Hybridization of the Atlantic salmon (*Salmo salar* L.) and brown trout (*S. trutta* L.)

A.A. Makhrov

Makhrov, A.A. 2008. Hybridization of the Atlantic salmon (*Salmo salar* L.) and brown trout (*S. trutta* L.). *Zoosystematica Rossica*, **17**(2): 129-143.

Hybrids between the Atlantic salmon and brown trout can be identified on the basis of genes coding for several protein and DNA markers. Hybrids are found in all regions where the Atlantic salmon and brown trout are sympatric. The main causes of the hybridization are the sneaking of mature male parr, escape and release of cultivated fishes, unstable river discharges, and overfishing. In numerous experimental crosses, the survival of F_1 hybrids varies from zero (a complete loss) to normal. Post-F_1 hybridization sometimes results in gynogenesis, hybridogenesis and introgression. The role of hybridization in the evolution of *Salmo* is discussed.

A.A. Makhrov, Vavilov Institute of General Genetics RAS, Gubkin str. 3, GSP-1, Moscow, 119991, Russia. e-mail: makhrov12@mail.ru

Introduction

Interspecific hybrids are interesting in terms of evolutionary genetics as well as conservation genetics. Hybridization is an important factor of evolution: many animal species have originated through distant hybridization (reviews: Serebrovskiy, 1935; Dowling & Secor, 1997; Barton, 2001; Arnold & Burke, 2005; Mallet, 2007). However, the environmental impact of human activities may also promote hybridization (reviews: Allendorf et al., 2001; Levin, 2002; Seehausen et al., 2007).

Interspecific hybridization is common for many fishes, including salmonids (reviews: Day, 1888-89; Hubbs, 1955; Nikolyukin, 1972; Dangel et al., 1973; Chevassus, 1979; Schwartz, 1981; Verspoor & Hammar, 1991; Smith, 1992; Yakovlev et al., 2000; Scribner et al., 2001; Taylor, 2004). Possibly, the hybrid between the Atlantic salmon and brown trout was the first hybrid fish ever to be described; natural hybridization of these species was mentioned by Willughbeii (1686). The Atlantic salmon and brown trout were hybridized artificially for the first time as early as in the 19th century (Shaw, pers. comm., 1841 (cited by Day, 1888-89); Coste, 1853; Rouiller et al., 1858; Fatio, 1890).

The hybridization between the Atlantic salmon and brown trout is a good model for studying the factors and consequences of interspecific hybridization. In addition, these fishes are key components of water ecosystems of Northern Europe and popular objects of aquaculture and angling. This article is a review of published data on natural and artificial hybridization between these species.

Methods of hybrid identification

Life history characters

"Typical" Atlantic salmon spawners are large anadromous fish. Anadromous brown trout (sea trout) do not travel so far to the sea and may visit freshwaters without spawning. The brown trout is better adapted to freshwater than Atlantic salmon (reviews: Calderwood, 1930; Nall, 1930; Frost & Brown, 1967; Smirnov, 1971; Mills, 1989; Klementsen et al., 2003).

A hybrid origin of large anadromous trout ("salmon-trout" or "bull trout"), particularly from the Tay and Tweed rivers in the United Kingdom, was extensively discussed (Lacepede, 1847; Day, 1887; Calderwood, 1930; Nall, 1930; Mills, 1989). Indeed, intense hybridization was observed in the Tweed River; however, genetic studies failed to detect hybrids in the Tay (Jordan & Verspoor, 1993).

A possible hybrid origin of mature male parr Atlantic salmon (T.G., 1834; Yarrell, 1836: 47; Davy, 1840: 64) was also considered. Classical experiments (Shaw, 1839) showed that most mature male parr were not hybrids. Mature female parr of Atlantic salmon were found in some rivers. "These individuals could be hybrids between Atlantic salmon and brown trout" (Bagliniere & Maisse, 1985: 259). However, genetic analysis of a mature female parr studied showed that it was a "pure" Atlantic salmon (Hindar & Nordland, 1989).

A hybrid origin of the landlocked salmon population from Lake Onega (the Baltic basin) was supposed (Novikov, 1938; Smirnov, 1971). However, this was not confirmed by genetic studies (Zelinskiy & Smirnov, 1972; Zelinskiy & Medvedeva, 1985; Makhrov et al., 2004, unpubl.).

A few immature anadromous "winter salmon" (possible hybrids) have been found in rivers of the Baltic basin (Narova, Luga and Svir) where Atlantic salmon and brown trout are artificially hybridized (Khristoforov & Murza, 2001).

Morphology

Identification of wild hybrids based on external appearance under the field conditions was confirmed by genetic data on smolts (Solomon & Child, 1978; Leonko & Chernitskiy, 1986) and spawners (Youngson et al., 1992; Jansson & Ost, 1997). The smallest hybrid parr were very similar or identical to salmon or trout in external appearance, but among older parr the hybrids could be distinguished more reliably (Garcia de Leaniz & Verspoor, 1989; Paaver et al., 2001). Young hybrids are often difficult to detect on the basis of external characters alone (Hurrell & Price, 1991; Jansson et al., 1991; Wilson et al., 1995).

A number of researchers have performed morphological comparison of young Atlantic salmon, brown trout, and their hybrids (Day, 1887; Arens, 1894; Jones, 1947; Winge & Ditlevsen, 1948; Alm, 1955; Evropeitseva & Belyayeva, 1963; Piggins, 1967; Wilkins et al., 1994; Hedenskog et al., 1997). Individual morphological characters of the hybrids are sometimes similar to those of one or the other species in any character.

This means that early reports on the hybrids should be considered with caution. For example, a fish from Norwegian Lake Bugglandsfiord "bears a peculiar mottled of tigred colour pattern, which I have previously seen in crosses between salmon and trout…" (Dahl, 1927, p. 21). However, a genetic study of "marmorated trout" from this lake did not detect hybridization (Skaala & Solberg, 1997).

Moreover, morphological characters, as well as life history characteristics, are not diagnostic outside the sympatry area of the Atlantic salmon and brown trout. The size and morphology of brown trout from the Black Sea, Caspian Sea, and some large lakes of the White Sea basin are similar to those of Atlantic salmon and/or hybrids, but genetic studies have not found any admixture of Atlantic salmon genes in these areas. So, this is an example of character displacement (review: Makhrov, 2005).

Adult Atlantic salmon, brown trout, and their hybrids differ from one another in osteological characters (Fehlmann, 1926; Henking, 1929; Seppovaara, 1962; Kazakov, 1990). However, the shape of bones of young hybrids was similar to those of young brown trout or intermediate between those of the two species (Dorofeyeva et al., 1990).

Genetic methods

It was shown that Atlantic salmon, brown trout and their F_1 hybrids differ in the number of chromosomes (Prokofieva, 1934; Svardson, 1945; Nygren et al., 1975; Giedrem et al., 1977; Johnson & Wright, 1986; Dorofeyeva, 2001). The genomes of the Atlantic salmon and brown trout contain 54-60 and 76-84 chromosomes, respectively (reviews: Phillips & Rab, 2001; Zelinsky & Makhrov, 2001).

However, chromosome counting is rather complicated, and its application is limited. On the other hand, molecular genetic methods allow F_1 hybrids to be effectively distinguished in natural populations.

Loci encoding proteins, including esterase (*EST-2**) (Nyman, 1970), glucose-6-phosphate isomerase (*GPI-A1**, *GPI-B1**) (Guyomard, 1978), transferrin (*TF**) (Solomon & Child, 1978), phosphoglucomutase (*PGM-1*, PGM 2**) (Beland et al., 1981), superoxide dismutase (*sSOD-1**) (Sutton et al., 1983), malic enzyme (*sMEP-2**), xanthine dehydrogenase (*XDH**) (Vuorinen & Piironen, 1984), esterase D (*ESTD**) (Semeonova & Slyn'ko, 1988a,b), formaldehyde dehydrogenase (*FDHG**), phosphoglycerate kinase (*PGK-2**) (Galbreath & Thorgaard, 1995), isocitrate dehydrogenase (*sIDHP-1**), mannose-6-phosphate isomerase (*MPI**), para-albumin (*PALB**) (Giuffra et al., 1996), fumarate hydrotase (*FH-2,3**), and octanol dehydrogenase (*ODH**) (Osinov & Lebedev, 2000), have been described as diagnostic for the Atlantic salmon and brown trout. The maternal species of an individual can be determined by electrophoresis of egg yolk proteins (Paaver, 1991).

Locus encoding eye-specific lactate dehydrogenase (*LDH-C**) have also been described as diagnostic proteins (Joyce et al., 1973; Johnson & Wright, 1986). Nevertheless, alleles of their genes regarded as specific for the Atlantic salmon have been found in brown trout populations (Osinov & Lebedev, 2000). Repression of some alleles in hybrids is the main obstacle to species diagnosis (Nyman, 1970; Payne et al., 1972; Nygren et al., 1975; Ueda & Kobayashi, 1990; Jansson et al., 1991; Jansson & Dannewitz, 1995).

Analysis of nucleotide sequences is free from this drawback. To date, the Atlantic salmon and brown trout have been shown to differ with respect to several homological regions of nuclear DNA (histone genes, minisatellite DNA, the preprogonadotropin releasing hormone gene, ribosomal RNA genes, short interspersed nuclear elements, and the transferrin gene) (review: Artamonova, 2007).

The maternal species of the hybrids can be determined by analysing mitochondrial DNA (mtDNA) (see Table 1). The exceptional case of Atlantic salmon and brown trout mtDNA recombination was found (Ciborowski et al., 2007).

Thus, genetic methods are the most suitable for identification of the hybrids. However, some cases of introgression cannot be detected. Only data on natural hybrids identified by genetic methods are considered below.

Prezygotic reproductive isolation and natural hybridization

Factors of prezygotic reproductive isolation

Several processes are involved in prezygotic reproductive isolation. These are biotopic isolation, differences in the reproduction season, behavioural differences, and mechanical isolation (Mayr, 1970).

Biotopic isolation between the Atlantic salmon and brown trout is known to exist. These species usually have different spawning grounds even when they live in the same river (Nall, 1930; Smirnov, 1971; Heggberget et al., 1988; Martynov, 2007).

