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ECOLOGICAL PHYSIOLOGY

# Role of Temperature in Regulation of the Life Cycle of Temperate Fish[1]

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**Abstract**—The review provides information on adaptive responses of fish metabolic processes in response to temperature reduction of habitat, including the direction of adjustment of energy metabolism and mechanisms to improve the adaptive capacity and reparative capacity of tissues in response to lower temperatures. It presents data on the effect of temperature on the reproductive function of fish and fish development processes in the early stages of ontogeny.

*Keywords*: fish, adaptation, low temperatures, reproductive function, fish ontogeny

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## INTRODUCTION

Contemporary dominance of teleosts became possible due to their high ecological plasticity, which has ensured the successful adaptation of species to different environmental conditions determined by seasonal changes in photoperiod, hydrochemical and hydrologic parameters and temperature conditions. At present, little is known about the mechanisms responsible for the perception of the fish changes of ambient temperature and adaptive reorganization of metabolic processes.

However, the problem of the temperature adaptation of fish retains its relevance in view of the fact that, firstly, the global climate changes have a significant impact on the life cycle of fish.

Second, considerable attention is paid to research and evolutionary aspects of thermoregulation thermoreception vertebrates.

Third, no less weighty is the proportion of scientific and practical research, providing a more rational use of marine biological resources, scientific study and development of advanced technologies acclimatization, breeding and cultivation of new aquaculture.

### *Thermoreception in Fish*

The ambient temperature determines the body temperature of fish and intensity of the flow of metabolic processes. Obviously, the thermal regime of the habitat of freshwater fish of mid-latitudes, fish living in waters of the polar circle, and pelagic fish species of the World Ocean is distinguished not only the absolute values of optimum temperature, but also a range of tolerance values of water temperature, which gives the right to consider the temperature of water environment as a leading factor in forming the boundary of habitats of aquatic organisms [92]. Accordingly, the nature of adaptive adjustment of basic metabolic processes in fish can be quite significant specific features depending on the particular environmental conditions of habitat and species specificity of the flow of metabolic processes. However, the number of review publications argues for evidence of the general principles of adaptation of fish to changes in temperature [34, 51, 92]. According to some researchers, another plane of existence of this problem is well-defined differences between the ability of fish to an adequate reconstruction of metabolic processes as the changing seasons of the year and adapt fish to a new thermal regime, formed on the background of global climate change [99, 92]. Integral stimulus, formed under the influence of diurnal and seasonal fluctuations in environmental conditions, including fluctuations in water temperature for fish is an important signal that regulates their life cycle [9, 34]. In contrast, disruption of the natural characteristics of the dynamics of environmental factors dramatically narrow the adaptive potential effects on fish, reducing their viability, preventing legitimate cyclical physiological processes. In this sense, it is natural question about the physiological mechanisms responsible for the perception of a fish in ambient temperature. On the one hand, it is clear that as fish do not have the ability to provide constant body temperature, the decrease or increase in water temperature can directly cause corresponding changes in the kinetic parameters of biochemical reactions without any

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mechanisms of thermoreception. However, it is now well established that fish have a thermal sensitivity due to the specialized nerve endings that contain a set of specific ion channels—"thermoTRPs" susceptible to temperature fluctuations, characterized by well-established temperature sensitivity thresholds, as well as participating in chemoreception. The higher vertebrates acquire the ability to osmoreception [81, 89]. According to the author's cited publications, the role of temperature-sensitive nerve endings is the formation of behavioral responses of fish in response to heat and cold exposure. Trying to avoid the fish chilled water layers, most likely, is the earliest manifestation of reaction to the cold stimulus [105]. However, the authors point out that in bony fishes cooling water environment leads to rapid changes in the activity of neuro-humoral and sensorimotor functions of the central nervous system. In general, the thermal regime of the environment has a significant effect on the bioelectrical activity of excitable tissues of fish, directly modulates the activity of neuro-endocrine control of homeostasis-level fish [68], inducing changes in the metabolic processes in the nervous tissue [102], as well as restructuring of the activity of ion-transporting proteins in cardiomyocytes of fish [24, 38]. It is reported that one species of fish acclimatized to different temperature conditions, revealed changes in the parameters of bioelectrical activity of the muscles of the digestive tract and the dynamics of growth rates of gastric blood flow after a meal [31].

