Journal of Coastal Life Medicine

journal homepage: www.jclmm.com

Original article doi: 10.12980/jclm.4.2016J5-244 ©2016 by the Journal of Coastal Life Medicine. All rights reserved.

Dynamics of the content of H_2O, Na, K, Ca and Mg in the eggs of bream, *Abramis brama* L. in natural conditions and under stress

Vladimir Ivanovich Martemyanov*

Papanin Institute for the Biology of Inland Waters, Russian Academy of Sciences, 152742 Borok, Yaroslavl Oblast, Russia

ARTICLE INFO

Article history:
Received 2 Dec 2015
Received in revised form 17 Dec 2015
Accepted 16 Feb 2016
Available online 6 Apr 2016

Keywords:
Bream, *Abramis brama*
Oocytes
Water
Sodium
Potassium
Calcium
Magnesium

ABSTRACT

Objective: To study the dynamics of H_2O, Na, K, Ca and Mg content in the oocytes of bream, *Abramis brama* observed in prespawning period on breeding ground and in reply to catching, transportation and subsequent remaining of spawners in a cage.

Methods: For research on the dynamics of H_2O and cations content in the oocytes of bream females, *Abramis brama* in the course of eggs transition from maturity Stage IV to Stage V, fishes were caught from breeding ground in the coastal zone of the Volga Reach of the Rybinsk reservoir at the Vereteya Station. For studying the influence of stress, the bream (76 individuals) were caught from breeding ground by hauling the seine during 15 min. Capture, sorting and transportation for 3 h to the ponds were the stress factors. Samples of oocytes from 6–8 fishes were taken immediately after capturing, then two more were taken during transportation. Later fishes were removed from the cage in certain time intervals. Concentration of Na and K in the dissolved samples of oocytes was measured by the spectrometer (Flapho-4, Carl Zeiss, Iena, Germany) and content of Ca and Mg was measured by atomic-absorption spectrometer-1 (the same producer).

Results: In natural conditions before spawning in the course of maturation of oocytes from maturity Stage IV to V, H_2O content in the ovicells of bream has increased by 3.3% and concentration of Na, K, Ca and Mg has decreased by 24.9%, 38.1%, 56.2% and 65.7%, accordingly. Stress caused by capturing, transportation and the subsequent remaining of bream spawners in a cage did not change parameters of water-salt exchange of the oocytes.

Conclusions: In natural conditions before spawning, the maturation of oocytes of bream from maturity Stage IV to V take place. Stress caused by capturing, transportation and the subsequent remaining of bream spawners in a cage prevents the transition of eggs from maturity Stage IV to V. It is suggested that in order to develop optimal technique stimulating oocytes maturation and the process of ovulation in industrial conditions, study of these reactions of spawners of one or another species in natural environment is preferentially conducted. Conditions of incubation and combination of hormonal preparations selected on the basis of these data should invoke similar effects as the ones spawners experience in natural habitat.

1. Introduction

Reproduction of many commercially valuable species of fishes due to a number of reasons has suffered an essential decrease. Due to this reason, they try to achieve the increase in population of this or that fishes species through receipt of young fishes in factory conditions and subsequently they are released into natural conditions. In this method, spawners as a rule are captured in nature, delivered to factories and kept in artificial conditions. It is shown that such procedures cause stress in fishes which is followed by changes in parameters of their neuroendocrine systems[1-8], carbohydrate[2-5,7-11], protein[12] and water-salt exchange[4,11,13-25]. In condition of stress, spawners' synthesis of gonadotropic hormone and sex steroid concentration of 17,20β-dihydroxy-4-pregnen-3-one decline reproductive function[6,26-31]. In captivity, spawners of many fish species can not make the transition from maturity Stage IV to V. To understand the reasons of this phenomenon, it is necessary to study the processes which fishes experience in prespawning period during maturing of reproductive products in natural environment on breeding ground and in reply to catching, transportation and keeping of spawners in artificial conditions.

This study presents the dynamics of H_2O, Na, K, Ca and Mg content in the oocytes of bream, *Abramis brama* studied in prespawning period on breeding ground and in reply to catching, transportation and the subsequent remaining of spawners in a cage.

*Corresponding author: Vladimir Ivanovich Martemyanov, Papanin Institute for the Biology of Inland Waters, Russian Academy of Sciences, 152742 Borok, Yaroslavl Oblast, Russia.
Tel: +79611565975
E-mail: martem@ibiw.yaroslavl.ru

Foundation Project: Supported by the budgetary state project: Studying of adaptations of organisms, populations, communities of aquatic organisms and modeling ecosystems to environmental factors (State Registration No. 01201351909).
The journal implements double-blind peer review practiced by specially invited international editorial board members.

