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Ecological and Biochemical Status of the Atlantic Salmon *Salmo salar* L. and the Brown Trout *Salmo trutta* L. at Early Stages of Development

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Abstract—A review of original and published data on the biochemical status of two salmonid species, the Atlantic salmon *Salmo salar* L. and the brown trout *Salmo trutta* L., encompasses the results on fish embryogenesis and the early development of fry of different ages during the freshwater period of life at different stages of life history (fingerling, parr, smolt) with inhabitation of the riverine biotopes of the northwest Russia, which differ in ecological and hydrological conditions. Data on the total lipid content, reserve lipids (triglycerides and cholesterol ester) and structural lipids (phospholipids and their fractions, cholesterol), fatty acids, activity of enzymes of carbohydrate metabolism, energy metabolism, and intracellular proteolysis are considered, along with some molecular-genetic indices of muscular tissue growth (the expression level of genes controlling myogenesis, as well as myostatin and heavy chain of myosin). Biochemical differences are already found in the embryos of the studied salmon fish; they determine the specifics of the interaction of larvae and fry with the habitat. As a result, when leaving the redds, some hatchlings may have certain metabolic advantages that facilitate their settling on better nursery grounds. Among all of the studied age groups, the "youngest" groups (0+, 1+) stand out, both in regard to the level of biochemical metabolism and the degree of difference between phenotypic groups inhabiting microbiotopes with different ecological, trophic, and hydrological conditions.

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INTRODUCTION

The research on the salmon fish inhabiting northern Europe is especially interesting in terms of the search for common mechanisms and specific features of the formation of adaptive reactions characteristic of their early development and in regard to the particular species, habitat conditions, and the specifics of the food supply. The early development of salmonids includes the processes of the differentiation of the same generation of embryos, larvae, and fry, which ultimately leads to the formation of a complex age and subpopulation structure that supports the intraspecific biodiversity and stability of population reproduction (Kazakov et al., 1992; Kazakov and Veselov, 1998; Khristoforov and Murza, 1998; Pavlov et al., 2010). It should be noted that the living conditions in the river period are extremely important in order to replenish the salmon population; this period of life is characterized by significant morphological and functional transformations (Shustov, 1983; Pavlov et al., 2007; Zubchenko et al., 2007). The article reviews the data on changes in the biochemical status of eggs during the process of embryonic development and in juvenile fish of different ages belonging to the family Salmonidae, genus *Salmo* (Atlantic salmon and brown trout), and those inhabiting the rivers of the northwestern part of Russia at different stages of the life cycle (yearlings, parrs, smolts).

BIOCHEMICAL STATUS OF YOUNG SALMON FISH

1. System of Indicators of the Biochemical Status of Fish

A system of biochemical indicators based on an analysis of our own and published data has been developed, theoretically justified, and tested. It covers the most important metabolic pathways for the transformation of macromolecules, ensuring the maintenance of the necessary homeostasis at the early developmental stages and during the growth of juvenile salmon fish (Murzina et al., 2014, 2016; Nemova et al., 2014; Nefedova et al., 2016). The proposed system includes some parameters of the biochemical status of lipids, fatty acids, enzymes of energy and carbohydrate metabolism, and intracellular proteolysis. It is known that lipids have two main functions: reserve and structural. They are also involved in hormonal and signal regulation, especially during ontogenesis (Kreps, 1981; Sidorov, 1983; Hochachka and Somero, 2002; Tillman and Cascio, 2003; Nemova, 2005; Arts and Kohler, 2009; Kainz and Fisk, 2009). Fatty acids (FAs) act as structural components and sources of metabolic energy (Hochachka and Somero, 2002). The higher the starting level of lipids in pre-spawning eggs is, including some FAs, the greater is the potential for further survival of the larvae.

