelian haplotype AAACA is found as unmixed in Astervajoki and Oulankajoki. Further, unmixed AAACA it is found in isolated brooks in Purkuputaanoja, Uopajanpuro, Pihlajajärvi, Olekseinlampi and Lohilampi. Only the Finnish farm stocks Kuusinkijoki and Kitkajoki (below Jyrävä) are mixed by haplotype CAABA (blue), from Kitkajoki above the waterfall Jyrävä. This unfortunate mixing has been reported in the stock description (Makkonen et al., 2000).

We calculated the Fst based on haplotype frequencies along the transect, including the farm stocks. Fst between the groups above vs. below Jyrävä was estimated as 20% (P = 0.012), but the real difference of pristine populations is larger.

Discussion

Comparison of our PCR-RFLP results with Hansen and Mensberg (1998) was not successful, probably due to too different fish material in Denmark and Finnish-Russian border. To avoid confusion, it is to be stressed that our naming system is not directly comparable with that of Hansen and Mensberg (1998), even if the labels look similar. Both haplotyping systems can only be connected by further DNA sequencing. We have sequenced (few) representatives of all our RFLP haplotypes (Fig. 1, manuscript in preparation), but only few of the Danish types have been sequenced (GenBank accession numbers AF117716-AF117719).

Similarly, the global analysis of brown trout by Bernatchez (2001) can not yet be directly connected with the data presented here. His marker was D-loop, which is poorly variable among Atlantic clade of brown trout. Later, the connection can be created by additional sequencing work, and the Danish and global analyses can be combined to achieve a full picture of the recolonization of north-eastern Europe.

Variation in mitochondrial DNA

First observation on the variation is that brown trout in this limited area contains more variability than Atlantic salmon in the same area (Asplund et al., 2004).

RFLP was used here to identify mitochondrial haplotypes, which are known to differ more from each other than just by those few variable cutting sites. This was indicated by the preliminary sequencing. E.g., haplotypes AAACA and AAAAA have only one divergent *Hae*III site, but along the 1200 bp sequenced, they have four nucleotide substitutions. Types AAACA and CAABA differ by two cutting sites (*Hae*III, *Ava*II), due to single substitution, and the sequenced 1200 bp differ by three substitutions. Thus, a detailed study of this material should be based on large scale sequencing.

As a first draft aiming to a phylogeographic analysis, the PCR-RFLP method works well, indicated by some clear geographic divides in the map in Fig. 2. About the remaining problems we may mention that AAAAA haplotype is found in all parts of the study area, often in high frequencies. It is not yet clear, if it indeed is identical in Baltic and White Sea drainages. Longer sequences, and comparison with Danish and Swedish populations is needed to solve the true identity of AAAAA.

The contact zone in upwaters of Kovda river system: Geological history of lake Kitka

Heikkinen and Kurimo (1977) have studied the history of Lake Kitka in details, by shoreline trend analysis, pollen stratigraphy, and radio-carbon dating. The area was deglaciated 9400-9500 B.P., and the lake was from the beginning isolated, stituating higher than the highest shores of Ancylus lake in the west (shoreline at present 200 m. a.s.l.), and Karelian Ice Lake in the east (170 m a.s.l.). The Maanselkä watershed was at the narrowest only some 40 km wide, when present Baltic -White Sea minimum distance is 400 km (Koutaniemi, 1999).

In the beginning Lake Kitka was a bifurcation lake, draining to the west through Livojärvi and Livojoki, which reached the Ancylus lake some 35 km downstream. This early Baltic phase is expected to be the colonization phase for trouts in Lake Kitka. Later, the postglacial land uplift tilted the lake so that the western outflow dried up 8400 B.P., when the eastern threshold did find a deeper way for outflow. The water level dropped suddenly nine meters, almost to the present 240 m a.s.l.

In Fig. 4, the study area between Baltic Sea and White Sea is depicted, with historical shorelines of the Baltic phase Ancylus Lake (9500 B.P.) and the White Sea (Karelian) Ice Lake. Names of the sampled rivers and lakes (Fig. 3) are presented. The history of the populations can be inferred by the comparison of the genetic structure and geological history of the area, giving us well-dated details (Heikkinen, Kurimo 1977; Koutaniemi 1999).