Temporal segregation is the main mechanism preventing the hybridization between the Atlantic salmon and brown trout. The peak of the spawning of the brown trout is earlier than that of sympatric populations of the Atlantic salmon in Europe (Calderwood, 1930; Nall, 1930; Menzies, 1936; Alm, 1955; Heggberget et al., 1988; Lura & Segrov, 1993; Skaala & Solberg, 1997). There is no temporal segregation between the native Atlantic salmon and the introduced brown trout in North America (M. O'Connell, pers. comm., cited by McGowan & Davidson, 1992b); extensive hybridization was found in this region (Verspoor, 1988; McGowan & Davidson, 1992b). Possibly, the temporal segregation of these species in Europe results from reinforcement (reproductive character displacement), which is known for many species (review: Servedio & Noor, 2003).

Behavioural differences between Atlantic salmon and brown trout spawners have been poorly studied. "The main reproductive difference between brown trout and Atlantic salmon in southern European rivers is the lack of evidence for sneaking behaviour in small maturing brown trout" (Garcia-Vazquez et al., 2001, p. 148).

Mechanical isolation between these species is unknown. It was suggested that Atlantic salmon have larger spermatozoa and egg micropyle than brown trout, which is a mechanical obstacle to fertilization of brown trout eggs by Atlantic salmon spermatozoa (Day, 1887, 1888-89). Actually,

Table 1. Sequences of mitochondrial DNA that were described as diagnostic for Atlantic salmon and brown trout.

Locus	References
Total mitochondrial DNA (restriction)	Gyllensten & Wilson, 1987; Palva et al., 1989; Youngson et al., 1992, 1993; Hartley, 1996; Beall et al., 1997; Thompson et al., 1998; Gephard et al., 2000; Garcia-Vazquez et al., 2001
Gene encoding 16S rRNA	Patarnello et al., 1994
NADH dehydrogenase 5/6 region	Largiader et al., 1996
Control region	Bernatchez, 2001; Snoj et al., 2002; Sušnik et al., 2004
NADH dehydrogenase-I region	Matthews et al., 2000
ATPase subunit VI	Giuffra et al., 1994
Cytochrome b	McVeigh & Davidson, 1991; McGowan & Davidson, 1992b; Giuffra et al., 1994; Palsson & Arnason, 1994; Patarnello et al., 1994; Jansson & Ost, 1997; Phillips et al., 2000; Paaver et al., 2001; Snoj et al., 2002; Ayllon et al., 2004; Sušnik et al., 2004

brown trout spermatozoa are wider than Atlantic salmon spermatozoa (Murza & Christoforov, 1993).

Factors promoting natural hybridization

Some **mature male parr** of brown trout retain active gonads for a long time (Scrochowska, 1969). Moreover, mature male parr of salmonids have distant contact with females before spawning, e.g., the sneaker tactic (review: Fleming & Reynolds, 2004). The sex steroid hormone content of plasma is increased in mature male parr of both species in the presence of females of either species (Olsen et al., 2000, 2002). There is evidence for the existence of hybrid offspring of both Atlantic salmon mature male parr (Gephard et al., 2000; Garcia-Vazquez et al., 2001) and brown trout resident males (Hindar, 1998; Thompson et al., 1998; Taggart et al., 2001).

Hybridization is caused by **changes in the hydrology** of rivers. High proportions of hybrids were found in samples from rivers where small spawning grounds were restored (Jansson et al., 1991; Jansson & Ost, 1997).

Introduction of the Atlantic salmon and brown trout to non-native regions has been found to be associated with hybridization (Verspoor, 1988; McGowan & Davidson, 1992b; Ayllon et al., 2004). Moreover, intentional or unintentional artificial hybridization occurs during supportive breeding (Fatio, 1890; Lamond, 1916; Fehlmann, 1926; Henking, 1929; Alm, 1955; Seppovaara, 1962; Evropeitseva & Belyayeva, 1963; Roth & Geiger, 1972; MacCrimmon & Gots, 1979; Vuorinen & Piironen, 1984; Semyonova & Slyn'ko, 1988b; Schreiber et al., 1994; Christoforov et al., 1995; Ayllon et al., 2004; Makhrov et al., 2004).

It has been shown that escaping **farmed salmon** cross with brown trout more frequently than wild salmon do (Youngson et al., 1993; Mjolnerod, 1999; Matthews et al., 2000). This may be related to changes in the behaviour of farmed fishes. Sometimes, the spawning period of cultured salmon overlaps with that of brown trout (Lura & Segrov, 1993). Hybridization may also be caused by the fact that the conditions of artificial breeding determine a greater morphological similarity between the species (Wilkins et al., 1994).

Deficiency of spawners of either species (usually male salmon) may also induce hybridization (Fries et al., 1895, p. 861; Regan, 1911, p. 32–33; Cordier-Goni, 1939; Garcia de Leaniz & Verspoor, 1989). At least three cases of hybridization have been detected in the small Nilma River on the White Sea coast, where the numbers of the Atlantic salmon had decreased because of overfishing (Makhrov et al., 1998; Ponomareva et al., 2002). Sneaking male Atlantic salmon can fertilize brown trout ova in the absence of male trout under natural conditions (Garcia-Vazquez et al., 2002).

A case was described where hybridization was induced by all the five factors listed above. The hybrid was found in a North American river upstream of the dam where young hatchery salmon had been released. Female Atlantic salmon couldn't come back to their spawning grounds because of the dam, and mature male parr of Atlantic salmon fertilized female brown trout (Gephard et al., 2000).

Frequency of the natural hybrids and their genetic characters

Thus, several types of human activity facilitate the hybridization. Apparently, this is why monitoring showed a significant increase in the hybridization during several years (Hindar & Balstad, 1994). In Scandinavia, the frequency of the hybrids is lower than in other European regions where rivers have been much more affected (Elo et al., 1995). As shown in Table 2, the hybridization is observed in all regions where Atlantic salmon and brown trout coexist.

Selection may increase the hybrids rate in natural population. For example, hybrids are more resistant to the dangerous parasite *Gyrodactylus salaris* than Atlantic salmon are (Bakke et al., 1999; Bazilchuk, 2004; Johnsen et al., 2005). Selection against the hybrids is possible too (see the next section).

Analysis of mitochondrial DNA demonstrated that natural hybrids may result from crosses between female brown trout and male Atlantic salmon (McGowan & Davidson, 1992b; Hartley, 1996; Beall et al., 1997; Jansson & Ost, 1997; Gephard et al., 2000; Garcia-Vazquez et al., 2001, 2004; Paaver et al., 2001; Johnsen et al., 2005), as well as between female Atlantic salmon and male brown trout (Youngson et al., 1992, 1993; Hartley, 1996; Hindar, 1998; Thompson et al., 1998; Matthews et al., 2000; Paaver et al., 2001; Taggart et al., 2001; Johnsen et al., 2005). There are field observations of courtship of a female Atlantic salmon by a male brown trout (Fries et al., 1895, p. 861; Regan, 1911, p. 32-33; Cordier-Goni, 1939; Scott et al., 2005).

Unfortunately, the data obtained under natural conditions are insufficient for estimation of consequences of the hybridization. There were few cases when adult wild hybrids were caught (Payne et al., 1972; Youngson et al., 1992; Beall et al., 1997; Jansson & Ost, 1997; Paaver et al., 2001; Johnsen et al., 2005).

There are data on wild post-F_1 hybrids (Beland et al., 1981; Verspoor & Hammar, 1991; Youngson et al., 1993; Verspoor & McCarthy, 1997; Hindar,

Table 2. The frequencies of hybrids in samples from natural populations.

Region	Number of studied river systems	Number of river systems with hybrids	Species observed, life-history stage*	% of hybrids: range and mean	Reference
Spain	4	2	AS,p	0.0-3.1 (2.3)	Garcia de Leaniz &Verspoor, 1989
France, Spain	7	7	AS,BT,p,a	0.9-3.1 (2.2)	Beall et al., 1997
British Isles	11	5	AS,a	0.0-0.9 (0.4)	Payne et al., 1972
Britain	3	3	AS,BT,p	0.0-4.0 (1.4)	Hurrell & Price, 1991
	23	8	AS,p	0.0-3.4 (1.0)	Jordan & Verspoor, 1993
	1	1	AS,p	18.18	Hartley, 1996
	16	7	AS,p	0.0-8.2 (1.0)	Youngson et al., 1993
N. Ireland	1	1	BT	3.6	Crozier, 1984
Ireland	13	8	As,BT,p	0.0-2.7 (1.2)	Matthews et al., 2000
	1	1	BT,p	?	Ferguson & Taggart, 1991
Estonia	5	4	AS,BT,p	0.0-6.6 (2.8)	Paaver et al., 2001
Sweden	1	1	AS,BT,p	13.0	Jansson et al., 1991
	5	1	AS,BT,?	0.0-28.0 (1.6)	Gross et al., 1996
	1	1	AS,BT,a	1.6	Jansson & Ost, 1997
	1	1	AS,BT,p	41.5	Jansson & Ost, 1997
Norway	4	0	AS,BT,e	0	Heggberget et al., 1988
Norway, 1980-1986	?	?	AS,BT,p	0.0-2.0 (0.24)	Hindar & Balstad, 1994
Norway, 1987-1992	?	?	AS,BT,p	0.0-8.0 (0.87)	Hindar & Balstad, 1994
Norway, Finland	2	2	AS,BT,p,a	0.1-0.3 (0.15)	Elo et al., 1995
Kola peninsula	3	1	AS,a	0.0-0.09	Semeonova & Slyn'ko, 1988b
White Sea basin	3	2	AS,BT,p	0.0-6.67 (1.21)	Makhrov et al., 1998
North America	1	1	As,BT,p	1.8	Beland et al., 1981
	10	5	AS,BT,psa	0.0-5.45 (0.9)	Verspoor, 1988
	9	8	AS,BT,p	0.0-18.75 (4.67)	McGowan & Davidson, 1992b
	1	1	AS,BT,p	0.81	Gephard et al., 2000
Kergelen Islands	1	1	AS,BT,p,a	5,9	Ayllon et al., 2004

Notes: * AS – Atlantic salmon, BT – brown trout, a – adults, p – parrs, s – smolts, e – eggs and fry in redds.

1998; Johnsen et al., 2005; Ciborowski et al., 2007). Apparently, the data obtained in the first of the cited studies were incorrect because of artefact bands in the electrophoregrams (Crozier, 1984). Common variants may reflect parallel mutations (Verspoor et al., 2005). Therefore, we should use experimental data to estimate the possible consequences of hybridization.

