EESTI NSV TEADUSTE AKADEEMIA TOIMETISED. BIOLOOGIA
ИЗВЕСТИЯ АКАДЕМИИ НАУК ЭСТОНСКОЙ ССР. БИОЛОГИЯ
PROCEEDINGS OF THE ACADEMY OF SCIENCES OF THE ESTONIAN SSR.BIOLOGY
1984, 33, 2

УДК 575.174:597.553.2

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ELECTROPHORETIC VARIATION OF PROTEINS AND GENETIC DIFFERENTIATION IN SOME STOCKS OF RAINBOW TROUT FROM ESTONIAN FISH HATCHERIES

Rainbow trout (*Salmo gairdneri*) is one of the most important fish species cultivated in ponds all over the world. There are several trout farms in Estonia, too. However, little is known about the origin, genetic structure and possible relationships between Estonian rainbow trout populations.

The main purpose of the study was to detect polymorphic enzymes in rainbow trout and describe with their help the genetic structure of various rainbow trout stocks cultivated in Estonia. Comparing our experimental results with literature data, we tried to find out the differences and relationships between rainbow trout stocks of different origin.

Material and methods

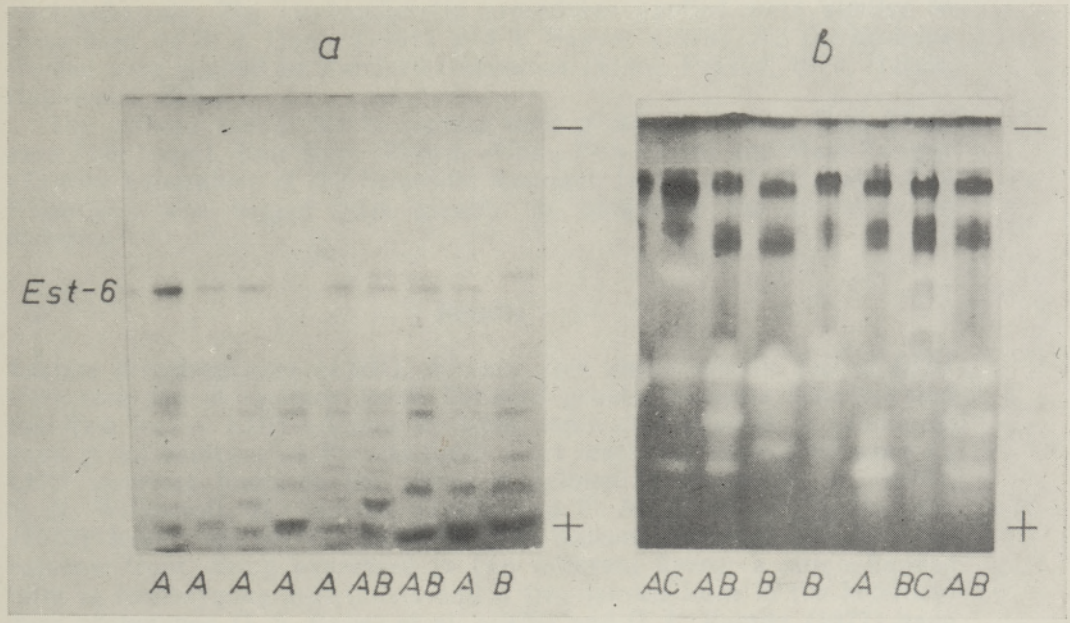
The material used in the study was collected in the following rainbow trout hatcheries in the Estonian SSR:

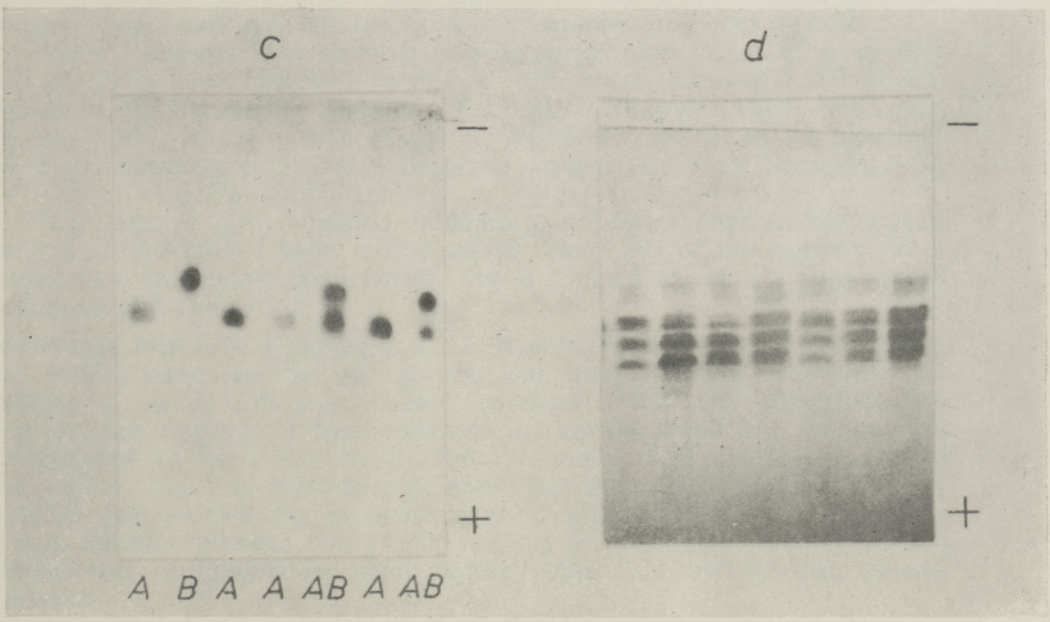
1. Keila-Joa — 50 specimens (age group 0+);
2. Keila-Joa+Vohnja+Roosna-Alliku — 101 specimens (mixed material, age group 0+);
3. Aravuse — 132 specimens (mixed material, 2, 3 or 4 years old);
4. Põlula — 25 specimens (2 years old);
5. Roosna-Alliku
5.1. caught in December 1981 — 49 specimens (2 years old);
5.2. caught in March 1982 — 50 specimens (2 years old);
6. Pidula — 30 specimens (3 years old).

Practically all the domesticated rainbow trout strains in the world are descendants of Californian rainbow trout (Busack et al., 1979). Rainbow trout was introduced into Estonia before World War II. Systematic rainbow trout farming began in the Estonian SSR in the late forties. In 1948 rainbow trout was introduced from the German DR into the Soviet Union (Ropsha Experimental Fish Farm near Leningrad). In 1952 rainbow trout was introduced from Ropsha into Estonia, into the Põlula Fish Hatchery (Post, 1976). Most trout stocks cultivated in Estonia nowadays have taken their origin from the Põlula stock, but almost all of them have been mixed with new introductions from Czechoslovakia, Finland and Denmark.

We studied two selections (December 1981, March 1982) of the recently introduced materials from Japan, the USA and Finland which had been reared in the Roosna-Alliku hatchery. Both choices consisted of 150 fish, 50 in each group. We did not have at our disposal more detailed data on the origin of the introduced fish.

Samples were taken from the liver, white skeletal muscle, blood and





Est-6 types (*a*), SOD types (*b*), PGM types (*c*) and MDH types (*d*) in the rainbow trout.

erythrocytes. Twelve protein systems were studied by polyacrylamide gel electrophoresis. The electrophoretic procedures applied were similar to those used by B. J. Davis (1964) and T. Paaver (1979). All the proteins studied were stained by standard techniques (Shaw, Prasad, 1970; Harris, Hopkinson, 1976).

The authors would like to express their gratitude to Ilme Post (Aravuse Fish Farm), Enn Soon (Roosna-Alliku Fish Farm) and Mart Kangur (Tallinn Laboratory of the Scientific Research Institute of the Baltic Sea Fisheries), who helped them greatly in obtaining the investigation material.

