ISSN 2658-3518

LIMNOLOGY & FRESHWATER BIOLOGY

2019, № 2

> abiotic and biotic water components;
> ecosystem-level studies;
> systematics and aquatic ecology;
> paleolimnology and environmental histories;
> laboratory experiments and modeling

Limnology and Freshwater Biology 2019 (2): 199-204 DOI:10.31951/2658-3518-2019-A-2-199

Original Article

ISSN 2658-3518
LIMNOLOGY FRESHWATER BIOLOGY
www.limnolfwbiol.com

Influence of food on morphological characteristics of *Daphnia galeata* (Cladocera, Daphniidae) from Lake Baikal

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ABSTRACT. The study shows the influence of feeding conditions on morphological characteristics of *Daphnia galeata* (Sars, 1863) in different areas of Lake Baikal. At high food concentrations and in the absence of invertebrate predators of the species *Leptodora kindti*, the daphnids have a large body size, low helmets and short tail spines. At low food concentrations, crustaceans with small-sized shells, poorly developed helmets and tail spines dominate. In the presence of the predators, an abrupt shift of adaptive variation occurs: at low food concentrations, the crustaceans have a large body size, and at high ones, small adult daphnids with well developed protective patterns dominate.

Keywords: Lake Baikal, *Daphnia galeata*, food, morphological variability, the influence of predator

1. Introduction

The influence of food supply on the biology of cladocerans was widely studied as the most important environmental factor. The results of these studies showed that food quality and quantity influences body size, eggs size and amount, protective patterns development, life and development duration (Zhukova, 1953; Manuylova, 1964; Vijverberg, 1976; Gilyarov, 1987; Burns, 1995; Boersma and Vijverberg, 1996; Czeczuga et al., 2003; Freese and Martin-Creuzburg, 2013; Garbutt and Little, 2014). Food supply conditions strongly depend on temperature, illuminance, water currents velocity (Jacobs, 1987; Dodson, 1988; Manca et al., 2008; Gall et al., 2017). High water temperatures cause an increase in crustacean growth rate, requiring more food and, thus, this phenomenon occurs at high food concentrations (Zhukova, 1953; Vijverberg, 1976; Manca et al., 2008; Masclaux, 2009; Gorbi et al., 2011; Sarpe et al., 2014; Sicora et al., 2014). Body length is one of the most important features in the determination of daphnids weight and potential productivity. Moreover, it is one of the cyclomorphic traits. Hutchinson showed its role in adaptive reactions to environmental changes (Hutchinson, 1967). In our studies of influence of contrast feeding conditions, we showed that the majority of *D. pulex* clones manifests the same reaction at high food concentration (Pitul'ko et al., 2009). This is an increase in body size and of tail spine length, acceleration of development until maturation as well as a rise of reproduction and abundance of survived crustaceans.

The impact of invertebrate predators on the variability of morphological features of daphnids is well known; as a rule, it concerns premature and small adult crustaceans, and there is no direct impact on juvenile and mature crustaceans of elder age groups (Lagergren et al., 2007; Manca et al., 2008; Zuykova and Bochkarev, 2010). Under favorable feeding conditions, the predators do not impact the daphnids body size, but helmets and tail spines are well developed (Brooks, 1946; Dodson, 1988; 1989; Laforsh and Tollrian, 2004; Hülsmann et al., 2011).

The influence of concentration of available food and invertebrate predators on morphological characteristics of daphnids has not been studied for Lake Baikal. *Daphnia galeata* (Sars, 1863) is a widely distributed species of the genus *Daphnia* in the lake (Sheveleva, 1996; 2001). These cladocerans inhabit bays, sors and near-shore shallow waters. They play a considerable role in the formation of food resources for the organisms of the next level of the food chain during several summer and autumn months. Phytoplankton, detritus, bacteria, and protozoa are the main food of planktonic crustaceans. They consume cells within the size range of 3-30 μm (Monakov, 1998). The daphnids prefer small protococci with a diameter of 3.5 μm, then, *Scenedesmus* (15 μm) and *Chlorococcum* (20-30 μm), as well as species of the genus *Chroomonas: Ch. acuta* μm and *Ch. sp.* (7-11 μm long and 3-7 μm wide) and *Stephanodiscus binderanus* (diameter of 7.5-12.3 μm) found in Lake Baikal phytoplankton (Bondarenko et al., 1991; 1995). Algae of the genus *Chroomonas* dominate phytoplankton. In Baikal, maximum phytoplankton abundance is in Chivyrkuy and Barguzin Bays, the minimum abundance is in Southern and Northern Baikal (Antipova, 1963; Bondarenko et al., 1991;1995).

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The aim of this study is to assess the influence of accessible food concentration on some morphological traits of *Daphnia galeata* and to analyze adaptive responses of these crustaceans by the studied features in the presence or absence of the predator *Leptodora kindtii*.

2. Materials and methods

Crustaceans *D. galeata* and *L. kindti* were collected with Juday net (inlet area is 0.1 m^2, filter cone mesh is 90 μm) in the Lake Baikal pelagic area and bays in August-September, 1993, 1995 and 1997 at 36 stations. The samples were fixed with 4 % formalin. Main materials were obtained in two large bays (Barguzin and Chivyrkuy Bays – St. 18-33), as well as in the pelagic area of Central Baikal (St. 10-17). In addition, we used the data on the near-shore shallow-water area near the Ushkany Islands (St. 27), Selenga area (St. 8-9), the near-shore area of Southern Baikal (St. 1-9), and Northern Baikal (St. 34-36) (Fig. 1). At stations located mainly in Central Baikal and bays (6, 10, 18, 23-26, 28-31), *L. kindti* was recorded. At low food concentration, there were 5 such stations out of 16 ones, and at high food concentration – 10 stations out of 12 ones.

The obtained and selected daphnids were classified as mature, premature and juvenile females. In total, 2525 specimens were studied. The morphological variation in *D. galeata* was measured by the following characteristics: body length, height of the helmet and tail spine length (Fig. 2), as well as the calculated relationship between these traits, the relative height of the helmet and the relative length of the tail spine (Manuylova, 1964; Havel, 1985; Ranta and Tjossem, 1987; Dodson, 1988; 1989; Ranta et al., 1993; Riccardi et al., 2002). We determined body length, helmet height and tail spine length (Fig. 2) as well as calculated the ratio of helmet height and tail spine length to body length. Relative characteristics showed allometric growth of body parts under certain existence conditions and assessed the development of cyclomorphic features (Havel and Dodson, 1985).

To characterize the food supply level of daphnids, we used the daily production of phytoplankton in mg of carbon per m^3 (mg C/m^3). This is an integrated indicator showing total food concentrations in daphnids habitats. Previous reports imply distribution of bacterioplankton and phytoplankton abundance in the food of inferior crustaceans in the Lake Baikal water area. Based on the data shown in Bondarenko et al. (1991), we established seven grades of food concentration. Its minimum (19 mg C/m^3) was recorded in Southern Baikal (Stations 1-7). In the range areas of Chivyrkuy and Barguzin Bays, food concentrations were 30.0 and 35.0 mg C/m^3, respectively (St. 19, 25, 26, 30, and 33). In Central and Northern Baikal, values of phytoplankton daily production were 38 mg C/m^3 (St. 11-17, 27 and 34-36). In the Selenga shallow-water area, this value is 160 mg C/m^3 (St. 8-10). Within Barguzin and Chivyrkuy Bays, food concentrations were 190 mg C/

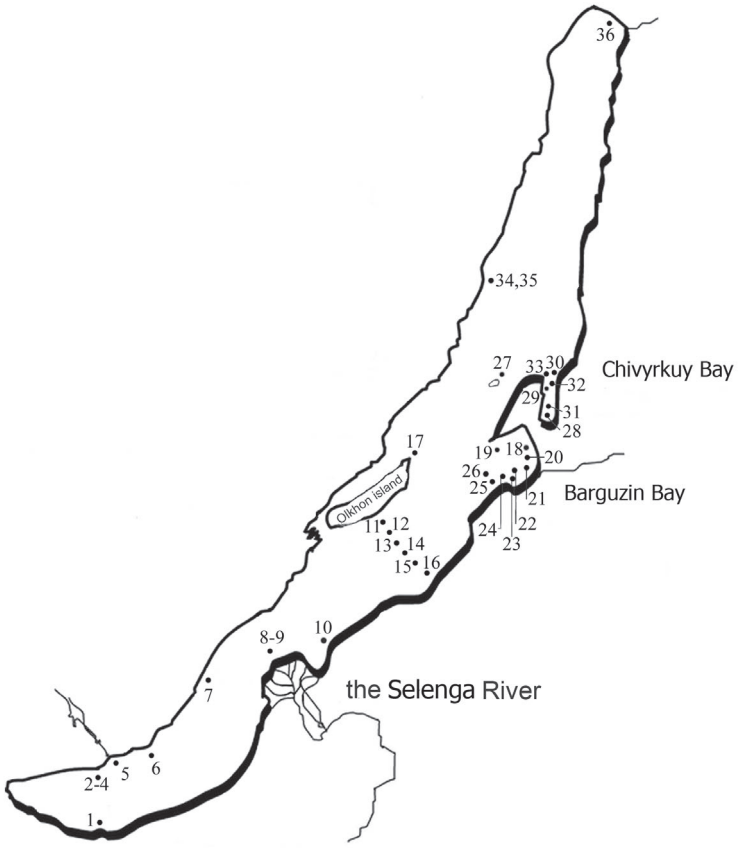

Fig.1. Stations of zooplankton sampling in Lake Baikal in 1993-1997. Numbers are stations

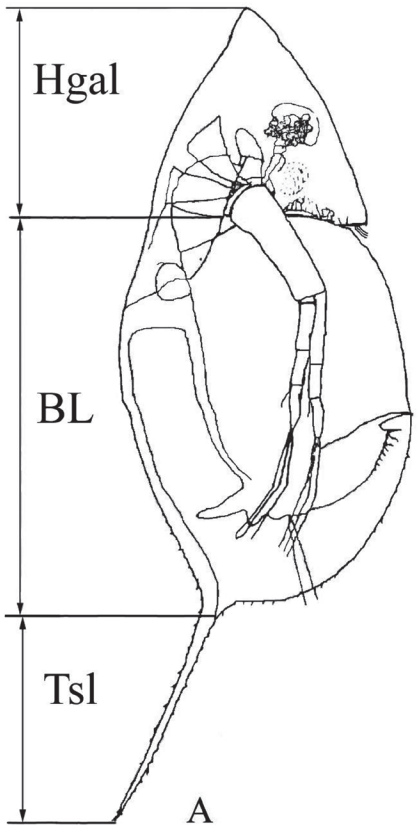

Fig.2. Scheme of morphological traits measurements: HH – helmet height, BL – body length, Tsl – tail spine length

m^3 (St. 18, 20 and 22-24) and 250 mg C/m^3 (St. 28-29 and 21-32), respectively. According to the above data, the established grades are two qualitatively different groups. In the first four ones, the concentrations were by one order of magnitude lower than in the other three ones. Due to this fact, we indicated food concentrations of 19-38 mg C/m^3 as low, and those of 160-250 mg C/m^3 as high.

In order to distinguish the influence of predator and a certain concentration of accessible food on the variability of morphological features, we used the following approach. Firstly, we analyzed the morphological variability of daphnids at low and high food concentrations for the whole data set. Then, based on the same concentrations, we used two selected groups in the presence and absence of the invertebrate predator *L. kindti* in the samples.

The results were statistically processed using standard methods. According to the obtained data, the average value of the trait and the error of the average were calculated. Differences were estimated using Student's test. (Rokitskii, 1973).

3. Results

Table 1 shows variations of the studied features under different conditions (food concentration and presence or absence of predators). Notably, the studied age stages differ significantly by body size. The analysis of results for the whole data set has indicated that body length in juvenile, premature ($t = 4.77$, $t = 6.99$, $P < 0.001$) and adult crustaceans ($t = 2.32$, $P < 0.05$) is indeed larger at high levels of food supply than at low ones. However, mature and premature crustaceans without and with predators clearly demonstrate a different response to feeding conditions. In predator-free sets, their body length is considerably larger at high concentrations, whereas in the sets with predators, mature daphnids are indeed larger at low food level ($t = 4.48$, $P < 0.001$) than at high one, and premature daphnids do not differ statistically ($t = 0.55$). With predators, the body length at all daphnids age groups is larger under different feeding conditions, except for adult specimens at high food supply. Large sizes of crustaceans allow them to have large reserves of nutrients and avoid selective predation due to the size, since invertebrate predators consume mainly small crustaceans. In various elder age groups, juvenile crustaceans do not differ in body size regardless of food concentrations, as well as the presence or absence of predator.

According to all available data, the helmet height in juvenile, premature and mature crustaceans is obviously larger at high concentrations of accessible food. In predator-free set, all studied age stages have no valuable differences in the helmet height, both at low and at high food concentrations. In the presence of predators, juvenile, premature and mature crustaceans have considerably higher helmets at high food concentrations ($P < 0.001$). On the whole, in the presence of predator, both at low and at high food concentration, the helmet is higher than at the same food concentration but without predator. Typically, in predator-free sets, specimens of all age groups have low helmets, without any difference in daphnids sampled at different food concentrations, while in the sets with predators, all specimens of any age stage have high helmets at any food concentrations. This suggests that the presence of predators rather than by food concentration influences the helmet height. In samples with predators at all food concentrations, the helmet is higher than in the absence of predator ($P < 0.001$). In general, the reaction of organisms estimated by the height of the helmet to the studied conditions is obvious.

According to all available data, tail spines at high food concentrations are significantly longer at high concentrations of food than at low ones. At the same time, in predator-free sets, mature and premature crustaceans have no obvious differences in this feature both at high and low food levels. However, the tail spine length in juvenile crustaceans is considerably larger at high food concentrations ($t = 5.83$, $P < 0.001$). In sets with predators, mature and premature crustaceans have obviously longer tail spines at high food concentrations ($t = 5.09$, $P < 0.001$ in mature specimens and $t = 4.33$, $P < 0.001$ in premature specimens). In juvenile crustaceans, the tail spine length does not differ significantly, both at low and at high food concentration. Under all trophic conditions, in the presence of predators, specimens of all age stages have considerably longer tail spines.

Relative helmet height in all analyses indicates the highest values in premature and juvenile crustaceans and the lowest ones in mature daphnids. According to all obtained data, relative helmet size in daphnids of all age stages is large at high food concentrations ($P < 0.001$). However, in predator-free sets, this value is obviously lower in mature and juvenile crustaceans at high food concentrations ($t = 2.42$, $P < 0.05$; $t = 2.51$, $P < 0.05$, respectively), and does not differ in premature ones. In the presence of predators, all age groups have a considerably greater relative helmet height at high food concentrations ($P < 0.001$); moreover, this value is considerably higher at all food concentrations than under predator-free condition. It should be noted that in the presence of predators, at high food concentrations, values of this feature in mature crustaceans increase significantly compared to predator-free conditions.

