INTRODUCTION
Examining the morphological and genetic characteristics of cisco populations in northeastern Europe is likely to lead to important insights into both the evolution and biogeography of this group. As seen in other fish species (e.g., Kottelat and Freyhof 2007), many members of the Coregoninae quickly diverge into distinct forms (Hudson et al. 2007). These are, sometimes prematurely, given a status of species (Svärdson 1988, Kottelat and Freyhof 2007). These morphologically ‘distinct’ forms, however, are also known to revert to a more common form when reared in controlled environments, suggesting that the presence of morphological characteristics does not actually mean that each population should deserve the ‘species’ status (Vonlanthen et al. 2012).
Northern Europe is a region where a significant overlap exists between European and Siberian fauna. Many species, particularly those which have originated from Siberia, have been relatively poorly studied (Segerstråle 1976, Kuderski 1987, Bănărescu 1991, Pervozvansky 1999, Makhrov and Bolotov 2006). Insofar as coregonids are concerned, the wider geographical area where both European and Siberian forms are present has been subject to scientiﬁc scrutiny for nearly a century (see references in Borovikova and Makhrov 2009). The existence of such transitional zones means that determining the distributional boundaries of European and Siberian coregonids, as well as describing their taxonomic status and phylogenetic relations is difﬁcult.

One of the ﬁrst references to the presence of a Siberian form, least cisco, Coregonus sardinella Valenciennes, 1848, in Northern Europe can be found in Berg (1916). He described a sub-species of the White Sea cisco, Coregonus sardinella marisalbi based on specimens caught near the Solovetsky Archipelago. Pokrovskij (1967) later demonstrated that the distribution of this sub-species was more widespread. He suggested that the same sub-species could be found in water bodies in the catchments bordered by the Arctic Ocean (basins of rivers Pechora, Indiga, and Mezen; lakes of Bolshezemelsky tundra and Kolguyev Island), and the Baltic Sea (e.g., Volodzero Lake in the Onega Lake sub-catchment). Another sub-species of least cisco—C. sardinella vescicus—was described from Lake Beloye which is located in the upper reaches of the Volga River near the watershed between the Baltic and White seas (Drăgin 1933).

The presence of ﬁsh with intermediate morphological characters in the Solovetsky lakes and from Lake Beloye, suggested that specimens captured from these sites could be classiﬁed as being either least cisco or vendace (Drăgin 1933, Kuziśin et al. 1999, Dvorânkin 2005). Additional studies have, by contrast, suggested that the ciscoes from the lakes of Bolshoy Solovetsky Island are ‘typical’ Coregonus albula (Linnaeus, 1758) (see Zahvatkin 1927, Muhomediarov 1963).

Interestingly, Kuziśin et al. (1999) observed changes in the external morphology of vendace from Lake Kransoye over a period of 25 years. So whilst this population had been earlier identiﬁed by Muhomediarov (1963) as being ‘typical’ vendace, the specimens obtained from Lake Kransoye in 1989 were morphologically more similar to least cisco (Kuziśin et al. 1999).

Confusion relating to the taxonomic status of ciscoes from Solovetsky Archipelago has been further complicated by the use of different diagnostic characteristics by the various authors. To correct this, Rešetnikov (2003) attempted to streamline the identiﬁcation of vendace using basic morphological characteristics. Using these ‘rules’, ﬁsh can be identiﬁed as a vendace if the antedorsal length (expressed as a percentage of fork length) exceeds 42% and vertebral counts are 54 to 59 (more commonly 55–56). Least cisco has 57–64 vertebrae, and this ﬁgure is often more than 60. Using these basic morphological criteria it has been suggested that the distribution of least cisco in Europe is limited by the outermost northeastern part (Chesha Bay and Pechora basin), and does not include the Solovetsky Archipelago (Rešetnikov 2003).

Determining the taxonomic status and likely origin of ciscoes populations from the Solovetsky Archipelago is crucial if we are to fully understand of the phylogeny and phylogeography of ciscoes of northeastern Europe.

This study attempts to improve our understanding of the nature of the transitional zone between European and Siberian ciscoes in northeastern Europe. To do that we tested the working hypothesis that the Coregonus ﬁsh (ciscoes) inhabiting the above-mentioned transitional zone represent a single species (Coregonus albula). We examined populations of ciscoes from Solovetsky Archipelago, using a combined analysis of multiple morphological characteristics and molecular markers from nuclear and mitochondrial genomes.

