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On the Origins of the Negative Impact of Invasive Pink Salmon *Oncorhynchus gorbuscha* on Natural Populations of Atlantic Salmon *Salmo salar* (Salmonidae)

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Abstract—This paper considers the causes of the decline of catches of Atlantic salmon *Salmo salar* from the basins of the Barents and White seas. In addition to hydraulic engineering construction, timber rafting, and pollution of salmon rivers with domestic and industrial wastewater, the impact of aquaculture of this species in the form of possible changes at the genetic level and disease distribution, as well as the effect of increased volumes of approaches of pink salmon *Oncorhynchus gorbuscha* for spawning, can also be observed. It is necessary to develop effective technologies, including taking into account the expansion of an invasive species, Far Eastern pink salmon, to preserve and restore natural populations of Atlantic salmon in the basins of the Barents and White seas, which are an important depository of genetic material; the importance of preservation of this material increases under conditions of increasing volumes of commercial breeding.

Keywords: Atlantic salmon, pink salmon, biological invasions, growth rate, life strategies, population structure, evolutionary history, zoogeography, embryophysiological characteristics

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INTRODUCTION

The reduction of biodiversity in natural ecosystems is one of the most important problems of our time, which has been reflected in a number of international and national documents. These problems are also directly related to wild populations of Atlantic salmon *Salmo salar* Linnaeus, 1758 from the basins of the Bering and White seas, which represent a strategically important gene pool not only in Russia but also at the global level. In addition to the impact of increasing anthropogenic pressure on aquatic ecosystems, the impact of negative aspects of legal and illegal fishing on salmon populations has been also aggravated by risks due to both the intensively developing industrial aquaculture of Atlantic salmon and the results of the introduction of alien species. The purpose of this publication is to comprehensively consider the features of relationships between wild populations of Atlantic salmon and the invasive pink salmon *Oncorhynchus gorbuscha* (Walbaum, 1792) from the basins of the Barents and White seas during the freshwater period of their life using diverse scientific material (morphobiological, genetic, ecological, paleogeographic, embryophysiological, and other data).

Characteristics of the State of Atlantic Salmon Stocks and Causes of Reduction in Their Abundance

Atlantic salmon is a large migratory fish that lives in the northern part of the Atlantic Ocean basin. It migrates for spawning to rivers in areas from the western coast of Portugal to the Baltic and North seas, the coasts of Scandinavia, and the Arctic Ocean and eastward to the Kara River. Along the North American coast, salmon is common from Greenland to Cape Cod (Nikol'skii, 1971). Atlantic salmon is a traditional commercial species in the Russian North. Based on the available statistical data from the International Council for the Exploration of the Sea (ICES, 2023), we can distinguish periods demonstrating a deterioration of the state of stocks of the natural Atlantic salmon with respect to the level of its catch from the White and Barents sea basins. Thus, whereas the average annual catch was 1.5 to 2.9 (mean 2.2) thousand tons from 1956 to 1987, it was about 1.0 thousand tons from 1988 to the end of the 2000s. The second decade of this century was characterized by a further progressive decrease in catch volumes to an average of 77 tons per year (Zubchenko, 2006). Therefore, the second half of the last century and the beginning of this century are characterized by a decrease in the stocks of Atlantic salmon in basins of the Barents and White

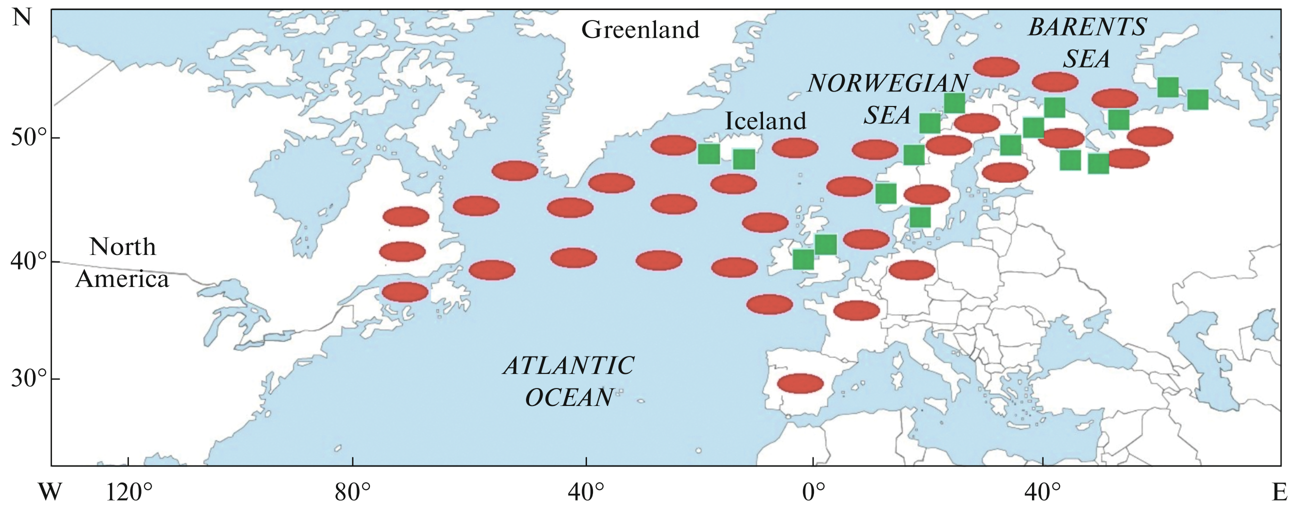

Fig. 1. Current distribution of natural populations of Atlantic salmon *Salmo salar* (●) and pink salmon *Oncorhynchus gorbuscha* acclimatized in the second half of the last century (■) in the North Atlantic region.

seas (Alekseev et al., 2006, 2023; Alekseev and Zubchenko, 2017).

