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Physiological and biochemical basis of salmon young fishes migratory behavior

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ABSTRACT

The review presents data on structural changes, physiological and biochemical reactions occurring at salmon young fishes during smoltification. It is shown, that young salmon fishes located in fresh water, in the process of smoltification undergo a complex of structural, physiological and biochemical changes directed on preparation of the organism for living in the sea. These changes cause stress reaction which excites young fishes to migrate down the river towards the sea. Measures to improve reproduction of young salmon fishes at fish farms are offered.

1. Introduction

Initial stages of salmonid fishes development are carried out in freshwater. At the first stage young fishes form structures and systems connected with ability to live in freshwater. At the second stage a complex of structural, physiological and biochemical changes directed on preparation of the organism for downstream migration and seawater entry takes place[1]. After completion of smoltification under certain conditions young fishes migrate downstream the river towards the sea. The cause of migratory state occurrence and conditions of young salmonid fishes migration downstream the river towards the sea remain obscure.

The purpose of this work is to find out probable cause for occurrence of the migratory condition stimulating young fishes to roll downstream the river towards the sea based on comparative analysis of structural, physiological and biochemical processes occurring during smoltification. Solving this task has important theoretical value and plays an important role in optimization of measures to improve reproduction of valuable salmonid fishes in industrial conditions at fish farms.

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2. Structural, physiological and biochemical transformations at the young salmonid fishes during smoltification

During smoltification organism of the young salmonid fishes undergoes two groups of processes. The first group is connected with processes determined by preparation of young fishes to the sea mode of life (Figure 1, right part). The second group testifies that during smoltification the stress reaction (Figure 1, left part) is realized.

2.1. The processes connected with preparation of young salmonid fishes to the sea life

During smoltification hypertrophy and hyperplasia of hypophysis somatotropic cells occurs resulted in increased excretion of growth hormone[1-4] leading to rising of its concentration in blood[1,5-8]. The growth hormone form parameters allowing smolts to survive in the seawater[3-6,9,10]. It is shown[11] that the hypophysectomized young coho salmon and young chinook survive in freshwater but die in seawater. However, if fishes with the removed hypophysis are injected with growth hormone period of their survival in seawater elongates.

During the period of smoltification tirotropotsity adenohypophysis activate leading to amplified inflow of thyritropic hormone in

