Food base and nutrition of endemic lenok (*Brachymystax savinovi*) in Lake Markakol and in the reservoir of the river Uidene

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Abstract. The feeding characteristics of the Markakol lenok *Brachymystax savinovi* (Mitrofanov, 1959) from two mountain reservoirs of East Kazakhstan, the Lake Markakol and the reservoirs of the river Uidene, were observed in the spring-summer period of 2021-2022. It has been established that the same-aged lenoks from Lake Markakol have higher size and weight indicators than from the reservoir on the river Uidene, which is due to different levels of trophicity of water bodies. The food base of Lake Markakol has high stocks of large benthic invertebrates, which are well used by fish as food, and to a greater extent are gammarus and leeches. At the reservoir on the river Uidene only the estuarine part of the reservoir is characterized by an increased level of trophicity (due to the mass development of chironomids) in terms of macrozobenthos, but other areas show a moderate or very low level of trophicity. A significant difference in the food base of the two reservoirs determines the nutritional spectrum of *B. savinovi*. In lenoks from Lake Markakol, the main component in the food bolus were gammarus and leeches, the most numerous and accessible food. Lenok from Lake Markakol have the widest range of nutrition in individuals aged 6+ to 8+ years. In the lenok from the reservoir on the river Uidene the largest number of food fragments was noted for individuals of 3 to 4 years old. The leading position in the food bolus is occupied by the common gudgeon and chironomid larvae. Fish in the stomach of a lenok from a reservoir on the river Uidene was registered in all age groups. To strengthen the food base of the reservoir on the river Uidene, it is necessary to introduce food benthos, in particular gammarids.

Key Words: COI gene, nutritional spectrum, macrozoobentos, stomach filling index, trophic status.

Introduction. *Brachymystax* (Günther 1866) genera that include is a freshwater fishes of the *Salmonidae* family that lives in the foothills of rivers and mountain cold lakes, being distributed in the rivers of the Far East and Siberia, Mongolia, China, West Korea. In the Kazakhstan basin of the Irtysh River, *Brachymystax savinovi* is common, as well as in the rivers of the Southern Altai region, such as the Karakaba, Kalzhir, Kurchum and others. A fairly large population of *B. savinovi* (Fricke 2023) lives in Lake Markakol, where its local name is uskuch. The population of the Markakol lenok is isolated from the penetration of other fish of this species. During a long isolated evolution, the Markakol lenok acquired a number of morphological differences (Baimukanov 2009). Discussions on the taxonomic position of the lenok from Lake Markakol did not subside until now. Mitrofanov identified lenok from Lake Markakol as the Markakol subspecies *Brachymystax lenok savinovi* (Mitrofanov 1959) based on the analysis of plastic and meristic characters. However, subsequent studies (Vasilyeva 1978; Osinov et al 1990; Mina 1986) showed that Markakol lenok belongs to the sharp-snouted form of lenok, and its special morphological features are a manifestation of the phenetic diversity of the complex species *B. lenok*. To confirm the species we used a short (650 bp) DNA fragment from the mitochondrial 5'-terminal region of the cytochrome c oxidase I (COI) gene is widely used as a universal standard DNA barcode for identification of metazoan species (Hebert et al 2003).

Due to quite significant differences in the abiotic and biotic factors of the two water bodies, lenoks differ both in terms of plastic and meristic characteristics, and in terms of sexual maturation. The lenok from the Uidene population is characterized by higher head and eye indices than the lenok from Lake Markakol, with a lighter coloration of the body and with larger and fewer spots that are located on the back, and not all over the body, as in lenok from Lake Markakol (Figure 1, Figure 2).

Figure 1. Appearance of *Brachymystax savinovi* from Lake Markakol.

Figure 2. Appearance of *Brachymystax savinovi* from the reservoir on the river Uidene.

Of the entire array of scientific data on the hydrochemical regime, analysis of the food base (zooplankton and macrozoobenthos), ichthyological studies, etc. (Institute of Hydrobiology and Ecology 2017), the nutrition of *B. savinovi* in various water bodies remains the least studied. The nutritional characteristics of the Markakol lenok were studied and covered in the literature by domestic scientists in the period 1957-2008. The results of later studies on the nutrition of the *B. savinovi* are not known.

The purpose of this study was to determine the degree of development of the macrozoobenthos of Lake Markakol and reservoirs on the river Uidene as a food base for *B. savinovi*, as well as the food spectra and food preferences of *B. savinovi* from the Lake Markakol and from the reservoirs on the river Uidene.

Material and Method

Research location. Lake Markakol is located on the territory of the Markakol State Natur Reserve, which was organized in August 1976 on the territory of the Kurchum district of the East Kazakhstan region and is located in the southeastern part of the Southern Altai Mountains, being the periphery of the mountain-taiga landscapes of Southern Siberia. The total area of the reserve is currently 102,971 hectares. About 45%

of the Markakol Natural Reserve is occupied by Lake Markakol. The lake has an elongated oval shape and extends from the northeast to the southwest, its absolute height is of 1449.5 m above sea level. The length of the lake is 38 km, the width is 19 km, the length of the coastline is 106 km, the depth is up to 27 m (on average 14.3 m), the area is 455 sq km. The total catchment area is 1180 sq km. About 50 different streams flow into Lake Markakol, but only one river flows out: the Kalzhyr (length 128 km), which is a tributary of the Black Irtysh (Baimukanov 2009). The climate of Southern Altai is sharply continental, with severe snowy winters and warm, and moderately humid summers. Lake Markakol freezes for the winter. Ice occurs between November 6 and December 4, with a median of the period on November 20. Only the source of the river Kalzhir remains non-freezing. On the beds of some rivers (Topolevka, Urunkhaika) there are small air-holes all winter. The opening of the lake occurs on average on May 9, and the latest date for the complete clearing of the lake from ice is May 28. In summer, there are significant fluctuations in the temperature of the surface water layer of the lake from 6.8 to 20.50ºC, averaging 16.4ºC. Lake Markakol belongs to the category of fresh water bodies according to the classification of natural waters (Alekin 1970), being characterized as low-mineralized. The water in the lake is soft, belonging to the hydrocarbonated class and calcium group, having a neutral reaction, with pH fluctuations in the range of 6.54-6.98. The content of nutrients is low and corresponds to the level of clean water bodies according to the Institute of Hydrobiology and Ecology (2017).