MATERIALS AND METHODS

Collection and preservation of material. A total of 344 ciscoes were caught with set nets (mesh size 12–20 mm) from five lakes on Bolshoy Solovetsky Island from 1995 up to 2009 (Fig. 1, Table 1). Collection of the ﬁsh was performed in accordance with permits of the administration of the culture preserve “Solovetsky”. It is important to mention that four lakes (Bolshoye Krasnoye, Nizhniy Pert, Sredniy Pert, and Bolshoye Gremyachye) are connected by canals while Lake Goreloye is not included in this canal systems.

Morphological analysis was carried out on all ﬁsh captured during this research project. Studies relating to genetic polymorphism, using nuclear- (creatinine kinase isoclini) and mitochondrial (ND-1 fragment of mtDNA) markers, were only performed using samples obtained during the period of 2008–2009. To study polymorphism using creatine kinase samples of the white muscles, which were quickly frozen in liquid nitrogen (–70°C), were used. For mtDNA analysis the muscle tissue samples were ﬁxed in 96% ethanol.

Morphological analysis. Morphological characteristics were described using the methodology previously used for coregonids from northeastern Europe (Pravdin 1966) (Fig. 2). Since Berg (1916) does not provide data on the number of vertebrae in the type specimen of Coregonus sardinella marisalbi, we counted their number on the X-ray image of the type specimen from Zoological Institute (Russian Academy of Sciences).

Analysis of creatine kinase isoclini CK-41,2*. Each sample of white muscle tissue (piece measuring 5 × 5 × 5 mm3) was placed in an amount equal to its volume of TRIS extraction buffer (containing 0.015 mol Tris-HCl, pH 7.5, and 20% sucrose). It was then homogenized at 0 to 4°C. Vertical polyacrylamide gel electrophoresis was performed in 7.5% polyacrylamide using Tris-Borate-EDTA (TBE) buffer. Gel, stock solutions and Tris-Borate-EDTA (TBE) buffer were prepared according Peacock et al. (1965). Voltage was applied for 20 min before addition of
the samples. Twelve mL of extract from white muscle were applied to each slot. For cooling of cells water at 0 to 4°C was used throughout the run. If the length of gel was 8–10 cm a potential difference 230–260 V was applied which resulted in a current of approximately 60–80 mA at the end of the run (2 h). Vertical electrophoresis was performed in cells designed by Truveller and Nefëdov (1974).

Creatine kinase loci $CK-1,2^*$ analysis allows Coregonus albula and $C. sardinella$ from Siberia to be differentiated via the presence or absence of some alleles (Perelygin 1992, Sendek 2002). Staining for general protein, including products of the creatine kinase loci, was carried out according to the method described by Gaá et al. (1980). It should be noted for improving of the results we slightly modified this method. So we changed the ratio

Fig. 1. The map of Northwestern Russia with the main water bodies discussed in the study; LGM = Last Glacial Maximum (according to Svendsen et al. 2004); 1 = Lake Onega; 2 = Lake Beloye; 3 = Lake Vodlozero; 4 = Lake Puruvesi; 5 = Solovetsky Archipelago; 6 = Mezen River; 7 = Chesa Bay; 8 = Indiga River; 9 = Kolguiev Island; 10 = Lake Nizhniy Pert; 11 = Lake Sredniy Pert; 12 = Lake Bolshoye Krasnoye; 13 = Lake Bolshoye Gremyachye; 14 = Lake Goreloye; Roman numerals indicate refugia; Arrows indicate the main hypothesized directions of the ciscoes’ spread before and after last glacial period

Table 1

| Lake                        | Coordinates      | Year sampled | Sample size | Total |
|-----------------------------|------------------|--------------|-------------|-------|
|                            | Latitude | Longitude |             | MA  | IA  | MTA |     |
| Sredniy Pert                | 65°03′N    | 35°43′E    | 1995        | 63  | —   | —   | 63   |
| Nizhniy Pert = Khutorskoe#  | 65°02′N    | 35°41′E    | 1995        | 11  | —   | —   | 11   |
|                            |            |            | 1996        | 90  | —   | —   | 90   |
|                            |            |            | 2008        | 55  | 55  | 55  | 165  |
|                            |            |            | 1996        | 5   | —   | —   | 5    |
| Bolshoye Krasnoye          | 65°05′N    | 35°42′E    | 1997        | 35  | —   | —   | 35   |
|                            |            |            | 2008        | 53  | 53  | 53  | 160  |
|                            |            |            | 1997        | 5   | —   | —   | 5    |
| Bolshoye Gremyachye        | 65°07′N    | 35°42′E    | 2008        | 7   | 7   | 7   | 12   |
| Goreloye = Bolshoye Ostrechye# | 65°08′N | 35°50′E    | 2009        | 20  | 20  | 20  | 60   |
| Total                       |            |            |             | 344 | 135 | 135 |      |

