

Article

The Contact Zone of Phylogenetic Lineages of Freshwater Fish in Arctic Eurasia: Genetic Polymorphism of Coregonid Populations

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Abstract: The reconstruction of regional fauna history is very important in the context of recent climate change and anthropogenic transformation. We analyzed the mitochondrial *nd1* gene polymorphism in populations of whitefish *Coregonus lavaretus* and certain widespread Eurasian ciscoes species: vendace *Coregonus albula* and least cisco *Coregonus sardinella*, inhabiting waterbodies from the Anadyr River in the east (the Pacific Ocean basin) to Loch Lomond in the west (the Atlantic Ocean basin). Distinct phylogenetic lineages and secondary contact zones have been found in these species. Most of these are species-specific with the exception of the zone from the Pechora River basin to at least the western part of the Taymyr Peninsula, in which whitefish, vendace, and least cisco share with each other and with various cold-water hydrobionts. We associate differences in the geographical position and propagation of the secondary contact regions with the species-specific morpho-ecological features, in particular, with the ability for long-term migrations. Based on the data obtained, we also discuss certain limitations of the phylogeography and phylogeny of the considered coregonid species and the correctness of the taxonomic status of certain populations or their groups.

Keywords: mitochondrial *nd1* gene; *Coregonus lavaretus*; *Coregonus albula*; *Coregonus sardinella*; phylogeography; secondary contact



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1. Introduction

The ichthyofauna of water bodies of northern temperate and arctic zones have repeatedly undergone significant transformations due to cyclic climate changes, namely alternating periods of warming and cooling [1]. In accordance with the paleogeographic data, more than twenty glaciation cycles occurred in the Pleistocene [2], each lasting about 100 thousand years, while interglacial periods lasted 10–12 thousand years [3–5].

Pleistocene glaciers radically modified freshwater systems, with some waterbodies being destroyed and new lakes and rivers being formed everywhere. These changes dramatically affected the distribution of hydrobionts, leading to the repositioning, association, and/or fragmentation of their populations [4,6–8]. The occupation of newly formed waterbodies, as well as those now freed from ice, provided an opportunity for rapid evolutionary transformations, while multiple cases of isolation in different periglacial waterbodies and refugia led to the accumulation of genetic differences between populations [9]. These processes resulted in the formation of distinct intraspecific phylogenetic lineages with their own histories and distributions [10,11]. Repeated climate fluctuations also facilitated secondary contacts between isolated groups [4,7,12–15], which also affected the specific structures of modern populations [16].

The study of contact zones can allow researchers to obtain a better understanding of the mechanisms of intraspecific differentiation, hybridization, and speciation in general [17–23], etc. It helps elucidate the nature of the observed diversity and correctly reflects it in the taxonomy of groups [24–28], etc. Moreover, the reconstruction of the history of the regional

fauna is very important for modern biodiversity management, especially in the contexts of climate change and anthropogenic transformation, accompanying biological invasions, and the translocations of species [29,30].

The majority of northern Eurasian freshwater fishes are characterized by the presence of several intraspecific phylogenetic lineages of mitochondrial DNA (mtDNA) (Table 1).

Table 1. The contact zone regions of the main species of Eurasian cold-water ichthyofauna.

Species	NL	Contact Zone in Arctic Eurasia	Source of Data
<i>Salmo trutta</i>	5–7	Great Britain, the basins of the North and Baltic Seas, southern Europe	[31–33]
<i>Salvelinus alpinus</i>	5	Western Greenland, lakes of the Norilo-Pyasinskaya water system (Taymyr Peninsula), the Beringian region	[34–38]
<i>Thymallus arcticus</i>	2	for <i>T. thymallus</i> : basins of the Danube and Weser rivers, Lake Constance area; for <i>T. arcticus</i> and <i>T. thymallus</i> : the northern European regions (Norway, Sweden, Finland), the Kola Peninsula, the northern Dvina River, basins of the Pechora and Ob rivers; for <i>T. thymallus</i> and other Siberian <i>Thymallus</i> sp.: Lake Khantayskoye	[39–44]
<i>Osmerus mordax</i>	7	the Kandalaksha Bay, the Kolguyev Island	[21,45,46]
<i>Osmerus eperlanus</i>			
<i>Esox lucius</i>	3	basins of the Baltic and North Seas, the Middle Danubian drainage, southern Europe	[28,47]
<i>Rutilus</i> sp.	2	Aegean and Baltic Seas' basins, the White Sea basin (the Northern Dvina and Onega rivers), the Black Sea basin (the Upper Dnieper and lower reaches of the Don River), the Caspian Sea basin (the Volga River basin)	[25,48]
<i>Lota lota</i>	5	the Baltic region	[49]
<i>Gasterosteus aculeatus</i>	6–7	the north-eastern part of the Atlantic Ocean, the Phô ne River, the White and Barents Seas, the Black Sea	[23,50]
<i>Pungitius</i> sp.	3	from the north of France (the North Sea, English Channel, Seine, Meuse, and Rhine drainages) to the Netherlands	[24,51]
	2	the Baltic Sea, Skagerrak/Kattegat	[52]
<i>Perca fluviatilis</i>	3–9	the Oslofjord (Norway), the eastern part of the Baltic region, the North Sea basin, the Danube River, southern Europe, Lake Constance	[53–55]
<i>Cottus gobio</i>	7	Northern Scandinavia (the northern Baltic), the Lower Rhine	[56–58]

NL—number of mtDNA phylogenetic lineages.

The patterns of these lineages' propagation are commonly species-specific, however, areas of secondary contact are similar. The mixing of different lineages is associated with resettlement from the refugia via the same water corridors. Additionally, contact zones may be formed in the piedmonts due to settlement through the low mountain passes during periods of climate warming [59–61]. According to the literature, the contact zones are most often noted in the basins of the North and Baltic Seas, the Alpine region, certain water basins of southern Europe, the waterbodies of the Putorana Plateau and the Taymyr Peninsula, and the Beringia region. Thus, *Perca fluviatilis* [53], *Thymallus thymallus* [40], and *Cottus gobio* [57,58] recolonized Europe from several glacial refugia located around the Scandinavian ice sheet. The postglacial invasion of *Esox lucius*, *Coregonus albula*, and *Salvelinus alpinus* occurred along the east–west and/or south–north axes [26,34,47]. Many European hydrobionts have distinct lineages, “local”, i.e., originating from European refugia, and arrivals that penetrated into Europe from the east or west through the coastal waters of the seas [62]. It is worth noting that in many of the above-listed cases, the study of the history of the recolonization of territories rarely goes beyond the limits of the last Quaternary Interglacial (115 thousand years ago) [32].