The reservoir on the river Uidene is located in the East Kazakhstan region, in the south and east it borders the Xinjiang Uygur Autonomous Region of China, 18 km southwest of the city of Zaisan, at the coordinates 47°21'46.02"N and 84°46'44.25"E. The total length of the reservoir is 4.4 km, with a maximum width of 3.8 km, and a maximum depth of 63.5 m. The reservoir is located in the mountains, which stretch in the latitudinal direction, with the Saur and Manyrak ridges. The climate of the region is sharply continental with large daily air temperature amplitudes. According to the climatic conditions, the territory of the region belongs to the desert-steppe or dry and alpine tundra-meadow zones. Summers are dry and hot, winters are cold and harsh. The average annual rainfall is 281 mm. The average annual air temperature is -4°C. The absolute minimum temperature falls on January at -50°C, the absolute maximum in July is 46°C. The duration of the frost-free period is 130-150 days. Snow cover is established in the second half of November and disappears in early April. The average height of snow cover by the end of winter reaches 20-30 cm, with fluctuations in some years from 5 to 40 cm.

The reservoir of the river Uidene belongs to the artificial type and is currently used for energy purposes, recreation and irrigation. The target of the dam is located in the mountainous part of the Sauro-Tarbagatai Range. The river Uidene originates in the northern spurs of the Saur Range at an altitude of about 2,600 m. The river is fed mainly from springs, as well as from snow and glaciers. The river receives 6 minor tributaries-springs, before leaving the mountains, it flows in a narrow rocky gorge with steep, sometimes sheer banks according to Gidrometeoizdat (1987). The bottom of the reservoir is composed of rocks, in some places covered with loose gravel-pebble deposits, and along the banks it is covered with loamy soils. The annual variation of the water level in the river Uidene is characterized by an extended flood wave with separate peaks. The water of the river Uidene is fresh, suitable for drinking and industrial purposes, its mineralization is 250-350 mg L^{-1} with a predominance of calcium bicarbonate. The pH value changed from 8.7 to 9.0, classifying the waters as alkaline (Kushnikova & Kuanyshbekova 2021). The hardness value corresponded to 0.9 mg-eq dm^{-3}, which corresponds to "very soft" waters. Thus, according to Alekin (1970), surface waters of the reservoir of the river Uidene belong to the bicarbonate-calcium class, type one. Research was carried out on the Lake Markakol and on the reservoir on the river Uidene in the spring-summer period 2021-2022. The sampling of macrozoobenthos, ichthyological samples for bioanalysis, as well as the collection of biomaterial for fish nutrition were carried out at combined stations (Figure 3, Figure 4).

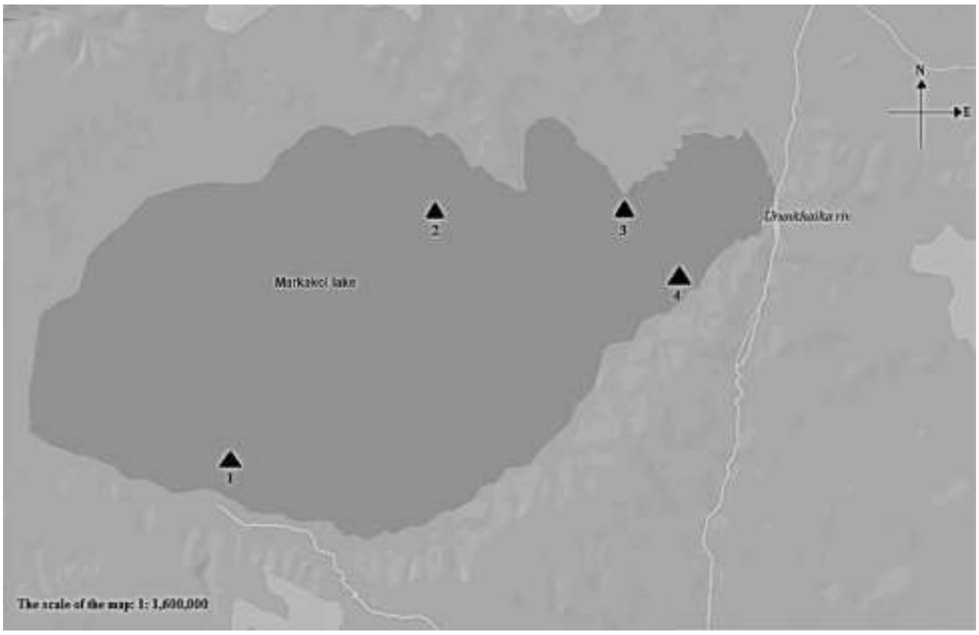

Figure 3. The material collection area on Lake Markakol. Symbols: 1 - Matabay station (MS); 2 – Yelovka station (YS); 3 – Topolevka station (TS); 4 - Urunkhaika station (US).

Figure 4. The material collection area at the reservoir on the river Uidene. Symbols: 1 - wellhead part station (WPS); 2 - dam station (DS); 3 - central part station (CPS); 4 - right-bank station (RBS); 5 - left bank station (LBS).

Macrozoobenthos was sampled with a Petersen grab (with a capture area of 1/40 m^2), followed by washing the soil through a No. 19 sieve (0.5 mm mesh) and fixing with a 4% formalin solution according to Nauka (1974). Three grabs were taken at each station. To calculate the biomass and abundance of zoobenthos per m2, a conversion factor of 20 was used. A total of 102 quantitative samples of macrozoobenthos were collected and processed. The organisms were counted in a modified Bogorov chamber under an MBS-9 microscope. Invertebrates were weighed with an accuracy of 0.1 mg on a torsion balance. The abundance (ind m^{-2}) and biomass (g m^{-2}) of zoobenthos were calculated by station. Determination of the taxonomic affiliation of organisms was carried out according to Nauka (1994-2004). The coordinates of the sampling center are given in Table 1.

Table 1

Names and coordinates of the stations used for the selection of hydrobiological and ichthyological samples from the Lake Markakol and the reservoir of the river Uidene, May-August, 2021 and 2022

Name of research stations	*Abbreviation*	*Coordinates*
Lake Markakol, Urunkhaika station	US	N 48°47'28.12" E 86° 0'46.02"
Lake Markakol, Topolevka station	TS	N 48°47'33.58" E 85°56'3.81"
Lake Markakol, Yelovka station	YS	N 48°48'39.12" E 85°45'13.77"
Lake Markakol, Matabay station	MS	N 48°40'47.54" E 85°38'49.35"
Reservoir on the river Uidene, wellhead part station	WPS	N 47°20'47.98" E 84°46'22.15"
Reservoir on the river Uidene, left bank station	LBS	N 47°21'50.04" E 84°46'26.24"
Reservoir on the river Uidene, right bank station	RBS	N 47°21'58.40" E 84°47'0.16"
Reservoir on the river Uidene, central part station	CPS	N 47°21'59.70" E 84°46'37.72"
Reservoir on the river Uidene, dam station	DS	N 47°22'21.29" E 84°46'35.53"

Table 2

The volume of collected biological material in May and August, 2021 and 2022, respectively, from the Lake Markakol and reservoirs on the river Uidene

