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THEORETICAL PAPERS
AND REVIEWS

Dispersal Routes and Species Identification of Freshwater Animals in Northern Europe: A Review of Molecular Evidence

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Abstract—According to genetic data, North European freshwater areas were colonized from refugia along the eastern Atlantic coast, in southern and eastern basins of Baltic Sea, in Siberia, North America, and areas of the Caspian and Black seas. Probably, a refugium also existed in Southern Norway. Colonization from the sea also took place. The taxonomic position of some forms, such as members of the complex groups of Arctic chars and coregonids, was refined in the course of combined studies including morphological analysis and molecular markers.

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Genogeography was founded more than 70 years ago [1, 2]. Since then, not only molecular markers have appeared, but also theoretical concepts of population genetics have been developed. It became obvious that the processes of speciation may differ dramatically from processes occurring in populations [3]. Scientists face the problem of "separating population structure from population history" [4]. A new field of research, phylogeography, was established, which deals with the history of emergence of populations and species [5].

At present, reviews on colonization of Europe by various species [6–8] and on Arctic phylogeography [9] are available. In this article, we summarize the results of molecular studies on the routes of colonization of North European freshwater bodies and identification of species inhabiting these bodies.

These studies are of considerable theoretical and practical importance. Many species of northern water bodies are involved in aquaculture, and breeding programs require knowledge of their gene pools. Many forms are on the brink of extinction, and their species attribution is necessary for their salvation. It is necessary to find out the causes and predict invasions, in particular, parasite invasions [10].

The results of faunistic (review in [11]) and parasitological (review in [12]) studies of aquatic animals in northern Europe provide reliable grounds for genetic studies. The long-term work of experts in systematics and fauna has been compiled into *Guide to Freshwater Fishes of Russia* [13] and the voluminous *Key to Freshwater Invertebrates of Russia* [14, 15]. These books provide the bulk of information on the occurrence and systematics of aquatic animals. Other publications will be referred to in the text. However, many theoretical and practical problems could not be solved by conventional methods.

In this study, we consciously avoided consideration of paleogeographical reconstructions, because these are controversial, ranging from complete absence of continental glaciations to a huge glacial "cap" covering the northern part of the globe [16–20]. However, there is no doubt that the history of northern Europe includes significant coolings, as confirmed by pollen fossil analysis. Apparently, the freshwater fauna became depauperated or completely extinct during these periods.

Also, we leave aside the deduction of the time of divergence between phylogenetic lineages from genetic data. Such conclusions are only possible in the framework of the molecular clock notion, which is derived from the neutral theory. However, neither the neutral theory nor the existence of the molecular clock has been experimentally confirmed, (see review in [21]). In particular, a rapid rearrangement of the genetic structure of populations is observed in the case of one of the objects of our analysis, Atlantic salmon (for review, see [22]).

Because of space limitations, we only briefly present genogeographic data for some aquatic animals. Data on molecular markers used are presented in Table 1. In Conclusions, we summarize these data and attempt to determine the locations of refugia and major routes of dispersal of freshwater fish and invertebrate species in northern Europe.

FISHES

Sturgeons, Genus Acipenser

Atlantic sturgeon, *Acipenser sturio* Linnaeus, is widespread in Europe. It is occasionally found even in

Table 1. Methods used in genogeographic studies of freshwater animals of northern Europe

