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The origin of sympatric forms of European whitefish (*Coregonus lavaretus* (L.)) in Lake Ladoga based on comparative genetic analysis of populations in North-West Russia

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Four sympatric forms of Lake Ladoga European whitefish (*Coregonus lavaretus* (L.)) were analyzed at 29 enzyme loci. The genetic distances between these populations were highest when the lake form and the lake-river form from the southern part of the lake (both of them low-density-rakered) were compared with two lake forms ("black" and "white") from the north-western coastal zone of Lake Ladoga ($D_N = 0.003$–0.006). No genetic differences between the low-density-rakered "white" form and the medium-density-rakered "black" European whitefish were found. Analysis of allelic distribution and genetic divergence among European whitefish populations in North-West Russia failed to support the identity of the low-density-rakered forms of Lake Ladoga whitefish with eastern populations of *C. lavaretus pidschian*. Based on these data, the hypothesis of possible penetration of the White Sea coregonid fauna into Lake Ladoga can be rejected. A more plausible hypothesis is that European whitefish and vendace originated in the Lake Ladoga basin via colonization from a Baltic periglacial lake.

Introduction

Lake Ladoga is the largest lake in Europe, and occurs within the Baltic Sea basin connected to the Gulf of Finland via the short Neva River, 74 km long. Two coregonid species, European whitefish (*Coregonus lavaretus* (L.)) and vendace (*Coregonus albula* (L.)), populate Lake Ladoga. Both species are represented by several well-distinguished forms that differ both ecologically and morphologically (Berg 1948, Pravdin 1954, Reshetnikov 1980).

Based on gillraker morphology alone, European whitefish are divided into three different forms of Lake Ladoga: low-density-rakered and benthic feeding; high-density-rakered and plankton feeding; and medium-density-rakered forms with variable feeding preferences (Svärdson 1952, Reshetnikov 1980). There are two viewpoints on the origin of such forms in Europe: (1) different sympatric feeding types originated from a common ancestor through ecological differentiation (Steinmann 1951); and (2) all forms originated from two to five geographically isolated ancestral populations (Himberg 1970, Svärdson 1998). It is interesting that high-density-rakered and medium-density-rakered forms that are typical of Western Europe are almost completely absent eastwards from lakes Ladoga and Onega; only low-density-rakered European whitefish or pidschian, *C. lavaretus pidschian* Gmelin, live along the Arctic coast.

During the Pleistocene epoch, glaciation in the Baltic shield took place several times, resulting in the almost complete disappearance of preglacial and interglacial sediments on this shield. The absence of fish fossils in the layers older than late glacial time and Holocene prevents reconstruction of the modern fish fauna of northern Europe, including the Lake Ladoga region (Kudersky 1998). The use of paleolimnological, zoogeographical and population genetic data could throw light on the history of distribution and evolution of coregonid fishes at the edge of the Baltic and White Sea basins.

This research focuses on a genetic comparison of European whitefish populations from adjoining regions in North-West Russia and the origin of sympatric forms of Lake Ladoga whitefish. The aim of the present research is to study the hypothesis of similarity of low-density-rakered whitefish forms from Lake Ladoga with pidschian (*C. l. pidschian*) from northern coastal drainage systems of Russia (Svärdson 1998).

Materials and methods

Samples from four well-distinguished forms (or populations) of Lake Ladoga European whitefish were caught between 1995 and 2002 using different methods (trap-net, gill-net, and angling). The average number of gill rakers was calculated for every sample (Table 1). Two lake forms ("white" — with a white-colored ventral side, and "black" — with a black-spotted ventral side) were caught in the northwestern part of this lake near Konevec island (Fig. 1). The "white" form was identified as the low-density-rakered (LGR) *C. lavaretus ludoga* (mean number of gill rakers = 25.6, range = 22–28), while the "black" form was identified as the medium-density-rakered (MGR) *C. lavaretus mediospinatus* (mean number of gill rakers = 32.1, range = 28–37). (Here, and further in the text, the species designation is according to Pravdin 1954). The other LGR lake form of European whitefish, *C. lavaretus baeri* n. *ladogae*, (mean number of gill rakers = 22.2, range = 20–25), was represented by a sample from the Motornoje fish hatchery. In natural conditions, this form (trivial name is common lake whitefish) usually occurs along the southwestern coast of the lake. The sample of lake-river LGR Volkhovsky form (*C. lavaretus baeri*, mean number of gill rakers = 23.3, range = 21–26) was taken from brood stock at the Sukhodolskoje fish farm. Since the 1920s, when

Table 1. List of populations sampled with their sample size (*n*) and mean number of gill rakers.

Region	Location (form)	*n*	Mean gillraker number
Baltic Sea	L. Ladoga ("Black" whitefish)	41	32.1
	L. Ladoga ("White" whitefish)	44	25.6
	L. Ladoga (Volkhovskij whitefish)	50	23.3
	L. Ladoga (Common whitefish)	20	22.2
	Ladmozero (*C. l. karelicus*)	6	21.2[1]
White Sea	Kandalaksha Bay	23	23.4
	Zimniaja Zolotitsa River	4	29–33[2]
	Severnaja Dvina River	48	23.4[3]
	Mezen' River	2	19–23[3]
Barents Sea	Volonga River	10	23.4
	Pechora River	328	23.1
Kara Sea (Western Siberia)	Severnaja Sos'va River (Ob' River tributary)	199	24.0
	Ob' River lower current	29	24.4

[1] Yu. Sharova, pers. comm.

[2] A. Novoselov, pers. comm.

[3] Koz'min and Shatova 1999.

