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# THEORETICAL PAPERS AND REVIEWS

# Genetic Markers in Population Studies of Atlantic Salmon *Salmo salar* L.: Karyotype Characters and Allozymes

# V. S. Artamonova

Vavilov Institute of General Genetics, Russian Academy of Sciences, Moscow, 119991 Russia; e-mail: valar99@mail.ru

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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 first part of the review concerns karyotype features and allozyme markers of *Salmo salar*. The latter are effectively used for distinguishing populations and subpopulations of Atlantic salmon, as well as for genetic monitoring of its populations. It is shown that the distribution of alleles of some allozymes may be related to selection for resistance to certain environmental conditions.

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# INTRODUCTION

Genetic diversity of many plant and animal species has been studied throughout the 20th century, but the mechanisms of appearance and maintenance of this diversity are still under debate. Understanding these mechanisms is essential for evolutionary reconstructions and adequate planning of conservation and rational management of living organisms (see monograph [1]).

Regularities of the formation of genetic diversity are studied mainly on so-called model organisms. For instance, a number of important principles of population genetics were inferred from studying salmonids fishes, especially Pacific salmons of the genus *Oncorhynchus*. In recent years, the range of model species has been expanded. In particular, studies of Atlantic salmon *Salmo salar* L. have been accumulating (see monograph [2]).

Atlantic salmon has both freashwater and anadromous forms (in northern Russia, the anadromous form is called *semga*). This species inhabits a wide range, extending on both sides of the Atlantic. On the North American coast, the species range extends northwards to 68° N and formerly reached 41° N southwards. At the other side of the Atlantic, the range of Atlantic salmon totally covers the European coast (including Iceland, British Isles, and the Baltic basin) from Portugal to the Kara River, including the coasts of the White and Barents seas [3]. Atlantic salmon is an important component of the ecosystem of northern rivers, a valuable object of fishery and aquaculture.

Genetic studies of Atlantic salmon have been performed for over 70 years. The earliest work on genetics of this species was conducted in the Soviet Union by an associate of the Institute of Genetics, A.A. Prokof'eva-Bel'govskaya [4]. Since then, hundreds of studies have been published, but generalization and analysis of the available evidence are hindered by the language barriers and by remarkable diversity of methodical approaches employed by researchers.

The authors of earlier reviews focused on comparing genetic characteristics of different populations [5-10]. Several reviews were devoted to karyotype variability in Atlantic salmon [11-15]. Recently, a review appeared summarizing abundant data on allozyme diversity in this species [16].

However, studies comparing the results of different authors using DNA markers of different types in their population studies are still lacking. Moreover, there are no theoretical works presenting comparative characteristics of different methods of analysis, their resolution power, and fields of application.

A comprehensive survey of genetic markers, used in studying Atlantic salmon, is required to include this species in the category of model organisms for population genetic investigation and use the bulk of the accumulated factual data for theoretical generalizations.

The first part of the present review\* presents data on karyotype characters and allozymes as markers which were first employed in the early studies of Atlantic salmon genetics and have been used for decades since then. Based on them, a number of important facts have been found in the studies, main results of which are discussed in the present review.

### KARYOTYPE CHARACTERS

Resolution ability of karyological analysis is generally low, and in a number of species of a polyploid origin this method does not always yield reliable results,

<sup>\*</sup> The second part of the review see in the Russian Journal of Genetics, 2007, vol. 43, no. 4.

which limits its use. Atlantic salmon has passed a tetraploid stage and has numerous small chromosomes. The modal (i.e., the most frequent) number of chromosomes (2n) in its populations varies from 54 to 60, the number of chromosome arms, from 72 to 74 [11–15]. At that, in individuals from one population, the chromosome number can be represented by all possible variants, and two populations sometimes differ only in the frequency of a particular variant [11].

However, the modal chromosome number (2n) in a related species, brown trout *Salmo trutta*, ranges from 76 to 84 in different populations, in spite of significant similarity of this species with Atlantic salmon [14, 15]. This allows using karyological analysis for identification of hybrids between brown trout and Atlantic salmon. These hybrids are typically viable and sometimes even fertile. Nevertheless, they are of no commercial value and can genetically pollute natural populations. Consequently, their identification by various methods is fairly relevant: such fish were sometimes developed artificially and also found in natural populations (see [17] for review).

