

Morphometric Characters and Feeding Habits in the Early Ontogenesis of Kildin Cod *Gadus morhua kildinensis* (Gadidae) from Lake Mogilnoe (Kildin Island, Barents Sea)

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Abstract—Kildin cod *Gadus morhua kildinensis* is a subspecies of Atlantic cod with extremely small population size, listed in the Red Data Book of the Russian Federation, which inhabits the waters of a small meromictic lake on the Kildin Island (Barents Sea). Comparative studies of morphobiological characteristics and feeding habits of Kildin cod in the juvenile period were conducted for the first time. Comparison of sample sets of adult Kildin cod and fingerlings on the basis of multivariate analysis of variance demonstrates a high degree of differences in the complex of morphometric characters. The diet of the analyzed sample set of Kildin cod fingerlings consisted of ostracodes (Ostracoda), larvae of polychaetas (Polychaeta), cladocerans (Cladocera), and gammarids (Gammaridae). The special features of changes in the diet of Kildin cod in the early ontogenesis are discussed.

Keywords: Kildin cod *Gadus morhua kildinensis*, morphometry, nutrition, Red Data Book, Lake Mogilnoe

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INTRODUCTION

Kildin cod *Gadus morhua kildinensis* Derjugin, 1920 is an isolated self-reproducing population of an extremely small size inhabiting Lake Mogilnoe on Kildin Island (Barents Sea). The subspecies is listed in the Red Data Book of the Russian Federation (Shilin and Stroganov, 2021). Its descriptions have been presented in multiple works devoted to the study of Lake Mogilnoe: a small relict meromictic water body that had formed ~1.5 thousand years ago as a result of the cut-off of the sea bay by the rocky–pebble spit (barrier) from the water area of the Kildin Strait under the complex influence of a number of factors (seabed uplift, glacial accumulation, abrasive-accumulative activity of the sea, etc.) (Fausek, 1891; Schmidt, 1891; Rippas, 1915; Deryugin, 1925; Gurevich and Liyva, 1975; Tarasov, 1975; Kotsubko and Kravchenko, 2002). Although information on Lake Mogilnoe on Kildin Island is found on nautical charts of English and Dutch travelers since the middle 16th century (Titov et al., 2002), the first description of the lake cod was only made at the beginning of the 19th century by Ozeretskovsky (1804). For more than 200 years, studies have been conducted on the biology, morphology,

parasite fauna, and genetic and other characteristics of the Kildin cod (Deryugin, 1920, 1925; Esipov, 1930; Dogel, 1936; Tseeb, 1975; Tseeb, Astafeva, 1975; Antsiferov and Trofimov, 2002; Karasev, 2002; Mukhina, etc., 2002; Zhivotovsky et al., 2016; Stroganov et al., 2017). The mechanisms of its adaptation to the specific conditions of the lake are analyzed. It is shown that the process of the subspecies separation from the maternal form occurred while retaining some biological features (cannibalism and high fecundity) and changing other features, such as reduction of the diversity of characters and their specialization (only one type of coloration out of the spectrum of different colors in the original form, head becoming larger and wider, transition of adult individuals mainly to territorial behavior, etc.) (Stroganov et al., 2017). Studies were conducted mainly on adult individuals. Meanwhile, insufficient attention was paid to the study of the morphobiological characteristics and feeding habits of juvenile Kildin cod, among other reasons due to difficulties in obtaining material. For example, in the 1966–1969 studies of the Murmansk Marine Biological Institute, out of 160 analyzed specimens of the Kildin cod, there were only three fingerlings (Tseeb, 1975).

The aim of the present study is to obtain and analyze data on morphometry and diet of the Kildin cod in its juvenile period. The study significantly expands the available information on the juveniles of the subspecies. Studying the food spectrum of the juvenile Kildin cod is also of particular interest due to the fact that representatives of both brackish-water and marine zooplankton inhabit the lake at different depths with different salinity values (Strelkov et al., 2019).