The causes of the deterioration of the natural reproduction of Atlantic salmon are poaching and industrial development of territories. The latter reason is diverse and includes a wide range of areas. Hydraulic engineering construction for generating electricity and providing cities with water has led to the reduction in the area of breeding grounds (BGs) and degradation of Atlantic salmon populations, e.g., in rivers such as the Niva, Teriberka, Voronya, and Solza (Zubchenko, 2006). Wood drifting, practiced in a number of rivers, has caused negative consequences in the form of clogging of the bottom with driftwood, siltation of BGs, and hydrolysis of cellulose; pollution of salmon rivers with domestic and industrial wastewater increases near large human settlements and mining and metallurgical facilities (Zubchenko et al., 2003). It has been noted that the content of sulfates increases and the level of alkalinity decreases in water in a number of rivers of the Kola Peninsula in the direction from east to west, which can negatively affect the reproduction of salmonid fishes (Salmonidae) (Moiseenko et al., 1996; Matishov et al., 2010).

The development of commercial aquaculture of Atlantic salmon, which has been active since the 1990s (the volume of global cage rearing of Atlantic salmon was 158.0 thousand tons in 1990, 2435.9 thousand tons in 2018, 2719.6 thousand tons in 2020, 2866.0 thousand tons in 2022, and up to 2906.0 thousand tons in 2023) (FAO, 2022; *Analiz rynka lososevykh*..., 2023[1]), also puts increasing pressure on wild Atlantic salmon populations due to habitat pollution, the distribution of diseases (e.g., gyrodactylosis), possible genetic pollution by farmed salmon escaping from commercial aquaculture farms, and other reasons (Zilanov, 1996; Aleksandrova, 2021; Vasil'ev and Aleksandrova, 2021; Dzyuba et al., 2023).

The results of activities to increase the bioproductivity in northern waters (including by introducing new objects), which were most active in the second half of the last century, currently also create conditions for the negative impact of the introduced representative of Far Eastern salmon, pink salmon, on natural populations of Atlantic salmon (Fig. 1) (Zubchenko et al., 2004; Gordeev et al., 2023; Stroganov et al., 2023).

There is also a natural reason for the decline in Atlantic salmon stocks. In recent decades, the mortality of wild Atlantic salmon has increased in the rivers of the Kola Peninsula due to a poorly studied disease, ulcerative dermal necrosis (UDN) of salmon skin, which is presumably of viral etiology. The disease is observed in sexually mature individuals (mainly in Atlantic salmon and sea trout *Salmo trutta* Linnaeus, 1758) (Provotorov et al., 2023) during anadromous migration to spawning grounds and has been recorded in the Kola and Tuloma rivers in the Murmansk region since 2015 and in the Umba River since 2019. There is information about the expansion of the geography of UDN detection, in the Varzuga and Keret rivers (Pashenkova, 2021[2]). Against the background of the registration of another outbreak of this disease and its further distribution in the second decade of the current century and taking into account the poor study of UDN, it cannot yet be ruled out that this may also be

[1] Salmon market analysis and 5-year forecast of salmon production and consumption, 2023 (https://рыбоводы.рф/news/19-rybovodstvo/445-strizh. Version 01/2024).

[2] Pashenkova, M., 2021. The number of rivers with diseased wild salmon has increased in the Murmansk region (https://www.murmansk.kp.ru/online/news/4360290/. Version 10/2023).

somewhat determined by approaches of pink salmon to its spawning grounds.

Below, we consider the possible consequences of the introduction of pink salmon into the salmon rivers of the White and Barents sea basins for the natural reproduction of Atlantic salmon.