Results

Lactate dehydrogenase (LDH). At least five tissue specific loci of LDH were recorded in rainbow trout. Detailed genetic analysis demonstrated that two loci of LDH (A and B) were duplicated. Studies in salmonids have given evidence of the existence of at least one locus producing C_4 LDH isozymes found in the retina of salmonids (Bailey et al., 1976). S. N. Williscroft, H. Tsuyuki (1970) and F. M. Utter, H. O. Hodgins (1972) have reported the LDH-B^2 gene variant found in the liver of rainbow trout, being expressed in two different forms: a single-banded form in homozygous individuals and a five-banded form in the heterozygous phenotypes. G. S. Bailey et al. (1976) and G. L. Reinitz (1977) have detected the polymorphism of the same locus in the blood and some other tissues. R. Guyomard (1981) has studied the LDH phenotypes from the muscle, heart and eye. He describes five monomorphic loci of LDH.

Several authors have studied the polymorphic locus of LDH in greater detail. They have observed functional differences between LDH phenotypes in the swimming stamina (Tsuyuki, Williscroft, 1977; Northcote, Kelso, 1981), in pH optima (Tsuyuki, Williscroft, 1973), in the tolerance of high temperatures and low dissolved oxygen (Redding, Schreck, 1979; Klar, Stalnaker, Farley, 1979).

We detected a five-banded monomorphic LDH system in the muscle and a single-banded form in the serum. The LDH of the rainbow trout liver was not clearly perceivable, but it seemed to be a single-banded monomorphic system.

Esterases (Est). N. Kingsbury, C. J. Masters (1972) and F. M. Utter et al. (1974) have reported one polymorphic liver esterase locus with two alleles. G. A. E. Gall and his co-researchers (1976) have described two independent systems of liver esterases in rainbow trout. The systems are designated as Est-1 and Est-2 (from the slowest to the fastest anodal migration). Est-2 is monomorphic, Est-1 has two alleles. G. D. Grossman (1977) has studied the polymorphism of plasma esterases in rainbow trout. He has recorded two allelic systems of plasma esterases with two phenotypes: single-banded slow homozygotes and two-banded heterozygotes.

We studied the polymorphism of the liver and blood esterases in rainbow trout. In the liver we detected at least six esterase loci. We designated them as Est-1, ..., Est-6 (from the fastest to the slowest anodal migration). Est-1 was monomorphic. The others seemed to be polymorphic, but in most of the series studied the patterns were not clear enough. Est-6 was studied in greater detail (Figure, *a*). In this zone the usual two-allele polymorphism was observed, containing one band in the homozygotes and two bands in the heterozygotes. The frequencies of the genotypes and the alleles of Est-6 are presented in Table 1. We suggest that Est-6 is identical with the esterases investigated by N. Kingsbury, C. J. Masters (1972), F. W. Allendorf et al. (1975) and G. A. E. Gall et

Table 1

Comparison of Est-6 gene frequencies of the investigated rainbow trout stocks

Stock	Sample size	Genotype			Gene frequency		χ^2
		AA	AB	BB	A	B	
Aravuse	132	47 (8.49)	49 (65.58)	36 (27.93)	0.54	0.46	8.40**
Keila-Joa	49	24 (22.66)	19 (21.32)	6 (5.02)	0.68	0.32	0.52
Keila-Joa+Vohnja+ Roosna-Alliku	99	57 (51.32)	29 (39.92)	13 (7.76)	0.72	0.28	7.16**
Roosna-Alliku, 1981	49	14 (14.29)	25 (24.34)	10 (10.37)	0.54	0.46	0.04
Roosna-Alliku, 1982	50	22 (22.45)	23 (22.11)	5 (5.45)	0.67	0.33	0.09
Roosna-Alliku, 1981+1982	99	36 (36)	48 (48)	15 (15)	0.60	0.40	—
Pidula	30	6 (8.11)	19 (14.98)	5 (6.91)	0.52	0.48	2.16
Põlula	25	10 (10.24)	12 (11.52)	3 (3.24)	0.64	0.36	0.05
American, 1981	48	40 (37.92)	5 (9.40)	3 (0.58)	0.89	0.11	12.27***
American, 1982	52	36 (31.64)	9 (17.85)	7 (2.52)	0.78	0.22	14.0***
American, 1981+1982	100	76 (68.89)	14 (28.22)	10 (2.89)	0.83	0.17	25.39***
Finnish, 1981	48	24 (20.91)	15 (21.54)	9 (5.55)	0.66	0.34	4.59*
Finnish, 1982	51	14 (12.75)	23 (25.5)	14 (12.75)	0.50	0.50	0.49
Finnish, 1981+1982	99	38 (33.30)	38 (48.23)	23 (17.46)	0.58	0.42	4.59*
Japanese, 1981	50	29 (28.88)	18 (18.24)	3 (2.88)	0.76	0.24	0.01
Japanese, 1982	49	25 (28.30)	24 (17.88)	— (2.82)	0.76	0.24	2.47
Japanese, 1981+1982	99	54 (57.18)	42 (36.12)	3 (5.70)	0.76	0.24	2.48