No definite trends have been found in geographic (including intercontinental) distribution of chromosome variants. There is also no distinct difference between populations of anadromous and resident forms. However, differences in the modal chromosome number between some geographically distant or isolated populations are in some cases quite clear, even if two isolated populations inhabit the same river system [11].

Practical application of chromosome markers is very limited. Today these markers are virtually not used in population studies. Nevertheless, using these markers Garcia-Vazquez et al. [18] have shown that survival of Scottish salmon transplanted into Spanish rivers was lower than that of the local fish [18]. Later, this finding was supported by studies with the use of molecular markers (see below).

# DIVERSITY AT THE PROTEIN LEVEL

Protein analysis has significantly higher resolution than karyological analysis. The former is less laborconsuming and allows to examine large samples concurrently at several genetic markers. In taxonomic and in population genetic studies, analysis of allozymes (allelic protein variants) [1] has been widely used. In context of this approach, allelic variants refer to the proteins encoded by the same genetic locus not only in one, but also in different, systematically close species.

#### Differences among Closely Related Species

Allozyme analysis provides a reliable and simple way to distinguish Atlantic salmon from a related species, brown trout. In these species, different allozyme alleles are fixed at some loci, while at other loci, sets of alleles characteristic for each of the species, do not coincide (at least in sympatric areas).

To distinguish Atlantic salmon and brown trout, as well as their hybrids, various electrophoretically detectable proteins were used at different time. These include enzymes: esterase(locus *EST*-2\*), glucose phosphate isomerase (loci *GPI-B1*\* and *GPI-A*\*, which was formerly designated *GPI-1*\* and *GPI-3*\*), phosphoglucomutase (*PGM-1*\*, *PGM-2*\*), superoxide dismutase (*sSOD-1*\*, formerly *SOD*\*), xanthine dehydrogenase (*XDH*\*), malic enzyme (*sMEP-2*\*, formerly *MEP-3,4*\*), esterase *D* (*ESTD*\*), formaldehyde dehydrogenase (*FDHG*\*), phosphoglycerate kinase (*PGK-2*\*), mannose phospate isomerase (*MPI*\*), as well as protein transferrin (*TF*\*) (see [17] for references).

In addition to the proteins listed above, the following proteins can be used to identify hybrids between Atlantic salmon and brown trout: fumarate dehydrogenase, expressed in muscle tissues (locus  $FH-2,3^*$ ); liver octanol dehydrogenase ( $ODH^*$ ) [19], isocitrate dehydrogenase expressed in the eye ( $sIDHP-1^*$ ), and blood para-albumin ( $PALB^*$ ) [20]. The species affiliation of the mother can be determined by electrophoretic analysis of storage egg proteins [21].

## Intercontinental, Interpopulation, and Intrapopulation Differences

Wide use of allozyme analysis for detecting hybrids is possible, among other reasons, because Atlantic salmon is a young and relatively low-polymorphic species that have many single-allele loci. In mean heterozygosity, it ranks lower than brown trout and Pacific salmons [19, 22].

However, for the same reason, the spectrum of protein markers used to characterize intraspecies variation, is rather narrow in Atlantic salmon, though within-population diversity accounts for the main part (about 70– 75%) of the total genetic diversity. Interpopulation and intercontinental differences constitute only 15–20% of the total protein variability [22].

In practice, Atlantic salmon populations are characterized typically on the basis of only nine loci, which in further text are referred to as characterological. These are *sAAT-4*\*, *ESTD*\*, *FLABAD*\*, *IDDH-1*\*, *IDDH-2*\*, *sIDHP-3*\*, *sMDH-B1,2*\*, *mMEP-2*\*, and *TPI-3*\*, for which alternative alleles were found in most populations of the species. Moreover, these loci are highly polymorphic: in some populations, the frequency of alternative alleles for each of them exceeds 10%. Loci *mME*\*, *PER*\*, and protein locus *TF*\* are likely highly polymorphic, but since they are either poorly studied or used for analysis only in a few laboratories, the data on them can hardly be used for broad generalizations. A complete list of loci, for which alternative alleles were described in Atlantic salmon, is given in the table.

