ECOLOGICAL PHYSIOLOGY AND BIOCHEMISTRY OF AQUATIC ORGANISMS

Content of Sodium, Potassium, Calcium, and Magnesium in the Body of Larvae of Sibling Species *Chironomus balatonicus* and *Chironomus plumosus* Depending on the Salinity of the Medium

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Abstract—The tolerance range of water salinity reaches 0.09-9.3 and 0.008-6.0 g/L for the larvae of *Chirono-mus balatonicus* Devai, Wülker et Scholl, 1983 and *Ch. plumosus* L., 1758, respectively. In the tolerance range of salinity of the medium, the sodium, potassium, calcium, and magnesium concentrations in the body of *Ch. balatonicus* are within 33.9-77.1, 7.7-13.7, 11.9-37.6, and 54.7-110.6 mmol/kg wet weight, respectively. In larvae of *Ch. plumosus* (developmental stage III), the concentrations of sodium, potassium, calcium, and magnesium are within 62.7-80.8, 10.6-18, 6.7-12, 2.9-6.0 mmol/kg wet weight, and in larvae of *Ch. plumosus* (developmental stage IV)-49.6-62.3, 9.7-14.8, 42.5-62.2, 47.9-83.4 respectively. In the optimal salinity range of 0.8-5.3 g/L, the sodium concentration in the body of *Ch. balatonicus* is maintained at a constant level, decreases in the critically low zone of 0.8-0.09 g/L, and increases in the critically high zone of 5.3-9.3 g/L. In critically low and high salinity zones, the organism's ability to survive is reduced. The content of sodium in the body of freshwater aquatic organisms serves as a reliable criterion for assessing optimal, critically low, and critically high salinity zones.

Keywords: *Chironomus balatonicus, Chironomus plumosus*, tolerance range, optimal, critical low and critical salinity zones, sodium, potassium, calcium, magnesium

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INTRODUCTION

Populations of Chironomus balatonicus Devai, Wülker et Scholl, 1983 and Ch. plumosus L., 1758 live together in a number of sites in the bays of the Baltic Sea (Belyanina, Loginova, 1993). In the Curonian Lagoon of the Baltic Sea, there is a pronounced gradient from fresh to brackish water of a certain salinity. The larvae of *Ch. plumosus* are ubiquitous in this bay, although larvae of Ch. balatonicus are found in brackish water and absent in freshwater areas (Markiyanova, 2015; Kornijow et al., 2019). In acute experiments, Ch. balatonicus does not tolerate fresh water dilution. but is more resistant to increased salinity compared with Ch. plumosus (Markiyanova, Ezhova, 2013). The reason for the different response of the larvae of these species to the salinity of the medium remains unclear. It may be due to differences in the mechanisms that maintain ionic homeostasis in chironomid larvae.

Salinity is one of the most important environmental factors affecting the distribution of species, as well as stability, development, growth, and physiological processes of aquatic organisms (Kilgour et al., 1994; Berezina, 2003; Khlebovich and Aladin, 2010; Krupa and Grishaeva, 2019). Organisms of certain species of aquatic organisms can survive within certain limits of salinity (tolerance range). Optimal, critically low, and critically high salinity zones are distinguished within the tolerance range. In the optimal salinity range, the content of various cations in the internal environment and in the tissues of aquatic organisms is maintained in a narrow concentration range, providing stable conditions for the functioning of various body cells, regardless of external conditions. Outside the optimal range (in areas of low and high salinity), the levels of inorganic ions in the body deviate sharply from the norm. If the indicators deviate beyond the limits compatible with the vital activity of cells, the organism dies (Martemyanov, 2011; Martemyanov and Borisovskaya, 2012). Such a pattern of regulation of ion levels in the body makes it possible to use it as a criterion for distinguishing the boundaries of the tolerance and optimal ranges, as well as critically low and critically high salinity zones.

