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Natural Hybrids of *Salmo salar* with *Salmo trutta* in the Rivers of the White Sea Basin

A. A. Makhrov*, K. V. Kuzishchin, and G. G. Novikov****

* *Institute of General Genetics, Russian Academy of Sciences, ul. Gubkina, 3, Moscow 117809 Russia,*
E-mail: makhrov@vigg.ru
** *Biological Faculty, Moscow State University, Vorob'evy gory, Moscow 119899 Russia*

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Abstract—Among *Salmo salar* and *S. trutta* parr in the Keret and Nilma rivers: White Sea Basin, hybrids between these species have been identified by means of electrophoresis. The loci coding the enzymes esterase-D (ESTD*) and mannose-6-phosphateisomerase (MPI*) were used for their diagnostics. It is supposed that the origin of hybrids between these two species in nature has resulted mainly from anthropogenic influences.

INTRODUCTION

The origin of interspecific hybrids is interesting for a researcher as a good example of relativity of the reproductive criteria of species. Studies in hybridization of *Salmo salar* with *Salmo trutta* also have a practical value. A high mortality rate during ontogenesis and disturbances in gonad structure have been observed in their first generation hybrids. Hybrids of the second generation and backcrosses usually die at early developmental stages (Alm, 1955). So, the appearance of hybrids between these two species in fish hatcheries and in natural populations is undesirable. However, the identification of hybrids of these species is related to some difficulties. The differences of these hybrids from parental species in morphological characters are insignificant (Jones, 1947). *S. salar*, *S. trutta*, and their hybrids differ in chromosome numbers (Svardson, 1945; Nygren *et al.*, 1975). However, karyological analysis takes a lot of time and has little use for the studies of large numbers of fishes. The hybrids also differ from parental species in some osteological characters (Kazakov *et al.*, 1982), the level of variability of the mass of ovulated eggs (Kazakov and Il'enkova, 1982), and the morphology of gill rakers (Kazakov *et al.*, 1984). However, these characters have only been used for the identification of hybrids among spawners in fish hatcheries.

The identification of natural hybrids between *S. trutta* and *S. salar* by the use of genetic methods is also possible among the young. These species possess differences in the electrophoretic mobility of some proteins: esterases (Nyman, 1970), glucosephosphate isomerase (Guyomard, 1978), phosphoglucomutase (Beland *et al.*, 1981), octanol dehydrogenase (Osinov, 1984), superoxide dismutase (Crozier, 1984), malik-enzyme, xantine dehydrogenase (Vuorinen and Piironen, 1984), and esterase-D (Semenova and Slyn'ko, 1988). Differences between these species have also been found in the structure of mitochondrial (Gyllensten and Wilson, 1991) and nuclear (Gross *et al.*, 1996) DNA.

Genetic markers allowed the discovery of the hybrids between *S. salar* and *S. trutta* in almost all regions where these species are sympatric: the rivers of North America (Beland *et al.*, 1981; Verspoor, 1988; McGowan and Davidson, 1992), northern Spain (Garcia de Leaniz and Verspoor, 1989; Moran *et al.*, 1993), the British Isles (Payne *et al.*, 1972; Solomon and Child, 1978; Taggart *et al.*, 1981; Crozier, 1984; Hurrell and Price, 1991; Youngson *et al.*, 1992, 1993; Jordan and Verspoor, 1993; Wilson *et al.*, 1995; Hartley, 1996), the Rhine drainage (Schreiber *et al.*, 1994), the Baltic Sea basin (Semenova and Slyn'ko, 1988; Jansson *et al.*, 1991; Gross *et al.*, 1996), Norway (Stahl, unpublished data, in Heggberget *et al.*, 1988), and in the Barents Sea Basin (Semenova and Slynko, 1988; Elo *et al.*, 1995).

Hybrids between *S. salar* and *S. trutta* have not been found in rivers of the White Sea basin (Semenova and Slyn'ko, 1988), and the suggestion on the hybrid origin of *S. trutta* in Pyaozero Lake (Mel'yantsev, 1951) has not been confirmed (Makhrov, 1995). This paper contains data on the hybrids identified in the study of the genetic variation of *S. trutta* and *S. salar* in the White Sea basin.