The system of intracellular proteolysis includes enzymes that provide irreversible processes of intracellular protein degradation: proteasome, calpains, and cathepsins. It is known that proteolysis processes underlie cellular differentiation, adaptive metabolism, and many other biological processes (Nemova et al., 2010; Lysenko et al., 2011). The main pathways of intracellular proteolysis—lysosomal autophagic, proteasomal, and calpain-mediated—are responsible for the degradation of proteins in skeletal muscles; the last pathway dominates in fish. In general, the rate of accumulation of muscle protein mass and growth depends on the ratio of the rates of protein synthesis and degradation (Mommsen, 2004; Salem et al., 2006; Overturf and Gaylord, 2009; Salmerón et al., 2013, 2015), and the rate of protein synthesis in the fish muscle prevails over the rate of its degradation to ensure a nondeterministic growth characteristic of most representatives of bony fish (class Teleostei), including family Salmonidae (Johnston et al., 2011). The intensity of catabolism as a tool for basic cellular protein metabolism and quality control is directly related to the rate of protein synthesis, which is especially high during the period of active growth of juvenile salmon. Intensive hydrolysis of skeletal muscle proteins with subsequent utilization of amino acids also contributes to the survival of fish with increased energy consumption, i.e., during the periods of spawning, starvation, and migration. The exceptional importance of energy metabolism for vital activity and the growth and development of juvenile fish makes it necessary to study the level and proportions of the aerobic and anaerobic pathways of energy metabolism (Pavlov, 2007; Churova et al., 2011; Nemova et al., 2015).

In research on the early development of salmonids, the activities of several carbohydrate conversion enzymes are considered: cytochrome *c* oxidase (COX), lactate dehydrogenase (LDH), aldolase, 1-glycerophosphate dehydrogenase (1-GPDH), and glucose-6-phosphate dehydrogenase (G6PD) (Childress, 1980; Treberg et al., 2002; Johansen and Overturf, 2006; Gauthier et al., 2008). An indicator of the level of aerobic metabolism is the activity of the mitochondrial respiratory-chain enzyme cytochrome *c* oxidase, the activity of which characterizes the oxidation of all energy substrates: intermediate products of the breakdown of carbohydrates, proteins and lipids during aerobic metabolism, and the associated aerobic synthesis of ATP. Lactate dehydrogenase (LDH) catalyzes the reaction of the mutual conversion of lactate to pyruvate. The activity of this enzyme in the muscles is an indicator of the intensity of anaerobic metabolism and anaerobic synthesis of ATP. The energy metabolism of cells is inextricably linked to carbohydrate oxidation, since the use of carbohydrates for ATP synthesis by aerobic and/or anaerobic pathways increases if significant energy is consumed. Although aldolase is not a limiting glycolysis enzyme, it may be used to evaluate the processes of carbohydrate oxidation in glycolysis for a comprehensive assessment of the metabolic pattern. The activity of glucose-6-phosphate dehydrogenase (G6PD) indicates the rate of pentose-phosphate oxidation of carbohydrates, during which pentoses form. They are necessary for the synthesis of nucleic acids, as well as NADPH equivalents for the reduction reactions of lipid biosynthesis and the restoration of glutathione. 1-Glycerophosphate dehydrogenase (1-GPDH), along with the shuttle mechanism, is involved in the formation of 1-glycerophosphate, a precursor of structural and storage lipids, thus providing a link between the carbohydrate and lipid metabolism (Harmon and Sheridan, 1992; Treberg et al., 2002).

Myosin is one of the main proteins in muscles; it accounts for 25% of the total protein content of the whole body and 50% of the amount of all muscle proteins (Watabe and Ikeda, 2006). The expression level of the myosin heavy chain gene (MyHC) correlates with the growth rate and size of the fish; therefore, it may be used as an indicator reflecting the growth rate of fish and the growth rate of their muscle mass (Overturf and Hardy, 2001; Dhillon et al., 2009). A study of the level of expression of regulatory factors of myogenesis (MyoD, Myf5, myogenin) and proteins that inhibit muscle growth (myostatin) makes it possible to describe the processes of the regulation of muscle growth and the features of muscle tissue formation in ontogenesis with respect to the stage of fish development and environmental conditions (Johansen and Overturf, 2006; Bower et al., 2009; Overturf et al., 2010). Considering the biochemical status of young salmon fish at early developmental stages, conclusions may be drawn about the state and functional activity of the organism as a whole, its growth, development, physical activity, ability to adapt to environmental conditions, etc. (Pavlov, 2007; Churova et al., 2011; Nemova et al., 2015).