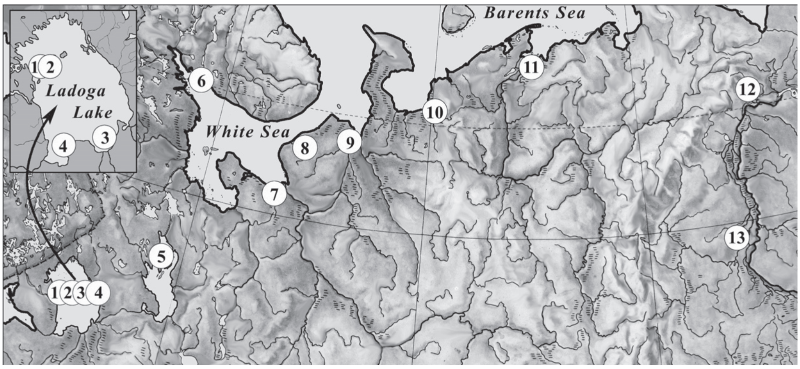

Fig. 1. Sampling sites of whitefish populations. 1. Lake Ladoga, “black”; 2. Lake Ladoga, “white”; 3. Lake Ladoga, Volkhovsky; 4. Lake Ladoga, Common lake; 5. Ladmozero; 6. Kandalaksha Bay of White Sea; 7. Severnaja Dvina River; 8. Zimniaja Zolotitsa River; 9. Mezen’ River; 10. Volonga River; 11. Pechora River; 12. Fellow Channel of the Ob’ River Lower current; 13. Severnaja Sos’va River (Ob’ River tributary).

the main spawning site of this form was dammed in the Volkhov River, the Volkhovsky whitefish persists solely as the result of artificial breeding. At the present time, the Volkhovsky whitefish is a protected species in Russia. The progeny of common lake whitefish and Volkhovsky whitefish were analysed; for hatchery purposes the spawners of these two forms were taken from the southern part of Lake Ladoga (Fig. 1).

The sampling of LGR *C. l. pidschian* was carried out in different locations on the White Sea and its drainage (Severnaja Dvina River, Mezen’ River, Kandalaksha Bay), the Barents Sea drainage (Pechora River, Volonga River) and two sites of the Kara Sea basin of Western Siberia (the Fellow Channel of the Ob’ River lower current and Severnaja Sos’va River — Ob’ River tributary of the middle stream). The sample of MGR European whitefish was taken from Zimniaja Zolotitsa River (White Sea basin) as well as the sample of LGR form of European whitefish (*C. lavaretus karelicus*) from Ladmozero in Karelia (Onezhskoje Lake basin; Table 1).

All samples of muscle and liver tissue were kept frozen before biochemical analysis. Twelve enzyme systems were studied with polyacrylamide gel electrophoresis. The list of enzyme systems and the 29 associated loci are described in Sendek (2002) except the loci *mMEP-1,2** and *sMEP-3,4**. Standard measurements of genetic variability (percentage of polymorphic loci (*P*, 99% criterion) and mean expected heterozygosity (H_{exp})) were calculated with the original program of Swofford and Selander (1981), and a modified version, BIOSYS-2, created by Black (1997). Contingency chi-square analysis was performed on the data from the polymorphic loci for population comparisons. The extent of gene exchange between pairs of populations was evaluated from *F* estimates (Wright 1978). The programs NEIGHBOR and CONSENSE of the PHYLIP3.5C package (Felsenstein 1993) were used to determine confidence of the tree topologies that were constructed from 100 UPGMA trees based on bootstrapped distance matrices.

Results

The average number of gill rakers was calculated for part of the series (Table 1). In every case, their variation corresponded with a normal distribution.

In all analyzed populations, 13 loci were monomorphic: *sAAT-2**, *CK-A1**, *CK-A2**, *GPI-B1**, *GPI-B2**, *sIDHP-3**, *LDH-B1**, *MDH-A2**, *MDH-B2**, *PGDH**, *PGM-4**, *sSOD**, *mSOD**. For European whitefish populations of the Severnaja Sos’va, Pechora and Severnaja Dvina Rivers, allele frequencies had been published earlier (Sendek 2002). The allele frequencies of polymorphic loci for all populations are presented in schematic form in Table 2. Two *LDH-A2** alleles (*LDH-A2*105* and *LDH-A2*137*),

Table 2. Percentage of polymorphic loci (P, 99% criterion), mean expected heterozygosity (H_{exp}) and allele frequencies of polymorphic loci in the studied populations. Uppercase letters are used for alleles with mean frequencies of ≥ 0.1; lowercase letters for alleles with mean frequencies between $0.01 \leq q < 0.1$; lowercase letters in parentheses for alleles with mean frequencies of < 0.01.

Loci	Periglacial races and populations (forms)												
	Baltic Sea race				White-Barents Seas race							Siberian race	
	“White” (L. Ladoga)	“Black” (L. Ladoga)	Volkhovsky (L. Ladoga)	Comm.lake (L. Ladoga)	Ladmozero	Kandalaksha Bay	Severnala Dvina R.	Zimniaja Zolotitsa R.	Mezen’ R.	Volonga R.	Pechora R.	Severnaja Sos’va R.	Lower Ob’ R.
*sAAT-1**	A	A	A	A(0.98)	A	A(0.98)	A	A	A	A	A(0.99)	A(0.99)	A
											(b)		
				c		c							
											(d)	d	
*G3PDH-1**	A(0.99)	A(0.96)	A	A	A	A	A	A	A	A(0.95)	A(0.98)	A(0.99)	A
	c	c									(c)		
		d								d	d	d	
*G3PDH-2**	A(0.89)	A(0.95)	A(0.84)	A(0.88)	A	A	A(0.97)	A	A	A	A(0.98)	A(0.92)	A(0.95)
											d		
	E	e	E	E			e				(e)	e	e
*G3PDH-3**	A	A	A	A	A(0.58)	A(0.97)	A(0.66)	A	A(0.75)	A(0.55)	A	A(0.70)	A(0.50)
	E(0.80)	E(0.84)	E(0.53)	E(0.55)	E	e	E		E	E	E(0.57)	E	E
			f										
			g										
*GPI-A1**				a									
	B	B	B(0.99)	B(0.92)	B	B	B	B	B	B	B	B(0.98)	B
			d									d	
				g									
*GPI-A2**	A(0.89)	A(0.83)	A(0.98)	A(0.95)	A(0.50)	A(0.63)	A		A(0.50)	A(0.75)	A(0.72)	A	A
	B	B	b	b	B	B	B(0.53)	B	B	B	B		
*IDDH-1,2**	A(0.67)	A(0.67)	A(0.65)	A(0.63)	A(0.68)	A(0.73)	A(0.64)	A(0.75)	A(0.75)	A(0.70)	A(0.77)	A(0.76)	A(0.67)
	–	–	C	C	C	C	C	C	C	C	C	C	C
											(d)		
											(e)		
						f	F		F	F	f		
											(g)		
*sIDHP-4**	A(0.83)	A(0.77)	A(0.83)	A(0.97)	A	A(0.97)	A(0.92)	A(0.88)	A	A(0.95)	A(0.96)	A(0.97)	A(0.93)
	b	b	b			b	b	B			b	b	b
	C	c	C	c									
			d								(d)		
	f	f					f			f	f	f	
*LDH-A1**	A(0.97)	A(0.98)	A(0.87)	A(0.93)	A	A	A(0.98)	A(0.75)	A	A(0.95)	A(0.99)	A(0.98)	A
	b						b	B		b	b	b	
	c	c	C	c									