Postzygotic reproductive isolation and experimental hybridization

F_1 hybrids

Some putative hybrids obtained in 1959 (Piggins, 1965) had the chromosome number 2n = 80, which is typical of the brown trout (Nygren et al., 1975). The electrophoretic mobility of the proteins that are diagnostic for these species was studied for the F_2 offspring of these "hybrids". It was similar but not identical for these offspring and for brown trout (Haen & O'Rourke, 1968; Nyman, 1970; Jouce et al., 1973). In this case, all the F_1 hybrids were obtained from one pair of spawners, and the species of one of the spawners may have been determined incorrectly. I used only the data on the hybrids obtained in 1963 (Piggins, 1965, 1967).

The survival of hybrids between the Atlantic salmon and brown trout was estimated in numerous experiments (Day, 1887; Arens, 1894; Haak, 1894; Grote et al., 1909; Winge & Ditlevsen, 1948; Demoll & Steinmann, 1949; Fontaine & Vibert, 1950; Alm, 1955; Buss & Wright, 1956; Spaas & Heuts, 1958; Evropeitseva & Belyayeva, 1963; Piggins, 1965; Zelinsky & Smirnov, 1972; Refstie & Giedrem, 1975; Blanc & Chevassus, 1979, 1982; Refstie, 1983; Kazakov, 1990; McGowan & Davidson, 1992a; Gray et al., 1993; Galbreath & Thorgaard, 1994; Babiak et al., 2002; Garcia-Vazquez et al., 2002).

The results varied considerably, from the absence of fertilization of brown trout eggs to a normal survival of the hybrids. Probably, the populations of the parental species differ in some genetic characters important for survival of the hybrids (Winge & Ditlevsen, 1948; Zelinsky & Smirnov, 1972; Chevassus, 1979). Possibly, one of these characters is the spawning time. Peak spawning periods of Atlantic salmon populations vary (Heggberget, 1988).

Brown trout usually spawns earlier than Atlantic salmon (see references above), and brown trout eggs may be overripe when male Atlantic salmon reach maturity. Apparently, this is why hybrids developing from the eggs of brown trout were less viable than those developing from Atlantic salmon eggs (Arens, 1894; Grote et al., 1909; Demoll & Steinmann, 1949; Alm, 1955; McGowan & Davidson, 1992a; Gray et al., 1993; Garcia-Vazquez et al., 2002). There is an exception (Refstie & Giedrem, 1975); however, control Atlantic salmon had high mortality in this experiment too.

Many crosses between female Atlantic salmon and male brown trout have been carried out in Europe. The survival of these hybrids was lower than those of the parental species (Day, 1887; Winge & Ditlevsen, 1948; Alm, 1955; Piggins, 1965; Refstie & Giedrem, 1975; Blanc & Chevassus, 1979; Refstie, 1983). However, the hybrids had the same (McGowan & Davidson, 1992a) or higher (Gray et al., 1993; Galbreath & Thorgaard, 1994) survival rate compared to that of Atlantic salmon in experiments performed in North America. Possibly, this was also a result of reinforcement.

Developmental instability as measured by the fluctuating asymmetry of meristic traits is significantly greater in the hybrids (Wilkins et al., 1995). Morphological abnormalities (Winge & Ditlevsen, 1948; Buss & Wright, 1956; McGowan & Davidson, 1992a) and disturbances in the development of gonads (Winge & Ditlevsen, 1948; Alm, 1955; Evropeitseva & Belyayeva, 1963; Youngson et al., 1992) have been described in the hybrids. The hybrids were unfertile in one experiment (Demoll & Steinmann, 1949). "Meiosis of the hybrid (in the male) shows disturbances" (Svardson, 1945, p. 58).

However, the hybrids exhibit a specific relationship between physiological characters and temperature (Spaas & Heuts, 1958; Kusakina, 1959), and they are sometimes more resistant to high temperature and other adverse factors than the parental species are (Evropeitseva & Belyayeva, 1963). Heterosis is typical of many interspecific hybrids.

Backcrosses

In one experiment, numerous mitotic disturbances were observed (Svardson, 1945), the offspring of backcrossing in all combinations dying (Alm, 1955). However, in another experiment, "some hatchery-reared backcrosses proved to be viable and to contain early-maturing, fertile males" (Hindar, 1998, p. 30). The results of other works are presented below.

Female brown trout × male hybrid. The survival rate of the hybrids was low (Day, 1887; Arens, 1894). The offspring died at embryonic stages (Winge & Ditlevsen, 1948, Garcia-Vazquez et al., 2004). Only a few fish hatched and died soon in other experiment (Nygren et al., 1975). Almost all the offspring died before the beginning of feeding. One live fish was confirmed to be a recombinant triploid hybrid (Galbreath & Thorgaard, 1995).

Female Atlantic salmon × male hybrid. The survival rate was very low in two studies. The chromosome numbers of these fish vary from 58 to 69 (Nygren et al., 1975; Garcia-Vazquez et al., 2004). Molecular analysis of four individuals with 2n = 68-69 showed that the 5S rRNA genes were identical to F_1 hybrids (Garcia-Vazquez et al., 2004). In another study, all the fish studied had genotypes for two studied loci that were typical of the F_1 hybrid too (Semeonova & Slyn'ko, 1988b). In one more study, the offspring died before the start of feeding (Galbreath & Thorgaard, 1995). The mortality was also high in the fifth experiment. The few survivors had recombinant genotypes. However, more than 80% of eggs triploidized by heat shock survived through hatching (Wilkins et al., 1993).

Thus, in almost all crosses of male hybrids and females of the parent species, a high mortality of the offspring was observed. F_1 hybrids may produce gametes identical to those of brown trout (Semeonova & Slyn'ko, 1988b; Garcia-Vazquez et al., 2004). Possible, it is due to spatial isolation of parental chromosome sets that is known to both species (Prokofieva-Belgovskaya, 1964).

Female hybrid × male Atlantic salmon. The resultant yearlings were immature; the males had "tube-like testes, and the females normal immature ovaries. One fish had what appeared to be an ovary on one side and a tube-like testis on the other" (Jones, 1947). In another experiment, it was shown that backcrosses were gynogens and triploids. All the triploids expressed one copy of brown trout alleles and two copies of Atlantic salmon alleles for all loci examined. One Atlantic salmon chromosome was lost in one fish (Johnson & Wright, 1986). In the other studies, all the offspring were triploids (Galbreath & Thorgaard, 1995; Garcia-Vazquez et al., 2003). Some triploids that were found in this last study were fertile (see below).

A difference was found between crosses of hybrids originating from female Atlantic salmon and from female brown trout. In the former case, the survival was high and all the offspring were triploids. In the latter case, the survival was low and the chromosome number of one fish was 69: hybrid female produced a trout-like haploid gamete (Garcia-Vazquez et al., 2004). However, this is not so for other experimental crosses of hybrids originating from female brown trout (Johnson & Wright, 1986). Moreover, natural triploid hybrids found in two Norwegian rivers were offspring of crosses between male Atlantic salmon and female hybrids that also originated from female brown trout and male Atlantic salmon (Johnsen et al., 2005).

Female hybrid × male brown trout. Six hundred and sixty-seven parr were obtained from 1000 eggs (Day, 1887). The survival rate was several percent in another study (Arens, 1894). The offspring survival until the beginning of feeding was zero in two studies (Galbreath & Thorgaard, 1995; Garcia-Vazquez et al., 2004). In the fifth study, most backcrosses were triploid. However, some individuals were diploid for one locus but triploid for the other loci (Dannewitz & Jansson, 1996).

Gynogens were obtained from eggs of female hybrids activated with UV-irradiated rainbow trout (*Parasalmo mykiss*) sperm. A DNA fragment was missing in one of these fishes (Galbreath et al., 1997). Therefore, gynogenesis and the loss of a few chromosomes (aneuploidy) are typical of the offspring of female hybrids.

Thus, crossing of female hybrids and males of the parent species may yield viable hybrids, because female hybrids are capable of gynogenesis and can produce diploid eggs.

Triploid hybrids and introgression

There are publications on triploid hybrids that were obtained via heat shock. These hybrids showed a poor survival (Gray et al., 1993; Galbreath & Thorgaard, 1994). The saltwater survival of triploid hybrids and Atlantic salmon was similar, but maturation of hybrid females was not observed (Galbreath & Thorgaard, 1997). The survival was zero for all the offspring backcrossing with triploid male hybrids (Galbreath & Thorgaard, 1995).

Fertile triploid hybrids between backcrosses of female Atlantic salmon × brown trout hybrids with male Atlantic salmon have been found. Mature triploid males were crossed with females of the parental species. All the embryos hatching from brown trout eggs died before yolk sac absorption. Only 0.69–3.01% of embryos hatching from Atlantic salmon eggs survived until yolk sac absorption. Forty-eight out of 74 studied alevins exhibited a brown trout specific variant for a least one genetic marker (Castillo et al., 2007).

The ova of one mature triploid female were fertilized by two mature male parr of Atlantic salmon in an experimental stream. Five living fry (1.2% survival) carried three or two brown trout specific variants. The offspring of the triploid female, as well as the offspring of triploid males, were similar to Atlantic salmon with respect to the DNA content and chromosome number. This is evidence for introgression (Castillo et al., 2007).

F_2 hybrids

In experiments performed in Europe, either all the hybrids of the second generation died (Fehlmann, 1926; Alm, 1955) or the survival rate was only several percent (Arens, 1894). However, crossing performed in North America yielded fertile offspring (Catt, 1950). Unfortunately, the description of this last experiment is very brief.

Hybridization and the evolution of *Salmo*: The present, past and future

Hybridization of brown trout and endemic species of Salmo

The results of *S. trutta* hybridization with *S. salar* considerably differ from the results of the hybridization of *S. trutta* and other *Salmo* species. The data on experimental hybridization and natural hybrids detected by genetic methods alone are listed below.

The Sevan trout (*S. ischchan*) is endemic of Caucasian Lake Sevan. Artificial hybridization of *S. ischchan* and *S. trutta* was performed, and the offspring was entirely viable (pers. comm. of Jermuk hatchery staff, from Osinov, 1990). A hybrid population of these species appeared after the introduction of Sevan trout to another Caucasian lake, Tabatzkuri (Rukhkian, 1989).

