ISSN 1062-3590, Biology Bulletin, 2011, Vol. 38, No. 2, pp. 138–145. © Pleiades Publishing, Inc., 2011.
Original Russian Text © A.A. Makhrov, V.S. Artamonova, V.S. Sumarokov, A.N. Pashkov, S.I. Reshetnikov, M.V. Ganchenko, S.A. Kulyan, 2011, published in Izvestiya Akademii Nauk, Seriya Biologicheskaya, 2011, No. 2, pp. 178–186.

ZOOLOGY

# Variation in the Timing of Spawning of the Black Sea Brown Trout *Salmo trutta labrax* Pallas under Artificial and Natural Conditions

**A. A. Makhrov[a], V. S. Artamonova[a], V. S. Sumarokov[b], A. N. Pashkov[b], S. I. Reshetnikov[b], M. V. Ganchenko[c], and S. A. Kulyan[d]**

[a] *Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninskii pr. 33, Moscow, 119071 Russia*
*e-mail: makhrov12@mail.ru*
[b] *Kuban State University, ul. Stavropol'skaya 149, Krasnodar, 350040 Russia*
[c] *Department of Agriculture and Processing Industry of Krasnodar Krai, ul. Rashpilevskaya 36, Krasnodar, 350000 Russia*
[d] *Adler Experimental Production Salmon Breeding Hatchery, ul. Partizanskaya, Monastyr' village, Sochi, Krasnodar krai, 354386 Russia*

Received April 16, 2010

**Abstract**—Analysis of the maturation and spawning times of the Black Sea brown trout bred at the fish-farming plants and inhabiting natural waterways of the Northwestern Caucasus has demonstrated a considerable variation depending on environmental conditions, first and foremost, temperature. This fact, as well as the analysis of literature data, suggests that the duration and timing of the spawning season cannot be used as self-sufficient criteria for identifying species of the genus *Salmo*.

**DOI:** 10.1134/S1062359011020075

The fish belonging to the genus *Salmo* display a high ecological plasticity: several intraspecific forms can coexist even in a small aquatic system. Some of them were described as separate species (Gunther, 1866); however, further studies confirmed the species status of only the Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) as well as several endemic species (*S. marmoratus, S. letnica, S. ischchan, S. carpio,* and *S. platycephalis*) (Berg, 1962; Frost and Brown, 1967; Behnke, 1968; Dorofeeva, 1998). Just recently, this list was supplemented with a number of endemic species (Zerunian and Gandolfi, 1990; Delling, 2003).

Nonetheless, Kottelat and Freyhof (2007) without any additional studies separated several other species of the genus *Salmo*. In particular, based only on the differences in spawning ground and time, they proposed to regard sympatric forms of the brown trout from Lake Ohrid (Balkan Peninsula) as the separate species *S. aphelios*, *S. balcanicus*, and *S. letnica*. It is demonstrative that any genetic distinctions between these species were undetectable even by such a sensitive method as microsatellite analysis (Susnik et al., 2006, 2007); thus, the authors believe that prezygotic reproductive isolation can serve as an independent criterion of species.

The goal of the work was to analyze the maturation and spawning times of one of the brown trout subspecies—the Black Sea brown trout *Salmo trutta labrax*—bred at fish-farming plants and inhabiting rivers of the Northwestern Caucasus and to study the appropriateness of this trait as a criterion for identifying salmon species.

## MATERIALS AND METHODS

The background for this work was data on the maturation and spawning times of the Black Sea brown trout obtained at the Adler Experimental Production Salmon Breeding Hatchery (hereinafter, AEPSB hatchery) as well as for the fish inhabiting several rivers on the Black Sea coast of the Northwestern Caucasus, namely, the Mzymta River and its tributary, the Chvizhepse River, and Shakhe, Psezuapse, Psakho, and Pshada (Fig. 1).

The AEPSB hatchery is located on the bank of the Mzymta River 35 km from Adler. Characteristics of this hatchery are listed in the paper by Kulyan (1999). The hatchery has a captive broodstock of the Black Sea brown trout, which has been formed for several years of the fingerlings obtained from anadromous breeders caught in the Mzymta River. These breeders were kept to spawning in cages in the river and released after reproduction.

Currently, the AEPSB hatchery has both captive and replacement broodstocks of the Black Sea brown trout as well as the raised fingerlings. The fingerlings are raised in a closed room in direct-flow tanks with a volume of about 640 l until an age of 1 year and then are either transferred into ITsA-2 (Russia) shed tanks with a circular flow and a volume of 1900 l or released into the Mzymta and Shakhe rivers.

Granulated combined feeds (according to the fish age and weight) are used when raising the replacement broodstock; during the maturation period, the feeding is ceased, and males are kept separately from females.