MATERIALS AND METHODS

Materials were collected in the systems of three rivers of the White Sea basin, where populations of *S. salar* and *S. trutta* exist, namely the Kachkovka, Nilma, and Keret (Fig. 1). These rivers differ in the extent of anthropogenic influence. Uncontrolled fishing of *S. salar* takes place in all three rivers, but less so in the Kachkovka where no settlements exist. In the Keret' River, the fishing of *S. salar* has been performed

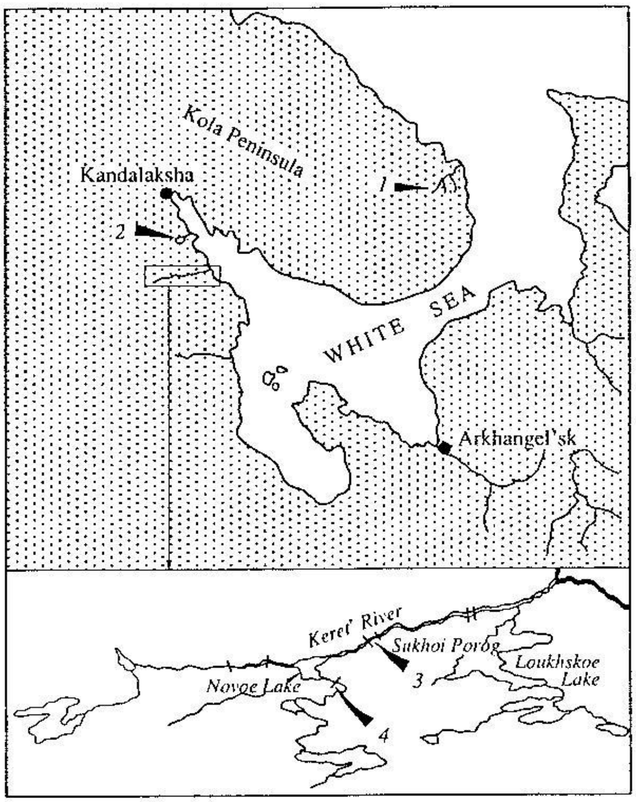

Fig. 1. Regions of material collecting: (*1*) the Kachkovka River; (*2*) the Nilma River; (*3*) Sukhoi rapid; (*4*) rapid upwards from Novoe Lake.

since 1968 by the concentrated catch method. Fifty percent or more of spawners were realized in the river, and a proportion of caught fishes were used for artificial breeding. Since 1991, the catches have decreased significantly, and since 1994 spawners have been caught only for breeding purposes. Currently, more than a half of producers of *S. salar* in the Keret' are artificial in origin (data from Karelrybvod).

The materials were collected over the whole length of the Nilma River, in the Kachkovka River system (from the tributary of the Nizhnyaya Kottevaya near the place of its confluence in the Kachkovka). In the Keret' River, the materials were collected from Sukhoi Porog and from rapid above the Novoe Lake (Fig. 1). Fishes were collected using electrofishing. The samples studied were represented mainly by the young and dwarf males. The fishes caught from the Keret' were significantly smaller than the young from the hatchery released in to this river. Therefore, they had a natural origin. The years of material collecting and sample sizes are shown in table. After biological analysis (Pravdin, 1966), the fishes were frozen and transported in this condition.

We used white muscles for the analysis. The electrophoresis of proteins was performed in 7.5% polyacrylamide gel in the apparatus described by Truveller and Nefedov (1974), using a tris-gel buffer EDTA-borate (Peacock *et al.*, 1965). The activity of the enzymes esterase-D (Ahmad *et al.*, 1977) and mannose-b-phosphate isomerase (Allendorf *et al.*, 1977) were identified in the gels.

RESULTS

Esterase-D is quite suitable for the identification of hybrid individuals. This enzyme keeps its activity for a long time during storage, is easily identified in gel, and the identification of genotypes does not face any difficulty. The locus ESTD* coding the esterase-D is monomorphic in the *S. trutta* samples studied by us but polymorphic in *S. salar*. The allele ESTD*71 was fixed in *S. trutta*, the alleles ESTD*100 and ESTD*92 in *S. salar*, which correspond to data from Semenova and

Slyn'ko (1988), although these authors indicate other values of the electrophoretic mobility of allele variants of esterase-D.