Title of work	*Number of samples on Lake Markakol*	*Number of samples at the reservoir on the river Uidene*
Macrozoobenthos samples	48	54
Biological analysis of fish (spec.)	328	264
Fish nutrition (spec.)	148	126

The collection and processing of ichthyological and trophological material was carried out according to generally accepted methods (Pravdin 1966). Fishing was carried out with fixed nets with a mesh size of 20 to 50 mm. Two sets of nets, each extending for a length of 100 meters, were deployed for a duration of 8 hours. During the sampling from the research net catches, the following parameters were recorded: Smith length (FL) and body weight, low weight (without viscera), sex, degree of maturation of gametes. Age was determined by gill covers using a LOMO MSP-2 binocular microscope. The stomachs were fixed with 4% formaldehyde solution. The mass of the food bolus was calculated as the difference between the mass of the filled and empty stomach. The food bolus was analyzed under an MBS-10 binocular microscope. The surviving animals (and their fragments) were identified to a possible taxonomic unit, counted, dried on filter paper, and weighed on an OHAUS model PR224/E electronic balance (50 g)*(0.01 g^{-1}). The gastric filling index (GFI, expressed in ‰) was calculated as the ratio of food mass to total body weight according to Nauka (1974). To assess the importance of different food objects in the diet, their frequency of occurrence, as well as their share in the total weight of the food bolus were determined.For molecular genetic analysis, a small fragment (2x2 mm) of the pectoral fin was cut out from each individual using sterilized scissors. Tissues were immediately preserved in 96% ethanol.

The isolation of genomic DNA was performed using DNA-EXTRAN-2 reagents (Sintol, Russia) in the DNA extraction process. For cell lysis, 5-10 mg of tissue was added to a 2 mL tube, then 300 μL of lysing solution, 1 μL of 2-mercaptoethanol and 10 μL of proteinase K were left overnight at 56°C. To precipitate proteins, 100 μl of precipitating solution 1 was added to the lysate, the contents were mixed on a vortex for 20 seconds, and the mixture was centrifuged for 5 min at 13,000 rpm, a dense precipitate formed at the bottom of the tube. For DNA precipitation, 2 μL of glycogen was added to clean 2 mL tubes. The supernatant containing DNA was transferred in its entirety to the test tubes with DNA precipitator, 300 μL of precipitating solution 2 was added, and mixed by inversion until a visible DNA precipitate appeared. The mixture was centrifuged for 5 minutes at 13,000 rpm, the supernatant was carefully poured off and the tubes were blotted on filter paper. To wash and dissolve the DNA, 400 μL of washing solution were added, centrifuged for 2 min at 13,000 rpm, the supernatant was removed and the tubes were blotted on filter paper. After that, the open tubes were dried in a thermostat at 37°C for 10 minutes until completely dry. Then, 50 μL of the elution solution was added to the precipitate, mixed and heated at 65°C for 5 minutes until the DNA dissolved. The resulting DNA solution was stored at –20°C until further use. DNA integrity was checked by applying a molecular weight marker, 8 μl of isolated DNA, onto a 1.4% agarose gel stained with SYBR Green I, an intercalating dye whose fluorescence intensity increases by several orders of magnitude when incorporated into double-stranded DNA. A working 1X Tris-acetate buffer (TAE) containing tris, acetic acid and EDTA (ethylenediaminetetraacetic acid) was used to perform horizontal DNA electrophoresis on agarose gel. The DNA concentration was estimated using a nano-volume spectrophotometer (NanoDrop One; Thermo Fisher Scientific Inc., Waltham, MA, USA) and stored at −20°C for further use.

The amplification of cytochrome oxidase subunit 1 gene fragments was performed using the PCR technique. The primers used in the PCR process were FishF2_t1 TGT AAA ACG ACG GCC AGT CGA CTA ATC ATA AAG ATA TCG GCA C and FishR2_t1 CAG GAA ACA GCT ATG ACA CTT CAG GGT GAC CGA AGA ATC AGA A (Ivanova et al 2007). The PCR cycle profiles were as follow: 5 minutes initial denaturation at 94°C, followed by 37 cycles of 1 minute at 94°C, annealing for 45 seconds at 55°C and an extension for 1 minute at 72°C,followed by a final extension for 10 minutes at 72°C. The sequencing reaction was carried out in amplifier C1000/T100 (Bio-RAD) or similar in accordance with the instructions for the device. PCR products were visualized on 1% agarose gel. 8 μL of the PCR product was loaded into agarose gel and electrophoresed at 150 volts for 30 minutes. The size of the amplicons was determined using 100 base pair molecular weight ladder. Purified PCR products were directly sequenced in both forward and reverse directions with an Nanophore 05 (Volkov et al 2021) sequencer with a BigDye™TerminatorKit v.1.1/3.1 (Applied Biosystems, Waltham, MA, USA). The forward and reverse sequences of the samples were assembled using Geneious Pirme bioinformatics software package (Kearse et al 2012). After the consensus editing, the generated sequences were pasted and matched to the Basic Local Alignment Search Tool (BLAST) of the National Center for Biotechnology Information (NCBI) to facilitate molecular identification.

Results and Discussion. DNA barcoding has been proven to be a fast and accurate tool for standardized molecular identification system (Lakra et al 2011; Frézal & Leblois 2008). Identification of species in a particular area is vital in implementing efficient assessment and management of the stocks. A total of 16 COI sequences belonging to *Brachymystax* genera and *B. savinovi* species from the two locations (Lake Markakol and Uidene river of East Kazakhstan) were analyzed. After the sequence assembly and consensus editing, sequences with an average length of 565 base pair long were read. Average nucleotide for two lenok's population frequencies are as follows: G: 18.3%, C: 27.7%, T: 29.4% and A: 24.6%. Overall GC content is 46%. The database revealed maximum identity matches of 99 % for all the sequences In Genbank Accession No. KT716377.1. Evaluation of the food base of *B. savinovi* in Lake Markakol and reservoirs on the river Uidene was carried out on macrozoobenthos, since macrozoobenthos is one of the main food components of lenoks at different stages of development and growth (Levanidov 1951; Shuba 1989; Lim & Lee 2019). As part of the macrozoobenthos of Lake Markakol in 2021-2022, 18 taxa of invertebrates were found, including 8 taxa of chironomid larvae, 3 taxa of leeches, 2 taxa of mollusks and gammarus, and 1 taxon of oligochaetes, bugs and chaoborus (Table 3). The maximum frequency of occurrence was noted in the Baikal gammarus *G. lacustris* (100%) and large leeches *Erpobdella octoculata* (100%). More than 50% frequency of occurrence was observed in amphipods of the species *G. fasciatus* (86%) and oligochaetes (65%). The remaining invertebrates in the samples were recorded rarely and their frequency of occurrence did not exceed 50%. In benthic samples, some species of bedbugs, larvae of mayflies and caddis flies, which were numerous in previous years, were absent (Stuge et al 2009; Kirichenko & Devyatkov 1999; Devyatkov & Kushnikova 2019).