This study aims to determine the concentration of sodium, potassium, calcium, and magnesium in the body of *Ch. balatonicus* and *Ch. plumosus* to search the

Salinity, g/L NaCl, mmol/L Na	no.	<i>n</i> ₁	<i>n</i> ₂	Content of cations, mmol/kg wet weight			
				sodium	potassium	calcium	magnesium
0.09(1.5)	1	10	1	39.2	7.7	18.0	67.0
0.3 (5.1)	2	10	6	37.0 ± 3.1	8.4 ± 0.4	25.6 ± 7.3	101.4 ± 9.2
0.8 (13.7)	3	10	6	50.9 ± 0.7	8.2 ± 0.4	19.1 ± 2.2	95.1 ± 10.4
1.6 (27.3)	4	10	2	54.3 ± 3.2	10.4 ± 0.8	19.4 ± 2.5	63.8 ± 9.1
3.3 (56.4)	5	10	5	45.4 ± 4.7	11.2 ± 0.7	24.3 ± 1.9	95.2 ± 4.1
4.3 (73.5)	6	10	5	46.5 ± 2.7	10.5 ± 0.5	20.1 ± 2.1	81.3 ± 4.3
5.3 (90.6)	7	10	5	47.0 ± 3.8	9.9 ± 0.6	24.2 ± 3.5	87.1 ± 5.9
6.3 (107.7)	8	10	5	56.6 ± 4.5	11.3 ± 0.7	16.8 ± 2.4	89.3 ± 12.4
7.3 (124.8)	9	10	6	62.4 ± 6.6	11.0 ± 0.9	16.6 ± 2.0	91.2 ± 9.2
8.3 (141.9)	10	10	6	64.2 ± 9.2	10.4 ± 1.3	28.8 ± 8.8	83.2 ± 15.4
9.3 (159.0)	11	10	3	73.1 ± 4.0	12.1 ± 1.6	13.6 ± 1.7	70.3 ± 17.8
10.3 (176.1)	12	10	1	67.9	9.1	30.0	100.0
Range				33.9-77.1	7.7-13.7	11.9-37.6	54.7-110.6

Table 1. Content of cations in the body of *Chironomus balatonicus* larvae in the tolerance range of salinity of the medium

Here and in Table 2, no. is the container number, n_1 is the number of individuals at the beginning of the experiment, and n_2 is the number of surviving individuals at the end of the experiment.

boundaries of the tolerant and optimal ranges for these species, as well as to define their critically low and critically high salinity zones.

MATERIALS AND METHODS

Larvae of *Ch. balatonicus* weighing 1.6–12.0 mg (developmental stage IV) were collected on June 6, 2013, in the Vistula Lagoon of the Baltic Sea (54°37'36" N, 20°7'19" E; 54°40'18" N, 20°19'59" E). The ion concentrations in water were 42.0, 0.9, 5.1, and 4.8 mmol/L for sodium, potassium, calcium, and magnesium, respectively. Live chironomids were delivered to the Marine Ecology Laboratory of the Atlantic Branch of the Institute of Oceanology, Russian Academy of Sciences. Species identification of larvae was carried out using the karyological method (Demin and Shobanov, 1990). The resulting karyotypes were analyzed using standard species cytophotomaps (Kiknadze et al., 1991).

In the experiment, larvae were placed in 12 glass containers (ten individuals each) containing ~1-cm-thick soil at the bottom and a certain amount of water from the Vistula Lagoon (no. 1, 10 mL; no. 2, 25 mL; no. 3, 50 mL; nos. 4-12, 100 mL each). Distilled water (10 mL) was added into containers nos. 1-3 twice a day until the final volume reached 100 mL. In container no. 4, the larvae were kept in the ambient water from the Vistula Lagoon (salinity of 3.1 g/L). A total of 25-50 mg of NaCl was added to containers nos. 5-12 four times a day until the final concentrations were reached (Table 1).

Two series of experiments were carried out with larvae of *Ch. plumosus*. In the first experiment, larvae (16.0–25.2 mg, stage IV) were caught on July 8, 2013, in the Curonian Lagoon of the Baltic Sea ($55^{\circ}206''N$, 20°40'08'' E). The cation concentrations in the water were 1.55, 0.26, 1.4, and 0.8 mmol/L for sodium, potassium, calcium, and magnesium, respectively. After the larvae were delivered to the laboratory, they were placed in five containers (ten individuals each) containing soil (1 cm in thickness) at the bottom and filled with 100 mL of ambient water from the Curonian Lagoon with a salinity of 0.09 g/L. Four times a day, 25 mg of NaCl were added to four containers until certain concentrations were reached (Table 2).