In general, contact zones have different scales. In Europe, contact zones are formed along the trajectories of the main resettlement pathways. For example, the Danube contact zone exists along the Danube invasion corridor [63]. The Putorana Plateau is an example of the Trans-Siberian contact zone, where the European and Siberian lineages converge [26,36,38]. Transcontinental contact zones are located in the Beringian region and the northern part of the Atlantic, where the mixing of the lineages of the two continents occurs [37,45,47,64].

Populations living in the contact zones are commonly characterized by a high level of genetic polymorphism relative to the populations belonging to separate phylogenetics [4,47,55,58], etc. However, the distribution pattern of genetic polymorphism does not always correspond to modern zoogeographic concepts since it is determined by geological objects and the climate phenomena of the past [65].

Populations from the secondary contact zones often display morphological polymorphism as well. However, they may contain representatives of the same morphotype, but with different origins, i.e., formed independently in distinct phylogenetic lineages [66–69]. This phenomenon indicates the similarity of the mechanisms and consequences of adaptive radiations in different phylogenetic lineages in response to similar environmental cues. They may also include a number of distinct morphotypes formed in the phylogenetic lineages prior to their secondary contact. Without appropriate genetic studies, such morphotypes are often mistaken for intraspecific or even supraspecific units of different origin [70].

Here, we focus for the first time on the distribution pattern of the main mtDNA phylogenetic lineages and their contact zones in whitefish *Coregonus lavaretus* and certain widespread Eurasian ciscoes species, namely vendace *Coregonus albula* and least cisco *Coregonus sardinella*, over a vast region of Arctic Eurasia from the Anadyr River in the east (the Pacific Ocean basin) to Loch Lomond in the west (the Atlantic Ocean basin). Previous studies considered the questions of the phylogeography of the populations of these species only in limited areas [66,71–73], etc.

2. Materials and Methods

2.1. Sample Collection

We used both our own information and NCBI data on the nucleotide sequences of the mitochondrial NADH dehydrogenase subunit 1 gene (*nd1* mtDNA) in coregonids: 240 sequences of ciscoes from 51 populations, and 562 sequences of whitefish from 79 populations were analyzed, including sympatric forms with a controversial systematic status (Table S1). Thus, we discuss two forms of ciscoes of the Pechora River, named saurey and zeld; different forms of whitefish, namely predator and mokchegor, from Lake Sobach'ye (the Putorana Plateau); the lacustrine and lacustrine–riverine whitefishes with a different number of gill rakers of Lake Dorong (the Transbaikal region), etc. A number of endemic coregonid populations were also included in the study: the vendace of Lake Pleshcheyevo (the Volga River drainage); the whitefish of Lake Teletskoye and reservoirs of the Todzha River basin; and the dwarf form of whitefish of Lake Kubenskoye (the White Sea basin), *C. lavaretus nelmuschka*.

Fish from natural populations were caught with gillnets from 2003 to 2021. Some samples of coregonid from waterbodies of the Yamal Peninsula were collected as a part of the Yamal LNG (Liquefied Natural Gas) monitoring investigations. For subsequent genetic analysis, tissue samples from the liver, white muscles, or adipose fin were stored in 96% ethanol (1:5).

2.2. mtDNA Extraction and Sequencing

Total genomic DNA was extracted with the use of DIAAtom™ DNAPrep100 (Isogen Lab Ltd., Moscow; www.rugenlab.ru; accessed on 30 October 2022. www.dnalab.ru/diagnostic-kits/dna-extraction accessed on 30 October 2022) or DNA-Extran-2 (Syntol, Moscow; <https://www.syntol.ru/catalog/nabory-reagentovdlya-vydeleniya-dnk-i-rnk/>

accessed on 30 October 2022) reagent kits. In several cases, the sequencing of the *nd1* gene was preceded by the PCR-RFLP (polymerase chain reaction, restriction fragment length polymorphism) analysis of ND1 fragment 2052 base pairs (bp) long, included a part of the *16S rRNA* gene and several *tRNA* genes flanking the protein gene [26,74]. This technique allowed us to reduce the loss of information regarding the polymorphism of coregonid populations during the random selection of specimens from large samples. For sequencing of the mtDNA region, which was about 2000 bp long, several pairs of primers were used [26,75–77]. Additionally, some of the primers were designed by us (Table S2). PCR conditions as well as the composition of reaction mixtures are given in the description of Table S2.

Sequences were run on an ABI 3500 automated analyzer (Applied Biosystems, United States/Hitachi, Japan) at the Papanin Institute for Biology of Inland Waters of the Russian Academy of Sciences (Borok, Yaroslavl region, Russia) after the purification of PCR products by DNA precipitation with an ethanol–ammonium acetate mixture (http://www.genomecentre.ru/downloads/NH4Ac_EtOH.pdf accessed on 30 October 2022). The sequence reactions were carried out using a BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Austin, United States) as recommended by the manufacturer.

The length of the obtained sequences varied from 1846 bp to 1975 bp, and the sequences taken from NCBI were also of different lengths. Therefore, it was decided to use only the *nd1* gene sequence, 975 bp long, without its flanking regions. As discussed earlier, there was no significant loss of information during this manipulation, while at the same time, it was possible to avoid the formation of star structures and closed loops in the network [26]. All sequences derived by us, as well as those from NCBI, were aligned in MEGA7.0 [78]. During this work, we deposited 93 *nd1* gene sequences in the GenBank: OQ026245–OQ026322 and OQ030167–OQ030187 (Table S1).

2.3. Phylogenetic and Phylogeographic Analyses

The analysis of the sequence polymorphism of the *nd1* gene of coregonids was carried out using the MEGA7.0 and DNAsp5.0 [79] software. For each sample, the average number of nucleotide differences (k), the number of polymorphic sites (S), and haplotype (H_d) and nucleotide (π) diversities were estimated. Additionally, we calculated intra- and interpopulation p -distances using the TN93 model of nucleotide substitutions [80]; bootstrapping (500 replications) was used to calculate the standard error of the distance. Intrapopulation p -distance values were used to discuss the level of polymorphism of coregonid populations from contact zones. Median-joining networks of ciscoes and whitefish *nd1* haplotypes were constructed using Network 10.2.0.0 software [81].