List of loc	ci for which alternativ	e loci were de	escribed in Salm	o salar L.						
E.C. NO.	Enzyme	Quaternary structure	Tissue, in which the locus is expressed	Locus	Frequently used syn- onyms	Allele	Allele frequency in European populations	Literature sources (Europe)	Allele frequency in North Ameri- can populations	Literature sources (North America)
3.5.4.4.	Adenosin deami- nase	Monomer	Liver	ADA-2*	I	06*	0.000-0.028	[23]	0.000	[24]
4.2.1.3.	Aconitase (aconitate dehydrogenase)	Monomer	Liver	sAH*	I	*80	0.000-0.010	[25]	0.000	[25]
1.1.1.1	Alcohol dehydroge- nase	Dimer	Liver	ADH*	I	*-50 (*50)	0.000-0.030	[25]	0.000	[25]
			Muscle	mAAT-1,2*	mAAT-1*; mAAT-2*; AAT-1,2*	<i>•00</i> *	0.000-0.014	[26]	I	I
			Mucolo boout	. V V T 1*	SAAT-1,2*;	*50	0.000	[20]	0.000-0.150	[20, 24, 27]
7611	Aspartate ami-	Dimer	IVIUSCIE, IIEAIL	- I- IEES	AAT-1,2*	*130	0.000-0.011	[28]	0.800	[20]
1.1.0.2	notransferase		Eye	sAAT-3*	AAT-3*	*83	0.000-0.010	[28]	I	I
			T iver	24 AT 7*	AAT-4*; AAT-3*;	*50	0.000-0.620	[16, 23, 25, 26, 28-34]	0.631-1.000	[25, 27, 35–37]
				L- 11776	sAAT-3*; AATs-2*	*25	0.000-0.500	[16, 23, 25, 26, 28-33]	0.000-0.005	[27]
4.4.1.5	Glyoxalase (lactoyl- glutathionliase)	Dimer	Muscle	GLO*	*T9T	*115	0.000-0.006	[23]	I	I
	_Alnha_alvreronhos_				AGP-1,2*;	*50	0.000-0.007	[33]	0.000	[33]
1.1.1.8	phate dehydrogenase	Dimer	Muscle	G3PDH*	G3PDH-1*; G3PDH-2*	*130	0.000-0.016	[33]	0.000	[33]
	Glucose-6-nhos-		Musela	GPI_R1*	GPI-1*; GPI-1?*;	*140	0.000	[33]	0.000-0.044	[24, 27, 33, 36]
5310	phate isomerase	Dimer	Alachta	14-110	PGI-I*	*185	0.000-0.019	[33, 37]	0.000-0.010	[24, 27, 33]
	isomerase, phos-		Musele liver	GPL-A*	GPI-3*;	<i>06</i> *	0.000-0.010	[16]	0.000-0.016	[24, 27]
	(ven tuttuetuun gulid		אין	01 I-1 IO	PGI-3*	*110	0.000-0.009	[38]	0.000-0.190	[24, 27, 35, 36]