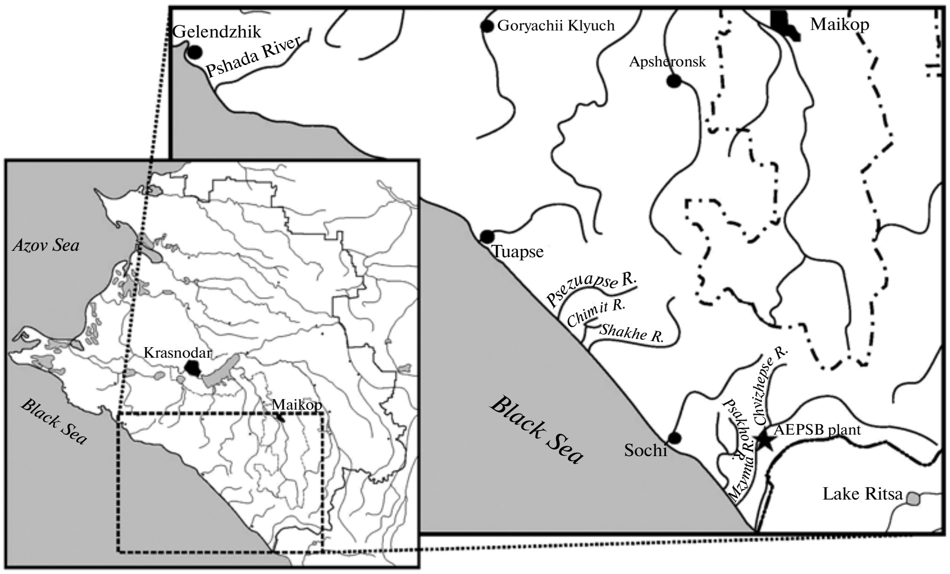


**Fig. 1.** Sites of sample collection. The inset shows the location of study areas on the territory of Krasnodar krai.

In our work, we recorded the dates of spawning of the females of generation of 1999 and 2000 bred at the AEPSB hatchery and their mothers, wild females that spawned in 1999 and 2000. In addition, biological analysis of 29 individuals (10 males and 19 females) of the generation of 2000 was performed on September 27–28, 2003.

In addition to the artificially bred fish, we also analyzed wild fish caught in rivers running into the Black Sea. The hydrological characteristics of these rivers are described by Borisov (2005) and Reshetnikov and Pashkov (2009). The caught underyearlings and the individuals originating from breeding facilities were discarded from analysis. The latter individuals were distinguished from the wild ones according to the fin rays bent as a result of necrosis (Dombrovsky and Usik, 2001). The age of wild fish was determined by the same person according to scales.

The main biological characteristics of the studied wild and artificially bred Black sea brown trout individuals, the volumes of studied samples, and catching dates are listed in Table 1. Black Sea brown trout fishing is limited because this form is rare; therefore, we examined the samples of a rather small volume. The body length to the caudal fin fork was measured in the majority of fish according to Smith (AC). In the case of individuals with a damaged caudal fin, AC was not measured; the body length to the end of the scale covering (AD) was used instead. The degree of gonad maturation was assessed according to the scale proposed by Murza and Khristoforov (1991). The stage of maturation was determined by one person for all individuals.

## RESULTS AND DISCUSSION

The females of generation 1999 obtained from wild breeders but raised at the AEPSB hatchery spawned for the first time in the winter of 2002–2003, i.e., during the third year of their life. The spawning campaign extended to the end of spring (Table 2). In January–March of 2003, the spawn was not taken from part of the mature females; thus, the number of individuals that reached maturity during this period was even larger than is shown in Table 2. In early June 2003, we necropsied a dead female at the fifth stage of gonad maturity.

In September 2003, the females of generation 2000 from the AEPSB hatchery population were at the second–third to fourth stages of gonad maturity and the males, at the second and fourth stages (Table 3). From December 2003 to June 2004, the fish from both studied generations (1999 and 2000) matured; the spawning peak was observed in January. Because of insufficient number of tanks, the breeders were mixed, preventing us from recording the spawning dates for each generation individually.

In September–October, the gonads of wild fish from the Mzymta, Shakhe, Chvizhepse, Psezuapse, and Psakho were at the second, third–fourth, fourth, and fifth stages of maturation (Table 3). The “wild” breeders of the anadromous brown trout form caught in the Mzymta River for further breeding reached maturity in November–December (Table 2).

The wild fish caught in September 2005 in the Pshada River were least developed (Table 3). Note that this was an abnormal year, since the water in the Pshada River was very low due to a dry summer and the brown trout residential form localized to a deep pool near the entry of a spring-fed brook.