Similarly, viable offspring was obtained from experimentally crossing *S. (trutta) marmoratus* (an endemic species or subspecies from the Adriatic basin) with *S. trutta* (Kosoric & Vukovic, 1969), as well as from backcrossing hybrid F_1 males with female brown trout (Gharbi et al., 2006). Moreover, large-scale introgressive hybridization of these species is a result of non-native fish stocking (Largiader & Scholl, 1995; Giuffra et al., 1996; Snoj, 1997; Berrebi et al., 2000; Delling et al., 2000; Jug et al., 2004, 2005).

Salmo carpio, an endemic species or subspecies from Lake Garda (Italy), is considered to have resulted from natural hybridization between *S. trutta* and *S. marmoratus* (Giuffra et al., 1996; Antunes et al., 2002).

Two endemic trout live in Lake Ohrid (the Adriatic basin): *S. (trutta) letnica* and *Salmo (Acantolingua) ohridanus*. A post-F_1 hybrid of these two forms has been found in Lake Ohrid (Susnik et al., 2006).

Reciprocal hybrids capable of living were obtained from crossing *S. trutta* with an endemic species from Adriatic coast, *Salmothymus (Salmo) obtusirostris* (Kosoric & Vukovic, 1969). Natural introgressive hybridization of these species was detected using molecular markers (Razpet et al., 2007a,b; Snoj et al., 2007; Susnik et al., 2007).

All crosses between *S. obtusirostris* and *S. marmoratus* died within several months (Kosoric & Vukovic, 1969).

Taxonomy and evolution of Salmo

Thus, species of the genera *Salmo* can be divided in two groups according to the results of hybridization: (1) Atlantic salmon and (2) brown trout and endemic forms. There is a correlation between the taxonomic relationship and the success of hybridization of fishes, including salmonids (Nikoljukin, 1972; Chevassus, 1979).

Recently, the species *S. trutta*, *S. ischchan*, *S. letnica* and *S. carpio* were combined onto the subgenus *Trutta,* and *S. salar* was included into the monotypic subgenus *Salmo* (Dorofeyeva, 1998). The results of interspecific hybridization suggest that *S. marmoratus*, *S. ohridanus*, and *S. obtusirostris* should be included into the subgenera *Trutta.* Possibly, other endemic forms from the Mediterranean basin are member of this group too.

This suggestion agrees with the results of recent morphological (Delling, 2003), karyological (reviews: Phillips & Rab, 2001; Zelinskiy & Makhrov, 2001), and molecular genetic (Patarnello et al., 1994; Giuffra et al., 1996; Phillips et al., 2000; Bernatchez, 2001; Antunes et al., 2002; Presa et al., 2002; Snoj et al., 2002; Phillips et al., 2004; Sušnik et al., 2004) studies.

Morphological differences between the two subgenera are small (see above), but genetic differences are very large. It is suggested that genome reorganization accompanied the speciation of the Atlantic salmon (Zelinsky & Makhrov, 2001).

Delayed consequences of the hybridization between the Atlantic salmon and brown trout

Several possible results of mass interspecific hybridization are known. These are extinction of paternal species because of sterility or mortality of the hybrids (Zaslavskiy, 1967; Rhymer & Simberloff, 1996; Levin, 2002), reinforcement of reproductive isolation (reproductive character displacement) (review: Servedio, Noor, 2003), introgression (Anderson, 1949), hybridogenesis (review: Devlin & Nagahama, 2002) and hybrid speciation (review: Mallet, 2007). What is likely to occur in our case?

Death of the hybrids is a usual result of experimental hybridization between Atlantic salmon and brown trout. Therefore, extinction of some local Atlantic salmon populations because of the combined effect of hybridization with brown trout and another negative factor (overfishing, destruction of spawning grounds, or parasite invasion) is possible. The destruction of population is self-strengthening processes: number of spawners decreasing resulted in hybridization increasing and increasing of mortality.

Reproductive character displacement is a result of natural selection against hybridization. Character displacement is well known in fish, including salmonids (reviews: Mina, 1991, Robinson, Wilson, 1994). Some evidence for reproductive character displacement in Atlantic salmon and brown trout in Europe are presented in this article. An increase in hybridization should increase differences between these species in the time and place of spawning, especially in North America.

Introgression is also widespread among fishes, including salmonids (reviews: Verspoor & Hammar, 1991; Smith, 1992; Taylor, 2004). Some evidence for introgression during natural and experimental hybridization between the Atlantic salmon and brown trout have been mentioned above. It is possible that an "alien" allelic variant is adaptively advantageous and will spread over other species.

Hybridogenesis is process of parental chromosome exclusion during meiosis. Atlantic salmon and brown trout hybrids may produce gametes identical to those of brown trout (Semeonova & Slyn'ko, 1988b; Garcia-Vazquez et al., 2004). Incomplete exclusion of parental chromosomes may be reason of introgression.

Several natural hybrids of fishes use gynogenesis as a normal mode of reproduction (review: Devlin & Nagahama, 2002). Females of experimental hybrids between the Atlantic salmon and brown trout are capable of gynogenesis. Moreover, a triploid hybrid is the result of natural reproduction of hybrids between the Atlantic salmon and brown trout via gynogenesis (Johnsen et al., 2005). Therefore, a new gynogenetic hybrid form (a "reproductive parasite") has appeared. It is an initial stage of hybrid speciation, which calls for detailed research in this field. Moreover, the gynogenetic hybrid form is a potential effective competitor of both the Atlantic salmon and brown trout.

Conclusion

To date, the methods of detecting first-generation hybrids between the Atlantic salmon and brown trout have been well developed. These hybrids are numerous in rivers deteriorated as a result of human activity. However, remote descendants of F_1 hybrids are be detected only occasionally.

Widespread hybridization will have negative consequences. Usually, this is waste of gametes. The appearance of a gynogenetic hybrid form (a "reproductive parasite") and introgression are also possible. Further research in the natural post-F_1 hybridization, including the competition between the hybrids and parental species, is necessary. Interspecific hybridization is dangerous for the gene pools of natural populations. However, this is a good model of hybrid speciation.

Acknowledgments

I thank M.L. Arnold, T.A. Bakke, E. Beall, O.L. Christoforov, B. Delling, T.E. Dowling, E.A. Dorofeyeva, K. Elo, I.A. Fleming, P.F. Galbreath, E. Garcia-Vazquez, E. Giuffra, K. Hindar, W.C. Jordan, C.R. Largiader, V.G. Martynov, I.B. Mjolnerod, I.G. Murza, A.G. Osinov, T. Paaver, S. Palsson, R.B. Phillips, K.T. Scribner, O. Skaala, E.B. Taylor, A.R. Templeton, E. Verspoor, J.A. Vuorinen, N.P. Wilkins, I.F. Wilson, T. Ueda, and Yu.P. Zelinsky for reprints.

The study was supported by the program of the Russian Academy of Sciences "Biodiversity and Dynamics of Gene Pools".

References

Allendorf, F.W., Leary, R.F., Spruell, P. & Wenburg, J.K. 2001. The problems with hybrids: setting conservation guidelines. *Trends in Ecology and Evolution,* **16**: 613-622.

Anderson, E. 1949. *Introgressive Hybridization*. New York: John Wiley & Sons, Inc.; London: Chapman & Hall, Limited. 109 p.

Antunes, A., Templeton, A.R., Guyomard, R. & Alexandrino, P. 2002. The role of nuclear genes in intraspecific evolutionary inference: genealogy of the transferrin gene in the brown trout. *Molecular Biology and Evolution,* **19**: 1272-1287.

Arens, C. 1894. Ueber den Lachsbastard. *Allgemeine Fischerei-Zeitung,* **19**: 346-347.

Arnold, M.L. & Burke, J.M. 2006. Natural hybridization. *In:* Fox, C.W. & Wolf, J.B., (Eds.) *Evolutionary Genetics: Concepts and Case Studies*: 399-413. Oxford: Oxford University Press.

Artamonova, V.S. 2007. Genetic markers in population studies of Atlantic salmon *Salmo salar* L.: analysis of DNA sequences. *Russian Journal of Genetics,* **43**: 341-353.

Ayllon, F., Martinez, J.L., Davaine, P., Beall, E. & Garcia-Vazquez, E. 2004. Interspecific hybridization between Atlantic salmon and brown trout introduced in the subantarctic Kerguelen Islands. *Aquaculture,* **230**: 81-88.

Babiak, I., Dobosz, S., Kuzminski, H., Goryczko, K., Ciesielski, S., Brzuzan, P., Urbanyi, B., Horvath, A., Lahnsteiner, F. & Piironen, J. 2002. Failure of interspecies androgenesis in salmonids. *Journal of Fish Biology,* **61**: 432-447.

Bagliniere, J.L. & Maisse, G. 1985. Precocious maturation and smoltification in wild Atlantic salmon in the Armorican massif, France. *Aquaculture,* **45**: 249-263.

Bakke, T.A., Soleng, A. & Harris, P.D. 1999. The susceptibility of Atlantic salmon (*Salmo salar* L.) × brown trout (*Salmo trutta* L.) hybrids to *Gyrodactylus salaris* Malmberg and *Gyrodactylus derjavini* Mikailov. *Parasitology,* **199**: 467-481.

Barton, N.H. 2001. The role of hybridization in evolution. *Molecular Ecology,* **10**: 551-568.

Bazilchuk, N. 2004. Salmon crisis in Norway. *New Scientist,* **181**: 14.

Beall, E., Moran, P., Pendas, A., Izquiedo, J. & Garcia-Vazquez, E. 1997. Hybridization in natural populations of Salmonids in south-west Europe and in an experimental channel. *Bulletin Francais de la Peche et de la Pisciculture,* **344-345**: 271-285. (In French, English summary).

Beland, K.F., Roberts, F.L. & Saunders, R.L. 1981. Evidence of *Salmo salar* × *Salmo trutta* hybridization in a North American river. *Canadian Journal of Fisheries and Aquatic Sciences,* **38**: 552-554.

Bernatchez, L. 2001. The evolutionary history of brown trout (*Salmo trutta* L.) inferred from phylogeographic, nested clade, and mismatch analyses of mitochondrial DNA. *Evolution,* **55**: 351-379.