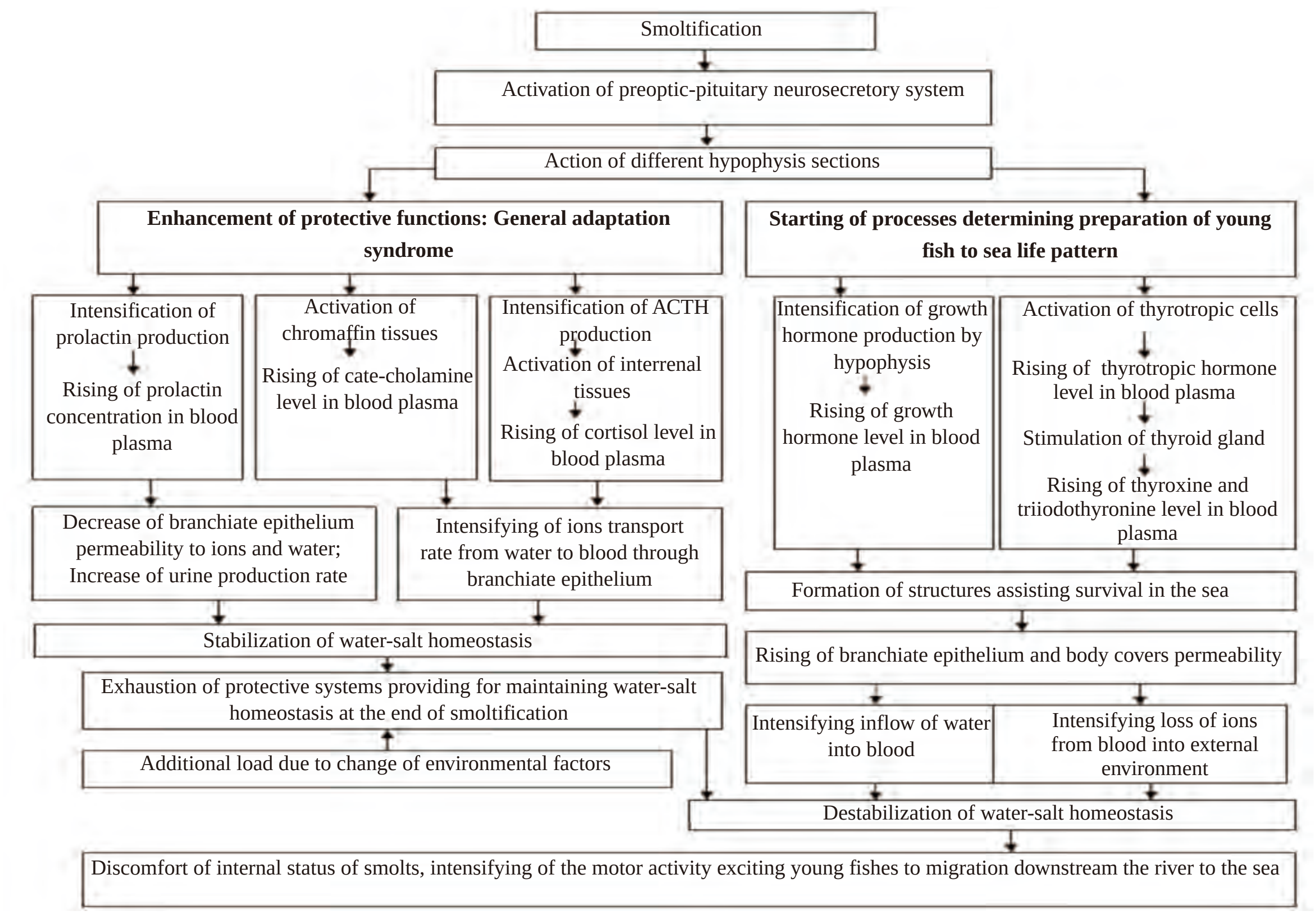

Figure 1. Schematic diagram of the conjugated processes related to the general adaptation syndrome (left part) and structures facilitating survival of young fishes in the sea (right part) during smoltification.
ACTH: Adrenocorticotrophic hormone.

blood. This hormone stimulates thyroid gland, stimulating release of triiodothyronine and thyroxine in blood[1,8,12-14]. Activities of thyroid gland hormones are associated with various morphological, behavioral and physiological changes, preparing salmons for life in seawater[15]. Intensifying of salinous water preference by smolts match with rise of thyroxine in fishes blood[16,17]. Increase of thyroid hormone level in blood of Pacific salmons results in preference of salinous water and its reduction – in preference of freshwater[18,19].

Salmonid fishes with evident dysfunction of thyroid gland are not capable to grow in seawater, and placements of pre-smolts in sea water leads to growth inhibition and even death of fishes[10,17]. Additionally, to the mentioned functions, hormones of thyroid gland stimulate mobilization of lipids, enhance synthesis of proteins, influence vitamin and carbohydrate metabolism[20,21], as well as control olfactory imprinting during downstream migration[22,23]. Thyroid gland of euryhaline fish *Fundulus heteroclitus* L. participates in maintenance of water-salt homeostasis during adaptation to seawater[24]. Inhibition of thyroid gland of the individuals of this species acclimated to freshwater, does not affect their vitality and regulation of osmotic and ion exchange whereas in seawater fishes die within 3 weeks. Meanwhile, rising of osmotic pressure and concentration of sodium occur in blood serum. It is recorded[15] that effects of thyroid gland hormones and growth hormone to the big extent complement each other.

During the period of salmons smoltification structural changes are registered in intercellular contacts and chloride cells of gill apparatus[25,26], rising of succinate dehydrogenase ferments[2,27] and Na^+-K^+-ATPase[4,9,12,13,27-30] activity in gills. The number, size and activity of chloride cells in the gills increase in smolts in freshwater[26]. The chloride cells of smolts in freshwater are more similar to those of seawater fish than to those of freshwater salmon. During smoltification, the intestine, as well as the other osmoregulatory tissues, will pre-adapt for a life in seawater, while the fish are still in freshwater[31]. The absorptive form of the Na^+-K^+-2Cl^- cotransporter-like isoform (subapically located Na^+-K^+-2Cl^- and/or Na^+, Cl^- co-transporter) of intestinal increased during smoltification and further after seawater transfer[32]. It is observed that kidneys of smolt rearrange to the sea type of regulation[33-36]. *Salmo salar* exhibited sufficient hypo-osmoregulatory capacity at the initiation of downstream migration[37]. It is shown that when smolts are moved from freshwater to seawater, they survive in it[2,38-40].