**Table 1.** Characterization of the studied samples of the Black Sea brown trout

| Sampling site and date | Sex | Age | *n* | AC length, mm | AD length, mm | Weight, g |
|---|---|---|---|---|---|---|
| AEPSB plant; September 27–28, 2003 | Males | 2+ | 10 | – | 380–442 (409) | 765–1265 (976) |
| | Females | 2+ | 19 | – | 387–456 (424.4) | 855–1320 (1060.6) |
| Mzymta River; September 25, 2003 | Males | 1+ | 2 | 92–103 (97.5) | 84–94 (89) | 7.9–10.8 (9.35) |
| | | 2+ | 1 | 138 | 128 | 26.2 |
| | Males | 1+ | 3 | 91–114 (103.3) | 84–106 (95.7) | 8.2–14.6 (11.53) |
| | | 2+ | 6 | 129–158 (143.3) | 119–147 (133.2) | 20.5–39.5 (30.33) |
| Same site; October 5, 2004 | Male | 3+ | 1 | 246 | 227 | 154.7 |
| Chvizhepse River; September 24, 2006 | Males | 2+ | 4 | 142–169 (153.8) | 130–156 (141.8) | 34.1–52.2 (41) |
| | | 3+ | 5 | 176–213 (200.6) | 162–196 (184.8) | 64.7–111.4 (87.7) |
| | Females | 2+ | 4 | 150–161 (155) | 139–149 (143.8) | 35.4–43.8 (39.2) |
| | | 3+ | 9 | 175–230 (197.4) | 160–212 (181.4) | 59.4–130.9 (86.9) |
| Psakho River; September 8, 2006 | Males | 1+ | 2 | 136–146 (141) | 126–134 (130) | 27.1–32.5 (29.8) |
| Shakhe River; September 29, 2003 | Males | 1+ | 4 | 153–200 (172.8) | 142–186 (159.8) | 34.7–70.6 (52.2) |
| | Females | 1+ | 5 | 162–196 (177) | 150–181 (164.2) | 41.7–65.6 (50.36) |
| Same site; October 6, 2004 | Males | 1+ | 1 | 104 | 96 | 12.7 |
| | | 2+ | 2 | 168–197 (182.5) | 157–184 (170.5) | 40.6–72.1 (56.35) |
| Psezuapse River; September 14, 2006 | Males | 2+ | 9 | 162–192 (178.1) | 149–178 (164.4) | 44.8–70.8 (59.39) |
| | | 3+ | 1 | 212 | 195 | 93.3 |
| | Females | 2+ | 2 | 181–198 (189.5) | 167–183 (175) | 64.2–85 (74.6) |
| | | 3+ | 3 | 190–213 (201.7) | 176–198 (187.3) | 75.5–114.4 (89.6) |
| Pshada River; September 21, 2005 | Males | 1+ | 3 | 153–183 (167.7) | 142–171 (156) | 35.3–58.3(47.8) |
| | Females | 1+ | 6 | 154–175 (165.3) | 144–164 (154.2) | 35.6–50.6 (43.52) |

Note: The minimal and maximal values and the mean (parenthesized) are given for length and weight; *n* is the sample volume, individuals (for Tables 1 and 3).

**Table 2.** Maturation time and the number of mature wild females of the Black Sea brown trout from the Mzymta River (1999 and 2000) and the females bred at the AEPSB hatchery (2002–2003)

| Group | November | December | March | April | May |
|---|---|---|---|---|---|
| Wild females | 1 | 6 | 0 | 0 | 0 |
| Females bred at the AEPSB hatchery | 0 | 13 | 5 | 6 | 6 |

What are the possible reasons for the differences in the maturation and spawning times of the artificially bred and wild Black Sea brown trout as well as of individuals from different populations?

The brown trout has several intraspecific forms; the most widespread of them are migratory (anadromous) and residential. The latter one (especially males) is actively involved in the spawning of migratory individuals of the same species, i.e., both forms can constitute a single population. The self-reproducing populations of the brown trout residential form are found only in the regions of aquatic systems that are not visited due to some reasons by the anadromous fish (Barach, 1962; Kuzishchin, 1997; Klementsen et al., 2003; Pavlov and Savvaitova, 2008; Tuniev, 2008).

Autumn spawning is characteristic of both anadromous and residential forms of the brown trout. The autumn spawning period only occasionally extends to January (Menzies, 1936). Some males retain the sperm fertilizing ability until spring; however, the spawn of the females that had not spawned by the fall is unable to develop in spring (Scrochowska, 1969).

According to our data (Tables 2, 3) and the literature data (Murza and Khristoforov, 1988; etc.), the

**Table 3.** Distribution of the studied fish according to maturation stages

| Sex | Date | Catching site | Age, years | *n* | Fish distribution according to maturation stages, % | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Second | Second–third | Third | Third–fourth | Fourth | Fifth |
| Males | September 2003 | Mzymta River | 1+ | 2 | 100 | 0 | 0 | 0 | 0 | 0 |
| | | | 2+ | 1 | 100 | 0 | 0 | 0 | 0 | 0 |
| | October 2003 | | 3+ | 1 | 0 | 0 | 0 | 0 | 100 | 0 |
| | September 2003 | Shakhe River | 1+ | 4 | 50 | 0 | 0 | 25 | 25 | 0 |
| | October 2003 | | 1+ | 1 | 0 | 0 | 0 | 0 | 0 | 100 |
| | | | 2+ | 2 | 100 | 0 | 0 | 0 | 0 | 0 |
| | September 2006 | Chvizhepse River | 2+ | 4 | 0 | 0 | 0 | 0 | 100 | 0 |
| | | | 3+ | 5 | 0 | 0 | 0 | 0 | 100 | 0 |
| | September 2006 | Psezuapse River | 2+ | 9 | 33 | 0 | 0 | 11 | 56 | 0 |
| | | | 3+ | 1 | 0 | 0 | 0 | 0 | 100 | 0 |
| | September 2006 | Psakho River | 1+ | 2 | 0 | 0 | 0 | 0 | 100 | 0 |
| | September 2005 | Pshada River | 1+ | 3 | 0 | 0 | 67 | 33 | 0 | 0 |
| | September 2003 | AEPSB plant | 2+ | 10 | 60 | 0 | 0 | 0 | 40 | 0 |
| Females | September 2003 | Mzymta River | 1+ | 3 | 100 | 0 | 0 | 0 | 0 | 0 |
| | | | 2+ | 6 | 100 | 0 | 0 | 0 | 0 | 0 |
| | September 2003 | Shakhe River | 1+ | 5 | 100 | 0 | 0 | 0 | 0 | 0 |
| | September 2006 | Chvizhepse River | 2+ | 4 | 50 | 0 | 0 | 0 | 50 | 0 |
| | | | 3+ | 9 | 0 | 0 | 0 | 0 | 100 | 0 |
| | September 2006 | Psezuapse River | 2+ | 2 | 0 | 0 | 0 | 0 | 100 | 0 |
| | | | 3+ | 3 | 0 | 0 | 0 | 33 | 67 | 0 |
| | September 2005 | Pshada River | 1+ | 6 | 66 | 17 | 17 | 0 | 0 | 0 |
| | September 2003 | AEPSB plant | 2+ | 19 | 0 | 5 | 47 | 32 | 16 | 0 |