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Table (C	ontd.)									
E.C. NO.	Enzyme	Quaternary structure	Tissue, in which the locus is expressed	Locus	Frequently used synonyms	Allele	Allele frequency in European populations	Literature sources (Europe)	Allele frequen- cy in North American populations	Literature sources (North America)
	Iditol dehydro- genase (sorhi-		Liver	IDDH-1*	Earlier, <i>SDH-2*</i> ; in PAAG often <i>IDDH-2*</i>	*80	0.000-0.320	$\begin{bmatrix} 16, 25, 26, 28, \\ 31, 32, 37, 38 \end{bmatrix}$	0.000-0.062	[25, 27]
1.1.14	tol dehydroge- nase)	Tetramer	Liver	IDDH-2*	Earlier, <i>SDH-1</i> *; in PAAG often	06-*	0.000-1.000	[25, 29-33, 37, 38]	0.400-1.000	$\begin{bmatrix} 20, 24, 25, 27, \\ 33, 35 - 37 \end{bmatrix}$
					IDDH-I*	$00I_* > X + *$	0.000-0.188	[29]	I	I
			Eye	I-HHUIs	IDHP-2*	*160	0.000-0.010	[25]	0.000	[25]
1.1.1.42	Isocitrate dehy- drogenase	Dimer	Liver, eye	sIDHP-3*	IDHP-3*; sIDHP-2*; IDHP-2*; IDH- 4*	*116	0.000-0.708	[16, 25, 28-32, 34, 37]	0.000-0.190	[24, 25, 27, 35–37]
C C L C	Creating Lines	Dimer	Musula	CV 40*	CK-2*;	*65	0.000	[20]	0.000-0.012	[24, 27, 35]
7.0.1.7	CIVALIIN MIIAN		OLOGUIAI	7U-WO	$CK$ - $I^*$	*87	0.000	[20]	0.000-0.071	[24, 27]
			Muscle	LDH-AI*	LDH-I*	f > *I00	0.000-0.003	[20]	0.000	[24]
						$\tilde{O}_*$	I	I	0.000-0.085	[27]
1.1.127	Lactate dehy- drogenase	Tetramer	Liver	LDH-B2*	LDH-4*	*75	0.000-0.030	[25, 28, 33, 39]	0.000-0.014	[25, 27, 33]
	)					*140	1	I	0.000-0.020	[33]
			Eye	LDH-C*	LDH-5*	$00I_{*} > X_{+*}$	0.000-0.028	[40]	I	I
			Liver, eye	sMDH-AI*	*I-HQW	*50, *(-200)	0.000-0.056	[16, 25, 33]	0.000-0.100	[24, 25, 27, 33, 35, 36]
1.1.1.37	Malate dehy- drogenase	Dimer	Muscle	*IA-HUMs	MDH-B1,2*; MDH-3 4*·	*75	0.000-0.194	$\begin{bmatrix} 16, 25, 26, 29, \\ 31 - 34, 37 \end{bmatrix}$	0.000-0.165	[25, 27, 33, 36, 37]
					MDH-3*	*120	0.000-0.020	$\begin{bmatrix} 16, 25, 26, 29, \\ 31 - 33, 37 \end{bmatrix}$	0.009-0.888	[24, 25, 27, 35–37]
1 1 1 30	Malic enzyme	Tatramer	Mucha	$_{mMF*}$	$ME^*$ ;	*80	0.000-0.020	[25, 41]	0.000-0.541	[25, 27, 41]
C.1.1.1	(NAD <sup>+</sup> )	ן כון מוווכו	Alucuta	имп	ME-NAD*	011*	0.000-0.160	[41]	0.000	[41]

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Table (C	Contd.)									
E.C. NO.	Enzyme	Quaternary structure	Tissue, in which the locus is expressed	Locus	Frequently used syn- onyms	Allele	Allele frequen- cy in European populations	Literature sources (Europe)	Allele frequen- cy in North American populations	Literature sources (North America)
1.1.1.40	Malic enzyme (NADP <sup>+</sup> )	Tetramer	Muscle	mMEP-2*	MEP-2*; ME-2*	*125	0.000-0.984	[16, 25, 26, 28–32, 37]	0.200-1.000	[24, 25, 27, 35, 35, 36, 37]
						*Tf-2 > *100	0.000-0.125	[23, 40, 42]	0.000	[42, 44, 45]
I	Transferrin	Monomer	Blood serum	$TF^*$	I	*Tf-3 (rare)	0.000	[42, 43]	0.000-0.160	[42, 46]
						*Tf-4 < *100	0.000	[42]	0.070-0.915	[42, 44–46]
5311	Triosophosphate	Dimer	T iver ave	TD1_3*		*103	0.000-0.500	[16, 25, 28, 29]	0.000	[25]
1.1.0.0	isomerase		בוענו, נשי	6-111	I	*97	0.000-0.030	[25]	0.000	[25]
1.1.1.44	Phosphoglucon- ate dehydrogenase	Dimer	Muscle	PGDH*	PGD*	*87	0.000-0.043	[26]	I	I
						*–120 (*75)	0.000-0.144	[16, 28, 31–34]	0.000	[25, 33]
6675	Phosphoglucomu-	Monomer	Muscle, liver	PGM-2*	(PGM-1*)	*-140	0.000-0.010	[28]	I	1
1.1.E.C	tase					*45	I	I	0.000-0.008	[27]
_			Liver	PGM-1r*	PGM1-t*	$0\widetilde{O}^{-*}$	0.000	[25]	0.000-1.000	[24, 25, 27, 36]
1111	Darovidaca	Monomer	I iver	pY_7*	PX*; PO*; PFR*.	*120	0.230-0.640	[30]	I	1
1.1.1.1				7-7/1	PER-2*	*140	0.000-0.150	[30]	I	1
4.1.2.13	Fructose-biphos- phate aldolase	Tetramer	Eye	FBALD-3*	FBALD-2*	*50	0.040-0.480	[16, 25, 28, 29]	0.000-(0.071)	[24, 25]
3.1.1	Esterase	Monomer	Liver	EST-5*	I	06*	0.000-0.070	[28]	I	I
3.1	Esterase D	Dimer	Muscle	ESTD*	EST-D*; ESTD-2*	*80	0.000-0.540	[16, 25, 30]	066.0	[25]