It is shown that in blood serum, liver, intestines, red and white muscles of parr content of polyunsaturated fats is relatively low, and content of linoleic acid is high that is typical of freshwater fishes[41]. During smoltification concentration of polyunsaturated fats with lengthy chain increases in these tissues that is typical for marine fishes.

The given data show that as a result of smoltification young salmonid fishes being in freshwater form structures and systems necessary for survival of smolts in seawater. However, formation of structures and systems necessary for sea mode of life during smoltification is accompanied by negative consequences connected with increase of body covers and branchiate epithelium permeability to water and ions. It is known[42], that euryhaline species in freshwater have low permeability of body covers and gills to ions and water, while with moving fishes to seawater permeability sharply grows. Increase of excreted urine amount during smoltification[43] testifies intensifying of water penetration into the organism. This can be connected with rising permeability of body covers and gills to water. It is registered that losses of ions of sodium and chloride from smolts blood to environment dominate[44-46], what points at increase of branchiate epithelium and body covers permeability to these ions. In order to confront these consequences unfavorable for the organism, functions connected with general adaptation syndrome strengthen during smoltification (Figure 1, the left part).

2.2. Realization of stress reaction of young salmonid fishes during smoltification

During smoltification activity of preoptic-pituitary neurosecretory system intensify[47,48], therefore, concentration of adrenocorticotrophic hormone in blood plasma increases. This hormone stimulates interrenal cells[4,47,49], stimulating release of corticosteroid hormones in blood. Therefore, during smoltification concentration of cortisol, mainly, in blood plasma essentially grows[8,13,28,50-56].

This hormone affects various aspects of vital activity of the organism. Its role in regulation of water-salt exchange is acknowledged[57-59]. Removal of freshwater fishes’ interrenal gland causes slowing down of sodium uptake from external environment into the organism. It is accompanied by fall of salts level in fishes’ blood. Injections of cortisol in low doses cause intensifying of sodium uptake from freshwater, resulting to recovery of its level in fishes’ blood. Consequently, corticosteroids have an effect on fishes adapting to freshwater, as the factor intensifying active transport of sodium from external environment. Therefore, increase of the level of these hormones during smoltification alongside with other functions is directed on maintaining ionic homeostasis by means of the increase of sodium absorption from external environment.

During smoltification concentration of catecholamines in blood plasma rises[60,61]. These hormones are responsible for various functions including regulation of ion exchange between the organism and environment. Adrenalin enhances uptake of sodium by gill[62,63] and prevents desalination of the fish organism adapted to freshwater. Consequently, catecholamines, as well as corticosteroids, compensate unfavorable consequences of increased permeability by means of intensifying the rate of ions transport from water through gills.

It is shown[2] that during smoltification activity of hypophysis cells intensifies, resulting in rising of prolactin level in blood plasma[8]. In teleost fishes, prolactin was identified as the “freshwater-adapting hormone”, promoting ion-conserving and water-secreting processes by acting on the gill, kidney, gut and urinary bladder[64]. Removing hypophysis of freshwater fishes causes essential increase of sodium ions and chloride efflux from the organism leading to sharp drop of osmotic pressure and concentration of electrolytes in blood[65-67]. Injection of repetitive doses of prolactin into hypophysectomized animals facilitates recovery of salts level. It is shown that ionic disbalance induced by hypophysectomy is conditioned by increase of electrolytes efflux from organism whereas their absorption remained at the former level. It is concluded[59,68,69] that corrective effect of prolactin is directed on reduction of permeability of body covers and gills to ions. Prolactin facilitates excretion of water from the organism by means of intensifying diuresis[59]. It is shown[65] that prolactin stimulates secretion of slime by mucous cells of branchiate epithelium and body covers. Slime is considered to be a protective factor reducing permeability of branchiate epithelium and body covers for ions and water.

Other data show, that prolactin controls permeability of cellular membranes. It is known, that calcium carries out important role in maintaining functional integrity of membranes through reducing their permeability to sodium and chloride ions[70]. Reduction of calcium concentration in water is accompanied by increasing activity of prolactin-synthesizing cells of hypophysis. On the contrary, adding calcium to water provokes reverse reaction[71]. Survival of hypophysectomized bulltrout *Salmo trutta* L. in freshwater was prolonged either by injections of prolactin or by increasing content of calcium in environment approximately up to 5 mmol/L[72]. It can be concluded that calcium in environment and prolactin in the organism substitute each other in the process of regulating permeability of branchiate epithelium and body covers to sodium ions. Based on physiological role of prolactin, it is possible to conclude that intensifying secretion of this hormone during smoltification is directed on stabilization of water-salt exchange by means of reducing permeability of branchiate epithelium and body covers to ions as well as increasing the speed of diuresis.