Berrebi, P., Povz, M., Jesensek, D., Cattaneo-Berredi, G. & Crivelli, A.J. 2000. The genetic diversity of native, stocked and hybrid populations of marbled trout in the Soca river, Slovenia. *Heredity,* **85**: 277-287.

Blanc, J.M. & Chevassus, B. 1979. Interspecific hybridization of salmonid fish. I. Hatching and survival up to the 15th day after hatching in F_1 generation hybrids. *Aquaculture,* **18**: 21-34.

Blanc, J.M. & Chevassus, B. 1982. Interspecific hybridization of salmonid fish. II. Survival ang growth up to the 4th month after hatching in F_1 generation hybrids. *Aquaculture,* **29**: 383-387.

Buss, K. & Wright, J.E. 1956. Results of species hybridization within the family Salmonidae. *Progressive Fish-Culturist,* **18**: 149-158.

Calderwood, W.L. 1930. *Salmon and Sea Trout*. London: Edward Arnold & Co. 242 p.

Castillo, A.G.F., Beall, E., Moran, P., Martinez, J.L., Ayllon, F. & Garcia-Vazquez, E. 2007. Introgression in the genus *Salmo* via allotriploids. *Molecular Ecology,* **16**: 1741-1748.

Catt, J. 1950. Some notes on brown trout with particular reference to their status in New Brunswick and Nova Scotia. *Canadian Fish Culturist,* **7**: 25-27.

Chevassus, B. 1979. Hybridization in salmonids: Results and perspectives. *Aquaculture,* **17**: 113-128.

Christoforov, O.L., Murza, I.G., & Dorofeeva, E.A. 1995. Introgressive hybridization in artificially propagated populations of Atlantic salmon and sea trout in the north-west part of Russia. *In:* Svennevig, N. & Krogdahl, A. (Eds.) *Quality in Aquaculture. Short Communications and Abstracts*: 341-342. Gent, Belgium.

Ciborowski, K.L., Consuegra, S., Garcia de Leaniz, C., Beaumont, M.A., Wang, J. & Jordan, W.C. 2007. Rare and fleeting: an example of interspecific recombination in animal mitochondrial DNA. *Biology Letters,* **3**: **554-557.**

Cordier-Goni, P. 1939. Hypothese sur un hybride du saumon et de la Truite (*Salmo salar* L. – *Salmo (Trutta) fario* L.). *Riviera Scientifique (Nice),* **26**: 3-10. (In French).

Coste, M. 1853. *Instructions Pratiques sur la Pisciculture*. Paris: Librairie de Victor Masson. 140 p. (In French).

Crozier, W.W. 1984. Electrophoretic identification and comparative examination of naturally occurring F_1 hybrids between brown trout (*Salmo trutta* L.) and Atlantic salmon (*S. salar* L.). *Comparative Biochemistry and Physiology,* **78B**: 785-790.

Dahl, K. 1927. The "blege" or dwarf-salmon. A landlocked salmon from lake Bugglandsfiord in Setesdal. *Skrifter utgitt av det Norske Videnskaps-Akademi i Oslo. I. Matem.-Naturv. Klasse,* **9**: 1-25.

Dangel, J.R., Macy, P.T. & Withler, F.C. 1973. Annotated bibliography of interspecific hybridization of fishes of the subfamily Salmonidae. *NOAA Technical Memorandum NMFS,* **NWFC-1**: 1-48.

Dannewitz, J. & Jansson, N. 1996. Triploid progeny from a female Atlantic salmon × brown trout hybrid backcrossed to a male brown trout. *Journal of Fish Biology,* **48**: 144-146.

Davy, H. 1840. *Salmonia*. Leipzig: Verlag von Leopold Vob. 328 p. (In German).

Day, F. 1887. *British and Irish Salmonidae*. London & Edinburgh: Williams et Norgate. 298 p.

Day, F. 1888-89. Notes on hybridization. *Proceeding of the Cotteswold Club*: 334-373.

Delling, B. 2003. Species diversity and phylogeny of *Salmo* with emphasis on southern trouts (Teleostei, Salmonidae). Doctoral dissertation. Stockholm: Department of Zoology, Stockholm University. 25 p.

Delling, B., Crivelli, A.J., Rubin, J.-F. & Berrebi, P. 2000. Mophological variation in hybrids between *Salmo marmoratus* and alien *Salmo* species in the Volarja stream, Soca River basin, Slovenia. *Journal of Fish Biology,* **57**: 1199-1212.

Demoll, R. & Steinmann, P. 1949. *Praxis der Aufzucht von Forellenbesatzmaterial*. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung. 98 p. (In German).

Devlin, R.H. & Nagahama, Y. 2002. Sex determination and sex differentiation in fish: an overview of genetic, physiological, and environmental influences. *Aquaculture,* **208**: 191-364.

Dorofeyeva, E.A. 1998. Systematics and distribution history of European salmonid fishes of the genus *Salmo*. *Journal of Ichthyology,* **38**: 419-429.

Dorofeyeva, E.A. 2001. Using of karyotype characteristics for the identification of reciprocal hybrids of lake Atlantic salmon *Salmo salar* and lake trout *Salmo trutta* (Salmonidae). *Proceedings of the Zoological Institute (Russian Academy of Sciences),* **287**: 221-231.

Dorofeyeva [Dorofeeeva], E.A., Kazakov, R.V., Ilyenkova, S.A. & Urbanas, E.V. 1990. Osteological characteristics of the juvenils of the salmon (*Salmo salar* L.), brown trout (*Salmo trutta* L.) and their hybrids. *Proceedings of the Zoological Institute USSR Academy of Sciences,* **222**: 132-143. (In Russian, English summary).

Dowling, T.E. & Secor, C.L. 1997. The role of hybridization and introgression in the diversification of animals. *Annual Review of Ecology and Systematics,* **28**: 593-619.

Elo, K., Erkinaro, J., Vuorinen, J.A. & Niemela, E. 1995. Hybridization between Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in the Teno and Naatamo river systems, northernmost Europe. *Nordic Journal of Freshwater Research,* **70**: 56-61.

Evropeitseva, N.V. & Belyayeva, G.V. 1963. Experimental-ecological analysis of young hybrids of Baltic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta trutta* L.) from ponds. *Proceeding of the Institute of Biology (Latvian Academy of Sciences),* **23**: 297-308. (In Russian).

Fatio, V. 1890. *Faune des Vertebres de la Suisse*. V. 5. Geneve et Bale: H. Georg, Libraire-Editeur. 576 p. (In French).

Fehlmann, W. 1926. *Die Ursachen des Ruckganges der Lachsfischerei im Hochrhein*. Schaffhausen: Buchdruckerei Meier & Cie. 112 p. (In German).

Ferguson, A. & Taggart, J.B. 1991. Genetic differentiation among the sympatric brown trout (*Salmo trutta*) populations of Lough Melvin, Ireland. *Biological Journal of the Linnean Society,* **43**: 221-237.

Fleming, I.A. & Reynolds, J.D. 2004. Salmonid breeding systems. *In:* Hendry, A. & Stearns, S. (Eds.). *Evolution illuminated: Salmon and their relatives*: 265-294. Oxford: Oxford University Press.

Fontaine, M. & Vibert, R. 1950. Sur un parr de saumon hermaphrodite parvenu a maturite sexuelle. *Journal du Conseil,* **16**: 216-226. (In French).

Fries, B., Ekstrom, C.U. & Sundevall, G. 1895. *A History of Scandinavian Fishes*. Second edition. Revised and completed by F.A. Smitt. Part 2. Stockholm: P.A. Norstedt & soner. 1240 p.

Frost, W.E. & Brown, M.E. 1967. *The trout*. London: Collins. 286 p.

Galbreath, P.F., Adams, K.J., Wheeler, P.A. & Thorgaard, G.H. 1997. Clonal Atlantic salmon × brown trout hybrids produced by gynogenesis. *Journal of Fish Biology,* **50**: 1025-1033.

Galbreath, P.F. & Thorgaard, G.H. 1994. Viability and freshwater performance of Atlantic salmon (*Salmo salar*) × brown trout (*Salmo trutta*) triploid hybrids. *Canadian Journal of Fisheries and Aquatic Sciences,* **51**(Suppl. 1): 16-24.

Galbreath, P.F. & Thorgaard, G.H. 1995. Sexual maturation and fertility of diploid and triploid Atlantic salmon × brown trout hybrids. *Aquaculture,* **137**: 299-311.

Galbreath, P.F. & Thorgaard, G.H. 1997. Saltwater performance of triploid Atlantic salmon *Salmo salar* L. × brown trout *Salmo trutta* L. hybrids. *Aquaculture Research,* **28**: 1-8.

Garcia de Leaniz, C. & Verspoor, E. 1989. Natural hybridization between Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, in northern Spain. *Journal of Fish Biology,* **34**: 41-46.

Garcia-Vazquez, E., Ayllon, F., Martinez, J.L., Perez, J. & Beall, E. 2003. Reproduction of interspecific hybrids of Atlantic salmon and brown trout in a stream environment. *Freshwater Biology,* **48**: 1100-1104.

Garcia-Vazquez, E., Moran, P., Martinez, J.L., Perez, J., de Gaudemar, B., & Beall, E. 2001. Alternative mating strategies in Atlantic salmon and brown trout. *Journal of Heredity,* **92**: 146-149.

Garcia-Vazquez, E., Moran, P., Perez, J., Martinez, J.L., Izquierdo, J.I., de Gaudemar, B. & Beall, E. 2002. Interspecific barriers between salmonids when hybridization is due to sneak mating. *Heredity,* **89**: 288-292.

Garcia-Vazquez, E., Perez, J., Ayllon, F., Martinez, J.L., Glise, S. & Beall, E. 2004. Asymmetry of post-F_1 reproductive barriers among brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*). *Aquaculture,* **234**: 77-84.

Gephard, S., Moran, P. & Garcia-Vazquez, E. 2000. Evidence of successful natural reproduction between brown trout and mature male Atlantic salmon parr. *Transactions of the American Fisheries Society,* **129**: 301-306.

Gharbi, K., Gautier, A., Danzmann, R.G., Gharbi, S., Sakamoto, T., Hoyheim, B., Taggart, J.B., Cairney, M., Powell, R., Krieg, F., Okamoto, N., Ferguson, M.M., Holm, L.-E. & Guyomard, R. 2006. A linkage map for brown trout (*Salmo trutta*): Chromosome homeologies and comparative genome organization with other salmonid fish. *Genetics,* **172**: 2405-2419.