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## Intercontinental Differences

It follows from the data presented in the table that Atlantic salmon from the east and west coasts of the Atlantic differ but slightly. In any case, general characteristics of gene diversity widely overlap for most proteins. However, the available data are scarce for some low-polymorphic loci: the loci have been examined only in some populations, sometimes within a continent.

Intercontinental differences are clear at loci *PGM-1r\**, *sMDH-B1\**, *mME\**, as well as probably *sAAT-4\** and *TF\**, and partly *ESTD\**.

For instance, Atlantic salmon from North America is polymorphic at the regulatory locus of phosphoglucomutase, *PGM-1r*\*. Allele *Q0*, responsible for reducing the enzyme activity [47], occurs at high frequency in all populations of the Atlantic west coast, but has not yet been found in European salmon.

The malate dehydrogenase locus *sMDH-B1*<sup>\*</sup> is polymorphic in both American and European populations. In all of them, allele \*75 occurs at a low frequency. However, in all North American populations studied, another allele, \*120, is found. In many cases, the latter prevails even over the \*100 allele. In a few populations of East Atlantic allele 120<sup>\*</sup> is very rare, being absent in most of them.

Vespoor and McCarthy [41] examined the distribution of alternative alleles mME\*80 and mME\*110 of the malic enzyme (NADP<sup>+</sup>) across the main part of the Atlantic salmon range (75 populations from the both sides of the Atlantic) and found that the slow allele of this enzyme is generally present at a significant frequency in the American, but not the European, populations of the species. The fast allele is lacking in the populations of the western part of the range, being extremely rare in the eastern part, as well as the slow allele.

The data for locus  $sAAT-4^*$  are somewhat contradictory. For instance, some authors (see references in the table), in particular Vespoor [27, 35, 36], who had examined many Atlantic salmon populations from both Europe and North America, report a high frequency of allele \*50 in American populations but either do not find in them allele \*25, or very rarely record it at an extremely high frequency. Yet, in his comparison of populations from the two continents, Stahl [33] recorded wide distribution of allele \*50. Since the discrepancy between the results by Stahl and the data reported by other authors may be explained by a technical error of the former, the data for the  $sAAT-4^*$  locus in the table are given without accounting for [33].

The data on the frequency range of minor *sAAT-4*\* alleles show that European and American populations are clearly different at this locus.

Some studies discuss intercontinental differences at the transferrin locus  $TF^*$  [42, 45, 46, 48, 49]. In addition to the shared allele, which is usually denoted \*Tf-1,

in European populations is found allele \*Tf-2, and in American populations, rare allele \*Tf-3 and widespread allele \*Tf-4. Note, however, that transferrins of Atlantic salmon, especially European salmon, are poorly studied: only three Swedish populations from the Baltic Sea basin, as well as several populations from the British Isles and Ireland have been examined with regard to these proteins. Corresponding data on the European North of Russia, Norway, and Atlantic Swedish coast are lacking in literature.