Genus, species	Markers	Reference
Acipenser	Sequencing of the D-loop (mtDNA) and the region flanking microsatellite loci Aox-23	[23]
Salmo salar	ALL	[24–32]
	PCR–RFLP *ND-1* and *16S rRNA* (mtDNA)	[33–35]
	Microsatellites, PCR–RFLP of major histocompatibility complex genes	[36]
	ALL, PCR-RFLP *ND-1* (mtDNA)	[37, 38]
	PCR-RFLP of the gene coding for growth hormone (GH1)	[39]
	Sequencing of the gene coding for growth hormone (GH1)	[40]
	Microsatellites, ALL, PCR–RFLP *ND-1*, and *16S rRNA* (mtDNA)	[41]
	Microsatellites	[42]
Salmo trutta	ALL	[43–46]
	ALL, sequencing of the D-loop, PCR–RFLP of the D-loop, *ND-5/6*, and *CO* (mtDNA)	[47, 48]
	Sequencing and PCR-RFLP D-loop, *ND-5/6* and *CO* (mtDNA)	[49]
	Sequencing of rRNA ITS	[50]
Salvelinus alpinus	ALL	[51–54]
	Microsatellites	[55, 56]
	Sequencing of the D-loop (mtDNA)	[57]
Coregonus albula, C. sardinella	ALL	[58–64]
	ALL, PCR-RFLP of the D-loop, and *ND-1* (mtDNA)	[65]
	Partial sequencing of *ND-3* and the D-loop (mtDNA)	[66]
Coregonus	Partial sequencing the D-loop (mtDNA)	[67]
Coregonus lavaretus	DNA hybridization	[68]
	ALL	[62, 69–72]
	PCR-RFLP of mtDNA	[73]
	PCR-RFLP of *ND-1* and *ND-5/6* (mtDNA), microsatellites	[74]
	Conformational polymorphism of the *CO* and *ND-3* genes (mtDNA)	[75]
	Microsatellites	[76]
Stenodus leucichthys	ALL, RAPD	[77]
Thymallus	ALL	[78]
	PCR-RFLP of mtDNA	[79, 80]
	Microsatellites	[81]
Osmerus	ALL	[82]
Osmerus eperlanus	PCR-RFLP of mtDNA	[83]
Esox lucius	Sequencing of the D-loop (mtDNA)	[84]
	Microsatellites	[85]
Anguilla	ALL	[86]
	ALL, PCR-RFLP of mtDNA	[87]
	Microsatellites	[88]
	Amplified fragment length polymorphism (AFLP)	[89]
Leuciscus cephalus	Sequencing of *CYTb* (mtDNA)	[90]
Cobitis taenia	Sequencing of *CYTb* (mtDNA)	[91]
Lota lota	Sequencing of *CYTb* (mtDNA)	[92]
	Partial sequencing of the D-loop (mtDNA)	[93]
Perca fluviatilis	Sequencing of the D-loop (mtDNA)	[94]

Table 1. (Contd.)

Genus, species	Markers	Reference
Cottus gobio	ALL, PCR-RFLP, or sequencing of the D-loop (mtDNA)	[95, 96]
	Sequencing of the D-loop (mtDNA)	[97]
Cottus poecilopus	Sequencing of the D-loop and genes for *CYTb*, ATPase6, and ATPase8 (mtDNA)	[98]
Triglopsis quadricornis	ALL	[99, 100]
	Sequencing of genes CYTb, ATPase6, and ATPase8 (mtDNA)	[101]
Gyrodactylus	Sequencing of rRNA ITS and the V4 domain of the gene for the small rRNA subunit	[102]
	Sequencing of spacers between genes for rRNA	[103, 104]
	Sequencing of the gene for *COI* (mtDNA)	[105, 106]
	Sequencing of rRNA ITS	[107]
	Sequencing of the gene for *COI* (mtDNA) and rRNA ITS	[108]
Mysis	ALL	[109, 110]
	ALL, partial sequencing of the gene for *COI* (mtDNA)	[111]
	ALL, partial sequencing of genes for *COI*, *16S*, *CYTb* (mtDNA), ITSI, 18S	[112]
Gammaracanthus	ALL, partial sequencing of the gene for *COI* (mtDNA)	[113]
Gammarus lacustris	ALL	[114]
Pontoporeia	ALL	[115]
Daphnia	PCR-RFLP of mtDNA, RAPD	[116]
Daphnia pulex	ALL	[117]
	PCR-RFLP of genes for *ND-4* and *ND-5* (mtDNA)	[118]
Daphnia magna	Partial sequencing of the gene for *COI* (mtDNA)	[119]
Margaritifera	ALL, partial sequencing of the gene for *COI* and *16S* (mtDNA)	[120]

Note: ALL, allozymes; mtDNA, mitochondrial DNA; *CYTb*, gene for cytochrome b; *CO*, gene for cytochrome oxidase; *COI*, gene for cytochrome oxidase subunit 1; *ND*, gene for NADH dehydrogenase; PCR-RFLP, restriction fragment length polymorphism; rRNA ITS, inner transcribed spacer of the gene for rRNA; RAPD, polymerase chain reaction with random primers.

the White Sea. Siberian sturgeon *A. baeri* Brandt occurs, though uncommonly, in the Pechora River. However, study of DNA from fossil sturgeon bones shows that in the period from 1200 to 800 years ago, Atlantic surgeon in the Baltic Sea basin was replaced by another species, *A. oxyrinchus* Mitchill, formerly believed to occur only in North America [23].

Atlantic Salmon, Salmo salar Linnaeus

This species is widespread in Western and Northern Europe, including the British Isles and Iceland, and on the northeastern coast of North America. The populations are dominated by the anadromous form, whereas the resident form is scarce.