2. Correlation of Biochemical Status with the Characteristics of the Growth and Development of Juvenile Salmon Fish of Different Ages (0+, 1+, 2+, 3+, and 4+)

Salmon juveniles of all studied ages from different biotopes differ in the content of storage lipids in the form of triacylglycerols (TAGs) and cholesterol esters (Chol esters) (Pavlov et al., 2008; Nefedova et al., 2016). Reserve lipids in the form of TAGs prevail in the total lipids of juvenile salmon of all studied ages; their content does not significantly differ in fish of different ages. The TAG content characterizes the process of the accumulation of energy reserves. It reflects the provision of juveniles with food and may serve as one of the mechanisms determining the strategy of motor activity of fish associated with the distribution of juveniles after hatching in different biotopes and their physical capabilities to move against the stream (rheoreaction). The decrease in the content of phospholipids (PLs) and reserve Chol esters in juveniles of age 1+ as compared to those of age 0+ is probably due to the active use of these compounds, primarily as structural components of biomembranes (BMs), as well as sources of FAs—Chol esters (Perevozchikov, 2008). In a comparison of the lipid spectrum of brown trout of different ages (parrs 0+, 1+, 2+, 3+, and smolts) from Krivoi Ruchei River, Olkhovka River (0+, 1+, and 2+), Indera River (4+) (the White Sea basin, the "northern" rivers), and juveniles (1+, 2+, and 3+) from Orzega River (Onega Lake basin, the "southern" river), a similarity was found for the content of total lipids (TLs) in parrs (1+) in a range of 9.51–10.03% dry weight and a higher content of TLs in older age groups of juveniles (2+, 3+) from Orzega River (22.36 and 19.43% dry weight, respectively) (Murzina et al., 2017a; Nefedova et al., 2018). Young brown trout (1+, 2+, and 3+) from Orzega River (the southern river) has larger size and weight characteristics as compared with those inhabiting the rivers Olkhovka and Krivoi Ruchei (northern rivers). Older age groups, such as smolts 4+ (Indera River), have higher size and weight characteristics as compared to the parrs 3+ and smolts from Krivoi Ruchei River and with parrs 3+ from Orzega River, which correlate with increased ratios of n-3/n-6 polyunsaturated FAs (PUFAs) and unsaturated FAs to polyunsaturated FAs (MUFA/PUFA). Quantitative differences, including variations in the spectrum of certain lipids in young salmon of different ages, especially in smolts, may be affected by the degree of activity of metabolic processes, depending on the fish age.

Comparison of the activity of the enzymes of energy and carbohydrate metabolism and myogenesis indices in yearlings, parrs, and smolts of juvenile Atlantic salmon and brown trout of different ages from different biotopes of the White Sea basin (Varzuga, Indera, Krivoi Ruchei and Olkhovka rivers) and Lake Onega basin (Orzega River) indicate the presence of age-related changes in energy metabolism and the intensity of carbohydrate use, as well as in the processes of muscle growth (Churova et al., 2015, 2017a, 2017b). A positive relationship was found between the studied parameters and the fish body weight within the age groups, which indicates a high level of aerobic and anaerobic metabolism in larger "fast-growing" specimens (Churova et al., 2015). The age-related dynamics of enzyme activity in parrs from different biotopes was similar. With allowance for the activity of COX, LDH, and aldolase enzymes, which are involved in the metabolic processes of carbohydrate metabolism, a certain tendency of a decrease in the level of aerobic ATP synthesis, and an increase in the process of anaerobic energy production and the degree of carbohydrate use in anaerobic ATP synthesis with age are observed in different juvenile age groups. An increase in the activity of 1-glycerophosphate dehydrogenase (1-GPDH) in accordance with the age of juveniles indicates an intensification of the conversion of carbohydrates to glycerophosphate (a precursor of structural and storage lipids) (Churova et al., 2015, 2017a, 2017b).

A high level of expression of the myosin heavy chain gene (MyHC) and the transcription regulation gene genes in two-year-old (1+) Atlantic salmon and brown trout was found for muscle proteins of the parrs of both species, which reflects the intensive growth and increase in muscle mass at this age (Churova et al., 2015, 2017a, 2017b). The decrease in MyHC expression in the parrs of brown trout 2+ and in the Atlantic salmon aged 2+ and 3+ occurs against the background of a decrease in the activity of cytochrome *c* oxidase (COX), which is an indicator of a slowdown in the muscle growth of fish during this period (Churova et al., 2015, 2017a, 2017b). It is possible that age-related changes in the regulation of muscle growth are associated with the expression of the MyoD1a and MyoD1b genes in Atlantic salmon and the Myf5 gene in brown trout, which may indicate the presence of specific features of the expression of myogenesis regulation genes during ontogenesis (Churova et al., 2015, 2017a, 2017b).