*LDH-A2**	A(0.98) f g	A	A	A	A	A	A	A	A	A	A	A	A
*LDH-B2**	A(0.89) D	A(0.99) d	A	A	A	A	A	A	A	A	A	A	A
*MDH-A1**	A	A	A(0.93) b	A(0.80) B	A	A	A(0.91) b	A	A(0.75) B	A(0.80) B	A(0.78) B	A	A
*MDH-B1**	A(0.99) b	A(0.95) b c	A	A(0.98) b	A(0.92) c	A	A	A	A	A	A(0.98) b (c)	A	A
*PGM-3**	A(0.81) B	A(0.88) B	A(0.94) b	A(0.75) B	A(0.75) B	A(0.79) B	A(0.93) b	A(0.88) B	A(0.75) B	A(0.70) B	A(0.73) B	A B(0.68)	A B(0.66)
*EST-D**	A	A	A	A	A	A(0.98) b	A	A	A	A	A(0.98) b	A	A
P (%)	44.8	37.9	34.5	41.4	17.2	27.6	31.0	17.2	20.7	31.0	44.8	34.5	27.6
H_{exp}	0.091 0.066 (0.027)	0.82 0.075 (0.027)	0.090 (0.031)	0.103 (0.032)	0.074 (0.033)	0.064 (0.027)	0.090 (0.033)	0.062 (0.026)	0.098 (0.041)	0.102 (0.034)	0.092 (0.030)	 (0.026)	 (0.030)
Total allele number	30	29	28	27	20	23	25	19	19	24	37**	25	20

** For Pechora River population the ten alleles with frequencies less than 0.01 are also taken into account.

not previously observed in coregonid fishes, were found in the population of the "white" form of Ladoga whitefish. The phenotypes observed at the loci *IDDH-1,2** in the Pechora River, Severnaja Dvina River and Lake Ladoga populations suggested that *IDDH-1,2** was polymorphic at both loci. The method of Waples (1988) was used to estimate the allele frequencies at each of the loci for all studied populations.

For the most part, the genotype distributions did not deviate from Hardy-Weinberg expectations, except at the locus *PGM-3** in the "white" ($p = 0.024$) and the "black" ($p = 0.047$) Lake Ladoga forms. Some lack of heterozygotes was noted in both series, and is probably an artifact of the limited sample sizes. For the pidschian sampled from the Mezen' and Zimniaja Zolotitsa rivers, as well as for European whitefish taken from Ladmozero, deviations from H-W equilibrium at some loci were related to very small sample sizes (Table 1).

The percentage of polymorphic loci ranged from 34.5% to 44.8% (0.99 criterion) for Lake Ladoga populations. The average index of expected heterozygosity was lowest (0.082) for the "black" form of whitefish and highest (0.103) for LGR lake form (*C. lavaretus baeri* n. *ladogae*; Table 2). Among pidschian populations of the Arctic coast and Siberia, the populations of the Barents Sea demonstrated the highest levels of genetic variability: $P(\%) = 44.8$ in the Pechora River and $H_{exp} = 0.102$ in the Volonga River.

Contingency table analysis of 15 polymorphic loci revealed high genetic differentiation between the four forms of Lake Ladoga European whitefish: eight loci demonstrated significant differences for the samples studied: $p < 0.001$ for *G3PDH-3**; $p < 0.01$ for *GPI-A1**; $p < 0.01$ for *GPI-A2**; $p < 0.01$ for *sIDHP-4**; $p < 0.05$ for *LDH-A1**; $p < 0.001$ for *LDH-B2**; $p < 0.001$ for *MDH-A1**; and $p < 0.01$ for *PGM-3**. In contrast, for two Siberian samples only one out of eleven polymorphic loci were significantly different ($p < 0.001$ for *G3PDH-3**) and, for the seven populations from the White and Barents Seas, five out of thirteen loci were significantly different: $p < 0.001$ for *G3PDH-3**; $p < 0.001$ for *GPI-A2**; $p < 0.001$ for *LDH-A1**; $p < 0.001$ for *MDH-A1**; and $p < 0.01$ for *PGM-3**.

Among Lake Ladoga populations, genetic

Table 3. The values of unbiased genetic distances (Nei 1978) among studied populations (below diagonal) and the levels of *F* (Wright 1978) for within-race populations comparisons (above diagonal).