MA = morphological analysis; IA = analysis of polymorphism of creatine kinase isoloci $CK-A1,2^*$; MTA, PCR–RFLP analysis of mtDNA; # denotes lakes which are known by two names.
of the coomassie, trichloracetic acid, and ethanol and concentration of trichloracetic acid (0.005 g coomassie was diluted in 0.100 L ethanol and the total volume was brought to 1 L with 15% trichloracetic acid). The gel made of the mix was left for 12–16 h for staining to develop. Fifteen specimens of ‘typical’ vendace from Lake Puruvesi, Finland, were used as controls.

**PCR–RFLP analysis of mitochondrial ND-I fragment.**

Total cell DNA was isolated from ethanol-preserved specimens by the phenol-chloroform extraction protocol (Green and Sambrook 2012) or the DNA kit Diatom®DNAPrep100 (manufactured by “Izogen”, Moscow, www.rugenlab.ru).

For PCR-RFLP analysis the amplified mtDNA fragment of ~2050 bp including the gene that encodes subunit 1 of NADH–dehydrogenase complex (ND-1; hereafter referred to as ND–I fragment) was used. The amplification was performed using the primers developed by Cronin et al. (1993): 5’ACCCCGCCTGTTTACCAAAAACAT3’ (LGL381, forward) and 5’GGTTCATTAGTGAGGGAAGG3’ (LGL563, reverse).

Synthesis of fragments (polymerase chain reaction, PCR) was conducted in 25 𝜇L of ×1 amplification buffer from “Bion-m” (Moscow): 0.010 mol Tris-HCl (pH 8.8); 0.050 mol KCl; 2.5 mmol MgCl₂, and 0.08% Nonidet P40. The amplification mixture contained 100–300 ng of total cell DNA, 10–15 pmol of each of the two primers, 200 nmol dNTPs, and 0.5–1 units of Taq polymerase (“Bion-m”, Moscow or “Fermentas”, Lithuania). A small amount of mineral oil was added on the surface during PCR to avoid evaporation.

Amplification program of ND–I fragment included initial DNA denaturation step at 95°C for 5 min; 32 cycles of fragment synthesis at 95°C for 1 min, 53°C for 1 min 45 s, and final elongation at 72°C for 5 min.

The amplified fragments of mtDNA were investigated by means of 14 restriction endonucleases (AseI, BstNI, BstUI, DdeI, DpnII, HaeIII, HhaI, HincII, Hinfl, HphI, MspI, NciI, RsaI, TagI). Seven 𝜇L of reaction mix contained 0.7 𝜇L of ×10 buffer as recommended by the manufacturers (“Sibenzyme”, Novosibirsk or “Fermentas”, Lithuania), 2–4 𝜇L of PCR product and 0.5–1 units of the enzyme. For DdeI and HaeIII we used 14 𝜇L of reaction mix, because the products were analyzed both in agarose and polyacrylamide gels. Endonuclease treatment of samples was carried out for 3–4 h at the temperature recommended by manufacturers.

Fragment length analysis of the cut amplification products were performed in 2% gel for all endonucleases except BstNI. For the latter, the fragment lengths were analyzed in 1.3% agarose gel. Electrophoresis was done using Tris-Acetate-EDTA (TAE) or Tris-Borate-EDTA (TBE) buffer systems (Green and Sambrook 2012). To reveal polymorphisms of low-weight molecular fragments, the products of cutting ND–I fragment by DdeI and HaeIII were also run in 11% polyacrylamide gel with TBE buffer. After electrophoresis agarose and polyacrylamide gels were stained with ethidium bromide. Composite haplotypes were created for each sample and labelled following Borovikova (unpublished) and Borovikova and Makhrov (2009).

**Data analysis.** Differentiation of the ciscoes populations on number of vertebrae was tested with χ². For estimate of the significance of mean values’ differences Student’s 𝑡-test was performed (Ivanter and Korosov 2003). In case of the morphological traits expressed as the percentage for improve normality we transformed data using arcsine transformation.

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*Borovikova E.A. 2009. Filogeografiâ râpušek Coregonus albula (L.) i C. sardinella Valenciennes evropejskogo severa Rossii. [Phylogeography of the ciscoes Coregonus albula (L.) and C. sardinella Valenciennes in the European North of Russia.] Avtoreferat na soiskanie učenoy stepeni kandidata biologičeskih nauk. [PhD Thesis.] Peoples’ Friendship University of Russia, Moskva/Moscow. [In Russian with English summary.]*
RESULTS

** Morphological characteristics of ciscoes from Bolshoy Solovetsky Island.** All specimens were small in size, ranging between 16 and 20 cm fork length with only a few specimens exceeding 21 cm. Total weight varied between 13 and 167 g (Table 2).