No hybrids were found in the Kachkovka River. Three hybrid individuals were found in the Keret' River, in a rapid above Novoe Lake. Their proportion was 10.4%. One of these individuals had genotype ESTD*71/100, two others ESTD*71/92. All these were brood of the year: 0+. One hybrid with genotype ESTD*71/100 at the age of 3+ (proportion 1.6%) was caught from the Nilma River in 1993 (table). One more individual, brood of the year with the same genotype, was identified in the sample of young *S. salar* (n = 100, proportion 1.0%) caught from the Nilma River in 1996, and was kindly provided for study by M.V. Ofitserov. Therefore, these individuals belong to different generations.

Initially, we did not plan to use mannose-b-phosphate isomerase for the identification of hybrids. Variability of the locus MPI* coding mannose-b-phosphate isomerase has been examined only in the samples of *S. trutta* where the alleles MPI*100 and MPI*105 have been identified. However, in the course of the study, we have found that all hybrids identified using the analysis of variation of the locus ESTD*, had genotype MPI*100/107. Studies of the sample of *S. salar* from the Nilma River (n = 20) revealed that the allele MPI*107 is fixed in *S. salar* (Fig. 2), i.e., the locus MPI* is also diagnostic for *S. trutta* and *S. salar.*

DISCUSSION

Identification of hybrids. Earlier, the locus MPI* did not fit in the diagnostic for *S. salar, S. trutta,* and their hybrids, although some researchers have compared them in these species (Johnson and Wright, 1986; Elo *et al.*, 1995). Apparently, this related to the fact that these authors used other gel buffer for analysis.

The results of the analysis by loci ESTD* and MPI* coincide. All hybrids found have a "hybrid" phenotype by both diagnostic loci. Therefore, they seem to be first generation hybrids (F_1). No individuals having a "hybrid" phenotype by only one diagnostic locus, i.e., backcrosses and second generation hybrids (F_2), were found. At the same time, it should be noted that the backcrosses obtained artificially had "hybrid" genotypes by many loci (Semenova and Slyn'ko, 1988). The progeny from the crossing of females of the hybrid and males of *S. salar* (Johnson and Wright, 1986) were represented by gynogenetic individuals and triploids. The progeny from the crossing of hybrid female and *S. trutta* males were represented mainly with triploids but some individuals were diploids (Dannewitz and Jansson, 1996).

Recombinant genotypes were identified only in progeny from the crossing of hybrid males and *S. salar* females (Nygren *et al.*, 1975; Wilkins *et al.*, 1993). In these experiments, substantial mortality rated of backcrosses were observed at early stages of development. However, it cannot be excluded that under certain conditions they can survive and produce progeny. Many facts evidence the introgression of genes from the population of *S. salar* to that of *S. trutta* and back (Verspoor and Hammar, 1991). At the same time, it has been demonstrated that the expression of some genes of one of the parental species may be suppressed in F_1 hybrids (Nygren *et al.*, 1974; Jansson and Dannewitz, 1995). Such individuals may be considered as F_2 hybrids or backcrosses.

Rivers, years of material collecting, and sample sizes

Water body	Year	Sample sizes, spec.		
		Salmo salar	*Salmo trutta*	hybrids
the Nilma River	1992	1	29	–
	1993	9	51	1
	1994	16	63	–
	1995	37	14	–
the Kachkovka River	1994	29	35	–
the Keret' River, Sukhoi rapid	1995	16	–	–
the Keret' River, above Novoe Lake	1995	18	8	3

Level of hybridization in different rivers. In our study, as in the majority of others, hybrids have been found among young fish. At the same time, hybrids among spawners have been described (Payne *et al.*, 1972; Youngson *et al.*, 1992). The proportion of hybrids among spawners is extremely high, 18.8–31.4% in the Narva River, the Baltic Sea Basin (Semenova and Slyn'ko, 1988). In all probability, these hybrids have appeared mainly due to crossing of *S. salar* and *S. trutta* in the Narva Fish hatchery (Kazakov *et al.*, 1982).

The highest proportion of hybrids was noted by us in the Keret' River exposed to the most intensive fishing. In the more favorable Nilma River the proportion of hybrids is lower. In the Kachkovka River, under the lowest anthropogenic pressure, no hybrids were found. Hybrids were not found or were very rare in other rivers of the Kola Peninsula (Semenova and Slyn'ko, 1988), as well as in many rivers of Norway and northern Finland (Heggberget *et al.*, 1988; Elo *et al.*, 1995), which face lower anthropogenic pressures than other salmon rivers of Europe.