MATERIAL AND METHODS

The material was obtained from the collections of the expedition on Lake Mogilnoe by the Department of Ichthyology of Lomonosov Moscow State University (2011 and 2012), the Department of Ichthyology and Hydrobiology of St. Petersburg State University (2016), and Polar Branch of Russian Scientific Research Institute of Fisheries and Oceanography (1997–2000). Cod specimens in Lake Mogilnoe were collected by the catch-and-release method (in accordance with the permits of the Ministry of Natural Resources and Environment of the Russian Federation) with hook-and-line and net gear. We measured the length and weight of the caught fish, took photos with the number of a given specimen and a ruler in the frame, after which the cod was returned to the lake.

Morphometry was performed using the photographs (from the side, top, and bottom angles of view). The basis for morphometric studies consisted of measurements performed on a sample set of fingerlings before their transition from pelagic to benthic lifestyle (the so-called settlement). Only individual specimens of older juveniles of the Kildin cod (two-year old) living in the vicinity of the bridge (Stroganov et al., 2022), were available for measurements due to a secretive lifestyle associated, among other things, with cannibalism: the juveniles represent a significant portion in the food spectrum of the large cod (Mukhina et al., 2002). The results of measurements of morphometric characters of the juveniles were compared with measurements of the large cod, also made using photographs.

During morphometric analysis, 12 morphometric characters were measured: *TL*, total length; *SL*, standard length (to the end of the scale covering); *c*, head length; *cH*, head depth; *ao*, snout length; *cir*, length of the chin barbel; *io*, interorbital distance; *o*, eye diameter; *H*, greatest body depth; *h*, shortest body depth; *aD*, antedorsal distance; *pD*, postdorsal distance (Fig. 1). Measurements were performed with an accuracy of 1 mm, the characters were expressed as indices (the ratio to the total and standard length of the body and to the length of the head) (Aleev, 1963). Statistical analysis was performed according to the standard methods (Rokitsky, 1967; Ivanter and Korosov, 2003). The level and significance of the differences in morphometric indices were evaluated in Excel and STATISTICA software packages on the basis of single-fac-

tor (one-way ANOVA) and multivariate analysis of variance (MANOVA). It should also be noted that according to the conditions of application of the software, the sample set of fingerlings was arbitrarily divided into two parts.

The cod fingerlings from the collection of the Polar Branch of Russian Scientific Research Institute of Fisheries and Oceanography were used to study the feeding habits. We measured the total length of a fingerling (with an accuracy of 1 mm) and the weight of a specimen, contents of the stomach, and each component of the food (with an accuracy of 0.001 g). We estimated the proportion of food components by weight (%), the frequency of occurrence of each component (%) (Zharnikova, 2013), and the Fulton's condition factor (Lokshina and Shatunovsky, 1978). We analyzed the feeding rate, which is quantitatively expressed by the indices of stomach fullness: the total fullness index (the ratio of the weight of the whole food bolus to the mass of the fish, multiplied by 10 000) and the partial fullness index (the ratio of the weight of one food component to the weight of fish, multiplied by 10 000), expressed in permyriads (‰) (Kotlyar, 2004; Ryzhkov et al., 2013). We also calculated the relative importance index (%), taking into account both the frequency of occurrence and the weight portion of each food component (Popova and Reshetnikov, 2011) according to the formula: $IR = (F_i P_i / \sum F_i P_i) \times 100$, where F_i is the frequency of occurrence of each food type, P_i is its weight portion, and the value of i itself varies from 1 to n (n is the number of species of forage organisms). Since the index is normalized, it varies between 0–100% regardless of the number of forage organisms, and as a result, the value of each food object by weight in the composition of the food bolus is adjusted for the frequency of occurrence.

RESULTS

The analysis of morphometric characters showed that the head of the Kildin cod fingerlings is rather large, with length of 0.27–0.30 *SL*, but relatively narrow: the *io/c* index was 0.15–0.25. Indices of other signs in %*SL*: *aD*, 0.29–0.37; *pD*, 0.51–0.58; *H*, 0.15–0.20; and in %*c*: *ao*, 0.19–0.36; *o*, 0.28–0.33; *cir*, 0.12–0.18.