Relative tail spine length has high values in juvenile and mature specimens and low ones – in mature crustaceans. The analysis of the results for the whole data set on mature ($t = 5.53$, $P < 0.001$), premature ($t = 2.21$, $P < 0.5$) and juvenile ($t = 4.15$, $P < 0.001$) stages showed that relative tail spine length is considerably greater at high food concentrations. Under predator-free conditions, at high food concentrations, this value is obviously lower in adult and premature daphnids ($t = 3.86$, $P < 0.001$ and $t = 4.18$, $P < 0.001$, respectively). In juvenile crustaceans, the relative tail spine length is considerably higher at high food concentrations ($t = 2.40$, $P < 0.001$) than

Table 1. Morphological features of *Daphnia galeata* of different age groups at low and high levels of food supply

Characters	Age	Analysis options					
		All data		Without predators		With predators	
		Low food concentration	High food concentration	Low food concentration	High food concentration	Low food concentration	High food concenration
Number of studed individuals	Mature	818	405	595	78	223	327
	Premature	274	108	174	20	100	88
	Juvenile	590	330	432	90	158	240
Body length (μm)	Mature	948.2 ± 4.14	965.1 ± 6.01*	927.2 ± 4.82	976.4 ± 15.91**	1004.3 ± 6.81	962.4 ± 6.40***
	Premature	790.0 ± 4.04	840.7 ± 6.03***	757.0 ± 4.20	829.1 ± 10.16***	847.5± 4.12	843.2 ± 6.91
	Juvenile	615.4 ± 4.63	654.0 ± 6.65***	590.6 ± 4.84	609.7 ± 11.62	682.9 ± 9.18	670.6 ± 7.78
Helmet height (μm)	Mature	121.9 ± 0.98	160.1± 2.91***	118.4 ± 0.94	112.9 ± 3.67	131.3 ± 2.46	171.3 ± 3.20***
	Premature	114.8 ± 1.80	174.2 ± 6.25***	105.3 ± 1.76	111.3± 4.04	131.3 ± 3.29	189.0 ± 7.10***
	Juvenile	98.8 ± 1.26	129.2 ± 2.89***	90.9 ± 1.19	87.9 ± 2.32	120.4 ± 2.77	144.7 ± 3.37***
Tail spine length (μm)	Mature	459.9 ± 2.67	496.3 ± 4.29***	454.2 ± 3.10	441.3 ± 9.46	474.7 ± 5.10	509.4 ± 4.52***
	Premature	422.4 ± 3.14	469.1 ± 7.80***	411.8 ± 3.29	407.8 ± 8.34	440.9 ± 6.01	482.6 ± 8.73***
	Juvenile	348.9 ± 3.46	397.7 ± 3.86 ***	330.5 ± 3.96	369.3 ± 5.36***	399.2 ± 5.34	408.3 ± 4.73
Relative helmet height	Mature	0.130 ± 0.0028	0.169± 0.0033***	0.129 ± 0.0010	0.118 ± 0.0044*	0.132 ± 0.0025	0.181 ± 0.0036***
	Premature	0.145 ± 0.0021	0.206 ± 0.0074***	0.140 ± 0.0023	0.135 ± 0.0050	0.155 ± 0.0039	0.223 ± 0.0079***
	Juvenile	0.162 ± 0.0018	0.198 ± 0.0039***	0,156 ± 0,0020	0.146 ± 0.0036*	0.177 ± 0.0035	0.217 ± 0.0046***
Tail spine relative length	Mature	0.489 ± 0.0028	0.519± 0.0048***	0.493 ± 0.0032	0.458 ± 0.0101***	0.476 ± 0.0056	0.534 ± 0.0051***
	Premature	0.537 ± 0.0041	0.558 ± 0.0086*	0.546 ± 0.0049	0.493 ± 0.0116***	0.521 ± 0.0070	0.573 ± 0.0096***
	Juvenile	0.587 ± 0.0506	0.615 ± 0.0046***	0.584 ± 0.0061	0.614 ± 0.0093*	0.583 ± 0.0089	0.615 ± 0.0054**

Note: * – $P < 0.05$; ** – $P < 0.01$; *** – $P < 0.001$

at lower ones. In the presence of predators, specimens of all age stages have considerably longer tail spines at high concentrations ($t = 5.09$, $P < 0.001$) than at lower ones. We indicate that in the presence of predators at high food concentrations, this ratio has maximum values in all age groups.

4. Discussion

The obtained results show that both food concentration and predators affect morphological variability of *D. galeata* in Lake Baikal. Moreover, daphniids are likely to be affected by temperature, since high food concentrations were recorded in the bays with higher water temperature (Bondarenko et al., 1991).

The body size of adult and premature daphniids is larger in the absence of predators and at high food concentrations than at low food concentrations. Under such conditions, *Daphnia* grow faster at all stages and their growth continues after reaching maturity (Vijverberg, 1976; Gilyarov, 1987; Romanovsky, 1989; Burns, 1995; Czeczuga et al., 2003; Rinke and Vijverberg, 2005; Freese and Martin-Creuzburg, 2013; Sarpe et al., 2014; Sicora et al., 2014; Gall et al., 2017). Juvenile daphniids have the smallest body size in the absence of predators and at high concentrations of food, since they have minimum sizes with birth and a limited supply of nutrients (Zhukova, 1953; Jacobs, 1987; Dodson, 1989; Gorbi et al., 2011). Mature *Daphnia* have smaller body size in the presence of predators and at high food concentrations. This may be due to the selection in food for numerous predators (Dodson, 1988; 1989; Riccardi et al., 2002; Lagergren et al., 2007; Manca et al., 2008; Korzun and Pitul'ko, 2010; Hülsmann et al., 2011).

The largest crustaceans are recorded in the presence of predators and at low food concentrations. Their large body size prevents from capture by predators and ensures their efficient filtering of food (Havel, 1985; Havel and Dodson, 1985; Dodson, 1988). We have determined that the body size of juvenile and premature crustaceans do not differ in the presence of predators at low and high food concentrations. However, their body size is larger at all food concentrations compared to

Daphnia without predators. Thus, predators positively influence on the growth rate of immature crustaceans. A helmet, tail spine and their relative sizes are less developed in the absence of predators and vice versa. Previously it was shown that the portion of *Daphnia* morphotypes with a high helmet and long tail spine (spined morphotype) is increased under high densities of predators (Korzun and Pitul'ko, 2010; Tams et al., 2018). Consequently, the studied structures have a protective function against predators.

5. Conclusion

Thus, the body size increases but the helmet size and tail spine length decrease at high concentrations of available food. The presence of a predator favours strong development of protective structures in mature and premature *Daphnia*. Juvenile crustaceans in the absence of predators have the smallest dimensions, whereas in their presence they are larger regardless of the food concentration. Therefore, *D. galeata* possess different adaptive responses to changes in food conditions in the presence or absence of predators. Without predators and at low food concentrations, crustaceans grow slower until maturity; then, the growth stops. These crustaceans have a smaller body size but a higher helmet and longer tail spine. In the bays with rich food, the body grows fast throughout life. Different adaptive responses are observed in crustaceans in the presence of predator depending on the conditions of the food supply. Large mature daphnids survive in a lack of food and under pressure of predators; however, they possess weak protective structures. At high food concentrations and strong pressure of predators, mature crustaceans have a smaller body size with more developed protective structures than those at low food concentrations. Therefore, food conditions play a crucial role in adaptive strategies. Different adaptive responses caused by changes in various environmental parameters favour sustainable conservation of *Daphnia* populations and the prevention of their death.

Acknowledgements

We thank V.M. Korzun for the help, advice and friendly criticism in the course of the work on the manuscript and Julia Kaplyukova for translation of the manuscript from Russian into English. The work was performed within the project No. 51.1.1.10 "State, biodiversity and ecology of the coastal zone of Lake Baikal." O.A. Timoshkin).

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Limnology and Freshwater Biology 2019 (2): 205-209 DOI:10.31951/2658-3518-2019-A-2-205

Original Article

ISSN 2658-3518
LIMNOLOGY FRESHWATER BIOLOGY
www.limnolfwbiol.com

The vertical distribution of zooplankton in stratified mesotrophic Lake Arakhley (Eastern Transbaikalia)

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ABSTRACT. We have studied the vertical distribution of zooplankton of a stratified mesotrophic lake. Thus, in August 2011 and 2013, copepods dominated the composition of the zooplankton of the mesotrophic Lake Arakhley and had a density maximum either in the upper euphotic layer or in the area of the metalimnion, with a gradual decrease in the lower layers of water. By 2013, the zooplankton community changed and mainly consisted of cladocerans, and they both dominated in numbers.

Keywords: zooplankton, species composition, vertical distribution, temperature, Lake Arakhley, East Transbaikalia

1. Introduction

The zooplankton community is a complex and multicomponent system determined by many factors. The change in its species composition, quantitative and qualitative parameters with the depth of the water body as well as the factors that determine them are of great theoretical and practical interest. In recent decades, climate warming has been observed, which affects various processes occurring in aquatic ecosystems, including zooplankton communities. In Transbaikalia, air temperature increases by 1.0-1.5 ˚C in winter and by 0.5-1.0 ˚C in summer (Vezhnovets et al., 2012; Feniova et al., 2016). The increase in the surface water temperature by 1.21 ˚C was recorded in Lake Baikal (Moore et al., 2009). The 2011 and 2013 years of the study are from the arid climatic period.

The lake during these years, despite the large area of 59.0 km^2 and the water volume of 0.60 km^3, had an average depth of 10.2 m and a maximum depth of 17.0 m. The transition between the low-water and high-water years is 2017. Temperature, dissolved oxygen concentration, food resources, etc. have a significant effect on the distribution of zooplankton organisms. At the same time, temperature and oxygen are the most important factors in the regulation of zooplankton communities, as well as its spatial and temporal scale of lake ecosystems, since they affect the abundance and structure of zooplankton communities. In this regard, the impact of climate warming reflected in the increase in water temperature on the vertical structure of zooplankton and on subsequent changes in the ecosystem arises the question.

2. Materials and methods of research

Zooplankton studies were performed in the mesotrophic Lake Arakhley (52 ˚ 12’20 “N, lat. 112 ˚ 52’01” E) during the period of thermal stratification of the lake in August from 2011 and 2013. The sampling of zooplankton was carried out at the central station of the lake using a Patalas bathometer (volume 6 l) with triplicate from eight vertical layers every two meters of the water column. Samples were fixed with 4 % formalin. Quantitative processing of the collected material performed in the Kolkwitz and Bogorov chambers. Organisms were calculated and measured on LOMO Micmed-1, MBS-10 microscopes. Animals were determined on Nikon Eclipse E200 and AXIO SCOPE A1 microscopes. Quantification was performed based on generally accepted methods. The species composition of zooplankton was determined by the corresponding determinants. The temperature of the water was measured with a mercury thermometer embedded in the bathometer. At the same time, the temperature was considered together with the sampling of the zooplankton along the horizons of the water column – 0, 2, 4, 6, 8, 10, 12, and 14 m. The water transparency values for the Secchi disk for these years ranged from 4.5 to 6.4 m. Quantitative accounting of the number was carried out on the basis of generally accepted methods (Guidelines ..., 1983). The species composition of zooplankton was determined by the corresponding determinants (Manuylova, 1964; Kutikova, 1970; Borutsky et al., 1991).

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3. Results and discussion

Tables 1 and 2 show the species composition, number and relevance of each species to the selected horizons. In these tables, among all years studied we discuss 2011 and 2013 due to the fact that they have the most distinctive features in the distribution of zooplankton and the number of species. Thus, the dry 2013 showed rotifers of the genera *Brachionus* and *Synchaeta*, which were not previously observed. The number of individual species and the ratio of taxonomic groups in the vertical layers of water in August 2011 and 2013 significantly differed at the level of identical species composition.

The number of zooplankton in the surface layer of water in 2011 was small (2.6 thousand indiv./m^3) and consisted mainly of nauplial copepodite stages of diaptomus, cyclops and rotifers. The maximum number of zooplankton (76.2 thousand indiv./m^3) was observed in the epilimnion at a four-meter depth with 79 % dominance of the copepods, mainly *E. graciloides*. The number of zooplankton in the metalimnion (at a depth of 10 m) was 38.19 thousand indiv./m^3. Cladocerans *D. galeata* represented 60 % of the total number. In the hypolimnion, 52 % of the animals were rotifers – *K. longispina* and *A. priodonta*. Unlike crustaceans, rotifers in August were not the dominant zooplankton group in the epilimnion. Notably, there was a very significant increase in their share at the lower boundary of the metalimnion and in the hypolimnion. Thus, in 2011, different species dominated in number in different vertical layers of water (Table 1).

In 2013, the temperature rise in the surface layers of water reached up to 22 ˚C. Under these conditions, zooplankton animals were distributed over the vertical layers of the water column more or less evenly. The maximum number was observed in the water layer from two to eight meters (up to 69.48 thousand indiv./m^3). Unlike 2011, in 2013, the crustacean *D. galeata* (thermophilic species presented in summer hypolimnion (Stolbunova, 2006; Rivier, 2012)) dominated all layers, and the situation differed fundamentally in Lake Arakhley: the largest proportion of Cladocera (81 %) was in the uppermost oxygenated epilimnion layer at a temperature of 20.0-21.9 ˚C, in metalimnion, with a decrease in temperature to 19.8 ˚C, *D. galeata* also dominated, but was 62 % of the total number of zooplankton. As the depth in the hypolimnion increased (at a temperature of 10.0 ˚C), the relative abundance of *D. galeata* continued to decrease, reaching 52 % in the bottom layer of water. This year, there was a change in the percentage of taxonomic groups due to an increase in the proportion of cladocerans and rotifers in the total number and a decrease in the share of copepods.

The dominant species of zooplankton in different years are presented in Table 3.

Thus, in 2011 *D. galeata* and *E. graciloides* were 22-24 %, and in 2013 *D. galeata* was 65 % of the total number of zooplankton.

Therefore, an increase in temperature can cause a change in the vertical structure of zooplankton and even in the dominant species. The vertical distribution of zooplankton communities in stratified lakes during summer is due to temperature, the abundance of food and the presence of oxygen. These factors affecting the state of the ecosystem regulate the structure and abundance of zooplankton communities. While in August 2011 the surface temperature of water ranged from 18 to 19 ˚C, in 2013 water temperature rose to 21.9 ˚C. We determined that with increasing water temperature there was a change in the percentage of taxonomic groups of zooplankton towards an increase in the proportion of cladocerans and a decrease in the share of copepods. Hence, an increase in the water temperature in low-water and high-water years affects the dominant zooplankton complex in different ways. Thus, with an increase in water temperature in the low-water period, cladocerans and rotifers dominate the zooplankton community, and in the high-water period − copepods (Table 2).

In the vertical distribution of zooplankton over the studied years, the identified features of the species composition, abundance of zooplankton show that in August 2011 copepods *E. graciloides* dominated at a water temperature of 18-19 ˚C, comprising 16-56 % in the upper layers (0-2 m), 73-75% at a depth of 4-6 m, and 49-37 % in metalimnion (8-10 m). In the hypolimnion (12-14 m), the number of organisms was 26-29 % of the number of zooplankton. Therefore, copepods *E. graciloides* were the most dominant at a depth of 4-6 m.

With a further increase in the water temperature to 21.9 ˚C in August 2013, cladocerans, mainly *D. galeata*, dominated the zooplankton community, accounting for 70-80 % in the upper water horizons (0-6 m) with a decrease to 50-67 % in the number of zooplankton in the corresponding layer of water in the horizons of 8-14 m. In 2013, the zooplankton community differed from the previous years. There were changes in the percentage of taxonomic groups towards an increase in the proportion of cladocerans in the total number of zooplankton and a decrease in the proportion of copepods.

We have obtained a vertical distribution of structural changes in zooplankton communities associated with the transformation of the temperature factor over the horizontal layers of the water column (species composition, abundance of zooplankton).

Conclusions

1. We studied the effect of water temperature on the vertical distribution of zooplankton in a stratified mesotrophic lake on the example of Lake Arakhley in the low-water period (when the water level of the lake was 0.35-0.43 m).
2. We revealed that the surface layer of water in August 2011 warmed up to a temperature of 18.1-19.3 ˚ C, and in the warmest 2013 the temperature reached 21.9 ˚C.
3. We found that copepods dominated the zooplankton community in 2011, whereas cladocerans dominated in warm 2013.