Works on Pink Salmon Acclimatization

Well-known figures of fisheries science (Knyazev and Lazarev, 1961; Smirnov, 1971, 1975a) put forward proposals for the introduction of representatives of Far Eastern salmon (genus *Oncorhynchus*), which are characterized by a rapid growth rate and a high commercial quality, beyond their natural habitats. They justified their proposals not only by the availability of food resources against the background of the underuse of products of the pelagic and benthic ecosystems of the White Sea by largely local White Sea fish species (Zhitnii, 2005), but also by the problems of restoration of the Atlantic salmon population and the need to increase the fish productivity in northern rivers based on species that, in the opinion of the developers, were not competitors for representatives of the native ichthyofauna. Thus, an idea of acclimatization of Far Eastern salmons in the Russian North was put forward in 1931. To give acclimatization works a systematic, scientifically sound, industrial character, a "Team for Acclimatization of Fishes and Invertebrates" was created in 1946 under the Ministry of Fisheries of the USSR. It included famous representatives of biological science: L.A. Zenkevich (Moscow State University), A.F. Karpevich (Russian Federal Research Institute of Fisheries and Oceanography), V.V. Vasnetsov (Moscow State University), B.S. Il'in (Russian Federal Research Institute of Fisheries and Oceanography), N.I. Kozhin (Russian Federal Research Institute of Fisheries and Oceanography), and G.V. Nikol'skii (Moscow State University) (Kershtein et al., 2008). Works on the introduction of pink salmon in Russia were started in 1956, when 3.8 million pink salmon eggs were brought from southern Sakhalin to the Taibol Fish Hatchery in the Murmansk Region, followed by the release of the juveniles into the Barents Sea. In 1957 and 1958, pink salmon was released under the ice from Kola Peninsula fish hatcheries at the larval stage in April–May and there was no return from these releases. Although the natural reproduction of pink salmon was recorded both in the rivers of the Kola Peninsula, Karelia, and Cheshskaya Bay and in Norway after performing certain changes in the technology in 1960, the work on pink salmon releases in 1959–1964 did not produce a significant positive effect according to general estimates. It is believed that this is determined by lower, unfavorable temperatures in northern European rivers, which contributed to a slowdown of gametogenesis and led to a later onset of oocyte vitellogenesis in pink salmon females and a delay of the return of the latter for spawning (Kuderskii, 2005; Kershtein et al., 2008; Dorofeeva, 2009; Rafikov and Zakharov, 2019). The effect of pink salmon naturalization and the formation of its self-reproducing population were achieved later, in 1985 and 1986, based on releases of juveniles from the delivered eggs of the "Magadan" batch from the Ola and Yana rivers into the White Sea basin (the catch of pink salmon from the White Sea basin reached 156 thousand individuals in 2001) (Karpevich et al., 1991). At the end of the last century–the beginning of this century, pink salmon is naturalized along two generatively isolated lines of even and odd years. It is noted that the specific conditions of the spawning rivers in the Russian North with an intensive decrease in water temperatures at the beginning of the autumn period presumably contributed to the formation of pink salmon populations with short and early spawning; among them, groups spawning in odd years have an adaptive advantage (Dyagilev and Markevich, 1979; Alexeev et al., 2019; Rafikov and Zakharov, 2019). The increase in the abundance of naturalized pink salmon and the trend towards an increase in the heat content of Arctic waters at the beginning of this century have led to an increase in the range of introduced pink salmon eastward to the Kara River and Baydaratskaya Bay of the Kara Sea. The results of comprehensive studies showed that the odd line of pink salmon acclimatized in the White Sea maintained stable approaches of spawners for ten generations. An early spawning population is formed mainly through adaptations during sexual maturation (the downstream juveniles do not experience a slowdown in the rate of early ontogeny; females entering for spawning are ready to spawn within a period favorable for the development of juveniles) (Dorofeeva, 2009). The most abundant approaches of pink salmon to spawning grounds in the current century have been recorded in 2021 (Zubchenko et al., 2022).

Peculiarities of Interaction between Atlantic Salmon and Pink Salmon

The conditions of the decrease in the stocks of the representative of the autochthonous ichthyofauna, Atlantic salmon, make the issues of its relationship with the invasive pink salmon particularly significant. Moreover, whereas researchers using previous data rejected the possibility of the formation of competitive interactions of the introduced group of pink salmon with representatives of the native ichthyofauna (the most significant of which is Atlantic salmon) in the White Sea, it is possible to expect even the suppression of Atlantic salmon populations in a number of rivers of the White Sea basin under conditions of the growth of the abundance of the pink salmon group in odd years. The Russian statistics on Atlantic salmon and pink salmon catches show that two oppositely directed processes are observed in the current century against the background of the trend of increasing heat content of