At the same time, the proportion of hybrids *S. salar* × *S. trutta* is very high in some rivers of Sweden, up to 23% (Jansson *et al.*, 1991) and in England up to 18.2% (Hartley, 1996), although for rivers of the British Isles their much lower proportion has been indicated earlier (Paine *et al.*, 1972; Solomon and Child, 1978; Crozier, 1984; Hurrell and Price, 1991; Jordan and Verspoor, 1993). The frequency of hybridizations of *S. salar* with

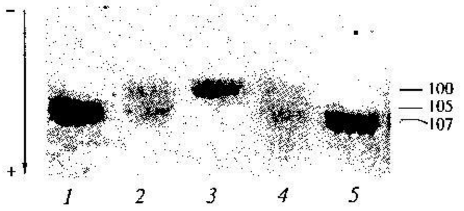

Fig. 2. Electrophoretic phenotypes of mannose-b-phosphate isomerase: (*1*) *S. trutta*, MPI*105/105; (*2*) *S. trutta*, MPI*100/105; (*3*) *S. trutta*, MPI* 100/100; (*4*) hybrid, MPI*100/107; (*5*) *Salmo salar*, MPI*107/107.

S. trutta seem to the increase with increase of anthropogenic pressure on natural water bodies.

Anthropogenic factors promoting hybridization. The origin of hybrids in the Nilma and Keret' rivers may relate to the population decline of *S. salar*, resulting from fishing. Hybrids may appear when single fishes, reaching spawning sites, cannot find a partner of the same species. In addition, with the population decline in *S. salar*, the proportion of dwarf males seems to increase (Gibson, 1978). In the Nilma River, the majority of *S. salar* males mature without migrating the sea (Kuzishchin, 1997). Hybrids *S. salar* × *S. trutta* are often encountered in rivers where the proportion of dwarf males is high in populations of *S. salar* (Garcia de Leaniz and Verspoor, 1989; Jansson *et al.*, 1991; McGowan and Davidson, 1992; Elo *et al.*, 1995). *S. salar* dwarf males may participate in the insemination of eggs together with anadromous males, but usually the larger anadromous males push out the dwarfs from the female before spawning (Myers and Hutchings, 1987). This seems to prevent dwarf males recognize the female correctly and they may mate with the female of *S. trutta*.

The gonads of dwarf males of *S. trutta* can be mature for a long time before spring (Scrochowska, 1969). Consequently they can also participate in the spawning of *S. salar*, which takes place later than that of *S. trutta*. Analysis of mitochondrial DNA revealed that hybrids can be formed as a result of the reciprocal crossing of *S. trutta* and *S. salar* (McGowan and Davidson, 1992; Youngson *et al.*, 1992, 1993; Hartley, 1996).

Probably, hybridization can be promoted by the presence of spawners from fish hatchery on the Keret' River, as it was noted that artificially reared *S. salar* females crossed with *S. trutta* more often than wild ones (Younson *et al.*, 1993). A.G. Osinov (personal communication) has found hybrids of *S. salar* with *S. trutta* in the Luven'ga River where the reared young of *S. salar* are released.

Undoubtedly, hybridization sometimes occur in rivers not influenced by anthropogenic factors. However, as a rule, sympatric populations of *S. salar* and *S. trutta* differ in time of reproduction and, to a lower extent, in the place of spawning (Heggberget *et al.*, 1988).

Apparently, the hybridization of *S. salar* with *S. trutta* in natural habitats largely resulted from anthropogenic influence. To prove it, we need yearly monitoring of the level of hybridization of these species in rivers influenced by anthropogenic activity.

Unfortunately, we should indicate that the hybridization of *S. salar* with *S. trutta* should be added to a long list of unfavorable consequences of anthropogenic influences on the White Sea rivers where *S. salar* reproduces. In this way, the appearance of natural hybrids among spawners used in salmon fish hatcheries is possible. To prevent this, it is necessary to realize the control of species of spawners; most desirably by the use of genetic methods.

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REFERENCES

Ahmad, M., Skibinski, D.O.F., and Bearmore, J.A., An Estimate of the Amount of Genetic Variation in the Common Mussel (*Mytilus edulis*), *Biochem. Genet.*, 1977, vol. 15, no. 9/10, pp. 833–846.