Table 1. Species composition and abundance (thousand indiv./m^3) of zooplankton in the water column of Lake Arakhley in August 2011

Species	Depth, m							
	0	2	4	6	8	10	12	14
Cladocera, Crustacea								
Daphnia galeata Sars	0.06	1.56	14.76	11.34	13.08	19.56	3.54	2.76
Ceriodaphnia pulchella Sars	0	0	0.18	0	0.12	0	0	0
Bosmina longirostris (O.F.Muller)	0.06	0	0	0	0.33	0	2.28	2.28
Leptodora kindtii (Focke)	0	0.06	0.24	0.30	0.24	0	0.06	0
Bythotrephes longimanus Leydig	0	0	0.06	0	0.06	0	0.06	0
Alona rectangula Sars	0.06	0	0	0	0	0	0	0
Acroperus harpae Baird	0	0	0	0.06	0	0	0	0
Total Cladocera	0.18	1.62	15.24	11.76	13.83	19.56	5.88	5.04
Copepoda, Crustacea								
naplii	1.02	3.90	0.66	0.36	0.18	0	0.12	0
copepodit	0.42	2.64	1.44	0.45	2.04	2.34	1.80	1.86
Mesocyclops leuckarti *Thermocyclops crassus* (Fisher)	0	0.54	0.06	0.06	0.78	1.47	0.18	0.15
Eudiaptomus graciloides (Lilljeborg)								
naplii	0.36	4.44	1.02	0.72	0.36	0.06	0.78	0.12
copepodit	0.06	1.86	3.62	0.24	1.14	0.36	0.24	0.60
adults	0	9.00	53.10	30.84	17.60	13.26	8.46	8.76
Total Copepoda	1.98	22.38	60.24	32.67	22.08	17.49	11.76	11.64
Rotifera								
Asplanchna priodonta Gosse	0.06	0.12	0.12	0	0.24	0.18	7.92	3.18
Kellicottia longispina (Kellicott)	0	0	0.06	0.06	2.16	0.9	10.5	11.88
Keratella cochlearis (Gosse)	0	0.06	0	0	0	0	0	0
Euchlanis dilatata Ehrenberg	0.30	0.06	0.06	0	0	0	0	0
Conochilus unicornis Rousselet	0.06	0.66	0.33	0	0	0	0	0
Polyarthra vulgaris Carlin	0	1.65	0	0	0	0	0	0
Pompholyx sulcata Hudson	0	0.18	0.18	0	0.18	0	0.12	0.06
Trichocerca multicrinis (Kellicott)	0	0.30	0	0	0.36	0.06	0	0.06
Filinia longiseta (Ehrenberg)	0	0	0	0	0	0	0.24	0.66
Total Rotifera	0.42	3.03	0.75	0.06	2.94	1.14	18.78	15.96
Total	2.58	27.30	76.23	44.49	38.85	38.19	36.42	32.64

Note: 0 – the species is absent.

Table 2. Species composition and abundance (thousand indiv./m^3) of zooplankton in the water column of Lake Arakhley in August 2013

Species	Depth, m							
	0	2	4	6	8	10	12	14
Cladocera, Crustacea								
Daphnia galeata Sars	32.52	55.74	33.46	24.96	34.02	34.98	37.38	19.92
Ceriodaphnia pulchella Sars	0	0	0	0	1.32	0.18	0	0
Bosmina longirostris (O.F.Muller)	3.12	1.92	1.62	1.44	4.56	4.32	1.74	1.98
Leptodora kindtii (Focke)	0	0	0.06	0	0.36	0.12	0.06	0
Bythotrephes longimanus Leydig	0	0	0.06	0	0	0	0	0
Chydorus sphaericus (O.F. Muller)	1.08	0.12	0	0	0	0	0	0
Total Cladocera	36.72	57.78	35.20	26.40	40.26	39.66	39.18	21.90
Copepoda, Crustacea								
naplii	1.74	2.04	1.98	1.74	11.76	4.02	1.80	1.80
copepodit	1.50	2.46	1.20	1.32	6.12	5.06	5.64	8.40
Mesocyclops arachlensis Alekseev	0.12	1.86	1.38	2.04	1.56	0.42	1.44	0.84
Thermocyclops crassus (Fisher)	0.42	0	0	0.06	0.12	0.36	5.82	2.70
Macrocyclops albidus (Jurine)	0.06	0	0	0	0	0.12	0.12	0
Eudiaptomus graciloides (Lilljeborg)								
naplii	0.96	0.90	0.90	0.36	5.10	2.16	0.12	0.54
copepodit	0	0	0	0	0	0	0	0.06
adults	0	0	0	0	0	0	0	0.06
Total Copepoda	4.80	7.38	6.18	5.85	24.72	12.14	14.94	14.4
Rotifera								
Asplanchna priodonta Gosse	0.18	0.12	0.18	0.06	0.24	0.48	0.54	0.06
Kellicottia longispina (Kellicott)	0.60	0.66	0.60	0	0.54	0.84	0.24	0.48
Keratella cochlearis (Gosse)	0.90	0.36	0.30	0.24	0.78	0	0.18	0.18
K.quadrata (Muller)	0.06	0	0.18	0	0.12	0.18	0	0.12
Euchlanis dilatata Ehrenberg	0	0	0	0	0	0.54	0	0
Conochilus unicornis Rousselet	0.06	0.06	0.12	0	0	0	0	0
Polyarthra vulgaris Carlin	0.24	0.18	0	0.33	0.24	0.12	0.12	0.54
Pompholyx sulcata Hudson	0	0	0	0	0.06	0.30	0	0.18
Trichocerca multicrinis (Kellicott)	2.10	2.94	1.92	2.16	1.14	1.50	0.18	0.12
Filinia longiseta (Ehrenberg)	0.06	0	0	0.06	0	0.06	0.18	0.9
Synchaeta sp.	0	0	0	0	0.18	0	0	0
Brachionus sp.	0.12	0.06	0	0	0	0	0	0.06
Total Rotifera	4.32	4.32	3.24	2.97	3.30	4.02	1.44	2.70
Total	45.84	69.48	44.62	35.22	68.28	55.82	55.56	39.10

Table 3. The dominant zooplankton complex of Lake Arakhley in 2011 and 2013

2011	% of the total abundance	2013	% of the total abundance
Eudiaptomus graciloides	22	*Daphnia galeata*	65
Daphnia galeata	24	*Eudiaptomus graciloides*	22
Kellicottia longispina	9	*Trichocerca multicrinis*	3

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Limnology and Freshwater Biology 2019 (2): 210-217 DOI:10.31951/2658-3518-2019-A-2-210

Original Article

ISSN 2658-3518
LIMNOLOGY FRESHWATER BIOLOGY
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Microbiological water quality of Lake Baikal: a review

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ABSTRACT. The article provides information about the sanitary-bacteriological studies conducted in the water area of Lake Baikal. We show the data on the long-term observations of the spread and abundance of fecal indicator bacteria and potentially pathogenic bacteria in the pelagic and littoral waters of the lake. We also present a review of the standards and methods for the sanitary-bacteriological water quality worldwide, techniques for detecting fecal indicator bacteria, including those specific for human microbiota, methods for microbial source tracking, as well as studies of the spread and retaining of fecal indicator bacteria in various ecotopes, such as bottom sediments and biofilms. For the sanitary-bacteriological monitoring of Lake Baikal, we propose an integrated approach based on the application of modern techniques that correspond to world practice. This approach would allow identification of the sanitary adverse sites and more reliable and standardized assessment of the Baikal water quality.

Keywords: monitoring, surface water, water pollution, fecal indicator bacteria, coliforms, enterococci, Lake Baikal

Sanitary and microbiological characteristics of Lake Baikal: history and current state

Water is an essential condition of life as well as a necessary resource for the implementation of economic activities. The surface waters of the planet are subject to the intensive anthropogenic impact, since the population uses them for many purposes, such as recreation, water consumption, irrigation, fishery, wastewater discharge, reservoir construction, etc. Nowadays, the ecological state of freshwater bodies as the main sources of drinking water is deteriorating throughout the world, which leads to the disruption of the evolutionary formed microcenoses and the development of the pathogenic and opportunistic bacteria in them (Thevenon et al., 2012; Sales-Ortells et al., 2015; Strathmann et al., 2016; Lenart-Boron et al., 2017; Korajkic et al., 2018). The problem of chronic fecal pollution has long been recorded for the complexes of Great Lakes of North America and African Great Lakes that serve as a source of drinking water for hundreds of millions of people. Thus, during the past decade waters and beaches of Lake Huron and Upper Lake are considered as dangerous for swimming and recreation due to high concentrations of coliform bacteria and enterococci (Kon et al., 2007; Newton et al., 2013; Ran et al., 2013; Harwood et al., 2017). The water quality of Victoria and Kivu lakes also have poor sanitary state (Byamukama et al., 2000; Olapade, 2012). Chronic fecal pollution of freshwater bodies has also become one of the primary problems in European countries. Monitoring of the sanitary state of Lithuanian and Belgian lakes and rivers indicated the low microbial quality of waters (Ouattara et al., 2011; Staradumskyte and Paulauskas, 2012). Sediments of Lake Geneva and tributaries of Lake Onega showed a high abundance of opportunistic microflora (Thevenon et al., 2012; Tekanova et al., 2015).

In recent years, the water quality of the world's oldest and deepest Lake Baikal has been also evidently deteriorating. The volume of fresh water in the lake is 20 % of all fresh water in lakes and rivers of our planet (Atlas of Lake Baikal, 1993). It is a source of water consumption and recreation for locals. The large settlements located directly on the Baikal coast, where the industrial and agricultural activities are carried out, are significant sources of pollution. These are the Slyudyanka and Baikalsk towns, the Kultuk settlement, the Severobaikalsk town, the Nizhneangarsk town, the Goryachinsk settlement, and the Babushkin town. The Selenga River, which places the capital of the Republic of Buryatiya, a city of Ulan-Ude, also poses a potential danger as a source of pollution (Grachev, 2002).

Microbiological studies of Lake Baikal have been conducting for more than a hundred years (Parfenova et al., 2016; Belykh and Drucker, 2018). According to long-term observations, microbial indicators in the pelagic zone of Lake Baikal were rather constant for a long time. The pelagic waters of Lake Baikal contained mainly single quantities of fecal indicator bacteria (FIB).

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FIB in surface waters were found mostly in summer, near settlements and the mouths of large tributaries of the lake (Drucker et al., 1993; Parfenova et al., 2009a). Observations conducted in the second half of the 20th century detected significant number of FIB mainly in the southern basin of the lake, in the surface waters of the littoral zone near the wastewater discharge of Baikalsk Pulp and Paper Mill (BPPM) (Goman, 1973; Maksimova and Maksimov, 1989; Maksimova et al., 1998; Shchetinina et al., 2003; 2013; Verkhozina et al., 2003). In the littoral zone of the same wastewater discharge area, there was contamination with hepatitis A viruses and rotaviruses. In deep areas, there were no anthroponotic viruses and FIB (Maksimov et al., 2003; Shchetinina et al., 2013). For 47 years of the BPPM operation, the waters of the Southern Baikal have been subject to constant anthropogenic load in the form of the BPPM wastewaters as well as domestic sewage of the Baikalsk town, which is fed to the treatment facilities until now. From 2000 to 2009, there was an increase in the sanitary-bacteriological indicators near the BPPM wastewater discharge (Shchetinina et al., 2013). The deterioration of the sanitary situation initiated studies of the diversity and antibiotic resistance of bacteria isolated from the lake areas with a high anthropogenic impact (Shchetinina and Maksimov, 1999; Verkhozina, 2003; Savilov et al., 2008). The distribution and determination of species composition of potentially pathogenic bacteria (PPB): bacteria of Enterobacteriaceae family and non-enzymatic group (Panasyuk, 2002) as well as bacteria of the genus *Enterococcus* (Kravchenko, 2009), were of special attention. The PPB distribution throughout the water area of the lake was uneven and associated with the settlements, the mouths of the main tributaries and the sites discharging insufficiently treated domestic sewage. They showed the highest abundance in the south of Baikal (the Bolshiye Koty, Listyanka, Port Baikal settlements and Baikalsk town) as well as in the central part of Baikal (Barguzin and Chivyrkuy bays and the Selenga delta). The PPB number naturally increased during the summer and autumn and decreased in the winter months. The isolated PPB showed poly-resistance to antibiotics, haemolytic activity and ability to adapt to low-temperature environmental conditions; hence, they have a potential epidemic hazard to human health. In addition, the results of the research implied using extra FIB for control of the water quality. They can be considered as specific indicators of the fecal water influx. These FIB are *Pseudomonas aeruginosa*, *Enterobacter cloacae*, *Citrobacter freundii*, *Burkhalderia cepacia* and bacteria of the genus *Enterococcus* (*E. faecium, E. avium, E. faecalis, E. mundtii, E. hirae, E. durans,* and *E. gallinarum*), which were detected in the water area of the lake (Panasyuk, 2002; Panasyuk et al., 2002; Drucker and Panasyuk, 2006; Parfenova et al., 2008; 2010; Kravchenko, 2009; Parfenova, 2009).

In recent years, the Baikal ecosystem has been experiencing a serious ecological crisis. The coastal areas have signs of eutrophication, i.e. intensive development of algae that are non-specific for the littoral zone of Lake Baikal, a mass death of sponges and toxic cyanobacterial blooms (Kravtsova et al., 2012; 2014; Belykh et al., 2016; Khanaev et al., 2016; Kobanova et al., 2016; Potapskaya et al., 2016; Suturin et al., 2016; Timoshkin et al., 2014a; 2014b; 2015; 2016; 2018). The poorly treated sewage from the settlements located on the coast are discharged to the lake waters; the tourist load and the number of vessels increase. The number of tourists visiting the Baikal coast has increased manifold over the period of 2012-2015. The annual number of the officially registered tourists at Lake Baikal is approximately 2.2 million people (2015), which is associated with the active development of the infrastructure in this industry, particularly, the accommodation sector. More than 40 recreational development zones have formed directly on the Baikal coast. They concentrate most of the tourist accommodation facilities, i.e. tourist camps, hotels, holiday houses, etc. (Evstropyeva, 2016). The sanitary-bacterial monitoring from 2010 to 2017 indicated FIB in the waters of the lake for the entire research period. There were near-mouth sites of the Turka, Barguzin, Buguldeika, Goloustnaya, and Sukhaya Anga rivers as well as the Selenga delta, where a high FIB abundance was detected most frequently during this period. In 2011, there was the exceeding the RF standards throughout the pelagic zone of Lake Baikal and in most of its major tributaries. Furthermore, in 2012 pelagic water in the southern part of the lake had an unfavourable microbiological and sanitary state. The littoral zone showed significant number of FIB near the Listvyanka settlement and the Baikalsk town in the southern basin of Baikal, in the waters of the Maloye More and Olkhonskiye Vorota straits and the Selenga delta – in the central basin, as well as, in the coastal waters of the Severobaikalsk town and the Zarechny settlement – in the northern basin (Kovadlo and Drucker, 2010; Timoshkin et al., 2014a; Verkhozina et al., 2014a; Bondarenko et al., 2015; Shtykova et al., 2016; 2017; 2018a; 2018c; Suslova et al., 2017a; 2017b; 2018a). PPB characterized by resistance to a wide range of antibiotics were present and accumulated in various ecotopes of the Baikal coastal zone (in the water column, epilithic and neuston biofilms, sponges and bottom sediments) (Verkhozina et al., 2014b; Shtykova et al., 2018b).

The studies have shown that the waters of Lake Baikal experience an intensive anthropogenic load, which has been steadily increasing recently. The FIB distribution is uneven and local in nature mainly due to the association with the sites of the anthropogenic impact on the lake, which the data on chemical analysis also confirm (Khodzher et al., 2017). They show the maximum abundance in the estuarine zones of the rivers, and it gradually decreases with the river waters flowing to the lake (Parfenova et al., 2009b). The results of the studies suggest that under the influence of the anthropogenic factors in the coastal areas of the lake, there is a shift of the autochthonous microbiota towards the allochthonous one, which is highly resistant to antibiotics. The presence of the additional factors that contribute to the PPB persistence and reproduction would reduce the ability of the coastal Baikal waters to

self-purification to such a degree that their use would be epidemiologically dangerous. This leads to the need to develop a water quality management strategy for Lake Baikal.