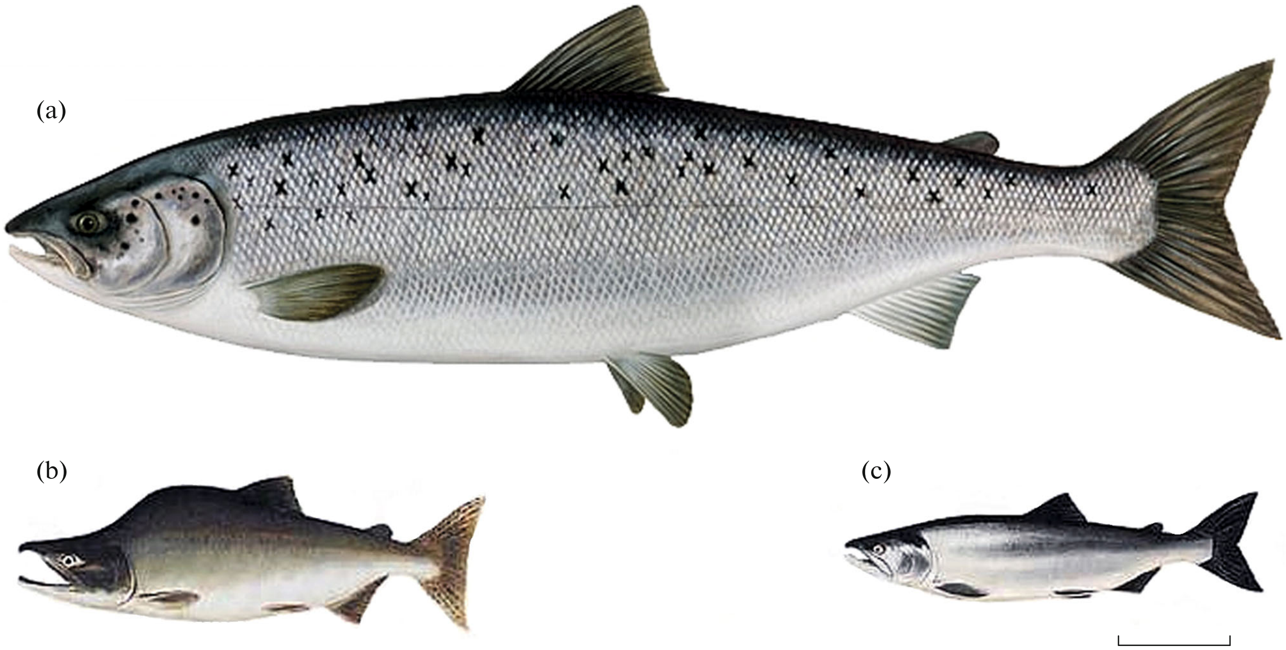

Fig. 2. Atlantic salmon *Salmo salar* (a) and pink salmon *Oncorhynchus gorbuscha*: male (b) and female (c); comparative size characteristics. Scale: 10 cm. The drawing of the Atlantic salmon was taken from the publication by R.E. Parkhomenko (https://poklev.com/vidy-ryb/prohodnye-i-poluprohodnye/semga. Version February, 2024). The drawings of the pink salmon were taken from an open source.

waters in the Barents Sea region: the state of Atlantic salmon populations is deteriorating in the White and Barents sea basins and, at the same time, the volumes of pink salmon approaches to spawning grounds increase under these conditions, which is most clearly defined for the pink salmon group in odd years, which has many times exceeded both the pink salmon group in even years and Atlantic salmon populations in catch volumes in recent years (Fig. 2; Tables 1, 2).

As is known, the White Sea region is not rich in fishing grounds and the potential growth of pink salmon stocks helps to attract the attention of fishermen. Undoubtedly, this also increases the social significance of pink salmon as a factor in raising the standard of living of the human population in this region. This involves more intensive discussions of the benefits and harms of pink salmon with respect to Atlantic salmon. Accordingly, against the background of inter-

Table 1. Total annual catch volumes of Atlantic salmon *Salmo salar* and pink salmon *Oncorhynchus gorbuscha* from the White Sea (Republic of Karelia, Arkhangelsk Region, and Nenets Autonomous Okrug) in the current century, t

Year	Atlantic salmon	Pink salmon	Year	Atlantic salmon	Pink salmon
2000	118.8	11.0	2012	64.1	0.1
2001	99.4	339.6	2013	63.5	200.5
2002	98.7	1.2	2014	63.7	10.1
2003	82.9	151.4	2015	65.9	161.1
2004	72.6	1.2	2016	44.7	7.2
2005	72.0	125.6	2017	28.8	369.9
2006	78.2	1.3	2018	57.1	4.3
2007	55.4	235.3	2019	34.4	414.7
2008	50.5	0.5	2020	28.1	0.7
2009	60.0	138.5	2021	28.7	712.2
2010	66.9	–	2022	36.9	4.1
2011	68.2	98.2	2023	–	47.1

Here and in Table 2: –, no data.

Table 2. Total annual catch volumes of Atlantic salmon *Salmo salar* and pink salmon *Oncorhynchus gorbuscha* from the Barents Sea (Komi Republic, Murmansk Region, and Nenets Autonomous Okrug) in the current century, t

Year	Atlantic salmon	Pink salmon	Year	Atlantic salmon	Pink salmon
2000	6.5	0	2012	17.6	0.1
2001	19.4	0	2013	15.8	0.5
2002	21.4	0	2014	19.1	1.0
2003	20.9	0	2015	14.4	1.1
2004	10.2	0	2016	11.2	0
2005	7.6	0	2017	21.4	3.6
2006	9.8	0	2018	24.8	2.9
2007	8.4	0	2019	24.7	3.1
2008	11.4	0	2020	21.6	0.2
2009	13.3	0	2021	15.8	2.4
2010	20.1	0.2	2022	18.2	0.8
2011	21.9	0.1	2023	–	156.2

est in increasing the fishery of pink salmon, the position of its harmlessness for Atlantic salmon is more actively discussed, since their groups in the river are temporally separated as a result of the earlier spawning of pink salmon. Moreover, a certain benefit of pink salmon is even assumed, since its post-spawning death may contribute to an increase in the bioproductivity of rivers. Field studies at spawning grounds in the first and second decades of the current century examined in fairly sufficient detail the features of relationships between Atlantic salmon and pink salmon during the spawning period. In the rivers of the Kola Peninsula, pink salmon spawns in late July–early August on pebble riffles and shallow reaches of both the main channel and tributaries with grounds 1–20 mm in fraction size. The area of BGs suitable for pink salmon spawning is less than 4% of the total area of BGs. The estimates of BGs showed that there were rather few areas combining the optimal granulometric composition of the ground (gravel and small pebbles (1–5 cm)), depth (up to 0.5 m), and flow velocity (0.4–1.0 m/s)), and this is a significant limiting factor in the reproduction of pink salmon in the White Sea rivers. Indeed, there is some difference here: Atlantic salmon spawns at greater depths (up to 1.5 m) and usually uses ground with larger fractions for nesting. However, observations have shown that pink salmon also occupies the spawning grounds of Atlantic salmon when the area of preferred spawning grounds is insufficient. In some cases, Atlantic salmon even avoids spawning grounds occupied by pink salmon. During large approaches of pink salmon and its dominance in a river, it enters into competitive and even antagonistic relations with Atlantic salmon in spawning grounds and demonstrates a high degree of aggressiveness (Zubchenko et al., 2004; Gordeev et al., 2023; Efremov, 2023). This is also confirmed by the census data on approaches to spawning grounds; thus, according to the data for the Varzuga River, the number of approaches of Atlantic salmon clearly tends to decrease against the background of an increase in pink salmon approaches (Fig. 3).