However, Norwegian populations inhabiting the regions adjacent to Russia, populations of Kola Peninsula and western Baltic Sea coast substantially differ from the populations of the Baltic basin, British Isles, and other European regions. Only here on the European continent occurs allele *ESTD*\*80, which is close to fixation in most North American populations, its frequency being quite high in some populations of Kola Peninsula [25, 29, 30, 50–52]. The appearance of carriers of this allele in the Baltic region [25, 53] is probably related to the introduction of fish of the Canadian origin in one of the rivers of this basin.

Unfortunately, population of the European North of Russia are scarcely studied at such characterological loci as *FBALD-3\**, *TRI-3\**, locus *TF\**, and most low-polymorphic loci. This sometimes hinders comparison of the data on the Russian populations with the data obtained for other parts of the species range.

Such studies appear important because there are increasingly more data indicating that in the post-glacial period, Kola Peninsula was colonized by fish from three different refugia: American, West European, and Baltic. Exactly in this part of the species range, the highest genetic diversity in allozyme loci and mito-chondrial DNA (see below) is observed [52]. Here occur allelic enzyme variants that are characteristic for North American populations (see the table) but absent in the other populations of Europe. For instance, in addition to *ESTD\*80*, the rare allele *GPI-A\*110* was found in Kola Peninsula [38].

This new evidence indicating a contact between salmons of the two continents in the post-glacial period, shed doubt on the presence of two isolated subspecies of Atlantic salmon, which are recognized by some authors [42].

## Interpopulation Differences and Differences among Intrapopulation Fish Groups

Interpopulation differences within the European continent in total exceed the differences among the North American populations. This is evidenced by the range of variation of the frequencies of minor protein alleles within each continent (table).

Differences among populations of different rivers within regions have been shown in a number of works (see [16] for review and references in the table). In particular, several studies deal with genetic differentiation of populations from the European North of Russia [29, 30, 50, 52, 54, 55].

Various authors have repeatedly noted the existence of intrapopulation groups of Atlantic salmon in some rivers (both of Europe and America), inferred from allozyme analysis of fish originating from different tributaries [16, 26, 33, 37, 39, 56–63] or inhabiting different rapids [64]. The differences among subpopulations were sometimes so great that exceeded the differences among the populations of rivers within the region [16, 37], but in other cases, no differences among the tributaries were recorded [65, 66].

A special intrapopulation group is constituted by dwarf males that cross with anadromous females. One of the characteristic features of this group is high allozyme heterozygosity [67], which is probably explained by the fact that this group includes fish with high maturation and growth rate, and these parameters correlate with heterozygosity [68]. There are also data on association of dwarf size with the presence of the \*0Q allele of the regulatory locus *PGM-1r*\* in the genome [47].

Though very infrequently, allozyme markers prove to be helpful in more fine-scale intrapopulation studies. For instance, genetic differences between spawners of different running times within a river were revealed by allozyme analysis [69, 70]. The immunological method did not detect differences between "winter" and "summer" individuals from the same population, although this method permitted to distinguish fish samples from different populations [71].

In experimental conditions, allozymes were used for estimating the proportion of progeny of anadromous and dwarf males in the population. Even in the presence of anadromous males, dwarf males proved to be able to fertilize nearly one-third of all eggs [72, 73].

# Differences among Anadromous and Freshwater Forms

Significant differences between the anadromous and freshwater populations in frequencies of different allelic protein variants, even within a river system, were shown by many authors [36, 44, 74–77]. The mean heterozygosity was generally lower in freshwater Atlantic salmon populations than in anadromous ones, which suggested strong effect of gene drift in freshwater isolates [36, 76, 78].

The differentiation among the freshwater population of each region is higher than that among the anadromous populations. The freshwater populations do not form an isolated group in genetic similarity dendrograms, having at the same time little similarity with the neighboring anadromous populations. Sometimes they are clustered with populations from other regions or even another continent, i.e., the differences between anadromous and freshwater populations can reach the level of intercontinental differences [36, 55, 76]. There are two basic viewpoints on the origin of this diversity of freshwater populations. Some authors believe that it is associated with the history of colonization of the water reservoirs [36, 55], while others explain it by stochastic reasons, mainly the founder effect or gene drift [36, 76].