While average antedorsal length (as a percentage of fork length) was typical for vendace, we also found specimens whose measurements were characteristic of least cisco. Notably, the number of vertebrae in the fish caught in Solovetsky lakes was also greater than might be expected in a ‘typical’ vendace. Our specimens had an average of 57–58 vertebrae with some reaching 59–60. Note that the type specimen of White Sea cisco described by Berg (1916) had 59 vertebrae.

The ciscoes from Bolshoye Gremyachye Lake were somewhat different, however: it had the smallest number of vertebrae, which made it more similar to the European form compared to other populations (Tables 2, 3). At the same time, the dorsal fin had an anterior position which

| Trait | Population code |
|------|------------------|
| FL [mm] | G | BOD | SP | SPD | NP | BK | BKM | BG |
| 167–208 | 52 | 36–64 | 26 | 15–154 | 26–93 | 72 | 7 |
| W [g] | 43.4–69.5 ± 57.9 | 39.2–117.1 (64) | 17.7–167.0 (98) | 13.3–84.2 (92) | — | — | 13.9–34.7 |
| NV | 56–59 | 56–60 (51) | 56–59 | 55–60 (112) | 55–60 (83) | 54–58 | 55–58 |
| NED | ± 1.6 | 74.0 ± 2.3 | — | 50.1 ± 2.8 | 31.8 ± 1.0 | 24.8 ± 2.5 |
| LUJ | ± 1.6 | 69.7 ± 0.5 | 83.5 ± 0.9 | 85.8 ± 0.4 | 85.7 ± 0.6 | 81.9 ± 0.7 |
| % HL | 23.5–29.4 | 57.8 ± 0.1 | 57.7 ± 0.1 | 56.7 ± 0.1 | 56.7 ± 0.4 |

Values shown for each trait: range, number of fish measured (in brackets), mean value ± standard error of the mean; M value of the index calculated based on the data from Muromedžar (1963); G = Goreloye (=Bolshoye Ostreche), this study; BOD = Bolshoye Ostreche (=Goreloye), data from Dvorânk (2005); SP = Sredniy Pert, this study; SPD = Sredniy Pert, data from Dvorânk (2005); NP = Nižnij Pert, this study; BK = Bolshoye Krasnaya, this study; BKM = Bolshoye Krasnaya, data from Muromedžar (1963); BG = Bolshoye Gremyachye, this study; n = sample size; FL = fork length; W = total weight; NV = number of vertebrae; NSLL = number of scales in lateral line; NGR = number of gill rakers; NDBR = number of branched rays in dorsal fin; NABR = number of branched rays in anal fin; NVBR = number of branched rays in ventral fin; NPBR = number of branched rays in pectoral fin; VA = ventral distance; AD = antedorsal distance; AV = anteventral distance; AV as % of AD 49.4–59.5 (61) 49.4–59.9 (6) 56.1 M 44.4–59.9 (6)

Some meristic and plastic traits of ciscoes from Bolshoy Solovetsky Island

| Trait | Population code |
|------|------------------|
| VA as % of AD | 42.3–46.1 |
| AD | 42.3–46.1 |
| VA | 21.7–27.0 |
| AV | 44.6–49.7 |
| PV | 26.9–30.4 |
| Hmax | 17.8–21.9 |
| LCP | 12.6–17.6 |
| HL | 17.4–20.5 |
| NED | 23.5–29.4 |
| LUJ | 36.9–46.1 |
| % HL | 34.0–47.4 |

Values for shown each trait: range, number of fish measured (in brackets), mean value ± standard error of the mean; M value of the index calculated based on the data from Muromedžar (1963); G = Goreloye (=Bolshoye Ostreche), this study; BOD = Bolshoye Ostreche (=Goreloye), data from Dvorânk (2005); SP = Sredniy Pert, this study; SPD = Sredniy Pert, data from Dvorânk (2005); NP = Nižnij Pert, this study; BK = Bolshoye Krasnaya, this study; BKM = Bolshoye Krasnaya, data from Muromedžar (1963); BG = Bolshoye Gremyachye, this study; n = sample size; FL = fork length; W = total weight; NV = number of vertebrae; NSLL = number of scales in lateral line; NGR = number of gill rakers; NDBR = number of branched rays in dorsal fin; NABR = number of branched rays in anal fin; NVBR = number of branched rays in ventral fin; NPBR = number of branched rays in pectoral fin; VA = ventral distance; AD = antedorsal distance; AV = anteventral distance; AV as % of AD 49.4–59.5 (61) 49.4–59.9 (6) 56.1 M 44.4–59.9 (6)
differed from fish obtained from other lakes of Bolshoy Solovetsky Island. Thus, according to this feature the ciscoes from Bolshoye Gremyachye Lake can be described as being ‘typical’ for a Siberian form. It should be noted, however, that the size sample from Bolshoye Gremyachye Lake was quite small. The smallest-sized fish were caught from Bolshoye Krasnoye Lake (Tables 2, 3). The cisco from Goreloye