Phylogenetic reconstructions were performed using the Bayesian inference (BI) approach. First, the sequences were collapsed into common haplotypes using DNAsp 5.10.01. For further analysis, two haplotype data files (for whitefish and ciscoes separately) were converted using programs Geneious 7.0.6 (Biomatters Ltd., Auckland, New Zealand; <https://www.geneious.com/> accessed on 25 July 2022) and ALTER [82]. Then, we determined the best-fitting models of nucleotide substitution for each (first, second, and third) nucleotide position in the codon using the PartitionFinder 2.1.1 software [83] on the basis of the Bayesian information criterion (BIC). The models of nucleotide substitutions were identified as follows: for the ciscoes group, 1st *nd1*–K80 + I, 2nd *nd1*–HKY + I, and 3rd *nd1*–GTR + G; for the whitefish group 1st *nd1*–K80 + G, 2nd *nd1*–F81 + I, and 3rd *nd1*–GTR + G. Bayesian phylogenetic inference (BI) was carried out in MrBayes v.3.2.5 software [84]. Two simultaneous analyses were run for 10,000,000 generations each with four MCMC chains sampled every 1000 generations. The first 25% of runs were discarded as burn-in. The phylogenetic trees resulting from the BI analyses were visualized and edited using FigTree v.1.4.2 software [85]. During phylogenetic and phylogeographic analyses, other species of genera, *Prosopium* and *Coregonus*, were included in the study: *P. cylindraceum* MF621767; *C. anaulorum* MT995292–MT995300; *C. clupearformis* JQ390060, JQ661482–JQ661487, MH301057, and MH301058; *C. fluviatilis* KX151804–

KX151807; *C. chadary* KX431963, KX431964; *C. migratorius* MN394787–MN394789; *C. nasus* JQ390058; and *C. ussuriensis* KX431965–KX431971 (all species names are given according NCBI sequences annotations).

Demographic analysis was performed according to [66,86,87]. For time estimates, we used a mean generation length of 6 years. The assumption of neutrality was tested by Tajima’s *D*-test [88,89] in DNAsp 5.10.01 software. As this test has low statistical power [90], we additionally used the *F_s* value [91] with a higher power. The *F_s* values were calculated in Arlequin 3.01 software [92]. Estimates for expansion time at the rate of 1–2% sequence divergence per million years were given only for clades with significant negative values of Fu’s test and Tajima’s *D*-test. It is important to note that since variances in estimates of the timing of the population expansion are large, results are suggestive only.

3. Results

The analysis of both haplotype networks and phylogenetic trees showed the existence of several mtDNA phylogenetic lineages in whitefish *C. lavaretus* and cisco-considered species, namely vendace *C. albula* and least cisco *C. sardinella* (Figure S1–S4). Our data confirmed the nonrandom distribution of the identified phylogeographic groups. There were two large clusters with a similar time of dispersal start for both species (Table 2), the first at 220–110 thousand years ago and the second at 180–90 thousand years ago. In addition, the architecture of haplotype networks is also similar. Star structures were typical for both species, which indicated dispersal after a period of isolation in the refugium. However, the species differed in the patterns of the geographical distribution of haplotype groups and the contact zones of different phylogenetic lineages (Figures 1 and 2).

Table 2. Pairwise sequence divergence statistics (mismatch analysis) based on the frequency of haplotypes in considered cisco species (*C. albula* and *C. sardinella*) and whitefish (*C. lavaretus*) phylogenetic lineages.

Lineages	Level of Clades Subdivision	N	S	k	τ	Theta Obs.	Theta ₀	R _i	Tajima’s D	F _s	Time Since Expansion
Cisco species											
All haplotypes	2–1	240	137	6.706	1.770	24.770	4.936	0.008	−2.259 **	−24.611 ***	91 425–45 712
IC	1–1	59	53	4.414	4.414	11.838	0	0.018	−2.130 *	−25.751 ***	227 052–113 529
IIC	1–2	167	93	3.967	3.591	17.392	0.396	0.030	−2.421 **	−25.691 ***	184 912–92 456
IIIC	1–3	7	3	1.238	0.566	1.224	0.673	0.277	0.050 NS	0.406 NS	–
IVC	1–4	7	5	2.095	2.095	2.041	0	0.091	0.132 NS	−1.447 NS	–
Whitefish											
All haplotypes	3–1	562	175	6.058	4.967	27.939	1.091	0.006	−2.313 **	−24.406 ***	255 242–127 621
IW	2–1	330	123	5.072	4.280	20.550	0.791	0.010	−2.272 **	−24.898 ***	219 938–109 969
IIW	2–2	232	99	3.526	3.526	17.437	0	0.026	−2.447 **	−25.798 ***	180 820–90 410
IW1	1–1	91	12	1.878	0.998	2.361	0.880	0.027	−0.550 NS	−1.242 NS	–
IW2	1–2	239	113	4.646	4.202	19.830	0.444	0.018	−2.355 **	−25.211 ***	215 930–107 965

N—number of sequences, S—number of polymorphic sites, k—mean number of pairwise differences, τ —mutational time since demographic expansion, theta—the mutation parameter as observed and prior to (theta₀) expansion. R_i—Harpending’s raggedness index, F_s—Fu’s test value. * *p* < 0.05, ** *p* < 0.01, *** *p* < 0.001, NS—not significant, “–” no data.