Age-related differences were found in the activity of intracellular proteinases in the muscles of juvenile Atlantic salmon (Lysenko et al., 2015, 2017; Kantserova et al., 2017b). Calpains are considered the main proteinases that ensure the degradation of muscle (myofibrillar and sarcoplasmic) proteins in fish. The contribution of other proteolytic systems (proteasomal and lysosomal) is less significant and plays a secondary role, since calpains, in particular, play a leading role in the disassembly of myofibrillar protein complexes (Goll et al., 2008). There are data on a positive correlation of the level of activity of cathepsin D, calpains, and proteasome in muscle tissue with the growth rate of salmon of different age groups (Lysenko et al., 2015). The most actively growing specimens (parrs 0+) are characterized by a higher level of proteolysis, followed by parrs 1+–4+; as growth rates decrease, the activity of these proteinases decreases, too. The age-related dynamics of the activity of lysosomal proteinase, cathepsin B, the contribution of which to the exchange of myofibrillar proteins is insignificant, has a different pattern than the rest of the proteinase cohort: the content of this enzyme increases with age, which apparently reflects its special role in growth processes. During smoltification, the growth rate and accumulation of proteins in the Atlantic salmon are inversely related to the activity of proteinases in the fish muscles: the intensive growth of the fish, which enters the stage of smoltification and thus undergoes physiological rearrangements for migration from rivers to the sea, is accompanied by a decrease in the degree of protein degradation in skeletal muscles of juveniles (Kantserova et al., 2017a, 2017b). In brown-trout smolts, the activity of calpains and cathepsin B is significantly higher than that in parrs; the opposite pattern is observed for proteasome proteases. Most likely, this is a qualitative difference in trout smolts with respect to the formation degree of their osmoregulatory apparatus: in the absence of ability to carry out active ionic regulation, trout smolts survive due to individual adaptive mechanisms, including tissue enrichment with osmotically active substances (amino acids). After they migrate from the river, brown-trout smolts remain for a long time in the desalinated water of the estuary, which ensures a gradual "inclusion" of the osmoregulatory function. This apparently indicates the species-specific role of proteinases in smoltification. The inhibition of proteolysis of muscle proteins serves as a mechanism to enhance the growth of muscle mass of the Atlantic salmon presmolts, and the enhanced proteolysis of muscle proteins in brown-trout presmolts provides their tissues with osmolytes and contributes to their survival in the marine environment with an unformed system of osmoregulation.

Biochemical indicators and lipid-status indices characterizing the readiness of juveniles of the Atlantic salmon and brown trout for smoltification have been reported (Nefedova et al., 2018). The quantitative ratios of Chol/PL and TAG/PL, as well as MUFA/PUFA (16:0/18:1(n-9), 18:2n-6/18:3n-3, 22:6n-3/18:3n-3, and 20:4n-6/18:2n-6), are the primary indicators. These parameters determine the changes in the synthesis of both storage and structural lipids, i.e., the readiness for migration to the sea and for feeding; they also demonstrate "subtle" adaptation mechanisms when the fish change the habitat from fresh water to marine water. In particular, variations in the cholesterol/PL ratio may indicate an adjustment of the lipid microenvironment of membrane integral enzymes, including osmoregulatory ones, in order to maintain their activity at an optimal level. This may be indicated by the predominance of FAs of the n-3 family over FAs of the n-6 family (Tipsmark et al., 2010; Sundell and Sundh, 2012). The initiation of modification of the FA composition of the freshwater type in the direction of the marine type is also indicated by an increase in the content of phosphatidylserine (PS) in parrs (1+) and especially in smolts; PS is an effective regulator of the activity of the key osmoregulation enzyme, Na^+/K^+-ATPase, which supports the biochemical mechanism of fish adaptation to a marine habitat. There are no significant differences in these parameters in brown-trout juveniles from the southern rivers of Karelia, which may indicate its belonging to the residential form and can be considered as an explanation of the biological features of this species in rivers, where trout smoltification does not occur (Murzina et al., 2017a; Nefedova et al., 2017).

The results of studies of the biochemical status of juvenile Atlantic salmon and brown trout of different ages indicate the presence of age, size, and stage-specific differences associated primarily with variations in the use of carbohydrates, proteins, and lipids in energy and plastic metabolism at the early stages of ontogenesis. These differences may serve as an example of ecological and biochemical adaptation of cellular metabolism, leading ultimately to the size–weight diversity of juveniles and the formation of its phenotypic groups upon resettlement into biotopes with a different combination of hydrological and environmental factors.