| Population code | Trait |
|-----------------|-------|
|                 | FL    | W    | NV   | NSLL | NGR  | NDBR | NABR | NVBR | NPBR |
| G vs. BOD       | —     | —    | 1.66** | —    | 4.92*** | —    | 0.00ns | —    | —    |
| G vs. SP        | 48.08*** | 5.75*** | 1.90** | —    | 2.91** | 0.71ns | 1.34ns | 0.71ns | 3.54*** |
| G vs. SPD       | —     | —    | 0.83** | —    | 4.30*** | —    | 1.34ns | —    | —    |
| G vs. NP        | 22.98*** | 2.42* | 0.95** | —    | 0.60** | 0.71ns | 0.45ns | 0.19* | 1.26ns |
| G vs. BK        | 97.94*** | 13.83*** | 0.63** | —    | 1.94** | 2.83** | 1.34ns | —    | —    |
| G vs. BKM       | 90.78*** | —     | —     | 0.95** | 5.66*** | —    | 4.47*** | —    | —    |
| G vs. BG        | 28.78*** | 11.15*** | 1.60** | —    | —     | —    | —    | —    | —    |

| Population code | Trait |
|-----------------|-------|
|                 | FL    | W    | NV   | NSLL | NGR  | NDBR | NABR | NVBR | NPBR |
| BOD vs. SP      | —     | —    | 0.00ns | —    | 2.40* | —    | 1.34ns | —    | —    |
| BOD vs. SPD     | —     | —    | 1.06** | —    | 0.40** | —    | 1.34ns | —    | —    |
| BOD vs. NP      | —     | —    | 1.34** | —    | 6.84** | —    | 0.45ns | —    | —    |
| BOD vs. BK      | —     | —    | 1.79** | —    | 4.71*** | —    | 1.34ns | —    | —    |
| BOD vs. BKM     | —     | —    | —     | —    | 7.49** | —    | 4.47*** | —    | —    |
| BOD vs. BG      | —     | —    | 3.13** | —    | —     | —    | —    | —    | —    |
| SP vs. SPD      | 73.19*** | 6.60*** | 2.12* | 1.41** | 3.40*** | 0.00ns | 2.83** | 1.34ns | 2.85** |
| SP vs. NP       | 158.76*** | 16.83*** | 2.83** | 1.02** | 1.60** | 2.12* | 0.00ns | —    | —    |
| SP vs. BK       | 151.61*** | —     | —     | 3.49*** | 3.35** | 4.95*** | 4.95*** | —    | —    |
| SP vs. BGM      | 54.04*** | 14.48*** | 3.40** | —    | —     | —    | —    | —    | —    |
| SPD vs. NP      | —     | —    | 0.00ns | —    | 2.34* | 5.40*** | —    | 2.83** | —    |
| SPD vs. BK      | —     | —    | 0.45** | —    | 2.03* | 3.60*** | —    | 0.00ns | —    |
| SPD vs. BKM     | —     | —    | —     | —    | 1.40** | 5.59*** | —    | 4.95*** | —    |
| SPD vs. BG      | —     | —    | 2.46* | —    | —     | —    | —    | —    | —    |
| NP vs. BK       | 68.87*** | 6.15*** | 0.71** | 0.14** | 2.12* | 2.12* | 2.83** | —    | —    |
| NP vs. BKM      | 61.72*** | —     | —     | 4.84*** | 0.55** | 4.95*** | 7.78*** | —    | —    |
| NP vs. BG       | 16.71*** | 6.74*** | 2.67** | —    | —     | —    | —    | —    | —    |
| BK vs. BKM      | 11.31*** | —     | —     | 4.12*** | 1.94** | 2.83** | 4.95*** | —    | —    |
| BK vs. BG       | 12.55*** | 2.60* | 2.43* | —    | —     | —    | —    | —    | —    |
| BKM vs. BG      | 9.41*** | —     | —     | —    | —     | —    | —    | —    | —    |