In the second experiment, larvae (8.0-20.0 mg)stage III) were caught on July 16, 2014, in the Curonian Lagoon of the Baltic Sea (55°2'06"N, 20°40'08"E). The cation concentrations in the water were 0.54, 0.16, 0.39, and 0.1 mmol/L for sodium, potassium, calcium, and magnesium, respectively. In the laboratory, larvae were placed in ten containers (ten individuals each) containing soil (1 cm in thickness) at the bottom and a certain amount of ambient water from the Curonian Lagoon (no. 1, 10 mL; no. 2, 25 mL; no. 3, 50 mL; and nos. 4-10, 100 mL). A total of 10 mL of distilled water was added to containers nos. 1-3 twice a day until a volume of 100 mL was reached in each one. In container no. 4, the larvae were kept in the ambient water of the Curonian Lagoon with a salinity of 0.032 g/L. A total of 25-50 mg of NaCl was added four times a day until certain concentrations were reached (Table 2). The larvae were acclimated to the given constant conditions for ≥ 10 days. The water temperature during the experiments varied within 17–18°C.

After acclimation, chironomids were removed one by one from the container, washed in distilled water,

Salinity, g/L NaCl , mmol/L Na	no.	<i>n</i> ₁	<i>n</i> ₂	Content of cations, mmol/kg wet weight							
				sodium	potassium	calcium	magnesium				
Developmental stage IV (experiment in 2013)											
0.09 (1.5)	1	10	2	57.8 ± 3.2	13.4 ± 1.4	56.1 ± 6.1	57.1 ± 9.2				
1.1 (18.8)	2	10	2	59.1 ± 3.2	13.0 ± 0.2	49.2 ± 1.7	56.5 ± 9.4				
2.1 (35.9)	3	10	2	60.1 ± 1.0	12.6 ± 0.2	46.6 ± 1.1	65.2 ± 1.0				
3.1 (53.0)	4	10	1	53.3	11.1	42.5	65.4				
4.1 (70.1)	5	10	3	52.0 ± 2.4	11.1 ± 1.4	46.8 ± 7.6	76.8 ± 6.6				
Range				49.6-62.3	9.7-14.8	42.5-62.2	47.9-83.4				
Developmental stage III (experiment in 2014)											
0.008 (0.14)	1	10	2	79.5 ± 1.2	17.9 ± 0.1	7.8 ± 0.7	5.3 ± 0.9				
0.0 11 (0.19)	2	10	4	75.6 ± 1.8	11.7 ± 1.5	10.5 ± 1.1	3.4 ± 0.5				
0.016 (0.27)	3	10	8	80.2 ± 0.6	13.0 ± 1.1	11.0 ± 1.0	5.6 ± 0.4				
0.032 (0.51)	4	10	5	68.0 ± 2.6	11.3 ± 1.6	10.5 ± 0.7	5.0 ± 0.2				
1.03 (17.6)	5	10	5	64.9 ± 0.2	11.1 ± 1.5	11.3 ± 0.7	5.5 ± 0.2				
2.03 (34.7)	6	10	5	64.5 ± 1.2	10.7 ± 0.1	8.6 ± 0.5	5.1 ± 0.2				
3.03 (51.8)	7	10	3	66.2 ± 0.5	11.6 ± 0.7	10.0 ± 1.8	5.3 ± 0.7				
4.03 (68.9)	8	10	3	64.3 ± 0.5	11.2 ± 0.6	8.5 ± 1.3	4.3 ± 0.2				
5.03 (86.0)	9	10	3	63.0 ± 0.3	15.4 ± 1.6	8.3 ± 1.6	4.9 ± 0.5				
6.03 (103.1)	10	10	1	67.0	16.7	7.0	4.2				
Range				62.7-80.8	10.6-18.0	6.7-12.0	2.9-6.0				

Table 2. Content of cations in the body of *Chironomus plumosus* larvae depending on water salinit

blotted with filter paper, and guickly weighed on an MV 210-A electronic laboratory balance (ZAO Sartogosm, St. Petersburg, Russia) with a 0.00001-g accuracy. The specimens were placed individually into the plastic test tubes, and then 0.5 mL of concentrated nitric acid was added. After ashing, distilled water was added to dilute the sample 1000 times. The concentration of sodium and potassium in the samples was determined using propane on a flame spectrophotometer Flapho-4, Carl Zeiss, Jena, Germany. The content of calcium and magnesium was measured on an atomic absorption photometer Saturn (OKBA NPO Khimavtomatika, Severodonetsk, Ukraine). The cation concentrations in the body of chironomid larvae were expressed in mmol/kg wet weight. Mathematical processing of the results was carried out in MS Excel. Data are represented as mean and standard error. The significance of differences was assessed using Student's t-test at p < 0.95.