2. Materials and methods

For research on dynamics of H_2O and cations content in the oocytes of bream females, *Abramis brama* in prespawning period, fishes were caught from breeding ground in the coastal zone of the Volga Reach of the Rybinsk Reservoir at the Vereteya Station. Data regarding roach was published earlier[32]. For studying the influence of stress, the bream [76 individuals; the weight of (1 162 ± 44) g] was caught from breeding ground in the Volga Reach of the Rybinsk Reservoir at the Vereteya Station by hauling the seine during 15 min. Capture, sorting and transportation for 3 h to the ponds of experimental base (Sunoga) of Institute of Biology of Internal Waters were stress factors. Such procedures were inevitably present in research work and aquaculture. Samples from not less than 6–8 fishes were taken immediately after capturing, then two more were taken during transportation. Later fishes were removed from the cage in certain time intervals. Fish bodies were placed in polyethylene packages and put in thermostatic boxes with ice. Cooled fish bodies were delivered to the laboratory where they were weighed and opened and a sample of oocytes weighing of 120–150 mg was taken from the middle part of the ovary. Samples of eggs were placed on the decalcified paper and weighed by the laboratory weigher (VLR-200) with the accuracy of 0.05 mg. Afterwards, samples were kept for about 1 week at room temperature. Then they were dried at 105 ˚C up to constant mass. Dried samples were placed in teflon cups with added 2 mL of the concentrated nitric acid and were evaporated on electric cooker up to carbonization. Afterwards, bidistilled water was added in teflon cup with the quantity necessary to delude the substance 500 times as calculated from the mass of crude tissue.

Concentration of Na and K in the dissolved samples was measured in air-propane flame by the spectrometer (Flapho-4, Carl Zeiss, Iena, Germany) and content of Ca and Mg (absorptive mode in air-acethylene flame) was measured by atomic-absorption spectrometer-1 (the same producer). The water content was calculated as the difference between wet and dry weights of eggs and were expressed in percent of total wet weight. In the oocytes, Na, K and Mg ions were dissolved in water, therefore, concentration of these cations was calculated as per 1 kg of water. Ca ions in caviar were connected with proteins[32]. Therefore, content of Ca in oocytes was calculated as per 1 kg of dry mass. The data were presented as means and errors of means. Accuracy of differences was evaluated with the help of Student's factor at significance level $P < 0.05$.

3. Results

In natural conditions, content of H_2O in the oocytes of female bream and roach spawners with ovary maturity Stage IV in prespawning period was regulated at certain stable levels (Table 1). Shortly before spawning, (24–72 h) content of H_2O in the oocytes of bream increased by 3.3% and by 3.4% in the oocytes of roach. In the course of maturation of oocytes from maturity Stage IV to V, concentration of Na, K, Ca, Mg in the ovicells of bream has decreased by 24.9%, 38.1%, 56.2% and 65.7%, accordingly. At transition to maturity Stage V, content of Na in the oocytes of roach increased by 44.6%, whereas levels of K, Ca and Mg did not change.

Stress caused by capturing, transportation and the subsequent remaining of bream spawners in a cage did not change parameters of water-salt exchange of the oocytes, preventing their transition from maturity Stage IV to V (Figure 1).