Comparison of the Kildin cod fingerlings with large (adult) individuals on the basis of 11 indices of morphometric characters using MANOVA is shown in Fig. 2. The degree of overlap of scattering fields (at the level of 95%) within the 1st and 2nd discriminant functions illustrates the high degree of differences in the character complex.

The results of one-way ANOVA, which allows us to estimate the level of differences of individual morphometric characters, showed that the differences between the sample sets of large Kildin cod and finger-

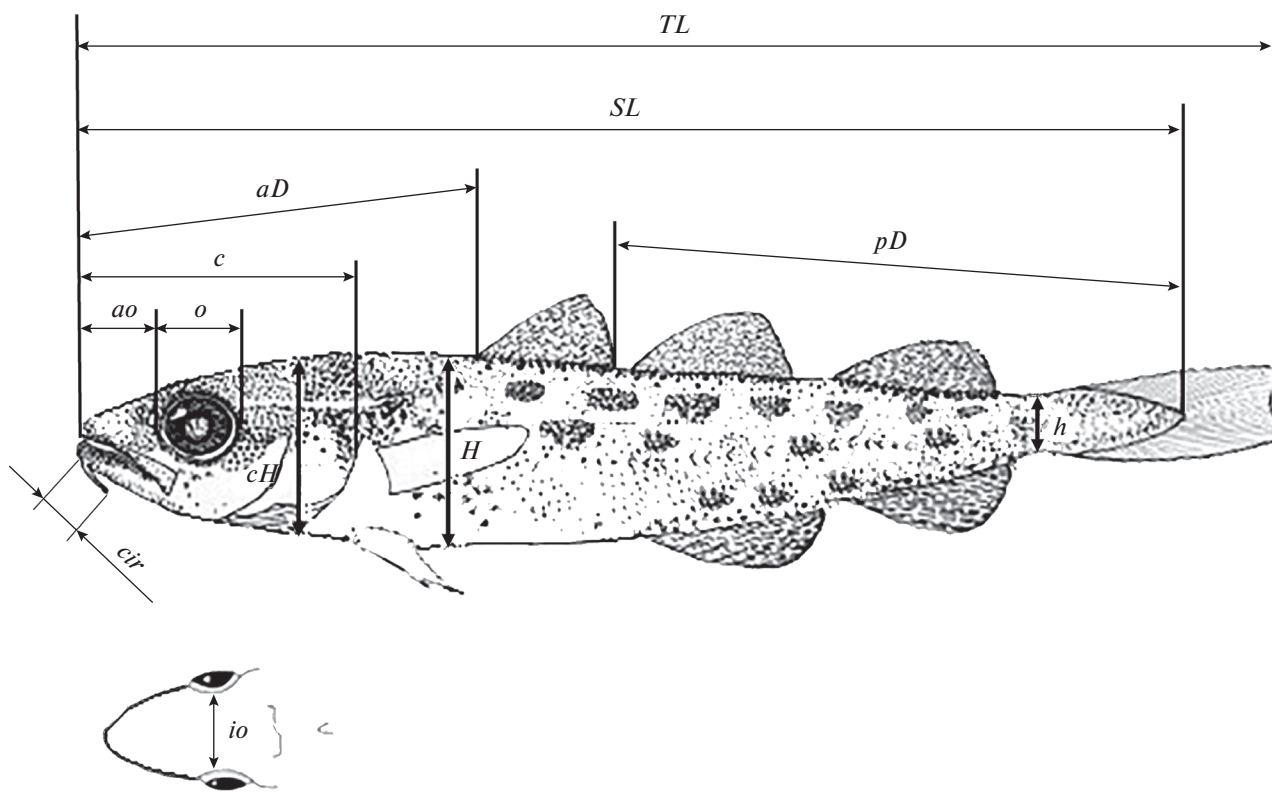


Fig. 1. Schematic illustration of measurements of *Gadus* sp. (according to Rass, 1946; Voskoboinikova et al., 2012, modified). *TL*, total length; *SL*, standard length (to the end of the scale covering); *c*, head length; *cH*, head depth; *ao*, snout length; *cir*, length of the chin barbel; *io*, interorbital distance; *o*, eye diameter; *H*, greatest body depth; *h*, shortest body depth; *aD*, antedorsal distance; *pD*, postdorsal distance.