Allendorf, F.M., Mitchell, N., Ryman, N., and Stahl, G., Isozymes Loci in Brown Trout (*Salmo trutta*): Detection and Interpretation from Population Data, *Hereditas*, 1977, vol. 86, pp. 179–189.

Alm, G., Artificial Hybridization between Different Species of the Salmon Family, *Rep. Inst. Freshwater Res. Drottninholm*, 1955, no. 36, pp. 13–56.

Beland, K.F., Roberts, F.L., and Saunders, R.L., Evidence of *Salmo salar* × *Salmo trutta* Hybridization in North American River, *Can. J. Fish. Aquat. Sci.*, 1981, vol. 38, pp. 552–554.

Crozier, W.W., Electrophoretic Identification and Comparative Examination of Naturally Occurring F_1 hybrids between Brown Trout (*Salmo trutta* L.) and Atlantic Salmon (*S. salar* L.), *Comp. Biochem. Physiol.*, 1984, vol. 78B, no. 4, pp. 785–790.

Dannewitz, J. and Jansson, N., Triploid Progeny from a Female Atlantic Salmon × Brown Trout Hybrid Backcrossed to Male Brown Trout, *J. Fish Biol.*, 1996, vol. 48, no. 1, pp. 144–146

Elo, K., Erkinaro, J., Vuorinen, J.A., and Niemela, E., Hybridization Between Atlantic Salmon (*Salmo salar*) and Brown Trout (*Salmo trutta*) in the Teno and Naatamo River

Systems, Northernmost Europe, *Nordic J. Freshwat. Res.*, 1995, vol. 70, pp. 56–61.

Garcia de Leaniz, C. and Verspoor, E., Natural Hybridization Between Atlantic Salmon, *Salmo salar*, and Brown Trout, *Salmo trutta*, in Northern Spain, *J. Fish Biol.*, 1989, vol. 34, no. 1, pp. 41–46.

Gibson, R.J., Recent Changes in the Population of Juvenile Atlantic Salmon in the Matamak River, Quebec, Canada, *J. Cons. Int. Explor. Mer.*, 1978, vol. 38, no. 2, pp. 201–207.

Gross, R., Nilsson, J., and Schmitz, M., A New Species-Specific Nuclear DNA Marker for Identification of Hybrids Between Atlantic Salmon and Brown Trout, *J. Fish Biol.*, 1996, vol. 49, no. 3, pp. 537–540.

Guyomard, R., Identification par Electrophorese d'hybrides de Salmonides, *Ann. Genet. Sel. Anim.*, 1978, vol. 10, no. 1, pp. 17–27.

Hurtley, S.E., High Incidence of Atlantic Salmon x Brown Trout Hybrids in a Lake District Stream, *J. Fish Biol.*, 1996, vol. 48, no. 1, pp. 151–154.

Heggberget, T.G., Haukebo, T., Mork, J., and Stahl, G., Temporal and Spatial Segregation of Spawning in Sympatric Populations of Atlantic Salmon, *Salmo salar* L., and Brown Trout, *Salmo trutta* L., *J. Fish Biol.*, 1988, vol. 33, no. 3, pp. 347–356.

Gurrell, R.H. and Price, D.J., Natural Hybrids Between Atlantic Salmon, *Salmo salar* L., and Trout, *Salmo trutta* L., in Juvenile Salmonid Populations in South-West England, *J. Fish Biol.*, 1991, vol. 39, suppl. A, pp. 335–341.

Iyullesten, U. and Wilson, A.K., Mitochondrial DNA of Salmonid Fishes (Study of Intra- and Interspecific Variability Using Restriction Ferments), in *Populyatsionnaya genetika i upravlenie rybnym khozyaistvom* (Population Genetics and Fishery Management), Moscow: Agropromizdat, 1991, pp. 354–371.

Jansson, H. and Dannewitz, J., Repression of the Brown Trout GPI-1* Locus in Atlantic Salmon x Brown Trout Hybrids, *Hereditas*, 1995, vol. 122, no. 3, pp. 293–294.

Jansson, H., Holmgren, I., Wedin, K., and Andersson, T., High Frequency of Natural Hybrids Between Atlantic Salmon, *Salmo salar* L., and Brown Trout, *S. trutta* L., in a Swedish River, *J. Fish Biol.*, 1991, vol. 39, suppl. A, pp. 343–348.

