

# European whitefish *Coregonus lavaretus* of the Nizhnetulomskoye Reservoir (Tuloma River basin, Murmansk region) and its habitat conditions

LIMNOLOGY  
FRESHWATER  
BIOLOGY

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**ABSTRACT.** The modern biological characteristics of the most common polymorphic species of European whitefish *Coregonus lavaretus* (L.) in Northern Europe were studied in the conditions of its habitat in the oldest riverbed reservoir in the Murmansk region. A number of features of the functioning of the ecosystem of the Nizhnetulomskoye Reservoir (hereinafter NTR) have been identified, including eutrophication of the reservoir, accompanied by the development of cyanoprokaryotes in phytoplankton communities, including potentially toxic species. The introduction of the Onega smelt *Osmerus eperlanus* (L.) into the Tuloma River system half a century ago led to the transformation of the structure of the NTR fish community from whitefish-salmon to whitefish-smelt. Whitefish (hereinafter, this species name is only used in regard to the European whitefish) in the NTR are represented by a polymorphic population and, according to length-weight characteristics, belong to the group of medium-sized whitefish of the Murmansk region watercourses with early maturation. Based on the type of feeding, it can be classified as a benthophage with a wide range of consumption of food organisms. The stomach contents of whitefish in the summer-autumn period correlate well with the seasonality of the development of aquatic invertebrates. Artificial feeds used by the farms of rainbow trout *Oncorhynchus mykiss* (Walbaum) in the reservoir are currently of great importance in the feeding of the NTR whitefish. Understanding the mechanisms of structural and functional differentiation of whitefish populations is both of fundamental importance in revealing the mechanisms and direction of microevolution and adaptation of fish in changing environmental conditions and of fundamental practical importance in the implementation of protection and rational fishing, their artificial reproduction.

**Keywords:** European whitefish *Coregonus lavaretus*, biological characteristics, Nizhnetulomskoe Reservoir

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## 1. Introduction

The Murmansk region is one of the areas with a high level of electrical energy consumption, which is determined by the high energy intensity of mining and processing enterprises and non-ferrous metallurgy. Around two-thirds of the total electrical energy consumption in the region is accounted for by these sectors (Kuznetsov et al., 2020). The creation and development of the electric power system on the Kola Peninsula in the initial stage were primarily reliant on the construction of hydroelectric dams (Kuznetsova and Konovalova,

2021). Between 1930 and 1972, the construction of dams on certain large lakes and rivers in the Murmansk region, resulted in the creation of approximately 20 reservoirs. Reservoirs can be classified as natural-technogenic geosystems, the development of which occurs under the influence of internal (natural processes) and external (various types of anthropogenic and natural influences) factors (Dvinskikh and Kitaev, 2008; 2014). Artificially created ecosystems of reservoirs, combining elements of lotic and lentic systems are characterized by an unstable balance of ecological interactions among their four main components: the atmosphere, hydro-

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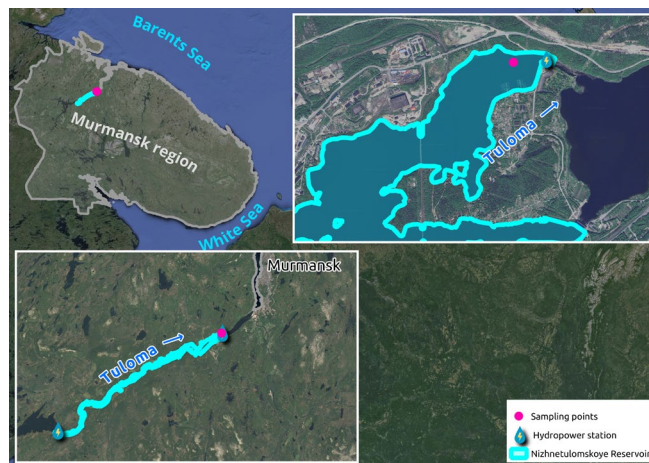
sphere, lithosphere and biosphere. It is determined by a regulated hydrological regime, usually different from the natural one (Dvinskikh and Kitaev, 2014). Especially in the conditions of the Extreme North, this leads to disruptions in biogeochemical cycles, the seasonality of biotic processes, and, ultimately, a decrease in biological diversity and the transformation of the hydrobiotic community structure.