RESULTS

During the experiment, a certain number of larvae died at different salinities of the medium (Tables 1, 2). Single individuals survived in the zones of critically low and critically high salinity.

Sodium. In the salinity range of 0.8-5.3 g/L, larvae of *Ch. balatonicus* maintained the sodium concentration

in the body at an average level of 49.4 ± 1.7 mmol/kg wet weight, regardless of the environmental factor. In relation to this level, the sodium concentration in the body of the larvae of *Ch. balatonicus*, acclimated to a salinity of 0.09–0.3 g/L (gradually diluted water of the Vistula Lagoon), was 23% lower (Table 1). In larvae of *Ch. balatonicus*, acclimated to a salinity of 5.3–9.3 g/L, the sodium content in the body significantly increased by 48%.

In the experiment held in 2013, the sodium content in the body of larvae IV of *Ch. plumosus*, acclimated in the salinity range of 0.09-4.1 g/L, did not differ between different treatments, maintaining an average level of 56.2 ± 1.6 mmol/kg wet weight (Table 2). In 2014, the sodium content in the body of larvae III of *Ch. plumosus* was maintained at higher levels compared with that in 2013. At the same time, the ranges of sodium concentration regulation in the body of chironomids, obtained in 2013 and 2014, did not overlap. In the experiment of 2014, the sodium concentration in the body of *Ch. plumosus*, acclimated at low salinity of 0.008-0.016 g/L, was maintained at a significantly higher level compared to that obtained for animals in the range of 1.0-6.0 g/L.

Potassium. In the salinity range of 0.8-10.3 g/L, larvae of *Ch. balatonicus* regulated the potassium concentration in the body at an average level of 10.7 ± 0.3 mmol/kg wet weight, regardless of the environ-

mental factor. Larvae of *Ch. balatonicus*, acclimated to a low salinity of 0.09–0.8 g/L, maintained a significantly lower level of potassium ions in the body (Table 1).

In larvae of *Ch. plumosus*, the content of potassium in the body did not depend on the salinity of the medium, being at an average level of 12.3 ± 0.6 mmol/kg wet weight in 2013 and 12.4 ± 0.5 mmol/kg wet weight in 2014 (Table 2). The ranges of regulation of potassium concentration in the body of chironomids, obtained in 2013 and 2014, overlapped with each other. The range of regulation of potassium concentration in the body of *Ch. balatonicus* largely overlapped with that obtained for *Ch. plumosus*.

Calcium. The content of calcium in the body of larvae IV of *Ch. balatonicus* did not depend on the salinity of the medium, being maintained at 22.4 \pm 1.5 mmol/kg wet weight (Table 1). This level of calcium was more than half as low as that recorded in *Ch. plumosus* of similar age.

The calcium concentration in the body of *Ch. plumo*sus larvae also did not depend on the salinity of the medium, keeping at an average level of $49.1 \pm 3.2 \text{ mmol/kg}$ wet weight in 2013 and $9.9 \pm 0.4 \text{ mmol/kg}$ wet weight in 2014 (Table 2). The level of maintenance of calcium in the body of larvae III of *Ch. plumosus* in 2014 was five times lower than that obtained for larvae IV in 2013.

Magnesium. The content of magnesium in the body of *Ch. balatonicus* larvae did not depend on the salinity of the medium, being maintained at a level of $85.2 \pm 3.0 \text{ mmol/kg}$ wet weight. This level was 22% higher than that obtained for *Ch. plumosus* of similar age.

The concentration of magnesium in the body of *Ch. plumosus* also did not depend on the salinity of the medium, being at an average level of $66.5 \pm 4.3 \text{ mmol/kg}$ wet weight in larvae IV in 2013 and $5.0 \pm 0.2 \text{ mmol/kg}$ wet weight in larvae III in 2014 (Table 2). The level of maintenance of magnesium in the body of *Ch. plumosus* larvae III was 13.3 times lower than that obtained for larvae IV.