timing of spawning for the anadromous and residential Black Sea brown trout individuals in the Mzymta River and the majority of other rivers of the Russian Black Sea shore does not differ from that typical of the species. These data are also confirmed by the information obtained from local residents, although one of the experienced fishermen mentioned a form of brown trout in the Mzymta River that spawned in August.

However, the maturation of the females from the Pshada River is somewhat delayed as compared with the females of other waterways. The period when breeders from the captive broodstock of the AEPSB hatchery became ready to spawn considerably expands towards the spring season (Table 2). This fact was noticed in two generations of the brown trout raised at this hatchery. The extension of maturation and spawning periods of the Black Sea brown trout towards the spring months is annually recorded at the other fish-farming facility, the Adler federal state hatchery. The spawning there is recorded from November to early April (Babii et al., 2002; Nikandrov and Shindavina, 2007; V.A. Yankovskaya, personal communication) (Fig. 2).

Analysis of the published data demonstrates that the spawning time is inherited in some salmon species (Heggberget, 1988; Nikandrov et al., 2002). On the other hand, it has been shown that the genes controlling the spawning time had formed before the genome duplication accompanying the origination of salmon fish (O'Malley et al., 2002). Thus, it is most likely that such genes regulating maturation are present in all the salmon species. However, in some cases that we studied (AEPSB hatchery), the extension in the maturation period and spawning time took place almost during one generation in the majority of individuals of a certain group; therefore, we cannot speak about the genetic nature of this phenomenon—the effect of the environment is evident.

As is known, several environmental factors influence the time of fish spawning in addition to the genotype (Lam, 1983; Koshelev, 1984). For example, the spawning commencement in salmonids is to a consid-

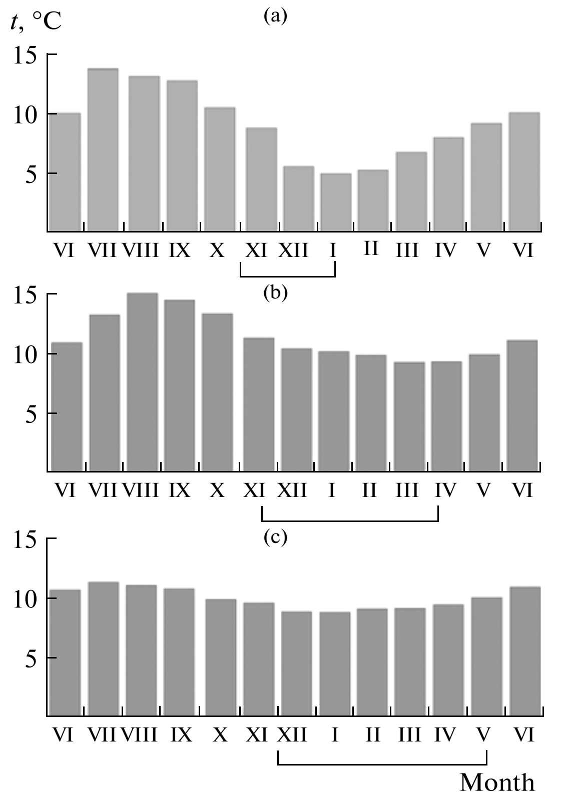


**Fig. 2.** Annual temperature variations in (a) Mzymta River, (b) tanks of the Adler plant (Nikandrov et al, 2002), and (c) the AEPSB plant. The abscissa shows the spawning period of brown trout (Murza and Khristoforov, 1988; Babii et al., 2002; Nikandrov and Shindavina, 2007).

erable degree determined by the photoperiod (Bromage et al., 1989). However, extension of the spawning period and its advance towards spring was also observed in the Black Sea brown trout breeders from the Adler hatchery. The fish at this facility are kept in unshaded tanks, so the photoperiod does not differ from the natural conditions.

The extension of the spawning period and its advance towards spring in the brown trout breeders raised at the AEPSB hatchery is likely to be connected with the water supply from springs. As for the Adler hatchery, the fish there are kept in the water taken from under the riverbed of the Mzymta River. Correspondingly, the temperatures necessary for activation of sex product maturation at these facilities are reached later than in rivers, while the seasonal changes in temperature are less pronounced than in nature (Fig. 2).

Most likely, these particular specific features of the temperature regimen to a considerable degree determine the slowed and less concurrent maturation of the breeders from both artificial populations. The temperature changes at the AEPSB hatchery more considerably differ from the natural conditions as compared with the Adler hatchery (Fig. 2); correspondingly, the change in the timing of spawning is more distinctly pronounced. Presumably, a certain delay in the gonad development of the wild fish from the Pshada River was also connected with the fact that they spent the summer in cold spring water.