Table 3

Taxonomic composition and occurrence frequency (OF, %) of macrozoobenthos of Lake Markakol in May and August, 2021 and 2022

Taxon	*Research region*								*OF %*
	Matabay		*Urunkhaika*		*Topolevka*		*Yelovka*		
	Spring	*Summer*	*Spring*	*Summer*	*Spring*	*Summer*	*Spring*	*Summer*	
Amphipoda									
Gammarus lacustris	+	+	+	+	+	+	+	+	100
Gmelinoides fasciatus	+	+	+	+	+	-	+	+	86
Oligohaeta									
Oligohaeta gen. sp.	+	-	+	-	+	-	+	+	65
Mollusca									
Sphaerium nucleus	+	-	-	-	-	-	+	-	12
Euglesa lilljebogi	-	-	-	-	+	-	-	-	6
Hemiptera									
Corixa linnaei	-	+	-	-	-	-	-	+	12
Hirudinea									
Erpobdella octoculata	+	+	+	+	+	+	+	+	100
Glossiphonia complanata	-	-	+	+	+	-	+	-	13
Helobdella stagnalis	+		+		+		+		25
Chaoboridae									
Chaoborus flavicans	-	-	+	-	+	+	+	+	31
Chironomidae									
Chironomus dorsalis	-	-	-	-	+	-	-	+	6
Cryptochironomus defectus	+	-	-	+	+	-	-	+	25
Cladotanytarsus mancus	-	-	+	-	-	-	+	-	12
Procladius ferrugineus	+	-	-	-	-	+	-	+	13
Endochironomus albipennis	-	-	+	-	-	-	+	-	12
Glyptotendipes gripekoveni	+	-	-	-	+	-	+	-	38
Stictochironomus histrio	-	-	+	-	-	+	-	-	12
Tanytarsus gregarius	+	-	+	-	+	-	+	-	38
Total	10	5	11	4	10	5	12	7	

Quantitative indicators of macrozoobenthos differ by years of study. In 2021, the maximum number of macrozoobenthos was noted at Topolevka station - 770 ind m^{-2} with a biomass of 9.98 g m^{-2} (Table 4), where gammarus *G. fasciatus* prevailed in abundance and biomass, which accounted for 60% of the biomass and 73% of the population. At the stations Matabay and Yelovka, leeches *E. octoculata* dominated in terms of biomass: 4.78 g m^{-2} (56% of the total biomass) and 4.0 g m^{-2} (51%), respectively. In terms of abundance at all stations, gammaruses significantly prevailed. The minimum abundance indicators were observed in the area of Matabay station, 470 ind m^{-2}, and the minimum biomass indicators at Urunkhaika station, 6.01 g m^{-2}. All study areas, according to the generally accepted classification (Kitaev 2007), belong to the middle trophic class (β-mesotrophic).

Table 4

Average values of abundance (A, ind m^{-2}) and biomass (B, g m^{-2}) of macrozoobenthos of Lake Markakol in 2021 by research station

Benthos group	*Matabay*		*Urunkhaika*		*Topolevka*		*Yelovka*		*Average*	
	A	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*
Oligochetes	10	0.02	10	0.02	50	0.05	40	0,11	28	0.05
Leeches	40	4.78	40	2.61	40	3.42	40	4,0	40	3.70
Gammaruses	270	3.57	450	2.81	560	5.99	480	2.57	440	3.73
Chironomid larvae	150	0.18	130	0.54	110	0.49	90	0.19	120	0.35
Other invertebrates	-	-	10	0.03	10	0.03	20	0.92	10	0.25
Total	470	8.55	640	6.01	770	9.98	670	7.79	638	8.08

In 2022, the quantitative indicators of macrozoobenthos were higher compared to 2021. The stocks of benthos were unevenly distributed among the observation stations. The maximum values for biomass were registered in the area of Yelovka station, 24.91 g m^{-2}, which corresponds to a high level of trophicity (Table 5).

Table 5

Average values of abundance (A, ind m^{-2}) and biomass (B, g m^{-2}) of macrozoobenthos of Lake Markakol in 2022 by research station

Benthos group	*Matabay*		*Urunkhaika*		*Topolevka*		*Yelovka*		*Average*	
	A	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*
Oligochetes	20	0.01	40	0.25	-	-	-	-	15	0.07
Mollusk	20	0.61	-	-	20	0.13	40	10.22	20	2.74
Leeches	20	0.22	60	8.47	100	3.70	40	8.43	55	5.21
Gammaruses	460	3.21	520	5.77	680	7.00	420	5.42	520	5.35
Chironomid larvae	20	0.13	20	0.04	-	-	80	0.19	30	0.09
Other invertebrates	-	-	20	0.07	20	0.13	40	0.73	20	0.23
Total	540	4.18	660	14.6	820	10.96	620	24.9	660	13.66
Type of reservoir	α-mesotrophic		α-eutrophic		α-eutrophic		β-eutrophic		α-eutrophic	
Class of trophicity	Moderate		Elevated		Elevated		High		Elevated	

Gammarus *G. lacustris* and *G. fasciatus* formed the basis of abundance (68%), mollusks *S. nucleus* (41%), leeches (34%), and all the same gammaruses (22%) were the leaders in terms of biomass. At Urunkhaika and Topolevka stations, the abundance of benthic invertebrates was not inferior to Yelovka station, but due to the absence of large mollusks, the biomass indicators were significantly lower, 14.6 and 10.96 g m^{-2}, respectively. At Urunkhaika station, leeches accounted for 58.0% of the biomass, and at Topolevka station, gammarids accounted for 64%. The minimum amount of macrozoobenthos was noted at Matabay station, 540 ind m^{-2} and 4.18 g m^{-2}. Both in terms of abundance (85%) and biomass (77%), gammarus dominated. The average value of the number of benthic invertebrates was 660 ind m^{-2}, the average value of biomass was 13.66 g m^{-2}, which corresponds to a reservoir of increased trophicity according to the scale of S.P. Kitayev. Studies of the macrozoobenthos of Lake Markakol showed that the food base of Lake Markakol has high reserves of large benthic invertebrates, namely gammarus and leeches. A completely different situation in terms of food base has developed in the reservoir on the river Uidene. As a result of the spring-summer studies of 2021-2022, 12 taxa of benthic invertebrates were noted in the composition of the macrozoobenthos of the reservoir on the river Uidene, including the larvae of mayflies, stoneflies, caddis flies, chironomids, as well as bedbugs and oligochaetes. The most diverse macrozoobenthos is at the estuary of the river Uidene. Oxirheophilous larvae of stoneflies, mayflies, caddisflies, chironomids, and oligochaetes occur on stony-pebbly soils (Table 6).