**Bold** denotes comparisons of the number of contemporary ciscoes samples from same lake; FL = fork length; W = total weight; NV = number of vertebrae; NSLL = number of scales in lateral line; NGR = number of gill rakers; NDBR = number of branched rays in dorsal fin; NABR = number of branched rays in anal fin; NVBR = number of branched rays in pectoral fin; NPBR = number of branched rays in pectoral fin; VA = ventroanal distance; AD = antedorsal distance; AV = antevelar distance; PV = pterocentral distance; Hmax = maximum body depth; LCP = caudal peduncle length; HL = head length; NED = horizontal eye diameter; LUJ = upper jaw length; VA%AD = VA as % of AD; G = Goreloye (=Bolshoye Ostreche), this study; BOD = Bolshoye Ostreche (=Goreloye), data from Dvoránkin (2005); SP = Sredniy Pert, this study; SPD = Sredniy Pert, data from Dvoránkin (2005); NP = Nizhnii Pert, this study; BK = Bolshoye Krasnoye, this study; BKM = Bolshoye Krasnoye, data from Muhomediârov (1963); BG = Bolshoye Gremyachye, this study; The level of significance: ns $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; Time interval between collections varied from 5 years for comparisons G vs. BOD and SP vs. SPD to 55 years for comparison BK vs. BKM.
Lake (which is not part of the canal system which connects the other sampled lakes) did not exhibit substantial morphological differences from other populations.

**Polymorphism of creatine kinase isolooci (CK-A1,2*).** Polymorphism within the creatine kinase isolooci was studied using 135 fish obtained from four lakes located in the Bolshoy Solovetsky Island (Table 1) and 15 fish from a Finnish lake (Lake Puruvesi), which served as a control. All fish possessed the allele *100* typical of the vendace. The allele variant *116* characteristic for Siberian ciscoes was not found in any of the sampled populations (Fig. 3).

**Polymorphism of mitochondrial ND-1 fragment.** Ciscoes obtained from the lakes of Bolshoy Solovetsky Island exhibited a low level of mtDNA polymorphism. All populations were dominated by the composite haplotype E, which corresponds to the haplotype PE2 in Politov et al. (2000). This composite haplotype is common in vendace, and has also been recorded in specimens of least cisco and peled, _Coregonus peled_ (Gmelin, 1788) (see Borovikova unpublished*, Borovikova and Artamonova unpublished data). The samples from Lake Bolshoye Krasnoye were the only ones which contained fish with two unique haplotypes (SOL1 and SOL2). Another haplotype ALB1, commonly associated with vendace populations in Northern Russia was also found in some specimens of this lake. Interestingly, one specimen from Bolshoye Krasnoye Lake exhibited heteroplasmy in mtDNA after treatment of the ND-1 fragment by _AseI_ endonuclease (Fig. 4).

The difference between the common haplotype E and the three other haplotypes recorded during this study is one

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*See footnote on page 186.