3. General and Specific Features of Metabolic Changes in Juvenile Salmon Fish That Settled in Different Biotopes after Leaving the Spawning Nests

After hatching and leaving the spawning nests located in the main riverbed of Varzuga River (the White Sea basin), part of the school of Atlantic salmon fry remains in the main channel of the river, and the other part settles in tributaries and streams for 10–12 days, where hydrological, trophic, and ecological conditions are the most favorable for growth and development (Veselov and Kalyuzhin, 2001; Nefedova et al., 2014; Nemova et al., 2015a, 2015b; Murzina et al., 2016). During the summer, juveniles stay between bare boulders in local stream flows, leading a sedentary lifestyle, and the Atlantic salmon yearlings do not migrate between the tributary and the main channel. The growth rate of the Atlantic salmon larvae and fry living in the more favorable conditions of shallow water and well-warmed tributaries with significant oscillation of day and night temperatures is higher than that of individuals inhabiting the river bed. The tributary-associated phenological group is characterized by faster growth (individuals became 1.5 times larger in 1.5 months of observation) (Nemova et al., 2017). Among the studied age groups, juveniles of ages 0+ and 1+ stand out both in terms of indicators of biochemical metabolism and in the degree of differences between phenotypic groups living in biotopes with different ecological, trophic, and hydrological conditions (Pavlov et al., 2009; Nefedova et al., 2014; Nemova et al., 2015a, 2015b; Murzina et al., 2016).

Different combinations of fodder objects for juvenile salmon fish form in different streams (Murzina et al., 2017b). The proportion of food items available for juvenile salmon feeding varies significantly, from 28 to 99%, 80% on average (Murzina et al., 2017b). The variations in the FA composition of the macrozoobenthos of the studied freshwater biotopes indicate differences in the qualitative and quantitative composition of primary producers in these biotopes, which is reflected in the transfer of matter and energy in the form of FAs to the consumers of higher trophic levels, particularly, to macrozoobenthos and juveniles of salmonids (Voronin et al., 2016; Murzina et al., 2017b).

The study of metabolic characteristics in juveniles that inhabit the main riverbed of Varzuga River and its tributary Pyatka River did not find differences in the activity of the aerobic metabolism enzyme COX, while fry from the tributary showed a higher total LDH activity and higher activity of group A of LDH isoenzymes, as well as higher aldolase activity. Since anaerobic metabolism is directly related to the energy supply of motor activity, it may be assumed that the increased activity of the studied enzymes in the Atlantic salmon fry from the tributary determines their good physical activity and adaptive capabilities upon relocation and habitation in the stream.

The metabolism of juvenile Atlantic salmon living in the tributary is characterized by a higher activity of 1-GPDH, which, along with data on changes in lipid status in the same juvenile, indirectly indicates a more intense formation of 1-glycerophosphate, which may be used in the synthesis of reserve and structural lipids (Harmon and Sheridan, 1992; Treberg et al., 2002).

It is possible that the good forage basis of the tributaries as compared to that of the river channel makes it possible both to use and store nutrients to maintain the necessary level of vital activity (Meshcheryakova et al., 2017).

Yearlings living in a tributary (Pyatka River) demonstrated a higher activity of intracellular proteolysis enzymes as compared to those in the main channel of Varzuga River, which indicates an increased intensity of intracellular protein metabolism (Nemova et al., 2017). The mechanism of selective regulation of calpain activity in these individuals may be associated with the specific lipid composition of their biomembranes, including higher contents of phosphatidylinositol, arachidonic acid, and unsaturated FAs. Both direct and indirect effects of lipid components on the activity of calpains were described previously. In particular, the association of calpains with phosphatidylinositol on the inner surface of membranes is a necessary step in the activation of calpain zymogen (Zalewska et al., 2004), and an increase in the microviscosity of membranes leads to an increase in the passive transport of calcium ions, the main activator of calpains, into the cell (Kyavyaryainen et al., 2005; Kantserova et al., 2012).