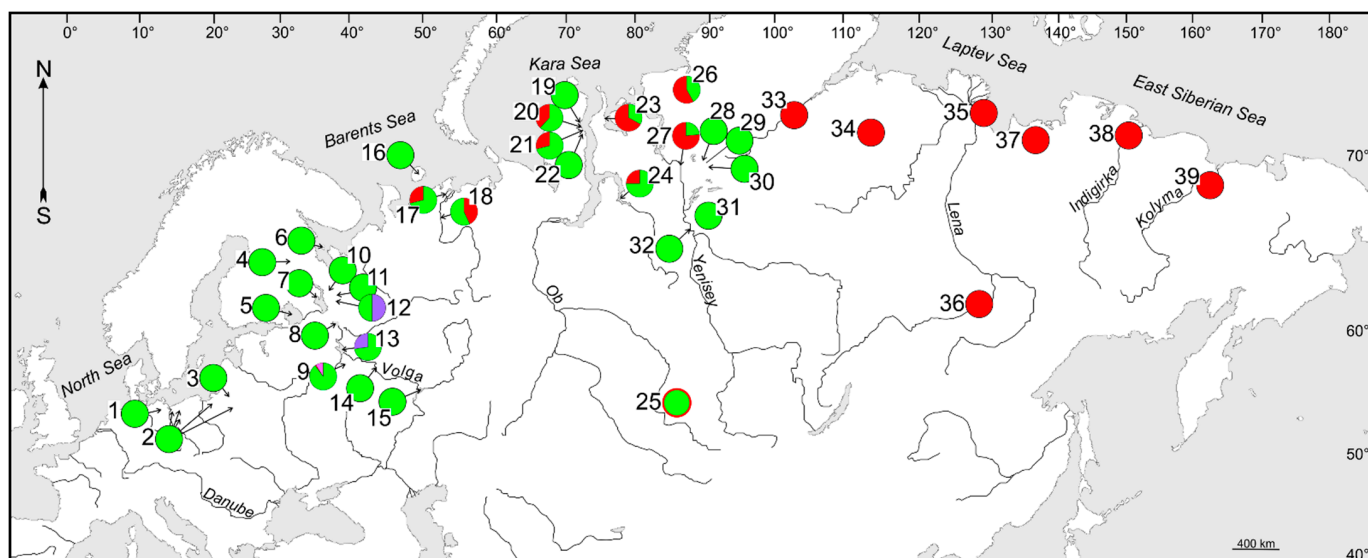


Figure 1. The distribution of phylogenetic mitochondrial lineages of considered cisco species over waterbodies of Arctic Eurasia: red circles—lineage IC, green—IIC, light purple—IIIC, pink—IVC. Location of populations: 1–Lake Stechlin (*C. albula* and *C. fontanae*); 2–lakes of Poland: Bytyń, Płociowe, Drawsko, Marta, Miedwie, Morzycko, Wigry, Ostrowieckie, Żerdno, and Narie; 3–Lake Vištytis, Kaliningrad Region; 4–Lake Khedo; 5–Lake Ladoga; 6–lakes of the Solovetsky Archipelago: Bol’shoye Krasnoye, Gremyacheye, and Bol’shoye Ostrech’ye; 7–Lake Onega; 8–Lake Belaye; 9–Lake Pleshcheyevo; 10–Lake Vodlozero; 11–Lake Kenozero; 12–Lake Lyokshmozero; 13–Rybinsk Reservoir; 14–Gorky Reservoir; 15–Kuybyshev Reservoir; 16–waterbodies of the Kolguyev Island; 17–Pechora River, Lake Golodnaya Guba, saurey; 18–Pechora River, watercourse and estuary, zeld; 19–Nyakharvangata-Yakha River; 20–Sabetta-Yakha River; 21–Venujmue-Yakha River; 22–Lake Yoserotato; 23–Nyojta-Yakha River; 24–Messo-Yakha River; 25–Lake Ingol (introduced population of *C. albula*, denoted by red circle); 26–Pyasina River; 27–Yenisey River; 28–Lake Lama; 29–Lake Sobach’ye; 30–Lake Kutaramakan; 31–Kureyka Reservoir; 32–Yenisey River, Kureyka River mouth; 33–Khatanga River; 34–Anabar River; 35–Tiksi Bay; 36–Lena River; 37–Yana River; 38–Indigirka River; 39–Kolyma River. More detailed information about ciscoes samples is given in Table S1.

3.1. Phylogenetic Lineages and Their Contact Zones in Considered Cisco Species

In the case of the considered ciscoes, the geographical distribution of the four differentiated lineages was confined to certain regions. The first lineage, IC, is most common in Siberian waterbodies, and the frequencies of its haplotypes decrease from east to west. The haplotypes of this lineage were the only ones to be found in the populations of the Lena, Yana, Indigirka, and Kolyma rivers (Figure 1). There are also numerous carriers of this lineage in the Yenisey River, waterbodies of the Taymyr and Yamal peninsulas, and in the Ob and Pechora rivers and their basins, where they already coexist with carriers of haplotypes of the second large Eurasian lineage—IIC. Lake Pleshcheyevo (the Volga River basin, Yaroslavl region) is the westernmost point, where the haplotype belonging to the IC lineage is revealed.

The lineage IIC is associated with western waterbodies. In all of the studied European populations of cisco to the Ural Mountains, the haplotypes of other lineages were noted only in lakes Lyokshmozero and Pleshcheyevo, in the Rybinsk Reservoir, and the Pechora River (Figure 1; Table S3). However, even to the east of the Ural Mountains, there are populations where the frequency of the haplotypes of this lineage reaches 100%, namely in the lakes of the Putorana Plateau—Lama, Kutaramakan, and Sobach’ye. The frequency of occurrence of IIC haplotype carriers is also high in the waterbodies of the Yamal Peninsula, and in the Yenisey and Pyasina rivers. Only east of the Yenisey, haplotypes of this lineage were not found. It should be noted that the IIC lineage is younger than the IC (Table 2).