Giuffra, E., Bernatchez, L., Guyomard, R. 1994. Mitochondrial control region and protein coding gene sequence variation among phenotypic forms of brown trout *Salmo trutta* from northern Italy. *Molecular Ecology,* **3**: 161-171.

Giuffra, E., Guyomard, R. & Forneris, G. 1996. Phylogenetic relationships and introgression patterns between incipient parapatric species of Italian brown trout (*Salmo trutta* L. complex). *Molecular Ecology,* **5**: 207-220.

Gjedrem, T., Eggum, A. & Refstie, T. 1977. Chromosomes of some salmonids and salmonid hybrids. *Aquaculture,* **11**: 335-348.

Gray, A.K., Evans, M.A. & Thorgaard, G.H. 1993. Viability and development of diploid and triploid salmonid hybrids. *Aquaculture,* **112**: 125-142.

Gross, R., Nilsson, J. & Schmitz, M. 1996. A new species-specific nuclear DNA marker for identification of hybrids between Atlantic salmon and brown trout. *Journal of Fish Biology,* **49**: 537-540.

Grote, W., Vogt, C. & Hofer, B. 1909. *Die Susse-wasserfische von Mittel-Europa*. Frankfurt a. M.: Druck von Werner u. Winter; Leipzig: Commissions-Verlag von Wilhelm Engelmann. 558 p. (In German).

Guyomard, R. 1978. Identification par electrophorese d'hybrides de Salmonides. *Annales de Genetique et de Selection Animale,* **10**: 17-27. (In French, English summary).

Gyllensten, U. & Wilson, A.C. 1987. Mitochondrial DNA of Salmonids: inter- and intraspecific variability detected with restriction enzymes. *In:* Ryman N. & Utter F. (Eds.) *Population Genetics and Fishery Management*: 301-317. Seattle & London: University of Washington Press.

Haak 1894. Lachsbastarde auf der Schweizerischen Fischerei-Ausstellung in Zurich. *Allgemeine Fischerei-Zeitung,* **19**: 280-281. (In German).

Haen, P.J. & O'Rourke, F.J. 1968. Proteins and haemoglobins of salmon-trout hybrids. *Nature,* **217**: 65-67.

Hartley, S.E. 1996. High incidence of Atlantic salmon × brown trout hybrids in a Lake District stream. *Journal of Fish Biology,* **48**: 151-154.

Hedenskog, M., Petersson, E., Jarvi, T. & Khamis, M. 1997. Morphological comparison of natural produced Atlantic salmon (*Salmo salar* L), anadromous brown trout (*S. trutta* L), and their hybrid. *Nordic Journal of Freshwater Research,* **73**: 35-43.

Heggberget, T.G. 1988. Timing of spawning in Norwegian Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences,* **45**: 845-849.

Heggberget, T.G., Haukebo, T., Mork, J. & Stahl, G. 1988. Temporal and spatial segregation of spawning in sympatric populations of Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L. *Journal of Fish Biology,* **33**: 347-356.

Henking, H. 1929. Untersuchungen an Salmoniden mit besonderer berucksichtigung der art- und rassefragen. Teil 1. *Rapports et Proces-Verbaux des Reunions,* **61**: 1-99. (In German, English summary).

Hindar, K. 1998. Interbreeding of farmed salmon and wild trout: does this risk the genetic integrity of wild populations? *In:* Youngson, A.F., Hansen L.P. & Windsor M.L. (Eds.) *Interactions between Salmon Culture and Wild Stocks of Atlantic salmon*: 30-31. Bath, England, UK: ICES and NASCO.

Hindar, K. & Balstad, T. 1994. Salmonid culture and interspecific hydridization. *Conservation Biology,* **8**: 881-882.

Hindar, K. & Nordland, J. 1989. A female Atlantic salmon, *Salmo salar* L., maturing sexually in the parr stage. *Journal of Fish Biology,* **35**: 461-463.

Hubbs, C.L. 1955. Hybridization between fish species in nature. *Systematic Zoology,* **4**: 1-20.

Hurrell, R.H. & Price, D.J. 1991. Natural hybrids between Atlantic salmon, *Salmo salar* L., and trout, *Salmo trutta* L., in juvenile salmonid populations in southwest England. *Journal of Fish Biology,* **39**(Suppl. A): 335-341.

Jansson, H. & Dannewitz, J. 1995. Repression of the brown trout *GPI-1** locus in Atlantic salmon × brown trout hybrids. *Hereditas,* **122**: 293-294.

Jansson, H., Holmgren, I., Wedin, K. & Andersson, T. 1991. High frequency of natural hybrids between Atlantic salmon, *Salmo salar* L., and brown trout, *S. trutta* L., in a Swedish river. *Journal of Fish Biology,* **39**(Suppl. A): 343-348.

Jansson, H. & Ost, T. 1997. Hybridization between Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in a restored section of the River Dalalven, Sweden. *Canadian Journal of Fisheries and Aquatic Sciences,* **54**: 2033-2039.

Johnsen, B.O., Hindar, K., Balstad, T., Hvidsten, N.A., Jensen, A.J., Jensas, J.G., Syversveen, M. & Ostborg, G. 2005. Atlantic salmon and *Gyrodactylus* in the river Vefsna and Driva. *NINA rapport,* **34**: 33 p. (In Norwegian, English Abstract).

Johnson, K.R. & Wright, J.E. 1986. Female brown trout × Atlantic salmon hybrids produce gynogens and triploids when backcrossed to male Atlantic salmon. *Aquaculture,* **57**: 345-358.

Jones, J.W. 1947. Salmon and trout hybrids. *The Proceedings of the Zoological Society of London,* **117**: 708-715.

Jones, J.W. 1959. *The Salmon*. London: Collins. 192 p.

Jordan, W.C. & Verspoor, E. 1993. Incidence of natural hybrids between Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L, in Britain. *Aquaculture and Fisheries Management,* **24**: 373-377.

Joyce, P., Hearn, J., Kelly, M. & Duke, E.L. 1973. Genetic and biochemical aspects of lactate dehydrogenase isozymes in the salmonid eye. *Biochemical Genetics,* **9**: 327-342.

Jug, T., Berrebi, P. & Snoj, A. 2005. Distribution of non-native trout in Slovenia and their introgression with native trout populations as observed through microsatellite DNA analysis. *Biological Conservation,* **123**: 381-388.

Jug, T., Dovc, P., Pohar, J. & Snoj, A. 2004. RAPD analysis as a tool for discriminating marble trout from hybrids (marble trout × brown trout) in the zones of hybridization. *Journal of Animal Breeding and Genetics,* **121**: 156-162.

Kazakov, R.V. 1990. *Artificial forming of anadromous salmonids populations*. Moscow: Agropromizdat. 239 p. (In Russian)

Khristoforov, O.L. & Murza, I.G. 2001. Seasonal races of the Atlantic salmon (*Salmo salar* L.): some features of a physiological status and behaviour of migrants. *In:* Veselov, A.E., Danilov, P.I., Ieshko, E.P., Kitaev, S.P., Kuznetsov, O.L. & Nemova, N.N., (Eds.) *Biodiversity of the European North. International conference. September 3-7, 2001. Abstracts*: 253-254. Petrozavodsk: Institute of Biology of Karelian Research Centre. (online: http://biology.krc.karelia.ru/conferences/biodiv2001/)

Klementsen, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. & Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish,* **12**: 1-59.

Kosoric, D. & Vukovic, T. 1969. A research of possibilities of hybridization of Salmonidae species of the Neretva river confluence. *Ichthyologia,* **1**: 57-67. (English summary).

Kusakina, A.A. 1959. Cytophysiological investigation of muscle tissue in some interspecies fish hybrids at heterosis. *Cytology (USSR),* **1**: 111-119. (In Russian).

Lacepede. 1847. *Histoire Naturelle*. v. 2. Paris: Furne et C[ie], Editeurs. 648 p. (In French).

Lamond, H. 1916. *The sea-trout*. London: Sherratt and Hughes. 219 p.

Largiader, C.R., Guyomard, R. & Roche, P. 1996. Evidence for natural reproduction of Atlantic salmon (*Salmo salar* L.) in a French tributary of the Rhine based on genetic analysis of eggs collected from redds. *Bulletin Francais de la Peche et de la Pisciculture,* **343**: 183-188. (In French, English summary).

Largiader, C.R. & Scholl, A. 1995. Effect of stocking on the genetic diversity of brown trout populations of the Adriatic and Danubian drainages in Switzerland. *Journal of Fish Biology,* **47**(Suppl. A): 209-225.

Leonko, A.A. & Chernitskiy, A.G. 1986. Comparative analysis of smolt migration of Atlantic salmon, *Salmo salar*, and sea trout, *Salmo trutta*. *Journal of Ichthyology,* **26**: 113-120.

Levin, D.A. 2002. Hybridization and extinction. *American Scientist,* **90**: 254-261.

Lura, H. & Segrov, H. 1993. Timing of spawning in cultured and wild Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in the river Vosso, Norway. *Ecology of Freshwater Fish,* **2**: 167-172.

MacCrimmon, H.R. & Gots, B.L. 1979. World distribution of Atlantic salmon, *Salmo salar*. *Journal of the Fisheries Research Board of Canada,* **36**: 422-457.

Makhrov, A.A. 2005. "Dialectical" speciation: from brown trout (*Salmo trutta* L.) to Atlantic salmon (*S. salar* L.). *In:* Vorobjeva, E.I. & Striganova, B.R. (Eds) *Evolutionary factors of the formation of animal life diversity*.): 248-256. Moscow: KMK Scientific Press Ltd. (In Russian, English summary).

Makhrov, A.A., Artamonova, V.S., Christoforov, O.L., Murza, I.G. & Altukhov, Yu.P. 2004. Hybridization between Atlantic salmon *Salmo salar* L. and brown trout *S. trutta* L. upon artificial propagation. *Russian Journal of Genetics,* **40**: 1258-1263.

Makhrov, A.A., Kuzishchin, K.V. & Novikov, G.G. 1998. Natural hybrids of *Salmo salar* with *Salmo trutta* in the rivers of the White Sea basin. *Journal of Ichthyology,* **38**: 61-66.

