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THEORETICAL PAPERS AND REVIEWS

Genetic Markers in Population Studies of Atlantic Salmon *Salmo salar* L.: Analysis of DNA Sequences

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Abstract—The review, which consist of two parts, summarizes literature data on all genetic markers used in population studies of Atlantic salmon. The second part of the review concerns analysis of DNA sequences: fragments of known genes, anonymous genome sequences, mini- and microsatellites, mitochondrial DNA. The main results of studies of the Atlantic salmon gene poll using DNA markers are discussed. Most of the markers examined in certain conditions may be under selection. The resolution power of various methods of DNA analysis and the fields of their use are considered in reference to Atlantic salmon.

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INTRODUCTION

Since the 1990s, population genetic studies of Atlantic salmon were increasingly based on DNA sequence analysis. The scope of issues which researchers are trying to solve using this approach is largely traditional, including identification of hybrids between Atlantic salmon and brown trout and search for intercontinental and interpopulation differences.

However, high resolution of many methods of DNA analysis, up to the possibility to identify individual fish, allows performing finer studies, including those aimed at detecting within-population interactions. Based on these methods, new approaches are developed to resolve the problems that were not solved by means of investigating fish morphology, physiology, and behavior. The spreading of DNA analysis is also promoted by the fact that they permit determining genotypes of live fish: a sufficient DNA amount can be isolated from scales, several drops of blood, or a fragment of fatty fin of salmon.

IDENTIFICATION OF INTERSPECIES HYBRIDS BY MEANS OF DNA ANALYSIS

Methods Using Anonymous DNA Sequences

Treatment of the total nuclear DNA with frequent-cutting restriction endonucleases followed by fragment end tagging and their fractionation in polyacrylamide gel produces a band pattern formed by repeated genome elements. These bands include species-specific ones. This method called taxon printing, in principle allows distinguishing Atlantic salmon from brown trout [1], but it is labor-consuming and requires high-quality DNA samples, and therefore is not used in routine studies.

RAPD (random amplified polymorphic DNA) analysis is amplification of random genome sequences using one or more short (decamer, i.e., consisting of about ten nucleotides) primer with a randomly selected sequence. This method detects genome rearrangements of tens to hundreds of base pairs in size. In the case in question, it is used only to species identification of Atlantic salmon, brown trout, and their hybrids. Using this method, Elo et al. [2] failed to reveal intrapopulation polymorphism in freshwater Atlantic salmon from a tributary of Saimaa Lake (Finland), although the authors employed 40 different decamer primers. However, this negative result may be explained by the specific features of the population examined: since the 1970s, this population is artificially maintained, and as shown by allozyme analysis, has a very high level of inbreeding [2].

Analysis Using Known Nuclear DNA Sequences

One of the methods of DNA analysis used to identify interspecies hybrids is restriction analysis. The genomic DNA is digested with restriction endonucleases, the DNA fragments are gel fractionated, transferred onto nitrocellulose or nylon membrane and hybridized with a radioactive probe, containing a known DNA sequence.

Hybridization with a cloned fragment of histone genes [3–5], amplified DNA region encoding preprogonadotropin-releasing hormone (GnRH), the peptide hypothalamus hormone [6] or a transferring gene fragment [7] permitted to distinguish Atlantic salmon from brown trout and to identify interspecies hybrids by the positions of hybridization zones.

Minisatellite analysis is a variant of restriction mapping, in which a digested sample of total DNA is hybridized with a tagged probe of a repeated fragment. The minisatellite locus may contain two to several hun-

dred tandem repeats nine–ten to a hundred nucleotides in size; a particular locus may occur one or several times in the genome (mono- and multilocus probes). To identify interspecies hybrids, monolocus probes were used [8].

However, the simplest method of identification of species and first-generation hybrids was proposed with the use of a fragment of the 5S rRNA gene: the size of the amplified fragments in Atlantic salmon and brown trout proved to be different, which permitted to omit additional technical procedures such as restriction or hybridization [9].