lings by all the studied characters are significant, with the exception of h/SL , aD/SL , and cir/c (Table 1). With age, the relative mean values of the head length decreased, the maximum body depth and postdorsal distance (pD) increased. The decrease in the mean value of the SL/TL index with age indirectly reflects the relative increase in the length of the caudal fin. The characters of the head related to its length also changed with age: the depth and width (interorbital distance) of the head and the snout length increased; at the same time, the relative diameter of the eye decreased. The insufficient number of two-year-old fish made it impossible to include their measurements in the statistical analysis; nevertheless, we can note that the index values for Kildin cod of age 1+, corresponding to the trends of allometric growth, had intermediate values of H/SL , ao/c , and io/c values between the corresponding indices in fingerlings and large cod.

The food spectrum of Kildin cod fingerlings included ostracodes (Ostracoda) (13.05%), polychaete larvae (17.05%), cladocerans (Cladocera) (23.54%), and juvenile gammarids (Gammaridae) (38.74%). Gammarids also had the highest frequency of occurrence (36.48%) (Tables 2 and 3).

Despite the fact that the variability of fingerling length was low ($CV = 5.3$), the feeding rate varied greatly. The stomach fullness index of fingerlings in different individuals was 5.423–578.069‰, which is probably caused by differences in the diet of individual fishes. This is supported by the size measurements: there were neither fishes with distinctly slow growing rate fish in the sample set nor overgrown individuals. This may indicate a good supply of the necessary and available food for the juvenile cod in Lake Mogilnoe, which is supported by the calculated indices of the condition factor, which varied within small range between different individuals in the sample ($CV = 8.3$). The average values of the partial fullness index demonstrated the priority of gammarids (108.976‰). For cladocerans and polychaete larvae, the partial indices of stomach fullness had similar values (88.395 and 89.808‰, respectively). The lowest values were calculated for ostracodes (61.014‰).

The relative importance index had the highest values for gammarids (52.5%) and consistently decreased for cladocerans, polychaetes, and ostracodes (24.3, 12.4, and 10.7%, respectively).

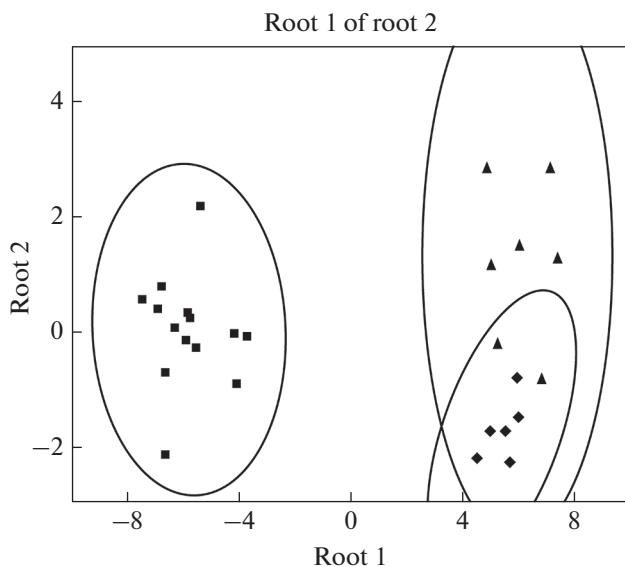


Fig. 2. Diagram of scattering of sample sets of Kildin cod *Gadus morhua kildinensis* from Lake Mogilnoe in the space of most significant canonical roots for canonical values (95% level) based on 11 indices of morphometric characters. Sample set of fingerlings was arbitrarily divided into two parts to fulfill the conditions of application of STATISTICA software package (Sm and Sm1). (■), mature specimens; (▲), Sm fingerlings; (◆), Sm1 fingerlings.