Thus, morphological, structural, physiological and biochemical reconstruction connected with preparation of young fishes to living in the seawater (Figure 1, right part), which takes place during smoltification, causes rising of branchiate epithelium and body covers permeability to water and salts in the organism of smolts. In its turn, it facilitates, on the one hand, water influx, on the other hand, intensifying leakage of sodium and chloride ions from the smolts organism. Confronting these harmful consequences is implemented by means of intensifying protective mechanisms of the general adaptation syndrome (Figure 1, the left part) which are directed on decreasing permeability of branchiate epithelium and body covers to water and ions, increase of dieresis speed and intensive transport of sodium from water.

Augmentation of tension in the organism during smoltification is happening gradually due to slow formation of structures and systems of the sea type. Because of this permeability of body covers and gills to water and ions also rises gradually. Protective mechanisms connected with the neuroendocrinal system (Figure 1, left part) during initial period of smoltification compensate not only damaging consequences provoked by rising of permeability but also function in abundance creating a certain “resistance reserve” in the organism. There is certain data testifying it. During smoltification, especially at an early stage, it is registered that locomotor ability of young fishes to stand against water flow[73] increases and speed of loosing sodium ions from the organism decreases[74].

During progressing of smoltification the load level gradually strengthens due to further continuation of structural reconstruction connected with preparation of fishes to sea life. Simultaneously, activity of compensatory systems increases in order to neutralize permeability gradually growing during smoltification. It is proven by the following fact. It is shown[28], that concentration of cortisol in blood plasma of smolts during smoltification gradually rises up to maximum values. By the end of smoltification structural changes complete, and permeability of body covers and gills reaches its maximum value, characteristic for marine fishes. In this situation compensatory systems connected with general adaptation syndrome are forced to function in intensive regime which cannot continue for a very long time. In due course there comes a moment when protective functions of the organism exhaust (“exhaustion stage” according to Selye[75]), they are not able to completely compensate unfavorable processes caused by hyperpermeability of body covers and gills. Exhaustion stage of freshwater spawners is observed straight after spawning[76] and demonstrates similar damaging as of smolts.

Exhaustion is accompanied by decrease in resistance of smolts organism to other factors and loads. It is shown that in comparison with parr, smolts are more susceptible and less resistant against effect of unfavorable factors[51,77-82]. Smolts reveal fall of locomotor opportunities[73,83,84]. It has been registered that before the beginning and during migration downstream smolts' protective systems ability to keep concentration of chloride[85] and sodium[2,33,36,45,86] in blood plasma and body tissues[87,88] deteriorate at stably raised levels. Decrease of the content of these ions in blood and tissues of smolts correlated with predominance of their losses into environment[44-46,89].

These facts form the basis for the theory of "demineralization". It has been assumed that a way out of such condition for smolts can be only migration[88,90,91]. Series of studies[92-94] have been devoted to substantiation of this assumption. However, this point of view is criticized because falling of electrolytes levels in blood plasma and tissues of smolts does not always reveal.

In some cases proved decrease of salts in the blood of smolts has not found[38,39,82,95,96], and in other studies even rising has been observed[27,97]. Chernitskii[98] has observed various scenarios of changes in concentration of sodium in blood serum of Atlantic salmon smolts: rising of young fishes in the river of Salaca, the tendency to decrease of young fishes in the river of Keret, absence of changes of fishes in the rivers of Luvenga and Ligma. It turned out that identical for all groups is increasing variability of the given parameter. Such various reactions are connected with differences in environmental factors.

3. Influence of external factors on physiological and migratory condition of young salmonid fishes

Action of external factors reveals in two ways. Favourable conditions which improve physiological state of smolts, slow down or even completely terminate migration of young fishes downstream the river. Unfavorable factors creating additional load on physiological processes of smolts enhance migration of young fishes downstream the river. This is testified by the data received by several researchers.