This method was also used for identifying fish eggs found on redds [10] as well as for identifying hybrid origin of live Atlantic salmon and brown trout in rivers of Estonia [11] and South Europe (Spain and France) [12]. It was also employed for identifying hybrid individuals in experimental conditions [5] and in assessing the level of hybridization occurring upon concurrent introduction of may be under selection and brown trout to Kerguelen islands in the subantarctic zone [13]. Using this method, Bagliniere et al. [14] showed that a large salmon caught in 1999 in the Mediterranean basin, beyond the natural Atlantic salmon range, was not brown trout or hybrid, but indeed Atlantic salmon (in all probability, a wild rather than farm fish).

DNA screening in 15 salmonid species aimed at revealing phylogenetic relationships within the family detected another genetic element, whose length was different in Atlantic salmon and brown trout [15]. If this element proves to lack intraspecies polymorphism, it could be used for identification if individuals of dubious species status and detection of interspecies hybrids.

Using allozyme and DNA analysis allowed estimating the proportion of hybrids in natural habitats. This proportion varied from 0 to 4.67% (in North America where brown trout have been introduced) (see [16] for review).

INVESTIGATION OF INTRASPECIES GENETIC DIVERSITY OF ATLANTIC SALMON AND ROUTES OF ITS SPREADING

Intraspecies Diversity of Nuclear Sequences

Comparison of primary gene sequences. Sequence analysis of transcribed spacer regions of the ribosome repeat DNA (rDNA) has shown that the divergence between Atlantic salmon and brown trout in this region was below 2.0–4.5% [17], not exceeding the intraspecies diversity level of brown trout, though the substituted nucleotide positions upon intra- and interspecies polymorphism generally do not coincide [18]. For the terminal transcribed regions, the differences are greater, attaining nearly 18%, but they are practically overlapped by the differences among Atlantic salmon individuals (about 17%) [17]. For the transferrin gene fragment, not only interspecies differences were shown, but also nucleotide sequence variants were described responsible for the presence in the *Salmo salar* genome of an allele encoding this protein (apparently *TF-1*: relative to the brown trout allele **100*, it was identified as **80*) [19].

One of the most variable exons in the Atlantic salmon genome was a sequence within a gene of the major histocompatibility complex. For this sequence, intraspecies differences constituted over 14%; they were shown to be adaptive. Among nine variants found, alleles were identified, whose carriers were resistant to bacterial infection or very susceptible to it; under conditions of infection, the latter were strongly selected against [20–23].

Examination of wild populations showed that selection at this locus plays a role in maintaining polymorphism both among and within populations [24–27]. Another mechanism of maintaining genetic variation at this locus was demonstrated experimentally. It was shown that in spawning, wild Atlantic salmon prefer partners that maximally differ from them in alleles of the major histocompatibility complex, which confer to the progeny resistance to a wide spectrum of infectious agents [28]. Not only mature fish but also juveniles are able to recognize carriers of particular alleles of at least one locus [29]. There was no preference of genetic markers that are traditionally thought as neutral [28].

Another gene with numerous alleles is the gene coding for the growth hormone (*GH1*). Complete sequencing of *GH1* in individuals of different populations revealed differences only in noncoding sequences [30].

Frequencies of different alleles of this gene tag groups of artificially reared juveniles of the same age but different size [31]; European populations of Atlantic salmon differ in them [32]. The populations of North America and Europe are also different in frequencies of these alleles, but variants similar to the "American" ones were recorded in northern Europe [30].

This finding is in agreement with the hypothesis on the participation of North American immigrants in colonizing northern Europe, which was advanced on the basis of allozyme analysis (see the first part of this review)[1] and mtDNA analysis (see below).

Restriction mapping and microsatellite diversity. Restriction mapping has shown that hybridization with the cloned ribosome repeat sequence detects high-molecular (3600- and 2600- bp) fragments in some fragments and none in other fragments [33]. However, the conclusion that this type of DNA polymorphism permits to discriminate between the European and North American Atlantic salmon, which was made in [33], does not seem likely, since the individuals examined represented mainly populations from rivers of Scotland Atlantic salmonid Newfoundland. Moreover, the use of high-molecular DNA markers requires high-quality DNA samples, and the illustrations presented in [33] show that DNA of fish from the European popula-

[1] *Russian Journal of Genetics,* 2007, vol. 43, no. 3, pp. 293–307.

tions have degraded to a far higher degree than the DNA of North American fish.