In the literature, considerable attention is paid to mechanisms for quality adjustment of the functional activity of mitochondria in fish under the influence of changing the thermal regime. The most characteristic features of this process are: an increase in mitochondrial inner membrane cristae seal, the modulation of the activity of transport proteins, inner mitochondrial membrane and modification of phospholipid composition, changing the ratio between saturated and unsaturated fatty acids, lipid bilayer membranes [34]. The review authors indicate definite differences in the changes in the functional properties of mitochondria from cold-and heat-loving species. In the last decade produced a considerable amount of experimental data convincingly demonstrate the high sensitivity of the genome of fish to changes in temperature environment. Therefore, in the literature, this issue is given particular importance, given the specificity of the reaction of fish to cold and heat stimulus, and the role of control mechanisms of transcription, depending on changes in temperature [6, 29, 34, 99, 106].

An important aspect in the study of adaptation of fish to thermal regime changes is to compare the body's response to acute and long-lasting changes in ambient temperature. Response to acute exposure to thermal factor at the level of behavioral responses [81, 89, 105], and metabolic processes in fish [34] is formed within a few seconds. Then, as for the restructuring of metabolism in response to sustained changes in water temperature may take several days or weeks [34].

In addition, in our opinion, deserve special attention a study of mechanisms of influence of temperature on the processes of morphogenesis of fish in the early stages of individual development [48, 60, 75].

Fish are cold-blooded animals, but the fish's body temperature is slightly above the temperature of the environment. During the high physical activity or during a meal production of heat increases, so the changes of hemodynamic parameters recorded in these conditions, it is permissible to consider, on the one hand, as a response to increased delivery needs or outflow, respectively, substrate or product of metabolism. On the other hand, is a way to realize the need for restructuring of the circulation of intravascular fluid, considered as a coolant? Also attracted the attention of the regular data redistribution in cold blood of vertebrates, including fish, during the winter in freezing waters [34]. Taken together, given evidence indicates that mechanisms of thermoregulation in fishes, which include how the processes of heat production and heat transfer. Striking proofs of the possibility of effective thermoregulation in fishes are the tunas. Anatomical structure of the circulatory system of these fish helps to maintain optimum temperature of the skeletal muscles, sensory systems and organs in warm and cold water, providing high mobility and ability to find and get food [30].

### *Adaptation of Metabolic Processes in Fish to Changes in Ambient Temperature*

A number of publications illustrates deep restructuring of metabolism in fish, showing reaction to thermal stimulus in the system, organ, cellular and subcellular levels. Of course, this approach allows forming a clearer picture of the "global" nature of the reaction to ambient temperature changes affecting all levels of organization of living matter. A central place is occupied by research on the effect of temperature changes in energy metabolism. Since the thermally induced rearrangement of structural and functional properties of mitochondria is essential for the success of the temperature adaptation of fish. However, the development of a universal scale qualitative and quantitative characteristics of the modification of mitochondria as the basic criterion of the effectiveness of the temperature adaptation of fish needs to be some clarification regarding the functional characteristics of the organelles in not only in different tissues, but in different populations of cells of one tissue, as well as differences in the activity of energy metabolism in the mitochondria still hibernating fish, fish are able to lead an active lifestyle in cold water and polar zones [34, 58, 69].