The conditions of unregulated growth of the abundance of pink salmon and its penetration into rivers may involve environmental consequences due to the occurrence of “kill” conditions in the river, primarily due to the overcrowding and concentration of pink salmon individuals, followed by their pre-spawning death, as well as due to the biologically determined total post-spawning death of pink salmon, followed by the decomposition of corpses and contamination of the river. At the same time, it is necessary to take into account the possible negative impact of “kills” on the juvenile Atlantic salmon living in the river for a number of years (from 3 to 5–6 years, depending on the temperature background) before migrating downstream to the sea (Lysenko et al., 1999[3]; Zubchenko et al., 2004; Bogdanov and Kizhevatov, 2015; Rafikov and Zakharov, 2019).

As noted above, there are also suggestions that the post-spawning mortality of pink salmon may contribute to the growth of the bioproductive capacity of spawning rivers owing to the additional supply of biogenic elements. This thesis is true to a certain extent for the conditions of the North Pacific basin, but proved to be completely unsuitable for the conditions of the Russian North. The thing is that the fauna of microorganisms, invertebrate detritivores, and vertebrate scavengers is poor in the acidified and cold waters of the rivers of the Murmansk region and the decomposition of dead fish is slower here than in the Far East. Therefore, the decrease in the intensity of

[3] Lysenko, L.F. and Berestovskii, E.G., 1999. Salmons from the Varzuga River (http://kola-salmon.ru/public/kola_peninsula/salmon/varzuga_salmon.htm. Version 02/2024).

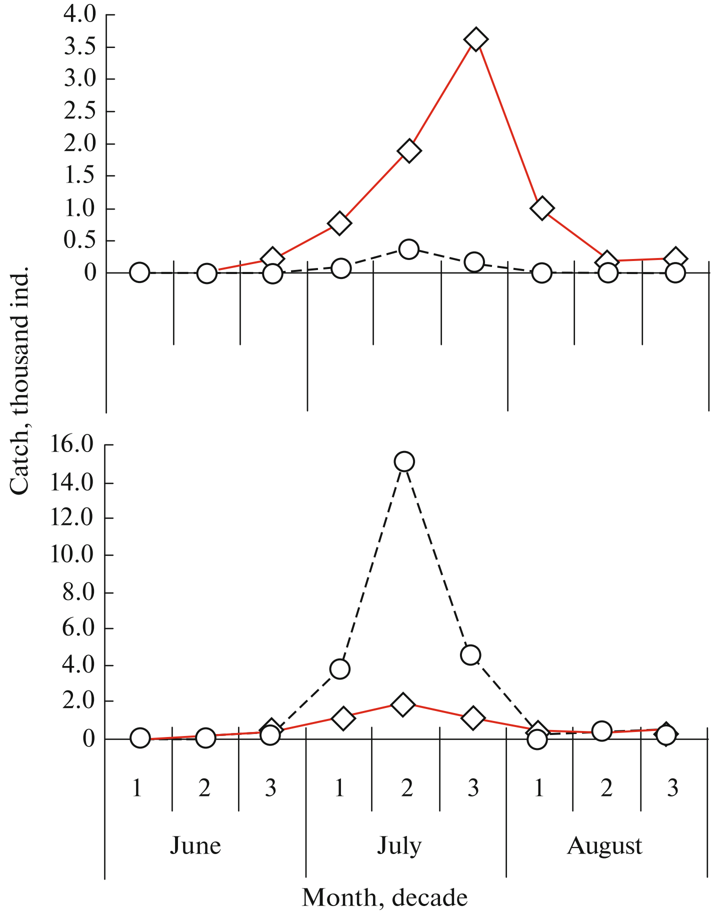

Fig. 3. Dynamics of the run of Atlantic salmon *Salmo salar* (◇) and pink salmon *Oncorhynchus gorbuscha* (○) in the Varzuga River in 1991 (a) and 2001 (b) (according to Zubchenko et al., 2004, with changes). A.V. Zubchenko kindly permitted the use of the materials from his monograph.

mineralization processes initiates the process of river eutrophication (Kalyuzhin, 2004). Although Atlantic salmon does not seem to have any visible problems with spawning, an increase in organic matter contributes to the deterioration of the conditions for the development of eggs in nests: from a decrease in the level of oxygen supply to embryos during silting of pebble grounds to an increase in the degree of damage by pathogenic microorganisms. For instance, eutrophication inevitably involves an increase in the level of damage to eggs in nests by fungi of the genus *Saprolegnia* as a result of the creation of unfavorable zoohygienic and sanitary conditions in the watercourse (Neish and Hughes, 1980).

Thus, we can see that opinions about the pattern and degree of interaction of Atlantic salmon (a representative of the native ichthyofauna) and pink salmon (the result of a set of acclimatization measures) during the spawning and freshwater periods of life can dramatically differ from each other (Gritsenko and Bakshtanskii, 1975; Alexeev et al., 2019; Tortsev and Studenov, 2022; Gordeev et al., 2023; Efremov, 2023). According to the publications, this may be determined mainly by insufficient scientific development of the idea of introduction of pink salmon, as well as by the lower level of scientific knowledge about salmon fishes in the first half of the last century than about their current state.