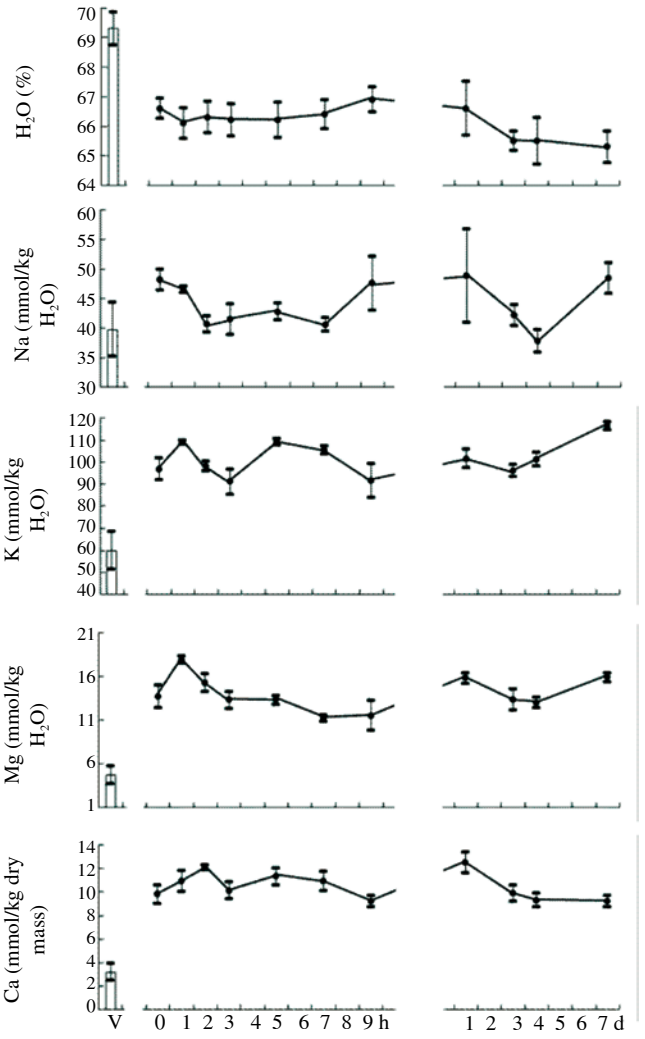

Figure 1. Dynamics of H_2O, Na, K, Ca and Mg content in the eggs of bream at maturity Stage IV in reply to catching, transportation and subsequent holding of spawners in a cage.

4. Discussion

It is stated that degree of oocytes watering before ovulation of the fishes spawning caviar in fresh and saltish water is at a lower level than of those spawning in the sea environment[33]. Shortly before spawning, content of water in the oocytes of bream increased by 3.3% and by 3.4% in the oocytes of roach. Concentration of

Table 1

Dynamics of H_2O, Na, K, Ca and Mg content in the oocytes of bream and roach during transition of gonads maturity from Stage IV to stage V in natural conditions.

Date		*n*	Stages	H_2O (%)	Na (mmol/kg H_2O)	K (mmol/kg H_2O)	Mg (mmol/kg H_2O)	Ca (mmol/kg dry weight)
Bream	25.04.1990	7	IV	67.1 ± 0.5	54.6 ± 4.0	95.9 ± 6.9	14.1 ± 1.8	7.6 ± 0.9
	03.05.1990	11	IV	67.0 ± 0.3	53.0 ± 3.1	96.8 ± 4.8	13.7 ± 1.3	7.3 ± 0.7
	08.05.1990	6	V	69.3 ± 0.6**	39.8 ± 4.6*	59.9 ± 8.3**	4.7 ± 1.0**	3.2 ± 0.7**
Roach[32]	03.05.1988	6	IV	65.4 ± 0.3	58.1 ± 2.9	94.7 ± 4.1	16.1 ± 1.3	19.6 ± 2.2
	05.05.1988	11	IV	66.0 ± 0.3	57.0 ± 1.6	98.9 ± 2.3	14.5 ± 1.0	16.6 ± 1.7
	06.05.1988	5	V	67.6 ± 0.2**	82.4 ± 3.3**	100.8 ± 2.0	12.9 ± 0.9	15.6 ± 1.5

*: $P < 0.05$; **: $P < 0.01$, differences between the maturity Stage IV and V.

water in the oocytes of sea halibut (*Hippoglossus hippoglossus*) raised before ovulation by 42.9% at the average and the oocytes of common killifish (*Fundulus heteroclitus*) raised by 90%[34,35]. The oocytes of black sea bass (*Centropristes striata*) at the final maturing stage increased their volume more than 3 times within 24 h due to water inflow[36]. The comparison shows that in oocytes of the sea fish, watering degree is considerably higher than in the oocytes of freshwater bream and roach. Water level in the oocytes of leopard frogs (*Rana pipiens*) spawning caviar in fresh water environment increased before spawning by 32%[37]. It is obvious that such rate of oocytes watering is characteristic for caviar of the sea fish species. Apparently, degree of oocytes watering depends not only on salinity of environment but also on taxonomic location of species. For various animal species, watering of oocytes before ovulation is a universal process, indicating readiness of breeders to spawn.

The reasons of oocytes watering before ovulation are connected with receipt of inorganic ions, accumulation of peptides and free amino acids resulted from yolk hydrolysis[33].

In natural conditions during transition of oocytes from maturity Stage IV to V, the content of cations in eggs of bream decreased. Lowering of ions level in oocytes was followed by the decrease of osmotic concentration and therefore prevented the watering of oocytes. Increase of H_2O content in oocytes of bream in the transition from maturity Stage IV to V is possible only if concentration of free amino acids by means of hydrolysis of yolk proteins is increased. At the same time, gain of amino acids should additionally compensate outflow of ions from oocytes.