In particular, according to some authors, the acclimatization of fish to low temperature may be accompanied by an increase in mitochondria, which, in turn, not only provides an opportunity to strengthen the work of the components of energy metabolism, but also provide a more efficient flow of oxygen into the cell [34, 59]. In this case, the process by increasing the mitochondria, on the one hand, due to induction of de novo synthesis of proteins and phospholipids, which is implemented through the activation of transcription of nuclear and mitochondrial genomes. On the other hand, unlike most mammals, in fish at low temperatures retard the degradation of proteins, which also helps increase their number in the mitochondria. Thus, the published studies indicate that the increase in mitochondria in cold acclimation of fish can not only compensate for a deficiency macroergs due to an increase of enzyme activity of the tricarboxylic acid cycle and fatty acid oxidation, but also to strengthen the flow of oxygen into the cell, which is particularly demonstrate some Antarctic fish, completely devoid of hemoglobin and myoglobin [59, 79]. Reducing the water temperature has a significant impact on the biophysical properties of the membrane, which negatively affects the activity of enzymes associated with the membrane and the intensity of transport processes. Recovery of these parameters by increasing the proportion of specific fatty acids and phosphatidylethanolamine facilitates optimization of the basic biophysical properties of lipid bilayer membranes [34, 69]. It is reported that the processes of cold adaptation of energy metabolism and gas exchange at the tissues of fish accompanied by an increase of production of reactive oxygen species that can act as a physiological regulator of mitochondrial biogenesis, but are a direct threat to damage biological structures of the cell [69]. Published studies show that fish cold-stimulated increased prooxidant potential is proportional to the increase in enzyme activity of aerobic metabolic reactions in mitochondria and increased levels of polyunsaturated fatty acids in the lipid bilayer [32]. Significant contribution to the strengthening of production of reactive oxygen species in the fish in cold adaptation can contribute to family proteins uncoupling protein (uncoupling proteins), responsible for the stimulation of thermogenesis in adipocytes, but under the influence of cooling rates of the body of their expression increased in almost all tissues [102]. The authors give information about that in *Danio rerio* as the temperature of the environment recorded increased activity of antioxidant defense enzymes (superoxide dismutase, glutathione peroxidase) in skeletal muscle. However, specific and tissue-specific expression of particular components of an enzymatic level to strengthen the system antioxidant antiperoxide protection in response to cold stimulus in fish requires further study. On the other hand, the observed number of cases in the neutral dynamics of the activity of this group of enzymes may be due to a significant contribution of low molecular weight antioxidants (glutathione, vitamin E, ascorbic acid, ubiquinone) in the process of neutralization of reactive oxygen species [32, 102].

Along with the above facts, we believe it is appropriate to recall some features of the antioxidant defense system of fish, the important role that is assigned a specific carotenoid astaxanthin enough [72]. Astaxanthin is present in the body of aquatic organisms—phytoplankton, aquatic invertebrates and fish, but is virtually absent in terrestrial vertebrates. Astaxanthin, as well as alpha-tocopherol, effectively interrupts the chain reaction of lipid peroxidation in the lipid phase [3], induced by reactive oxygen [91] and nitrogen [39]. Antioxidant properties of astaxanthin are significantly higher than that of alpha-tocopherol and beta-carotene [107]. In addition, it is known that in fish, metabolic pathways and accumulation of astaxanthin are working closely with the metabolism of unsaturated fatty acids [3, 82]. However, the role of specific carotenoids in cold adaptation of fish requires a better understanding.

It is also necessary to point out that in modern studies of the adaptation of fish to changes of the thermal regime the considerable attention is paid to the mechanisms of genetic control of metabolic adjustment [29, 69, 71, 99]. On the one hand, this mechanism is under the control of systemic humoral regulators of cell metabolic reactions, such as corticosteroids [41]. On the other hand, at the cellular and subcellular level is a delicate coordination of expression of the genome of the nucleus and mitochondria [34, 69]. It is notable that the representatives of the various fish populations of one species from habitats that are located at different latitudes have quite distinct tissue-specific differences in adaptation processes of respiration to temperature changes [21]. The presence of such a complex multilevel process control of tissue-specific transcription allows for the restructuring of metabolism in fish in strict accordance with the dynamics of temperature [41, 71, 106].