Analysis of genetic markers reveals differences, including qualitative ones, between populations of the European Atlantic coast and the Baltic Sea basin. These differences are likely to have been caused by dispersal from different refugia [24, 28, 33, 34, 39, 41]. It is conjectured that the Atlantic refugium occurred near the British Isles [32].

Genetic differences were found between populations of the northwestern and southeastern parts of the Baltic area, although the boundaries of these parts are fuzzy [31, 32, 42]. The northwestern salmon populations are similar to those of the Atlantic coast, probably, being derived from them [31, 33, 36, 42].

An alternative or additional hypothesis assumes colonization of the northwestern Baltic Sea from the northern part of the White Sea basin [34]. However, this seems unlikely, because the Baltic populations are virtually devoid of the ESTD* allele, common in the northern White Sea area, as indicated below. This allele is present in the population of Lake Kuito, located on the path of the conjectured dispersal [41]. The occasional findings of this allele in the Baltic Sea are related to the introduction of fish from Canada to a Sweden river [28, 121].

Apparently, the southeastern salmon populations are represented by the progeny of fish that survived the glaciation in a separate refugium [31, 34, 36, 39]. According to simple sequence repeat (microsatellites) analysis, the southeastern group of populations can be subdivided into two, probably originating from refugia in the southern and eastern parts of the Baltic area [42]. We will refer to these refugia as South-Baltic and Eastern.

Qualitative genetic difference is also observed between northwestern and southeastern populations in the Arctic Ocean basin as well. As in the Baltic Sea, the southeastern populations are likely to include the progeny of fish from the Eastern refugium [25–27, 35, 38].

The issue of the location of this refugium is controversial. Some authors [35] place it in hypothetical "Komi Lake" in the basin of the modern Pechora River, because the haplotype tagging the Eastern refugium is fixed in the populations of this region. However, glacial lakes are not a convenient habitat for Atlantic salmon [122].

Moreover, it is presently known that the haplotype tagging the Eastern refugium is also fixed in the population of the Onega River (southern White Sea basin). This population was connected with the Baltic basin system several thousand years ago [38]. Therefore, it is reasonable to suggest that the Atlantic salmon came to the White Sea area and then the Pechora from a refugium in the eastern Baltic basin, through Onega Lake and the Onega River. This suggestion agrees with all available genetic data. Similar dispersal routes is assumed for some other species.

For example, two groups of brown trout populations are identified in the White Sea basin (see next section). The boundaries of the occurrence of the groups of Atlantic salmon and brown trout are very close. Probably, the refugia of both species were located in the same areas. At present, no brown trout occurs in the Pechora basin [123], and there is no evidence that it occurred there in colder times.

Northwestern populations (Kola Peninsula and adjacent areas), as well as northwestern Baltic populations, are similar to the Atlantic ones, their putative ancestors [30, 35, 38]. However the ESTD* allele commonly occurring in the Kola Peninsula is the same as the allele almost fixed in North American populations [28, 29]. Populations of the Kola Peninsula and northern Norway also contain mtDNA haplotypes typical of North American [33, 35, 38]. Taken together, these facts indicate that salmon from North America colonized the Kola Peninsula either before or synchronously with colonization from the East Atlantic Ocean [35, 37, 38].

This viewpoint is additionally confirmed by the fact that populations of the Teno and Pechora Rivers have a growth hormone allele differing in a single mutation from the allele typical of North American populations [40]. Note that the presence of the American allele in the Pechora is in poor agreement with the suggestion of a salmon refugium in this region.

A wide zone of introgressive hybridization in northern Europe hampers discrimination between the European and American salmon forms, and does not allow them to be considered different species, as opposed to Kottelat's opinion [124].

Brown Trout, Salmo trutta Linnaeus

This species occurs in Europe, Northern Africa, and Southeastern Asia. Being very plastic, it includes numerous ecotypes and forms. The subspecies *Salmo trutta trutta* occurs in Western and Northern Europe, including the British Isles and Iceland.

This form has qualitative genetic features, discriminating it from others. It bears an endemic clade of haplotypes and several specific alleles of protein-encoding genes. However, these alleles are occasionally detected in southern brown trout populations, probably, as a result of spreading. The EST-2* allele, probably identical to that widespread in Caspian populations, has been found in the population of Lake Bunnersjoarna, Sweden [48]. However, there is evidence for introduction of brown trout of unknown origin into this lake [125]. This may be fish from Poland, grown in Sweden and characterized by the same rare LDH-1* allele found in Lake Bunnersjoarna [126].