Mallet, J. 2007. Hybrid speciation. *Nature,* **446**: 279-282.

Martynov, V.G. 2007. *Atlantic salmon Salmo salar L. in the North of Russia*. Ekaterinburg: UD RAS. 414 p. (In Russian, English summary).

Matthews, M.A., Poole, W.R., Thompson, C.E., McKillen, J., Ferguson, A., Hindar, K. & Wheelan, K.F. 2000. Incidence of hybridization between Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in Ireland. *Fisheries Management and Ecology,* **7**: 337-347.

Mayr, E. 1970. *Populations, Species, and Evolution*. Massachusetts: The Belknap Press of Harvard University Press.

McGowan, C. & Davidson, W.S. 1992a. Artificial hybridization of Newfoundland brown trout and Atlantic salmon: hatchability, survival and growth to first feeding. *Aquaculture,* **106**: 117-125.

McGowan, C. & Davidson, W.S. 1992b. Unidirectional natural hybridization between brown trout (*Salmo trutta*) and Atlantic salmon (*S. salar*) in Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences,* **49**: 1953-1958.

McVeigh, H.P. & Davidson, W.S. 1991. A salmonid phylogeny inferred from mitochondrial cytochrome b gene sequences. *Journal of Fish Biology,* **39(**Suppl. A): 277-282.

Menzies, W.J.M. 1936. *Sea Trout and Trout*. London: Edward Arnold & co. 230 p.

Mills, D. 1989. *Ecology and Management of Atlantic Salmon*. London & New York: Chapman and Hall. 351 p.

Mina, M.V. 1991. *Microevolution of Fishes. Evolutionary Aspects of Phenetic Diversity*. Rotterdam: A.A. Balkema. 215 p.

Mjolnerod, I.B. 1999. *Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (Salmo salar) revealed by molecular genetic techniques.* Dr. Scient. Thesis. Trondheim: The Norwegian University of Science and Technology, Department of Zoology. 29 p.

Murza, I.G. & Christoforov, O.L. 1993. Estimation of degree of maturity of gonads and prediction of age of attainment of sexual maturity in Atlantic salmon and sea trout (Methodological instructions) *Canad. Translat. Fish. Aquat. Sci*., **5599**: 1-106.

Nall, G.H. 1930. *The life of the sea trout*. London: Seeley, Service et Co, Ltd. 335 p.

Nikolyukin, N.I. 1972. *Distant hybridization in Acipenseridae and Teleostei, theory and practice*. Moscow: Pischevaia promuslennost. 336 p. (In Russian).

Novikov, P.I. 1938. *Atlantic salmon*. Petrozavodsk: State Press of Karelia. 60 p. (In Russian).

Nygren, A., Nyman, L., Svensson, K. & Jahnke, G. 1975. Cytological and biochemical studies in back-crosses between the hybrid Atlantic salmon × sea trout and its parental species. *Hereditas,* **81**: 55-62.

Nyman, O.L. 1970. Electrophoretic analysis of hybrids between salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.). *Transactions of the American Fisheries Society,* **99**: 229-236.

Olsen, K.H., Bjerselius, R., Petersson, E., Jarvi, T., Mayer, I. & Hedenskog, M. 2000. Lack of species-specific primer effects of odours from female Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*. *Oikos,* **88**: 213-220.

Olsen, K.H., Johansson, A.-K., Bjerselius, R., Mayer, I. & Kindhal, H. 2002. Mature Atlantic salmon (*Salmo salar* L.) male parr are attracted to ovulated female urine but not to ovarian fluid. *Journal of Chemical Ecology,* **28**: 29-40.

Osinov, A.G. 1990. On the origin of the Sevan trout: population-genetic approach. *The Journal of Fundamental Biology,* **51**: 817-827. (In Russian, English summary).

Osinov, A.G. & Lebedev, V.S. 2000. Genetic divergence and phylogeny of the Salmoninae based on allozyme data. *Journal of Fish Biology,* **57**: 354-381.

Paaver, T. 1991. Electroforetisk undersokning av romproteiner hos laxfisk. *Information fran Sotvattenslaboratoriet, Drottningholm,* **4**: 49-62. (In Swedish).

Paaver, T., Gross, R. & Vasemagi, A. 2001. Genetic characterization of Estonian salmon populations. *In:* Kangur, M. & Wahlberg, B (Eds.) *Present and potential production of salmon in Estonian rivers*: 77-84. Tallinn: Estonian Academy Publishers.

Palsson, S. & Arnason, E. 1994. Sequence variation for cytochrome b genes of three salmonid species from Iceland. *Aquaculture,* **128**: 29-39.

Palva, T.K., Lehvaslaiho, H. & Palva, E.T. 1989. Identification of anadromous and non-anadromous salmon stocks in Finland by mitochondrial DNA analysis. *Aquaculture,* **81**: 237-244.

Patarnello, T., Bargelloni, L., Caldara, F. & Colombo, L. 1994. Cytochrome b and 16S rRNA sequence variation in the *Salmo trutta* (Salmonidae, Teleostei) species complex. *Molecular Biology and Evolution,* **3**: 69-74.

Payne, R.H., Child, A.R. & Forrest, A. 1972. The existence of natural hybrids between the European trout and the Atlantic salmon. *Journal of Fish Biology,* **4**: 233-236.

Phillips, R.B., Matsuoka, M.P., Konkol, N.R. & McKay, S. 2004. Molecular systematics and evolution of the growth hormone introns in the Salmoninae. *Environmental Biology of Fishes,* **69**: 433-440.

Phillips, R.B., Matsuoka, M.P., Konon, I. & Reed, K.M. 2000. Phylogenetic analysis of mitochondrial and nuclear sequences supports inclusion of *Acantholingue ohridana* in the genus *Salmo*. *Copeia,* **2**: 546-550.

Phillips, R.B. & Rab, P. 2001. Chromosome evolution in Salmonidae (Pisces): an update. *Biological Reviews,* **76**: 1-25.

Piggins, D.J. 1965. Salmon and sea trout hybrids. *The Salmon Research Trust of Ireland,* **Report for 1964**: 27-37.

Piggins, D.J. 1967. Further studies on the specific characteristics of brown trout and salmon – sea trout hybrids. *The Salmon Research Trust of Ireland,* **Report for 1966**: 29-32.

Ponomareva, E.V., Ponomareva, M.V., Kuzishchin, K.V., Makhrov, A.A., Afanas'ev, K.I. & Novikov, G.G. 2002. Temporal variation in the population structure and genetic diversity of the Atlantic Salmon *Salmo salar* in the Nil'ma River. *Journal of Ichthyology,* **42**: 300-308.

Presa, P., Pardo, B.G., Martinez, P. & Bernatchez, L. 2002. Phylogeographic congruence between mtDNA and rDNA ITS markers in brown trout. *Molecular Biology and Evolution,* **19**: 2161-2175.

Prokofieva, A. 1934. On the chromosome morphology of certain pisces. *Cytologia,* **5**: 498-506.

Prokofieva-Belgovskaya, A.A. 1964. Heterocyclicity of the cell nucleus system at early stages of development of *Salmo faria*, *S. salar* and *Coregonus lavaretus baeri*. *Cytology (USSR)*, **6**: 553-559. (In Russian, English summary).

Razpet, A., Maric, S., Parapot, T., Nikolic, V. & Simonovic, P. 2007a. Re-evaluation of *Salmo* data by Gridelli (1936) – description of stocking, hybridization and repopulation in the River Soca basin. *Italian Journal of Zoology,* **74**: 63-70.

Razpet, A., Sušnik, S., Jug, T. & Snoj, A. 2007b. Genetic variation among trout in the River Neretva basin, Bosnia and Herzegovina. *Journal of Fish Biology,* **70**(Suppl. A) : 94-110.

Refstie, T. 1983. Hybrids between salmonid species. Growth rate and survival in seawater. *Aquaculture,* **33**: 281-285.

Refstie, T. & Giedrem, T. 1975. Hybrids between Salmonidae species. Hatchability and growth rate in the freshwater period. *Aquaculture,* **6**: 333-342.

Regan, T. 1911. *The freshwater fishes of the British Isles*. London: Methuen & Co Ltd. 287 p.

Rhymer, J.M. & Simberloff, D. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics,* **27**: 83-109.

Robinson, B.W. & Wilson, D.S. 1994. Character release and displacement in fishes: a neglected literature. *American Naturalist,* **144**: 596-627.

Roth, H. & Geiger, W. 1972. Brienzersee, Thunersee, and Bielersee: Effects of exploitation and eutrophication on the salmonid communites. *Journal of the Fisheries Research Board of Canada,* **29**: 755-764.

Rouiller, K., Borsenkow, J. & Usow, S. 1858. Ueber die Fischruchtungs-Anstalt des Herrn Wrasskji. *Archiv fur Wissenschaftliche Kunde von Russland,* **18**: 65-83. (In German).

Rukhkian, R.H. 1989. *Karyology and origin of the Transcaucasian trouts*. Erevan: Academy of Sciences of Armenian SSR. 166 p. (In Russian, English summary).

Schwartz, F.L. 1981. World literature to fish hybrids with an analysis by family, species, and hybrids. Suppl. 1. *NOAA Technical Report NMFS,* **SSRF-750**: 1-507.

Scott, R.J., Jurde, K.A., Ramster, K., Noakes, D.l.G. & Beamish, F.W.N. 2005. Interaction between naturalized exotic salmonids and reintroduced Atlantic salmon in a Lake Ontario tributary. *Ecology of Freshwater Fish,* **14**: 402-405.

Schreiber, A., Schenk, M., Lehmann, J. & Sturenberg, F.-J. 1994. Genetische Untersuchungen an Meerforellen- und Lachswildfangen aus dem Rheinsystem in Nordrhein-Westfalen. *Fischer & Teichwirt,* **2**: 52-53. (In German).

Scribner, K.T., Page, K.S. & Bartron, M.L. 2001. Hybridization in freshwater fishes: a review of case studies and cytonuclear methods of biological inference. *Reviews in Fish Biology and Fisheries,* **10**: 293-323.

Scrochowska, S. 1969. Migrations of the sea trout (*Salmo trutta* L.), brown trout (*Salmo trutta m. fario* L.) and their crosses. Part I. Problem, methods and results of tagging. *Polskie Archiwum Hydrobiologii,* **16**: 125-140.