DISCUSSION

In the salinity range of 0.09-10.3 g/L, larvae of *Ch. balatonicus* regulated the concentration of potassium, calcium, and magnesium in the body at certain levels, regardless of the environmental factor (Table 1). A different pattern was observed for sodium. At a salinity exceeding 0.3 g/L, the sodium content in the body of larvae was maintained at a high level; at a low salinity of 0.09-0.3 g/L (1.5-8.7 mmol/L Na), it was significantly lower. It was reported that the minimum concentration of sodium ions in water, necessary to maintain the ionic balance between the organism *Ch. balatonicus* and the medium, reached 0.60-0.62 mmol/L (Martemyanov and Markiyanova, 2018). Obviously, the sodium content in the body of

Ch. balatonicus is reduced even when the sodium level in the water is above the threshold values.

There is a pronounced gradient from fresh to brackish water of a certain salinity in the Curonian Lagoon of the Baltic Sea. The northern part of the lagoon is influenced by the brackish water of the Baltic Sea. Due to surge winds, sea water enters through a narrow strait near the city of Klaipeda, mixing with fresh water. As a result, a certain salinity and sodium ion level gradient is recorded from north to south. In the northern part of the Curonian Lagoon, the content of ions in the water is above the threshold values, allowing the larvae to stand the osmotic and ionic balance between the organism and the environment. Ch. balatonicus is found only in the brackish water of the northern part of the lagoon from the city of Klaipeda to the village of Juodkrante (Markiyanova, 2015).

In the central part of the lagoon (near the village of Morskoe), the level of sodium ions in the water approaches the threshold values (0.73 mmol/L) and becomes lower (0.50 mmol/L) when moving southwards (Martemyanov and Markiyanova, 2018). As a result, the larvae of *Ch. balatonicus* cannot maintain the ionic balance between the organism and the environment at such concentrations of sodium in water, which does not allow the species to develop the freshwater area of the Curonian Lagoon.

The population of *Ch. balatonicus* occurs sporadically in Lake Balaton (Specziár, 2008). The author believes that the population of this species, inhabiting the lake at the border of the range and with fluctuations in external conditions in certain periods, may go beyond the tolerance zone, which leads to the absence of some generations. Based on our data, we assume that the absence of generations of *Ch. balatonicus* in the Lake Balaton is associated with the periods when the sodium content in the water is not enough for its survival, development, and growth. However, special studies are required to clarify this issue.

When salinity decreases below certain values, the content of ions, mainly sodium, also drops sharply in the body of bivalve mollusks (Martemyanov, 2011) and fish (Martemyanov and Borisovskaya, 2012). Interspecific differences are manifested in the values of sodium concentration in water, which causes a decrease in the level of this ion in the body.

In the salinity range of 0.8-5.3 g/L, the sodium concentration in *Ch. balatonicus* is maintained at a constant level, decreasing in the range of 0.8-0.09 g/L and increasing at 5.3-9.3 g/L (Table 1). Such a response to salinity is characteristic of freshwater aquatic organisms (Martemyanov, 2011; Martemyanov and Borisovskaya, 2012). The content of sodium

in the body of freshwater aquatic organisms serves as a reliable criterion for assessing the optimal and critical zones of salinity of the medium. Within the optimal range, the sodium content in the body of various types of freshwater aquatic organisms does not depend on environmental factors. In relation to the tolerance range of the factor in the critically low zone, the concentration of sodium in the body decreases, while in the area of critically high salinity, the indicator increases.

Lower and upper limits of the salinity tolerance range for *Ch. balatonicus* are shifted towards higher salinity relative to those of *Ch. plumosus*. The total salinity zone, in which both species of chironomids can occur under natural conditions, reaches 0.09-6.0 g/L (1.5–102.0 mmol/L Na).

In *Ch. plumosus* larvae III, acclimated to the salinity range of 0.008-5.0 g/L, the content of sodium, potassium, calcium, and magnesium in the body did not depend on the environmental factor (Table 2). In the studied salinity zone, individuals of this age are able to maintain indicators of ion homeostasis at stable constant levels, allowing them to survive under these conditions. During the acclimation of larvae of *Ch. plumosus* to a salinity of 6 g/L, only one individual survived (Table 2); at a higher salinity, all individuals died. These data indicate that a salinity of 6 g/L is the upper limit for *Ch. plumosus* larvae III survival, so this species cannot colonize water bodies with salinity exceeding 6 g/L. However, the correctness of this statement needs to be verified by field research.