Indeed, Polish populations were shown to contain genotypes typical of southern brown trout populations [50]. Their origin in this region is unknown. Some authors suppose recent dispersal of the species from south to northern Europe [44]. However, no populations with "southern" genotypes have been found in the reconstructed dispersal paths [127]. In our opinion, there was a brown trout refugium in southern areas of the Baltic basin. Presence of a refugium in this region is proposed for Atlantic salmon (see above) and other species (see below).

The genetic diversity of brown trout is indicative of colonization of northern Europe from at least two more refugia [43, 48, 49]. Their location is not known with certainty. Analysis of the prevalence of alleles of isoloci sAAT-1.2* points to location of the refugia on the Atlantic coast and in the eastern Baltic basin. The latter refugium was the source of colonization of the southern White Sea basin, and the former, of Norway, the Kola Peninsula, and the western Baltic basin [45, 46].

Arctic Chars, Genus Salvelinus

Arctic char, *Salvelinus alpinus* (Linnaeus), occurs throughout the coast of the Arctic Ocean, in rivers and lakes. It can come to the sea for feeding. Numerous forms of unknown systematics occur in southern regions. In particular, large lakes of Fennoscandia are inhabited by lake char, *S. lepechini* (Gmelin).

According to studies of ecology and genetics of chars, three species were identified in Northern Europe: *S. alpinus*, *S. stagnalis*, and *S. salvelinus* [51]. However, further studies showed that these forms had no qualitative genetic differences, and thus could not be regarded as different species [52].

Several char forms inhabit Thingvallavatn Lake, Iceland. They have ecological, morphological, and, to a lesser extent, genetic differences [53]. The authors who described these forms did not recognize them to be different species, but Kottelat, did that in his survey [124]. He substantiated the establishment of the Iceland species solely by the fact that he could not compare them with other numerous char forms.

The analysis of the genetic diversity of Arctic char throughout its area suggests that Iceland was colonized by it from both Europe and North America [54]. Haplotypes belonging to the same clade as those occurring in Siberia were detected in populations of Spitzbergen and Kuolimo Lake (basin of Saimaa Lake), although other European regions are inhabited by a genetically different char form [57].

The diversity of microsatellites loci has been studied in the Arctic char forms of Northwestern Europe [56], Scandinavia and Finland [55], and Karelia (unpublished data from the Laboratory of Population Genetics, Vavilov Institute of General Genetics, Russian Academy of Sciences, and the Northern Research Institute of Fishery, Petrozavodsk State University). Microsatellites allow differentiation of some populations, but the level of differentiation between the regions is low.

Vendace and Least Cisco, Genus Coregonus

Here we consider two related *Coregonus* species: vendace *Coregonus albula* (Linnaeus) and least cisco *C. sardinella* Valenciennes. The former inhabits lakes in the basin areas of the North, Baltic, White, and Barents seas and in the upper Volga River. Least cisco has both anadromous and lacustrine forms. It is common in North America and Siberia. Its range is spread to the west up to the White Sea. Ranges of both species overlap in the Pechora River basin.

However, there are alternative views on their systematics and occurrence. For example, the fish of Vodlozero Lake (basin system of Onega Lake) was considered to be a subspecies of vendace [128], and the form of Beloe Lake in the upper Volga, as a subspecies of least cisco [129]. In Pokrovskii's opinion, the forms of both lakes belong to *C. sardinella* [130]. Genetic analysis confirms the overlap of the ranges and hybridization of the two species in the Pechora basin [61, 62]. It also points to the hybrid origin of the fish of Beloe [63, 64] and Vodlozero [65] lakes.

Recent studies have revealed mtDNA variants differing from the haplotypes of both species in the fish population from the Elbe basin area, in addition to haplotypes typical of vendace [66]. These may be ancient haplotypes inherited by vendace populations from the common ancestors of the species. Alternatively, they may be indicative of penetration of least cisco to the North Sea basin.

Large forms from Onega and Ladoga lakes were also suggested to belong to least cisco [131]. The large form from Ladoga Lake was even considered to be an endemic species [132]. However, these suggestions were not confirmed by genetic studies. No alleles typical of least cisco were found in populations of either lake. The large and small forms in both lakes proved to be genetically similar [59, 60].

One individual of the large Ladoga form had a haplotype differing from that typical of vendace but similar to those typical of omul *C. autumnalis* (Pallas) and similar North American forms [67]. This fish was caught in a Polish lake, where vendace had been introduced. However, proof of this interesting fact requires study of a larger number of individuals, including those from the original population.