### *Changes in Temperature as a Stressor*

It should be noted that the findings of an in-depth analysis of molecular and cellular mechanisms of adaptation of fish to changes in ambient temperature, are consistent with the established system of traditional concepts of stress effects on the fish body temperature drops [41, 102]. Basic principles of the reaction of fish to stressful environmental factors, including temperature changes, are detailed in the literature [2, 109]. Published data for more detailed studies have shown that even brief exposure to cold causes quite distinct behavioral responses of fish [105], while more prolonged exposure triggers the sequence of organ-adaptive reactions aimed not only to optimize the fundamental metabolic processes but also the restructuring of the structural and functional parameters of tissue [62] and increased antiperoxide protection of the body [102]. At the same coordinate body's reaction to the cold is not only in accordance with the absolute values of temperature reduction, but also takes into account the rate of cooling of the environment [105]. It is known that the abrupt cooling of the body can cause changes of system parameters of the ion balance, leading to gross violations of the metabolism of excitable tissues and locomotor activity [47]. In vertebrates, including fish, the primary humoral regulator of metabolism in response to the stress effect are glucocorticoids [90]. Meanwhile, in the body of teleosts glucocorticoids, cortisol and deoxicorticosterone (in elasmobranch fish—1-hydroxycorticosterone) combine the properties of the mineralocorticoid [96]. The physiological mechanisms by which glucocorticoids implement their anti-stress effects in fish fairly universal, regardless of the nature of the stress factor, however, showing some differences of peak values of glucocorticoids in response to the stresses reach their maximum in representatives of teleosts [2]. The review identifies several basic effects that accompany the release of glucocorticoids associated with changes in system parameters, ionic balance and metabolic rate, and hematologic effects, recorded on the background of increasing levels of heat-shock or stress proteins (HSPs). A number of review papers indicated the role of corticosteroids in the regulation of reproductive cycles of fish [74, 109].

The results of recent research show that shift of the thermal regime in the rate of secretion of glucocorticoids may determine the intensity of the endogenous production of sex steroids in the early stages of ontogenesis of fish by controlling the formation and the final formation of gender, regardless of the status of an genetically determined individual [37].

As already noted, the direct damaging effects of cold on fish tissue can be achieved through stimulation of lipid peroxidation [102]. In turn, the reaction to the thermally induced damage is to increase the secretion of a number of pleiotropic cytokines, including hypoxia inducible factor hypoxia inducible factor (HIF-1). Recall that the level of expression of HIF-intraorganic 1alpha and HIF-2alfa depends not only on the values of oxygen tension, but can also stimulation angiotensin-II and $Ca^{2+}$ to cobalt [35]. In addition, a molecule of nitric oxide can inhibit prolyl 4-way hydroxylase metabolic clearance HIF-1alpha, contributing to the increase of its concentration. Activation of HIF-1alpha synthesis and HIF-2alfa, aimed at adapting to the damaged tissue oxygen deficit: optimizing the metabolic processes by mobilizing the anaerobic glycolytic path and the stimulation of tissue glucose uptake, the restoration of tissue oxygenation due to the activation angiopoesis, erythropoesis and iron metabolism. On the one hand, increased production HIF in fish, with a decrease in ambient temperature can be regarded as a consequence of lack of oxygen in tissues, since cold adaptation may be associated with pronounced changes in the parameters of systemic and hemodynamic intraorganic [34, 105], remodeling of the branchial apparatus [93, 104] and, in some cases, the compensatory increase in gas exchange function of hemoglobin [51, 78]. However, the literature suggests that the stimulation of HIF in fish is under the direct influence of temperature on the background of normoxia [86].

It is known that HIF stimulates the secretion of cytokines involved in cell cycle regulation, controlling apoptosis, cell proliferation, as well as the mechanisms of cell-cell and cell-matrix interactions. In general, stressing the important role of HIF in the process of adaptation of tissues to oxygen deprivation, it should be emphasized that, firstly, the positive influence HIF depends on the duration of hypoxia, and secondly, along with a stimulating effect on HIF production of cytokines with distinct cytoprotective properties, HIF can increase the rate of production of TGF-beta1, pleiotropic cytokine that has immunomodulatory and prosclerotic effects. The relevance of these facts in terms of adaptation of fish to lower the ambient temperature is confirmed by studies that induction of hypoxia inducible factor in fish can be carried out as in hypoxic conditions, and as a result of exposure to low temperatures [86].