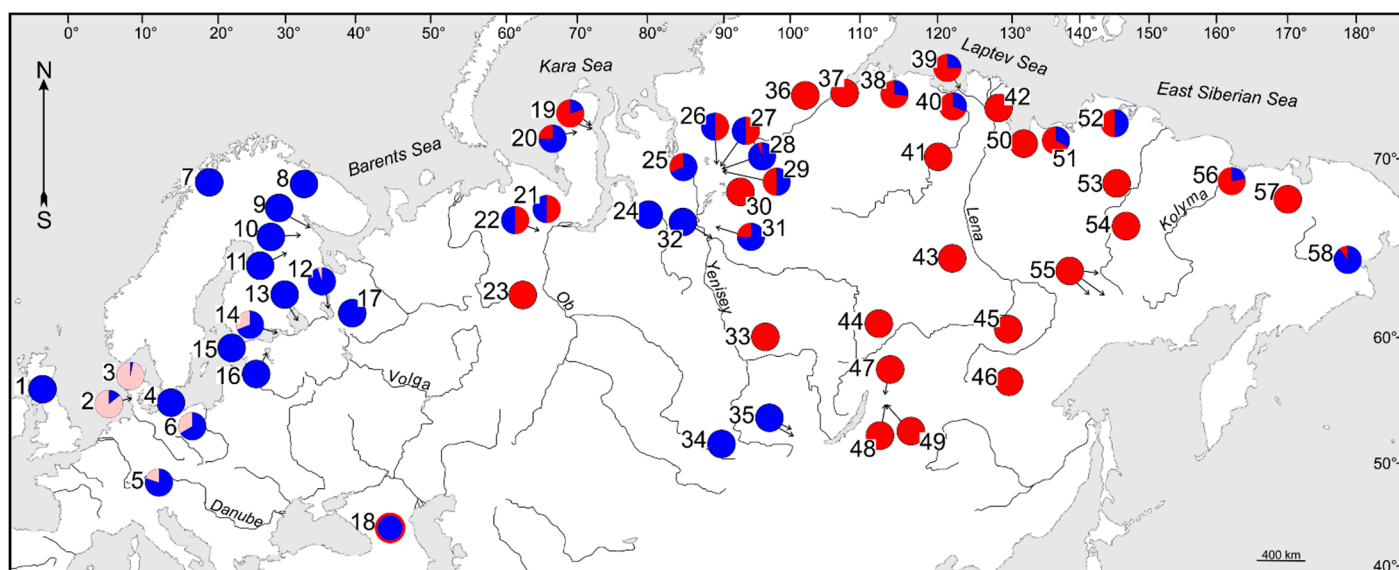


Figure 2. The distribution of phylogenetic mitochondrial lineages of whitefish over water bodies of Arctic Eurasia: red circles—lineage IW, subclade IW2, light pink—lineage IW, subclade IW1, blue—IIW. Location of populations: 1—Loch Lomond; 2—Vidaa River (*C. oxyrhynchus*); 3—waterbodies of Denmark: Nissum and Ringkøbing fjords, Kilen, lakes Tange and Flyder; 4—Achterwasser; 5—Lake Hallstatt and Koppentraun; 6—lakes of Poland: Sremski, Insko, Miedwie, Morzycko, and Marianovo; 7—Havgajävi; 8—Tuloma River; 9—Keret’ River; 10—Lake Topozero; 11—Lake Kamennoye; 12—Lake Onega; 13—Lake Ladoga; 14—the Gulf of Finland; 15—Baltic Sea, Estonian coast, 16—Lake Peipus; 17—Lake Kubenskoye (dwarf form of whitefish); 18—Lake Sevan (introduced population, denoted by red circle); 19—Sabetta-Yakha and Venujmue-Yakha rivers; 20—Lake Langtibeito; 21—Sob River; 22—Lake Varchaty and Voykar River; 23—Northern Sosva River; 24—Taz River; 25—Yenisey River; 26—Lake Lama; 27—Lake Sobach’ye, mokchegor; 28—Lake Sobach’ye, predator; 29—Lake Kutaramakan; 30—Irkingda River, lakes Keta and Khantayskoye; 31—Kureyka River; 32—Nizhnyaya Tunguska River; 33—Ayakhtha River; 34—Lake Teletskoye; 35—Lake Todzha and Khamsara River; 36—Zakharova Rassokha River; 37—Popigay River; 38—Anabar River; 39—Olenek channel of the Lena River; 40—Olenek River (settlement of Taymylyr); 41—Olenek River (middle course); 42—Tiksi Bay; 43—Markha River; 44—Upper Lena River; 45—Buotoma River; 46—Lake Bolshoye Toko; 47—Lake Dorong; 48—Lake Kapylyushi, pidschian; 49—Lake Kapylyushi, *C. l. baunti*; 50—Omoloy River; 51—Yana River; 52—Khroma River; 53—Suturuokha River; 54—Moma River; 55—Kuydusun River, lakes Ichilyakh and Labyntyk; 56—Kolyma River; 57—Lake Ilirney; 58—Anadyr River. More detailed information about whitefish samples is given in Table S1.

Two more lineages found in *C. albula* are rare, and their areas of occurrence are significantly limited. Lineage IIIC is found in Lake Lyokshmozero (the White Sea basin) and the Rybinsk Reservoir (Volga River), where it mixes with the IIC lineage. The IVC lineage is revealed in Lake Pleshcheyevo, where it coexisted with carriers of the IC and IIC lineages; the origin and distribution of this lineage was discussed in our previous publications [26,93,94]. Obviously, the IVC clade is the most ancient in vendace. Its *p*-distance with other lineages equals 2.6–2.9%, while the distance between the IC and IIC lineages is only 0.7% (Table S4). The genetic differentiation of IC and IIC lineages with whitefish haplotype groups is 3.4 and 3.7%, respectively.

It is worth noting that we cannot correlate lineage IC with least cisco, and lineage IIC with vendace. Haplotypes of both the first and second lineages are noted in the populations of both species. In our previous work, we discussed the close relation of these species (Table 3) and suggested their conspecificity [26].

Table 3. Inter- and intraspecies *p*-distance values (as %) for coregonid species; minimum, maximum, and mean values are given.