However, analysis of a minisatellite locus in fact showed conclusive differences between salmon from different continents, which was demonstrated on extensive material including fish from 35 West European and 128 American populations [34]. Using this method, differences among the populations of different rivers [35, 36] and subpopulation from the same river basin [37, 38] were shown and temporal genetic stability of the populations examined was demonstrated [39].

High variability of minisatellite loci permits using this approach not only for detection of among-population differences. With the use of four to six single-locus probes of high-variable minisatellites, the combined allele combination of each individual in the experiment typically is unique, which allows to identify the progeny of individual spawners. Apart from single-locus probes, multilocus probes are usually employed in such studies: here, a successful selection of the repeated sequences immediately yields an individual variant of the hybridization pattern consisting of several bands. These approaches were used to assess reproductive success of individual fish [40–49]. (The identification method in which an individual is recognized by a set of alleles of loci containing repetitive sequences was termed *fingerprinting*).

To date, minisatellite loci are increasingly often used not as a separate group of markers, but in combination with analysis of other repetitive sequences—microsatellites [50, 51].

Microsatellite diversity. A microsatellite locus is a genome region consisting of tandem di-, tri-, and tetranucleotides flanked by unique sequences that are usually absent in other genome regions. Sometimes insertions of several nucleotides, breaking the repetitive motif, occur within the locus. The repeat number within a locus varies in a broad range. In salmonids in general, and in Atlantic salmon in particular, microsatellites have more repeat units then mammalian microsatellites [52, 53]. As in other vertebrates, the same dinucleotide motif occurs in the Atlantic salmon genome at intervals of about 90 000 bp [52].

In Atlantic salmon, the maximum number of alleles (58) was found for locus BHMS7-017 (Ssa90NVH) [54], being on average 10–20 alleles par locus [51, 55–59].

The number of microsatellite loci found in Atlantic salmon is several hundreds [51, 53, 54, 56, 58–62], but the great majority of them are dinucleotide ones. Tetranucleotide loci occur in the Atlantic salmon genome 10 to 15 times less frequently [51], although they are of most interest for researchers. Their variation is about twofold higher [56, 63], and significant differences in the length of the amplified fragments allow identifying alleles at high precision. Only six trinucleotide loci in Atlantic salmon were reported [57, 64].

The abundance of microsatellites together with their high variability allow to detect genetic differences among population of North America [65–68] and Europe [50, 51, 54, 69–73], determine their independence as population units [65, 66, 68, 74], and in some cases assess migration among populations [70, 73, 75]. Using these markers, the intrapopulation structure within a water system and stability of the observed differences in time were studied [63, 67, 74, 76–83].

Moreover, analysis of DNA isolated from collections of Atlantic salmon old scales, permits estimating changes in the population genetic structure for the period of nearly hundred years, as well as determining critical periods in their existence, characterized by reduction in allele diversity (bottlenecks) [70, 73, 74, 84–90].

The resolution power of microsatellite analysis is so high that allows reliably (88–95.8%, on average more than 90%) assigning individual fish to a particular population, if these populations were previously analyzed. The identification reliability increases with the number of loci tested; however, most authors agree that in practice six to eight most variably microsatellites are sufficient [54, 59, 91–94].

In practice, of particular importance is recognizing farmed and subjected to selection salmon that have escaped from salmon farms and in massive numbers enter West European and North American rivers (mating to wild fish, they destroy the set of local adaptations characteristic for the river). Many studies using microsatellite analysis have shown that genetically these farmed fish differ from the wild ones (their allele diversity is typically lower by a factor of 1.5 and more) and can be identified with high precision (as a rule, more than 95%) [54, 59, 95–101].