Population or form	1	2	3	4	5	6	7	8	9	10	11	12	13
1. "White" (Lake Ladoga)	–	0.003	0.016	0.018									
2. "Black" (Lake Ladoga)	0.000	–	0.023	0.026									
3. Volkhovsky (Lake Ladoga)	0.003	0.005	–	0.009									
4. Comm.lake (Lake Ladoga)	0.004	0.006	0.001	–									
5. Ladmozero	0.028	0.029	0.021	0.016	–	0.000	0.047	0.027	0.008	0.040	0.076		
6. Kandalaksha Bay	0.026	0.027	0.019	0.015	0.000	–	0.105	0.027	0.007	0.037	0.072		
7. Zimniaja Zolotitsa River	0.054	0.052	0.049	0.047	0.005	0.013	–	0.075	0.033	0.142	0.173		
8. Severnala Dvina River	0.016	0.015	0.014	0.012	0.002	0.005	0.011	–	0.005	0.016	0.029		
9. Mezen' River	0.010	0.010	0.007	0.003	0.000	0.000	0.001	0.000	–	0.004	0.005		
10. Volonga River	0.007	0.008	0.006	0.004	0.006	0.006	0.027	0.002	0.000	–	0.000		
11. Pechora River	0.008	0.008	0.009	0.006	0.014	0.013	0.033	0.006	0.000	0.000	–		
12. Lower Ob' River	0.012	0.016	0.015	0.008	0.021	0.020	0.056	0.024	0.008	0.006	0.012	–	0.007
13. Severnaja Sos'va River	0.020	0.025	0.020	0.011	0.017	0.016	0.051	0.026	0.006	0.008	0.014	0.001	–

distances (Nei 1978) were highest when the two LGR forms from the southern part of the lake were compared with the "white" and "black" forms of the northwestern coast (D_N = 0.003–0.006). No genetic divergence was found between LGR "white" and MGR "black" forms (D_N = 0.000; Table 3). Pairwise genetic comparisons of the Lake Ladoga forms did not reveal high values of *F* (Wright 1978): 0.003 < *F* < 0.026. The lowest values of this index were found for the pairs *C. lavaretus baeri* & *C. lavaretus baeri* n. *ladogae* (*F* = 0.009) and *C. lavaretus ludoga* & *C. lavaretus mediaspinatus* (*F* = 0.003), as well as for two samples from Siberia (*F* = 0.007), suggesting considerable gene flow between these sympatric populations. The *F* values ranged from 0.000 to 0.173 in pair-wise comparisons among the populations of the White and Barents Sea watersheds. As a rule, the results were in positive correlation with geographical distances between Arctic coastal whitefish populations (Table 3).

When the four forms of European whitefish in Lake Ladoga were compared with populations from the Barents Sea, White Sea, and Siberia, the mean levels of genetic divergence were between 0.016 and 0.018 (Table 4).

The analysis of the distribution of allelic diversity at the polymorphic loci demonstrated that two Siberian populations (total specimens *n* = 227) differed from the White and Barents Sea pool of populations (total specimens *n* = 421) for 12 alleles (including alleles with frequencies < 0.01), and there were 11 alleles in the populations from the White and Barents Seas that were absent in Siberia. Comparing the populations of Lake Ladoga (total specimens *n* = 155) with the populations of the White and Barents Seas, 11 alleles were unique to Lake Ladoga and eight alleles that were present in the White and Barents Seas were not detected among the Lake Ladoga

Table 4. Mean genetic divergence (Nei 1978) between different periglacial races of European whitefish (number of populations in parentheses).

	Baltic (4)	White-Barents (7)
White-Barents (7)	0.018	–
Siberian (2)	0.016	0.020

samples. Comparing the Lake Ladoga populations with Siberian ones, 16 alleles characteristic only to Lake Ladoga and two alleles unique to Siberia were found (Table 2).

Discussion

It has been proposed that a brackish boreal sea extended from the modern Baltic Sea to the White Sea and further eastward during the last interglacial period (60 000–50 000 to 25 000 years ago; Kudersky 1971). The anadromous fishes of the genera *Salmo*, *Salvelinus*, *Coregonus* and others inhabited this sea and its river systems. When the last glaciation (Valday) began, part of the aquatic fauna, including the fishes mentioned above, survived in periglacial refugia, acquiring specific genetic features during the period of long isolation. The reverse spread of aquatic creatures northward began when the ice cover retreated. Some paleolimnological reconstructions show (Kvasov 1975) that periglacial lakes, which extended from the southern part of the Baltic basin to the Ural mountains, were not a united system with a single outlet (as was described by Grosswald 1983).

Because of the absence of paleontological data and contradictions of the paleolimnological schemes, the history of cold water fish distribution from periglacial refugia, as well as detailed mechanisms of the speciation process, must be determined by means of population genetics. Such investigations have been done for many species including North American and European coregonids (Bodaly *et al*. 1992, Bernatchez & Dodson 1994, Bernatchez *et al*. 1999, Douglas *et al*. 1999).

Data on variability in the nuclear genes could answer the questions of the present study: (1) the kind of speciation (sympatric or allopatric) that took place for Lake Ladoga whitefish forms; and (2) if there were several ancestors of the modern forms of this lake, were any of them conspecific to pidschian, which lives along the Arctic coast at the present time?

Genetic relationships between four forms of Lake Ladoga whitefish

According to Pravdin (1954), Lake Ladoga was inhabited by seven ecological forms of European whitefish belonging to *C. lavaretus* (Table 5). All these forms had a spawning season typical for coregonid fishes that spanned from October to December. One MGR lake form and three LGR forms (among them two forms were lake spawning and one, Volkhovsky, was a river spawning form) were the objects of the investigation. Because the Svirsky lake-river whitefish from the southern coastal zone is morphologically and ecologically similar to the Volkhovsky lake-river whitefish from the same location (Pravdin

Table 5. The Lake Ladoga whitefish forms with their mean gill raker numbers, habitat locations, spawning time and places (according to Pravdin 1954). Form names set in boldface were included in the present study.

Latin name	Common name	GR number, mean	Habitat locations in the Lake	Spawning place	Spawning time
C. l. pallasi n. *aspius* Smitt	Vuoksinsky	41-42, HGR	N	Rivers	Oct.
***C. l. mediospinatus* n. *musta-siika* Pravdin**	“Black”	33-34, MGR	N, NW	Lake (rivers, rarely)	Oct.–Dec.
C. l. widegreni Malmgren	Valaamsky	26-27, MGR	N	Lake (deep water)	Nov.–Dec.
***C. l. ludoga* Poljakow**	Ludoga, “White”	23-25, LGR	N (winter) S (summer)	Lake (southern part)	Oct.–Nov.
C. l. baeri* Kessler	Volkhovsky	23-24, LGR	S, SE	Rivers (lake, rarely)	Oct.–Nov.
C. l .baeri n. *Swirensis* Pravdin**	Svirsky	24-25, LGR	S, SE	Rivers	Nov.–Dec.
***C. l. baeri* n. *ladogae* Pravdin**	Common lake	24-25, LGR	W, SW (E, N)	Lake (western part)	Nov.