	CA	CS	CF	CL	COx	CPr	CBt	CAn	CFl	CCl	CMg	CCd	CUs	CN	PC
CA	0–3.3 0.1														
CS	0–3.4 0.1	0–1.6 0.1													
CF	0–3.1 0.6	0.03–0.1 0.06	0.02–0.04 0.03												
CL	3.1–4.5 3.6	2.8–4.3 3.5	3.0–4.1 3.5	0–1.4 0.1											
COx	3.3–4.0 3.5	2.9–3.8 3.4	3.4–3.6 3.5	0–1.2 0.06	0–0.1 0.02										
CPr	2.9–4.7 3.7	2.8–4.2 3.5	3.4–3.8 3.6	0.01–1.4 0.06	0.02–0.1 0.06	0.01–0.1 0.03									
CBt	3.3–3.6 3.5	3.0–3.8 3.4	3.1–3.6 3.5	0–1.1 0.06	0.03–0.1 0.05	0.03–0.1 0.06	0–0.05 0.02								
CAn	4.0–4.7 4.1	3.9–4.2 4.0	3.9–4.4 4.1	2.9–3.4 3.1	2.5–3.6 3.1	2.5–3.4 3.1	2.6–3.5 3.0	0.01–0.1 0.04							
CFl	3.5–4.1 3.6	3.2–3.9 3.5	3.5–3.7 3.6	1.4–2.0 1.7	0.02–2.0 1.7	1.4–2.0 1.7	1.1–1.9 1.5	2.0–2.9 2.5	0.02–0.1 0.04						
CCl	2.9–3.6 3.1	2.7–3.4 3.1	3.1–3.3 3.15	1.6–2.2 1.9	1.8–2.1 1.9	1.6–2.2 1.9	1.7–2.1 1.8	2.5–3.4 2.8	1.7–2.2 1.9	0–0.03 0.01					
CMg	3.5–4.3 3.7	3.3–4.3 3.6	3.5–4.1 3.7	1.8–2.4 2.1	1.9–2.5 2.1	1.7–2.6 2.1	0–2.5 1.7	2.7–3.8 3.2	1.1–1.9 1.5	1.8–2.5 2.0	0.01–0.1 0.03				
CCd	4.5–5.3 4.7	4.5–5.1 4.6	4.4–4.9 4.7	2.6–3.3 2.9	2.8–3.2 3.0	2.8–3.3 3.1	2.4–3.1 2.8	3.2–4.0 3.6	2.3–2.8 2.6	2.9–3.1 2.95	2.4–2.8 2.6	0.04			
CUs	4.4–5.2 4.6	4.1–4.8 4.5	4.3–4.8 4.6	2.7–3.2 2.9	2.9–3.3 3.0	2.6–3.3 3.0	2.3–3.2 2.8	3.1–4.0 3.5	2.2–2.8 2.5	2.7–3.1 2.8	2.3–2.8 2.5	0.04–0.1 0.05	0–0.04 0.02		
CN	3.8–4.3 4.0	3.8–4.6 3.9	4.1–4.4 4.3	2.4–3.0 2.6	2.9–3.2 3.0	2.7–3.2 2.9	2.6–3.2 2.9	3.4–4.1 3.7	2.8–3.2 0.3	2.7–3.0 2.8	3.2–3.6 3.4	4.2–4.3 4.25	4.0–4.3 4.2	nc	
PC	17.1–17.5 17.2	17.0–17.6 17.3	17.4–17.7 17.6	16.9–17.5 17.3	17.7–17.9 17.8	17.5–18.0 17.7	17.7–18.0 17.9	16.6–17.0 16.8	17.0–17.1 17.05	17.9–18.0 17.95	17.9–18.4 18.1	17.5–17.8 17.7	17.5–17.9 17.7	17.9	nc

Species names are given according to NCBI sequences’ annotations: CA—*Coregonus albula*; CS—*C. sardinella*; CF—*C. fontanae*; COx—*C. oxyrhynchus*; CPr—*C. l. pravdinellus*; CBt—*C. l. baunti*; CAn—*C. anaulorum*; CFl—*C. fluviatilis*; CCl—*C. clupearformis*; CMg—*C. migratorius*; CCd—*C. chadary*; CUs—*C. ussuriensis*; CN—*C. nasus*; PC—*Prosopium cylindraceum*; nc—not calculated.

Thus, for considered cisco species, several areas were revealed where two or more phylogenetic lineages are mixed: lakes Pleshcheyevo and Lyokshmozero, the Rybinsk Reservoir, the Pechora River and its basin, and the waterbodies of the Yamal Peninsula, as well as the basins of the Taz and Gydan Bays of the Kara Sea, and the Yenisey and Pyasina rivers and their basins (the western part of the Putorana Plateau).

3.2. Phylogenetic Lineages and Their Contact Zones in Whitefish

An analysis of the haplotype network (Figure S3; Table S5) shows that the whitefish has two ancestral haplotypes, the dispersal of which, apparently, began at about the same time (Table 2). The formation of star structures by these haplotypes indicates their further wide distribution. At the same time, it should be noted that we do not exclude the possibility of the earlier existence of other mtDNA lineages in whitefish, the carriers of which obviously disappeared during the glaciation.

Two large mtDNA lineages, IW and IIW (Figure 2), are associated with ancestral haplotypes. These lineages do not have clearly defined distribution regions, and their haplotypes of each of them are found both in European and Siberian waterbodies, although the first haplogroup (IW) noticeably dominates in waterbodies of the upper reaches of the Lena, Yana, and Indigirka Rivers, while the second (IIW) is more common in western waterbodies. It should be noted that haplotypes forming a separate subclade of clade IW, namely IW1, were identified in a number of waterbodies of Denmark, Poland, the Baltic Sea, and Lake Onega, and were not found in Siberia (Figure 2). Obviously, the haplotypes of this subclade were formed through isolation in a separate refugium, with their offspring subsequently spreading into certain European water bodies.

The contact zones of the two identified whitefish lineages are quite wide: the haplotype carriers of the IW and IIW groups coexist in the North and Baltic Seas’ basins, in the water bodies of the Yamal and Taymyr peninsulas, and in the lower reaches of all of the Siberian rivers of the Arctic Ocean basin, as well as in the Anadyr River. Interestingly, in the areas of Yamal and Taymyr, the contact zones of the phylogenetic lineages

of whitefish and considered cisco species coincide. Moreover, the same region as a zone of secondary contact was also noted for other cold-water fish (Table 1), which indicates its importance in the distribution and formation of the intraspecific polymorphism of the northern Eurasian ichthyofauna.

4. Discussion

We analyzed the mtDNA polymorphism in populations of *C. lavaretus* and ciscoes *C. albula* and *C. sardinella*, inhabiting the waterbodies of northern Eurasia from the Anadyr River in the east (the Pacific Ocean basin) to Loch Lomond in the west (the Atlantic Ocean basin). Distinct phylogenetic lineages and secondary contact zones were revealed in both species. Most of them are species-specific, however, one is common for whitefish and considered cisco species. Here we would like to discuss several results of our investigation in more detail.

4.1. The Level of Population Polymorphism in the Contact Zones of Coregonids Phylogenetic Lineages

An assessment of the level of polymorphism in the whitefish, vendace, and least cisco populations inhabiting the contact zones revealed results inconsistent with our predictions. Contrary to our expectations, in some cases these populations do not display a high level of genetic polymorphism (Tables S6 and S7, p -distance values). Only for the vendace populations of lakes Pleshcheyevo (the Volga River basin) and Lyokshmozero (the White Sea basin) do the indicator intrapopulation p -distance significantly exceed those of other vendace and least cisco populations. However, it should be noted that significantly differentiated lineages—IIC and IVC—are found in these waterbodies (Table S3).