A proportion of the lake trouts in Lake Kitka have an unusual migratory behaviour: they *descend* to the river Kitka for spawning, and the smolts swim upward to grow by feeding on the vendace (*Goregonus albula*) in the lake. The spawning area extends down until the Jyrävä waterfall, which prevents all upward migration, but not necessarily down-drifting of the smolts (and parr). Below the waterfall, river Kitka is occupied by spawners *ascending* from Lake Paanajärvi. Huusko et al. (1990) studied the migration of fish released in different points of the water system, and also demonstrated the differentiation between populations by isoenzyme analysis.

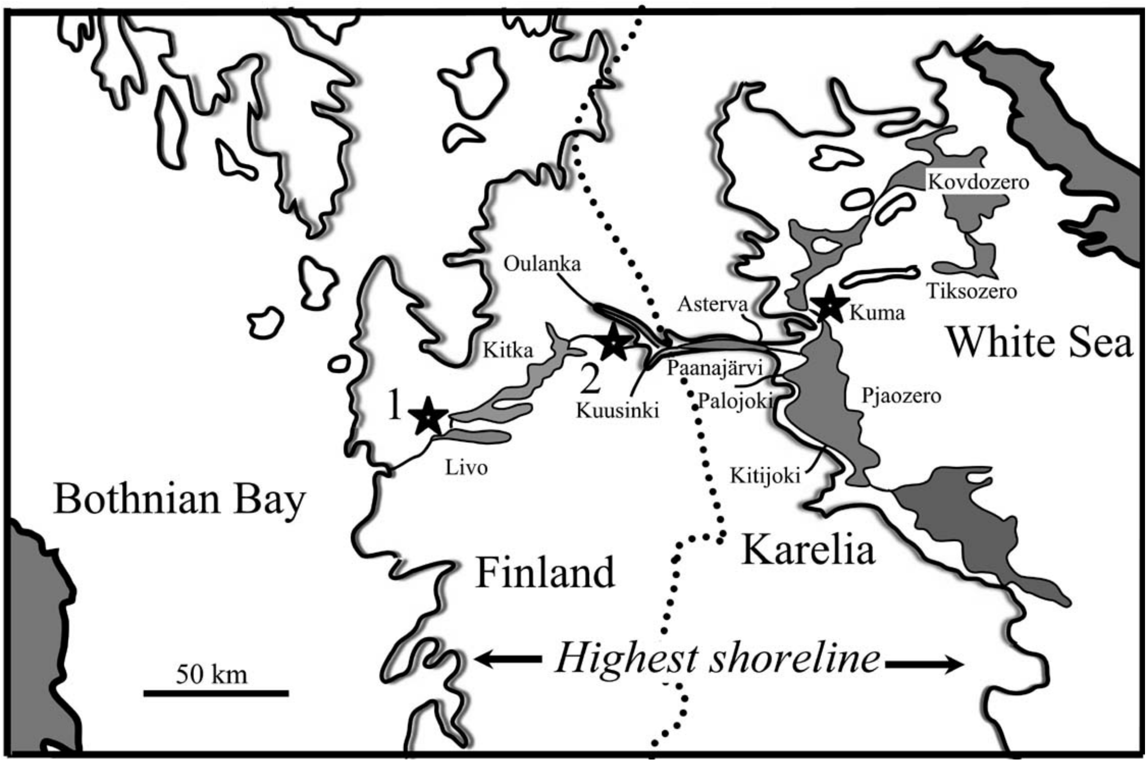

Fig. 4. The present and ancient shorelines of Baltic Sea (Bothnian Bay) and White Sea, and the location of Lakes Kitka, Paanajärvi, Pjaozero, Tiksozero and Kovdozero. Star #1 indicates the threshold between Livo and Kitka, which raised up 8400 BP and isolated Kitka trouts from the west. Star #2 approximates the location of Jyrävä waterfall. The map is based on information compiled by Koutaniemi (1999). Dotted line is the borderline between Finland and Russia

We also show that some mixing of the stocks used in the fisheries of the area can endanger the natural populations, and should be more strictly controlled. The natural stocks in this area represent a unique and valuable historical experiment, which should be maintained intact, for future research.

Geological history and colonization of the main parts of Kovda river system

The eastern part of the study area has been described by Koutaniemi (1999). The 9500 BP shoreline of the White Sea Ice Lake is also quite high in the modern landscape (Fig. 4). Lakes Paanajärvi and Pjaozero were deep under water, and the White Sea Ice Lake extended as a fjord into the Kuusamo highlands, reaching the present 166-170 m a.s.l. The fjord was 50 km long, 0.5-2 km wide and up to 200 m deep. In the river Oulanka, present rapid Taivalköngäs drained directly to the lake. The fjords to Kuusinkijoki and Kitkajoki were much shorter.