The spring-spawning form from Fennoscandian lakes was described as a distinct species, *C. trybomi* [131]. However, there is genetic evidence for independent formation of spring-spawning populations in various parts of the vendace area [58, 66]. Therefore, recognition of such populations as isolated species is not substantiated.

Whitefish, Coregonus lavaretus (Linnaeus)

Whitefish is common in the Russian regions of the Arctic Ocean basin. It occurs in the basin areas of the Baltic and North seas. A close form occurs in North America. The species is divided into numerous ecotypes and subspecies. Some authors recognize endemic species, in particular, in Northern Europe [124, 133]. It was also suggested that related whitefish species typical of Siberia and northeastern Europe occurred in Fennoscandia: peled (*C. peled* (Gmelin)) [134] and muksun (*C. muksun* (Pallas)) [135].

Early studies of whitefish failed to discriminate intraspecies forms and related species [68]. However, genetic markers were recently found that well discriminated most Siberian species of the genus *Coregonus*. The whitefish of Fennoscandia was studied with the use of these markers. The studies revealed no traces of *C. peled* in this region, except for basins where the species had been artificially introduced [69, 70].

No qualitative differences were found between the Siberian populations of *C. lavaretus* and *C. muksun* [136, 137]. This casts doubt upon the existence of the species *C. muksun* even in Siberia. No significant genetic differences between *C. lavaretus* and endemic *Coregonus* species (*C. oxyrhynchus* from the North Sea basin [74] and *C. baerii* and *C. ladoga* from the basin of Lake Ladoga) were found either [71].

The whitefish of northern Europe shows high diversity within the species. Earlier studies revealed two haplotype groups in this region. One occurs in Southwestern Scandinavia and the Baltic basin. Similar haplotypes are common in the Alps. The other is widespread in Europe and Siberia [73].

Later studies revealed two haplotype clades. In addition to the South-European and North-European, haplotypes typical of Siberian populations were detected: in the Northern Dvina basin, and, very seldom, in South Norway and the Baltic basin [75]. Ostbye et al. [75] suggested that the North-European haplotypes had originated from the refugium in the area of the present-day Pechora River. In our opinion, this hypothesis contradicts the limited occurrence of the Siberian haplotype in the Baltic basin.

Allozyme studies also point to restricted gene exchange between whitefish populations of the White Sea and Barents Sea basins (where the endemic IDDH-1.2* allele occurs), on one hand, and the Baltic basin, on the other [71, 72].

We agree with Sendek, who suggests a whitefish refugium in the Baltic basin [71], because there are alleles confined to this region. The cause of the specific gene pattern of the White Sea and Barents Sea whitefish populations is unknown. It may have been the presence of a refugium or colonization from Northern Scandinavia.

Recently, a combined study of morphological and genetic features of four whitefish forms inhabiting a Norway lake has been performed [76]. Its authors assume sympatric appearance of these forms in this case. This conclusion may be applied to other North European lakes inhabited by several whitefish species.

Inconnu, Stenodus leucichthys (Guldenstadt)

This large fish usually migrates to the sea for feeding. The Arctic Ocean coast from the White Sea to the American rivers Yukon and Mackenzie is inhabited by the *Stenodus leucichthys nelma* subspecies, and the Caspian Sea basin, by *S. leucichthys leucichthys*. Their genetic comparison revealed a significant divergence between the subspecies, although without qualitative difference [77].

Grayling, Genus Thymallus

Graylings are freshwater fishes. European grayling, *Thymallus thymallus* (Linnaeus), is widespread in Europe up to the Urals. Arctic grayling, *T. arcticus* (Pallas), occurs in Siberia and North America. It is also occasionally found in the Pechora basin area. Individuals with intermediate morphology (probably hybrids) have been caught in one of the Pechora tributaries [138].

Genetic studies confirm the cross between the two grayling species in the Pechora basin [78]. The mtDNA haplotype supposedly typical of Arctic grayling has been detected far west, in one of grayling populations of the Northern Dvina River [79].

Based on the genetic markers studied, the North European populations of European grayling are subdivided into two groups, to the west and east of the Baltic Sea. However, some Norway populations include haplotypes typical of the eastern group. The boundary between the two groups can also be traced on the southern coast of the Baltic Sea [79–81].

Smelt, Genus Osmerus

Smelt includes anadromous and freshwater forms. The area of European smelt, *Osmerus eperlanus* (Linnaeus), is similar to that of vendace. American smelt, *O. mordax* (Mitchill), occurs throughout the Northern Asia coast, up to the White Sea basin in the west.