| Population code | Trait | VA%AD | AD | VA | AV | PV | Hmax |
|----------------|------|-------|----|----|----|----|------|
| G vs. BOD      |      | 0.23ns| 2.68**| 1.12**| 1.39**| —  | 0.55ns|
| G vs. SP       |      | 1.63ns| 7.42***| 1.66**| 1.41**| 2.83**| 2.22' |
| G vs. SPD      |      | 0.28ns| 3.54***| 1.64**| 0.47ns| —  | 0.00ns|
| G vs. NP       |      | 2.89**| 7.16***| 4.74***| 1.39**| 4.24***| 5.69**|
| G vs. BK       |      | 0.22**| 6.34***| 2.50' | 1.11ns| 6.72**| 8.72**|
| G vs. BKM      |      | 1.10ns| 3.80***| 0.24**| —  | 0.00ns| —  |
| G vs. BG       |      | 1.50ns| 7.16***| 2.89**| —  | —  | —  |
| BOD vs. SP     |      | 2.18' | 6.71***| 0.71**| 0.55**| —  | 3.54**|
| BOD vs. SPD    |      | 0.11ns| 1.79**| 0.83| 2.77**| —  | 0.71ns|
| BOD vs. NP     |      | 3.43ns| 7.07***| 4.92***| 1.06**| —  | 8.94**|
| BOD vs. BK     |      | 0.51ns| 5.37***| 1.77**| 4.24***| —  | 10.82**|
| BOD vs. BKM    |      | —    | 2.68**| 1.39**| —  | —  | —  |
| BOD vs. BG     |      | 1.44ns| 6.31***| 2.42**| —  | —  | —  |
| SP vs. SPD     |      | 1.08ns| 3.89***| 0.28ns| 1.89**| —  | 2.83**|
| SP vs. NP      |      | 5.52**| 2.24* | 4.02***| 0.28ns| 1.41**| 4.47**|
| SP vs. BK      |      | 1.53ns| 1.06ns| 1.06ns| 2.77**| 3.89**| 8.04**|
| SP vs. BKM     |      | —    | 0.89ns| 1.94ns| —  | —  | —  |
| SP vs. BG      |      | 2.15' | 2.46' | 2.20'| —  | —  | —  |
| SPD vs. NP     |      | 2.22ns| 2.68**| 2.53**| 1.94**| —  | 8.05**|
| SPD vs. BK     |      | 0.50ns| 2.82**| 0.55ns| 0.55ns| —  | 10.26**|
| SPD vs. BKM    |      | —    | 1.57ns| 1.89ns| —  | —  | —  |
| SPD vs. BG     |      | 1.36ns| 4.92***| 1.97ns| —  | —  | —  |
| NP vs. BK      |      | 3.58**| 0.89| 2.68**| 3.18**| 2.47**| 6.01**|
| NP vs. BKM     |      | —    | 0.24| 5.06**| —  | 4.24**| —  |
| NP vs. BG      |      | 0.60ns| 3.89***| 0.99ns| —  | —  | —  |
| BK vs. BKM     |      | —    | 0.22ns| 2.77**| —  | 6.72**| —  |
| BK vs. BG      |      | 1.60ns| 3.13ns| 1.79ns| —  | —  | —  |
| BKM vs. BG     |      | —    | 2.65ns| 3.02**| —  | —  | —  |

Table footnotes are below Table 3a.
nucleotide substitute at one restriction site of three different restriction enzymes. These are located at the site of Rsal for SOL1, at the site of HaeIII for SOL2 and at the restriction site of Asel for ALB1. None of the composite haplotypes differ by more than two restriction sites substitutes.

**DISCUSSION**

**Taxonomic position of ciscoes from Solovetsky Islands.** The analysis demonstrated that plastic and meristic characters normally used to discriminate between European and Siberian ciscoes do not allow unambiguous identification of Solovetsky Island ciscoes. The morphological and molecular analyses appear contradictory.

Pairwise comparisons of the mean values of morphological traits between ciscoes populations from different lakes of Bolshoy Solovetsky Island (continuation)

| Population code | As % of FL | As % of HL | LCP | HL | NED | LUJ |
|-----------------|-----------|-----------|-----|----|-----|-----|
| G vs. BOD       | 7.07***   | —         | —   | —  | —   | —   |
| G vs. SP        | 0.63ns    | 0.45ns    | 2.23*| 4.07***| —   | —   |
| G vs. SPD       | 7.60***   | —         | —   | —  | —   | —   |
| G vs. NP        | 0.63ns    | 0.00ns    | 1.49ns| 3.85***| —   | —   |
| G vs. BK        | 2.22*     | 8.13***   | 4.46***| 1.49ns| —   | —   |
| G vs. BKM       | 1.94ns    | 11.18***  | 2.97** | —   | —   | —   |

| Trait           | LCP | HL | NED | LUJ |
|-----------------|-----|----|-----|-----|
| BOD vs. SP      | 9.39***| —   | —   | —   |
| BOD vs. SPD     | 1.34ns| —   | —   | —   |
| BOD vs. NP      | 8.94***| —   | —   | —   |
| BOD vs. BK      | 1.06ns| —   | —   | —   |
| BOD vs. BKM     | 2.24| —   | —   | —   |
| SP vs. SPD      | 12.73***| —   | —   | —   |
| SP vs. NP       | 0.00ns| 0.71ns| 1.39ns| 0.83ns| —   | —   |
| SP vs. BK       | 2.68**  | 10.73***| 3.06* | 3.80***| —   | —   |
| SP vs. BKM      | 4.02***  | 18.38***| 1.20| —   | —   |
| SP vs. BG       | —       | —   | —   | —   |
| SPD vs. NP      | 12.02***| —   | —   | —   |
| SPD vs. BK      | 2.68| —   | —   | —   |
| SPD vs. BKM     | 5.66***| —   | —   | —   |
| SPD vs. BG      | —       | —   | —   | —   |
| NP vs. BK       | 2.68**  | 10.29***| 4.99***| 3.58***| —   | —   |
| NP vs. BKM      | 4.02***  | 17.68***| 2.46* | —   | —   |
| NP vs. BG       | —       | —   | —   | —   |
| BK vs. BKM      | 5.30***  | 0.89ns| 1.40ns| —   | —   |
| BK vs. BG       | —       | —   | —   | —   |

Table footnotes are below Table 3a.