DISCUSSION

The results of a comparative analysis of the variability of a number of the main morphometrics characters between the age groups of the Kildin cod are quite consistent with the previous data obtained by different researchers at different times, indicating changes in the proportions of various body parts in fish during the development, which is associated with a consistent change in morphoecological adaptations of the organizational level (Alev, 1958, 1986; Abdurakhmanov, 1962; Dorofeeva, 1978). Our data demonstrate significant differences in most of the characters under consideration between the sample sets of fingerlings and large adult individuals of the Kildin cod. Fingerlings have a relatively larger head, larger eye diameter, and shorter body dept, which corresponds to changes common to many fishes during individual development (Reshetnikov and Popova, 2015). For fingerlings, we also noted lower values of the indices of snout length and interorbital distance, which is probably associated feeding on small objects and the need to reduce the frontal drag when inhabiting the pelagic zone (Alev, 1963). At the same time, it is necessary to note the similar values of the index of the chin barbel length in fingerlings and large individuals, which reflects the proportional increase of the chin barbel as the fish grows. Good development of this polysensory organ, which carries many various kinds of sensitive cells (Devitsina, 1997), is of particular importance for

the Kildin cod in ensuring the feeding efficiency of large individuals at the bottom among coastal rocks, including the desalinated part of the lake (Tseeb and Astafeva, 1975; Mukhina et al., 2002).

The size measurements of the Kildin cod in ontogenesis vary over great range. For example, the weight increases by 128000 times: from 0.030 g in larvae to 3840 g in a 12-year-old individual (Tseeb and Pozdnyakov, 1975; Stroganov et al., 2015). Accordingly, the species composition and sizes of food items change. Since there is still no description of successive changes in the diet of the Kildin cod by stages of individual development, starting with the transition of larvae to exogenous feeding, we, based on our own data and information from literature sources, have prepared the following generalization.

The early development of the Kildin cod as a representative of the ecological group of pelagophiles takes place in the water column. The transition of cod larvae to exogenous feeding on zooplankton is the most crucial period for determining their survival and further formation of the population size. Studies of the Murmansk Marine Biological Institute have shown that in Lake Mogilnoe, which has a complex structure of waters with different levels of salinity and density, among other features, the eggs and larvae of the cod in a floating state develop in a narrow layer of water at a depth of 6.7–7.3 m, where the salinity is 26–28‰ (Tseeb and Pozdnyakov, 1975). To support the survival and the active growth of small (*TL* 4–5 mm) cod larvae with low level of activity during the mixed feeding period, significant concentrations of marine zooplankton of appropriate size are required (Puvanendran et al., 2002). In Lake Mogilnoe, where zooplankton is abundant (its numbers are an order of magnitude higher than that in the Barents Sea), the following food objects are available to the larvae at appropriate depths. Firstly, the dominant over the entire column of the aerated waters in the lake is a small (0.3 mm in size) illoricate rotifer *Synchaeta* sp. Secondly, the nauplius forms of dominant species of lake copepods: *Pseudocalanus acuspes*, *Centropages hamatus*, and *Tisbe furcata*. Thirdly, the polychaete larvae of family Spionidae (size 0.1 mm and larger), the population of which periodically increases to a great size (more than 60% of the total plankton population). Finally, another dominant rotifer *Keratella* sp. (0.3 mm) may play an important role in the food spectrum of the cod larvae during the transition to mixed feeding; it forms significant aggregations in the uppermost (0–3 m) desalinated water layer, but also occurs deeper, (Strelkov et al., 2014).