During smoltification fatty[77] and carbohydrate[49] exchanges increase. As a result, sharp decrease in quantity of muscle fat[4,99], glycogen[100] and liver fat[2,4,77], coefficient of fatness and liver index of smolts is observed[101]. It is discovered[99] that migration of young fishes occurs at sharp decrease in muscle fatness of up to 2.6%. Under good feeding conditions ensuring maintaining of muscle fat at higher than 2.6% migration does not occur. The proportion of *Salmo salar* that reached Lake Vänern was significantly greater for fish fed fat-reduced feed than for fish given rations with higher fat content[102]. Also, successful migrants had a lower condition factor than unsuccessful ones[102,103].

It is shown[104], that augmentation of young salmonid fishes population in the river leads to deterioration of nutritional conditions and intensifying of migration. Reduction of density improves food consumption and weakens migration. These data show that at deficit of nutrition protective systems of smolts (Figure 1, the left part) are quickly being exhausted facilitating migration. At excess of nutrition resources the energy is sufficient to maintain adaptable reactions. As the result of it migration is being delayed. It is recorded[105] that among young salmonid fishes there is a significant part of smolts (up to 21%) not migrating down the river. These results can be explained as follows: not migrating fishes do not reach the depletion stage of their adaptable resources what allows them to remain in the river. In this perspective there is very interesting data regarding cultivation of salmon in a lake with excessive quantity of feed [106]. Young fishes reached migratory condition in the age of 13–14 months, however, they did not migrate down from the lake. During further cultivation in the lake fishes maintained silvery colour. At the age of 3+ maturation of males began and at 5+ of females.

Analysis of the data shows that migratory condition of smolts reveals when depletion of energy resources reaches the critical level. As a result, deficiency of energy required for functioning of smolts' physiological systems in strained regime arises. In such situation adaptable functions in due course exhaust and lose ability to keep vital parameters of water-salt homeostasis at stable levels. Such situation causes internal discomfort which results in raised motor activity of smolts stimulating them to migrate. Unfavorable external environmental conditions represent additional load on adaptable functions of smolts' organism. This accelerates reaching depletion of compensatory systems enhancing migration of young fishes. Improvement of environmental conditions leading to decrease of the load on protective functions of the organism weakens or even stops migration of young fishes. Migration of young salmons downstream the river is predetermined by excessive intensity of active processes in the organism back-grounded by energy deficiency. In such situation migration of smolts upstream the river demanding additional energy and physical efforts is doomed to be a failure.

Due to different reasons productivity of some commercially valuable species of salmonid fishes is dropping. Attempts are being made to correct this situation by means of cultivating young fishes at fish farms. In such conditions smolts do not realize migration downstream the river. Therefore young fishes are delivered to stations near the river mouth. This method does not allow to "imprint" the migratory route. Therefore return of mature salmons from to sea home does not exist. Return of mature fishes is observed in case smolts realize natural migration in which memorizing of migratory routes takes place. We believe that the basic drawback in the technological process of salmonid fishes reproduction is maintaining optimal conditions at the end of smoltification process. Such situation leads to decrease of load on physiological systems preventing reaching of maximum tension and initiation of migratory impulse. In our opinion, in order to achieve maximum stress and induce migratory impulse it is necessary to stop feeding young fishes at the end of smoltification process so that deficiency of energy is reached. For initiation of spontaneous migration it is necessary to increase load on physiological systems through deterioration of environmental conditions.

4. Conclusions

Analysis of the data has shown that during smoltification processes causing preparation of young fishes for the sea mode of life (Figure 1, right part) are put into effect. As a result of various structural changes permeability of body covers and gills to water and salts rises, facilitating watering and desalting of the organism. With the purpose of neutralizing damaging effects during smoltification protective mechanisms connected with the general adaptation syndrome (Figure 1, the left part) are activated. In the beginning of establishment the sea type structure invoke insignificant damaging consequences. Strengthening protective systems compensate unfavorable consequences facilitating resistance of the organism (stage of resistance according to Selye[75]). Along with developing of smoltification process and further formation of the sea type structures degree of increasing permeability of body covers and gills also rises. Parallel to this activity of compensatory systems increases with the purpose of neutralization of growing negative effects. By the end of smoltification structural changes finalize being accompanied by reaching maximum rising of permeability of body covers and gills. In due course there comes the moment of achieving energy deficiency and depletion of protective functions of the smolts' organism (stage of exhaustion according to Selye[75]). Such situation invokes internal discomfort and raised motor activity in the organism of smolts exciting them to downstream migration.

Conflict of interest statement

I declare that I have no conflict of interest.

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