The two smelt species have been shown to be completely different in the allelic states of many loci [82]; thus, they should be regarded as distinct species. The small smelt form from the Dvina Bay of the White Sea has been confirmed to belong to *O. mordax*.

The origin of the smelt of Syamozero Lake in the basin area of Onega Lake remains unknown [83], which is related to the fact that the authors took samples from only two of the numerous populations that could be the ancestors of the colonizers.

Pike, Esox lucius Linnaeus

This species is widespread in Northern Eurasia and North America. Pike has a low level of genetic differentiation among populations. It is suggested that the species dispersed relatively recently. Its origin is unknown [84, 85].

Eel, Genus Anguilla

Two eel species spawn in the Sargasso Sea, Atlantic Ocean. *Anguilla anguilla* (Linnaeus) fry comes to rivers throughout the Europe coast, and *A. rostrata* Le Sueuer fry, to North American rivers. The species are discriminated by a single morphological character, vertebra number. On the grounds of vertebra count, migration of *A. rostrata* and hybrids of the two species to northern Europe has been suggested [139].

The two eel species are clearly discriminated with a set of genetic markers (for review, see [140]). Genetic studies confirm the suggestion of regular migration of the hybrids of American and European eels to Iceland [86–89].

Chub, Leuciscus cephalus (Linnaeus)

Freshwater fish, widely occurring in Europe (except for the northernmost regions) and adjacent Asia regions, includes several subspecies. Four population groups where various haplotypes are close to fixation have been recognized in Europe. Only one haplotype has been found in the Baltic basin: the same as in northern parts of the Black Sea and Caspian Sea basins. Thus, Northern Europe appears to have been colonized from one, Ponto-Caspian, refugium [90].

Spined Loach, Cobitis taenia (Linnaeus)

This species inhabits freshwater bodies of the basins of the Baltic, North, Mediterranean, Black, and Caspian seas. Probably, it also occurs in Siberia. Several species are recognized in Southern Europe [124], where several clades of mtDNA haplotypes have been established. In the Baltic basin, haplotypes of only one clade are found: the same that is present in the Black and Caspian basins. Thus, spined loach also colonized Northern Europe from the Ponto-Caspian refugium [91].

Burbot, Lota lota (Linnaeus)

Burbot is widespread occurs in freshwater bodies of northern Eurasia and North America. Three population groups are recognized in Europe. They show qualitative differences in haplotype pattern. One group occurs in the Baltic basin and Central Europe; the second, in Western Europe and Denmark; and the third, in northwestern Fennoscandia. A haplotype typical of the third group has also been found in Onega Lake [92, 93].

Perch, Perca fluviatilis Linnaeus

It is a freshwater species, widespread in Northern Eurasia. Three haplotype clades have been recognized in Northern Europe. One of them is confined to this region (detected in several Norway populations). The second also occurs in Western Europe, and the third, in the Black Sea basin and in Siberia [94].

Bullhead, Cottus gobio Linnaeus

This fish is widespread in Europe except for northern Fennoscandia. The Russian bullhead subspecies *Cottus gobio koshewnikowi* Gratzianov is recognized by some authors. Other authors regard it as a species [133]. A similar species, *C. sibiricus* Kessler, occurs in Siberia.

Two genetic markers reveal qualitative differences among populations from the western, southeastern, and eastern parts of the Baltic basin [95, 96]. These populations are believed to have come from three different refugia. It is likely that the western populations dispersed from Central Europe [97]. The eastern populations correspond to the *koshewnikowi* form. Considerable introgressive hybridization has been noted in the zone of contact between the western and eastern forms [96].

Alpine Bullhead, Cottus poecilopus Heckel

Occurs in the Baltic basin, upper reaches of the Olanga River (White Sea Basin), and Siberia. North-European populations differ significantly from Carpathian ones. In northern Europe, population groups of northern Fennoscandia and of Southern Sweden and Denmark are recognized [98].

Fourhorn Sculpin, Triglopsis quadricornis (Linnaeus)

Occurs in coastal regions of northern seas. Freshwater forms occur in some Fennoscandian lakes. The systematics of these forms is unknown. The Baltic Sea populations and the Fennoscandian lacustrine populations show a significant genetic similarity [99–101].

INVERTEBRATES

Gyrodactyls, Genus Gyrodactylus

Worms, fish ectoparasites. This genus includes many species. In recent years, attention has been focused on *Gyrodactylus salaris* Malmberg, whose main host is Atlantic salmon. Formerly, this parasite occurred only in the Baltic basin. In 1975, it was first found in Norway, where it dispersed very rapidly and greatly impaired Atlantic salmon populations [41]. In 1992, it was found in the Keret River (western coast of the White Sea) [142], and in 2002, in the Pista River of the same region [143]. The parasite is spread with infected artificially reared fry.