* See footnote on page 186.
cal characters are not very reliable in distinguishing European and Siberian ciscoes, because to a large degree they are affected by environmental conditions. Thus, it appears that molecular-genetic methods are better suited for resolving the problems of taxonomic status, phylogenetic relations and distribution of the two forms (species).

According to our molecular data Bolshoy Solovetsky Island is inhabited by ‘typical’ vendace, *Coregonus albula*. This species is also found on the west and east coast of the White Sea (Sendek et al. 2012, Borovikova unpublished*). Further south, where the basins of Volga River, Baltic and White Seas connect, some populations carry genetic characteristics of both European and Siberian forms. For example, samples from Lake Vodlozero (the easternmost part of Baltic catchment) carried a haplotype of mtDNA characteristic of a Siberian species (Borovikova and Makhrov 2009). The populations of Lake Beloye (upper reaches of Volga), Lake Vodlozero and several other water bodies of Eastern Baltic basin, two lakes in the basin of Onega river (southern part of White Sea drainage basin) contained alleles of creatine kinase isocritic typical for least cisco (Gordeeva et al. 2009, Borovikova unpublished*). It should be noted that according Gordeeva et al. (2009) frequency one of these alleles in Lake Goreloye (Bolshoy Solovetsky Island) is 0.5. However, electrophoregram, on which this claim is based, is not included in the cited paper, which let us doubt the data these authors. The basin of the Pechora River had both populations with high frequency of an allele typical of *C. albula* and populations with great affinity to *C. sardinella* (see Sendek 2002).

All of the above is most likely related to the dispersal of ciscoes across northern Europe before and after the last glacial period. Before the last glacial period ciscoes were gradually colonizing European waters in a westward direction from Siberia. This formed a large ‘transitional’ area where ‘typical Siberian’ alleles were gradually substituted by ‘typical European’ ones. Later, the glacier cover of the Eurasian North divided the distribution range of this single species into three parts: European, Siberian (Fig. 1, refugium I), and a refugium near the present-day location of the Volga, Baltic and White Sea basins (Fig. 1, refugium II).

The populations located in this refugium are the descendants of the fish from the ‘transitional’ area that existed before glaciation (Fig. 1, refugium II). These fish may not seem to have contributed to the colonization of the newly available territories after ice retreat. These territories were colonized mainly by the ciscoes from the west (vendace) and by fish present in the basin of the present-day Onega Lake (Fig. 1, refugium III). It is likely, that near Pechora River, where the ciscoes dispersing from the west met the remnants of Siberian populations (least cisco), hybridization of the two forms took place. However, the two forms did not merge completely mainly, it appears, due to their differing ecology and, in particular, their vastly different habitat preferences (vendace inhabits lakes whereas least cisco is a semi-anadromous fish).

The differences in ecology might have led to changes in the morphological traits, so the changes in the body proportions being apparently adaptive (Borovikova and Makhrov 2012). We mentioned earlier the relation between the temperature during embryogenesis and the number of the vertebrae (Eckmann 1987, Lindsey 1988, Etheridge et al. 2012). Many of the head features could be changed by
the diet composition of fish (Menšíkov 1951, Meyer 1987, Balon 1989, Wimberger 1991). Body shape and position of the fins likely indicate ability to long-term migration (Belâeva 1951, Burmakin 1953).

Therefore many of the morphological features are likely to reflect the transition of the cisco from the semianadromous life history type to the lacustrine type, which is more characteristic of the European form. Thus, the speciation of the vendace is clearly adaptive, at least with respect to some traits. It should be noted, however, that the results of this study raise doubts as to whether the vendace has entirely diverged from the least cisco, and whether the speciation has been completed. At the same time, all available morphological and molecular genetic data show only slight differences between the vendace (Coregonus albula) and the least cisco (C. sardinella) (see Pokrovskij 1967, Bernatchez et al. 1991, Bodaly et al. 1991, Kuzišin et al. 1999, Romanov 2000, Sendek 2002, Borovikova and Makhrov 2009), along with wide transitional zone between these forms, makes it possible to hypothesise that Eurasian ciscos are actually a single species (C. albula). Thus our results support previous data about the existence, in northern Europe, populations characterized by transitional features between ‘typical’ vendace and ‘typical’ least cisco. This fact allows revising the current state of the systematic of the ciscos.

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