Johnson, F.R. and Wright, J.E., Female Brown Trout x Atlantic Salmon Hybrids Produce Gynogens and Triploids When Backrossed to Male Atlantic Salmon, *Aquaculture*, 1986, vol. 57, pp. 345–358.

Jones, J.W., Salmon and Trout Hybrids, *Proc. Zool. Soc. London*, 1947, vol. 117, pp. 708–715.

Jordan, W.C. and Verspoor, E., Incidence of Natural Hybrids Between Atlantic Salmon, *Salmo salar* L., and Brown Trout, *Salmo trutta* L., in Britain, *Aquacult. and Fish. Manag.*, 1993, vol. 24, pp. 373–377.

Kazakov, R.V., Dorofeeva, E.A., Kozlov, V.V., and Il'enkova, S.A., Use of Osteological Characters for the Identification of Reciprocal Hybrids Between *Salmo salar* L. and *Salmo trutta* L. (Salmonidae), *Vopr. Ikhtiol.*, 1982, vol. 22, no. 4, pp. 693–698.

Kazakov, R.V. and Il'enkova, S.A., Identification of Reciprocal Hybrids Between *Salmo salar* and *S. trutta* by the Variability Level of the Weight of Ovulated Eggs, *Genetika*, 1982, vol. 18, no. 1, pp. 154–160.

Kazakov, R.V., Il'enkova, S.A., and Kozlov, V.V., Peculiarities of Morphology of Gill Rakers in Hybrids of *Salmo salar* with *Salmo trutta* (Salmoniformes, Salmonidae), *Zool. Zhurn.*, 1984, vol. 63, no. 2, pp. 306–309.

Kuzishchin, K.V., *Osobennosti formirovaniya vnutrividovoi raznokachestvennosti u kumzhi Salmo trutta L. Belogo morya* (Peculiarities of Formation of Intraspecific Heterogeneity in *Salmo trutta* L. of the White Sea), Cand. Diss. (Biol.), Moscow: MGU, 1997.

Makhrov, A.A., Structure–Populational, Morphological, and Genetic Traits of *Salmo trutta* from the Drainage Basin of the Olanga River, in *Priroda i ekosistemy Paanayarvskogo natsional'nogo parka* (Nature and Ecosystems of Paanajarvi National Park), Petrozavodsk, 1995, pp. 122–126.

McGowan, C. and Davidson, W.S., Unidirectional Natural Hybridization Between Brown Trout (*Salmo trutta*) and Atlantic Salmon (*S. salar*) in Newfoundland, *Can. J. Fish. Aquat. Sci.*, 1992, vol. 49, no. 9, pp. 1953–1958.

Mel'yantsev, V.G., Data on the Biology of *Salmo trutta* L. morpha *lacustris* from Pyaozero, *Tr. Karelo-Finskogo Otd. Vses. NII Ozer. i Rech. Ryb. Khoz.*, 1951, vol. 3, pp. 58–68.

Moran, P., Garcia-Vazquez, E., Pendas, A.M., *et al.*, Status of Genetic Conservation in Salmonid Populations from Asturian Rivers (North of Spain), in *Genetic Conservation of Salmonid Fishes*, New York: Plenum Press, 1993, pp. 213–218.

Myers, R.A. and Hutchings, J.A., Mating of Anadromous Atlantic Salmon, *Salmo salar* L., with Mature Male Parr, *J. Fish Biol.*, 1987, vol. 31, no. 2, pp. 143–146.

Nygren, A, Nyman, L., Svensson, K., and Jahnke, G., Cytological and Biochemical Studies in Back-Crosses between the Hybrid Atlantic Salmon x Sea Trout and Its Parental Species, *Hereditas*, 1975, vol. 81, pp. 55–62.

Nyman, O.L., Electrophoretic Analysis of Hybrids Between Salmon (*Salmo salar* L.) and Trout (*Salmo trutta* L.), *Trans. Am. Fish. Soc.*, 1970, vol. 99, no. 1, pp. 229–236.

Osinov, A.G., *Analiz vnutrividovoi i mezhvidovoi differentsiatsii u nekotorykh vidov lososei roda Salmo po belkovym markeram genov* (Analysis of Intraspecific and Interspecific Differentiation in Some Species of Salmons from the Genus *Salmo* Using Gene Protein Markers), Cand. Diss. (Biol.), Moscow: MGU, 1984.