The Tuloma is one of the largest river systems in the Murmansk region (Catalogue..., 1962). Following the reconstruction of the Tuloma River territories, the majority of the river now belongs to the Verkhnetulomskoye and Nizhnetulomskoye riverbed reservoirs. At the same time, the state of the ecosystem after the river damming was studied only in the younger Verkhnetulomskoye Reservoir (VTR) (Fishery..., 1985). However, the state of the ecosystem in one of the oldest riverbed reservoirs in the Murmansk region, the Nizhnetulomskoye, has not been extensively studied. There are some papers on mollusks in the littoral zone of the NTR (Nekhaev, 2006; Frolov, 2009) and on the level of parasitic worm infections in fish in the reservoir (Karasev et al., 2020; Ivanitskaya et al., 2022). Some population characteristics of juvenile Atlantic salmon *Salmo salar* L. of the NTR have also been studied (Samokhvalov et al., 2014), there is an efficient operating fish ladder in the reservoir (Konovalova and Kuznetsov, 2020). This paper presents the results of biological characteristics studies of the whitefish *Coregonus lavaretus* (L.) of the NTR and its habitat conditions. Whitefish is the most common freshwater fish species in Northern Europe. Depending on habitat conditions, whitefish forms a variety of both allopatric and sympatric morphs and populations, differing in morphology, life cycle strategies, and ecological niches (Reshetnikov, 1980; Kahilainen et al., 2004; 2007; 2009; 2014; Østbye et al., 2005; Kahilainen and Østbye, 2006; Siwertsson et al., 2008; 2010; Harrod et al., 2010; Præbel et al., 2013, etc.). It is considered that the formation of sympatric morphs in conditions of low species diversity in northern watercourses allows the fish species to use efficiently available resources and determines the stability of water ecosystems as a whole (Reshetnikov, 1980; Moiseenko, 1983; Kashulin et al., 1999; Amundsen et al., 2004a; Kahilainen and Østbye, 2006; Siwertsson et al., 2008; 2010; Harrod et al., 2010; Laske et al., 2019; Skulason et al., 2019, etc.). Understanding the mechanisms of structural and functional differentiation of whitefish populations is both of fundamental importance in revealing the mechanisms and direction of microevolution and adaptation of fish in changing environmental conditions and of fundamental practical importance in the implementation of protection and rational fishing, their artificial reproduction (Mina, 1986; Altukhov, 2004).

## 2. Materials and methods

### 2.1. Study area

The Tuloma River basin is located in the northwest of the Murmansk region (Fig. 1). Before damming, the Tuloma River originated from Notozero Lake



**Fig.1.** Hydrochemical, hydrobiological and ichthyological sampling points in the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022.

(since 1962 is a part of the VTR with an area of 745 km<sup>2</sup>). The river flows into the Kola Bay of the Barents Sea (Fig. 1). After the Tuloma River regulation by the dams of hydropower stations (hereinafter HPP) Nizhnetulomskaya and Verkhnetulomskaya, the majority of the river is the NTR (Fig. 1). The length of the Tuloma River is 59.8 km, and the catchment area is 18231.5 km<sup>2</sup> (Catalogue..., 1962). The catchment area of the river is represented by complex and extensive lake-river systems draining the territory of the western part of the Murmansk region, where there are numerous hills and tundra. The Salnye Tundry are located in the watershed between the Barents and White Seas. The flow of the main tributaries of the Tuloma River, the Nota and Lotta rivers, which originate in Finland, is formed on the slopes of the hills and adjacent swampy plains. There are more than 5 thousand lakes in the Tuloma River catchment area. The river fall is 48 m, the average slope is 0.3%. In the mountainous section, the river is located in a narrow and deep gorge (incision depth is 200-300 m) and forms incised bends. There are many rapids on the river. In the lower reaches of the river (below the village of Murmashi), the influence of sea tides are felt. There are two HPP on the Tuloma River: Verkhnetulomskaya (since 1965) and Nizhnetulomskaya (since 1937), forming the VTR and NTR, respectively (Catalogue..., 1962; Surface..., 1969).

The NTR was filled in 1934-1936. When creating the reservoir, 170 ha of farmland were flooded. The area of the reservoir water surface is 38 km<sup>2</sup>, the volume is 0.39 km<sup>3</sup> (0.037 km<sup>3</sup> of which is useful), the length is about 16 km, the greatest width is 1.6 km, the average depth is 12 m, and the maximum depth is 20 m. The level of the upper pool of the reservoir is: forced – 18.5 m, normal – 18.0 m, minimum – 17.0 m; pressure: maximum – 20.3 m, minimum – 17.0 m; the average long-term flow rate is 234.0 m<sup>3</sup>/s. The rivers Pyaive and Sholgoch flow in the reservoir from the north, and – the Kercha River from the south (Catalogue..., 1962; Surface..., 1969). In the NTR water area, there are fish farms for growing rainbow trout *Oncorhynchus mykiss* (Walbaum).

The autumn ice phenomena on the Tuloma River begin in the first ten days of October. The river is covered with ice at the end of December. Ice sets in mid-November in the stretch areas of the river, and much later in rapid areas.. The river opens at the beginning of May, ice drifts until the beginning of June. In the downstream of the Nizhnetulomskaya HPP and further to the mouth, the Tuloma River is subject to a powerful tidal cycle under the influence of the Kola Bay. In addition, the river does not freeze in this part during winter (Catalogue..., 1962; Surface..., 1969).

In the Tuloma River basin, a study of whitefish and its habitat conditions was carried out in the NTR (Fig. 1).