Feasibility of such mechanism is indicated by the data on Ca. A number of researches show that concentration of free Ca ions in cytosol of oocytes of different animal species is extremely low (0.1–0.4 micromol/L)[38-44]. General concentration of Ca in oocytes of bream and roach is tens of thousands of times higher than free ions. It shows that almost all Ca ions in oocytes exist in the form linked with organic substances and only insignificantly small part is dissolved in the water phase of eggs.

At the transition of oocytes from maturity Stage IV to V, content of Ca in oocytes of bream has decreased for more than 2 times. Extremely low share of free Ca ions is not sufficient to support a process of such essential decrease. Consequently, the loss of Ca from oocytes of bream occurred by means of the part of ions linked with yolk proteins. Ca ions linked with proteins cannot be extracted from the oocyte. For this purpose, they should be transferred into free form. It is proven for a number of fish species that at transition of oocytes from maturity Stage IV to V, hydrolysis of yolk proteins takes place resulting in essential increase of the content of free amino acids[45-48]. This results in growing of osmotic concentration cause inflow of water into the oocyte. At transition of bream oocytes from maturity Stage IV to V as a result of protein hydrolysis, Ca ions were transferred to a free form and ousted from the oocytes. It is known that high levels of free Ca ions in cytoplasm of various types of cells destroy cytoskeleton and cause death[49,50].

At transition to maturity Stage V, content of Na in the oocytes of roach increased whereas levels of K, Ca and Mg did not change. Watering of the oocytes of roach is caused by the increase of osmotic concentration due to the raised level of Na in eggs. Constant content of Ca during maturing of the oocytes of roach indicates that there is no process of yolk proteins hydrolysis.

The period of transition of oocytes from maturity Phase IV to V is very quick and registering this process in field conditions is very difficult. In this connection, studies in this sphere are usually carried out in laboratory conditions applying the method of hormonal injections *in vivo* or incubation of oocytes in solutions with different hormones *in vitro*.

Before ovulation, intracellular concentration of Na raised to a certain level in the oocytes of starfish (*Astropecten aurantiacus*), black sea bass, common killifish and leopard frog[35-37,51]. Increase of Na concentration in oocytes at transition from maturity Phase IV to V facilitates the penetration of water into oocytes causing increase of their volume. Similar mechanism is discovered in adaptation of fishes to lack of oxygen in the water. It is shown that in condition of hypoxia and rise of outside temperature, increase of Na ions level accompanied by water absorption occurs in erythrocytes[52-55]. Consequently, the volume of erythrocytes increases resulting in increase of their oxygen bearing volume due to additional capture of oxygen[56]. It is believed that increase in the content of Na ions in erythrocytes in condition of adapting of fishes to lack of oxygen is connected with amplification of activity of Na^+/H^+ transporter[52,53]. Perhaps, this ionic pump also participates in increasing concentration of Na ions in oocytes during their transition from maturity Stage IV to V. To prove this, additional studies of oocytes *in vitro* are necessary.

The literature data concerning changes of K ions level in the oocytes of various species at the final stage of maturing also differ from each other. The same as of roach in the oocytes of leopard frog before ovulation changes in the content of K ions was not observed[37]. In other researches at the finishing stage of ovary maturing, the level of K ions raised in the oocytes of black sea bass, common killifish[35,36]. Increase of osmotic concentration in maturing eggs was happening simultaneously with changing of the level of K ions in oocytes[35]. Authors have drawn a conclusion that water inflow into maturing oocytes of common killifish is connected with entering of K ions into eggs.

Before ovulation in the oocytes of leopard frog, the level of linked Ca increased 18 times and the share of free ions reduced by 40%[37]. It shows that oocytes receive Ca proteins linked with ions from the liver. Observed watering of oocytes of this species was caused by the increase of the Na ions content.

In the oocytes of black sea bass at the final stage of maturing by means of protein proteolysis concentration of free amino acids increased 10 times[36]. Degree of proteolysis of yolk proteins precisely correlates with the rate of oocytes hydration[35]. It is shown that water inflow into oocytes during final maturing occurs through special water channels (aqua pores) which are discovered in the egg shell[57].

Thus, during the transition of fish oocytes from maturity Stage IV to V, content of water increases to a certain level by means of receiving Na or K ions or because of yolk proteins hydrolysis resulting to increased concentration of peptides and free amino acids. It is not clear how observed distinctions are defined. For finding it out, further research is required.