The White Sea Ice Lake introduced the brown trout to this area. The distribution of AAACA haplotype marks it's upper limits in our data. Karelian trout was not able to colonize the upper parts of river Kitka, because of the Jyrävä waterfall. No such waterfalls exist in river Kuusinki and Oulanka, and the trout could ascend higher. The isolated brook trouts in some small brooks above the 160 m.a.s.l were left behind when the water escaped from the area (e.g., Purkuputaanoja near Oulanka Biological station).

When the ice melted and released the freshwater Ice Lake to become White Sea, the surface level dropped fast, and Lakes Paanajärvi, Pjaozero and Topozero were isolated. The Kuma waterfall (natural drop 40 m) prevented later colonization of this area since 7000 BP.

Closely related species *Cottus gobio* and *Cottus poecilopus* (Kontula, Väinölä, 2001) have recolonized Karelia in the same way: *C. gobio* arrived along Baltic Ancylus lake phase, 9500-8500 years ago, and *C. poecilopus* from the White Sea (Karelian Ice Lake phase; Kontula, Väinölä, 2000). However, *C. poecilopus*, as well as Arctic charr (*Salvelinus alpinus*) somehow succeeded to cross the watershed, perhaps passing around, either in the north, or in the south. Fine details of their distribution in this contact zone are missing, but the vicariant distribution is obvious.

As a contrast to trouts, the grayling populations on both sides of the Kuusamo watershed were not much differentiated (Koskinen *et al*., 2000). However, the *Gyrodactylus salaris* parasite of grayling in Lake Kitka represents the western clade, and in Oulanka river the eastern parasite clade is present (Meinilä et al., 2004; Lumme et al., this volume).

In the Karelian waters below the Pjaozero level, some trout populations are of specific interest. Upstream of the rapids (now power plant) in Vincha River, the Tiksozero trouts *descend* for spawning; downstream, Kovdozero trouts *ascend*. No genetic difference was found between these subpopulations, both representing the endemic Karelian haplotype AAACA. The other interesting population was from Vilavatoje Ozero. Among the 19 individuals studied, 10 were of a mitochondrial haplotype AADAA, not found in any other populations in northeastern Europe. AADAA differs from widely distributed AAAAA by one nucleotide substitution (4236 A>G), removing an *Alu*I restriction site, so it might be a local mutation. Further studies on these two unusual populations may help to understand the postglacial colonization history of Russian Karelia.

References

Asplund T., Veselov A., Primmer C., Bakhmet I., Potutkin A., Titov S., Zubchenko A., Studenov I., Kaluzchin S., Lumme J. Geographical structure and postglacial history of mtDNA haplotype variation in Atlantic salmon (*Salmo salar* L.) among rivers of the White and Barents Sea basins // Ann. Zool. Fenn. 2004. V. 44. P. 465-475.

Bernatchez L. The evolutionary history of brown trout (*Salmo trutta* L.) inferred from phylogeographic, nested clade, and mismatch analyses of mitochondrial DNA variation // Evolution. 2001. V. 55. P. 351-379.

Bernatchez L., Osinov A. Genetic diversity of trout (genus *Salmo*) from its most eastern native range based on mitochondrial DNA and nuclear gene variation // Mol. Ecol. 1995. V. 4. P. 285-297.

Delling B. Species diversity and phylogeny of *Salmo* with emphasis on southern trouts (Teleostei, Salmonidae). PhD Thesis, Department of Zoology, Stockholm University. 2003.

Hall H. J., Nawrocki L.W. A rapid method for detecting mitochondrial DNA variation in the brown trout, *Salmo trutta* // J. Fish Biol. 1995. V. 46. P. 360-364.

Hansen M. M., Loeschke V. Genetic differentiation among Danish brown trout populations, as detected by RFLP analysis of PCR amplified mitochondrial DNA segments // J. Fish Biol. 1996. V. 48. P. 422-436.

Hansen M. M., Mensberg K. D. Genetic differentiation and relationship between genetic and geographic distance in Danish sea trout (*Salmo trutta* L.) populations // Heredity. 1998. V. 81. P. 493-504.

Heikkinen O., Kurimo H. The postglacial history of Kitkajärvi, North-eastern Finland, as indicated by trend-surface analysis and radio-carbon dating // Fennia. 1977. V. 153. P. 1-32.