Our conclusion agrees well with the literature data. For example, it has been shown that the brown trout spawns earlier in the upper reaches of rivers, where water cools faster, as compared with the lower reaches (Turyanin, 1982; Yakimov and Khatukhov, 2002). The spawning of the resident brown trout commences in January–March in the Russian spring-fed rivers (Vremya neresta..., 1893; Selegenenko, 1964). The brown trout reproduces in early spring in cold brooks of the Taurus Mountains, Turkey (Whittal, 1967). In an artesian-fed mountain brook in Spain, the spawning period of brown trout is extended from December to April (Gortazar et al., 2007), which is almost completely analogous to the spawning period of the brown trout at the AEPSB hatchery.

The spawning of the brown trout inhabiting cold mountain lakes of the Caucasus is also delayed. In particular, some individuals in Lake Tabistskhuri spawn in February (Kavraisky, 1896), as well as the brown trout *S. t. ezenami* in Lake Eizenam (Saidov and Magomedov, 1989). The brown trout of Lake Paravani spawns from the end of November to the beginning of February (Barach, 1964). The brown trout of Lake Visovacko in the Balkan Peninsula (described as an endemic species, *S. visovacensis*) spawns at the inflow and outflow of the Krka River, passing through the lake, in December and January and in the lake itself, according to survey data, in March and April (Taler, 1948).

A spring spawning of the May trout *S. schiffermulleri*, living in mountain lakes in the upper reaches of the Danube River, was described (Heckel and Kner, 1858). The carpione *S. carpio*, inhabiting mountain Lake Garda (Italy), spawns in winter and spring; moreover, some individuals maturate twice a year (Melotto and Alessio, 1990). The forms of the Sevan trout *S. ischchan* (Savvaitova et al., 1989) and Ohrid trout *S. letnica* (Soric, 1990) with winter and spring–summer spawning are described. The spawning season of bojak, a race of the Sevan trout, advanced from October–November to January–February and even March, when the spawning grounds dried making the fish move to deeper sites for spawning (Smolei, 1966).

Of special interest are the trout from the mountain lake Posta Fibreno (Italy). The water temperature there is almost constant over the year, amounting to about 10°C (Zerunian, 2002). Two forms of trout inhabit the lake: one spawns in December–January and the other, in February–March (Gibertini et al., 1990). The former is described as an endemic species *S. fibreni* (Zerunian and Gandolfi, 1990).

Data on the dependence of spawning time on water temperature are also available for other salmonids, in particular, the Atlantic salmon (Vladimirskaya, 1960; Johnston et al., 1992; Pankhurst and King, 2010). This species also spawns at different times in the upper and lower reaches of rivers (Webb and McLay, 1996), and a gradual, without any pronounced peaks, seasonal change in water temperature delays the spawning of the breeders of this species (Dikhnich, 2004). The rainbow trout grown in warmer water commences spawning earlier and in colder water, delays its spawning (Khristoforov and Murza, 1988; Scott, 1990; Pankhurst and King, 2010).

Our studies and analysis of the published data demonstrate that the spawning period of the representatives of the genus *Salmo* can considerably vary being influenced by environmental conditions. Spawning in different seasons (twice a year) is possible even during the ontogenesis of one individual, as was observed in carpione (Melotto and Alessio, 1990).

According to the observations of the authors, spawning of the Black Sea brown trout can extend from November to April (for a half year) due to phenotypic plasticity, and the offspring is quite viable. The spawning period of these individuals overlaps the spawning periods of all three "novel" species of the Ohrid trout, which spawn from October to January, from January to February, and from May to July (Soric, 1990).

Thus, there are grounds to assume that the maturation period of the Ohrid trout forms described as separate species—*S. aphelios, S. balcanicus*, and *S. letnica*—is to a considerable degree determined by temperature conditions, while the discreteness of their spawning periods results from the availability of only a few spawning grounds differing in their abiotic conditions. It is likely that the maturation of the Ohrid trout forms is not discrete, since a characteristic of each form is numerous individuals reaching maturity by the end of the normal spawning season or even later (Soric, 1990). Presumably, these individuals do not "fit" the conditions of a particular spawning ground. The presence of such individuals is anticipated, if the spawning period is determined by the environment rather than genetic adaptation to a particular spawning ground.

The spawning grounds of some salmonids are also subject to high variation, since, as experiments have shown, the site for future spawning of salmonids is usually determined by remembering a site in the aquatic body from which juveniles leave for feeding (Stabell, 1984). For example, it was demonstrated that although a form of the Sevan trout, the winter bakhtak, spawned in Lake Sevan, its fingerlings released into a tributary of the lake returned for spawning to this particular waterway (Vladimirov, 1942). As was mentioned above, another form of the Sevan trout, bojak, commenced spawning at deep sites when its spawning grounds were dried (Smolei, 1966). Note that homing in the brown trout is not so strict as compared with the other salmonids, and spawning migration to a nonnatal river (straying) is regularly observed (Makhrov et al., 1999).

The differences in spawning periods or grounds of some *Salmo* forms alone are insufficient to regard them as separate species, especially when these differences are not confirmed by the most important criteria of species—genetic and morphological traits.

For example, a diagnostic trait for *S. aphelios* (a form from Lake Orchid that spawns in May–June) according to Kottelat and Freyhof (2007) is an orange meat color. As is known, the fish meat color is to a considerable degree determined by the food objects, and it is difficult to imagine a less stable trait.