In the oocytes of bream after its catching, transportation and subsequent remaining in a cage change of H_2O and ions concentration were not observed preventing oocytes transition from maturity Stage IV to V. In condition of stress, the process of oocytes maturing is detained. As a result, reproductive products of breeders in captivity do not reach spawning stage of maturity V. It can be assumed that in condition of stress, function of hypophysis and gonads is depressed which results in the decrease of 17,20β-dihydroxy-4-pregnen-3-one of sex hormone concentration in blood plasma[6,26,27]. Normal concentrations of 17,20β-dihydroxy-4-pregnen-3-one hormone, which promote final oocyte maturation rapidly increase just prior to ovulation and spawning, and remain elevated throughout the duration of spawning activity[58-60]. Watering of the oocytes of loach and sturgeon fishes was stimulated *in vitro* by combining influence of progesterone and chorial gonadotropin on follicles[61,62].

Nowadays, the methods of hypophysial and hormonal injections are widely used in fish-breeding for stimulation of oocytes maturing and ovulation process[63-69]. It is shown that the result depends on conditions of incubation and application of hormonal

preparations[61,62]. It is required to search optimal methods to stimulate maturing of oocytes and ovulation process in industrial conditions. In our opinion for this purpose, it is necessary to start with studying these reactions of breeders of this or that species in natural conditions. Then, on the basis of received data, incubation conditions and combination of hormonal preparations can be selected in such a way that they activate similar effects which breeders experience in natural environment. In this case, receipt of the best quality reproductive products can be expected.

In natural conditions before spawning in the course of maturation of oocytes from maturity Stage IV to V, water content in the ovicells of bream has increased by 3.3% and concentration of Na, K, Ca, Mg has decreased by 24.9%, 38.1%, 56.2%, 65.7%, accordingly. Stress caused by capturing, transportation and the subsequent remaining of bream spawners in a cage did not change parameters of water-salt exchange of the oocytes preventing their transition from maturity Stage IV to V. It is suggested that in order to develop optimal technique stimulating oocytes maturation and the process of ovulation in industrial conditions, study of these reactions of spawners of one or another species in natural environment is firstly conducted. The conditions of incubation and combination of hormonal preparations are selected so that they invoke similar effects as the ones spawners experience in natural habitat.

Conflict of interest statement

I declare that I have no conflict of interest.

Acknowledgments

This study has been financially supported by the budgetary state project: Studying of adaptations of organisms, populations, communities of aquatic organisms and modeling ecosystems to environmental factors. State Registration No. 01201351909.

References

[1] Mazeaud MM, Mazeaud F, Donaldson EM. Primary and secondary effects of stress in fish: some new data with a general review. *Trans Am Fish Soc* 1977; **106**: 201-12.

[2] Meka JM, McCormick SD. Physiological response of wild rainbow trout to angling: impact of angling duration, fish size, body condition, and temperature. *Fish Res* 2005; **72**: 311-22.

[3] Biswas AK, Seoka M, Takii K, Maita M, Kumai H. Stress response of red sea bream *Pagrus major* to acute handling and chronic photoperiod manipulation. *Aquaculture* 2006; **252**: 566-72.

[4] Abreu JS, Takahashi LS, Hoshiba MA, Urbinati EC. Biological indicators of stress in pacu (*Piaractus mesopotamicus*) after capture. *Braz J Biol* 2009; **69**: 415-21.

[5] Rapp T, Hallermann J, Cooke SJ, Hetz SK, Wuertz S, Arlinghaus R. Physiological and behavioural consequences of capture and retention in carp sacks on common carp (*Cyprinus carpio* L.), with implications for catch-and-release recreational fishing. *Fish Res* 2012; **125-126**: 57-68.

[6] Baker MR, Swanson P, Young G. Injuries from non-retention in gillnet fisheries suppress reproductive maturation in escaped fish. *PLoS One* 2013; **8**: e69615.

[7] Raby GD, Wilson SM, Patterson DA, Hinch SG, Clark TD, Farrell AP, et al. A physiological comparison of three techniques for reviving sockeye salmon exposed to a severe capture stressor during upriver migration. *Conserv Physiol* 2015; doi: 10.1093/conphys/cov015.

[8] Uhlmann SS, Broadhurst MK, Millar RB. Effects of modified handling on the physiological stress of trawled-and-discarded yellowfin bream (*Acanthopagrus australis*). *PLoS One* 2015; **10**(6): e0131109.

[9] French RP, Lyle J, Tracey S, Currie S, Semmens JM. High survivorship after catch-and-release fishing suggests physiological resilience in the endothermic shortfin mako shark (*Isurus oxyrinchus*). *Conserv Physiol* 2015; doi: 10.1093/conphys/cov044.

[10] Colotelo AH, Raby GD, Hasler CT, Haxton TJ, Smokorowski KE, Blouin-Demers G, et al. Northern pike bycatch in an inland commercial hoop net fishery: effects of water temperature and net tending frequency on injury, physiology, and survival. *Fish Res* 2013; **137**: 41-9.