The above observations are also characteristic of *C. lavaretus*. In fact, a sample of whitefish from the middle reaches of one of the longest Russian rivers, the Olenek River (the Laptev Sea basin), had one of the highest values of intrapopulation polymorphism. The p -distance between the haplotypes found in the sample was 0.72%, and the nucleotide diversity was 0.00748 (Table S7), although only one lineage of haplotypes, IW, was found here. It is important to note that the size of the analyzed sample does not matter: three sequences from Yana River demonstrated the maximum variability indicators and the same values of these indicators were revealed for 15 sequences from the middle reaches of the Olenek River. From Lake Onega, where the haplotypes of different lineages were found (Figure 2; Table S5), 19 sequences were included in the analysis and the p -distance between the identified haplotypes was low, namely 0.31%. In the sample of the dwarf form of whitefish (*C. l. nelmuschka*) from Lake Kubenskoye, the level of polymorphism (p -distance) was equal to the polymorphism of the Lake Onega sample, although only two sequences were analyzed from the first waterbody.

It has been proposed that the level of polymorphism in the populations of the considered species is more related to the time of the existence of the lineages and populations [95] than to a mixture of different lineages in the same waterbody or basin. This is especially well seen in the vendace and least cisco. Thus, the highest polymorphism level of the *nd1* gene was detected in the vendace from Lake Pleshcheyevo, where carriers of the most ancient IVC lineage (or ALBP2 haplogroup according to [26]) were revealed. The minimum level of diversity is typical for the vendace of Fennoscandia waterbodies [96] and the least cisco of the Putorana Plateau (Table S6). Obviously, this is due to the youth of these populations. Glaciers covered vast areas of the basins of the Baltic, White, and Barents Seas during the last glaciation, and the age of these populations cannot exceed a maximum of 10–15 thousand years [66,97–99]. Therefore, even the presence of two different lineages in young whitefish populations in Danish waterbodies does not significantly increase the indices of intrapopulation polymorphism (Table S7).

In the case of the least cisco populations of the Putorana Plateau, an effect that their relative youth also seems to produce is seen. Here, the younger lineage IIC clearly dominates, obviously spreading to the region from the west [26,100]. Perhaps the ancestor of the modern predatory form of whitefish of Lake Sobach'ye (the Putorana Plateau) penetrated

into this region simultaneously with ciscoes. The predatory whitefish of this lake differs from the benthophage–mokchegor whitefish that it lives sympatrically, in both ecology and morphological features [101,102]. The predatory whitefish is also characterized by a significant predominance of only one haplotype lineage in the population (Table S5) and is almost two times lower than the level of genetic diversity compared to the mokchegor (Table S7). It should be noted that the approximate time of the beginning of the dispersal of the predominant lineages in the predatory whitefish and least cisco from Lake Sobach'ye coincides (Table 2).

4.2. Possible Reasons for the Formation of the Observed Patterns of Contact Zones in Considered Cisco Species and Whitefish

The patterns of the contact zones of phylogenetic lineages in the considered ciscoes and whitefish of Eurasia differ significantly, as mentioned earlier. Only one similar feature can be identified, namely the mixing of different lineages in both species in the area from the Yamal Peninsula to the western part of the Putorana Plateau, including the lower reaches of the Yenisey River (Figures 1 and 2). Our results suggest that the main reasons for the formation of these specific patterns of the distribution of the lineages of two species are as follows: 1. their different ability for long-term migrations, including under conditions of high salinity, which manifests itself in the features of the body shape, ecology, and physiology of fish [103,104], and 2. the location and size of the refugia from where the resettlement began [105,106]. Migrants from large refugia are more successful, as a rule. The success of migrants from large refugia is not only caused by the fact that individuals in large waterbodies are already more adapted to long-term movement, but also by the fact that the number of migrants from a population with larger numbers will be greater than from a population of a smaller size. Additionally, adaptation to specific habitat conditions in small waterbodies, expressed in specific genetic polymorphism [107,108], can play a certain role in reducing the ability to disperse the carriers of a particular lineage. Such specialization can reduce the ability to adapt to slightly different conditions in newly developed water bodies, affecting competitiveness, and thereby limiting resettlement. Apparently, the time spent by the group in isolation is also of significance.

For example, for the whitefish, which are larger in size than the vendace and least cisco, long-term migrations along the mainland lineage of Eurasia were obviously not difficult, which led to a wide distribution of the haplotypes of both mtDNA lineages. However, it should be noted that carriers of IIW apparently still had an advantage, since the frequency of this lineage is higher in the lower reaches of all large rivers, not only in the Arctic Ocean basin but also in the Bering Sea (the Anadyr River). The same lineage is mostly represented in the populations of western Europe. The haplotypes of the IW lineage are more associated with the upper reaches of Siberian rivers, and in Europe, they are represented by a separate IW1 subclade, which has a rather limited distribution, as discussed above. At the same time, the time of the beginning of the propagation of the IW and IIW lineages is comparable (Table 2). All these factors led to the presence of a significant number of whitefish populations where the carriers of IW and IIW lineages coexist.

We have already discussed the features of vendace and least cisco phylogeography earlier [26,94,96]. It should be noted that representatives of these species seem to be less capable of long-term migrations, and this has led to a limited distribution of a number of haplotypes. In particular, haplotypes belonging to the IC lineage, which is dominant in eastern Siberia, are almost never found outside the basin of the Pechora River. The same is true for the haplotypes of the younger lineage, IIC, their distribution in the east is limited to waterbodies of the Putorana Plateau. These factors determined the position of the vast contact zone of two of the main ciscoes lineages, IC and IIC, from the basin of the Pechora River to the western part of the Putorana Plateau.

4.3. Comparison of Our Own Results with other Studies of the Phylogeography of the Whitefish and Considered Ciscoes Species of Eurasia

This work is not devoted to a detailed discussion of the paths of cisco and whitefish dispersal in periglacial waterbodies. However, we note that our results are in good agreement with numerous paleogeographic reconstructions [97–99,109–112] and the data of other authors (see Table 1).