This type of analysis showed that narrowing of genetic diversity may occur even when farming is aimed at maintaining the diversity, as in the case of Atlantic salmon transported to Tasmania from Canada. In spite of the fact that the progeny was obtained from 500 fish in each generation, the microsatellite diversity decreased since the 1960s by approximately 20–25%, though allozyme and mitochondrial DNA analyses did not detect appreciable gene poll changes [102].

Using a set of 3–15 microsatellite markers permits unambiguous identification of individual fish and their progeny under conditions of a laboratory experiment [103–106], hatchery, and breeding [91, 107], and with high precision detect relatedness between individuals experimentally in the wild [92, 107–115].

However, in spite of many advantages, microsatellite analysis, as any other method, has some limitations. For instance, it seems that its possibilities are restricted when dealing with dispersion pathways of a species and detection of differences among populations from different regions [27, 65, 94, 116, 117]. On the other hand, it has been convincingly demonstrated by means of microsatellite analysis that there are significant differences between the Atlantic salmon from West Europe and North America [55, 71, 100, 118–120].

When the results of microsatellite and allozyme polymorphism analyses were compared, the corresponding similarity dendrograms were sometimes concordant [60]. However, if the material analyzed was collected across a large part of the species range, the results could be discordant [94]. Microsatellite analysis showed the best results when the populations compared were from one region or two neighboring regions [121].

This discrepancy seems to be explained by the fact that both allozyme and microsatellite markers may be subject to selection (directly or owing to linkage with selected genes). In this case, the results of analysis will strongly depend on the set of markers used.

Indeed, it was repeatedly noted that some samples are in disequilibrium at tetranucleotide loci *Ssa171* [50, 68], *Ssa197* [68], and (or) *Ssa202* [68, 70], which are particularly popular with researchers. Moreover, one of the *Ssa202* alleles was found to occur at a high frequency (0.39–0.65) in a selection line of Atlantic salmon, being modestly represented in wild populations (0.018–0.180) [97]. At these loci, de novo mutations were also recorded [97, 122], microsatellite mutation rates being inferred from exactly these three loci: 3.4×10^{-4} [122] and 7.8×10^{-4} [91].

Special studies aimed at finding markers linked to the genes were performed [51, 64, 123]. It has been shown that 9 of 75 linked microsatellites exhibit marked deviation from neutrality (about 12%). Moreover, of 17 microsatellite loci, which we earlier used as neutral markers, 4 (i.e., more than 23%) were shown not to be neutral (the *Ssa197* locus among them) [51]. A similar conclusion was reached by Antunes et al. [123] who have studied the transferring locus that was under selection. They believe that the microsatellites linked to this locus also cannot be regarded as neutral [123].

Interestingly, if in all previous studies only one trinucleotide microsatellite locus was found in Atlantic salmon, in the study aimed at searching for microsatellites linked with genes, five of them were found [64]. This may be explained by the fact that within-gene insertions multiple to three nucleotides, in contrast to other insertions, do not shift the reading frame [124].

In the future, markers of this type are very likely to trace genes responsible for local adaptations [51]. In the meantime, the first works [125] appear showing that high genetic diversity, marked by microsatellite diversity, promotes better adaptation of fish groups to the environment. Although in one study the authors failed to find association between microsatellite heterozygosity and growth rate [126], in another study this association has been found [127]. In addition, there is evidence on differences in microsatellite allele frequencies between fish groups with different growth rate [128].

However, it is clear that loci that are directly or indirectly subject to selection cannot serve as markers characterizing the species dispersal: the leading role in this is played by environmental conditions [51]. For most microsatellites, the neutral status was not confirmed and sets of loci examined are considerably different, which hinders comparing the results obtained in different laboratories [59].

Single-nucleotide polymorphisms (SNPs). As these polymorphisms result from a point mutation in the genome, their loci as a rule have only two alleles. The advantage of these markers lies in the fact that SNPs occur in the genome far more frequently than microsatellites (approximately each 1000–2000 bp); moreover, point mutations appear both in coding and noncoding genome regions. The latter means that they may directly affect protein functions or expression, thus being the objects of application of evolutionary forces. Another SNP advantage is their suitability for automated analysis, which involves DNA microarrays, mass spectrometry, etc.