[11] Frick LH, Reina RD, Walker TI. Stress related physiological changes and post-release survival of Port Jackson sharks (*Heterodontus portusjacksoni*) and gummy sharks (*Mustelus antarcticus*) following gill-net and longline capture in captivity. *J Exp Mar Bio Ecol* 2010; **385**: 29-37.

[12] Bouck GR, Ball RC. Influence of capture methods on blood characteristics and mortality in the rainbow trout (*Salmo gairdneri*). *Trans Am Fish Soc* 1966; **95**: 170-6.

[13] Martemyanov VI. [Stress as a source of errors in ecologo-physiological and biochemical studies of fish]. In: Monakov AV, Poddubny AG, editors. [*The assessment of errors in methods of hydrobiological and ichthyological studies*]. Rybinsk: IBVV RAN; 1982, p. 124-34. Russian.

[14] Martemyanov VI. [Dynamics of concentration of electrolytes at freshwater fishes at a stress]. In: Monakov AV, editor. [*Freshwater aquatic organisms and biology*]. Leningrad: Nauka; 1983, p. 237-48. Russian.

[15] Martemyanov VI. [Sensitivity of fishes influence in natural and laboratory conditions]. *Voprosy Ichthyologii* 1985; **25**: 1042-4. Russian.

[16] Martemyanov VI. [The dynamics of concentration corticosterone and electrolytes in the bream blood plasma under stress conditions]. *Biol Vnutrennikh Vod Informatsionnyi Byull* 1987; **75**: 51-4. Russian.

[17] Martemyanov VI. [Content of cations in plasma, erythrocytes, muscles and gonads roach Rutilus rutilus from the natural environment and acclimate to laboratory conditions]. *Voprosy Ichthyologii* 1999; **39**: 278-81. Russian.

[18] Martemyanov VI. Patterns of changes in sodium content in plasma and erythrocytes of freshwater fish at stress. *J Ichthyol* 2013; **53**: 220-4.

[19] Martemyanov VI. Dynamics of sodium and potassium in plasma, erythrocytes, and muscles of freshwater species under the effect of long-term combined stress. *Inland Water Biol* 2014; **7**: 389-93.

[20] Martemyanov VI. [Assessment of acute and chronic stress in freshwater fishes based on parameters of water-salt exchange]. *Uspehy Sovremennoy Biologii* 2014; **134**: 249-56. Russian.

[21] Martemyanov VI. Dynamics of the content of various fractions of water in the organism of roach *Rutilus rutilus* L. in response to catching, transportation, and further acclimation to laboratory conditions. *Inland Water Biol* 2015; **8**: 402-5.

[22] Martemyanov VI. [Dynamics of water content in organism of perch *Perca fluviatilis* L. at stress]. *Water Chem Ecol* 2015; **4**: 54-9.

[23] Martemyanov VI. Stress reaction in freshwater fish in response to extreme impacts and during the reproduction period. *J Coast Life Med* 2015; **3**: 169-77.

[24] Martemyanov VI, Borisovskaya EA. Indices of hydromineral metabolism in tyulka (*Clupeonella cultriventris*; Clupeiformes, Clupeidae) introduced in the Rybinsk Reservoir in comparison to aboriginal and marine fish species. *Russ J Biol Invasions* 2010; **1**: 187-93.

[25] Martemyanov VI, Zaprudnova RA. [Dynamics of electrolyte concentration in the blood plasma, erythrocytes and muscular tissue of freshwater fish under stress]. *Biologicheskie Nauki* 1982; **10**: 44-9. Russian.

[26] Pickering AD, Pottinger TG, Carragher J, Sumpter JP. The effects of acute and chronic stress on the levels of reproductive hormones in the plasma of mature male brown trout, *Salmo trutta* L. *Gen Comp Endocrinol* 1987; **68**: 249-59.

[27] Kubokawa K, Watanabe T, Yoshioka M, Iwata M. Effects of acute stress on plasma cortisol, sex steroid hormone and glucose levels in male and female sockeye salmon during the breeding season. *Aquaculture* 1999; **172**: 335-49.

[28] Pankhurst NW, Van Der Kraak G. Effects of stress on reproduction and

growth of fish. In: Iwama GK, Pickering AD, Sumpter JP, Schreck CB, editors. *Fish stress and health*. Cambridge: Cambridge University Press; 1997, p. 73-93.

[29] Lambert Y, Thorsen A. Integration of captive and wild studies to estimate egg and larval production of fish stocks. *J Northwest Atl Fish Sci* 2003; **33**: 71-9.