The data on the differences in the frequencies of mitochondrial DNA haplotypes between the winter- and summer-spawning forms of the Ohrid trout described as *S. letnica* and *S. aphelios*, respectively, were obtained when studying a hypervariable region in mtDNA (control region 3'-end) and should not be taken into account in evolutionary and population studies (Susnik et al., 2006, 2007). Some small distinctions between the winter- and summer-spawning forms in the allelic frequencies of an allozyme locus (Wilson, 2004) may be a result of selection.

Thus, it is likely that neither the duration nor the timing of the spanning period is an appropriate self-sufficient criteria for species identification of the representatives of the genus *Salmo*.

## ACKNOWLEDGMENTS

The authors are grateful to the staff of the Sochi National Park for their assistance in sampling as well as to A.V. Dikhnich, E.A. Dorofeeva, K.V. Kuzishchin, M.V. Mina, I.G. Murza, V.Ya. Nikandrov, D.S. Pavlov, O.L. Khristoforov, N.I. Shindavina, and V.A. Yankovskaya for discussion of the issues covered in this paper.

This work was supported by the Presidium of the Russian Academy of Sciences under the program "Biodiversity: Inventory, Functions, and Preservation" (projects nos. 2.3.1 and 23-P) and the Russian Foundation for Basic Research and the Administration of Krasnodar krai (project nos. 05-04-49232, 06-04-96735, and 11-04-00-69-7-a).

## REFERENCES

Spawning Season of the Rainbow Trout, *Vestn. Ryboprom.*, 1893, no. 56, pp. 2–33.

Babii, V.A., Yankovskaya, V.A., Nikandrov, V.Ya., and Shindavina, N.I., Breeding the Black-Sea Salmon under Hatchery Conditions—A Promising Method for Restoration of Its Abundance, *Rybn. Khoz., Ser. Aktual. Nauch.-Tekhn. Probl. Otrasli*, 2002, vol. 2, pp. 59–63.

Barach, G.P., *Chernomorskaya kumzha (losos'-forel')* (The Black-Sea trout (Salmon–Trout)), Tbilisi: Izd. Akad. Nauk GruzSSR, 1962.

Barach, G.P., *Ozernye vodoemy Gruzii i ikh rybokhozyaistvennoe znachenie* (Lakes of Georgia and Their Fishery Significance), Tbilisi: Sabchota Sakartvelo, 1964.

Behnke, R.J., *A New Subgenus and Species of Trout, Salmo (Platysalmo) platycephalis*, from Southcentral Turkey, with Comments on the Classification of the Subfamily Salmonidae, *Mitt. Hamburg Zool. Mus. Inst.*, 1968, Band 66, pp. 1–15.

Berg, L.S., Distribution of Freshwater Fishes in Europe: An Overview, in *Izbr. Tr* (Selected Papers), Moscow: Akad. Nauk SSSR, 1962, vol. 5, pp. 238–319.

Borisov, V.I., *Reki Kubani* (Rivers of Kuban), Krasnodar: Kuban. Knizh. Izd., 2005.

Bromage, N., Randall, C., Duston, J., et al., The Environmental Control of Spawning in Salmonids, in *Proc. of the Satel. Symp. on Applicat. of Comparat. Endocrinol. to Fish Cult., Almunecar, Granada, Spain, May 22–23, 1989*, Garrillo, M., Zanuy, S., and Planas, J., Eds., Barcelona, 1989, pp. 47–57.

Delling, B., Species Diversity and Phylogeny of *Salmo* with Emphasis on Southern Trouts (Teleostei, Salmonidae), *Doctoral Dissertation*, Stockholm: Dep. Zool. Stockh. Univ., 2003.

Dikhnich, A.V., Biological Basics of Formation of Spawning Schools of Atlantic Salmon *Salmo salar* L. under Hatchery Conditions, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, St. Petersburg: GosNIORKh, 2004.

Dombrovskii, K.Yu. and Usik, M.V., Results of Release of Sea Trout Fries into Rivers of Leningrad Oblast, in *Bioraznoobrazie Evropeiskogo Severa: Tez. Dokl. Mezhdunar. Konf. Petrozavodsk, 3–7 sentyabrya 2001 g.* (Abstracts of Papers, Int. Conf. on Biodiversity of the European North, Petrozavodsk, September 3–7, 2001), Petrozavodsk, 2001, pp. 5–6.

Dorofeeva, E.A., Taxonomy and History of Radiation of European Salmons of the Genus *Salmo*, *Vopr. Ikhtiol.*, 1998, vol. 38, no. 4, pp. 437–447.

Frost, W.E. and Brown, M.E., *The Trout*, London: Collins, 1967.

Gibertini, G., Ceccarelli, E., and Zerunian, S., Contributo Alla Conoscenza della Riproduzione delle Trote Indigene Nel Laco di Posta Fibreno (Lazio) (Osteichthyes, Salmonidae), *Riv. Idrobiol.*, 1990, vol. 29, no. 1, pp. 247–267.

Gortazar, J., Garcia De Jalon, D., Alonso-Gonzales, C., et al., Spawning Period of a Southern Brown Trout Population in a Highly Unpredictable Stream, *Ecol. Freshwater Fish*, 2007, vol. 16, pp. 515–527.

Gunter, A., *Catalogue of the in the British Museum*, London: Print. Trustees, 1866, vol. VI.