Review of modern criteria and methods for assessing microbiological water quality

Sanitary and bacteriological assessment of water quality imply determination of a set of sanitary indicators, i.e. criteria that reflect compliance or non-compliance of the sanitary state of the studied water body with the requirements of regulatory documents. FIB serve as these sanitary indicators. They are used throughout the world to detect and prevent fecal contamination and its associated human health risk, since they indicate the probable presence of pathogenic bacteria and viruses. FIB include such bacteria as total coliforms, thermotolerant coliforms, fecal coliforms, *E. coli*, enterococci, *Bifidobacterium*, *Bacteroides*, and *Clostridium* spp. These FIB are widespread in faeces of humans and most animals. Their levels in wastewater and faeces are rather high; therefore, with fecal contamination, they are usually present in surface waters (Harwood et al., 2017; Aguirre et al., 2019). The surface water monitoring includes using FIB abundances. Various regulations establish FIB standards to determine water quality (Table 1).

In the Russian Federation, sanitary rules SanPiN 2.1.5.980-00 «Water disposal of the populated areas and sanitary protection of water bodies. Hygienic requirements for the protection of surface water» regulate the compliance of the quality of surface water sources with sanitary standards. This regulatory document divides water bodies into two categories. The category I includes water bodies or their sites used as a source of drinking and domestic water consumption as well as water supply for food industries. The category II includes water bodies or their sites used for recreational purposes. The water quality requirements established for the water use category II applies, inter alia, to all sites of water bodies within the boundaries of the populated areas (SanPiN 2.1.5.980-00). Indicator of total coliforms, which reflects the water treatment quality, and indices of thermotolerant coliforms and coliphages, which reflect the degree of fecal contamination, are the main standardized indicators in the Russian Federation that used in assessing the sanitary and microbiological state of the water body (MUK 4.2.1884-04; SanPiN 2.1.5.980-00; Tymchuk et al., 2013). In the presence of epidemiological evidence, the indicators of the abundance of *Clostridium* spp., enterococci, *Staphylococcus* spp., and *E. coli* are additionally used, and the coefficient of self-purification is determined through calculating the total number of mesophilic aerobic and facultative anaerobic microorganisms (total microbial number) capable of forming colonies on meat-peptone agar (MPA) at 37 ° C for 24 hours and at 22 ° C for 72 hours.

The Russian system of sanitary and microbiological standards differs in many aspects from its counterparts abroad. The analysis of the standards stipulated by the regulations listed above has shown that the Russian standards of water quality for recreation are rather strict compared to the European and American regulations (Table 1). They do not allow the presence of any pathogens of intestinal infections and even twice limit the total number of coliform bacteria than the water EU standard for the classification «Good». Unlike SanPiN2.1.5.980-00, its counterpart regulation does not standardize physical and chemical indicators as well as the level of radioactive contamination at all (Tsoupikova, 2016). However, it should be noted that in the EU countries and USA, FIB (*Escherichia coli*, *Enterococcus faecalis* and *Clostridium perfringens*), as well as bacterial genera *Bacteroides* and *Bifidobacterium*, which are more specific to human body and warm-blooded animals, have long been directly detected, since they typically present in human faeces in higher quantities compared to *Clostridium* spp., enterococci, *E. coli* and other coliforms (Newton et al., 2011; Tymchuk et al., 2013; Harwood et al., 2017). This makes the water quality assessment more standardized and reliable.

In the world practice of sanitary research, new methods and approaches to the assessment of the sanitary state of water bodies are constantly appearing and being introduced. To detect and count FIB, accelerated identification methods using chromogenic media (GOST 24849-2014, 2016) are used, and the studies focused on the direct detection of *E. coli* (litmus paper test «DipTest») are conducted (Gunda et al., 2017). However, the cultivation methods often yield false positive results and do not consider uncultivated bacteria; therefore, the development and use of sensitive methods for the rapid detection and counting of FIB in water are recently relevant. These rapid methods are the nucleic acid-based, immunology-based and biosensor-based detection (Deshmukh et al., 2016; Darkazanli et al., 2018). The U.S. Environmental Protection Agency has long ago developed and implemented standardized procedures for the accelerated identification of Enterococci and Bacteroidales using Quantitative Polymerase Chain Reaction (qPCR) (USEPA, 2010; 2012b; 2013).

Nevertheless, the detection of FIB in environmental waters does not provide the information about the pollution source, since many members of this group are ubiquitous in the environment. FIB can be both fecal and environmental (Leclerc et al., 2001). Identification of the source is crucial for risk assessment and its elimination, since not all fecal sources are equally hazardous to human health. For example, human fecal contamination generally has the greatest risk due to the possible presence of human viral and bacterial pathogens, whereas cattle fecal contamination indicates the possible presence of zoonotic pathogens. Therefore, the adequate assessment of the sanitary state of the water body and the protection of human health requires microbial source tracking (MST) of fecal contaminations. Such methods are being developed in many countries (Bower et al., 2005; Newton et al., 2011; 2013; Harwood et al., 2017). There are still no formal regulation or methodologies for conducting MST,

Table 1. The norms and standards of FIB in surface recreational waters

Area, state	Limit for fecal indicator bacteria	Guideline, norm, or standard
Russia	Main indicators: Absence of pathogenic bacteria; Coliphages 10 PFU/100 mL; Thermotolerant coliforms 100 CFU/100mL; Total coliforms 1000 CFU/100mL (water use category for drinking and domestic water supply), 500 CFU/100mL (water use category for recreational water, and within cities); Additional indicators: The ratio of the total microbial number (TMN) of 22 °C to TMN of 37 °C is 4 and above; *E. coli* 100 CFU/100mL; Enterococci 50 CFU/100mL; Staphylococci 10 CFU/100mL	Hygienic requirements for the protection of surface water (SanPiN 2.1.5.980-00); Sanitary-microbiological and sanitary-parasitological analysis of surface water bodies (MUK 4.2.1884-04)
EC (EU)	*Inland waters:* Classification «Excellent» (95th percentile of log10 densities): Enterococci 200 CFU/100mL, *E. coli* 500 CFU/100mL; Classification «Good» (95th percentile of log10 densities): Enterococci 400 CFU/100mL, *E. coli* 1000 CFU/100mL; Classification «Sufficient» (90th percentile of log10 densities): Enterococci 330 CFU/100mL, *E. coli* 900 CFU/100mL; *Coastal waters and transitional waters:* Classification «Excellent» (95th percentile of log10 densities): Enterococci 100 CFU/100mL, *E. coli* 250 CFU/100mL; Classification «Good» (95th percentile of log10 densities): Enterococci 200 CFU/100mL, *E. coli* 500 CFU/100mL; Classification «Sufficient» (90th percentile of log10 densities): Enterococci 185 CFU/100mL, *E. coli* 500 CFU/100mL	Directive 2006/7/EC of the European Parliament and of the Council of 15 February 2006 concerning the management of bathing water quality (Directive 2006/7/EC)
USA	*Recommendation 1* (for an estimated illness rate of 36/1,000): Enterococci (marine and freshwater) 35 CFU/100mL (geometric mean), 130 CFU/100mL (10% statistical threshold value); E. coli (freshwater only) 126 CFU/100mL (geometric mean), 410 CFU/100mL (10% statistical threshold value); *Recommendation 2* (for an estimated illness rate of 32/1,000): Enterococci (marine and freshwater) 30 CFU/100mL (geometric mean), 110 CFU/100mL (10% statistical threshold value); E. coli (freshwater only) 100 CFU/100mL (geometric mean), 320 CFU/100mL (10% statistical threshold value)	Recreational Water Quality Criteria (USEPA, 2012a)
Brazil	Total coliforms < 5000 CFU/100mL in 80% of at least 5 monthly samples; Fecal coliforms < 1000 CFU/100mL in 80% of at least 5 monthly samples	Regulation/GM/No. 0013: Classifying domestic water courses in order to protect their quality (Brazilian Ministry of Health, 1976)
Japan	Fecal coliforms 1000 CFU/100mL	Environmental Quality Standards Regarding Water Pollution (Japan Environment Agency, 1986)
Kenya	Fecal coliforms < CFU/100mL, Total coliforms CFU/100mL	Environmental management and coordination (Water quality) regulations (Republic of Kenya, 2006)

PFU − plaque-forming units; CFU – colony-forming units

but in the U.S. Environmental Protection Agency the standardized procedures are already being developed (Harwood et al., 2017).

Monitoring of the microbiological quality of surface waters is usually limited to testing the water column. At the same time, the studies show that fecal bacteria occur in the bottom sediments of freshwater bodies and can be resuspended from the sediments during human activities or natural processes, which would increase their number in the water column (Haller et al., 2009; Thevenon et al., 2012). Bottom sediments may contain from 100 to 1000 more FIB than the water column, since FIB can persist longer in bottom sediments due to a high content of organic compounds in them and protection from insolation (Davies et al., 1995). Moreover, FIB in bottom sediments may

represent a more stable indicator of the water quality than in the water column (Thevenon et al., 2012). Epilithic biofilms in freshwater bodies can also serve as a reservoir for pathogenic bacteria (Ksoll et al., 2007; Balzer et al., 2010; Gubelit et al., 2011). The presence of coliform bacteria in biofilms and bottom sediments of Lake Baikal has been already recorded (Namsarayev and Zemskaya, 2000; Shtykova et al., 2018b; Suslova et al., 2018b; Sukhanova et al., 2019). The presence of fecal bacteria in biofilms and bottom sediments suggests that in such a way these bacteria adapt to adverse environmental factors and circulate in the autochtonous community. The study of these processes is especially important, since at present the antibiotic-resistant PPB are distributed in water bodies. The water area of Lake Baikal also shows an alarming trend in the detection of antibiotic-resistant strains (Parfenova et al., 2008; Verkhozina et al., 2014b). The ingress of antibiotic-resistant strains into the environmental objects maintains a pool of resistant strains due to the transfer of resistance genes to the autochtonous bacterial communities of the ecosystem. The transfer of antibiotic-resistance genes in the environmental communities is of special attention worldwide. The spread of antibiotic-resistant genes among bacteria increases morbidity and mortality from the infections they cause (Ashbolt et al., 2013; Berglund, 2015; Xu et al., 2018).

In addition to the anthropogenic factors, climatic, hydrochemical and hydrological conditions also influence the sanitary-bacteriological state of water bodies, which should be considered during monitoring (Gutierrez-Cacciabue et al., 2014). The effective monitoring of surface waters requires processing a large amount of data using various multivariate statistical techniques. Multivariate data processing is widely used to characterize and assess surface water quality and is useful for identifying temporal and spatial changes caused by natural and anthropogenic factors. The use of multivariate techniques allowed for optimizing monitoring tasks (Aguirre et al., 2019).

Conclusion

Based on the analysis of long-term studies and foreign methodologies for sanitary assessment of water quality, there is an obvious need to develop an algorithm for monitoring the sanitary-bacteriological state of Lake Baikal. Monitoring would include not only the identification of indicator levels and their comparison with standards according to the RF regulatory documents but also the detection of a wider range of FIB using modern methods for identifying and tracking the sources of fecal contamination, which correspond to the world practice. In order to determine the sites that are most susceptible to anthropogenic impact, monitoring should be supplemented with the study of the diversity and distribution of PPB isolated from various ecotopes of the lake (water, bottom sediments and biofilms) as well as determination of the proportion of the antibiotic-resistant strains among these bacteria and autochtonous microbiota. Such an approach would allow not only detection of the potentially pathogenic bacteria in the ecosystem but also a complex diagnostics of their state in order to determine a degree of the potential hazard of the Baikal waters to human health. A holistic approach to monitoring requires using multivariate statistic techniques, considering climatic, hydrochemical and hydrological data.

The assessment of the current sanitary-bacteriological state of Lake Baikal is increasingly relevant each year in order to preserve its uniqueness. It is important to consider key threats to the Baikal ecosystem, including anthropogenic impact, i.e. lack of the wastewater treatment plants, the spontaneous development of the lake coast, the lack of communal infrastructure of tourist places, and the increase in water transport. The analysis of water used by the population as a source of domestic, recreational and even drinking water supply is becoming important due to the cluster organization of tourist zones in the coastal area of Lake Baikal. The application of modern techniques that correspond to the world level would allow assessment of the sanitary state of Lake Baikal as well as its possible use as a source of drinking water and a recreational object. The monitoring results would contribute to the protection of the lake ecosystem and human health.

Acknowledgements

This work was carried out within the state task, project No. 0345-2019-0003 (Microbial and viral communities in biofilms…; AAAA-A16-116122110061-6).

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Limnology and Freshwater Biology 2019 (2): 218-222 DOI:10.31951/2658-3518-2019-A-2-218

Original Article

ISSN 2658-3518
LIMNOLOGY FRESHWATER BIOLOGY
www.limnolfwbiol.com

Changes in diatom and chironomid assemblages of boreal taiga in East Siberia (58N, Lake Aunakit, Russia) during the last 4.2 ka

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ABSTRACT. In this study, we analysed a 64 cm long sediment record from Lake Aunakit located on the Kropotkin Range (East Siberia, Russia) for subfossil diatoms and chironomids to provide an improved reconstruction of the environmental changes in the area for the past 4.2 ka. Diatom record is divided into four zones (0-0.84, 0.95-1.25, 1.3-2.0 and 2.0-4.2 ka BP). Duration of chironomid record is 1.8 ka, and this record is divided into five zones 1.8-1.5, 1.5-1.4, 1.4-1.25, 1.25-0.6, and 0.6-0 ka BP.

Keywords: diatoms, chironomids, reconstruction, lake, bottom sediments, East Siberia

1. Introduction

In the global scale, contrasting climate changes, so-called the Subboreal and Subatlantic periods of the Holocene, characterise time interval during the past 4 ka. Modern warming appears clearly in the high latitudes of the Northern Hemisphere. Probably, the previous climate changes were also contrasting, which paleo records from high latitudes indicate.

Diatom and chironomid records are a good proxy of paleoclimate changes. Thus, chironomid records are sensitive to annual summer air temperatures (Brooks and Birks, 2001; Heiri et al., 2003), and a time lag between changes of air temperatures and chironomid taxa is probably minimal. Diatoms are well-known to depend on water temperature, duration of open and close water, insolation and supply of nutrients into the water.

Lake Aunakit is located in the northern part of East Siberia (Russia), on the Kropotkin Ridge (Fig. 1). Lake Aunakit (58º31'N, 114º86'E) is a small freshwater lake located at 1033 m above sea level, with an area of approximately 0.03 km^2. The climate in this region is continental, as reflected by the large differences of temperature. The annual temperatures are from -5 to -7 ºC, whereas the mean January temperatures are lower than -30 ºC with a drop to -60 ºC, and the mean July ones are 16-18 ºC and up to 38 ºC. There is a stable snow cover from October to May. The annual precipitation ranges from 220 to 380 mm, with the precipitation largely (55-60%) accumulating during the summer months. Duration of the warm period is *ca.*130 day/year.

In this study, we attempted to detail environmental changes in the northern part of East Siberia during the middle Holocene by the diatom and chironomid records.