Based on the facts, we can assume that mechanisms of adaptive adjustment of energy metabolism in fish in response to cold stimulus include two opposing but complementary vector. First, the increase in mitochondrial respiration and strengthening processes. Second, HIF-dependent stimulation of anaerobic glycolysis. This duality of cold-induced restructuring of the energy exchange is fixed in an earlier review publications [34].

It should be noted that the realization of the fish HIF-induced genetic program are somewhat different than in mammals [28]. However, the phenomenon of cold stimulation of angiogenesis in fish has been confirmed experimentally [40]. Therefore, since cooling of the body induces damage to the fish of biologically important macromolecules, cells and tissues, the stimulation of angiogenesis, most likely, it is permissible to consider as one of the basic elements of reparation mechanisms of initiation. It is now known that implementation of these processes are due to HIF-1alpha, which stimulates the production of a series of cytokines that have cytoprotective properties that contribute to the regeneration of damaged areas of tissue and blood vessels [76], thus ensuring the replenishment of lost cells and pool restoration of organ function [112].

Also, the literature contains information about the role of the family of regulatory proteins heat shock proteins (HSP), in the process of adaptation of fish to changes in temperature. However, most authors rightly emphasize the importance of HSP in the adaptive response of fish in response to temperature increase habitat [67, 99]. At the same time, there are some reports devoted to studying the role of HSP in the adaptive reactions of fish in response to lower water temperatures [80]. In particular, the authors of the cited publications indicate that the fish cytoprotective properties of HSP when the temperature is largely implemented through synergism HSP, corticosteroids and HIF, perhaps via HSP90. While stressing that HSP70 has the ability to inhibition of apoptosis, while noting some differences in the dynamics of expression of HSP bodies of fish and higher vertebrates.

Along with the already mentioned humoral mediators of the stress response of fish to changes in temperature, in the modern literature an important place molecule nitric oxide and thyroid hormone [69]. Note that the role of nitric oxide (NO) in regulation of physiological functions of fish has been insufficiently studied. On the one hand, the number of publications devoted to this problem is relatively small. However, the fundamental nature of the research [10, 43, 101, 110] goes beyond the interests of ichthyology, ecology and aquaculture water biocenosis science. However, the literature contains some publications devoted to analyzing the role of nitric oxide in the regulation of reproductive functions of fish [98, 101]. It is reported that the concentrations of chemically stable metabolites of NO in the ovarian tissue of fish reach a maximum in the phase previtellogenesis, however, sharply declining phase of vitellogenesis, indicating the important role of NO in the control of reproductive functions of fish, as well as the promise of dynamic analysis of NO metabolites as an indicator state of oogenesis in fish [101]. In our opinion, the value of research in the fact that in addition to information about the dynamics of NO-synthase expression in different stages of the reproductive cycle of fish, the authors present the results of analysis of changes intraorganic and system-level products of oxidation of NO—endogenous nitrite and nitrate, which are the main substrate (nitrate) reductase loop cycle of nitric oxide [85]. Meanwhile, it was found that NO and physiologically active products of oxidation play an important role in the adaptation of fish to oxygen deficiency [36, 43, 77].

It is known that, on the one hand, nitrites have cytoprotective properties and perform an important function in the process of adaptation of organ and tissue damage by blocking the mechanisms of apoptosis, reducing the severity of reperfusion injury of tissue, speeding up the normalization of metabolic processes in cells of damaged areas of the body, as well as contributing to restoration of hemodynamic intraorganic [26, 100]. We consider the ability of NO and its metabolites activate angiogenesis [54], reducing prosclerotic [44, 88] and proinflammatory [87] potential within the damaged tissue. Also attracted the attention of information on the mechanisms of interaction of NO and HIF-1alpha, perform an important function in the reconstruction of the metabolic processes of cells in response to injury [25]. According to the authors of the cited publications, tissue damage leads to increased expression and enzymatic activity of inducible NO-synthase and increased secretion of HIF-1alpha. The reduced metabolic clearance of the molecule HIF-1alpha, is largely determined by increasing the secretion of NO.