The content of reserve lipids (TAG + Chol esters) is the main energy reserve in the fish organism, and the optimal ratio of these lipids versus structural lipids may be considered one of the adaptive mechanisms that facilitate the resettlement of yearlings after hatching in different biotopes (Nefedova et al., 2014; Nemova et al., 2015a, 2015b). Atlantic salmon yearlings have different lipid and FA compositions after hatching and resettlement. The ratios of the lipid classes are within physiological limits; the most important ratios are TAG + Chol esters/PL + Chol and 18:3(n-3)/18:2(n-6) FA. For example, yearlings (0+) that migrate from the main riverbed of Varzuga River to the tributary (Pyatka River) differ from those remaining along the coast of the main stream of Varzuga River by a higher ratio of 18:3(n-3)/18:2(n-6), which indicates better feeding conditions in the tributary (Nefedova et al., 2016). Other authors noted earlier that Atlantic salmon juveniles from the tributary (Pyatka River) preferably consumed chironomid larvae rich in 18:3(n-3) acid (up to 17.12% of the total FA) among all other species of invertebrates (Shustov, 1995, 2012; Descroix, 2010). It is known that there are competitive relationships between n-3 and n-6 PUFAs (Navas et al., 2001). The present study shows an increase in the n-3/n-6 PUFA ratio in parrs (1+), which indicates an increase in the number of PUFAs of the n-3 family, including physiologically significant ones. This is most likely associated with the consumption of food objects rich in these acids, as well as the capacity of this age group of fish for the selective consumption of certain macrozoobenthos species.

According to the content of TAG, total PL, and essential 18:2(n-6) and 18:3(n-3) FAs, as well as the sum of monoene FAs, different qualities of yearlings of Atlantic salmon from biotopes of the main riverbed of Varzuga River and its tributaries are also retained in older age groups of parrs (1+, 2+) (Nefedova et al., 2017). These differences are determined by the quality of the food supply (species composition and lipid spectrum of the food objects) and the hydrological conditions of the studied biotopes. A qualitative difference is also shown between microbiotopes of one tributary (Nemova et al., 2015b). In particular, the yearlings of Atlantic salmon of similar size and weight originating from two nests (from Arenga River, a tributary of Varzuga River, and from the main channel of Varzuga River) are different; after hatching, they populated the rapids under the waterfall in the tributary (Arenga River, generation A) and the mouth of the same tributary (generation B). The compared biotopes differed in hydrology, trophicity, and temperature, which affected the lipid status of juveniles. No significant differences were found in the TL content and the sum of monoenic FAs (MUFAs) in the yearlings of two generations, but a higher content of total PL in generation A is observed due to an increase in the concentration of phosphatidylcholine (PC), phosphatidylethanolamine (PEA), phosphatidylserine (PS), and sphingomyelin (SM) and a decrease in the proportion of lysophosphatidylcholine (LPC). An increase in the content of total PL alters the cholesterol/PL index, which reflects the microviscosity and fluidity of biomembranes and affects their functional activity. Due to the increased PL content in yearlings of generation A, this ratio was slightly lower than that in juveniles of generation B. Moreover, a change in the cholesterol/PL index is one way to regulate the state of cellular biomembranes in the process of adaptation of the organism to certain environmental conditions. Among the complex of studied ichthyological and biochemical indices and their differences between the two generations of juveniles, a change in this parameter may also indicate increased motor activity in fry of generation A under conditions of intense turbulent flow in the rapids. In addition, yearlings of generation A are characterized by a higher content of the PUFA of the n-3 metabolic family. This is mainly due to decosehexaenoic acid (22:6(n-3)), which may result from increased motor activity. Yearlings of generation B from the mouth of Arenga River (tributary) as compared to those from under the waterfall (generation A) were characterized by a higher content of linoleic acid (18:2(n-6)); the coastal insects that form part of the diet of juvenile Atlantic salmon are rich in this FA. At the mouth, in the conditions of a flood meadow, there is the mass development of flying insects, which serve as food for fry of generation B. In the forest habitat of generation A, the food is mostly typical (benthic invertebrates). Quantitative variations of PLs and their FAs support the "liquidity" of biomembranes necessary for the functioning of enzymes and enzyme ensembles, which is important for adaptation to the environment. Differences have been found in biochemical parameters between the yearlings of the Atlantic salmon from other biotopes of the tributaries of the rivers Varzuga and Indera (Porokushka, Falaley, Krivoi Ruchei, Sobachii Porog, Sobachii Ruchei rivers, etc.) (Pavlov et al., 2009; Nefedova et al., 2014; Nemova et al., 2015a, 2015b; Murzina et al., 2016). In addition to temperature, the spectrum of food objects characterized by different contents of lipids and lipotropic substances, its mass, and its availability, are important in these processes.