No particular trends have been revealed in the distribution of allelic protein variant in freshwater populations. The PGM-1r\*0Q was thought to be the only exception: its frequency in freshwater populations of North America is very high, and in some cases it is even fixed; therefore, selection for this allele was thought possible [36].

However, observations of artificially reproduced Atlantic salmon populations, particularly captive broodstocks that are constantly kept in fresh water, yielded evidence showing that selection may play the leading role in the formation also of other genetic features of freshwater populations. For instance, we have shown [79] that the freshwater captive broodstock derived from the progeny of anadromous spawners from the Keret' River, in the frequencies of *mMEP-2\** alleles approached the Kuito Lake population of the White Sea basin.

#### Monitoring of the Population Genetic Structure

In a number of studies, allozyme allele frequencies were compared in samples collected from the same population in different years. The genetic structure of natural populations that are not under significant anthropogenic pressure generally does not change with time. Only sometimes these population experience slight fluctuations of allele frequencies at some loci [37, 39, 56, 61, 63, 66, 70, 74, 80–86]. By contrast, changes in allele frequencies were recorded in populations supplemented by artificially reared fish or in the populations of rivers subject to intense fishery [59, 74, 86–89], which in some cases may be selective [70].

It has been shown that selected lines of Atlantic salmon significantly differ from natural populations in allozyme frequencies, even if the former are derived from the latter [28, 56, 85, 90–97]. Thus, in some cases allozymes can be used for assessing the effect on the natural gene pool of both fish purposefully transplanted in the rivers from other populations, and commercial fish that have escaped pools [83, 88, 95, 98–105]. The listed studies showed that the survival of non-native fish in the "alien" river is far lower than that of the local fish, but in the case of mass introduction the impact of the foreign fish can be very strong [103].

The genetic structure of artificially maintained populations may differ form the structure of the original populations even in the absence of directional selection [33, 59, 74, 82, 106–108], because the former experience effects of a set of new factors. For instance, some authors found differences between juvenile generations in hatcheries [33, 82, 109–111], which they explained by gene drift or the founder effect. However, at least in some cases, these changes could be caused by uncontrolled selection [79, 112–117].

The set of factors affecting artificially raised juveniles and in general on populations of the rivers to which these juveniles are released, has long escaped due attention. However, in recent years some technologies have been developed to promote maintenance of the gene pool of artificially reproduced fish and the efficiency of these measures have been tested in practice [117–120].

# Adaptive Significance of Allozyme Polymorphism

To date, most authors agree that allozyme polymorphism has adaptive significance. For instance, many studies have shown that fish with higher allozyme heterozygosity exhibit higher rates of growth, development, and maturation [67, 68, 121, 122]. There is evidence indication an inverse relationship between multilocus heterozygosity and fluctuating asymmetry of morphological traits (the latter index measures developmental stability) [122–124], although this association was not found in other experiments [108, 125, 126]. In one of the above studies, the authors, nevertheless, note that the *IDDH-2*\* heterozygotes showed lower fluctuating asymmetry than the corresponding homozygotes [108].

Numerous data suggest adaptive character of polymorphism at particular protein loci, which include *TF*\* [44, 45], *sIDHP-3*\*, *PE*\* [127], the trypsin-encoding locus *TRP-2*\* [128–134], *mMEP-2*\* ([39, 70, 87, 94, 135–140]; see [16] for review), *PGM-1r*\* [47], *IDDH-2*\* [115], and *sAAT-4*\* [115, 140]. In these works, correlation between allele frequencies with environmental parameters (temperature) or differences between the carriers of different genotypes in adaptive traits (in most cases size) were recorded. The studies with technical errors are omitted from this list (their critical discussion see in [79]).

In Russian hatcheries direct evidence of selection at loci *sAAT-4\** [112], *mMEP-2\** [79, 113], *sIDHP-3\** [79, 114], *ESTD\** [116] upon two-year fish rearing. Unintentional processes of this kind are caused by low rates of juvenile growth under conditions of the North, and consequently a long hatchery cycle and high selective culling during the rearing process.

Thus, polymorphism at a high number of allozyme loci may be adaptive in particular environmental conditions.

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