[30] Baker MR, Schindler DE. Unaccounted mortality in salmon fisheries: non-retention in gillnets and effects on estimates of spawners. *J Appl Ecol* 2009; **46**: 752-61.

[31] Baker MR, Kendall NW, Branch TA, Schindler DE, Quinn TP. Selection due to nonretention mortality in gillnet fisheries for salmon. *Evol Appl* 2011; **4**: 429-43.

[32] Martemyanov VI. Dynamics of the water content and the concentrations of the ions of natrium, potassium, calcium, and magnesium in the gonads of mature roach *Rutilus rutilus* (Cyprinidae) during the reproduction cycle. *J Ichthyol* 2014; **54**: 715-22.

[33] Skoblina MN. [Hydration of oocytes in bony fishes]. *Ontogenez* 2010; **41**: 5-18. Russian.

[34] Finn RN, Østby GC, Norberg B, Fyhn HJ. *In vivo* oocyte hydration in Atlantic halibut (*Hippoglossus hippoglossus*); proteolytic liberation of free amino acids, and ion transport, are driving forces for osmotic water influx. *J Exp Biol* 2002; **205**: 211-24.

[35] Greeley MS Jr, Hols H, Wallace RA. Changes in size, hydration and low molecular weight osmotic effectors during meiotic maturation of *Fundulus* oocytes *in vivo*. *Comp Biochem Physiol Part A: Physiol* 1991; **100**: 639-47.

[36] Selman K, Wallace RA, Cerdà J. Bafilomycin A1 inhibits proteolytic cleavage and hydration but not yolk crystal disassembly or meiosis during maturation of sea bass oocytes. *J Exp Zool* 2001; **290**: 265-78.

[37] Morrill GA. Water and electrolyte changes in amphibian eggs at ovulation. *Exp Cell Res* 1965; **40**: 664-7.

[38] Cuthbertson KS, Whittingham DG, Cobbold PH. Free Ca^{2+} increases in exponential phases during mouse oocyte activation. *Nature* 1981; **294**: 754-7.

[39] Eisen A, Kiehart DP, Wieland SJ, Reynolds GT. Temporal sequence and spatial distribution of early events of fertilization in single sea urchin eggs. *J Cell Biol* 1984; **99**: 1647-54.

[40] Busa WB, Nuccitelli R. An elevated free cytosolic Ca^{2+} wave follows fertilization in eggs of the frog, *Xenopus laevis*. *J Cell Biol* 1985; **100**: 1325-9.

[41] Poenie M, Alderton J, Tsien RY, Steinhardt RA. Changes of free calcium levels with stages of the cell division cycle. *Nature* 1985; **315**: 147-9.

[42] Steinhardt RA, Alderton J. Intracellular free calcium rise triggers nuclear envelope breakdown in the sea urchin embryo. *Nature* 1988; **332**: 364-6.

[43] Grandin N, Charbonneau M. Intracellular free Ca^{2+} changes during physiological polyspermy in amphibian eggs. *Development* 1992; **114**: 617-24.

[44] Keating TJ, Cork RJ, Robinson KR. Intracellular free calcium oscillations in normal and cleavage-blocked embryos and artificially activated eggs of *Xenopus laevis*. *J Cell Sci* 1994; **107**: 2229-37.

[45] Carnevali O, Carletta R, Cambi A, Vita A, Bromage N. Yolk formation and degradation during oocyte maturation in seabream *Sparus aurata*: involvement of two lysosomal proteinases. *Biol Reprod* 1999; **60**: 140-6.

[46] Carnevali O, Cionna C, Tosti L, Lubzens E, Maradonna F. Role of cathepsins in ovarian follicle growth and maturation. *Gen Comp Endocrinol* 2006; **146**: 195-203.

[47] Matsubara T, Nagae M, Ohkubo N, Andoh T, Sawaguchi S, Hiramatsu N, et al. Multiple vitellogenins and their unique roles in marine teleosts. *Fish Physiol Biochem* 2003; **28**: 295-9.

[48] Raldúa D, Fabra M, Bozzo MG, Weber E, Cerdà J. Cathepsin B-mediated yolk protein degradation during killifish oocyte maturation is blocked by an H^+-ATPase inhibitor: effects on the hydration mechanism. *Am J Physiol Regul Integr Comp Physiol* 2006; **290**: R456-66.

[49] Boldyrev AA. [*Introduction to membrane biochemistry*]. Moscow: Vysshaya Shkola; 1986. Russian.

[50] Boldyrev AA, Mel'gunov VI. [*Achievements of science and technology, All-Union Institute of Scientific and Technical Information, Academy of Sciences of USSR, Series: Biophysics*]. Moscow: Nauka; 1985. Russian.