The sampling program included measurements of the reservoir productivity (total nitrogen (µg/L), total phosphorus (µg/L), chlorophyll *a* content (µg/m<sup>3</sup>) and phytoplankton biomass (g/m<sup>3</sup>)), prey availability (diversity, total abundance, and biomass of zooplankton (thousand individuals/m<sup>3</sup> and g/m<sup>3</sup>) and macrozoobenthos (individuals/m<sup>2</sup> and g/m<sup>2</sup>)), putative prey for much of the fish community, key characteristics of the fish community (species composition (%)), and biological characteristics of whitefish (intraspecific composition, morphology, sex and length-weight composition, growth rate, diet, and maturation).

2.2. Hydrochemical research

Water samples from the surface layer (1 m from the surface) and bottom layer (1 m from the bottom) of the NTR were taken with a 2.0 L plastic bathometer. The collected water samples were transported in 1.0 L plastic bottles. The chemical composition of water was determined at the center for collective use of the INEP of the Kola Scientific Center RAS using uniform methods (Standard..., 1999; Anthropogenic..., 2002; Sandimirov et al., 2019). The periods for collecting hydrochemical samples and their quantities are given in Table 1.

2.3. Hydrobiological research

Detailed information on the hydrobiological sample sizes and their collection time is presented in Table 1. Quantitative phytoplankton samples were taken with a 2.2 L Rüttner bathometer at a depth interval of 0-5 m, and qualitative phytoplankton samples were taken with a Juday net. Each sample obtained was fixed with Lugol solution, and concentrated in the laboratory by settling method (Guide..., 1992; Sandimirov et al., 2019). Phytoplankton biomass was calculated using the counting-volume method based on determining the individual volume of cells (or dense colonies) of each species, calculated using formulas for the volume of similar geometric figures (Guseva, 1959; Kuzmin, 1984; Tikkanen, 1986). Counting the abundance and taxonomic identification of algae and cyanoprokaryotes was carried out in a 0.1 ml Nageotte Chamber on a Motic BA300 light microscope with an immersion lens. Magnifications ranging from 400 to 1000 times were used. The names of taxa are given in accordance with the international algological database (Guiry and Guiry, 2024).

To assess the physiological state and photosynthetic activity of algae and cyanoprokaryotes, the content of chlorophyll *a* in plankton was analyzed; sampling was carried out monthly. Water samples with a volume of 600 ml were filtered through a membrane filter with a pore diameter of 0.47 µm using a Millipore syringe with a filter attachment. Filtration was carried out directly on the reservoir to avoid changes in the content of photosynthetic pigments during the transportation of water samples. Extraction of chlorophylls was carried out with an acetone solution (90% analytical grade), the optical density of the extracts was measured with a PE-5400UF spectrophotometer. Concentrations of photosynthetic chlorophyll *a* were calculated using standard methods generally accepted in international and domestic practices (Determination..., 1966; Mineeva, 2004; Denisov and Kashulin, 2013). The tro-

**Table 1.** Characteristics of the used hydrochemical, hydrobiological and ichthyological material from the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022

Research period of GCS	Research period of GBS		Number of samples			Research period of IS	n1	n2	n3	n4
	P, Z	M	GC	P, Z	M					
IV, V, VII, X 2019,	VII 2018,	monthly	16	176	46	XII 2018,	431	379	55	107
I-II, V, VII, IX, XII 2020,	monthly	from V to XI 2019-2022				monthly				
VI 2021,	from I to X 2019,					from V to XII 2019-2020				
II, VIII, XI 2022	I-III, V-XI 2020,					V, VIII-XII 2021				
	I-III, V-XII 2021,					III, VII-XII 2022				
	monthly									
	from I to XII 2022									

**Note:** GCS – hydrochemical samples, GBS – hydrobiological samples, IS – ichthyological samples, P – phytoplankton, Z – zooplankton, M – macrozoobenthos, n1 – the whitefish number with studied length, weight, age, stage of development of reproductive products and linear growth rate, n2 – with studied branchial arch, n3 – with studied body morphology, n4 – with studied stomach contents.

phic status of waters was assessed by the content of chlorophyll *a* according to the classification proposed by Kitaev (2007).

Quantitative zooplankton samples were taken with a 2.2 L Rüttner bathometer at the depths of 0-2, 2-5, 5-10, 10-20 m, and qualitative zooplankton samples were taken with an Apstein net (38 cm diameter, 30 µm mesh size). Vertical trawling provides more complete data on the plankton population of the studied reservoir. Stretching the plankton net from the bottom up – from the bottom of the reservoir to the surface. The fixative is Lugol solution (Guide..., 1992; Sandimirov et al., 2019).

Quantitative and qualitative macrozoobenthos samples from littoral zones (< 1 m depth) were collected using a net scraper fitted with a 25x25 cm frame, and the animals were selected from stones. The collected samples were stored in plastic buckets (Guide..., 1992; Sandimirov et al., 2019). Collected macrozoobenthos samples were fixed with 4% formalin solution or 70% ethanol solution.