* Protected species in Russia; exists owing to artificial breeding only.

** Probably extinct because the main spawning grounds in the Svir River were made inaccessible to anadromous fish by dams in the 1940s.

1954), we believe that all the LGR forms in Lake Ladoga were analyzed (moreover, the Svirsky whitefish seems to be extinct because the Svir River was dammed in the 1940s, and its main spawning grounds became inaccessible for anadromous fish).

The primary internal characters for genetic variation among the four Ladoga forms (percent polymorphic loci and mean expected heterozygosity) were not identical, ranging from 34.5 to 44.8, and from 0.082 to 0.103, respectively (Table 2). The data showed that genetic divergence between the samples was quite low ($D_N = 0.000–0.006$).

Nevertheless, it is possible to distinguish two clusters, composed of the "white" and "black" forms in one group (northern) and the common lake whitefish and Volkhovsky forms in the other group (southern). No significant genetic divergence was found within each cluster: $D_N = 0.000$ for the northern "white" and "black" forms; and $D_N = 0.001$ for the two forms in the southern group. Only two of all polymorphic loci demonstrated significant differences in allele frequencies between the two northern samples ($p < 0.05$ for *sIDHP-4** and $p < 0.01$ for *LDH-B2**). Contingency chi-square analysis revealed three such loci ($p < 0.05$ for *GPI-A1**, $p < 0.05$ for *MDH-A1**, $p < 0.01$ for *PGM-3**) in comparisons between the common lake and Volkhovsky forms.

Conversely, the genetic distinctions increased ($D_N = 0.003–0.006$), when the two southern forms were compared with the two northern ones (Table 3). Analogously, eight of the fifteen polymorphic loci were significantly differentiated by allele frequencies when four samples of European whitefish were tested ($p < 0.001$ for *G3PDH-3**, $p < 0.01$ for *GPI-A1**, $p < 0.01$ *for GPI-A2**, $p < 0.01$ for *sIDHP-4**, $p < 0.05$ for *LDH-A1**, $p < 0.001$ for *LDH-B2**, $p < 0.001$ for *MDH-A1**, $p < 0.01$ for *PGM-3**).

The levels of reproductive isolation of each whitefish form from the others could potentially differ. This suggestion could be supported by different F values received from the pairwise comparisons of Lake Ladoga populations. It is not surprising that the lowest values of this parameter were found in pairs that shared the same habitat locations in the lake (and, perhaps, partly spawning sites, too) and were genetically close to each other, namely, *C. lavaretus baeri*–*C. lavaretus baeri* n. *ladogae* (southern group, $F = 0.009$) and *C. lavaretus ludoga*–*C. lavaretus mediaspinatus* (northern group, $F = 0.003$).

Low values for F pairwise comparisons may also serve as evidence of some genetic exchange that could happen between these forms, and the values from other comparisons ranged from 0.016 to 0.026 (Table 3). Nevertheless, the levels of this potential genetic exchange are lower than in the two pairs of forms mentioned above. This viewpoint can be confirmed by some indirect facts: the "black" whitefish was noted several times in the lower current of Svir' River (southern part of the lake); and the common lake whitefish and Volkhovsky whitefish were rarely noted in the northern part of Lake Ladoga, i.e. in typical habitats of the "black" and "white" forms (Pravdin 1954).

On the other hand, it was shown for Baikal sculpins (*Cottidae*) and Laurentian Great Lakes ciscoes that geographic separation, which is due to the large size of these lakes, is a significant barrier to gene flow among the localized populations (Smith & Todd 1984). Consequently, the amount of introgression among whitefish populations is negatively correlated to the size of the water body they inhabit (Svärdson 1998). Lake Ladoga is the largest lake in Europe and its impressive geographic characteristics (area 17 700 km^2, maximum depth 230 m, mean depth 51 m) indicate that there are numerous ecological niches. Thus, in spite of the small values of the F-statistics that were revealed for the studied samples (mean $F = 0.025$ for Lake Ladoga), intensive introgression of sympatric populations would be unlikely to occur.

Thus, the data on genetic relationships of the European whitefish forms in Lake Ladoga serve as the evidence of their disunity. However, relatively low genetic differences between the three LGR forms and one MGR form could support the hypothesis for a sympatric origin for the Lake Ladoga forms.

Genetic relationships between *C. l. pidschian* populations

Kvasov (1975) showed that periglacial lakes of the drainages of the Barents and White Seas were part of the same watershed from 17 000 to

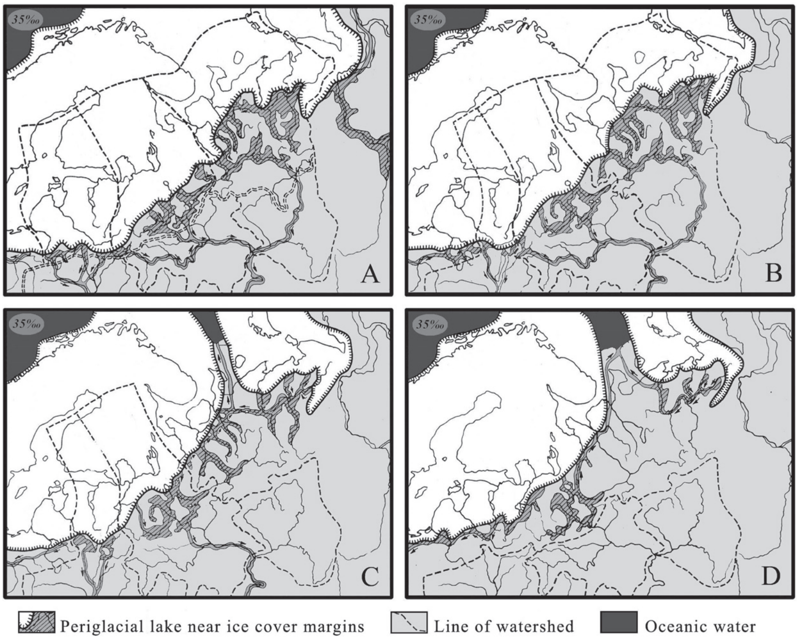

Fig. 2. Periglacial lakes of East Europe (from Kvasov 1975). — **A**: 17 000 BP; — **B**: 16 000 BP; — **C**: 15 000 BP; — **D**: 14 000 BP.