*$p < 0{,}05$; **$p < 0{,}01$; ***$p < 0{,}001$.

al. (1976), as it is the most intensively stained esterase zone, its pattern is similar and its allele frequencies and electrophoretic mobility are close to those referred in literature.

We did not observe blood plasma esterase polymorphism. The polymorphic esterase detected by G. D. Grossman seems not to be identical with that detected in the liver.

E. Diebig et al. (1979) have described the simple two-allele polymorphism of carbonic anhydrase (CA) in the rainbow trout liver, where β-naphthylacetate serves as the substrate of CA (usually it is also a substrate of unspecific esterases). We tried to detect CA polymorphism in

Comparison of SOD gene frequencies of the investigated rainbow trout stocks *Table 2*

Stock	Sample size	Genotype						Gene frequency			χ^2
		AA	AB	AC	BB	BC	CC	A	B	C	
Aravuse	132	1 (0.76)	17 (17.17)	1 (1.36)	97 (96.72)	15 (15.37)	1 (0.76)	0.07	0.86	0.07	0.44
Keila-Joa	50	— (0.61)	6 (5.61)	5 (4.18)	12 (13.01)	21 (19.38)	6 (7.22)	0.11	0.51	0.38	0.62
Keila-Joa+Vohnja+ Roosna-Alliku	100	1 (1.69)	20 (19.76)	4 (2.86)	58 (57.76)	16 (16.72)	1 (1.21)	0.13	0.76	0.11	0.80
Roosna-Alliku, 1981	49	2 (0.96)	9 (10.7)	1 (1.11)	31 (29.81)	5 (6.12)	1 (0.31)	0.14	0.78	0.08	3.2
Roosna-Alliku, 1982	51	1 (0.86)	11 (11.01)	— (0.53)	35 (35.13)	4 (3.39)	— (0.08)	0.13	0.83	0.04	0.13
Roosna-Alliku, 1981+1982	100	3 (1.96)	20 (22.69)	1 (1.68)	66 (65.61)	9 (9.72)	1 (0.36)	0.14	0.81	0.06	1.34
Pidula	30	— (0.08)	3 (2.61)	— (0.24)	22 (22.71)	5 (4.18)	— (0.19)	0.05	0.87	0.08	0.24
Põlula	27	3 (1.31)	6 (18.79)	— (0.48)	16 (14.79)	2 (1.60)	— (0.04)	0.22	0.74	0.04	3.27
American, 1981	50	4 (2.88)	16 (18.24)	—	30 (28.88)	—	—	0.24	0.76	—	0.76
American, 1982	52	6 (6.01)	23 (23.34)	—	23 (22.65)	—	—	0.34	0.66	—	0.02
American, 1981+1982	102	10 (8.58)	39 (42.0)	—	53 (51.42)	—	—	0.29	0.71	—	0.5
Finnish, 1981	48	5 (3.24)	15 (17.72)	— (0.75)	25 (24.20)	3 (2.04)	— (0.04)	0.26	0.71	0.03	1.86
Finnish, 1982	51	3 (2.70)	15 (17.36)	2 (0.70)	29 (27.93)	2 (2.26)	— (0.05)	0.23	0.74	0.03	2.83
Finnish, 1981+1982	99	38 (5.70)	30 (34.2)	2 (1.9)	54 (51.32)	5 (5.70)	— (0.16)	0.24	0.72	0.04	1.67
Japanese, 1981	50	6 (4.81)	19 (21.39)	—	25 (23.81)	—	—	0.31	0.69	—	0.62
Japanese, 1982	50	4 (4.81)	22 (20.46)	1 (0.93)	21 (21.78)	2 (1.98)	— (0.05)	0.31	0.66	0.03	0.33
Japanese, 1981+1982	100	10 (9.61)	41 (41.85)	1 (0.93)	46 (45.56)	2 (2.03)	— (0.02)	0.31	0.67	0.02	0.05