Fig.1. Location of Lake Aunakit

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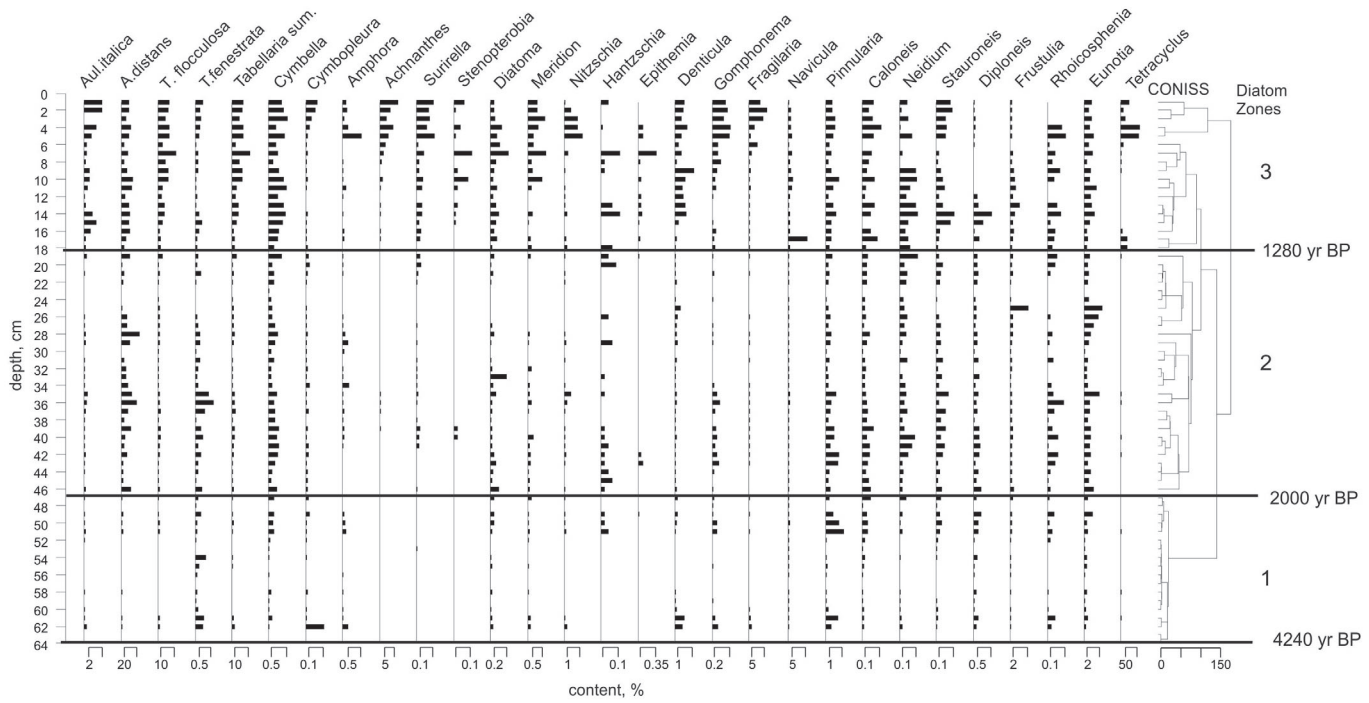

Fig.2. Distribution of main diatom taxa throughout of the sediment core and division of diatom zones (DZ) by CONISS method

2. Methods

In 2018, a sediment core was taken from the central part of Lake Aunakit (64 cm long) using a Uwitec Corer sampler. The water depth was 6 m at the core sampling site.

2.1 Diatom analyses

The cores were sampled with 1 cm intervals. Siliceous microfossils were quantitatively determined by counting permanent smear slides prepared according to the method described in Grachev et al. (1997). Diatom frustules (from 400 to 800 frustules per sample) were identified using keys, atlases and a reference collection (Round et al., 1990; Glezer et al., 1992).

2.2 Chironomid analyses

The cores were sampled with 1 cm intervals. Samples of 1cm^3 for chironomid analysis were immersed in concentrate HF; after 24 h the acid was washed out, and, then, the samples were washed through a 100-μm sieve with a sampling resolution of 1 cm. The remains of chironomid head capsules were identified according to Pankratova (1970; 1977; 1983) and Makarchenko (1982; 2006).

2.3 Depth-age model

The total radiocarbon content in the graphitized samples was quantified by AMS engineered at Budker Institute of Nuclear Physics (Novosibirsk, Russia). The total 14C content was measured relative to ^{13}C and normalized to NIST standards). Chemical pre-treatment and graphitization of samples were carried out in Laboratory of Radiocarbon Methods of Analysis at Novosibirsk State University using laboratory installation (Lysikov et al., 2018). Four sediment layers were dated (Table 1). Calendar date was evaluated from the radiocarbon one by CalPal ver.1.5.

3. Results and Discussion

Table 1. Results of AMS radiocarbon dating of the lake bottom sediments

Depth below sediment surface, cm	Lab.code	^{14}C age, yrs BP	Calendar age, yrs cal BP
7.5	BINP_NSU_1394	1077 ± 65	1006 ± 60
25*	BINP_NSU_1395	2416 ± 74	2524± 65
47.5	BINP_NSU_1396	2072 ± 66	2052± 65
63.5	BINP_NSU_1397	3783 ± 66	4172± 65

* the sample most likely contains old carbon.

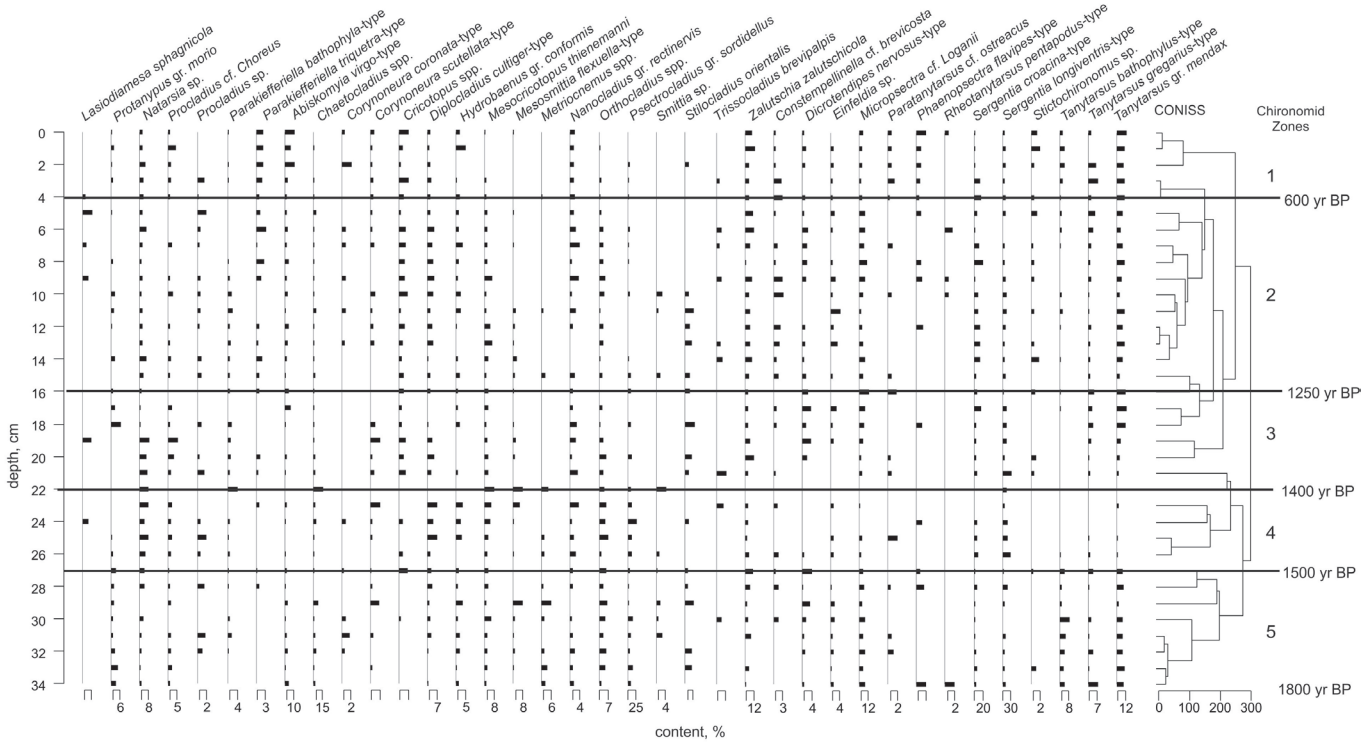

Fig.3. Distribution of main chironomid taxa throughout the sediment core and division of chironomid zones (ChZ) by CONISS method

According to the obtained dates, the bottom layer (64 cm) in sediment core was formed *ca.* 4.2 ka (Table 1). Only one data (25 cm) shows nonlinear chronology due to the presence of old carbon.

Ninety-two species represent diatom assemblages of the sediment core. The number of plankton diatoms changed from 0.02 to 126.6x10^6 frustules g^{-1} dry weight throughout the core. There were six plankton species, with *Aulacoseira italica* (Ehrenberg) Simonsen (up to 8.14x10^6 frustules g^{-1}), *A. distans* (Ehrenberg) Simonsen (up to 117.2x10^6 frustules g^{-1}), *Tabellaria flocculosa* (Roth) Kützing (67x10^6 frustules g^{-1}), and *T. fenestrata* (Lyngbye) Kützing (2.4x10^6 frustules g^{-1}) dominating in all records (Fig. 2). Single frustules of two species of the genera Cyclotella were found in the uppermost sediment layer. These dominant species are typical of oligotrophic-mezotrophic freshwater lakes with low or neutral pH (Barinova et al., 2006; Kharitonov and Genkal, 2012).

The number of benthic diatoms was 0.014-287.3x10^6 frustules g^{-1}. There was a great number of Tetracyclus (up to 228.7x10^6 frustules g^{-1}), Eunotia (up to 12.7x10^6 frustules g^{-1}), Frustulia (up to 12.7x10^6 frustules g^{-1}), and Achnanthes (up to 19.5x10^6 frustules g^{-1}). Content of chrysophycean cysts was 10-112x10^6 specimens g^{-1}.

Based on CONISS analysis, we divided diatom records into four local zones (DZ) (Fig. 2). In the DZ-1 (0-6 cm below the sediment surface, bss, *ca.* 0-0.84 ka BP), the total content of diatoms was 98.24-397x10^6 frustules g^{-1}. Benthic diatoms were dominant, 53.6-73.7% of total diatoms, with the highest content of Tetracyclus. *Aulacoseira distans* (14.2-24.0%) and *Tabellaria flocculosa* (10.4-18.2%) dominated plankton diatoms.

The DZ-2 (7-18 cm bss, *ca.* 0.95-1.25 ka BP) was characterised by a decrease in diatoms to 57.1-159.3x10^6 frustules g^{-1}. *A. distans* (16-56.7%) and *T. flocculosa* (6-43.3%) dominated diatom assemblages.

In the DZ-3 (19-46 cm bss, *ca.* 1.3-2.0 ka BP), the number of diatoms varied strongly between 0.41 and 141.84x10^6 frustules g^{-1}. The minimum content of frustules was at 23 cm bss. *A. distans* (21.3-82.6%), *T. flocculosa* (5.2-18.3%) and Eunotia (2.6-36.6%) fully dominated diatom assemblage.

In the DZ-4 (47-64 cm bss, *ca.* 2.0-4.2 ka BP), the total diatom content varied from 0.014 to 37.8x10^6 frustules g^{-1}. *A. distans* (18.8-46%), *T. flocculosa* (5.5-24.1%) and Eunotia (3.5-21.6%) prevailed in the zone.

In general, diatom records indicate that environmental condition contrast changed three times. The first period was since *ca.* 2.0 ka BP, when contents of plankton diatoms sharply began to increase. The second period was since *ca.* 1.7-1.3 ka BP, when contents of diatoms and chrysophycean cysts rapidly turned from the highest to the lowest ones. The third period is from 1.25 ka BP to the present time, when species diatom diversity is high.

We studied chironomidae assemblages for the upper 34 cm of the core. The assemblages showed 55 larval forms of 46 genera and 5 subfamilies (Podonominae, Tanypodinae, Diamesinae, Orthocladiinae, and Chironominae). Based on CONISS analysis, we divided chironomid records into five local zones (ChZ) (Fig. 3). The ChZ-1 (0-4 cm bss, *ca.* 0-0.6 ka BP) consisted of *Abiskomyia virgo*-type, *Zalutschia zalutschicola, Sergentia longiventris*-type and *Tanytarsus* gr. *Mendax*. *Natarsia* sp., *Procladius* cf. *choreus*, *Parakiefferiella triquetra*, *Chaetocladius* spp., *Diplocladius cultiger*-type, *Hydrobaenus* gr. *conformis*, *Nanocladius* gr.

rectinervis, *Psectrocladius* gr. *sordidellus*, and *Micropsectra loganii*-type were minor.

In the ChZ-2 (4-16 cm bss, *ca.* 0.6-1.25 ka BP) and the ChZ-3 (16-22 cm bss, *ca.* 1.25-1.4 ka BP) *Zalutschia zalutschicola, Sergentia longiventris*-type and *Tanytarsus* gr. *Mendax* dominated. *Procladius* cf. *choreus*, *Chaetocladius* spp., *Diplocladius cultiger*-type, *Hydrobaenus* gr. *conformis*, *Nanocladius* gr. *rectinervis*, and *Psectrocladius* gr. *Sordidellus* were minor. In addition, the number of head capsules of *Protanypus* gr. *Morio* sharply increased in the ChZ-3. Percentage of *Natarsia* sp., *Parakiefferiella bathophyla*-type, *Diplocladius cultiger*-type, *Nanocladius* gr. *rectinervis*, *Constempellinella* cf. *brevicosta*, *Dicrotendipes nervosus*-type, *Einfeldia* sp., *Micropsectra loganii*-type, *Sergentia croacina*-type, and *Tanytarsus gregarius*-type slightly increased in the ChZ-2 and 3 compared to those in the ChZ-1.

Throughout the ChZ-4 (22-27 cm bss, *ca.* 1.4-1.5 ka BP) *Natarsia* sp., *Diplocladius cultiger*-type, *Mesocricotopus thienemanni*, *Orthocladius* sp., *Psectrocladius* gr. *sordidellus*, and *Sergentia longiventris-type* dominated. However, the ratio of *Zalutschia zalutschicola* and *Micropsectra logani* reduced. In the sediment layer of 22-23 cm bss, *Diamesa aberrata*, *Parakiefferiella bathophyla*-type, *Chaetocladius* spp., *Metriocnemus* spp., *Mesosmittia flexuella*-type, *Smittia* sp., and *Sergentia longiventris*-type dominated.

The ChZ-5 (27-34 cm bss, *ca.*1.5-1.8 ka BP) is characterised by a sharp increase in *Diamesa stenboecki* and *Tanytarsus bathophylus*-type, as well as a great number of *Protanypus* gr. *Morio.*

Chironomid compositions of the ChZ-1,2,3 and 5 indicate that regional climate and lake ecological conditions were similar to modern ones. The ChZ-4 shows the low water level in the lake. Thus, *Protanypus* gr. *Morio* and *Zalutschia zalutschicola* inhabiting deep water (Walker et al., 1991; Olander et al., 1997) disappeared from chironomid assemblage. In addition, riverine and stream species also disappeared. It is likely that an inflow into Lake Aunakit strongly reduced. In addition, the number of frustules of plankton diatoms also was minimal within this span.

4. Conclusions

The core from Lake Aunakit formed over the past 4.2 ka BP. Ninety-two species represent diatom assemblages; however, only *A. distans*, *T. flocculosa*, Tetracyclus and Eunotia dominated the records. Four diatom zones divided 0-0.84, 0.95-1.25, 1.3-2.0, and 2.0-4.2 ka BP. The highest diatom diversity was in the past 1.25 ka. Chironomid assemblages of the upper 34 cm of the core showed 55 larval forms of 46 genera and 5 subfamilies (Podonominae, Tanypodinae, Diamesinae, Orthocladiinae, Chironominae). Changes in chironomid taxa occurred between 0-0.6-1.25-1.4-1.5-1.8 ka BP. The most dramatic changes in diatom and chironomid assemblages occurred 1.3-1.5 ka BP. Most likely, the lake level was low at that time.