Zooplankton and macrozoobenthos samples were transported to a field laboratory, identified using a microscope (mostly to genus level) (Merriitt and Cummins, 1984; Key..., 2000; 2001; 2016), sorted, counted (thousand individuals/m<sup>3</sup> and individuals/m<sup>2</sup> respectively) and weighed (g/m<sup>3</sup> and g/m<sup>2</sup> respectively) (Guide..., 1992). The Bogorov Chamber is used to count the zooplankton organisms in the sample. It is a thick plate of glass or plexiglass with a notch in the form of a labyrinth. Trophic status was assessed by zooplankton and macrozoobenthos biomass using the scale proposed by Kitaev (2007).

## 2.4. Ichthyological research

Detailed information on the samples sizes and catch times of fish presented in Table 1. The fish were collected using gill nets in all three sampled habitats of the NTR (littoral, pelagic, and profundal). In the NTR, catches were made with a standard set of nets 25-m-long and 1.5 m high with a mesh size of 10, 12, 16, 18, 20, 30, 35, 40, 45, 50, 55, and 60 mm. The nets are set overnight (c. 12h). Fish taken from the nets next morning (soak time c. 6-10 h.), were immediately killed with cerebral conclusion. All fish were identified in the laboratory or field to species (Fricke et al., 2024). A total of 408 whitefish were caught. All sampled whitefish were measured (Smith length (*FL*) ± 1 mm) and weighed (total weight (*W*) ± 1 g). Fifty-five whitefish were photographed using a Nikon d610 digital camera with a 60 mm f/2.8G ED AF-S Micro-Nikkor lens (Bochkarev et al., 2013; Melekhin et al., 2021). Whitefish morphs were identified based on the number of rakers on the first branchial arch (hereinafter *sp.br.*): 16 to 30 in sparsely rakered whitefish, 31 to 42 in medium rakered whitefish, 43 to 65 in densely rakered whitefish (Pravdin, 1954; Reshetnikov, 1980). Also, based on the number of perforated scales in the lateral line (*ll*), small scaled whitefish (76-83), medium scaled (83-86) and multi scaled whitefish (86-98) were identified (Bochkarev, 2022). *Sp.br.* were counted

under a microscope at magnification of ×10. To identify the structural features of the first branchial arch of whitefish, the length (± 0.1 mm) of the central gill raker (hereinafter *lsp.br.*) was also measured (Pravdin, 1966). The distance (± 0.1 mm) between the gill rakers (*ssp.br.*) was calculated according to the method of Kahilainen and Østbye (2006). Based on the obtained images of the fish, *ll* numbers in the lateral line of the whitefish were counted and, using the *ImageJ* program, measurements of morphometric whitefish body features (30 features) were made (± 0.1 mm) according to Bochkarev and Zuikova (2010) with minor changes: *H* – highest body height, *h* – caudal peduncle height, *aA*, *aV*, *aD*, *aP* – anteanal, anteventral, antedorsal, antepetral distances, respectively, *DC*, *VC*, *AC* – dorsocaudal, ventrocaudal and analcaudal distances, respectively, *PA*, *PV*, *VA* – pectroanal, pectroventral, ventroanal distances, respectively, *pA* – caudal peduncle length, *pD* – postdorsal distance, *ID*, *IA*, *IV*, *IP* – the length of the dorsal, anal, ventral and pectoral fins, respectively, *hD*, *hA* – length of the bases of the dorsal and anal fins, respectively, *C* – head length, *r* – snout length, *o* – eye diameter, *b* – pupil diameter, *po* – postorbital distance, *Ch1* and *Ch2* – head height at the level of the eye and the back of the head, respectively, *lmax* and *hmax* – length and height of the upper jaw respectively, *lmd* – lower jaw length.

Morphologic data (*lsp.br.*, *ssp.br.*, and morphometric body features) were first  $\log_{10}$ -transformed to reduce heterogeneity in variance and size-adjusted to the average length of the NTR whitefish samples using an allometric formula (Thorpe, 1975);  $X_i = 10^{Y_i}$ , where  $X_i$  is the size-adjusted morphologic measurement.  $Y_i$  is the logarithm of the adjusted morphologic measurement with the following relationship:  $Y_i = \log_{10} M_i - b(\log_{10} L_i - \log_{10} L_{tot})$ , where  $b$  is the pooled regression coefficient of  $\log_{10} M_i$  against  $\log_{10} L_i$ ,  $M_i$  is the morphologic measurement of *i*th whitefish,  $L_i$  is the total length of *i*th whitefish,  $L_{tot}$  is the average total length of all whitefish samples. Meristic counts were examined as raw data. For every trait, the mean (*M*) and standard error (*m*) were calculated. The normal distribution of the traits was tested in *Statistica 10* program (asymmetry and kurtosis, Kolmogorov-Smirnov, Shapiro-Wilk tests, two normal probability plots). Since visual analysis of the external structure of the NTR whitefish during catching and processing of the material, as well as evaluation of images of fish revealed some differences in the morphology of the head and body of individual sparsely rakered whitefish morph, morphometric (size-corrected) measurements were subjected to multivariate analysis (principal component analysis) in the *Statistica 10* program. The data obtained were compared, and the significance of differences in the traits demonstrating normal and non-normal (samples were large-volume) distribution was checked using Student's t-test. The differences were considered statistically significant at  $p \leq 0.05$ .