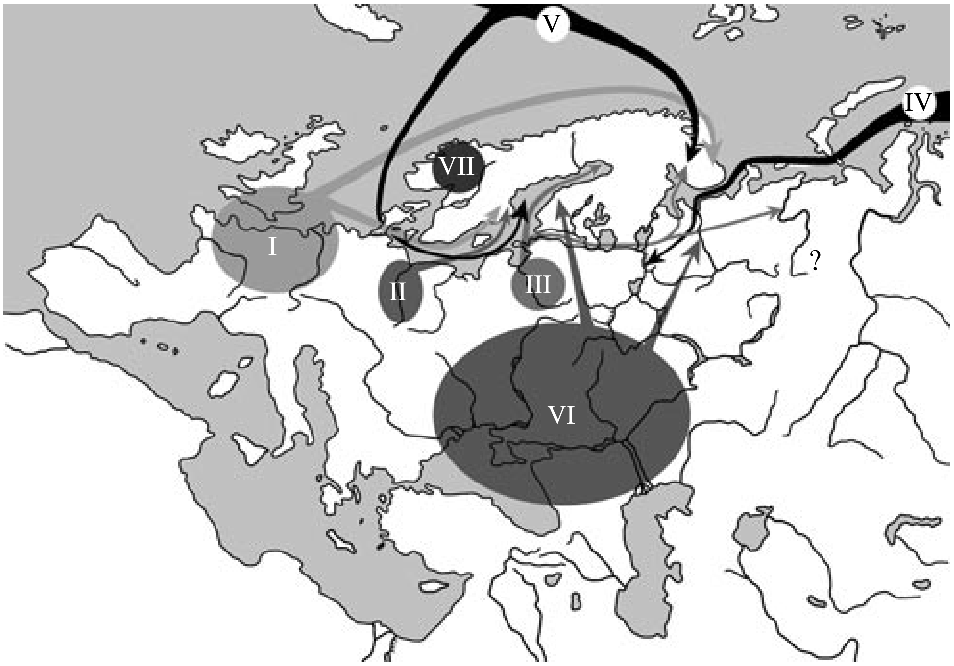
Several molecular studies have been involved with the diagnostics of species of the genus [102–105, 107, 108]. Special attention is paid to search for markers for discriminating *G. salaris* from morphologically similar *G. thymalli*, a grayling parasite. These species can be readily identified by analysis of some rDNA spacer sequences [103, 104].

Studies of intraspecies genetic diversity suggest that *G. salaris* came to Norway several times [105]. Four genetic groups of *G. thymalli* have been found in Fennoscandia: two in Scandinavia (probably dispersed from the Atlantic coast and the southern Baltic basin), one in the White Sea basin, and one in the eastern Baltic basin [108]. The last group also occurs in Kitka Lake, upper reaches of the Kovda River, flowing into the White Sea. Several thousand years ago, this lake belonged to the Baltic basin [106, 108].

Mysids, Genus Mysis

Small shrimp-like crustaceans. Opossum shrimp, *Mysis relicta*, is widespread in lakes of northern Eurasia and America. Six species of the genus occur in northern seas. Several related species occur in the basins of the Black and Caspian seas.

The Caspian species genetically diverged from the sea and freshwater North-European relatives [109, 112]. The *Mysis relicta* species includes four forms showing qualitative genetic differences. Three forms occur in Northern Europe, of which one is widespread, the second dwells only in the Arctic Ocean basin, and the third inhabits mainly in the Baltic basin [110, 111]. It is believed that two forms survived glaciation in the Baltic basin, one of them also surviving in a refugium near the British Isles [110]. The forms have also been



Sketch of refugia and dispersal routes of freshwater animals: I, Atlantic; II, South-Baltic; III, Eastern; IV, Siberian; V, American; VI, Ponto-Caspian; VII, Norway; ?, region of the "Komi Lake" (present-day Pechora).

found to differ in morphology and described as separate species [111].

Genus Gammaracanthus

Gammaracanthus lacustris Sars occurs in northern Eurasian lakes. According to genetic studies, the Caspian species *G. caspius* is closer to *G. aestuariorum*, occurring in the White Sea, than to Fennoscandian *G. lacustris* [113].