Peculiarities of Adaptation of Atlantic Salmon and Pink Salmon to Environmental Conditions during Evolution

Given the high degree of similarity between the modern representatives of the genera *Salmo* and *Oncorhynchus* in morphophysiological, biological, embryological, behavioral and other parameters, it is of interest to consider some of the features of their evolution. In the opinion of Mikulin (2003) on the features of the evolution of salmonids (Salmoniformes) (which eliminate some disagreements between representatives of the "freshwater" and "sea" concepts of origin of salmons), the ancestral forms of salmonids (Lower Paleogene), after inheriting the hydrodynamic body shape and anadromous lifestyle from their predecessors (Clupeiformes and Osmeriformes), initially dis-

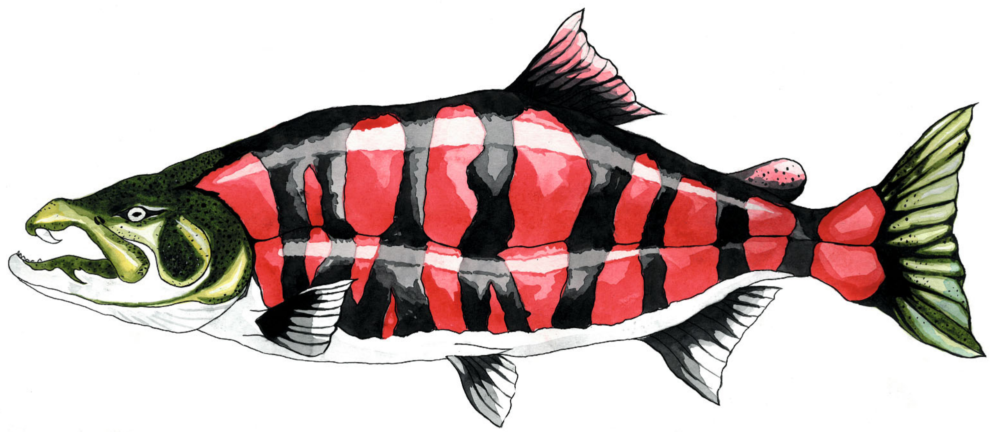

Fig. 4. Giant (more than 2 m) *Smilodonichthys* (*Oncorhynchus*) *rastrosus* from coastal Mio-Pliocene waters of the North Pacific (drawing by Diana Meshkova).

persed eastward from the Tethys Sea, covering the coast of Laurasia and adapting to the coastal waters of the northern part of the Paleo Pacific Ocean (Panthalassa Ocean). According to paleontological data, the North Pacific is not only the center of origin of salmonids, but also the region where their long evolution took place (at least their anadromous forms). This is also confirmed by finds of extinct representatives of the genera *Oncorhynchus*, *Paleolox*, *Smilodonichthys*, and *Salmo* from the Mio-Pleistocene in this region. Paleontological studies have shown that this area was inhabited by large representatives of salmonids, e.g., the giant (>2 m) planktophage *Smilodonichthys* (*Oncorhynchus*) *rastrosus* (Fig. 4) and *Salmo* (*Oncorhynchus*) *australis* with a range reaching the tropical region (Cavender and Miller, 1972, 1982; Zonenshain and Gorodnitskii, 1976; Glubokovskii, 1995; Gorodilov and Mel'nikova, 2003; Mikulin, 2003; Crespi and Fulton, 2004; Eiting and Smith, 2007; Waples et al., 2008; Mikulin and Lyubaev, 2010; Shedko et al., 2012; Zhivotovskii, 2015; *Alaska Arctic*..., 2016; Sankey et al., 2016; Stearley and Smith, 2016; Dolganov, 2022).

As is known, the modern representatives of the genus *Oncorhynchus* are localized in the North Pacific region and Atlantic salmons of the genus *Salmo* are distributed in the North Atlantic and in the western sector of the Arctic. At the same time, whereas the evolutionary biogeography of the Far Eastern salmons of the genus *Oncorhynchus* is illustrated and confirmed by the results of paleontological studies, which are considered one of the most reliable methods for verifying the directions and intensity of evolutionary processes (Mayr, 1970; Timofeev-Resovskii et al., 1977; Mikhailova and Bondarenko, 2006), the situation with the genus *Salmo* is not so clear. Although, according to Berg (1953), the exchange between the Atlantic and Pacific oceans through the Tethys Sea (with conditions characteristic of the tropical region) in the Mesozoic and Early Tertiary periods (including due to temperature limitations for poikilothermic organisms) was real only for tropical forms, and, accordingly, unrealistic for boreal, subarctic, and boreal–arctic forms, ideas about the penetration of ancestral forms of the genus *Salmo* into the Atlantic basin through the Tethys Sea are well known and substantiated by morphological and genetic data. Various types of water bodies in the North Atlantic region are populated by representatives of the genus *Salmo*; their species diversity increases from north to south and reaches its maximum value in the Mediterranean basin. At the same time, there is no paleontological evidence of this dispersal and one can even assume the opposite process, given the high biodiversity and the fact that these areas, unlike the North Atlantic and Arctic coasts, were not subject to active and repeated "abrasion" during numerous movements of Pleistocene glacial formations (Nikol'skii, 1953; Vinogradov and Neiman, 1965; Velichko, 1991; Glubokovskii, 1995; Zhivotovskii, 2015; Artamonova et al., 2020).