rainbow trout, using the same staining method as E. Diebig, but the proposed CA had the similar electrophoretic mobility as Est-6 and its phenotypes occurred to be identical with the phenotypes of Est-6. On the basis of that phenomenon we suggest that the CA reported by E. Diebig et al. (1979) is practically Est-6.

Superoxide dismutase (SOD). Breeding studies have proved that SOD is encoded by one locus in the rainbow trout liver (Utter et al., 1973). Three alleles have been detected for this enzyme (Utter, Hodgins, 1972; Diebig et al., 1979; Guyomard, 1981). The third allele, however, is very rare in American rainbow trout populations.

The study carried out by us supported the model of one polymorphic locus with three alleles (Figure, *b*). The homozygotes had one band, the heterozygotes had three bands. A comparison of allelic frequencies in different stocks of rainbow trout is given in Table 2.

Phosphoglucomutase (PGM). F. L. Roberts et al. (1969) have discovered the diallelic polymorphism of PGM in the skeletal muscle of rainbow trout. This model has also been approved by several authors (Utter, Hodgins, 1972; Gall et al., 1976; Guyomard, 1981).

We found two alleles of PGM in the muscles of rainbow trout (Figure, *c*). The homozygotes had one band and the heterozygotes had two bands. The allelic frequencies in some stocks of rainbow trout are given in Table 3.

Table 3

Comparison of PGM gene frequencies of the investigated rainbow trout stocks

Stock	Sample size	Genotype			Gene frequency	
		AA	AB	BB	A	B
Aravuse	82	72 (72.46)	10 (9.25)	— (0.30)	0.94	0.06
Keila-Joa	50	44 (44.18)	6 (5.64)	— (0.18)	0.94	0.06
Keila-Joa+Vohnja+ Roosna-Alliku	101	92 (92.92)	9 (7.76)	— (0.16)	0.96	0.04
Põlula	16	15 (15.04)	1 (0.93)	— (0.01)	0.97	0.03
Roosna-Alliku, 1981	50	45 (45.12)	5 (4.75)	— (0.13)	0.95	0.05
American, 1981	50	50	—	—	1.00	0
Finnish, 1981	51	37 (37.96)	14 (12.98)	— (0.14)	0.86	0.14
Japanese, 1981	50	32 (32.0)	16 (16.0)	2 (2.0)	0.80	0.20

Malate dehydrogenase (MDH). G. S. Bailey et al. (1970) have described two genetically distinct types (A and B) of supernatant MDH subunits in salmonids. The B type subunits predominate in the skeletal muscle. F. M. Utter and H. O. Hodgins (1972) assume that in rainbow trout there exists a duplicate locus producing a B type MDH. C. A. Busack et al. (1979) and R. Guyomard (1981) assume that the subsystem A is encoded by two loci denoted as MDH-1, MDH-2. MDH-1 is monomorphic, while MDH-2 is polymorphic. In rainbow trout the B subsystem also consists of two loci (MDH-3, MDH-4), both of them being polymorphic.

We detected a monomorphic zone of MDH in the rainbow trout muscle (Figure, *d*). However, the genotypes were not clearly distinguishable and there occurred a strong quantitative variation in the intensity of bands.