On the other hand, the literature discusses the nature of the effect of nitrite anions state of peroxidation processes [15, 100], since the rapid growth of intraorganic production of nitric oxide and its metabolites may be accompanied by the formation of cytotoxic products that cause serious violations gas exchange function of red blood cells, to stimulate their hemolysis [11, 12, 103].

Analyzing the possible role of iodothyronines in the adaptation of fish to lower temperatures, in our opinion, it is appropriate to recall that thyroid hormones do not only help to accelerate reparative processes such highly specialized cells, like neurons and cardiomyocytes, but also stimulate revascularization of damaged areas of tissue [95]. Emphasis is placed on evidence that thyroid hormones are closely involved in the regulation of cell cycle [63], the processes of regeneration of damaged tissues [4], neoangiogenesis [64]. It was established that iodothyronines can influence the course of reparative processes in stem cell mobilization by regulating the processes of division and differentiation [4, 33]. Participation of iodothyronines in reparation processes due to their direct influence on the genome of the cells [55], at the same time, tissue-specific mechanisms occurring tissue repair are likely to control the levels of expression of nuclear receptors for thyroid hormones [8, 50, 53] and indicators of the activity of certain isoforms intraorganic deiodinases [95]. Thus, the mechanisms of cell cycle control thyroid hormone may be associated with the effects of HIF-1 and do not depend on the oxygen regime in the tissues [64, 73].

In our opinion, the relevance of studying the role of thyroid hormones in the temperature adaptation of fish is of interest also because the literature reports of severe organ-specific expression of the dynamics deiodinases during metamorphosis taking place in the early stages of ontogenesis of fish, when the rate of change of environmental conditions of the environment are fast [13, 65].

### *Effect of Temperature on the Reproductive Function of Fish*

The effect of water temperature on the timing of maturation of gametes in fish is well known. This phenomenon is widely used in practical fisheries and ichthyological research. The mechanisms responsible for its implementation have important scientific and practical value, so are constantly in the center of attention [5, 16, 18, 68, 108]. Finding ways to optimize the temperature control process stages of artificial reproduction of fish is one of the most popular areas of research activities that seek the obvious practical results. Even an incomplete list of achievements in this field includs: the increase of the efficiency of use of expensive pituitary preparations to stimulate the producers of fish [19, 20] to achieve viability and increase the rate of growth of marketable products of the most valuable aquaculture [1, 48, 59, 60]; increase the effectiveness of the procedure and stimulate producers to improve the quality of the gametes [66, 83] to develop the optimum temperature regimes for transgenic downhole lines of valuable fish species [57].

In studies, the effect of temperature on the reproductive sphere of fish may be due to the high sensitivity to cold and thermal effects of the specialized neurons localized in the brain and in the pituitary gland [68]. It was shown that under conditions of acute cooling of the body parts of the fish central nervous system responsible for thermoreception one can record changes in thermal regime due to changes in the parameters of cerebral blood flow induced by cold stimulus [105]. Previously, it was found that increasing the temperature of the water content increases followed by gonadotropins in the pituitary tissue but not in the systemic circulation fish [5]. In the literature there is direct evidence for the important role of photoperiod in the regulation of the reproductive cycle of fish [14, 70]. However, the published experimental evidence of direct stimulatory effect of optimum spawning temperatures at rates of transcription of gonadotropin-releasing hormone, follicle-stimulating hormone and luteinizing hormone in the hypothalamic-pituitary axis of fish, other things being equal, the environment [16].