Despite the long period of divergence between the ancestral forms of *Salmo* and *Oncorhynchus* (about 20 million years), their current representatives retain a fairly large volume of similar morphobiological characteristics (up to the localization of spawning grounds and the features of grounds for the formation of redds). Representatives of the genera *Salmo* and *Oncorhynchus* effectively implement one of the main "evolutionary achievements" of anadromous salmons, namely, the use of the advantages of freshwater and marine periods of the life cycle. This determines not only their high abundance, but also high consumer properties of food produced from them (meat quality and caviar). Here, the main goal in the freshwater period is high survival, which is achieved by the development of large eggs with a large yolk reserve inside pebble substrate with protection from predators and with good "ventilation" by the underflow, as well as by an effective transition of the large larva to external feeding on drift invertebrates inside the pebble substrate (Novikov, 1953; Smirnov, 1975b; Kazakov and Mel'nikova, 1980; Kazakov, 1982; Martynov, 2007; Chernyaev, 2020). The task during the marine period is to achieve high growth rates under conditions of high food supply. Whereas this is mostly a uniform solution for the genera *Salmo* and *Oncorhynchus* in the marine period (implementation of feeding migrations in open sea and ocean waters), the maintenance of high abundance and productivity based on the features of the freshwater period of ontogeny is achieved in different ways. Pink salmon implements this task through early smoltification and downstream migration to the sea (larval period). Certainly, the transition of pink salmon to feeding in marine coastal waters can be accompanied by its low survival; however, this is compensated by mass downstream migration, which, given the high survival rate in the embryonic period, is generally determined by the receiving capacity of the spawning grounds. On the contrary, the size of large downstream migrating juveniles of Atlantic salmon as a result of the long freshwater period determines a high survival at sea and a high growth rate under conditions of high trophicity of marine waters and a high caloric value of prey, fish as the main food items of Atlantic salmon; at the same time, the amount of these juveniles is significantly limited by a rather low bioproductivity of oligotrophic salmon spawning rivers (Reddin, 1988; Reddin and Friedland, 1993; Reddin, 1998; Ponomareva et al., 2001; Jonsson et al., 2001; Haugland et al., 2006; Martynov, 2007; Antonov, 2011; Bugaev, 2015; Strøm et al., 2020).

The genera *Salmo* and *Oncorhynchus* have differences that give them advantages in their natural habitats. Thus, the genus *Salmo* is characterized by a spawning population of the second type (Monastyrskii, 1953), which contains repeatedly spawning individuals along with recruitment; Atlantic salmon juveniles differ both in the age of downstream migration and in the age of onset of sexual maturity. The genus *Oncorhynchus* is represented by spawning populations of the first type without respawning individuals. The highest level of specialization among the representatives of this genus is demonstrated by pink salmon, which differs not only in the homogeneity of the age of downstream migration of juveniles and age when the individuals reach sexual maturity (0 and 1+ years, respectively), but also in the reproductive isolation of even- and odd-year generations. Although this life strategy with monocyclicity and features of the population dynamics is fraught with the danger of the impossibility of population recovery in the event of the formation of negative conditions for reproduction, this factor in the realities of the relative stability of the climatic and oceanographic situation of the North Pacific basin is apparently of no decisive importance (Kuderskii, 2005). At the same time, as noted by Gritsenko and Bakshtanskii (1975), by generating a high population, pink salmon uses it as a tool to neutralize dangerous situations arising in a number of cases, e.g., by maintaining the necessary hydrological regime on spawning grounds, overcoming the barrier of coastal predators during the downstream migration of juveniles, etc. Therefore, following the evolutionarily established population model of pink salmon, it can be noted that the high abundance is not only its achievement, but also a necessary factor in maintaining stable existence. At the same time, the high number of approaches of pink salmon to spawning grounds also involves its negative, depressing effect on Atlantic salmon (Zubchenko et al., 2004; Zubchenko, 2006; Stroganov et al., 2023).

Differences in spawning population types may have also influenced differences in the distribution of representatives of the genera *Salmo* and *Oncorhynchus*. It is quite possible that this is determined by the peculiarities of the manifestation of Pleistocene glaciations in the North Atlantic and North Pacific regions. Harsh conditions with ocean regression, a significant reduction in the boreal zone against the background of the southward shift of the polar front in the North Atlantic, and a reduction in the range were successfully overcome by the Atlantic salmon group during glaciation periods (Kettle et al., 2010), including owing to the complex structure of the spawning population. An example of the high resistance of Atlantic salmon to significant changes in environmental factors is demonstrated by the only reproductively independent and spatially isolated (this is also shown by the results of genetic studies) population in Greenland, which reproduces only in one river (Kapisillit River) in the southern part of West Greenland (Arnekleiv et al., 2019).

Another confirmation of the greater resistance of spawning population species with the complex structure to unfavorable changing environmental factors can be the example of the Arctic char *Salvelinus alpinus* (Linnaeus, 1758); being to resistant to low temperatures, it dispersed, among other things, along the Arctic coast of Eurasia. Similarly to Atlantic salmon, the anadromous Arctic char is represented by spawning populations of the second type (Monastyrskii, 1953), which include repeatedly spawning individuals along with recruitment; the duration of embryonic–larval development can vary; the dates of both downstream migration of juveniles and the attainment of sexual maturity by individuals also vary. The long freshwater period with habitation in oligotrophic water bodies does not allow the formation of groups with high abundance: despite the circumpolar distribution, the level of catch of Arctic char in the world was only 538 tons in 2000 (Andriyashev and Chernova, 1995; Kotlyar, 2006; Esin and Markevich, 2017).