Heckel, J. and Kner, R., *Susswasserfische der Ostreichischen Monarchie*, Leipzig: Verlag von Wilhelm Engelmann, 1858.

Heggberget, T.G., Timing of Spawning in Norwegian Atlantic Salmon (*Salmo salar*), *Can. J. Fish. Aquat. Sci.*, 1988, vol. 45, pp. 845–849.

Johnston, C.E., Hambrook, M.J., Gray, R.W., and Davidson, K.G., Manipulation of Reproductive Function in Atlantic Salmon (*Salmo salar*) Kelts with Controlled Photoperiod and Temperature, *Can. J. Fish. Aquat. Sci.*, 1992, vol. 49, pp. 2055–2061.

Kavraiskii, F.F., *Lososevye (Salmonidae) Kavkaza i Zakavkaz'ya* (Salmonidae of the Caucasus and Transcaucasia, Tiflis: Tipogr. Kants. Glavnonach. Grazhdansk. Chast'yu na Kavkaze, 1896, vol. 1.

Klementsen, A., Amundsen, P.-A., Dempson, J.B., et al., Atlantic Salmon *Salmo salar* L., Brown Trout *Salmo trutta* L. and Arctic Charr *Salvelinus alpinus* (L.): A Review of Aspects of Their Life Histories, *Ecol. Fresh. Fish*, 2003, vol. 12, pp. 1–59.

Koshelev, B.V., *Ekologiya razmnozheniya ryb* (Fish Breeding Ecology), Moscow: Nauka, 1984.

Kottelat, M. and Freyhof, J., *Handbook of European Freshwater Fishes*, Kottelat, Cornol, Switzerland and Freyhof, Berlin, Germany, 2007.

Kulyan, S.A., The Black Sea Salmon Will Not Disappear, *Rybovodstvo Rybolovstvo*, 1999, no. 1, pp. 17–18.

Kuzishchin, K.V., Characteristic Features of Formation of Intraspecific Different Quality in Sea Trouts *Salmo trutta* L. in the White Sea, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Moscow: Mosk. Gos. Univ., 1997.

Lam, T.L., Environmental Influences on Gonadal Activity in Fish, *Fish Physiology*, Vol. IX, Part B, New York: Academic, 1983, pp. 65–116.

Makhrov, A.A., Kuzishchin, K.V., and Novikov, G.G., Genetic Differentiation of the Sea Trout (*Salmo trutta* L.) on the Coast of the Velikaya Salma Strait (White Sea), *Genetika*, 1999, vol. 35, no. 7, pp. 969–975 [Russ. J. Genetics (Engl. Transl.), 1999, vol. 35, no. 7, pp. 830–836].

Melotto, S. and Alessio, G., Biology of Carpione, *Salmo carpio* L., an Endemic Species of Lake Garda (Italy), *J. Fish Biol.*, 1990, vol. 37, no. 5, pp. 687–698.

Menzies, W.J.M., *Sea Trout and Trout*, London: Edward Arnold, 1936.

Murza, I.G. and Khristoforov, O.L., *Opredelenie stepeni zrelosti gonad i prognozirovanie vozrasta dostizheniya polovoi zrelosti u atlanticheskogo lososya i kumzhi (Metodicheskie ukazaniya)* (Determination of the Degree of Gonad Maturity and Prediction of the Age of Sexual Maturity in the Atlantic Salmon and Sea Trout: Guidelines), Leningrad: GosNIORKh, 1991.

Murza, I.G. and Khristoforov, O.L., Some Problems of Reproduction of the Black Sea Billtrout *Salto trutta* labrax Rall. of the Mzymta River and Consistent Patters of Its Sexual Maturation, *Sb. Nauch. Tr. GosNIORKh*, 1988, no. 276, pp. 147–159.

Nikandrov, V.Ya. and Shindavina, N.I., Characteristics of the Hatchery-Reared Black Sea Salmon *Salmo trutta labrax*, *Vopr. Ikhtiol.*, 2007, vol. 47, no. 2, pp. 238–246 [*J. Ichthyol.* (Engl. Transl.), 2007, vol. 47, no. 2, pp. 184–193].

Nikandrov, V.Ya., Shindavina, N.I., Babii, V.A., et al., Characteristics of the Rainbow Trout Breed Adler and the Prospects of Its Use, *Rybn. Khoz., Ser. Aktual. Nauch.-Tekhn. Probl. Otrasli*, 2002, vol. 2, pp. 33–58.

O'Malley, K.G., Sakamoto, T., Danzmann, R.G., and Ferguson, M.M., Quantitative Trait Loci for Spawning Date and Body Weight in Rainbow Trout: Testing for Conserved Effects across Ancestrally Duplicated Chromosomes, *J. Heredity*, 2002, vol. 94, no. 4, pp. 273–284.

Pankhurst, N.W. and King, H.R., Temperature and Salmonid Reproduction: Implications for Aquaculture, *J. Fish. Biol.*, 2010, vol. 76, pp. 69–85.

Pavlov, D.S. and Savvaitova, K.A., On the Problem of Ratio of Anadromy and Residence in Salmonids (Salmonidae), *Vopr. Ikhtiol.*, 2008, vol. 48, no. 6, pp. 810–824 [*J. Ichthyol.* (Engl. Transl.), 2008, vol. 48, no. 6, pp. 778–790].