We assigned fish to those taking part in spawning if their gonads were in sexual maturity stages III-IV, V, VI, VI-II (Reshetnikov and Bogdanov, 2011). The age of the fish was determined by scales using commonly

accepted methods (Van Oosten, 1929; Reshetnikov, 1966). The study of the back-calculated whitefish length on scales was conducted according to the method of Zubova et al. (2016). The percentage of whitefish individuals with empty stomachs and stomachs containing food components was determined from May to December. To analyze qualitative and quantitative features of whitefish feeding from May to December, 107 stomach contents were evaluated (Table 1) according to the known guides (Guide..., 1961; Methodological..., 1974). The stomachs were removed and fixed in 70% ethanol solution in less than 2-3 h after collection of nets from the lake. The treatment of the material was conducted in a laboratory using a microscope. Food items in stomachs were identified as far as possible to genus or family level (Key..., 2000; 2001; 2016), and the wet mass ( $\pm 0.1$  g) of each category was measured. To characterize the feeding spectrum, the *IR* (index of relative significance) was used:  $IR = (F_i P_i / \sum F_i P_i) \times 100\%$ , where  $F_i$  is frequency of occurrence of each component of food,  $P_i$  is share by mass; value  $i$  changes from 1 to  $n$  ( $n$  is the number of food components in the whole stomach contents) (Popova and Reshetnikov, 2011).

3. Results

3.1. Hydrochemical and hydrobiological characteristics

In terms of the content of total phosphorus and nitrogen in the water, the NTR can be classified as mesotrophic water bodies with signs of eutrophication (Table 2). At the same time, the average quantitative parameters (abundance, individuals/m<sup>3</sup>, and biomass, g/m<sup>3</sup>) of planktonic communities and chlorophyll *a* (mg/m<sup>3</sup>) correspond to the  $\alpha$ -oligotrophic trophic status (Table 2). Quantitative parameters are characterized by sharp changes throughout the year; phytoplankton vegetation processes continue during the subglacial period. Relatively long periods of autumn vegetation, almost until freeze-up, were observed, maintaining the zooplankton biomass at the level of summer values.

Phytoplankton communities were characterized by a species composition dominated by diatoms and golden algae, as well as the presence of representatives of charophyte (desmidia) algae. According to ecological characteristics, the bulk were made up of representatives of phytoplankton, characteristic of subarctic reservoirs of the northern taiga zone, as well as cosmopolitans with a wide biogeography: *Aulacoseira islandica* (O.Müll.) Simons., *Asterionella formosa* Hass., *Tabellaria fenestrata* (Lyngb.) Kütz., *Dinobryon divergens* Imh. The development of cyanoprokaryotes in communities is also observed (up to 85%), mainly in the autumn, including potentially toxic species that can cause algal blooms (*Aphanizomenon flos-aquae* Ralfs ex Born. & Flah., *Dolichospermum lemmermannii* (Rich.) Wack., L.Hoff. & Komár., and *Planktothrix gardhii* (Gom.) Anag. & Komár.).

The zooplankton communities of the studied reservoir were characterized by the dominance of eurybiont species typical of subarctic water bodies. In the studied water body, the taxonomic composition turned out to

be relatively poor (18-19 species). Rotifers dominated in abundance: *Keratella cochlearis* Gosse, *Polyarthra vulgaris* Carlin, *Synchaeta pectinata* Ehrb, the share of crustaceans was lower: *Eudiaptomus gracilis* Sars, *Bosmina obtusirostris* Sars, *Daphniasp.* (Table 2). According to the ecological characteristics, the zooplankton community corresponded to the rotary-cladoceran and rotary-copepod type, depending on the observation period.

Table 2. Average hydrochemical and hydrobiological parameters from the Nizhnetuloma Reservoir (Tuloma River basin), 2018-2022

Parameters	Values of parameters
Total phosphorus content, µg/L	13.3 ± 1.45
Total nitrogen, µg/L	228.5 ± 18.49
Trophic status*	mesotrophic with signs of eutrophicity
Phytoplankton biomass, g/m <sup>3</sup>	0.65
Chlorophyll α content, µg/m <sup>3</sup>	1.42
Trophic status**	α-oligotrophic
Zooplankton abundance, %	
rotifers	84.1
crustaceans	15.9
Zooplankton biomass, %	
rotifers	53.3
crustaceans	46.7
Total abundance of zooplankton, thousand individuals/m <sup>3</sup>	143.1
Total biomass of zooplankton, g/m <sup>3</sup>	0.4
Trophic status**	α-oligotrophic
Littoral macrozoobenthos abundance, %	
chironomids	72
caddisflies	2
bivalve mollusks	4
gastropod mollusks	3
oligochaetes	11
other groups of organisms	7
Littoral macrozoobenthos biomass, %	
chironomids	60
caddisflies	4
bivalve mollusks	2
gastropod mollusks	14
oligochaetes	10
other groups of organisms	10
Total abundance of littoral macrozoobenthos, individuals/m <sup>2</sup>	3642
Total biomass of littoral macrozoobenthos, g/m <sup>2</sup>	16.0
Trophic status**	eutrophic

Note: \* – along Likens, 1975, \*\* – along Kitaev, 2007.