Alpha-glycerophosphate dehydrogenase (α-GPDH). F. M. Utter and H. O. Hodgins (1972) report upon α-GPDH polymorphism found in the muscle of rainbow trout occurring as a single-banded enzyme form in homozygous individuals and as a three-banded in heterozygous phenotypes. The second, fixed locus is detectable in a particular buffer system only (Allendorf et al., 1975). C. A. Busack et al. (1979) and R. Guyomard (1981) have also described a single polymorphic locus with two alleles. However, the frequency of the second allele is very low.

In the present study we have assumed a model of a single polymorphic locus with two alleles. Homozygous individuals had one band and the heterozygotes had three bands. The frequency of the second allele was also very low in the material investigated.

Two loci of aspartate amino transferase (AAT) have been reported in rainbow trout (Allendorf et al., 1975). Only one of them (muscle AAT) occurred to be polymorphic (Busack et al., 1979). According to literature data, the glucose-6-phosphate dehydrogenase in rainbow trout (G-6-PDH) is polymorphic (Diebig et al., 1979). Monomorphism has been reported in such systems as PGI-phosphoglucoseisomerase (Avise, Kitto, 1973) and ADH-alcohol dehydrogenase (Allendorf et al., 1975; Busack et al., 1979; Guyomard, 1981).

We detected polymorphism of G-6-PDH and monomorphism in the general protein of the muscle and in hemoglobin. The AAT, PGI and ADH also seemed to be monomorphic, but unfortunately the resolution of those enzymes was very poor and the bands were unclear in our electrophoretic conditions.

Discussion

A comparison of the Estonian rainbow trout stocks has proved that they have a quite similar genetic profile.

On the basis of the results obtained we can draw a conclusion that the Estonian rainbow trout population is rather homogeneous due to its common origin. The latter mixing with new introductions has not changed its genetic structure to any significant extent. PGM is the best system to confirm it. Gene frequencies were almost equal in all the stocks studied (the frequency of the common allele fluctuated between 0.94 and 0.97). As to SOD, the differences in allele frequencies were not very significant, either. In all the groups studied there predominated the intermediate allele, ranging from 0.51 to 0.87, but in the Keila-Joa stock the frequency of the SOD-C allele was significantly higher.

The esterases were the most complicated system to explain. The distribution of the Est-6 phenotypes in the two Estonian stocks (Aravuse and Keila-Joa+Vohnja+Roosna-Alliku) and in the American steelhead group sharply deviated from the frequencies expected under the Hardy-Weinberg formula, showing a considerable deficiency of heterozygous individuals. Deviations, although not so great, were also observed in the Finnish group. The causes of the deviation may be of a random character, but they might be due to the mixing of different materials. The investigated material representing the Aravuse stock contained fish of various age groups (2, 3, 4), while the Keila-Joa+Vohnja+Roosna-Alliku material consisted of three different stocks.

Japanese, American, Finnish and Roosna-Alliku fish populations were examined twice. Samples representing two successive selections from the Japanese fish stock were almost identical, but in the other choices the

allele frequencies of SOD and Est-6 were slightly fluctuating. Thus we may conclude that the small random choices may occasionally differ from each other, and that they do not reflect the real genetic structure of a fish population.

A comparison of the European and American rainbow trout stocks on the basis of the results obtained by us and literature data indicates that their genetic profiles are quite different. In European rainbow trout there have been recorded three alleles of SOD. F. M. Utter and H. O. Hodgins (1972) have also pointed out the existence of the third allele, but they do not give the allele frequency. The other American investigators have not referred to the third allele of SOD, while in the rainbow trout populations cultivated in Europe this allele (the slowest one) has been recorded rather frequently (Diebig et al., 1979; Guyomard, 1981). The situation is different with the LDH polymorphism in European and American rainbow stocks. R. Guyomard (1981) and the authors of the present investigation have not detected any LDH polymorphism in rainbow trout, while the LDH-B^2 polymorphism has been reported by the American investigators. As to the other enzymes studied, PGM, α-GPDH, MDH, Est-6 appeared to be polymorphic, while ADH, PGI were monomorphic in both the American and European rainbow stocks. Thus the rainbow trout reared in Europe shows wide genetic variability. C. A. Busack et al. (1979) have proposed two possible explanations of the high variability of the domesticated trout strains: 1) the variability is a remainder of a high initial variability created by mixing trout from several sources to form strains, 2) much of this variability is maintained by balancing selection.