Table 6

Taxonomic composition of macrozoobenthos and frequency of occurrence of aquatic organisms (%) of the reservoir on the river Uidene

Taxon	*Ecological zone*				*Occurrence frequency*
	River part (r. Uydene)	*The open part of the reservoir*			
		Estuary	*Littoral*	*Pelagial*	
Class *Oligochaeta*	+		+	-	13
Class *Insecta*	-		-	-	-
Order *Hemiptera*	-		-	-	-
Sigara falleni Fieber	-	+	+	-	26
Order *Ephemeroptera*					
Epeorus pellucidus	+		-	-	13
Ephemerella ignita Poda	+		-	-	13
Brachycercus mimotus	+		-	-	13
Baetopus warnensis Keffermuller	-		+	-	13
Order *Plecoptera*	-		-	-	-
Leuctra fusca	+		-	-	13
Order *Trichoptera*					
Brachycentrus sumnubilus	+		-	-	13
Order *Diptera*					
Chironomys plumosus Linne	+	+	+	+	39
Chironomys dorsalis Meigen	-	+	-	+	13
Glyptotendipes gripekoveni Kieffer	+	+	+	+	91
Tanypus villipennis Meigen	-		+	+	52

In the open part of the reservoir there are water bugs, larvae of chironomids, oligochaetes, and single larvae of mayflies of the species *B. warnensis*. Chironomid larvae are most diversely represented, accounting for 67% of the total taxonomic wealth. The highest frequency of occurrence was noted for chironomids of the species *G. gripekoveni*, 91%. Ecological zones of the reservoir on the river Uidene also differ in quantitative indicators (Table 7).

In the river Uidene, with a population of 760 thousand ind m^{-2}, rather high biomass rates (13.29 g m^{-2}) are observed due to large larvae of amphibiotic insects. The basis of the number (37%) and biomass (69%) are mayfly larvae. According to the trophic scale of Kitayev (2007), in the estuary of the river Uidene, the predominant type of the water body is ȧ-mesotrophic, elevated trophic class. In the estuarine part of the reservoir, there is a very high abundance of chironomids, which create a significant biomass (19.44 g m^{-2}) and account for 96% of the abundance and 98% of the biomass of the entire macrozoobenthos. In terms of macrozoobenthos indicators, the estuarine part is characterized by an increased trophic class (Kitayev 2007). The ecological zones of the reservoir itself - pelagial and littoral - differ in qualitative and quantitative characteristics. In the littoral, macrozoobenthos is more diverse and is represented by chironomid larvae, bedbugs, and may fly larvae. In the pelagic zone, only chironomid larvae were recorded.

Table 7
Average values of abundance and biomass of macrozoobenthos of the reservoir on the river Uidene in May-August 2021-2022

Zoobenthos group	*Estuary part*		*Littoral*		*Pelagial*	
	Number ind m^{-2}	*Biomass g m^{-2}*	*Number ind m^{-2}*	*Biomass g m^{-2}*	*Number ind m^{-2}*	*Biomass g m^{-2}*
Chironomidae	9720	19.44	220	1.33	237	1.13
Hemiptera	40	0.42	160	2.02	-	-
Oligochaeta	-	-	40	0.08	-	-
Other	-	-	5	0.40	-	-
Total	9760	19.86	425	3.83	237	1.13
Type of reservoir	α-eutrophic		α-mesotrophic		α-oligotrophic	
Class of trophicity	Elevated		Moderate		Very low	

In terms of quantitative indicators, the littoral zone is in a higher position. In the littoral of the reservoir, the average abundance is 425 ind m^{-2} with a biomass of 3.83 g m^{-2}. According to the "trophic scale", the above indicators correspond to the α-mesotrophic type of the reservoir with a moderate trophic class (Kitayev 2007). The pelagic zone is characterized by a low trophic class with a biomass value of 1.13 g m^{-2}. Thus, in the reservoir on the river Uidene, a clear location of macrozoobenthos is currently observed in various ecological zones. Macrozoobenthos is the most numerous in the estuarine zone of the reservoir and the poorest in the pelagic zone. Only the estuarine part of the reservoir is characterized by an increased level of trophicity in terms of macrozobenthos, while in other areas it is moderate and very low. As is known, the food base largely determines the specific growth rate of fish, along with temperature and hydrological regime. On the growth rate of lenok from Lake Markakol and the reservoirs on the river Uidene, the influence of natural and climatic factors is minimal, since the reservoirs are located in the same natural and climatic zone and have a similar temperature regime. Therefore, the growth rate and biological parameters of fish from the two studied reservoirs directly depend on the food supply. According to the data of measurements and estimation of age by gill covers, the composition of the sample of lenok population consists of: 9 age groups, from- 3+ to 10+ years in the Lake Markakol and 7 age groups, from - 2+ to 8+ years, in the river Uidene. The results showed that it was just before the period of puberty (in *B. savinovi* from Lake Markakol puberty occurs at 4 years, in *B. savinovi* from the reservoir on the river Uidene at 6 years) the maximum specific growth rates were recorded, in particular, in *B. savinovi* from Lake Markakol 26-34% per year and for *B. savinovi* from the Uidene reservoir 33-49% per year. It was found that the weight and linear growth of the same-age groups of *B. savinovi* from the reservoir on the river Uidene is slower than in Lake Markakol (Figure 5).

Plastic features are more closely related not to age, but to the size and growth rate of fish (Reshetnikov & Popova 1988; Antonov 2012). Usually, slow-growing individuals have head and eye indices greater than in fast growing individuals. *B. savinovi* from the Uidene population is characterized by higher head and eye indices than the lenok from Lake Markakol (Kushnikova et al 2021). The nutritional features of the Markakol lenok were studied and covered in the literature by domestic scientists. The first detailed analysis of the nutrition of the Markakol lenok was presented in 1957 by Ten (Ten 1970). The nutritional spectrum of the Markakol lenok consisted of 45 components, of which 43 are invertebrates: these are larvae of chironomids, caddisflies, gammarus, mayflies, stoneflies, water bugs, and mollusks. Juvenile lenok feeds mainly on chironomid larvae and adults. With the growth of juveniles, the role of invertebrates decreases and, starting from the age of 7 years, lenok completely switch to a predatory lifestyle, consuming chars and minnows. But a significant role in the diet of lenok was played by benthic fauna, namely gammarus and caddisflies, up to 50% of occurrence and 26% by weight. All of the above indicates a wide range of nutrition of the Markakol lenok and the almost complete development of the food resources of Lake Markakol. Subsequent studies have shown the changes that have occurred in the nutritional spectrum of the *B. savinovi* of Lake Markakol (Kirichenko & Devyatkov 1999).