In conditions of higher temperatures in the sea layer of Lake Mogilnoe, the cod larvae during their growth process can rather quickly switch to feeding on larger zooplankton: older copepodites and adult stages of copepods *C. hamatus*, *Tachidius* sp., *P. acuspes*, and *T. furcata* (up to 1.8 mm in size); cladocerans *Pleopis*

Table 1. Morphometric characters of Kildin cod *Gadus morhua kildinensis* from different sample sets

Index	Large individuals <i>W</i> 980–2850 g, <i>TL</i> 48.2–74.0 cm; July 2011				Fingerlings <i>W</i> 0.564–1.453 g, <i>TL</i> 4.8–6.4 cm; August 2016				Two-year-old, 1 specimen .	
	<i>M</i>	σ	<i>CV</i>	<i>n</i>	<i>M</i>	σ	<i>CV</i>	<i>n</i>	<i>TL</i> 14.5 cm, 05.07.2011	<i>W</i> 15 g, <i>TL</i> 12.5 cm; 27.07.2012
<i>SL/TL</i>	0.92**	0.02	1.85	27	0.94	0.010	1.95	29	0.91	0.93
<i>c/SL</i>	0.24***	0.02	8.02	27	0.27	0.010	4.06	29	0.20	0.23
<i>H/SL</i>	0.20***	0.01	6.31	27	0.18	0.010	4.78	29	0.18	0.19
<i>h/SL</i>	0.05	0	9.25	27	0.05	0.002	5.43	29	0.05	0.05
<i>aD/SL</i>	0.32	0.03	9.22	26	0.33	0.010	5.47	29	0.33	0.32
<i>pD/SL</i>	0.56*	0.02	4.03	24	0.55	0.020	3.63	29	0.56	0.55
<i>cH/c</i>	0.67***	0.05	7.83	27	0.61	0.030	5.53	29	0.81	0.68
<i>ao/c</i>	0.32***	0.03	9.85	27	0.26	0.030	12.17	29	—	0.29
<i>o/c</i>	0.14***	0.02	13.73	24	0.31	0.010	4.02	29	0.33	0.31
<i>io/c</i>	0.32***	0.04	11.76	27	0.20	0.020	13.51	29	0.29	0.25
<i>cir/c</i>	0.15	0.02	12.06	15	0.15	0.010	10.83	14	—	—

TL, total length; *SL*, standard length; *c*, head length, *H*, greatest body depth; *h*, shortest body depth; *aD*, antedorsal distance; *pD*, post-dorsal distance; *cH*, head depth; *ao*, snout length; *o*, eye diameter; *io*, interorbital distance; *cir*, length of chin barbel; *W*, body weight; *n*, number of individuals, specimens; “—”, no data. The difference from the mean index value for fingerlings is significant at: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Here and in Table 2: *M*, mean value; σ , standard deviation; *CV*, coefficient of variation.

Table 2. Some characteristics of fingerlings of Kildin cod *Gadus morhua kildinensis*

Characteristic	<i>M</i>	min	max	σ	<i>CV</i>
Length (<i>TL</i>), cm	5.3	4.8	6.4	0.284	5.3
Body weight, g	0.814	0.564	0.691	0.145	17.8
Condition factor	0.540	0.432	0.691	0.045	8.3
Weight of food, g	0.008	0.001	0.049	0.007	87.5
Stomach fullness index, ‰	104.532	5.423	578.069	88.351	84.5

Min and max denote minimum and maximum values.

Table 3. Feeding spectrum of fingerlings of Kildin cod *Gadus morhua kildinensis*

Characteristic	Food component			
	cladocerans	ostracodes	gammarids	polychaete larvae
Portion of total weight, %	23.54	13.05	38.74	17.05
Frequency of occurrence, %	27.84	22.08	36.48	19.68
Index of relative importance, %	24.3	10.7	52.4	12.4
Private index of stomach fullness, ‰	$\frac{8.272-400.000}{88.395(75.622)}$	$\frac{6.053-145.000}{61.014(37.264)}$	$\frac{6.342-535.161}{108.976(98.433)}$	$\frac{4.596-268.551}{89.808(60.340)}$

Above the line: limits of variation range of the indicator; below the line: before the brackets, mean value; in brackets, standard deviation.