Huusko A., van der Meer O., Koljonen M.-L. Life history patterns and genetic differences in brown trout (*Salmo trutta* L.) in the Koutajoki river system // Pol. Arch. Hydrobiol. 1990. V. 37. P. 63-77.

Hynes R. A, Ferguson A., McCann M. A. Variation in mitochondrial DNA and post-glacial colonization of Northwestern Europe by brown trout // J. Fish Biol. 1996. V. 48. P. 54-67.

Kontula T., Väinölä R. Postglacial colonization of Northern Europe by distinct phylogeographic lineages of the bullhead, *Cottus gobio* // Molec. Ecol. 2001. V. 10. P. 1983-2002.

Koskinen M. T., Ranta E., Piironen J., Veselov A., Titov S., Haugen T. O., J. Nilsson M. Carlstein M., Primmer C. R. Genetic lineages and postglacial colonization of grayling (*Thymallus thymallus*, Salmonidae) in Europe, as revealed by mitochondrial DNA analyses // Molec. Ecol. 2000. V. 9. P. 1609-1624.

Koutaniemi L. Physical characteristics and palaeogeography of the Oulanka-Paanajärvi region of the Finnish-Karelian border // Fennia. 1999. V. 177. P. 3-9.

Makhrov A. A., Skaala O., Altukhov Yu. P. Alleels of sAAT-1,2* isoloci in brown trout: potential diagnsotic marker fro tracking routes of post-glacial colonization in northern Europe // J. Fish Biol. 2002. V. 61.

Makkonen J., Westman K., Pursiainen M., Heinimaa P., Eskelinen U., Pasanen P., Kummu P. Viljelykantarekisteri [Register of Farmed Fish Stocks]. Riista- ja kalatalouden tutkimuslaitoksen kalanviljelylaitoksissa ja maitipankissa säilytyksessä olevat kalalajit ja –kannat // RKTL, Kala- ja Riistaraportteja nr 2000. 2000.

Meinilä M., Kuusela J., Ziętara M. S., Lumme J. Initial steps of speciation by geographic isolation and host switch in salmonid pathogen *Gyrodactylus salaris* (Monogenea: Gyrodactylidae) // Int. J. Parasitol. 2004. V. 34. P. 515-526.

Nei M., Tajima F. DNA polymorphism detectable by restriction endonuclease // Genetics. 1981. V. 97. P. 145-163.

Nielsen E. E., Hansen M. M., Mensberg K.-L. D. Improved primer sequences for the mitochondrial ND1, ND3/4 and ND5/6 segments in salmonid fishes:application to RFLP analysis of salmon // Journal of Fish Biology. 1998. V. 53. P. 216-220.

Nielsen E. E., Hansen M. M., Loeschke V. Genetic structure of European populations of *Salmo salar* L. (Atlantic salmon) inferred from mitochondrial DNA // Heredity. 1996. V. 77. P. 351-358.

Nilsson J., Gross R., Asplund T., Dove O., Jansson H., Kelloniemi J., Kohlman K., Löytynoja A., Nielsen E. E., Paaver T., Primmer C. R., Titov S., Vasemägi A., Veselov A., Öst T., Lumme J. Matrilinear phylogeography of Atlantic salmon (*Salmo salar* L.) in Europe and postglacial colonization of the Baltic Sea area // Molecular Ecology. 2001. V. 10. P. 89-102.

Schneider S., Roessli D., Excoffier L. Arlequin ver. 2000: A software for population genetics data analysis. Genetics and Biometry Laboratory, University of Geneva, Switzerland. 2000.

Taggart J. B., Hynes R. A., Prodöhl P. A., Ferguson A. A simplified protocol for routine total DNA isolation from salmonid fishes // Journal of Fish Biology. 1992. V. 40. P. 963-965.

Tonteri A., Titov S., Veselov A., Zubchenko A., Koskinen M. T., Lesbarrères D., Kaluzchin S., Bakhmet I., Lumme J., Primmer G. R. Phylogeography of anadromous and non-anadromous Atlantic salmon (*Salmo salar*) from northern Europe // Ann. Zool. Fenn. 2005. V. 42. P. 1-22.

Weider L. J., Hobaek A. Postglacial dispersal, glacial refugia, and clonal structure in Russian/Siberian populations of the arctic *Daphnia pulex* complex // Heredity. 1996. V. 78. P. 363-372.