The revealed biochemical differences between the Atlantic salmon yearlings migrating to tributaries and those remaining in the coastal areas may be the basis for the formation of the subsequent (at the age of 1+, 2+) and stable differentiation of the fish into groups with different lipid status and size-weight indices. These differences may also influence the choice of life strategy by fish. Therefore, the genetically incorporated mechanisms for the regulation of the growth and early development of salmonids are implemented by a complex of biochemical features and adaptations that determine the choice of the optimal strategy for the early development of the Atlantic salmon juveniles and the specifics of the life cycle of this species.

4. Biochemical Diversity of Salmonids during Embryonic Development

Studies were carried out both in laboratory aquaria (salmon eggs were obtained from a fish hatchery on the Shuya River, Onega Lake basin) at several stages of development and at one of the "critical" stages (eye pigmentation stage) of embryogenesis of Atlantic salmon developing in natural spawning nests in the Rivers Varzuga and Umba. The biochemical heterogeneity that manifests itself in salmon embryos (at the stage of eye pigmentation) is characteristic primarily for the ratios of Chol/PL, PC/phenolic acid, and n-6/n-3 PUFAs and for the content of SM and the content of LPC (Nemova et al., 2015a). Lipid modifications are aimed at a reduction in BM viscosity and an increase in the activity of membrane-bound enzymes; an increase in the concentration of saturated and monoenic FAs before larva hatching is most likely associated with an increase in their synthesis *de novo*. The decrease in the proportion of polyene FAs (especially linoleic and linolenic FAs) may be explained by the lack of their intake with food at the stage of endogenous nutrition. In a comparison of the biochemical status of eggs of the Atlantic salmon at the stage of eye pigmentation (obtained from the spawning nests located in Umba River at a water temperature of 0.2–0.3°C) and eggs reared under artificial conditions (4°C), the stability of the TL content, in particular, classes (PL, TAG, Chol, Chol esters), as well as their ratios (Chol/PL and PL/TAG) observed in both cases, indicates the universal role of lipids in the genetic program of embryonic development (Nemova et al., 2015a). The relatively low rate of lipid metabolism in vivo at a lower temperature has an effect on some characteristics of PLs and FAs (i.e. increased concentrations of phosphatidylserine, sphingomyelin, oleic 18:1(n-9) and decosehexaenoic 22:6(n-3)), which can probably subsequently affect rates of egg growth and development. At the stage of eye pigmentation, the embryonic resistance to temperature variability increases, accompanied by increasing oxygen demand and followed by changes in the activity of aerobic metabolism of carbohydrates and lipids and the pentose phosphate pathway (COX, malate dehydrogenase, 1-GPDH, and G6PD) (Meshcheryakova et al., 2017). The characteristics of the biochemical status of juvenile Atlantic salmon, which are clearly seen already during embryogenesis, may serve as a determinant of fish development. As a result, the earliest larvae to hatch from spawning nests (larval hatching from one redd/nest lasts for 7–12 days) have certain advantages that allow active population of the best growing grounds. It should be noted that the formation of ecological groups is predetermined by the timing (early stages) of larval departure from the spawning nest and their successful resettlement to the growing grounds; rapids are particularly favorable microniches for habitat (Shustov and Smirnov, 1978; Shustov, 1983; Veselov and Kalyuzhin, 2001). The eggs differ in the volume of stored substances, size, and mass; this qualitative difference subsequently affects the rates of juvenile growth and development and determines different starting possibilities for the larvae to be resettled into biotopes with different living conditions. Surely, when the so-called “advanced” larvae inhabit biotopes with the best trophic and ecological living conditions, they grow and develop more intensively and are among the first to be ready for smoltification and seaward migration.