Reshetnikov, S.I. and Pashkov, A.N., *Ekosistemy malykh rek Chernomorskogo poberezh'ya Severo-Zapadnogo Kavkaza* (Ecosystems of Small Rivers of the Black Sea Coast of Northwestern Caucasus), Krasnodar: Biotekh-Yug, 2009.

Saidov, Yu.S. and Magomedov, G.M., *Srvnitel'no morfologicheskie osnovy sistematiki forelei i kaspiiskogo lososya* (Comparative Morphological Basics of Trout and Caspian Salmon Taxonomy), Moscow: Nauka, 1989.

Savvaitova, K.A., Dorofeeva, E.A., Markaryan, V.G., and Smolei, A.I., *Foreli ozera Sevan* (Trouts of Lake Sevan), Leningrad: ZIN AN SSSR, 1989.

Scott, A.P., Salmonids, in *Reproductive Seasonality in Teleosts: Environmental Influences*, Munro, A.D., Scott, A.P., and Lam, T.J., Eds., Boca Raton: CRC Press, 1990, pp. 33–51.

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

Selegenenko, N.V., To Understanding of Ecology and Biology of Spring Trout in the Central Caucasus, *Sb. Rabot Mol. Uch. Sev.-Osetin. S.-Kh. Inst.*, 1964, no. 1, pp. 300–306.

Smolei, A.I., Fecundity of Trouts in Lake Sevan, *Vopr. Ikhtiol.*, 1966, vol. 6, no. 1, pp. 77–83.

Soric, V., Salmonids in the Ohrid–Drim–Skadar System, *Acta Soc. Zool. Bohemoslov.*, 1990, vol. 54, no. 4, pp. 305–319.

Stabell, O.B., Homing and Olfaction in Salmonids: A Critical Review with Special Reference to the Atlantic Salmon, *Biol. Rev.*, 1984, vol. 59, pp. 333–388.

Susnik, S., Knizhin, I., Snoj, A., and Weiss, S., Genetic and Morphological Characterization of a Lake Ohrid Endemic, *Salmo (Acantholingua) ohridanus* with a Comparison to Sympatric *Salmo trutta*, *J. Fish. Biol.*, 2006, vol. 68, Suppl. A, pp. 2–23.

Susnik, S., Snoj, A., Wilson, I.F., et al., Historical Demography of Brown Trout (*Salmo trutta*) in the Adriatic Drainage Including the Putative *S. letnica* Endemic to Lake Ohrid, *Mol. Phyl. Evol.*, 2007, vol. 44, pp. 63–76.

Taler, Z., Visovacka Jezerska Pastrva (*Salmo visovacensis* n. sp.), *Glasnik biologiske sekcije. Hrvatsko prirodoslovno drustvo*, 1948, Serija II/B, vol. 2/3, pp. 118–158.

Tuniev, S.B., Exothermal Vertebrates of the Sochi National Park: Taxonomic Composition, Zoogeography, and Conservation, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, St. Petersburg: ZIN RAN, 2008.

Turyanin, I.I., *Fishes of Carpathian Water Bodies*, Uzhgorod: Karpati, 1982, vol. 144.

Vladimirov, V.I., Changes in Spawning Ecology of Trouts in Lake Sevan, *Izv. Arm. Fil. AN SSSR*, 1942, no. 34, pp. 157–163.

Vladimirskaya, M.I., Dependence of Atlantic Salmon Spawning in the Pechora River on Hydrological Conditions, *Vopr. Ikhtiol.*, 1960, no. 16, pp. 111–120.

Webb, J.H. and McLay, H.A., Variation in the Time of Spawning of Atlantic Salmon (*Salmo salar*) and Its Relationships to Temperature in the Aberdeenshire Dee, Scotland, *Can. J. Fish. Aquat. Sci.*, 1996, vol. 53, no. 12, pp. 2739–2744.

Whittal, H.M., Trout in Turkey, *Salmon Trout Mag.*, 1967, vol. 179, pp. 50–53.

Wilson, I., Low Genetic Variability in the Summer Koran (*Salmo letnica eestivalis* Stefanovic) of Lake Ohrid, *Alb. J. Nat. Techn. Sci.*, 2004, no. 16, pp. 3–13.

Yakimov, A.V. and Khatukhov, A.M., Altitude Aspect in the Spawning Pattern of Spring Trout (*Salmo trutta* morpha *fario* L.) in the Central Caucasus, in *Aktual'nye voprosy ekologii i okhrany prirody ekosistem yuzhnykh regionov Rossii i sopredel'nykh territorii: Mater. XV Mezhrespubl. Nauch.-Prakt. Konf. Krasnodar, 19 aprelya 2002 g.* (Proc. XV Interrepubl. Sci.-Pract. Conf. "Relevant Problems of Ecology and Nature Conservation of Ecosystems of Southern Regions of Russia and Adjacent Countries, Krasnodar, April 19, 2002), Krasnodar, 2002, pp. 162–163.

Zerunian, S. and Gandolfi, G., *Salmo fibreni* n. sp. (Osteichthyes, Salmonidae) Endemica Nel Bacino del Fibreno (Italia Centrale), *Riv. Idrobiol.*, 1990, vol. 29, no. 1, pp. 521–532.

Zerunian, S., *Iconography of Italian Inland Water Fishes*, Modena: Istituto Nazionale per la Fauna Selvatica "Alessandro Ghigi", 2002.