It was reported that the minimum concentration of sodium ions in water required to maintain the ionic balance between the organism of *Ch. plumosus* and the medium was 0.07–0.08 mmol/L (Vinogradov and Shobanov, 1990). The sodium content in most fresh water reservoirs, including low-mineralized ones, usually reaches 0.1 mmol/L and higher (Martemyanov and Mavrin, 2012). Therefore, the larvae of *Ch. plumosus* are able to live in almost all freshwater, as well as brackish-water reservoirs with a salinity of up to 6 g/L.

The sodium content in different parts of the Vistula Lagoon is 31.3–98.3 mmol/L (Martemyanov and Markiyanova, 2018), which falls into the general tolerant salinity range for both species, allowing chironomids to survive here. However, *Ch. plumosus* has not yet been found in this lagoon. Further research is needed to clarify the distribution of different chironomid species in the Vistula Lagoon.

Ranges of regulation of the content of sodium, calcium, and magnesium in the body of *Ch. plumosus* larvae in 2013 and 2014 differed significantly and did not overlap (Table 2). The reason for the observed differences may be due to different stages of development. In 2013, the larvae in the experiment were of developmental stage IV (almost prepupa), but in 2014 they were of the developmental stage III. Studies on various cultured cells and tissue preparations evidence that ions regulate the metabolism (Kachmar and Boyer, 1953; Sachs, 1957; Mantsavinos and Cannellakis, 1959; Kaye and Mommaerts, 1960; Atkinson, 1965; Atkinson and Walton, 1965; Mildvan and Cohn, 1965, 1966; Ballard, 1966; Bygrave, 1967; Chernavina, 1970; Low and Somero, 1975; Ledbetter and Lubin, 1977; Romanenko, 1978; Kal'tsii..., 1987; Prado et al., 1991; Avdonin and Tkachuk, 1994; De Baaij et al., 2015), genome operation (Kroeger, 1963; Lezzi and Gilbert, 1970; Patel and Kroeger, 1972), processes of cell division and differentiation, growth and development (Kafiani and Malenkov, 1976; Morrill and Robbins, 1984; Lannigan and Knauf, 1985; Takagi et al., 1986; Canaux et al., 1995; Barghouth et al., 2015). Presumably, the transition from stage of development III to IV is carried out due to changes in the content of ions in the body of chironomids, affecting metabolism, genome function, growth, and development processes. This assumption requires further research in this direction.

CONCLUSIONS

Tolerance salinity ranges for larvae of Ch. balatonicus and Ch. plumosus reach 0.09–9.3 and 0.008–6.0 g/L, respectively. Tolerance salinity range for Ch. balatonicus is shifted towards higher values compared to that of *Ch. plumosus.* Within the tolerance range, the potassium, calcium, and magnesium concentrations in organisms of both species do not depend on salinity, being maintained within certain narrow limits. In the range of 0.8-5.3 g/L, the sodium concentration in the body of Ch. balatonicus is maintained at a constant level, decreasing in the zone of low salinity of 0.8-0.09 g/L and increasing at high salinity of 5.3-9.3 g/L. Limits of the regulation of the concentrations of sodium, calcium, and magnesium in the body of Ch. plumosus of larval stage III are lower than that of larval stage IV.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

REFERENCES

Atkinson, D.E., Biological feedback control at the molecular level, *Science*, 1965, vol. 150, no. 698, p. 851.

Atkinson, D.E. and Walton, G.M., Kinetics of regulatory enzymes *Escherichia coli* phosphofructokinase, *J. Biol. Chem.*, 1965, vol. 240, p. 757.

Avdonin, P.V. and Tkachuk, V.A., *Retseptory i vnutrikle-tochnyi kal'tsii* (Receptors and Intracellular Calcium), Moscow: Nauka, 1994.

Ballard, F.J., Kinetic studies with liver galactokinasa, *Bio-chem. J.*, 1966, vol. 101, no. 1, p. 70.

Barghouth, P.G., Thiruvalluvan, M., and Oviedo, N.J., Bioelectrical regulation of cell cycle and the planarian model system, *Biochim. Biophys. Acta*, 2015, vol. 1848, p. 2629.

Belyanina, S.I. and Loginova, N.V., Cadastre of disc orders in polytene chromosomes of Chironomus species of the plumosus group. I. Karyofond *Chironomus balatonicus, Tsitologiya*, 1993, vol. 35, no. 4, p. 87.