Given the fairly high level of identity between Atlantic salmon and pink salmon at the morphological level during the period of embryonic–larval development, one might also expect a functional similarity. However, field observations, the results of introduction of pink salmon to the Russian North (especially in the 1960s), and further experimental works showed fundamental differences in the temperature resistance of Atlantic salmon and pink salmon embryos, at least in the first half of embryogenesis (before the formation of the circulatory system): the decrease in temperature below 6°C proved to be lethal for pink salmon embryos, while even the earliest embryos of Atlantic salmon demonstrate their resistance to water temperatures over a wide range, including around 0°C (Klinkchardt et al., 1987; Gorodilov, 2003; Gorodilov and Mel'nikova, 2003; Stroganov et al., 2006).

Homing of salmonids is well known; it actually serves as a basis for pasture aquaculture, i.e., when the release of salmon juveniles into the natural environment ensures the growth of the population in a given river with the corresponding opportunities to increase the catch of spawners returning to spawn. The situation with pink salmon is not quite the same due to a certain level of straying characteristic of this species (Klyashtorin, 1989; Kaev and Rudnev, 2007). At the same time, researchers do not exclude that straying of pink salmon has a somewhat adaptive nature, since it can recover populations in some rivers that have been negatively affected by environmental factors (e.g., lethal temperatures in some years, flood effects, freezing of spawning grounds during the winter low water period, etc.) (Kuderskii, 2005). In the 1960s. the release of pink salmon juveniles into the Barents and White sea basins was followed by the entry of sexually mature individuals into Norwegian rivers (the species was also recorded in Iceland and Scotland and near Spitsbergen); i.e., straying of pink salmon, characteristic of the Far Eastern region, was also manifested in its acclimatized individuals. It was more clearly defined under conditions with a limited volume of water areas used for acclimatization work (Alexeev et al., 2019). Moreover, the experience of the spawning season (fishing season) in 2023 shows that pink salmon spawners can radically change the routes of their anadromous migration during the formation of significant accumulations when they approach to spawning grounds in rivers. Given a certain time for the execution of the necessary permits, it is almost impossible to organize an effective catch of pink salmon on an industrial scale. This may involve even a situation with the unprofitability of the organization of pink salmon catch. In view of the above, it can be assumed that both field observations and experimental studies (Gorodilov, 2003; Gorodilov and Mel'nikova, 2003) confirm the opinions expressed by different authors (Azbelev and Yakovenko, 1963; Dyagilev and Markevich, 1979; Kamyshnaya and Smirnov, 1981) about the insufficient scientific development and, possibly, the erroneous implementation of decisions on carrying out works to acclimatize Far Eastern pink salmon in the White Sea—Barents Sea basin.

CONCLUSIONS

The above review clearly shows an ambiguous situation in the relationships between the invasive pink salmon and natural populations of Atlantic salmon in the spawning rivers in the Russian North. During the selection of an object for acclimatization in the White Sea—Barents Sea region in the first half of the last century, the task was to increase the fish productivity in northern rivers based on species that are not competitors for representatives of the native ichthyofauna. In fact, we can see that the selected object, Far Eastern pink salmon, demonstrates a fairly high degree of similarity with Atlantic salmon with respect to a number of characteristics (evolutionary, morphological, biological, etc.), which, as is known, can serve as a reason for interspecific competition. In turn, interspecific competition for BG resources, which is formed under certain conditions and influences the survival, growth, and reproduction efficiency, is an important factor in the formation of population abundance. In the Russian North, we can currently observe interspecific competition for breeding ground resources between Atlantic salmon and pink salmon, which is formed against the background of the high similarity of both their spawning biology and their spawning ground characteristics. At the same time, the level of differential use of the resource is inconsistent and depends on the abundance of spawning groups of pink salmon (Begon et al., 1986; D'yakov, 2020).

Thus, the large "bouquet" of factors negatively affecting the state of natural Russian populations of Atlantic salmon (poaching, construction of hydroelectric power stations, organization of drinking water reservoirs, and consequences of wood drifting; pollution of salmon rivers with domestic and industrial wastewater near large human settlements and mining and metallurgical facilities; chemical pollution, distribution of diseases and genetic pollution as a result of mass commercial cage farming of Atlantic salmon and epidemic of ulcerative dermal necrosis of salmon skin, etc.) has been also supplemented by another factor, the potential impact of which (the threat of its impact on Atlantic salmon) has increased in recent decades against the background of the increase in the return of pink salmon to spawning grounds—this is interspecific competition for breeding ground resources, which is implemented at a significant limitation of spawning areas in the basins of the Barents and White seas compared to the Far Eastern region.

Thus, regardless of the problems with pink salmon, it is necessary to set tasks and implement measures to restore and increase the stocks of wild Atlantic salmon populations in the Barents and White sea basins. For this purpose, it is primarily necessary to organize protection against poaching; clean and reclaim spawning rivers, where possible; create conditions for the formation of populations in those rivers where populations have disappeared. These directions for restoration

Atlantic salmon populations are consistent with and replicate the directions of measures that were carried out in Norway during the restoration of Atlantic salmon populations in more than 40 Norwegian rivers affected by the dispersal of the monogenetic salmon fluke *Gyrodactylus salaris* (Johnsen and Jensen, 1986, 2003).

Next, it is necessary to find a solution to the issues of relationships between Atlantic salmon and pink salmon that would make it possible to increase the bioproductivity in the White Sea–Barents Sea region against the background of the improvement and restoration of Atlantic salmon populations in the rivers of the White and Barents sea basins, including through the effective industrial use of the resource of acclimatized pink salmon and, possibly, taking into account the long-term and rich experience of working with salmons of the genus *Oncorhynchus* in the Far Eastern region (Zubchenko et al., 2004).

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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