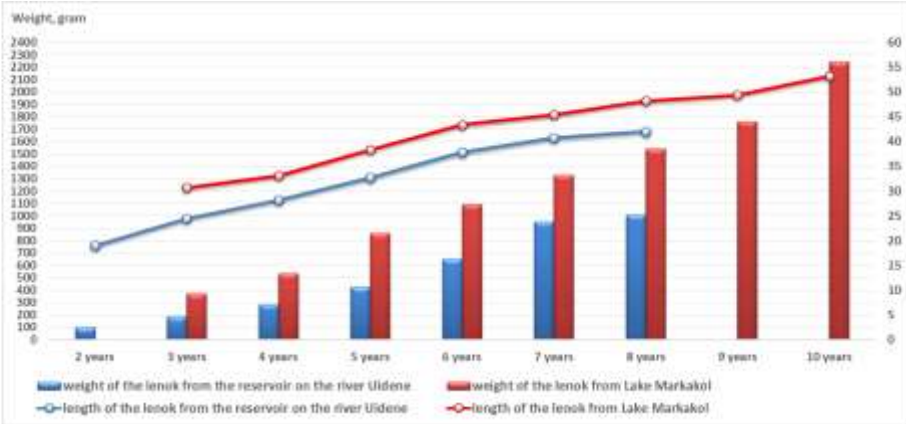

Figure 5. Dynamics of average size and weight indicators of *Brachymystax savinovi* from Lake Markakol and reservoirs on the river Uidene in 2021-2022.

The main part of the benthic component of fish food was gammarus (21.3%) and mollusks (10.9%). A significant role in the nutrition of the *B. savinovi* was played by chaoborus larvae (13.0% by weight) as well as fish (20.1% by weight). Feeding intensity was high – the general filling index for *B. savinovi* was 124.3^{0}/$_{000}$. Such high GFI values indicate a good supply of fish with food. The nutritional needs of *B. savinovi* are met by the high abundance and biomass of their prey items, benthic invertebrates. In our studies, the sample of *B. savinovi* is represented by individuals from 3+ to 10+ years old, with a predominance of 7-8 years old individuals. The ratio of males and females is 1:1.6. All examined stomachs were filled with food. The SFI (stomach filling index), which reflects the degree of nutrition intensity, widely varied from 7.57 to 292.0 ‰o (Table 8).

Table 8

Dimensional and weight indicators, and stomach filling index of *Brachymystax savinovi* of different ages, in the Lake Markakol, in 2021-2022

Age, years	*Number of fish, ind.*	*Length (FL), mm*	*Weight, G*	*Stomach filling index, ‰o*
3+	12	30.5±1.0 30.0 – 32.0	386.75±77.62 344.0 – 503.0	135.5±107.3 48.5 – 292.0
4+	7	37.14±3.57 33.0 – 41.0	764.28±259.04 440.0 – 1090.0	79.4±46.6 67.2 – 154.6
5+	17	37.33±3.21 35.0 – 41.0	830.33±230.79 635.0 – 1085.0	138.0±58.7 70.7 – 178.4
6+	21	44.00±1.33 41.0 – 46.0	1186.00±156.44 902.0 – 1355.0	112.7±91.9 14.1 – 288.9
7+	35	45.70±2.28 41.0 – 49.0	1424.82±173.57 1051.0 – 1705.0	140.1±65.2 14.8 – 243.9
8+	43	48.02±1.62 45.0 – 51.0	1582.64±184.01 1232.0 – 1880.0	87.8±57.5 7.57 – 216.4
9+	7	49.33±1.52 48.0 – 51.0	1841.33±222.48 1649.0 – 2085.0	131.1±53.4 76.1 – 182.7
10+	6	52.64±2.17 50.0 – 55.0	2384.29±316.37 1925.0 – 2615.0	63.2±23.7 33.3 – 96.5

Numerator - the mean value and standard deviation; denominator-the limits of the variation of the indicator.

The maximum values, of 292.0 ‱o, were noted for three-years-old, the youngest age group in the sample. The nutritional spectrum of the considered age groups is not large and is limited to 6 animal components and 2 plant components. These are the remains of macrophytes and detritus (Table 9). Mineral residues in the form of very small pebbles are classified as conditional food components. Food objects of animal origin are represented by various groups of benthic invertebrates: gammaruses (*Amphipoda*), leeches (*Hirudinea*), chironomid larvae (*Chironomidae*), water bugs (*Gerridae*), mollusks (*Mollusca*), which *B. savinovi* collected from the bottom of the lake. Remains of macrophytes were recorded in the nutrition of *B. savinovi*, which populates a significant part of the littoral of Lake Markakol and estuarine areas of rivers flowing into the lake. Despite the fact that *B. savinovi* belongs to predators by the type of food, no remains of fish or other vertebrates were found in the stomachs.

Table 9

Composition of food, the value of food components (% by weight) and the occurrence frequency (OF, %) in the diet of *Brachymystax savinovi* food components, in the Lake Markakol, in 2021-2022

Food component	*% by weight in food bolus*								*OF %*
Age, years	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	
Oligochaetes	1-3	-	-	-	1-2	-	-	-	4
Chironomidae larvae	2-5		1-2	1-2	1-2	1-2	1-2	1-2	25
Gammarus	95-100	95-98	98-99	15-100	10-100	2-100	98-100	96-100	91
Plant detritus, mineral remains	-	-	-	2-5	1-5	1-9	-	-	7
Macrophytes	-	-	-	1-2	-	1-2	-	-	4
Water bugs	-	2-7	-	1-31	1-85	1-26	-	1-4	13
Mollusks	1-2	2-5	1-3	1-2	1-2	1-2	-	-	14
Leeches	-	-	1-2	2-85	2-96	4-100	-	-	41
General filling index GFI, ‱	48.5-292.0	67.2-154.6	145.3-178.4	14.1-288.9	14.8-223.3	7.57-167.8	-	-	-
Number of specimens studied, ind.	12	7	17	21	35	43	7	6	
Of them with empty intestines, %	No specimens with empty intestines have been recorded.								