In 2006, Rengmark et al. [59] published a study, in which the first attempt at analyzing the Atlantic salmon population structure and estimating relatedness between individuals using SNPs was made. To detect mutations, they used a technique developed by Landegren et al. [129]: for each SNP locus, two oligonucleotides were selected, one of which contained at the 3' end a nucleotide corresponding to the variable nucleotide of one of the alleles (+ allele). The second nucleotide was joined to the 3'-end of the first one by its 5' end, when these nucleotides were annealed on the DNA template derived from the sample tested. The oligonucleotides could be ligated to each other only in the case when the 3' end of the first was exactly paired to the variable nucleotide of the DNA tested. The presence or absence of the ligation was detected by polyacrylamide gel electrophoresis.

Comparison of the results of microsatellite analysis at 16 dinucleotide loci with the results of analysis using 26 SNP markers showed that in the former case, individuals were unambiguously assigned to a concrete population in 95.8%, and in the latter, in 82.4% of the cases. This confirmed the assumption that SNPs are less informative than microsatellites. However, the resolution power of SNP analysis can be increased by enhancing the number of tested SNPs [59]. In addition, the authors believe that routine investigations require only eight most variable microsatellite loci or 12 SNP markers.

Intraspecies Diversity of Mitochondrial DNA Sequences

The main difference of mitochondrial DNA from nuclear one is the absence of recombination in the former. This means that the mutation accumulation in mtDNA proceeds consistently at rates five- to tenfold higher than in the nuclear genome. This provides the possibility not only for recording the presence of genetic diversity, but also for reconstructing the history of species dispersal [130].

Until lately, heteroplasmy has not been found in Atlantic salmon. Only very recently, we have recorded one such fish of the farm origin in the Keret' River, Karelia (Artamonova, Khaimina, unpublished data).

The complete sequence of the Atlantic salmon mitochondrial genome (16 665 bp) is known [131], which at present substantially facilitates the use of both the full-size mtDNA molecule and its fragments as genetic markers.

Differences among populations detected by RFLP (Restriction Fragment Length Polymorphism) analysis. In the early studies of the full-size mtDNA molecule by means of RFLP analysis, the authors addresses specific issues. Primarily, they hoped to find markers to discriminate between fish from different populations within a region [132, 133]. At the same time, another problem became relevant: to distinguish escaped farm fish from wild spawners [134].

Although at that stage researchers failed to gain adequate knowledge of the population structure, their works allowed revealing polymorphic restriction sites in the mtDNA molecule. The informative restriction endonucleases included *Ava*I [134], *Ava*II [132, 134, 135], *Bgl*II, *Bst*EII [135, 136], *Cla*I [135], *Dde*I [134, 136], *Dra*I [134–136], *Hae*III, *Hin*fI [132–134], *Hin*cII [136], *Mbo*I [137], *Pvu*II [136], and *Xba*I [138].

By comparing sets of restriction fragments, published by the authors who studied Atlantic salmon from some North American [138] and West European [132–134] populations separately, it was shown that some sites were apparently different in fish from the two continents. Restriction enzymes *Bgl*II, *Pst*I, and *Pvu*II were recognized as diagnostic [133]. In a similar fashion, it was established that the restriction fragments set for *Bgl*I is the same for Atlantic salmon from North America, Norway, Scotland, and some other European countries [132, 134, 138], but differs from that in Swedish fish studied [139].

Examining the complete mitochondrial genome, the authors were restricted to small sample sizes (typically up to ten individuals) from each sampling locality. The resolution of the method was comparable with that of allozyme analysis for standard sample sizes (i.e., about 40–50 specimens) [140] or even lower [141]. Special estimates have shown that samples should consist of at least 25–30 specimens to get an adequate picture of mitochondrial DNA diversity, while in cases, when precise assessment of different haplotype incidence is needed, they should be even larger [140]. Meeting these requirements, more refined studies were performed. For example, Birt et al. [136] revealed reproductive isolation between the anadromous and resident form of Atlantic salmon in the Gambo River system (Newfoundland).