It was previously shown that freshwater cyprinid fishes in the middle latitudes, the stimulation of oocyte maturation begins when water temperatures reach a certain threshold, significantly ahead of the peak values of gonadotropin secretion [5]. The presence of thresholds in the stimulating effect of temperature on gonadal maturation in teleost fish has been confirmed by further studies [70]. Furthermore, the authors of cited publications have reported that excess optimum temperature during spawning causes a decrease in the values of gonad-somatic index, against the background of increased secretion of gonadotropins and sex steroids. We can not exclude that, in connection with the search for unrecorded factors that could significantly complement our understanding of the influence of temperature on the sexual cycle of fish, it would be to analyze the results of studies that indicate a possible physiological and pathophysiological role of cytokines superfamily of transforming growth factor-beta (TGF-beta) in managing fish oocyte maturation. In the literature, individual data are presented of experimental studies of gonadotropic effects in fish TGF-beta [52] and morphogenesis of bone proteins—BMP [7]. Cytokines of the group carried out an intracellular signal transduction via the Smad-proteins. In teleosts, as in mammals available in two subpopulations of receptors of TGF-beta—TβRI and TβRII [52]. The authors of the cited publications found that the influence of these cytokines on the inhibition of oogenesis is determined by the stimulatory effect of gonadotropin and MIH—17α, 20β—dihydroxyprogesteron—DHP, the main sex steroid ovarian maturation-inducing fish eggs [52].

Note that temperature is a natural regulator of estrogen receptor expression in hepatocytes of fish [108]. This fact is directly related to the problem, since actively occurring processes of biosynthesis in the liver, an important condition for the normal maturation of the fish eggs [22, 56].

### *The Role of Temperature in the Early Stages of Fish Ontogeny*

Maintaining the optimum range of abiotic environmental factors is essential for normal fish development [17, 27, 37, 48, 84]. This line of research is of great practical importance because, first, to predict the reproduction of aquatic bioresources depending on the fluctuations of climatic factors. In particular, fluctuations in water temperature are considered as one of the main conditions determining the rate of growth of the fish and the mortality of young fish in natural ecosystems [48, 84]. Second, high-intensity techniques used in modern aquaculture can provide optimal conditions for breeding and rearing of fish, however, the methods of biotechnology of fish introduced into practice, in some cases, also require more in-depth analysis of the physiological mechanisms of the effect of thermal regime on growth and larval development of the oil field lines farmed aquaculture securities [48, 23, 57]. Some studies have reported that moderate cooling of the water, relative to optimum temperature during incubation of salmon can continue to provide a stimulating effect on the growth of muscle activity and foraging in juvenile fish [1, 48]. The authors suggested that the observed effect is of considerable interest to modern fisheries, because it allows to improve the quality and the amount of received marketable products. The literature discusses the possible species-specific mechanisms for the implementation of the observed effect and its practical significance for aquaculture [1, 59–61]. In contrast, the increase in water temperature during incubation salmon leads to anomalies of the heart, mediated by inadequate stimulation of the secretion of atrial natriuretic peptide (ANP) [97]. Meanwhile, the imbalance of the secretion of proteins of the family of natriuretic peptides, in addition to violations of the organogenesis of the cardiovascular system, may affect the status of water-salt homeostasis of fish [45, 46]. Since the early stages of postembryonic development of the ANP has an important function in maintaining the balance of salt and fluid in the body of larvae and juvenile fish [42].

At the same time, the nature of the influence of ambient temperature on the ontogeny of fish is the actual direction of the basic biology research [45, 48, 75, 111]. In a number of review publications [48] a fairly deep analysis of the influence of abiotic environmental factors was presented, including temperature, the timing and intensity of the processes of maturation and development of skeletal muscle in fish, taking into account known factors regulating miogenesis.

## CONCLUSIONS

Thus, the study of physiological and pathophysiological mechanisms of the effect of ambient temperature on metabolic processes of fish is a topical area of research.

Firstly, in our opinion, it should be noted that the published results cited in this review are the theoretical foundation of technology to improve reproduction and growth of cultivated species.

Second, it analyzed the problem of interest for fundamental biological science. Their theoretical value in the fact that the study of the restructuring of energy metabolism of fish in cold conditions, system performance analysis thermoreception and thermoregulation, as well as changes in particularly intraorganic blood flow during hibernation of fish allow us to estimate the evolutionary aspects of thermoregulation thermoadaptation and vertebrates.

However, at first glance, private matter humoral control of metabolic adaptation in fish under the influence of low temperatures, affect the very important aspects of the comparative physiology of regulatory effects of biologically active substances, as well as guidelines for their interaction.

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