The frequency of occurrence was dominated by gammaruses (*Amphipoda*), with 91%. Leeches (*Hirudinea*) were the second component in frequency of occurrence (42%). For gammarids and leeches, high selectivity indices (SI) were also established: 0.98 for gammarus and 0.89 for leeches. Chironomid larvae were recorded in a quarter of the analyzed individuals, but their share in the total weight of the food bolus is not significant. Water bugs and mollusks were next in frequency of occurrence, with values of 13% and 14%, respectively. The share of other components of the food bolus did not exceed 10%. Due to the fact that the determination of food components was carried out to a different level of taxonomic affiliation, the nutritional analysis of *B. savinovi* was carried out taking into account the proportion (%) of components by weight in the food bolus. Lenok of 6+ to 8+ years have the widest range of nutrition. The composition of the food bolus includes almost all the feed components observed in this reservoir. By the frequency of occurrence and share in the mass of the food bolus, gammarus were among the major components of food (Figure 6). In other age groups, the number of food components varied from 2 to 4. The dominant position in the food bolus also belongs to gammarus, they account for 95 to 100% of the weight of the food bolus. During the entire study period, no remains of fish or terrestrial insects were recorded in any stomach. The absence of larvae of stoneflies, mayflies, and caddis flies in the stomachs of fish indicates that fish do not rise to spawning rivers for food, where the above groups of macrozoobenthos form the basis of the biocenosis (Kushnikova 2022).

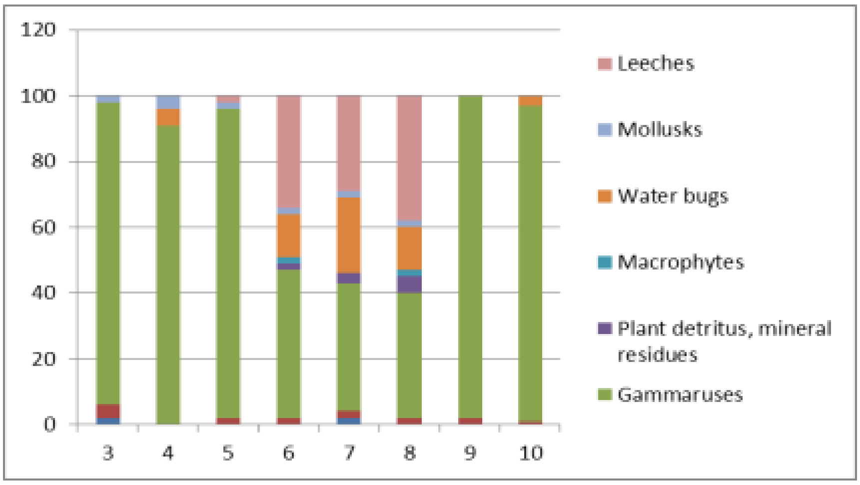

Figure 6. Nutritional spectrum of *Brachymystax savinovi* of different ages, in the Lake Markakol, in 2021 and 2022.

The nutritional spectrum of *B. savinovi* is partially explained by morphological features. In particular the sharp-snouted form of the mouth is closer to the benthophages; therefore, benthic organisms predominate in the diet. V.V. Shuba writes about this (Shuba 1989) when comparing the nutritional spectrum of the blunt-snouted and sharp-snouted lenoks. Some similarities in the nutritional spectrum with *B. savinovi* from Lake Markakol are described by Matveyev et al (2009), in the lake Balan-Tamur (basin of the Barguzin River), which is characterized by the optimal summer water temperature (8–12°C) for habitation and high quantitative indicators of zoobenthos. To analyze the nutritional spectrum of *B. savinovi* from the reservoir on the river Uidene the sample included individuals from 2+ to 8+ years old, with a predominance of 3 to 5 years old individuals. The ratio of males and females is 1:1. All stomachs taken for nutrition analysis were filled with food. The indexes of SFI (stomach filling index) varied widely from 29.1 to 251.0‰o. The minimum indicator was recorded for two-years-old (29.1 ‰o), and the maximum for five-year-old individuals (251.0 ‰o) (Table 10).

Table 10

Dimensional-weight indicators and stomach filling index of *Brachymystax savinovi* of different ages, in the reservoir on the river Uidene, in 2021-2022

Age, years	*Number of fish, ind.*	*Fish length (FL), mm*	*Weight, g*	*Stomach filling index, ‰*
2+	8	21.44±1.48 20.0 – 24.0	115.66±28.55 89.0 – 148.0	37.06±8.27 29.1 – 50.6
3+	25	28.12±3.44 25.0 – 36.0	263.87±122.10 171.0 – 551.0	133.13±60.42 31.6 – 207.0
4+	39	30.71±1.70 28.0 – 33.0	348.85±53.17 248.0 – 400.0	85.34±51.65 29.6 – 141.0
5+	27	32.69±1.87 30.2 – 35.5	563.63±32.56 520.0 – 610.0	90.26±8.06 79.8 – 102.5
6+	13	37.61±1.83 34.0 – 40.0	655.30±145.78 520.0 – 950.0	206.87±26.7 171.2 – 251.7
7+	9	43.77±0.90 42.5 – 45.0	1057.67±164.0 875.0 – 1275.0	185.37±22.13 156.2 – 211.4
8+	5	44.6±0.64 44.0 – 45.5	1216.0±58.24 1165.0 – 1295.0	174.38±9.85 164.2 – 188.9

Numerator - the mean value and standard deviation; denominator-the limits of the variation of the indicator.

The highest rates of SFI are typical for the older age group of 6-8 years. The nutritional spectrum of the considered age groups is not large and is limited to 5 animal components and 2 plant components. These are the remains of macrophytes and dendrites (Table 11).

Table 11

The food composition and the value of food components (% by weight) in the diet of *Brachymystax savinovi* in the reservoir of the river Uidene, in 2021-22

Food component	*% by weight in food bolus*							*OF*
	2 years	*3 years*	*4 years*	*5 years*	*6 years*	*7 years*	*8 years*	*%*
Cladocerans	< 1	-	-	-	-	-	-	3
Caddis fly larvae	< 1	-	-	-	-	-	-	5
Chironomid larvae	-	37-100	60-100	10-15	5-10	-	-	34
Water bugs	-	-	10-21	5-12	-	-	-	16
Fish	100	28-63	84-100	26-74	46-55	69-90	80- 100	53
Plant dendrite	-	1.4-21.5	15-20	-	-	-	-	11
Macrophytes	-	18-56	20-32	-	-	-	-	32
Stone	-	10-72	16-52	10-32	45-49	9-32	10-20	42
General filling index GFI, $^{0}/_{000}$	29.1-50.6	31.6-207.0	29.6-141.0	79.8-102.5	171.2-251.7	156.2-211.4	164.2 188.9	-
Number of specimens studied, ind.	8	25	39	27	13	9	5	-
Of them with empty intestines, %	No specimens with empty intestines have been recorded.							

It is necessary to note a significant proportion of pebbles in the food bolus up to 2.0-2.5 cm in size, which belongs to conditional food components (Figure 7).

Figure 7. Non-food components of the food bolus of *Brachymystax savinovi* from the reservoir on the river Uidene.