Payne, R.H., Child, A.R., and Forrest, A., The Existence of Natural Hybrids Between the European Trout and the Atlantic Salmon, *J. Fish Biol.*, 1972, vol. 4, no. 2, pp. 233–236.

Peacock, A.C., Bunting, S.L., and Quenn, K.G., Serum Protein Electrophoresis in Acrilamide Gel: Patterns from Normal Human Subjects, *Science*, 1965, vol. 147, pp. 1451–1452.

Pravdin, I.F., *Rukovodstvo po izucheniyu ryb* (Manual for Fish Studies), Moscow: Pishchevaya promyshlennost', 1966.

Schreiber, A., Schenk, M., Lehman, J., and Sturenberg, F.-J., Genetische Untersuchungen an Meerforellen- und Lachwildfangen aus dem Rheisystem in Nordrhein-Westfalen, *Fischer und Teichwirt*, 1994, no. 2, pp. 52–53.

Scrochowska, S., Migrations of the Sea Trout (*Salmo trutta* L.), Brown Trout (*Salmo trutta m. fario* L.) and Their Crosses. Pt. 1. Problem, Methods and Results of Tagging, *Pol. Arch. Hydrobiol.*, 1969, vol. 16, no. 2, pp. 125–140.

Semenova, S.K. and Slyn'ko, V.I., Protein Polymorphism in *Salmo salar* L. and *Salmo trutta* L. Populations and their Hybrids, *Genetika*, 1988, vol. 24, no. 3, pp. 548–555.

Solomon, D.J. and Child, A.R., Identification of Juvenile Natural Hybrids between Atlantic Salmon (*Salmo salar* L.) and Trout (*Salmo trutta* L.), *J. Fish Biol.*, 1978, vol. 12, pp. 499–501.

Svärdson, G., Chromosome Studies on Salmonidae, *Rep. Swed. State Inst. Freshwater Fish. Res. Drottningholm*, 1947, no. 23.

Taggart, J., Ferguson, A., and Mason, F.M., Genetic Variation in Irish Populations of Brown Trout (*Salmo trutta* L.): Electrophoretic Analysis of Allozymes, *Compar. Biochem. Physiol.*, 1981, vol. 69b, pp. 393–412.

Truveller, K.A. and Nefedov, G.N., Multigoal Apparatus for Vertical Electrophoresis in Parallel Plates of Polyacrilamide Gel, *Biol. Nauki*, 1974, no. 9, pp. 137–140.

Verspoor, E., Widespread Hybridization Between Native Atlantic Salmon, *Salmo salar*, and Introduced Brown Trout, *S. trutta*, in Eastern Newfoundland, *J. Fish Biol.*, 1988, vol. 32, no. 3, pp. 327–334.

Verspoor, E. and Hammar, J., Introgressive Hybridization in Fishes: the Biochemical Evidence, *J. Fish Biol.*, 1991, vol. 39, suppl. A, pp. 309–334.

Vuorinen, J. and Piironen, J., Electrophoretic Identification of Atlantic Salmon (*Salmo salar*), Brown Trout (*S. trutta*), and Their Hybrids, *Can. J. Fish. Aquat. Sci.*, 1984, vol. 41, pp. 1834–1837.

Wilkins, N.P., Courtney, H.P., and Curatolo, A., Recombinant Genotypes in Backcrosses of Male Atlantic salmon x Brown Trout Hybrids to Female Atlantic Salmon, *J. Fish Biol.*, 1993, vol. 43, pp. 393–399.

Wilson, I.F., Bourke, E.A., and Cross, T.F., Genetic Variation at Traditional and Novel Allozyme Loci, Applied to Interactions Between Wild and Reared *Salmo salar* L. (Atlantic Salmon), *Heredity*, 1995, vol. 75, no. 6, pp. 578–588.

Youngson, A.F., Knox, D., and Johnstone, R., Wild Adult Hybrids of *Salmo salar* L. and *Salmo trutta* L., *J. Fish Biol.*, 1992, vol. 40, no. 5, pp. 817–820.

Youngson, A.F., Webb, J.H., Thompson, C.E., and Knox, D., Spawning of Escaped Farmed Atlantic Salmon (*Salmo salar*): Hybridization of Females with Brown Trout (*Salmo trutta*), *Can. J. Fish. Aquat. Sci.*, 1993, vol. 50, no. 9, pp. 1986–1990.

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