Berezina, N.A., Tolerance of freshwater invertebrates to changes in water salinity, *Russ. J. Ecol.*, 2003, vol. 34, no. 4, p. 261.

Bygrave, F.L., The ionic environment and metabolic control, *Nature*, 1967, vol. 214, no. 5089, p. 667.

Canaux, S., Foulquier, F., Duprat, A., and Moreau, M., Regulation of Na⁺, K⁺-ATPase activity during meiotic maturation of *Pleurodeles waltl Oocytes*. Role of calcium, *Int. J. Dev. Biol.*, 1995, vol. 39, p. 327.

Chernavina, I.A., *Fiziologiya i biokhimiya mikroelementov* (Physiology and Biochemistry of Trace Elements), Moscow: Vysshaya Shkola, 1970.

De Baaij, J.H.F., Hoenderop, J.G.J., and Bindels, R.J.M., Magnesium in man: implications for health and disease, *Physiol. Rev.*, 2015, vol. 95, p. 1.

Demin, S.Yu. and Shobanov, N.A., Karyotype of the mosquito *Chironomus entis* from the group Plumosus in the European part of the USSR, *Tsitologiya*, 1990, vol. 32, no. 10, p. 1046.

Kachmar, J.F. and Boyer, P.D., Kinetic analysis of enzyme reactions. II. The potassium activation and calcium inhibition of pyruvic phosphoferase, *J. Biol. Chem.*, 1953, vol. 200, no. 2, p. 669.

Kafiani, K.A. and Malenkov, A.G., The role of cell ion homeostasis in the phenomena of growth and development, *Usp. Sovrem. Biol.*, 1976, vol. 81, no. 3, p. 445.

Kal'tsii—regulyator metabolizma (Calcium—A Metabolic Regulator), Tomsk: Nauka, 1987.

Kaye, L. and Mommaerts, W.H.M., The role of calcium ions in the acceleration of resting muscle glycolysis by extracellular potassium, *J. Gen. Physiol.*, 1960, vol. 44, no. 2, p. 405.

Khlebovich, V.V. and Aladin, N.V., The salinity factor in animal life, *Herald Russ. Acad. Sci.*, 2010, vol. 80, no. 3, p. 299.

Kiknadze, I.I., Shilova, A.I., Kerkis, I.E., et al., Kariotipy i morfologiya lichinok triby Chironomini. Atlas. (Karyotypes

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and Morphology of Larvae of the Tribe Chironomini: Atlas), Novosibirsk: Nauka, 1991.

Kilgour, B.W., Mackie, G.L., and Baker, M.A., Effects of salinity on the condition and survival of zebra mussels (*Dreissena polymorpha*), *Estuaries*, 1994, vol. 17, no. 2, p. 385.

Kornijow, R., Markiyanova, M., and Lange, E., Feeding by two closely related species of *Chironomus* (Diptera: Chironomidae) in south Baltic lagoons, with implications for competitive interactions and resource partitioning, *Aquat. Ecol.*, 2019, vol. 53, p. 315.

Kroeger, H., Chemical nature of the system controlling gene activities in insect cells, *Nature*, 1963, vol. 200, no. 4912, p. 1234.

Krupa, E. and Grishaeva, O., Impact of water salinity on long-term dynamics and spatial distribution of benthic invertebrates in the Small Aral Sea, *Int. J. Oceanogr.*, 2019, vol. 48, no. 4, p. 355.

Lannigan, D.A. and Knauf, P.A., Decreased intracellular Na⁺ concentration is an early event in murine erythroleukemic cell differentiation, *J. Biol. Chem.*, 1985, vol. 260, p. 7322.

Ledbetter, M.L. and Lubin, M., Control of protein synthesis in human fibroblasts by intracellular potassium, *Exp. Cell. Res.*, 1977, vol. 105, no. 2, p. 223.

Lezzi, M. and Gilbert, L.J., Differential effects of K^+ and Na⁺ on specific bands of isolated polytene chromosomes of *Chironomus tentans*, J. Cell Sci., 1970, vol. 6, no. 3, p. 615.

Low, P.S. and Somero, G.N., Protein hydration changes during catalysis: a new mechanism of enzymic rate—enhancement and ion activation/inhibition of catalysis, *Proc. Natl. Acad. Sci. U. S. A.*, 1975, vol. 72, no. 9, p. 3305.