Stones are present in the stomachs of individuals of all ages, except for two-years-old. The proportion of stones in the food bolus varies from 10 to 72%. Animals in the food bolus are represented by various groups of benthic invertebrates: cladocerans, caddisfly larvae, chironomid larvae, water bugs. In the diet of *B. savinovi*, remains of macrophytes and plant dendrite were noticed. The second representative of the ichthyofauna of the reservoir on the river Uidene, the common gudgeon *Gobio gobio (Linnaeus)*, was registered in the diet of the *B. savinovi*. The diet of *B. savinovi* from the reservoir on the river Uidene was rather monotonous, *B. savinovi* fed mainly on fish and chironomids. In terms of occurrence frequency, the gudgeon dominated among the food components (53% occurrence frequency). In second place, with the same occurrence frequency, are chironomid larvae (34%) and macrophytes (32%). The top three is completed by water bugs (16%). The share of other taxa in the food bolus is not significant and varies from 3 to 11%. The nature of nutrition differs significantly by age groups. It should be noted that the transition to carnivorous feeding begins at the age of two. Two-years-old feed mainly on common gudgeon and only a few representatives of zoobenthos are found, namely caddisfly larvae and planktonic organisms (cladocerans), which are not found in the stomachs of individuals of other age groups (Figure 8). The largest number of food fragments was noted for three-four-years-old. The leading position in this group is occupied by chironomid larvae (37-100%) and gudgeon (28-100%). In addition to them, water bugs and plant residues were identified in the food bolus.

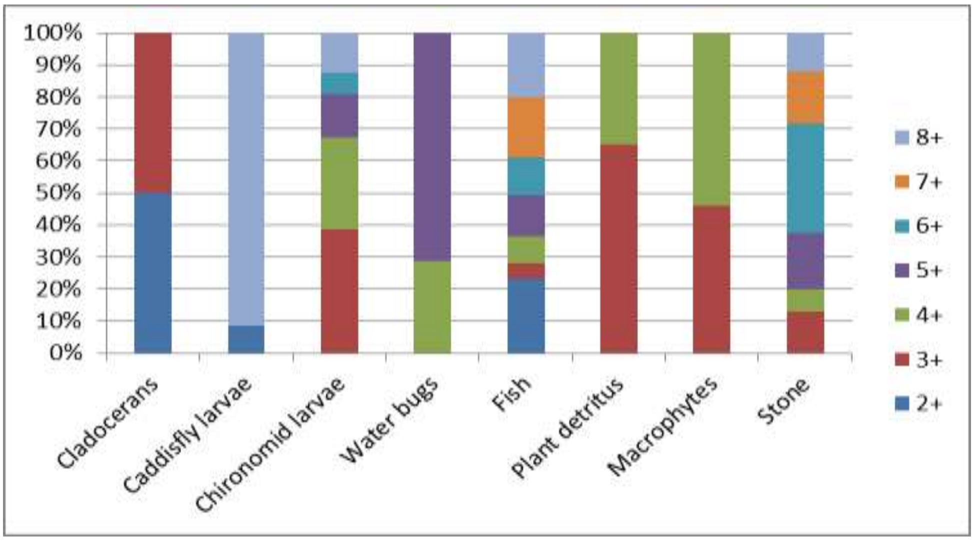

Figure 8. Nutritional spectrum of *Brachymystax savinovi* of different ages from the reservoir of the river Uidene, in 2021–2022.

With the transition to the next age groups, a decrease in food components of the food bolus is noted. In individuals five to eight years old, the basis of the food bolus components is the gudgeon, and the share of water bugs and chironomids accounts for 5 to 15%. The results of the study of macrozoobenthos and feeding of *B. savinovi* from the reservoir on the river Uidene suggest that lenok perform daily foraging migrations to the estuary and littoral parts during feeding, moving, in the daytime, to pelagic areas. The high probability of the *lenok*'s absence from the river explains the absence of river benthos in the food bolus of *B. savinovi*. According to Fulton, the average fatness values in lenoks from the Lake Markakol (1.25) and in the Uidene river's reservoir (1.27) are almost equal. In the current study, it was found that the concepts of 'selectivity' and 'availability' of food exhibited nearly identical meanings under the given conditions. The selectivity index for gammarus and leeches for the Markakol *B. savinovi* is close to 1, suggesting that the *B. savinovi* targets accessible and numerous groups of macrozoobenthos. Even the older age groups do not switch to eating fish, due to the excess of readily available food. *B. savinovi* from the reservoir of the river Uidene, on the contrary, switches very early to predation, due to the lack of other food objects.

Conclusions. *B. savinovi* lives in two reservoirs of the East Kazakhstan region: the Lake Markakol and the reservoir of the river Uidene. *B. savinovi* is a native species from these waters. An unintended introduction of organisms from Lake Markakol into the Uidene River reservoir led to the formation of a self-reproducing population. The food base of the studied reservoirs differs significantly both in quality and quantity. Markakol Lake's composition of macrozoobenthos is dominated by gammarus and leeches, while in the reservoir of the river Uidene it is dominated by chironomid larvae and water bugs. The trophic status of the Lake Markakol is classified as average and elevated, and in the reservoir on the river Uidene it is moderate to very low. A significant difference in the food base of the two reservoirs determines the nutritional spectrum of *B. savinovi*. For the *B. savinovi* from the Lake Markakol, gammarus and leeches were the main components in the food bolus, while for the Uidene's population, the basis of food is the gudgeon. *B. savinovi* from the Lake Markakol have the widest range of nutrition in 6+ to 8+ years individuals. The composition of the food bolus includes almost all the feed components, edible for *B. savinovi*, observed in this reservoir. By the frequency of occurrence and share in the mass of the food bolus, gammarus were among the dominant objects of food. In other age groups, the number of food components varied from 2 to 4. The dominant position in the food bolus also belongs to gammarus, accounting for 95 to 100% of the weight of the food bolus. In the *B. savinovi* from the reservoir on the river Uidene the largest number of food fragments was noticed for individuals of 3 to 4 years old. The leading position in this group is occupied by chironomid larvae (37-100%) and gudgeon (28-100%). In addition to them, water bugs and plant residues were identified in the food bolus. The most notable alterations in the dietary content of *B. savinovi* from the Uidene river reservoir occurred at the age of 7-8 years. During this period, their food intake primarily consisted of fish, with non-food items such as stones, making up an equal proportion in terms of weight, at a 1:1 ratio. A significant difference in the food base of the two reservoirs determined the feeding habits of the *B. savinovi*, which, in turn, affected the growth rate, the timing of puberty, and the formation of the morphotype. At the same age, lenok specimens from the Lake Markakol have higher size and weight indicators than those from the reservoir of the river Uidene. The results of the research support a recommendation for the users (the reservoir of the river Uidene is concessioned to the "Shygys" farm): to increase the food base of the reservoir through the introduction of gammarids.

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Conflict of interest. The authors declare no conflicts of interest.

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