Later, owing to the development of PCR, studies of mitochondrial genome became simpler. It has been shown that the most informative for Atlantic salmon population studies is the mtDNA fragment carrying (completely or partially) the gene for NADH dehydrogenase I (ND-1) [69, 76, 95, 96, 120, 142–146].

This fragment was examined with the use of more than 40 restriction endonucleases [77, 143, 144], of which the following proved informative: *Ava*II, *Hae*III, *Dra*I, *Hin*fI, *Nla*III, *Rsa*I, *Cfo*I, *Hae*II, and *Hha*I. The last two fragments detected genetic diversity of North American, but not European populations [144], and *Cfo*I was used only for studying Canadian populations [77].

RFLP analysis and sequencing of other mitochondrial genome regions—cytochrome b genes, *ND-3, ND-4, ND-5, ND-6*, and D-loop showed that these mtDNA sequences are low polymorphic and generally cannot serve as markers in population studies [76, 142, 147]. The exception is the D-loop sequence, which proved to be helpful in analysis of North American (but not European) populations. Polymorphism was observed at *Alu*I, *Mse*I, and *Tps*509 restriction sites [76, 77, 144].

Generally speaking, if the sample sizes are adequately large, the resolution power of RFLP analysis of the *ND-1* mtDNA gene sometimes permits to conclusively demonstrate genetic isolation of populations within a region and even record differences among subpopulations [76, 77]. However, this resolution often is not sufficient [142, 144], which is not surprising, because the among-population differences account for only 8% of the total mitochondrial genome diversity [143, 144], while within-population differences account for 48% of it [143].

Reconstruction of the species dispersal in the postglacial period inferred from mitochondrial DNA data. The advantage of markers (usually *ND-1*) of Atlantic salmon lies in the fact that, in contrast to allozyme and microsatellite loci, they can be employed for tagging population groups from particular geographic regions. For instance, it was shown that the differences between population groups from Baltic and North Atlantic explain up to 44% of the total genetic diversity, with frequencies of the characteristic haplotype groups showing a trend of decrease to the periphery of the region [143]. The differences between population groups from North Atlantic and North America are even higher, exceeding 68% [144].

Sequencing of a mitochondrial genome region carrying the *ND-1* gene confirmed that the mtDNA nucleotide sequences of fish from different European rivers, belonging to one haplotype, are identical with a singly exception: the mtDNA of one of the fish from the Swedish Atran River carried a unique substitution, which could not be identified by restriction analysis [145]. Examination of other genome sequences yielded the results that did not contradict the *ND-1* data analysis, but in this case the resolution was very low [142, 145].

The mtDNA haplotype diversity in North American Atlantic salmon was in general lower than that in European salmon. Although the American population as such proved to be nearly as diverse as the European

Comparative characterization of the methods used in population studies of Atlantic salmon

Task	Morphological traits	Allozyme markers	Mitochondrial DNA	Mini- and microsatellites	Nuclear gene fragments
Species assignment	++/+++	+++	(–/++++)	–	+++
Species assignment of mother	++	+++	[Detection of interspecies hybrids (++++)]	–	++++
Studying dispersion routes of species	+	++	+++	+	++
Studying among-population differences	+	++/+++	+++	++/+++	++
Studying within-population structure	++	++	++	+++	++
Assessment and monitoring of genetic diversity	++	++/+++	++/+++	+++	++
Establishment of relatedness among individuals	–	++	++	++++	++

Note: – the method cannot be used; + as a rule useless; ++ can be used in some cases or in combination with other methods; +++usually gives good results; ++++ reliable, recommended for use.

ones, the diversity was explained largely by variation at the D-loop locus, which was almost monomorphic in the European populations [144].

Reconstruction of Atlantic salmon phylogeny inferred from mitochondrial DNA data convincingly demonstrates differences between the fish from different continents: While within continents, the closest haplotypes differ usually in one point mutation, haplotypes of different continents are separated at least by ten mutations. This suggests very long isolation of the two continental groups (millions of years) [142–144].