15 000 years ago (Fig. 2). During this 2000 year interval, the isolated population of pidschian in this system could have acquired some specific genetic features by natural selection, founder's effect or genetic drift, which would distinguish it from neighboring Baltic and Siberian populations. That is why the populations of pidschian from the Pechora River, Volonga River, Severnaja Dvina River, Zimniaja Zolotitsa River, Mezen' River and Kandalaksha Bay could be considered as the White–Barents Sea (East-European) refugial race, which differs from Baltic and Siberian ones (Sendek 2000). The low values of genetic divergence revealed for these populations (D_N = 0.000–0.0013, excluding the population from the Zimniaja Zolotitsa River that stands somewhat apart) indicate their common origin. Perhaps, the LGR form of European whitefish from Ladmozero in Karelia (*C. l. karelicus*), which is typical for the northern part of the Lake Onega basin, also originated from an ancestor in the East-European refuge: *C. l. karelicus* is genetically more closely related to *C. l. pidschian* populations than with Lake Ladoga populations (Table 3). The explanation of this phenomenon could come from the specific geographical disposition of Lake Onega, which is situated very close to the watershed between the Baltic and White Seas, and the habitat of *C. l. karelicus* that is near the border between the two basins. Moreover, the Svir' River, which linked Lake Onega with Lake Ladoga (and, consequently, with the Baltic basin), arose not earlier than 11 800 years ago (Kvasov 1975).

The common origin of seven whitefish populations from the White and Barents Sea basins (including the Karelian Ladmozero population) was also confirmed by the contingency chi-square analysis data for polymorphic loci — only five out of thirteen loci demonstrated significant differences in the gene frequencies. This is not much if one takes into account the considerable geographic separation of these populations — more than 1 000 km between the most distant populations in the Pechora River and Kandalaksha Bay of the White Sea (Fig. 1).

The pairwise comparisons of these seven populations revealed low values of F (from 0.000 to 0.173; Table 3). These data also support a common origin of these populations from a single refugial race. It should be noted that the F values reflect the distances between coastal LGR whitefish populations of the White and Barents Seas (excluding the MGR population of the Zimniaja Zolotitsa River). This fact supports the idea about genetic exchange that could occur between river populations of the White and Barents basins, and the levels of such exchange are larger between neighbouring populations. It is known that anadromous whitefish could use brackish or salt water for feeding migrations. Some straying between coastal populations may take place during these migrations via brackish waters, which exist along sea coasts near estuaries of rivers. A similar phenomenon exists along the Arctic coast of Siberia because of the outfall of the great Siberian rivers into polar seas (Pirozhnikov 1967). Perhaps, owing to considerable straying between neighbouring populations, no significant genetic divergences were revealed for different anadromous coregonid species (including *C. lavaretus pidschian*) from West and East Siberia (Ermolenko 1992, Politov 2002, Sendek 2002).

The considerable genetic divergence revealed between the MGR population of Zimniaja Zolotitsa River and other pidschian populations could appear to be the result of the specialization of the first one. In contrast to anadromous pidschian populations, which were sampled downstream in the rivers or even in salt water (e.g., Kandalaksha Bay of the White Sea), the population of the Zimniaja Zolotitsa River is a fresh water river population (the fish were caught about 100 km up from the mouth of river). Owing to its isolation, the evolution of this MGR population proceeded without the influence of introgression from the nearest pidschian populations (Mezen' River to the east, Severnaja Dvina River to the west). Nevertheless, the origin of the MGR population in the Zimniaja Zolotitsa River (in fact, this is the most eastern population of MGR whitefish in Europe) should be connected with the White–Barents Sea refugial race because it doesn't share any special alleles, which is atypical for other populations of the same race (*see* below). Moreover, the genetic distinctness between the Zimniaja Zolotitsa River population and a potential donor population of the Baltic refugial race (the MGR "black" form from Lake Ladoga, for instance) is very high (Table 3).

The two pidschian populations from West Siberia are derived from a Siberian refugial race. Because the populations from the Severnaja Sos'va River and from the downstream Fellow Channel of the Ob' River represent the same river system, the genetic divergence between them was minimal, $D_N = 0.001$ (Table 3); only one of eleven polymorphic loci was significantly different ($p < 0.001$ for *G3PDH-3**). The mean genetic distance between the two Siberian populations and seven populations of the East-European refugial race was $D_N = 0.020$ (Table 4).

Genetic divergence between populations of different periglacial races

Based on extensive morphological and ecological investigations of whitefish populations from the north-western part of Russia, I. F. Pravdin (1954) pointed out that populations from the White and Barents Seas took an intermediate position between typical European whitefish, *C. l. lavaretus*, from the Baltic Sea basin and typical Siberian pidschian, *C. l. pidschian*. He even proposed to distinguish whitefish of the White and Barents Seas type with a special name *C. l. pidschianoides* (that is a synonym of *C. l. pidschian* n. *pidschianoides* by Berg (1948) given for whitefish from the same region).

From Svärdson's (1998) point of view, it was a pidschian from the White Sea region (originating from the East-European race, according to our data) that migrated from the fresh or brackish waters of the White Sea into Lake Ancylus around 9500 BP and could be the ancestral "storsik" found in northern Sweden and Finland. Their subsequent distribution from the great Lake Saimaa complex led to their occupation of vacant niches in Lake Ladoga. The same route of dispersal was proposed for *C. sardinella* (Svärdson 1998). In such a case, some genetic similarity of LGR Ladoga whitefishes and pidschian of the White–Barents Sea region should be expected.