The macrozoobenthos of the littoral zone of the NTR studied areas is typically freshwater. During the study period, invertebrates belonging to 13 systematic groups were recorded: flatworms (*Turbellaria*), nematodes (*Nematoda*), oligochaeta (*Oligochaeta*), leeches (*Hirudinea*), bivalves (*Bivalvia*), gastropods (*Gastropodae*), water mites (*Hydracarina*), chironomids (*Chironomidae*), flies (*Diptera*), true bugs (*Hemiptera*), caddisflies (*Trichoptera*), mayflies (*Ephemeroptera*), and alderflies (*Megaloptera*). The macrozoobenthos of the NTR littoral zone was characterized by a relatively high abundance and biomass – eutrophic trophic status (Table 2). The dominant complex was supplemented by inhabitants of the rocky littoral zone: gastropods (*Lymnaea* sp., *Valvata* sp.), caddisflies (*Polycentropus flavomaculatus* Pict., 1834, *Oxyethira* sp., *Limnephilidae*), leeches (*Glossiphonia complanata* L., 1758), heteropterans, mayflies, and alderflies were observed sporadically (Table 2).

### 3.2. Fish species composition

During our work from 2018 to 2022, ten species of fish were identified as part of the NTR ichthyofauna: rainbow trout, brown trout *Salmo trutta* Linnaeus, whitefish, European vendace *Coregonus albula* (Linnaeus), European smelt, European grayling *Thymallus thymallus* (Linnaeus), European perch *Perca fluviatilis* Linnaeus, burbot *Lota lota* (Linnaeus), and northern pike *Esox lucius* Linnaeus. The nine-spined stickleback *Pungitius pungitius* Linnaeus was observed in the stomachs of burbot and rainbow trout, as well as in the coastal zone of the reservoir. The dominant NTR species include whitefish, whose share in catches varies from 43 to 53% depending on the season (Fig. 2a, b). Thus, in the summer-autumn period, the number of whitefish in the sample reached more than 80%. In the summer-autumn period, 52% of whitefish were caught in the profundal zone of the reservoir and 48% in the littoral zone.

The abundance of European smelt (hereinafter smelt) in general during the entire study period reached 18-23% (subdominant species) (Fig. 2a, b). Less numerous in the catches were European vendace (vendace) and rainbow trout, which periodically escape from their rearing cages. The share of such fish ranges from 7 to 16% (Fig. 2a, b). European perch (perch) and burbot are less common. The number of perch reached almost 4% during the period of open water (Fig. 2a), while for burbot, a naturally higher occurrence in catches (9%) is typical for the winter period (Fig. 2b). Other fish species were encountered only sporadically.

### 3.3. Features of the distribution of intraspecific morphs of whitefish and their morphological characteristics

The catches from the NTR mainly contained the sparsely rakered (hereinafter *sr*) whitefish morph with the number of *sp.br.* from 16 to 28 ( $20.7 \pm 0.10$ ) (Fig. 3). Throughout the entire study period, only two whitefish individuals were caught with the number of *sp.br.* 32 and 39, which can be classified as the medium rak-