Salmons from the Baltic and North Atlantic apparently separated much later, although ample evidence suggests that they survived the last glaciation at least in two different refugia [143, 145, 148]. The results of analysis of mtDNA from Atlantic salmon bones of circa 32 000–41 000 years of age, which had been found in diggings on the Iberian Peninsula (Spain) indicates that the modern North-Atlantic mtDNA haplotypes then already existed in that region. Their frequencies had been likely very different from the current ones, but mitochondrial DNA haplotypes characteristic for the contemporary Baltic basin, were not found [148].

Another group of data suggests that in the period of Atlantic salmon colonization of its current range (after the retreat of the last glacier, 11 500–10 000 years ago), salmon groups from all of the three refugia had contacts and formed mixed populations. For instance, typically European mtDNA haplotypes were found in the rivers of Newfoundland Island, continental Canada, and Greenland [144, 147, 149], and typically American ones, in the northern Kola Peninsula [143, 150, 151].

In particular, RFLP in combination with allozyme analysis showed that Kola Peninsula was colonized by the Atlantic salmon that had originated from three different refugia, North American, North Atlantic, and Baltic [151]. The problem of colonization of the North Europe by Atlantic salmon is discussed in review [152].

Selection on mitochondrial DNA in wild populations of Atlantic salmon. Even very recently, DNA markers, including mitochondrial ones, were thought to be neutral. However, evidence to the contrary has been lately appearing at an increasing rate.

For instance, analysis of full-size mtDNA of Atlantic salmon from the Itchen River (South England) showed that spotted and running fish of the same generation significantly differ in frequencies of different mitochondrial DNA haplotypes, these frequencies being stable in time [137]. This means that the features of individual development in Atlantic salmon depend, among other factors, on the haplotype that carries the individual in question, which may turn ctitical in some environmental conditions for certain haplotypes.

Differences in mtDNA haplotype frequencies were also recorded in spawners of different running times. This suggests that selective fishery in certain seasons may destroy the historically formed population structure [153].

To explain the change in the mitochondrial DNA haplotype frequencies in Spain rivers during the last 40 000 years, Consuegra et al. [148] have advances a hypothesis according to which the frequency change (and particularly the substitution of the most common haplotype with another one) may be related to the constant elevation of water temperature.

In the Keret' River (Karelia), after invasion of the hazardous parasite *Gyrodactylus salaris*, in 15 years the most common haplotype, originating from the North Atlantic refugium, was replaced by another one, attributed to Baltic haplotype group, i.e., characteristic of *G. salaris*-resistant salmon, which initially occurred in no more than 10% of fish. Another Baltic haplotype (spread in the Ladoga Lake basin and in the Saimaa Lake, where *G. salaris* is rare or absent) which was also initially present in the population was not supported by selection ([154]; Artamonova et al., unpublished).

The examples of selection listed above do not depreciate the advantages of mtDNA as a suitable marker allowing to trance the dispersion pathway of the species, but emphasize the presence (absence) of each particular mtDNA variant in the population rather than haplotype frequencies. Moreover, a local narrowing of genetic diversity may indicate not the changed direction of the genetic flow, but action of selective forces at this point, which may involve temperature, parasites, etc.

CONCLUSIONS

Surveying methods of genetic analysis that are currently used in population studies of Atlantic salmon provides a possibility to draw some conclusions on the fields of application and resolving power of each of them (Table). In general, these conclusions agree with those obtained earlier for other species [130].

The evidence presented in this review suggests the appearance in the nearest future of a set of helpful nuclear markers, which will permit diagnostics not only of the first, but also of all subsequent generations. The development of the methods involving SNPs (in particular, allele-specific PCR) will allow performing fine-scale population studies in large samples without using costly methods of complete sequencing of large genome regions. In addition, it is expected that in the nearest future, many studies testing neutrality of genetic markers (especially microsatellites) will appear. The definite genes whose diversity is responsible for adaptation to particular environmental factors will be found by means of using genetic markers.

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