Acknowledgements

This study was supported by basic funding No. 0345–2016–0006 (AAAA-A16-116122110063-0), RFBR-17-29-05016 (financial support of laboratory materials and equipment) and RFBR-16-05-00342 (financial support of fieldwork and AMS dating). We thank T.O. Zheleznyakova for diatom analysis, E.V. Parkhomchuk, P.N. Kalinkin and S.A. Rastigeev for AMS dating.

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Limnology and Freshwater Biology 2019 (2): 223-231 DOI:10.31951/2658-3518-2019-A-2-223

Original Article

ISSN 2658-3518
LIMNOLOGY FRESHWATER BIOLOGY
www.limnolfwbiol.com

Phenetic relationships and diagnostic features of sculpins of the genus *Cottocomephorus* (Perciformes: Cottidae)

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ABSTRACT. The author has studied phenetic and taxonomic relationships of the Baikal endemic sculpins of the genus *Cottocomephorus* Pellegrin 1900. For this purpose, the author has performed a morphometric investigation by five meristic and 29 plastic characters, as well as analysed the characteristics of colouring and the number of preopercular spines. The author has confirmed the validity of three species: *C. grewingkii* (Dybowski, 1874), *C. inermis* (Yakovlev, 1890) and *C. comephoroides* (Berg, 1901). The differentiation of the studied species is based on the number of gill rakers and preopercular spines, the width of the interorbital distance, height and width of the head, the length of the pectoral fins and the characteristics of the in-life colouration. Based on the revision of the diagnostic features, the author has suggested a new key to identify species.

Keywords: *Cottocomephorus*, systematics, morphology, phenetic relationships, diagnostic features, Lake Baikal fauna

1. Introduction

J. Pellegrin (1900) determined the genus *Cottocomephorus*, which initially included the only species *C. megalops* Pellegrin, 1900. Subsequently, the composition of the genus changed several times. In general, during the research, along with *C. megalops*, its composition included five more taxa: species that were previously described in the composition of the genus *Cottus* – *C. grewingkii* (Dybowski, 1874), *C. inermis* (Yakovlev, 1890) and *C. comephoroides* (Berg, 1900) as well as varieties described later, *Cottocomephorus grewingkii* – var. *siemienkiewiczii* (Dybowski, 1908) and var. *alexandrae* (Taliev, 1935). Currently, the genus includes three species: *C. inermis*, *C. grewingkii* and *C. alexandrae*. The latter was formed by combining two taxa *C. comephoroides* and *C. grewingkii alexandrae* (Sideleva, 2001; 2003), which is doubtful. This fact requires a study aimed at clarifying the taxonomic boundaries of species and development of a new key to their identification.

2. Material and methods

The study was carried out on the material collected by the author in 1994 – 2012. Fishes were caught with gill nets. During sampling, species and intraspecific forms were identified by size of mature specimens, features of breeding colouration, time and localization of spawning area specified in the original descriptions and subsequent revisions (Yakovlev, 1890; Berg, 1900; Pellegrin, 1900; Taliev, 1935; 1955; Koryakov, 1972).

The nomenclature is shown according to the provisions of the International Code of Zoological Nomenclature (1999). Fig. 1 Shows the images of type specimens. Abbreviations of museum collections: ZISP – Zoological Institute RAS, St.-Petersburg, Russia; BMNH – Natural History Museum, London; ZMB – Humboldt-Universität, Museum für Naturkunde, Zoologisches Museum, Vertebraten (Wirbekltiere), Ichthyologie, Berlin; MNHN – Muséum National d'Histoire Naturelle, Paris.

C. inermis and *C. comephoroides* were caught in the period before spawning, from December to March, at depths of 100-200 m. Both species are characterized by relatively large dimensions: females reach 180 mm TL and males – 210 mm. The initial identification was carried out by colouration characteristics. Dark-purple colour of the back and head, as well as lack of dark stripes on the pectoral fins, are characteristic of *C. inermis*, whereas dark-olive colour of the back and head, as well as dark stripes of the pectoral fins, are characteristic of *C. comephoroides* (Fig. 2, Fig. 3).

C. grewingkii was caught in the zone of a shallow platform at a depth of 1-2 m during spawning in March, May, June, and September. This species has smaller sizes of up to 130-140 mm, spotty colouration (brown spots against an olive background) and bright yellow pectoral fins with dark stripes in males (Fig. 4). Spawned specimens identified as *C. grewingkii alexandrae* were caught in early June at a depth of 100 m near the

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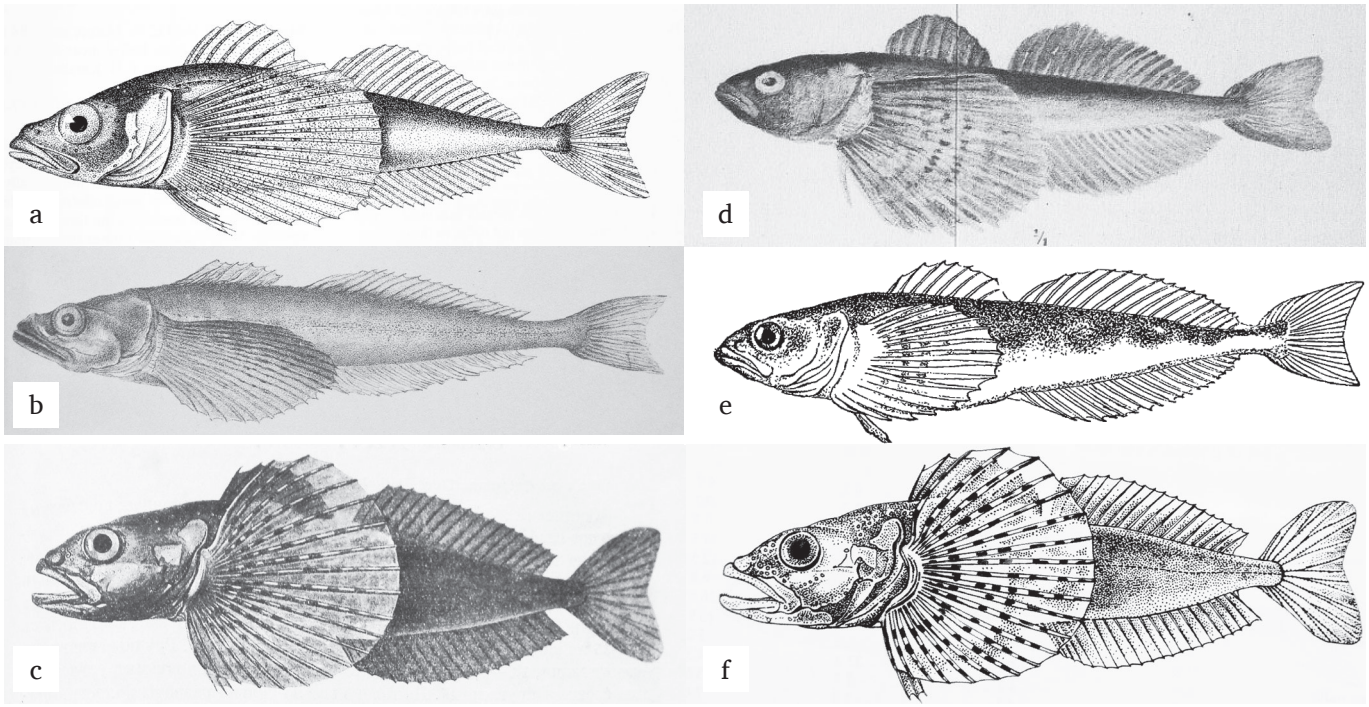

Fig. 1. Images of type specimens: a) neotype C. inermis ZISP 6350: male, 203 mm TL (Sideleva, 2003); b) syntype C. comephoroides ZISP ?: female, 159 mm TL (Berg, 1900); c) holotype C. siemienkiewiczii ZISP ?: male, 180 mm TL (Dybowski, 1908); d) lectotype C. grewingkii (?) BMNH 1897.7.5.4.(1): male, 130 mm TL (Dybowski, 1908); e) syntype C. grevingkii alexandrae: female, 102 mm TL (Taliev, 1935); f) ? 'lectotype-neotype' C. alexandrae: male, 170 mm TL (Sideleva, 2003)

eastern coast of the Northern Baikal, i.e. in the area indicated by Taliev (1955) as a likely breeding site of this form. These specimens differed from a typical form by the predominance of the brown colouration of the body and fins. Males also differed in the proportions of the head (Fig. 5) according to the original description (Taliev, 1955).

In total, we examined 53 specimens of *C. inermis*, 90 – *C. comephoroides,* 456 – *C. grewingkii*, including 38 specimens of *C. grewingkii alexandrae*.

The morphometric examination was carried out by five meristic and 29 plastic characters. We analysed: number of rays in the first (D_1) and second (D_2) dorsal, pectoral (*P*), and anal (*A*) fins, number of gill rakers (*sp.br*); length (*c*) and width (*bc*) of the head, length (*l*), height (*H*) and width (*w*) of the trunk; length (*lpc*) and height (*h*) of caudal peduncle; antedorsal (*aD*), postdorsal (*pD*), anteventral (*aV*), anteanal (*aA*), pectroventral (*P-V*) and ventroanal (*V-A*) distances; length of insertions of the first (lD_1) and second (lD_2) dorsal and anal (*lA*) fins; length of maximum rays in the first (hD_1) and second (hD_2) dorsal, anal (*hA*), pectoral (*lP*), and ventral (*lV*) fins; snout length (*ao*); longitudinal eye diameter (*o*); postorbital distance (*po*); head height near occiput (*cH*) and near vertical of the eye middle (*ch*); interorbital distance (*io*); and length of upper (*lmx*) and lower (*lmd*) jaws. Statistical processing of the material was performed by the generally accepted methods (Plokhinsky, 1980). Tables 1 and 3 show the variability of meristic and plastic characters. Selections were compared by factor analysis methods (PCA) using SPSS 8.0 software (Laerd Statistics, 2015). For assessment of the degree of differences, *CD* coefficient was used (Mayr, 1969).

Fig. 2. Lateral views of *C. inermis* (in top) and *C. comephoroides* (in bottom)

3. Results and discussion

Analysis of differences using the *CD* coefficient (Table 2, Table 4) has shown taxonomically significant differences between *C. inermis* and *C. comephoroides* by six characters in males and two characters – in females, between *C. inermis* and *C. grewingkii* – by five-nine characters and between *C. comephoroides* and *C. grewingkii* – by one-four characters. Differences are mostly in the number of rays in pectoral fins, fin base lengths and lengths of rays in fins, the height of the head, the interorbital distance and the diameter of the eye, which have highest values in *C. inermis*, the lowest values – in *C. grewingkii* and the intermediate ones – in *C. comephoroides*. There is an opposite pattern in the number of gill rakers. *C. inermis* have the lowest number (11-15), unlike the other species and forms that have 15-20 or 16-20 rakers.

There are discrete differences in the plastic characters between *C. inermis* and *C. grewingkii*, as well as the males of two *C. grewingkii* forms, typical and Northern Baikal one. At the same time, both forms have fewer differences between each other than with *C. comephoroides* and do not have taxonomically significant differences with other *C. grewingkii* populations.

Principal Components Analysis (PCA) of the variability of meristic and plastic characters in males has shown that the first and second principal components account for 36.3% of the total variance. The length of the pectoral fins yields the highest positive load on the first principal component, whereas the number of gill rakers – the negative one. For the second principal component, the width and height of the head at the occiput yield the highest positive load, and the ventroanal distance – the lowest one. In females, the first and second principal components account for 30.7% of the total variance. The number of rays in the pectoral fins and length of the head yield the highest positive load on the first principal component, whereas the length of the trunk and the length of the anal fin base – the negative one. For the second principal component, the highest positive load are the height of the body and height of the head at the occiput, and the negative one are the length of the body and snout.

Along with the above listed morphological features, these species differ in the combination of such characters as the number of preopercular spines (three to five in *C. inermis* and *C. comephoroides*, and one in *C. grewingkii*) and the colour

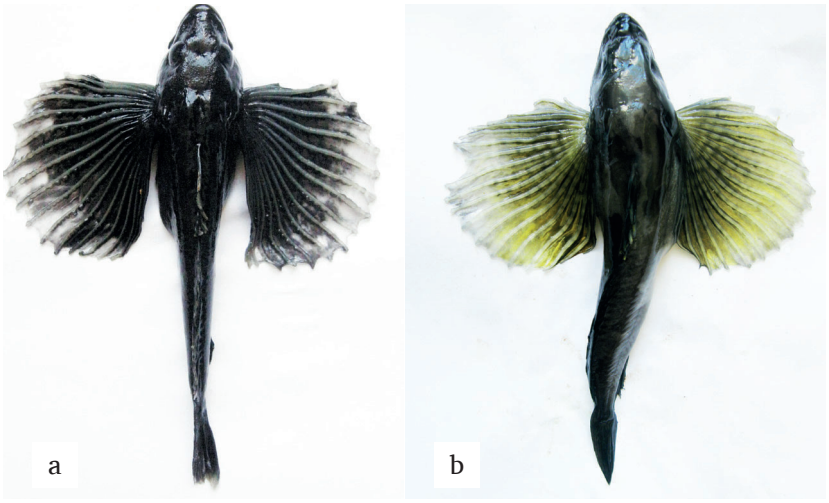

Fig. 3. Dorsal views of males in spawning coloration: a) *C. inermis*; b) *C. comephoroides*.

Fig. 4. Lateral views of *C. grewingkii* (June generation): a) male; b) female

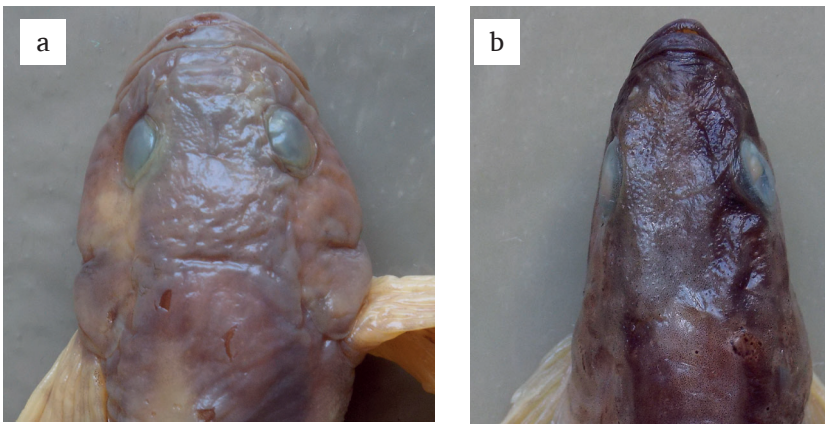

Fig. 5. Dorsal views of *C. grewingkii* males heads: a) 'typical form' (Southern Baikal, May generation); b) '*alexandrae* form' (Northern Baikal, March generation).