The temperature conditions are quite different in the water bodies of the Estonian hatcheries. At Roosna-Alliku, the temperature is almost stable all the year round as the hatchery receives its water from springs. But in the Aravuse ponds, for example, the temperature is more unsteady, for they receive their water from the river. The similar genetic profile in all the stocks confirms the absence of temperature-dependent ecological differences between electrophoretically distinct phenotypes of investigated enzymes.

Summary

The genetic composition of six rainbow trout stocks originating from the German DR and reared in Estonian hatcheries in several generations, and of three rainbow trout stocks recently introduced from the USA, Japan and Finland, was studied electrophoretically. Of the twelve proteins examined, LDH, ADH, AAT, My, PGI and Hb were monomorphic, while MDH, PGM, SOD, Est-6, α-GPDH and G-6-PDH were polymorphic. Gene frequencies of Est-6, PGM and SOD in the rainbow stocks investigated are given. A comparison of the Estonian rainbow trout stocks showed that their genetic profile was quite similar, being characteristic of all European trout populations. Deviations from the Hardy-Weinberg equilibrium in the distribution of Est-6 phenotypes were observed in two Estonian stocks, in American and Finnish steelhead stocks. The genetic profiles of American and European rainbow trout stocks were quite different. Different temperature conditions were not reflected in the distribution of the genotypes of polymorphic proteins.

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Received
March 31, 1983

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VALKUDE ELEKTROFOREETILINE VARIEERUVUS JA GENEETILINE DIFERENTSEERUMINE MÕNEDES EESTI VIKERFORELLIKARJADES

On uuritud erinevate Eesti kalamajandite vikerforellipopulatsioonide ja hiljuti USA-st, Jaapanist ja Soomest introdutseeritud vikerforellide geneetilist struktuuri. Kaheteistkümnest käsitletud valgust olid LDH, ADH, AAT, My, PGI ja Hb monomorfsed; MDH, PGM, SOD, Est-6, α-GPDH ja G-6-PDH aga polümorfsed. Tasakaaluarvutused Hardy-Weinbergi järgi andsid Est-6 genotüüpide osas suuri kõrvalekaldeid, mida võisid tingida juhuslikud katsevead, materjali ebaühtlane päritolu või mõne valikuteguri mõju Est-6 genotüüpidele. Eesti vikerforellikarjade võrdlev analüüs näitas nende geneetilise struktuuri sarnasust. Euroopa päritoluga vikerforellikarjade geneetiline struktuur erines Ameerika vikerforellide omast. Uuritud materjali puhul otsest keskkonnatingimuste mõju polümorfsete valkude genotüüpidele ei täheldatud.

Тийт ПААВЕР, Айли ЛИЛЛЕОРГ

ЭЛЕКТРОФОРЕТИЧЕСКАЯ ИЗМЕНЧИВОСТЬ БЕЛКОВ И ГЕНЕТИЧЕСКАЯ ДИФФЕРЕНЦИАЦИЯ НЕКОТОРЫХ СТАД РАДУЖНОЙ ФОРЕЛИ В ЭСТОНИИ

Исследовали генетическую структуру стад радужной форели из разных рыбхозов Эстонской ССР, а также недавно интродуцированной форели из США, Японии и Финляндии. Обнаружен полиморфизм у МДГ, ФГМ, СОД, Эст-6, АГФДГ, Г-6-ФДГ. Мономорфными оказались ЛДГ, АДГ, ААТ, Ми, ФГИ и гемоглобин. Рассмотрены отклонения распределения генотипов Эст-6 от равновесия по Харди—Вейнбергу. Показано сходство генетических структур популяции радужной форели в разных рыбхозах Эстонской ССР. Показаны различия между популяциями радужной форели в Европе и Америке.