Differences in the activity of enzymes of key reactions of energy and carbohydrate metabolism of the Atlantic salmon precondition the intensity and direction of biochemical processes in fish embryos and develop metabolic prerequisites for the formation of qualitative difference in the embryonic period by two factors: (1) energy status and (2) the use of carbohydrates in the processes of ATP synthesis and formation precursors for biosynthetic reactions (Meshcheryakova et al., 2016; Churova et al., 2017). Despite the significant lipid reserves in the embryo of Atlantic salmon, carbohydrates are mainly used as an energy source at the last stages of embryogenesis (Shatunovskii, 2001; Lahnsteiner, 2005). This is due to the fact that the shape and increased motor activity, especially before hatching, requires high energy costs, which may be easily compensated for by the rapid oxidation of carbohydrates in conditions of limited oxygen consumption. Salmon embryonic development occurs in sediment; therefore, the oxygen consumption by the embryo is very limited. In addition, the respiratory organs of the embryo still do not function; therefore, oxygen diffuses through the egg shell. The energy requirements of ATP in the embryonic period significantly exceed the capabilities of aerobic metabolism. Thus, the role of anaerobic synthesis of ATP is significant, as evidenced by the high activity of anaerobic LDH isoenzymes in salmon embryos. The enzyme activity shows a gradual decrease in the activity of COX at the end of embryogenesis and a sharp increase in the activity of LDH, aldolase, and 1-GPDH before hatching. These results indicate a decrease in the level of aerobic energy metabolism at the final stages of embryogenesis and an increase in the degree of carbohydrate use for energy purposes, on the one hand, and on the means of conversion to 1- or 3-glycerophosphate (a precursor of structural and storage lipids), on the other (Meshcheryakova and et al., 2017). Apparently, the biological indication of this is the need to preserve high-energy lipids for subsequent use by hatching larvae during a period of limited endogenous nutrition, since they are inactive and unable to feed for some time after hatching. Changes in the dynamics of intracellular proteolysis in the embryonic development of salmon, including those at the stage of eye pigmentation (in spawning nests), are associated with embryonic differentiation, morphogenesis, and growth. The so-called “critical” stages (start of gastrulation, eye pigmentation, time before hatching) have been proposed, and the maximum proteolysis activity is observed specifically at these stages (Nemova et al., 2010, 2017a). Lysosomal and cytoplasmic proteinases functionally interact during intracellular proteolysis. The initial stages of latter are carried out by calpains, and the subsequent cleavage of the resulting fragments into short peptides and amino acids is performed by cathepsins of lysosomes and by proteasome. During the development of salmon embryos at the gastrulation stage, when the reserve yolk proteins are actively used to cover the needs of embryo protein biosynthesis, a synergistic effect of the activation of cysteine-dependent intracellular proteinases of different localization, i.e., the lysosomal enzyme cathepsin B and cytosolic calpains (Nemova et al., 2010, 2017a), are observed. The activation of aminopeptidases of various specificity was detected at the stage of larval readiness for hatching. These enzymes are mostly trypsin-like peptidases, as evidenced by hydrolysis of the N-Bzl-L-Arg-p-NA substrate.

Biochemical studies of salmonid embryogenesis show that individual biochemical features are manifested during this developmental period. They are expressed as different levels of energy supply to the process of embryo development, which precondition the metabolic prerequisites for the formation of qualitative diversity in the embryonic period.

CONCLUSIONS

The results of studies of the early development of the Atlantic salmon and brown trout in northern Europe indicate that there are specific features that may be due to certain species and habitat conditions of salmonid juveniles in biotopes that differ in hydrological, trophic, and ecological conditions, along with the universal age-dependent dynamics of biochemical status common to all fish. It is possible that the biochemical heterogeneity found in our studies determines the adaptive abilities of larvae hatching from spawning nests already at the embryonic stages. As a result, the hatchlings have large energy resources, muscle mass, and physical activity; therefore, they actively migrate to tributaries with better conditions for further development, despite a high flow rate. The choice of habitat for juveniles of the Atlantic salmon is provided by behavioral mechanisms, which are apparently based on biochemical adaptations. Among all of the studied age groups (0+…4+), the younger age groups (0+, 1+) stand out, both in terms of indicators of biochemical metabolism and in the degree of differences between phenotypic groups living in biotopes with different ecological, trophic, and hydrological conditions. During this period, salmonid fry are still at the stage of choosing a life strategy (Shustov, 1983, 1995; Kazakov et al., 1992; Kazakov and Veselov, 1998; Veselov and Kalyuzhin, 2001; Pavlov et al., 2007, 2008, 2010; Zubchenko et al., 2007; Veselov et al., 2011). The observed differences in the biochemical status of the Atlantic salmon juveniles may determine the extension (by 1–3 years) of the onset of smoltification of salmon juveniles of one generation and, accordingly, early or late migration to the sea, which generally affects the formation of a complex age structure and intrapopulation biodiversity.

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COMPLIANCE WITH ETHICAL STANDARDS

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