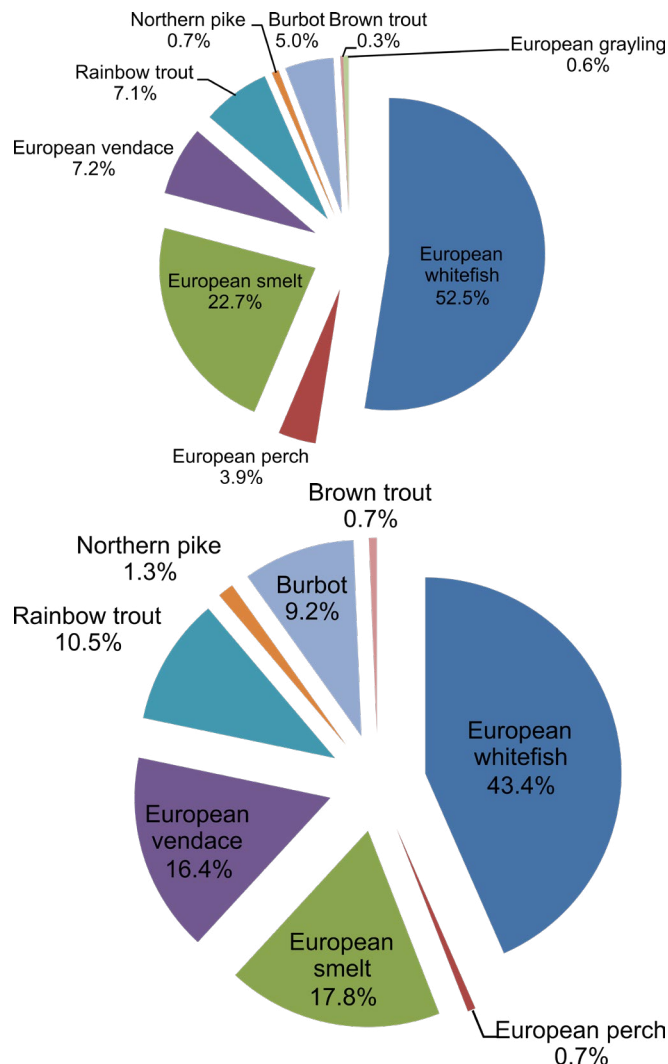


Fig.2. Composition of catches from the Nizhnetulomskoye Reservoir (Tuloma River basin) during the open water period (a) and the ice-covered period (b), 2018-2022.

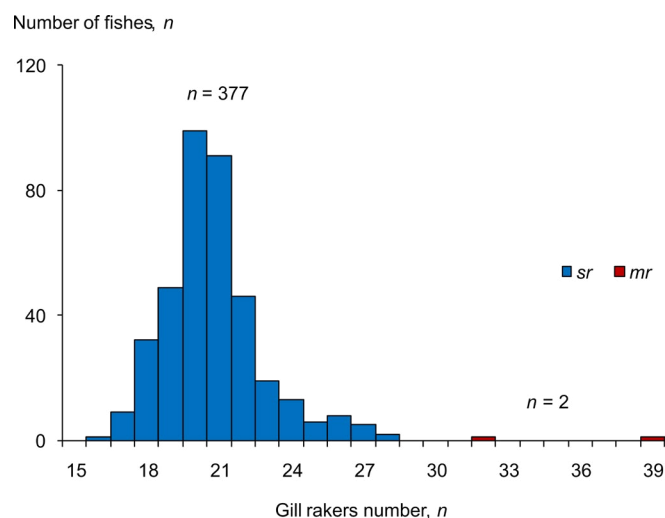


Fig.3. The European whitefish distribution by the number of gill rakers on the first branchial arch, *n* in the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022. *Sr* – sparsely rakered whitefish morph, *mr* – medium rakered whitefish morph.

ered (*mr*) whitefish morph (Fig. 3). Visual analysis of the external structure of whitefish from the NTR during catching and processing of the material, as well as the study of the resulting images of fish samples, revealed some differences in the morphology of the head and body of individual specimens of the *sr* whitefish morph. Thus, the NTR met:

1. whitefish with a complex-shaped head and a noticeable hump behind the head and a subterminal or terminal mouth (Fig. 4a, b) (hereinafter referred to as the “humpbacked” morphotype);
2. wide-bodied whitefish with a small head, a blunt snout and a subterminal or terminal mouth (Fig. 4c) (“wide-bodied” morphotype);
3. high-bodied whitefish with a sharper snout and terminal mouth (Fig. 4d) (“high-bodied” morphotype);
4. low-bodied whitefish with a sharper snout, a large eye and a terminal mouth (Fig. 4e) (“low-bodied” morphotype);
5. “dolphin-snouted” whitefish (“dolphin-snouted” morphotype) (Fig. 4f);
6. whitefish individuals that were difficult to classify by external characteristics into the above-described groups or morphotypes (“uncertain” morphotype).

The presence of the identified of *sr* whitefish morphotypes in the NTR was also confirmed by researchers of whitefish of the SB RAS and KSC RAS when studying images of the NTR whitefish (unpublished data).

The most detailed morphological characteristics were studied in 55 individuals of the *sr* whitefish morph from the NTR. The *sr* whitefish individuals were assigned to one of the six morphotypes described above. In five morphotypes (except for the “uncertain” morphotype), meristic and morphometric characteristics were analyzed and compared (Table 3). Thus, the number of *sp.br.* and *ll* of the identified morphotypes mostly overlapped (Table 3). Significant differences in the average number of *sp.br.* ( $p = 0.05-0.001$ ) and *ll* ( $p = 0.05$ ) have been found only in “high-bodied” whitefish compared to other morphotypes (Table 3): 26 *sp.br.* against 20-22 *sp.br.* and 91 *ll* against 86-88 *ll*, respectively.

