

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

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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<sub>1</sub> hybrids varies from zero (a complete loss) to normal. Post-F<sub>1</sub> hybridization sometimes results in gynogenesis, hybridogenesis and introgression. The role of hybridization in the evolution of *Salmo* is discussed.

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## 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; Klements 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 tighed 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<sub>1</sub> 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<sub>1</sub> 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), phosphoglucosomutase (*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 hydratase (*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 preprogo-

nadotropin 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; Mjølnerod, 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<sub>1</sub> 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	Heggeberget 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<sub>1</sub> 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 & Dav-

idson, 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 off-

spring 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<sub>2</sub> 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 (Rukhian, 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<sub>1</sub> 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<sub>1</sub> 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 (Paternello 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 (Zelinskiy & 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<sub>1</sub> 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<sub>1</sub> 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.

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