(*Podon polyphemoides* and *Podon leuckarti* (0.5–0.6 mm); and large polychaete larvae, which, in fact, is typical for the early ontogenesis of Atlantic cod (Grauman et al., 1989).

The transition from the metamorphic stage to the juvenile state of the cod is accompanied by the formation of muscles, fins, and swim bladder, which not only contributes to increased motor activity, but also makes it possible to expand the feeding zone to desalinated horizons of Lake Mogilnoe with an expanded food spectrum, which now includes *Keratella* sp. and cladocerans *Bosmina* sp. (0.5 mm in size) (Drobysheva, 2002; Mukhina et al., 2002; Strelkov et al., 2019; Stroganov et al., 2022).

The special feature of the cod from Lake Mogilnoe is that its pelagic juveniles enter the coastal zone and consume benthic forage organisms in addition to zooplankton. For example, in our work, it was shown that the proportion of combined ostracodes and gammarids by weight was >51%.

Another special feature of the feeding of the juvenile lake cod is that, while the Atlantic cod fingerlings in the Barents Sea switch to a bottom-dwelling lifestyle (settlement) in late August–September with a corresponding change in the food spectrum, the cod juveniles of Lake Mogilnoe continue to consume zooplankton for up to three years. At the same time, the first two years of life of the Kildin cod demonstrate a high growth rate, which is due to good food supply, as well as a more favorable temperature regime in the habitat (Tseeb, 1975; Antsiferov and Trofimov, 2002; Mukhina et al., 2002; Boitsov et al., 2003; Stroganov et al., 2022).

In 1997–2000, during the expeditions of the Polar branch of Russian Federal Research Institute of Fisheries and oceanography to the lake, studies were conducted on the feeding habits of the adult individuals of the Kildin cod. It was shown that in comparison with the Atlantic cod of the Barents Sea, which has more than three hundred food items, the food spectrum of the Kildin cod is much smaller. At the same time, two more representatives of bony fish living in the lake, the butterflyfish *Pholis gunnellus* and the three-spined stickleback *Gasterosteus aculeatus*, as well as worms, coelenterates, and insect larvae account for less than 10% of the food spectrum of the cod. Gammarids and cod juveniles form the basis of the food spectrum of the adult Kildin cod, and their portion in the food spectrum, according to researchers, varies greatly (10–80% and 16–69%, respectively) between different seasons and influenced by different values of environmental factors (Tseeb, 1975; Mukhina et al., 2002).

Thus, it was found that the Kildin cod, which exists in specific conditions of Lake Mogilnoe with a small water area, impoverished biotopes, and limited food resources for adults, demonstrates age-related changes in body proportions (the ontogenetic allometry, according to: Mina and Klevezal, 1976). Similar to

the juveniles of many fish species (Reshetnikov, 1980), the cod fingerlings are characterized by a large head, large eye size, and shorter body depth compared to the adult individuals. The feeding habits of the Kildin cod in different periods of ontogenesis vary significantly. Starting with the transition of larvae to a mixed diet, cod has the ability to expand the food spectrum: from small rotifers, copepod nauplii, and polychaete larvae to copepods of copepodite and adult stages. The transition to the fingerling state allows juvenile cod (in the pelagic phase and after the settlement) to feed not only on the zooplankton of the marine zone, but also the zooplankton of the desalinated layer, as well as on the zoobenthos. Good food supply during the early development of the Kildin cod under conditions of higher temperatures of the waters of Lake Mogilnoe contributes to a high growth rate in the first two years of life. The basis of the food spectrum of recruits and adult individuals of the species are gammarids and their own juveniles. The shortage of large forage organisms in the lake is the reason for the decrease in the growth rate of the large cod (Mukhina et al., 2002).

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