Genetic relationships (Nei 1978) between the studied populations are presented in Table 3. An UPGMA dendrogram (Fig. 3), constructed from the distance matrix, shows the aggregation of 13 populations into three pooled clusters which are complimentary to three sources of origin: Baltic periglacial race (four populations); White–Barents Sea race (six populations); and Siberian race (two populations). The mean genetic distances between them were roughly equal. It should be emphasized, however, that the position of most

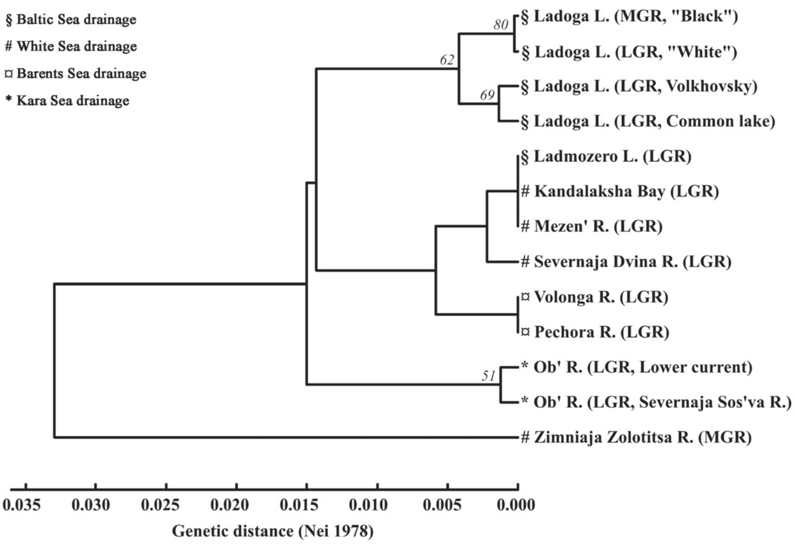

Fig. 3. UPGMA denrogram (Nei 1978) of unbiased genetic distances for studied populations.

of the branches was not supported by bootstrap values.

The levels of pairwise genetic divergence between four Ladoga forms and East-European pidschian populations averaged $D_N = 0.018$ (Table 4). Similar distances were noted between Lake Ladoga whitefish populations and Siberian pidschian ($D_N = 0.016$).

It should be noted, however, that there are at least two important facts that were not reflected in the dendrogram: two Lake Ladoga forms of the southern group (*C. lavaretus baeri* and *C. lavaretus baeri* n. *ladogae*) were genetically more closely connected to pidschian populations of the White and Barents Seas (Table 3). Moreover, the levels of genetic difference were quite low when whitefish forms of Ladoga were compared with the two Barents Sea populations (D_N = 0.004–0.009). It is especially difficult to explain the last fact taking into consideration the Pleistocene paleolimnological history of these geographically separated regions.

An additional cluster on the dendrogram was formed by the MGR population of Zimniaja Zolotitsa River. The considerable differentiation of this MGR population from the other populations of the East-European race is probably explained by its geographic isolation. However, the level of MGR population distinctness from other populations is very high and is probably due to chance selection from the small sample size of the Zimniaja Zolotitsa River population, at least in part. Genetic distance by itself could not prove the validity of similarities between pidschian populations from an East-European refugium and the four Lake Ladoga populations.

Analysis of allelic diversity

The greatest allelic diversity among populations of the White and Barents Seas was noted in the population of Pechora River pidschian (Table 2). This may be partly due to the greater quantity of samples from this location (n = 328) as compared with those of other populations from the White and Barents Sea basins. It is interesting to note, however, that there are 11 electrophoretic variants in the Pechora River population (12, if all the analyzed populations from the White–Barents region (n = 421) are considered) that are absent in the two Siberian populations of Ob' River (n = 227), and only one allele from the Ob' pidschian populations (*GPI-A1*d*) is absent in the East-European populations of *C. l. pidschian*. These observations could be explained by the penetration of the Siberian refugial race into Europe and its introgression with the native race of European whitefish. At the same time, a reciprocal transfer of genetic material was impossible because of spacial-temporal circumstances during the period of global rearrange-

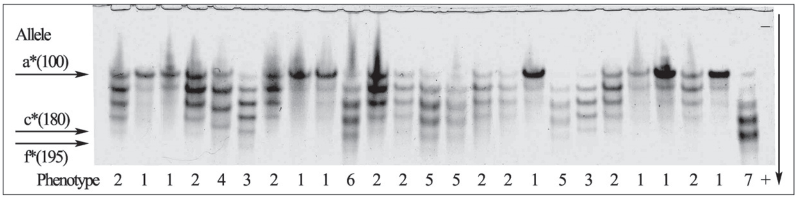

Fig. 4. Pattern of *IDDH-1,2** isozymes in pidschian population from Severnaja Dvina. Phenotype designations: 1. a/a/a/a/; 2. a/a/a/c; 3. a/a/c/c; 4. a/a/a/f; 5. a/a/c/f; 6. a/c/c/f; 7. a/c/f/f/.

ment of river drainages of the late Quaternary epoch. If such an exchange between the Siberian and European faunas did not take place, the populations of European whitefish disposed on both sides of the Ural mountains should differ by more alleles; according to our data their number theoretically could be 24 (12 alleles × 2 regions). Therefore, it was not surprising that the proportion of the distinct alleles turned to be 16 to 2 in favour of Baltic periglacial race when the four Lake Ladoga populations were compared with the two Siberian ones (Table 2).

Each of the four Lake Ladoga whitefish forms differed approximately equally from the pool of seven populations of the East-European refugial race by a number of exclusive alleles (17 alleles for the "black" form, 19 alleles for the common lake form, 20 alleles for the "white" form, and 22 alleles for the Volkhovsky whitefish). This order would change just slightly if Ladoga samples were compared with the two Barents Sea populations (16 alleles for the "black" form, 19 alleles for the "white" form, 20 alleles for the common lake form, and 21 alleles for the Volkhovsky whitefish). Thus, the close similarity between the southern group of Lake Ladoga forms and pidschian populations of the Barents Sea, suggested by genetic distances, was not supported by allelic distribution data.