Table 1. The total length (*TL*), fork length (*FL*), standard length (*SL*), weight (*W*) and morphometric characters of males of the species of the genus *Cottocomephorus*

	C. inermis	C. comephoroides	C. grewingkii		
	(n = 33)	(n = 60)	'typical form' (48)	'alexandrae form' (13)	other populations (208)
TL	192.9 177.0-210.3	171.0 131.8-201.3	120.6 103.8-134.5	119.8 113.0-127.4	115.6 80.3-134.5
FL	184.4 169.5-200.4	162.4 125.8-192.5	116.7 101.0-131.8	116.3 109.7-122.2	112.2 79.0-130.0
SL	162.5 151.0-177.5	145.6 107.4-172.4	103.8 88.7-116.7	102.8 96.2-107.9	99.5 69.3-116.3
W	92.5 51.4-210.0	55.8 14.9-96.8	21.0 16.4-24.9	12.0 6.5-19.2	16.8 5.8-24.9
Meristic characters					
D_1	8.4 ± 0.10 7-9; 0.55	8.0 ± 0.07 7-9; 0.58	8.5 ± 0.08 7-10;0.58	8.3 ± 0.23 7-10; 0.82	8.2 ± 0.03 7-10; 0.50
D_2	19.1 ± 0.14 18-21; 0.78	18.2 ± 0.11 17-20; 0.84	18.4 ± 0.12 17-20;0.83	19.1 ± 0.23 18-21; 0.83	18.5 ± 0.05 17-20; 0.73
P	20.7 ± 0.10 19-22; 0.58	19.9 ± 0.08 19-21; 0.63	18.8 ± 0.08 18-20;0.59	18.8 ± 0.15 18-20; 0.53	18.8 ± 0.04 17-21; 0.64
A	21.3 ± 0.12 20-23; 0.68	21.1 ± 0.09 20-23; 0.71	20.6 ± 0.12 19-22;0.80	21.5 ± 0.21 20-23; 0.75	21.0 ± 0.04 19-22; 0.61
sp.br.	13.1 ± 0.16 11-15; 0.95	17.5 ± 0.17 15-20; 1.28	18.8 ± 0.20 17-23;1.41	17.7 ± 0.20 16-19; 0.72	18.7 ± 0.09 16-23; 1.27
Plastic characters in % *SL*					
c	28.2 ± 0.17 26.6-30.9; 1.00	27.8 ± 0.13 25.2-31.4; 1.02	26.7 ± 0.14 24.0-28.8;0.98	26.5 ± 0.25 24.8-28.2; 0.89	25.7 ± 0.07 23.1-29.3; 1.04
L	76.5 ± 0.27 72.4-79.2; 1.55	75.1 ± 0.31 67.6-83.9; 2.41	74.1 ± 0.24 68.9-77.0;1.69	77.5 ± 0.51 74.6-81.2; 1.84	78.7 ± 0.10 73.8-85.8; 1.47
H	20.7 ± 0.30 17.8-25.4; 1.75	17.4 ± 0.23 14.3-21.3; 1.78	20.4 ± 0.14 18.5-22.9;0.94	14.2 ± 0.37 12.2-17.3; 1.35	17.3 ± 0.11 12.2-21.3; 1.64
h	4.4 ± 0.04 4.0-5.1; 0.24	3.9 ± 0.05 3.1-4.8; 0.41	4.2 ± 0.04 3.7-4.8;0.29	4.2 ± 0.08 3.8-4.7; 0.30	4.5 ± 0.03 3.6-6.0; 0.37
B	15.5 ± 0.30 12.1-18.4; 1.72	13.1 ± 0.17 9.5-16.0; 1.32	15.5 ± 0.15 13.5-17.4;1.05	11.2 ± 0.34 9.8-14.5; 1.22	13.5 ± 0.08 10.5-16.4; 1.20
aD	33.1 ± 0.22 30.2-35.1; 1.27	32.7 ± 0.15 30.0-35.6; 1.17	31.4 ± 0.17 28.7-33.9;1.19	30.5 ± 0.41 26.9-32.7; 1.47	31.4 ± 0.11 25.4-40.0; 1.52
pD	11.7 ± 0.20 8.8-14.5; 1.14	12.7 ± 0.15 9.1-15.3; 1.19	13.1 ± 0.14 11.1-14.9;0.95	13.0 ± 0.41 9.9-15.6; 1.46	13.0 ± 0.07 10.4-16.0; 1.06
aV	27.9 ± 0.35 24.0-32.4; 2.01	26.3 ± 0.19 23.4-30.0; 1.48	26.2 ± 0.31 15.1-29.8;2.15	24.7 ± 0.18 23.7-26.2; 0.66	25.3 ± 0.14 14.3-37.2; 2.07
aA	54.1 ± 0.31 50.2-58.0; 1.77	54.7 ± 0.24 50.1-58.5; 1.84	51.0 ± 0.28 44.9-54.6;1.93	50.5 ± 0.36 48.3-53.0; 1.30	50.1 ± 0.12 45.2-55.5; 1.77
pl	9.8 ± 0.12 8.3-11.5; 0.69	10.4 ± 0.11 8.6-12.5; 0.87	10.0 ± 0.26 7.8-17.7;1.78	9.8 ± 0.20 8.5-10.7; 0.71	9.7 ± 0.06 7.3-12.3; 0.88
PV	3.2 ± 0.10 2.0-4.4; 0.55	3.0 ± 0.08 1.7-4.5; 0.59	3.3 ± 0.07 2.4-4.8;0.49	2.4 ± 0.15 1.8-3.6; 0.53	2.9 ± 0.03 1.6-4.2; 0.45
VA	28.6 ± 0.42 24.8-33.5; 2.39	30.4 ± 0.23 26.8-35.1; 1.77	26.2 ± 0.26 21.0-30.4;1.80	27.9 ± 0.41 25.9-30.6; 1.46	26.6 ± 0.15 21.5-40.1; 2.17
lD_1	22.1 ± 0.22 19.0-25.4; 1.25	22.6 ± 0.20 19.5-28.7; 1.56	21.0 ± 0.22 17.4-23.8;1.55	20.6 ± 0.44 17.6-22.8; 1.59	21.1 ± 0.10 17.3-25.3; 1.50
lD_2	35.4 ± 0.26 32.6-39.1; 1.51	33.7 ± 0.20 30.5-36.9; 1.56	35.8 ± 0.26 31.6-39.6;1.82	36.3 ± 0.45 33.1-38.8; 1.64	35.4 ± 0.13 31.5-40.5; 1.83

	C. inermis	C. comephoroides	C. grewingkii		
	(n = 33)	(n = 60)	'typical form' (48)	'alexandrae form' (13)	other populations (208)
hD_1	11.8 ± 0.17 10.3-14.3; 0.96	10.5 ± 0.11 8.7-12.8; 0.83	9.9 ± 0.14 7.7-13.3;0.98	10.9 ± 0.20 9.6-12.3; 0.74	10.5 ± 0.05 8.1-13.1; 0.79
hD_2	14.4 ± 0.16 12.3-16.2; 0.92	12.1 ± 0.11 10.1-14.0; 0.89	11.9 ± 0.11 10.6-14.0;0.80	13.0 ± 0.25 11.5-14.6; 0.91	12.1 ± 0.05 9.7-15.2; 0.78
lA	37.2 ± 0.21 34.8-39.1; 1.19	36.2 ± 0.22 32.7-40.9; 1.70	39.6 ± 0.19 36.5-42.1;1.34	39.4 ± 0.31 37.2-41.8; 1.11	39.8 ± 0.11 35.6-44.4; 1.58
hA	15.1 ± 0.16 13.3-16.8; 0.93	12.7 ± 0.11 10.9-15.1; 0.89	12.4 ± 0.15 9.7-14.7;1.01	14.4 ± 0.37 12.0-16.0; 1.35	13.1 ± 0.06 10.8-16.2; 0.83
lP	44.1 ± 0.34 40.7-47.5; 1.95	36.3 ± 0.27 31.7-40.2; 2.08	34.8 ± 0.36 23.3-39.8;2.52	36.5 ± 0.48 32.9-39.5; 1.72	35.5 ± 0.15 29.9-42.6; 2.10
lV	17.9 ± 0.16 15.7-19.5; 0.92	13.9 ± 0.11 12.3-15.9; 0.83	13.9 ± 0.12 11.9-15.6;0.83	14.6 ± 0.24 13.6-16.3; 0.86	14.0 ± 0.06 11.6-16.7; 0.81
Plastic characters in % *c*					
ao	31.9 ± 0.24 29.2-34.4; 1.36	32.1 ± 0.20 28.7-35.4; 1.51	32.9 ± 0.26 28.9-37.5;1.79	29.5 ± 0.33 28.0-32.2; 1.19	31.1 ± 0.11 27.0-36.1; 1.63
o	25.1 ± 0.60 20.8-41.4; 3.42	23.6 ± 0.28 18.5-28.1; 2.14	22.4 ± 0.24 17.6-26.7;1.69	22.6 ± 0.30 21.1-24.5; 1.07	22.0 ± 0.10 18.2-25.6; 1.40
op	40.4 ± 0.30 37.0-44.3; 1.70	42.2 ± 0.24 38.0-47.1; 1.87	43.4 ± 0.32 38.9-48.8;2.25	44.9 ± 0.53 41.5-47.9; 1.92	43.2 ± 0.13 37.6-49.1; 1.92
bc	65.7 ± 1.08 52.6-78.0; 6.21	55.3 ± 0.71 45.7-68.5; 5.47	76.7 ± 0.91 64.4-89.6;6.31	55.6 ± 1.36 44.9-66.8; 4.92	64.7 ± 0.34 53.3-77.5; 4.87
hcz	66.9 ± 0.46 60.4-70.8; 2.66	55.2 ± 0.56 45.2-64.7; 4.35	66.7 ± 0.54 58.7-75.9;3.75	53.1 ± 0.79 46.8-58.3; 2.86	61.0 ± 0.26 51.8-70.8; 3.72
hco	53.5 ± 0.53 46.1-59.9; 3.04	44.0 ± 0.37 36.8-50.5; 2.87	54.7 ± 0.76 44.4-81.7;5.25	43.5 ± 0.54 40.1-46.5; 1.94	48.4 ± 0.25 38.7-61.2; 3.56
io	19.6 ± 0.40 16.2-24.9; 2.33	19.5 ± 0.28 15.3-24.8; 2.14	27.8 ± 0.26 24.0-32.7;1.77	25.6 ± 0.64 20.7-30.1; 2.30	24.4 ± 0.15 19.1-29.8; 2.22
lmx	51.9 ± 0.30 47.8-55.8; 1.70	47.9 ± 0.30 42.5-51.7; 2.35	47.6 ± 0.33 43.4-52.7;2.29	49.1 ± 0.48 46.4-51.5; 1.72	49.1 ± 0.14 43.0-55.1; 2.08
lmd	60.7 ± 0.36 57.1-65.4; 2.07	56.5 ± 0.26 50.2-61.2; 1.98	58.3 ± 0.46 53.7-66.8;3.17	56.7 ± 0.65 53.4-63.0; 2.33	57.9 ± 0.17 52.6-66.7; 2.41

Note: Above the line – mean value and its error; under the line – limits of variation of character and mean square deviation.

Table 2. Differences in the morphometric characters of males of species and intraspecific forms of the genus *Cottocomephorus* reaching a taxonomically significant level (CD > 1.28)

	1	2	3	4
1. *C. inermis*				
2. *C. comephoroides*	*sp.br., hA, lP, lV, hcz, hco*			
3. *C. grewingkii*: 'typical form'	*P, *sp.br., hD_2, lA, *lP, *lV, io*	*bc, hcz, hco, io*		
4. *C. grewingkii*: 'alexandrae form'	*P, *sp.br., *H, B, *lP, lV, hcz, hco, io*	*aA, io*	**H, B, bc, *hcz, hco*	
5. *C. grewingkii*: Other populations	*P, *sp.br., hD_2, lP, lV*	*aA*	–	–

Note: * - characters for which there is hiatus.

Table 3. The total length (*TL*), fork length (*FL*), standard length (*SL*), weight (*W*) and morphometric characters of females of the species of the genus *Cottocomephorus*

	C. inermis	*C. comephoroides*	*C. grewingkii*		
	(n = 20)	(n = 30)	'typical form' (30)	'alexandrae form' (25)	other populations (132)
TL	141.8 115.7-179.7	143.4 121.2-166.2	121.7 113.4-129.5	120.7 107.7-131.0	106.0 85.7-130.0
FL	134.3 110.0-170.5	135.3 113.6-157.0	119.3 111.2-127.2	116.6 104.4-126.5	102.0 10.7-126.6
SL	120.5 97.5-156.0	121.9 100.8-142.0	106.2 98.9-113.4	104.0 93.0-113.3	92.0 75.4-113.3
W	24.6 10.4-64.3	31.8 14.2-45.4	8.1 6.5-10.7	15.9 9.4-19.7	10.6 4.7-18.5
Meristic characters					
D_1	8.6 ± 0.11 8-9; 0.49	8.0 ± 0.07 7-9; 0.41	8.1 ± 0.09 7-10; 0.47	8.1 ± 0.05 8-9; 0.27	8.1 ± 0.04 7-9; 0.49
D_2	18.6 ± 0.15 17-20; 0.66	17.6 ± 0.14 16-19; 0.76	18.4 ± 0.14 17-20; 0.76	18.3 ± 0.15 17-20; 0.73	18.1 ± 0.05 16-20; 0.62
P	20.2 ± 0.13 19-21; 0.60	19.5 ± 0.11 18-21; 0.62	18.5 ± 0.12 17-20; 0.67	18.9 ± 0.12 18-20; 0.59	18.2 ± 0.05 17-20; 0.57
A	21.1 ± 0.11 20-22; 0.50	20.7 ± 0.08 20-21; 0.46	21.0 ± 0.12 20-22; 0.63	20.8 ± 0.17 19-22; 0.85	20.8 ± 0.06 19-22; 0.65
sp.br.	12.8 ± 0.23 11-15; 1.04	17.7 ± 0.27 15-20; 1.47	18.2 ± 0.20 15-20; 1.11	18.2 ± 0.19 16-19; 0.95	18.3 ± 0.10 16-20; 1.11
Plastic characters in % *SL*					
c	26.5 ± 0.17 24.8-28.0; 0.77	26.9 ± 0.16 24.7-28.5; 0.90	25.4 ± 0.16 24.0-27.2; 0.88	26.2 ± 0.19 24.0-28.8; 0.93	24.0 ± 0.10 21.7-26.9; 1.13
L	77.1 ± 0.23 75.5-79.4; 1.03	75.4 ± 0.29 70.1-78.4; 1.61	77.6 ± 0.22 75.2-79.9; 1.19	78.1 ± 0.23 75.5-79.9; 1.15	78.8 ± 0.13 69.8-81.7; 1.47
H	17.7 ± 0.36 15.1-22.4; 1.62	17.4 ± 0.37 13.6-21.7; 2.02	16.1 ± 0.19 14.1-17.9; 1.02	17.4 ± 0.26 15.0-19.9; 1.28	17.3 ± 0.23 11.7-22.5; 2.63
h	4.0 ± 0.06 3.3-4.5; 0.27	3.6 ± 0.05 3.0-4.5; 0.29	3.8 ± 0.04 3.4-4.1; 0.22	4.2 ± 0.04 3.7-4.5; 0.22	3.8 ± 0.02 3.2-4.7; 0.27
B	11.7 ± 0.40 9.1-15.5; 1.79	12.7 ± 0.28 9.7-15.2; 1.51	11.9 ± 0.19 9.4-13.7; 1.04	12.8 ± 0.21 10.5-14.8; 1.07	13.1 ± 0.15 8.6-19.2; 1.78
aD	31.2 ± 0.25 29.1-33.3; 1.11	32.6 ± 0.16 30.8-34.1; 0.89	31.0 ± 0.19 28.3-32.6; 1.04	31.4 ± 0.18 30.0-33.1; 0.90	30.2 ± 0.12 24.5-33.7; 1.38
pD	12.6 ± 0.27 10.5-14.6; 1.22	13.0 ± 0.20 10.5-14.9; 1.10	13.4 ± 0.15 11.4-14.9; 0.84	13.6 ± 0.17 12.1-15.8; 0.85	13.6 ± 0.10 10.6-16.1; 1.15
aV	25.4 ± 0.22 22.7-26.8; 1.00	26.1 ± 0.21 23.9-28.2; 1.13	24.1 ± 0.21 22.1-26.3; 1.17	25.2 ± 0.18 22.6-27.1; 0.92	23.7 ± 0.11 21.0-27.2; 1.23
aA	55.2 ± 0.35 53.4-60.0; 1.57	55.6 ± 0.83 34.7-61.4; 4.57	53.2 ± 0.26 50.7-55.7; 1.40	51.8 ± 0.34 47.8-56.1; 1.69	52.7 ± 0.14 48.7-56.3; 1.57
pl	10.8 ± 0.16 9.4-12.2; 0.72	11.0 ± 0.26 8.8-15.8; 1.42	10.2 ± 0.17 8.3-12.8; 0.95	10.3 ± 0.16 8.7-11.9; 0.82	10.2 ± 0.09 5.7-12.6; 1.04
PV	2.8 ± 0.14 1.7-3.9; 0.63	3.2 ± 0.12 2.1-4.2; 0.63	2.8 ± 0.07 2.0-3.3; 0.36	3.0 ± 0.16 1.7-4.8; 0.78	3.1 ± 0.05 1.8-5.7; 0.63
VA	31.6 ± 0.56 27.5-38.6; 2.49	31.8 ± 0.49 26.7-37.2; 2.71	30.0 ± 0.33 26.5-33.2; 1.82	27.8 ± 0.32 24.5-30.9; 1.58	30.0 ± 0.15 24.0-33.7; 1.78
lD_1	23.4 ± 0.33 20.9-26.5; 1.47	24.4 ± 0.21 21.4-26.4; 1.17	22.7 ± 0.22 20.7-25.0; 1.22	21.4 ± 0.20 19.5-23.0; 1.01	23.3 ± 0.15 18.7-34.1; 1.77
lD_2	33.2 ± 0.27 31.5-36.0; 1.22	31.3 ± 0.28 26.8-34.0; 1.51	33.7 ± 0.24 31.4-36.9; 1.30	33.3 ± 0.29 30.5-36.2; 1.43	33.5 ± 0.12 29.4-38.0; 1.41