[51] de Santis A, Ciccarelli C, Dale B. Free intracellular cations in echinoderm oocytes and eggs. *Eur Biophys J* 1987; **14**: 471-6.

[52] Motais R, Garcia-Romeu F, Borgese F. The control of Na^+/H^+ exchange by molecular oxygen in trout erythrocytes. A possible role of hemoglobin as a transducer. *J Gen Physiol* 1987; **90**: 197-207.

[53] Motais R, Borgese F, Fievet B, Garcia-Romeu F. Regulation of Na^+/H^+ exchange and pH in erythrocytes of fish. *Comp Biochem Physiol A Physiol* 1992; **102**: 597-602.

[54] Virkki LV, Salama A, Nikinmaa M. Regulation of ion transport across lamprey (*Lampetra fluviatilis*) erythrocyte membrane by oxygen tension. *J Exp Biol* 1998; **201**: 1927-37.

[55] Martemyanov VI. The regularities of changes in the sodium ion levels in fish erythrocytes during adaptation to a temperature. *Biol Bull* 2009; **36**: 412-6.

[56] Nikinmaa M, Cech J Jr, Ryhänen EL, Salama A. Red cell function of carp (*Cyprinus carpio*) in acute hypoxia. *Exp Biol* 1987; **47**: 53-8.

[57] Cerdà J, Zapater C, Chauvigné F, Finn RN. Water homeostasis in the fish oocyte: new insights into the role and molecular regulation of a teleost-specific aquaporin. *Fish Physiol Biochem* 2013; **39**: 19-27.

[58] Nagahama Y, Yamashita M. Mechanisms of synthesis and action of 17α20β-dihydrooxy-4-progen-3-one a teleost maturation-inducing substance. *Fish Physiol Biochem* 1989; **7**: 193-200.

[59] Lubzens E, Young G, Bobe J, Cerdà J. Oogenesis in teleosts: how fish eggs are formed. *Gen Comp Endocrinol* 2010; **165**: 367-89.

[60] Pramanick K, Kundu S, Paul S, Mallick B, Moulik SR, Pal P, et al. Changes in plasma steroid levels during oocyte development in Indian shad, *Tenualosa ilisha* (Hamilton, 1822): Role of gonadotropins on *in vitro* steroid production and development of oocyte maturational competence. *Anim Reprod Sci* 2013; **141**: 177-88.

[61] Saat TF. [Oocyte maturation and ovulation in the loach in different media and under different hormonal influences]. *Ontogenez* 1980; **11**: 545-54. Russian.

[62] Skoblina MN, Goncharov BF. Stimulation of *in vitro* oocyte ovulation by progesterone and homologous pituitary gonadotropic hormone in sturgeons. *Russ J Dev Biol* 2012; **43**: 157-63.

[63] Falahatkar B, Poursaeid S, Langroudi HE, Efatpanah I, Meknatkhah B, Rahmati M. Spawning induction in Kutum, *Rutilus frisii kutum* (Kamensky), with different hormones: analysis of hormone profiles and induced spawning success. *Arch Pol Fish* 2013; **21**: 271-81.

[64] Marte CL. Hormone-induced spawning of cultured tropical finfishes. *Adv Trop Aquac* 1989; **9**: 519-39.

[65] Rottmann RW, Shireman JV, Chapman FA. Hormone preparation, dosage calculation, and injection techniques for induced spawning of fish. Stoneville: Southern Regional Aquaculture Center; 1991. [Online]https://www.ncrac.org/files/biblio/SRAC0425.pdf [Accessed on 25th November, 2015]

[66] Miah MI, Mamun AA, Khan MMR, Rahman MM. Dose optimization with pituitary gland hormone for induced breeding of bata fish (*Labeo bata*). *Bangladesh J Anim Sci* 2008; **37**: 70-7.

[67] Ayoola SO, Kuton MP, Chukwu SC. Comparative study of piscine and non-piscine pituitary extract and ovulin for inducing spawning in catfish (*Clarias gariepinus*). *Afr J Food Agric Nutr Dev* 2012; **12**: 6809-22.

[68] Surnar SR, Kamble AD, Walse NS, Sharma OP, Saini VP. Hormone administration with induced spawning of Indian major carp. *Int J Fish Aquat Stud* 2015; **3**: 1-4.

[69] Mohammadi H, Khara H, Kazemi R. Effect of different doses of synthetic hormone lhrh-a_2 on serum sex hormones, ovulation percent and egg hatching rates of persian sturgeon acipenser persicus. *Croat J Fish* 2015; **73**: 58-62.