The comparison of the four Lake Ladoga populations (n = 155) with populations of the White and Barents Seas drainage (n = 421) revealed eleven alleles that were characteristic only for Lake Ladoga, and eight exclusive alleles for seven populations in the White and Barents Seas. This proportion would look like "Lake Ladoga (11) : White and Barents Seas (9)" if only the LGR populations were considered (three from Lake Ladoga and six from the East-European race). If the data on allelic diversity for populations from both sides of the Ural mountains are considered, the present observation is evidence of comparative genetic disunity of Arctic coastal populations of *C. l. pidschian* and Lake Ladoga whitefish populations.

It is particularly remarkable that allele *IDDH-2*f* (which is not known for any other coregonids) is not only widely distributed in the populations of the White–Barents Sea region, but in some cases has a frequency > 0.1 (Fig. 4). This means, considering selective neutrality for this allele and the possibility of penetration of pidschian into Lake Ladoga, that the presence of this electrophoretic variant should be expected at least in LGR forms. However, it was not observed.

From the other side, the marker alleles *LDH-A1*c* and *IDHP-4*c*, which are typical for each of the four Lake Ladoga whitefish forms and are not present in the populations of the East-European periglacial race, were found previously in whitefish of the western parts of the Baltic (Vuorinen & Piironen 1984, Bodaly *et al.* 1991).

The distribution of alleles in the studied area is similar to a comparative analysis of the fish fauna of Siberia and northern part of European Russia. It was demonstrated that among 19 species of Siberia (in particular the families *Coregonidae*, *Thymallidae* and *Salmonidae*), 13 inhabit the White Sea and Barents Sea as well, but only three of them inhabit the Baltic drainage. There are ten fish species of these families that are common to both the Baltic and White–Barents Sea drainages (Kudersky 1987). Thus, according to all these facts, Lake Ladoga was populated by coregonids from the west rather than from the east. The same conclusion was made earlier based on studies of two closely related species of cisco, *C. albula* and *C. sardinella* (Sendek 2000, 2002).

The origin of whitefish forms in Lake Ladoga

It was shown from paleolimnological investigations that periglacial lakes, which shifted to a depression at Lake Ladoga, developed independently for a long time from those periglacial lakes that moved to a depression at Lake Onega. A water outlet from the first group of lakes went westward and southward, while a outlet from the second chain of lakes went mainly to the Volga River basin (Kvasov 1975, Anon 1990). These phenomena caused some differences in the cold water fish fauna of lakes Ladoga and Onega: four-horned sculpins (*Triglopsis quadricornis lönnbergi*) from the two lakes diverged so much that they were described as two subspecies (Berg 1949); morphological and ecological differences exist between lake chars (*Salvelinus lepechini*) and the forms of large vendace *(Coregonus albula*), e.g. ripus (Lake Ladoga) and kiletz (Lake Onega). As for the *C. lavaretus* complex, thirteen forms of this species populate Lake Onega and its basin, while only seven forms were described in Lake Ladoga (Pravdin 1954). Such a disproportion probably could be explained by populating Lake Onega with two sources of whitefish such as the Baltic Sea basin and White Sea basin. If such a scenario is right, the forms conspecific to *C. l. pidschian* of the White and Barents Seas could be found among the other six forms of LGR (besides *C. l. karelicus*, which was an object of the present study).

It is very probable that the coregonid fauna of Lake Ladoga is quite old. Palynological analysis has shown that the salty waters of the Yoldia and Litorinia Seas did not penetrate into the Ladoga basin (Abramova *et al*. 1967). That is why reproductively isolated European whitefish and vendace populations (with origins from a Baltic periglacial lake) could live there constantly since Lake Ladoga was isolated about 9800 BP (Kvasov 1975).

From the data available, we could not conclude exactly what form of speciation within the Baltic basin (allopatric or sympatric) had led to the existence of numerous whitefish forms in Lake Ladoga at the present time. If we accept the hypothesis of an allopatric origin for the four examined forms of European whitefish, they could have originated from LGR and MGR ancestors from a Baltic periglacial lake, i.e. *C. holsatus* and *C. lavaretus* (designations according to Theinemann 1922, Svärdson 1998), respectively. Indeed, according to Svärdson (1998), these two species live sympatrically in the south-eastern Baltic (including Lake Ladoga). However, the low genetic divergence between LGR and MGR forms of Ladoga strongly refutes this point of view or perhaps reflects the consequences of introgression between *C. holsatus* and *C. lavaretus*.

Mitochondrial DNA analysis of European populations of European whitefish demonstrated that the whitefish populations of North and Central Europe belong to two distinct phylogenetic lineages, which probably evolved allopatrically. Moreover, any congruence was found between phenotypic and genotypic variation in whitefish (Bernatchez & Dodson 1994). The low values of allozyme distances revealed between the studied forms of Lake Ladoga whitefish strongly supported the idea that the populations with different gill raker numbers represented only one of these lineages. The evolution of these forms, which started about 10 000 years ago, could have happened according to the “species flocks” scheme (Smith & Todd 1984, Douglas *et al*. 1999). According to this model, various forms arose from a within-lake radiation of a single ancestral lineage; these forms represent distinct gene pools, and the morphological and ecological differences among them are not a product of phenotypic plasticity. Although the allozyme method is less sensitive than the microsatellite markers that were applied for the central Alpine *C. lavaretus* populations (Douglas *et al*. 1999), some of the genetic disunity observed among whitefish populations of Ladoga by isozymes could support the same hypothesis.

Allozyme markers could give some information on the real routes of whitefish colonization of Europe. Thus, the discovery of an exclusive allele, *IDDH-1*f*, in the low-density-rakered form “storsik” from the lakes of northern Sweden and Finland could confirm the hypothesis of an eastern origin for this form of European whitefish. The absence of *CK-A1*d* (which is typical for least cisco from Siberia) in the populations located westwards from the borderline of the natural ranges of Siberian species (peled, broad whitefish, arctic cisco) could also indicate the colonization of Eastern Europe by least cisco not earlier then 14 000 BP, at a time when the common periglacial drainages of Severnaja Dvina, Mezen' and Pechora disappeared and penetration of late Siberian colonists from the Pechora River basin further westward became impossible.

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