At the same time, the analysis of the new information presented here allows us to accurately supplement and refine the results of both our own earlier works on the phylogeography of coregonids [113] and the studies of other researchers. Thus, in the publication [66] where the phylogeography of the western European whitefish is considered in detail, three large mtDNA clades have been mentioned, which can be considered to correspond to the IW2, IW1, and IIW haplotype groups discussed by us. In addition, according to K. Østbye and coauthors [66], the carriers of the clade 3–1, which correspond to the IIW lineage in our work, dominate in European whitefish populations. From the data given in [66], the significant differentiation in the composition of the haplotypes of the European whitefish populations and the populations of the Pyasina and Khatanga Rivers can be seen. Indeed, according to our results, these Siberian rivers are inhabited by the carriers of the IW2 subclade haplotypes, which are not represented in western Europe (Table S5).

The phylogeography and phylogeny of whitefish are also discussed in the works of D.S. Sendek and coauthors [71–73,114–116], etc. However, most of these consider the origins of whitefish populations in rather limited areas, which leads to inconsistent conclusions. For example, the authors opine that the whitefish of Lake Pyaozero (Karelia, the White Sea basin), represented by different morpho-ecological forms, comes from three different phylogenetic lineages, including one from Siberia, due to its proximity to haplotypes from the Anabar River (the Laptev Sea basin) on the haplotype network [73]. According to our data, there are two phylogenetic lineages of whitefish in the Anabar River, the carriers of one (IIW) are apparently more capable of migration and have spread widely across Europe in addition to Siberian waterbodies (Figure 2; Table S5). Therefore, according to the illustrative material presented in the article [73], we believe that Lake Pyaozero is inhabited by the representatives of one lineage IIW, widespread in Europe, which is confirmed by the allozyme data of the authors themselves. Our data are also consistent with the conclusions of D.S. Sendek on the presence of cisco groups of different origins in the Pechora River [116,117]. However, it should be noted that differentiation does not occur between the saurey and zeld forms of cisco, the first of which is considered closer to the European vendace, and the second to the Siberian least cisco: each of these forms are almost equally represented by the carriers of haplotypes of both European and Siberian origin (Figure 1; Table S3).

Our data also do not confirm the existence of a number of whitefish species identified by other authors. Thus, whitefish from the Vidaa River (Denmark), which is considered to be a representative of the species *C. oxyrhynchus* [118,119], does not differ in the set of haplotypes either from other Danish populations or from a number of populations of the Baltic Sea basin (Figure 2; Table S5). In addition, according to our data, the whitefish from Lake Teletskoye (the Ob River basin) have a common origin. The differentiation of haplotypes revealed in this lake is low and equals 0.26% (Table S7). All haplotypes identified in the whitefish from this lake belong to the same phylogenetic lineage, IIW (Figure 2; Table S5). However, a number of authors [77,120] discuss the sympatric habitation of two subspecies in the lake, *C. l. pidschian* and *C. l. pravdinellus*, and do not exclude their allopatric origin. Some authors even believe that the separate species *C. pravdinellus* exists in Lake Teletskoye [121,122]. The species status of the medium-density rakered spring-spawning whitefish of Lake Kapylyushi (Transbaikalia), *C. baunti*, is also questionable since its differentiation with the sympatrically inhabiting whitefish is low. Common haplotypes were found for them [120]. At the same time, many of specific morpho-ecological features of whitefish, including the number of gill rakers and spawning time, are unstable and easily

changed [123]. This problem could be resolved by information on the karyology of all the above-discussed coregonids forms or RAD sequencing data, however, such data are not yet available.

The differentiation in the *nd1* gene sequences is also insignificant between the sympatric species *C. albula* and *C. fontanae* from Lake Stechlin (Germany). According to our data, these groups have the same haplotypes and belong to the same phylogenetic lineage common in Europe, IIC (Figure 1; Tables 3 and S3). This issue was discussed in more detail in our previous work [26].

5. Conclusions

The analysis of the polymorphism of the mitochondrial *nd1* gene in north Eurasian coregonid populations revealed four phylogenetic mtDNA lineages of considered cisco species, namely vendace and least cisco, and two lineages of whitefish. All species have zones of secondary contact. However, in some cases, the presence of representatives of different lineages in populations does not lead to the expected increase in intrapopulation genetic polymorphism. It should be noted that the locations and areas of the most contact zones are species-specific and depend on the species' morpho-ecological characteristics, such as the ability of long-term migration. In the area from the Yamal Peninsula to the western part of the Putorana Plateau, including the downstream of the Yenisey River, whitefish and ciscoes share a secondary contact zone with each other and with various cold-water hydrobionts [36,38,124], etc. Finally, one can conclude that the previously assigned species status of least cisco and several whitefish populations, such as *C. pravdinellus*, *C. baunti*, and *C. oxyrhynchus*, seems to be quite doubtful, and additional karyological and genetics studies are in high demand.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15020163/s1>, Table S1: The description of whitefish and considered cisco species samples; Table S2: Primers used for amplifying and sequencing of the mtDNA region of coregonids analyzed in this study; Table S3: Frequencies of the haplotypes of phylogenetic lineages in considered cisco species populations; Table S4: Genetic divergence (*p*-distances, as %) of different phylogenetic lineages and coregonids species; Table S5: Frequencies of the haplotypes of phylogenetic lineages in whitefish populations; Table S6: Values of intrapopulation polymorphism in considered cisco species; Table S7: Values of intrapopulation polymorphism in whitefish; Figure S1: Median-joining haplotype network of the considered cisco species based on the *nd1* gene sequences; Figure S2: BI consensus gene tree based on the *nd1* gene sequences for haplotypes of considered cisco species; Figure S3: Median-joining haplotype network of the whitefish based on the *nd1* gene sequences; Figure S4: BI consensus gene tree based on the *nd1* gene sequences for whitefish haplotypes.

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Institutional Review Board Statement: This article does not contain any studies with human participants performed by any of the authors. Fish samples were caught in accordance with annual permits for the provision of aquatic biological resources for use for fishing for research or control purposes. Vendace of Lake Pleshcheyevo was caught in compliance with the permission for fishing and hunting of wildlife objects included in the *Red Data Book* of the Russian Federation no. 51 of 21 March 2013; no. 136 of 28 August 2013; no. 38 of 11 April 2014; and no. 7 of 25 February 2015. In some cases, catching fish was carried out as a part of the business or research contract works according to the interests of fisheries and other organizations. In addition, parts of the samples were bought from local fishermen.

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