Mantsavinos, R. and Cannellakis, E.S., Studies on the biosynthesis of deoxyribonucleic acid soluble mammalian enzymes, *J. Biol. Chem.*, 1959, vol. 234, no. 3, p. 628.

Markiyanova, M.F., Species composition and distribution of sibling species *Chironomus Meigen* (Diptera: Chironomidae) in the Curonian Lagoon, *Povolzh. Ekol. Zh.*, 2015, no. 4, p. 400.

Markiyanova, M.F. and Ezhova, E.E., Salinity resistance of larvae of sibling species – *Chironomus balatonicus* Dévai et al. and *Chironomus plumosus* (L.) (Diptera: Chironomidae), *Tr. Zool. Inst. Ross. Akad. Nauk*, 2013, no. 3, p. 144.

Martemyanov, V.I., Influence of environmental mineral composition on the indices of water – salt metabolism in *Dreissena polymorpha* Pallas introduced in the Rybinsk reservoir, *Russ. J. Biol. Invasions*, 2011, vol. 2, nos. 2–3, p. 213.

Martemyanov, V.I. and Borisovskaya, E.V., Indices of salt and water metabolism in tubenose goby *Proterorhinus marmoratus* pallas, introduced into Rybinsk Reservoir, and in indigenous carp *Cyprinus carpio* L. Depending on environmental salinity, *Russ. J. Biol. Invasions*, 2012, vol. 3, no. 2, p. 110.

Martemyanov, V.I. and Markiyanova, M.F., Threshold concentrations of cations in the water necessary for maintaining the ionic balance between organism of *Chironomus balatonicus* Devai et al. larvae and environment, *Inland Water Biol.*, 2018, vol. 11, no. 1, p. 81.

https://doi.org/10.1134/S1995082917040071

Martemyanov, V.I. and Mavrin, A.S., Threshold environmental concentrations of cations defining the range of roach *Rutilus rutilus* L. in freshwater reservoirs, *Inland Wa*- *ter Biol.*, 2012, vol. 5, no. 1, p. 91. https://doi.org/10.1134/S1995082912010099

Mildvan, A.S. and Cohn, M., Kinetic and magnetic resonance studies of the pyruvate kinase reaction. I. Divalent metal complexes of pyruvate kinase, *J. Biol. Chem.*, 1965, vol. 240, no. 1, p. 238.

Mildvan, A.S. and Cohn, M., Kinetic and magnetic resonance studies of the pyruvate kinase reaction: II. Complexes of Enzyme, Metal, and Substrates, *J. Biol. Chem.*, 1966, vol. 241, no. 5, p. 1178.

Morrill, G.A. and Robbins, E., Changes in intracellular cations during the cell cycle in HeLa cells, *Physiol. Chem. Phys. Med. NMR*, 1984, vol. 16, no. 3, p. 209.

Patel, N. and Kroeger, H., Dependence of RNA and protein synthesis on electrolyte concentration, *Insect Biochem.*, 1972, vol. 2, no. 1, p. 137.

Prado, F.E., Lazaro, J.J., and Gorge, J.L., Regulation by Ca^{2+} of a cytosolic fructoso-1,6-bisphosphatase from spinach leaves, *Plant Physiol.*, 1991, vol. 96, no. 4, p. 1026.

Romanenko, V.D., *Pechen' i regulyatsiya mezhutochnogo obmena* (Liver and Regulation of Interstitial Metabolism), Kyiv: Naukova Dumka, 1978.

Sachs, H., A stabilized enzyme system for amino acid incorporation, *J. Biol. Chem.*, 1957, vol. 228, no. 1, p. 23.

Specziár, A., Life history patterns of *Procladius choreus, Tanypus punctipennis* and *Chironomus balatonicus* in Lake Balaton, *Ann. Limnol.*, 2008, vol. 44, no. 3, p. 181.

Takagi, K., Okabe, Y., Yoshimura, K., and Ichikawa, Y., Changes in intracellular K^+ and Na^+ ion concentrations during cell growth and differentiation, *Cell Struct. Funct.*, 1986, vol. 11, no. 3, p. 235.

Vinogradov, G.A. and Shobanov, N.A., Specific features of sodium metabolism in *Chironomus* larvae at different values of environmental salinity and pH, *Zh. Evol. Biokhim. Fiziol.*, 1990, vol. 26, no. 3, p. 308.

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