	C. inermis	*C. comephoroides*	*C. grewingkii*		
	(n = 20)	(n = 30)	'typical form' (30)	'alexandrae form' (25)	other populations (132)
hD_1	12.0 ± 0.20 10.0-13.3; 0.90	10.8 ± 0.16 9.0-12.8; 0.88	11.4 ± 0.18 9.6-13.5; 0.98	10.4 ± 0.16 8.1-11.7; 0.82	10.9 ± 0.08 7.8-13.7; 0.94
hD_2	12.7 ± 0.19 11.5-14.8; 0.87	11.4 ± 0.15 9.9-13.9; 0.81	11.7 ± 0.12 10.3-13.1; 0.65	11.4 ± 0.17 9.6-13.2; 0.86	11.1 ± 0.07 8.6-12.5; 0.79
lA	33.3 ± 0.33 30.0-36.0; 1.49	33.2 ± 0.27 29.8-35.8; 1.45	36.6 ± 0.21 35.1-39.7; 1.17	37.1 ± 0.25 34.7-39.7; 1.25	36.8 ± 0.13 28.2-43.1; 1.50
hA	12.2 ± 0.19 10.5-14.2; 0.86	11.2 ± 0.12 9.7-13.1; 0.65	11.5 ± 0.15 9.7-13.2; 0.84	11.8 ± 0.13 10.3-13.1; 0.63	10.9 ± 0.07 9.0-13.3; 0.85
lP	35.1 ± 0.50 31.3-38.6; 2.24	32.2 ± 0.34 29.6-37.6; 1.86	32.4 ± 0.35 28.3-36.4; 1.91	32.0 ± 0.41 27.6-36.0; 2.06	31.3 ± 0.16 22.4-35.2; 1.78
lV	14.4 ± 0.17 13.2-15.8; 0.76	12.0 ± 0.14 10.0-14.2; 0.74	12.1 ± 0.11 11.2-13.4; 0.63	12.7 ± 0.16 10.8-14.1; 0.80	11.9 ± 0.07 10.1-14.0; 0.79
Plastic characters in % *c*					
ao	29.5 ± 0.28 27.4-31.5; 1.26	31.3 ± 0.30 28.9-35.9; 1.62	28.8 ± 0.22 26.4-31.8; 1.19	29.5 ± 0.38 25.6-34.1; 1.92	30.2 ± 0.17 26.3-37.9; 1.98
o	31.3 ± 0.44 27.3-36.9; 1.95	27.9 ± 0.38 23.1-32.1; 2.10	25.4 ± 0.23 21.1-27.1; 1.24	24.1 ± 0.30 21.2-26.9; 1.52	25.0 ± 0.14 20.6-29.9; 1.55
op	37.7 ± 0.40 34.7-40.9; 1.79	39.2 ± 0.37 35.7-43.6; 2.00	41.3 ± 0.30 37.1-45.5; 1.66	44.2 ± 0.43 38.8-48.2; 2.15	41.1 ± 0.19 34.8-46.3; 2.15
bc	50.8 ± 0.95 44.6-60.8; 4.23	51.1 ± 0.78 42.6-58.5; 4.27	55.0 ± 0.50 49.2-62.0; 2.75	55.6 ± 0.67 48.9-62.0; 3.35	57.9 ± 0.43 46.5-84.9; 4.93
hcz	59.0 ± 0.76 52.9-66.8; 3.40	56.0 ± 0.93 43.3-62.9; 5.09	56.5 ± 0.53 50.4-63.2; 2.91	57.7 ± 0.73 48.6-63.2; 3.65	59.1 ± 0.34 49.4-68.5; 3.95
hco	46.3 ± 0.81 41.4-57.8; 3.60	42.5 ± 0.54 35.9-48.4; 2.97	43.6 ± 0.35 38.9-47.7; 1.93	43.6 ± 0.51 35.7-48.7; 2.53	44.5 ± 0.25 37.0-52.5; 2.86
io	14.6 ± 0.31 11.9-17.5; 1.40	17.3 ± 0.34 13.8-21.3; 1.85	21.6 ± 0.26 19.0-23.8; 1.41	24.1 ± 0.43 20.3-28.1; 2.13	22.4 ± 0.24 15.5-29.8; 2.75
lmx	46.0 ± 0.42 42.1-50.0; 1.89	45.6 ± 0.32 41.8-50.5; 1.77	44.0 ± 0.26 41.3-46.6; 1.41	44.8 ± 0.38 41.4-50.0; 1.89	43.9 ± 0.22 36.4-50.8; 2.49
lmd	57.0 ± 0.36 54.7-60.3; 1.59	56.5 ± 0.32 53.5-62.0; 1.74	55.0 ± 0.30 50.9-59.0; 1.65	55.2 ± 0.35 50.4-58.7; 1.76	55.5 ± 0.23 47.3-63.8; 2.60

Note: Above the line – mean value and its error; under the line – limits of variation of character and mean square deviation.

Table 4. Differences in the morphometric characters of females of species and intraspecific forms of the genus *Cottocomephorus* reaching a taxonomically significant level (CD > 1.28)

	1	2	3	4
1. *C. inermis*				
2. *C. comephoroides*	*sp.br., lV*			
3. *C. grewingkii*: 'typical form'	*P, sp.br., lA, lV, *o, *io*	*lA, io*		
4. *C. grewingkii*: 'alexandrae form'	**sp.br., lA, *o, po, *io*	lD_1, *lA, io*	–	
5. *C. grewingkii*: Other populations	*P, *sp.br., c, lV, o, io*	*c*	–	–

Note: * - characters for which there is hiatus.

of the pectoral fins with dark horizontal stripes in *C. comephoroides* and *C. grewingkii*, and without them in *C. inermis*.

The diagrams (Fig. 6) show that the spread of the first two principal components of the *C. grewingkii alexandrae* samples is not beyond the spread limits of other *C. grewingkii* populations, which confirms the statement of Koryakov (1972) that this subspecies is invalid.

The spread of *C. comephoroides* is intermediate between *C. inermis* and *C. grewingkii*. At the same time, the *C. comephoroides* males are very similar to *C. grewingkii* and the females – to *C. inermis*. This fact does not allow us to consider these fish as conspecific of either species.

The suggestion of Sideleva (2001) about the conspecificity of *C. grewingkii alexandrae* and *C. comephoroides*, as well as the consequent synonymy of *C. comephoroides* as an inadequate senior synonym, found no confirmation. Indeed, both forms similarly differ from the type species *C. grewingkii* by plastic characters and colouration. Only four and five characters of the 13 ones indicated by Taliev (1955) confirm taxonomically significant differences (Table 2). However, the number of preocular spines in *C. comephoroides* does not correspond to the diagnosis of *C. grewingkii alexandrae*, having three-five spines versus one spine. The name *C. comephoroides* is adequate from the original publication (Berg, 1900) and is the earliest name of this taxon according to the provisions of the Code (International Code…, 1999).

Therefore, the genus *Cottocomephorus* includes three valid species and has the following nomenclature:

Genus *Cottocomephorus* Pellegrin, 1900

Cottocomephorus Pellegrin, 1900: 354. Masc.

Cottocomephorus megalops Pellegrin, 1900. Type by monotypy

***Cottocomephorus inermis* (Yakovlev, 1890)**

Cottus inermis Yakovlev, 1890: 52 (holotype by monotypy is lost; Angara River near Irkutsk; collected by V.E. Yakovlev, December 1888); neotype: ZISP 6350 was designated by Sideleva (2003: 166, Fig 13.22); Irkut river (tributary of Angara River); collected by R.K. Maack, 1855.

Cottocomephorus megalops Pellegrin, 1900: 354 (holotype by monotypy MNHN 97–590; Angara River near Irkutsk; collected by L. Mangini, 1897).

***Cottocomephorus comephoroides* (Berg, 1901)**

Cottus comephoroides Berg, 1900: 338, Fig. 3, Table 8. (syntypes ZISP 11531 (19), 11532 (9) Baikal, Selenginskoye shoal, depth 255 m, collected by East Siberian branch of the Imperial Geographical Society, 1898; 11533 (20) Baikal near Goloustnoye village and 11535 (4) Baikal near Pesochnoye village, collected by Shostakevich and Soldatov, June 1898; 11534 (3) Baikal, collected by Botkin, 1897 (Berg, 1900) and BMNH 1905.12.4.18 (1) Lake Baikal, Selenginskoye shoal (Eshmeyer, 2006)).

Cottocomephorus grewingkii var. *siemienkiewiczii* Dybowski 1908: 559, Fig. 20 (holotype by monotypy not found in ZISP; Lake Baikal).

Cottocomephorus alexandrae (sic.) – Sideleva,

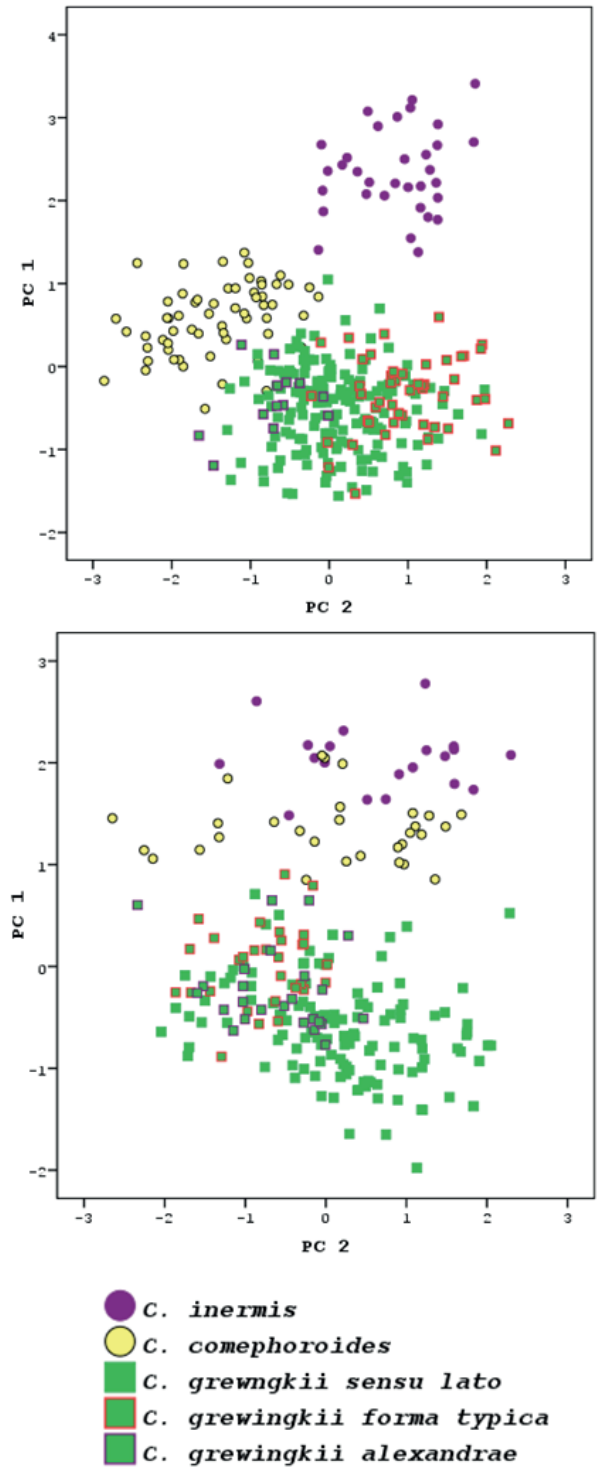

Fig. 6. Distribution of species of genus *Cottocomephorus* in space of a first (PC1) and second (PC2) principal components by meristic and plastic characters: males (in top) females (in bottom).

2003: 164, Fig. 13.19, Fig. 13.20, Table 42 (rediscription; lectotype ZISP 36608; Baikal, northern part; collected by A.A. Bazikalova, 1949); Sideleva et al., 2006: 295 (lectotype renamed to neotype). Both designations are unavailable under the Code (1999).

***Cottocomephorus grewingkii* (Dybowski, 1874)**

Cottus grewingkii Dybowski, 1874: 384, Pl. 1 (Fig. 1) (lectotype designated by B. Dybowski (1908), probably – BMNH 1897.7.5.4.(1), paralectotypes (8) – ZMB 7808(8); Lake Baikal, collected by B. Dybowski.

Cottocomephorus grewingki var. *alexandrae* Taliev, 1935: 64, Fig. 4, Table 1. (syntypes (7): (1) Baikal, near Marituy village, depth 100 m, 3 June 1930 and (2) Baikal, near Marituy village, depth 500 m, 15 June 1930, collected by Baikal Limnological Station (BLS) – whereabouts unknown; BLS 7010 (1) Baikal near Svyatoy Nos peninsula, depth 300 m, 14 August 1931 and BLS 7273 (3) Baikal, between of Tankhoy and Vydrino villages, depth 330 m, 31 August 1932 – not found in The Baikal Museum at the ISC SB RAS ex Baikal Limnological Station).

Cottocomephorus grewingki alexandrae Taliev, 1955: 287, Table 14. Fig., (rediscription; syntypes (28) whereabouts unknown; Kicherskaya bay, collected by Taliev, 17 November 1943). On figures 114 and 115 accompanying the description depicted specimens of *C. comephoroides* – probably ZISP 36608 and ZISP 36608a, collected by A.A. Bazikalova in 1949.

4. Conclusion

The results of the studies have confirmed the phenotypic isolation and diagnosability of three species of the genus *Cottocomephorus*: *C. inermis, C. comephoroides* and *C. grewingkii*. The revision of diagnostic characters suggests the following key to identify the species:

1 (4) The preopercle has three-five small sharp spines. The interorbital distance less than the diameter of the eye.

2 (3) The rays of the pectoral fins have dark spots forming horizontal stripes or arranged randomly. 16-12, less commonly 15, gill rakers: *C. comephoroides*

3 (2) The rays of the pectoral fins lack dark spots. 11-15 gill rakers: *C. inermis*

4 (1) The preopercle has one, less commonly two, rounded rudimentary spines. The interorbital distance more than the diameter of the eye.

The rays of the pectoral fins have dark spots forming horizontal stripes. 16-23, less commonly 15, gill rakers: *C. grewingkii*

Acknowledgements

The study was performed within the framework of LIN SB RAS State Task No. 0345–2019–0002: Molecular Ecology and Evolution of Living Systems of Central Asia under Global Ecological Changes.

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