Gammarus lacustris Sars

This amphipod occurs in northern Europe and Siberia. According to genetic data, Fennoscandian populations are divided into two major groups, possessing qualitative differences. One group is prevalent in the northeast of the region. It is genetically similar to Siberian specimens. Probably, it descended from Siberian colonizers. The other group is subdivided into two subgroups differing in the presence or absence of specific alleles. The group occurring on the Norway coast was probably formed by southwestern colonizers. Alternatively, it may have survived the glaciation on the drained Norway shelf [114].

Genus Pontoporeia

Small crustaceans. A single freshwater species, *Pontoporeia affinis* Lindstrom, occurs in northern Europe lakes and estuaries of rivers discharging into the Arctic Ocean. Genetic data reveal a high divergence between the freshwater *P. affinis* of Fennoscandia and the marine *P. femorata* of the Baltic Sea [115].

Genus Daphnia

Daphnias are widespread small freshwater plankton crustaceans. The dispersal is mediated by dormant eggs, able to survive drying and freezing. Molecular markers reveal a significant level of interspecies crosses, in particular, in Northern Europe [116].

According to genetic data, the *Daphnia pulex* species includes several strongly divergied groups. At least two groups are widespread in North America. They also have colonized Greenland, Iceland, and Spitzbergen and reached northern regions of continental Europe. One more group reached northern Europe from Siberia [118]. A high level of crosses among the groups is noted [117].

No cryptic species or dispersal routes have been found for another species, *Daphnia magna* [119].

Pearl Mussels, Genus Margaritifera

Freshwater pearl mussel *Margaritifera margaritifera* (L.) occurs in northeastern North America and northwestern Europe. Several endemic species of the genus occur in Southern Europe and North America [144]. In a recently published key [15], two endemic species, *M. elongata* (Lamarck) and *M. borealis* (Westerlund), are associated with northern Europe without indicating the precise location of findings.

Pearl mussel populations of the Kola Peninsula are genetically similar to some populations of Ireland and North America [120].

Table 2. Reconstruction of species inhabiting refugia (I–VII)

Genus, species	I	II	III	IV	V	VI	VII
Acipenser					+		
Salmo salar	+	?	+		+		
Salmo trutta	+	?	+			?	?
Salvelinus alpinus				+	?		
Coregonus sardinella				+			
Coregonus lavaretus	+		+	+			
Thymallus	+	+	+	+			
Osmerus				+			
Leuciscus cephalus						+	
Cobitis taenia						+	
Lota lota	+	+					?
Perca fluviatilis	+					+	?
Cottus gobio	+	+	+				
Cottus poecilopus	+		+				
Gyrodactylus thymalli	+	+	+	?			
Mysis	+		?	?			
Gammarus lacustris	+			+			?
Daphnia				+	+		
Margaritifera	+				?		

Note: For the designations of the refugia, see the legend to the figure.

Zebra Mussel, Dreissena polymorpha Pallas

The original area of this mollusk included the basins of the Black and Caspian Seas. In 19th and 20th centuries, it intensely dispersed over Europe, reached Southern Fennoscandia, and colonized the Northern Dvina basin. Judging from the prevalence of mtDNA haplotypes, the mollusk moved to northern Europe two ways: directly from the Caspian basin and through Western Europe (personal communication by I.S. Sergeeva and V.S. Artamonova).

CONCLUSIONS

According to genetic data, the freshwater bodies of northern Europe were colonized from refugia on the eastern Atlantic coast, in southern and eastern areas of the Baltic basin, in Siberia, in North America, and in the basins of the Caspian and Black Seas. Probably, there was one more refugium in Southern Norway (see the figure and Table 2). Fourhorn sculpin apparently colonized Fennoscandian lakes from the sea.

Dispersal routes also crossed divides. This was the case with zebra mussel, coming to the White Sea basin from the Volga basin. Spined loach, chub, and perch came to the Baltic basin from the south. Atlantic salmon, brown trout, gyrodactyls, and whitefish came from the Baltic basin to the White Sea basin, whereas burbot, Arctic char, least cisco, whitefish, and gammarus moved in the opposite direction.

The reconstructed routes are in good agreement with ecological features of the species. Thermophiles dispersed from southern water bodies and boreal species, from the Baltic basin. Psychrophiles, bulked by us into the Arctic subsaline fauna complex [145], dispersed from the Arctic Ocean basin.

It should be noted that genetic data generally agree with data from faunistic and morphological studies. Combined studies, including analysis of morphology and molecular markers, allowed refinement of the taxonomy of some forms, including Arctic chars, coregonids, and mysids. Significant levels of interspecies hybridization were found in eels, vendace, least cisco, graylings, and daphnias.

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