Seehausen, O., Takimoto, G., Roy, D. & Jokela, J. 2007. Speciation reversal and biodiversity dynamics with hybridization in changing environments. *Molecular Ecology,* **17**: 30-44.

Semeonova, S.K. & Slyn'ko, V.I. 1988a. Est D polymorphism in salmon (*Salmo salar* L.) and sea trout (*S. trutta* L.). *Isozyme bulletin,* **21**: 197.

Semyonova, S.K. & Slyn'ko, V.I. 1988b. Polymorphism of proteins in populations of Atlantic salmon (*Salmo salar* L.), brown trout (*S. trutta* L.), and their hybrids. *Genetica (USSR),* **24**: 548-555. (In Russian, English summary).

Seppovaara, O. 1962. Zur Systematik und okologie des Lachses und der Forellen in der Binnengewassern Finlands. *Annales Zoologici Societatis "Vanamo",* **24**: 1-86. (In German).

Serebrovskiy, A.S. 1935. Hybridization of Animals. Moscow, Leningrad: Biomedgiz. 290 p. (In Russian).

Servedio, M.R. & Noor, M.A.F. 2003. The role of reinforcement in speciation: theory and data. *Annual Review of Ecology and Systematics,* **34**: 339-364.

Shaw, J. 1839. Account of experimental observations on the development and growth of salmon-fry, from the exclusion of the ova to the age of two years. *Transactions of the Royal Society of Edinburgh,* **XIV**: 547-566.

Skaala, O. & Solberg, G. 1997. Biochemical Genetic Variability and Taxonomy of a Marmorated Salmonid in River Otra, Norway. *Nordic Journal of Freshwater Research,* **73**: 3-12.

Smirnov, Y.A. 1971. *Salmon of Lake Onego*. Leningrad: Nauka. 212 p. [Fisheries Research Board of Canada. Translation Series 2137]

Smith, G.R. 1992. Introgression in fishes: significance for paleontology, cladistics, and evolutionary rates. *Systematic Biology,* **41**: 41-57.

Snoj, A. 1997. Molecular biologic characterization of marble trout (*Salmo marmoratus*, Cuvier 1817). Dissertation Thesis. Domzale: University of Ljubjana. 109 p. (English summary).

Snoj, A., Melkic, E., Susnik, S., Muhamedagic, S. & Dovc, P. 2002. DNA phylogeny supports revised classification of *Salmothymus obtusirostris*. *Biological Journal of the Linnean Society,* **77**: 399-411.

Snoj, A., Razpet, A., Tomljanovic, T., Treer, T. & Sušnik, S. 2007. Genetic composition of the Jadro softmouth trout following translocation into a new habitat. *Conservation Genetics,* **8**: 1213-1217.

Solomon, D.J. & Child, A.R. 1978. Identification of juvenile natural hybrids between Atlantic salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.). *Journal of Fish Biology,* **12**: 499-501.

Spaas, J.T. & Heuts, M.J. 1958. Contributions to the compative physiology and genetics of the European Salmonidae. II. Physiologie et genetigue du developpement embryonnaire. *Hydrobiologia,* **12**: 1-26.

Sušnik, S., Knizhin, I., Snoj, A. & Weiss, S. 2006. Genetic and morphological characterization of a Lake Ohrid endemic, *Salmo* (*Acantholingua*) *ohridanus* with a comparison to sympatric *Salmo trutta*. *Journal of Fish Biology,* **68**(Suppl. A): 2-23.

Sušnik, S., Schöffmann, J. & Snoj, A. 2004. Phylogenetic position of *Salmo* (*Platysalmo*) *platycephalus* Behnke 1968 from south-central Turkey, evidenced by genetic data. *Journal of Fish Biology,* **64**: 947-960.

Sušnik, S., Weiss, S., Odak T., Delling B., Treer T. & Snoj, A. 2007. Reticulate evolution: ancient introgression of the Adriatic brown trout mtDNA in softmouth trout *Salmo obtusirostris* (Teleostei: Salmonidae). *Biological Journal of the Linnean Society,* **90**: 139-152.

Sutton, J.G., Goodwin, J., Horscroft, G., Stockdale, R.E. & Frake, A. 1983. Identification of trout and salmon bloods by simple immunological technigue and by electrofocusing patterns of red cell enzyme superoxide dismutase. *Journal of the Association of Official Analytical Chemists,* **66**: 1164-1174.

Svardson, G. 1945. Chromosome studies on Salmonidae. *Reports from the Swedish State Institute of Freshwater Fishery Research, Drottningholm,* **23**: 1-151.

T.G. 1834. The salmon par is neither a hybrid, nor a distinct species, of the genus *Salmo*, but a state of the common salmon. *The Magazine of Natural History,* **7**: 521-522.

Taggart, J.B., McLaren, I.S., Hay, D.W., Webb, J.H. & Youngson, A.F. 2001. Spawning success in Atlantic salmon (*Salmo salar* L.): a long-term DNA profiling-based study conducted in a natural stream. *Molecular Ecology,* **10**: 1047-1060.

Taylor, E.B. 2004. Evolution in mixed company: Evolutionary inferences from studies of natural hybridization in Salmonidae. *In:* Hendry, A. & Stearns, S. (Eds.) *Evolution illuminated: Salmon and their relatives*: 232-263. Oxford: Oxford University Press.

Thompson, C.E., Poole, W.R., Matthews, M.A. & Ferguson, A. 1998. Comparison, using minisatellite DNA profiling, of secondary male contribution in the fertilization of wild and ranched Atlantic salmon (*Salmo salar*) ova. *Canadian Journal of Fisheries and Aquatic Sciences,* **55**: 2011-2018.

Verspoor, E. 1988. Widespread hybridization between native Atlantic salmon, *Salmo salar*, and introduced brown trout, *S. trutta*, in eastern Newfoundland. *Journal of Fish Biology,* **32**: 327-334.

Verspoor, E., Beardmore, J.A., Consuegra, S., Garcia de Leaniz, C., Hindar, K., Jordan, W.C., Koljonen, M. L., Makhrov, A.A., Paaver, T., Sanchez, J.A., Skaala, O., Titov, S. & Cross, T.F. 2005. Population Structure in the Atlantic Salmon: Insights From 40 Years of Research into Genetic Protein Variation. *Journal of Fish Biology,* **67**(Suppl. A): 3-54.

Verspoor, E. & Hammar, J. 1991. Introgressive hybridization in fishes: the biochemical evidence. *Journal of Fish Biology,* **39**(Suppl. A): 309-334.

Verspoor, E. & McCarthy, E. 1997. Genetic divergence at the NAD+-dependent malic enzyme locus in Atlantic salmon from Europe and North America. *Journal of Fish Biology,* **51**: 155-163.

Vuorinen, J. & Piironen, J. 1984. Electrophoretic identification of Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and their hybrids. *Canadian Journal of Fisheries and Aquatic Sciences,* **41**: 1834-1837.

Wilkins, N.P., Courtney, H.P. & Curatolo, A. 1993. Recombinant genotypes in backcrosses of male Atlantic salmon × brown trout hybrids to female Atlantic salmon. *Journal of Fish Biology,* **43**: 393-399.

Wilkins, N.P., Courtney, H.P., Gosling, E., Linnane, A., Jordan, C. & Curatolo, A. 1994. Morphometric and meristic characters in salmon, *Salmo salar* L., trout, *Salmo trutta* L., and their hybrids. *Aquaculture and Fisheries Management,* **25**: 505-518.

Wilkins, N.P., Gosling, E., Curatolo, A., Linnane, A., Jordan, C. & Courtney, H.P. 1995. Fluctuating asymmetry in Atlantic salmon, European trout and their hybrids, including triploids. *Aquaculture,* **137**: 77-85.

Willughbeii, F. 1686. *Historia piscium* ... Oxonii: E. Theatro Sheldoniano, Anno Dom. 180 p.

Wilson, I.F., Bourke, E.A. & Cross, T.F. 1995. Genetic variation at traditional and novel allozyme loci, applied to interactions between wild and reared *Salmo salar* L. (Atlantic salmon). *Heredity,* **75**: 578-588.

Winge, O. & Ditlevsen, E. 1948. A study on artificial hybrids between salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Comptes Rendus des travaux du Laboratorie Carlsberg. Serie Physioloque,* **24**: 317-345.

Yakovlev, V.N., Slyn'ko, Yu.V., Grechanov, I.G. & Krysanov, E.Yu. 2000. Distant hybridization in fish. *Journal of Ichthyology,* **40**: 298-311.

Yarrell, W. 1836. *A history of British fishes*. London: John van Voorst. v. 2. p. 47.

Youngson, A.F., Knox, D. & Johnstone, R. 1992. Wild adult hybrids of *Salmo salar* L. and *Salmo trutta* L. *Journal of Fish Biology,* **40**: 817-820.

Youngson, A.F., Webb, J.H., Thompson, C.E. & Knox, D. 1993. Spawning of escaped farmed Atlantic salmon (*Salmo salar*): hybridization of females with brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences,* **50**: 1986-1990.

Ueda, T. & Kobayashi, J. 1990. Disapperance of Ag-NORs originated from maternal species in hybrids between female Atlantic salmon and male brown trout. *Chromosome Information Service,* **49**: 25-26.

Zaslavskiy, V.A. 1967. Reproductive self-destruction as an ecological factor (Ecological results of the genetic interaction of populations). *The Journal of Fundamental Biology,* **28**: 3-11. (In Russian).

Zelinskiiy, Yu.P. & Medvedeva, I.M. 1985. Analysis of chromosomal variability and polymorphism in Atlantic salmon, *Salmo salar* of lake Onego. *Journal of Ichthyology,* **25**: 70-77.

Zelinskiy, Yu.P. & Makhrov, A.A. 2001. Chromosomal variability, genome reorganization in phylogeny, and the systematics of *Salmo* and *Parasalmo* species (Salmonidae). *Journal of Ichthyology,* **41**: 209-216.

Zelinskiy, Yu.P. & Smirnov, Yu.A. 1972. A question about genetic purity of Pjalma stock of Onego lake salmon. *In:* Komulainen A.A. (Ed.) *Scientific conference of Karelian biologists. Abstracts*: 265-266. Petrozavodsk: Karelian Branch of USSR Academy of Sciences. (In Russian).

Received 20 June 2008, accepted 15 December 2008