When studying the head morphology of the identified whitefish morphotypes, the values of the size-adjusted parameters overlapped (Table 3). The closest indicators of head parameters were characteristic of “humpbacked” and “low-bodied” whitefish. They had significantly ( $p = 0.05-0.001$ ) greater length of the head, snout, eye and pupil, and upper and lower jaws (Table 3). The head height at the level of the eye and

**Table 3.** Some meristic and size-adjusted plastic characteristics of the sparsely rakered whitefish morphotypes from the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022

Parameters	<i>sr</i> whitefish morphotypes				
	«humpbacked»	«low-bodied»	«wide-bodied»	«dolphin-snouted»	«high-bodied»
<i>FL</i> , mm	$226 \pm 12.7$ 161 – 293 (10)	$206 \pm 2.4$ 196 – 213 (6)	$222 \pm 13.1$ 133 – 299 (12)	$234 \pm 13.7$ 177 – 263 (6)	$286 \pm 14.4$ 239 – 338 (7)
<i>sp.br.</i> , <i>n</i>	$20.2 \pm 0.32$ 18 – 21 (10)	$19.8 \pm 0.66$ 18 – 22 (6)	$20.5 \pm 0.69$ 17 – 24 (12)	$22.0 \pm 0.89$ 20 – 26 (6)	$26.2 \pm 0.87$ 22 – 28 (7)
<i>ll</i> , <i>n</i>	$86.0 \pm 1.21$ 80 – 92 (10)	$88.2 \pm 2.26$ 83 – 98 (6)	$87.8 \pm 1.23$ 82 – 93 (12)	$87.0 \pm 1.37$ 84 – 93 (6)	$91.0 \pm 1.46$ 86 – 97 (7)
<i>CXi</i> , mm	$45.9 \pm 0.46$ 42.4 – 47.5 (10)	$45.9 \pm 0.38$ 44.4 – 47.2 (6)	$43.5 \pm 0.40$ 41.2 – 45.9 (12)	$45.6 \pm 0.62$ 44.0 – 47.5 (6)	$43.4 \pm 0.66$ 40.7 – 45.5 (7)
<i>rXi</i> , mm	$11.2 \pm 0.18$ 10.0 – 12.0 (10)	$11.6 \pm 0.28$ 10.6 – 12.4 (6)	$10.5 \pm 0.18$ 8.8 – 11.2 (12)	$11.4 \pm 0.37$ 10.1 – 12.3 (6)	$10.6 \pm 0.45$ 8.7 – 12.1 (7)
<i>oXi</i> , mm	$11.8 \pm 0.28$ 10.5 – 13.0 (10)	$12.3 \pm 0.28$ 11.2 – 13.1 (6)	$11.5 \pm 0.26$ 9.5 – 12.6 (12)	$11.7 \pm 0.32$ 11.0 – 12.9 (6)	$10.8 \pm 0.35$ 9.8 – 12.3 (7)
<i>bXi</i> , mm	$5.5 \pm 0.19$ 4.6 – 6.5 (10)	$5.6 \pm 0.19$ 4.8 – 6.2 (6)	$5.0 \pm 0.14$ 4.3 – 5.7 (12)	$5.1 \pm 0.16$ 4.7 – 5.8 (6)	$4.8 \pm 0.14$ 4.4 – 5.4 (7)
<i>poXi</i> , mm	$23.0 \pm 0.50$ 20.9 – 26.2 (10)	$22.8 \pm 0.30$ 22.0 – 23.8 (6)	$22.2 \pm 0.29$ 20.4 – 23.9 (12)	$23.0 \pm 0.30$ 21.8 – 23.8 (6)	$22.6 \pm 0.23$ 21.9 – 23.7 (7)
<i>ChXi1</i> , mm	$21.4 \pm 0.27$ 20.2 – 22.6 (10)	$21.3 \pm 0.26$ 20.6 – 22.2 (6)	$22.1 \pm 0.49$ 18.9 – 25.2 (12)	$21.8 \pm 0.38$ 21.0 – 23.6 (6)	$21.0 \pm 0.49$ 17.7 – 21.8 (7)
<i>Ch2Xi</i> , mm	$32.1 \pm 0.36$ 30.2 – 33.5 (10)	$32.0 \pm 0.58$ 30.1 – 33.7 (6)	$32.9 \pm 0.59$ 29.8 – 36.1 (12)	$34.5 \pm 0.66$ 32.1 – 36.5 (6)	$30.8 \pm 0.48$ 29.0 – 32.3 (7)
<i>lmaxXi</i> , mm	$13.0 \pm 0.29$ 11.9 – 14.8 (10)	$13.6 \pm 0.29$ 13.9 – 14.7 (6)	$13.4 \pm 0.39$ 10.9 – 15.3 (12)	$13.2 \pm 0.32$ 12.1 – 14.5 (6)	$12.5 \pm 0.63$ 10.1 – 15.4 (7)
<i>lmdXi</i> , mm	$18.5 \pm 0.52$ 16.0 – 21.0 (10)	$17.7 \pm 0.72$ 15.6 – 20.1 (6)	$18.1 \pm 0.30$ 16.5 – 19.7 (12)	$17.9 \pm 0.38$ 16.4 – 19.1 (6)	$16.8 \pm 0.32$ 15.7 – 18.3 (7)

Parameters	sr whitefish morphotypes				
	«humpbacked»	«low-bodied»	«wide-bodied»	«dolphin-snouted»	«high-bodied»
HXi, mm	<u>55.1 ± 1.12</u> 48.6–59.4 (10)	<u>50.2 ± 1.61</u> 45.1–55.4 (6)	<u>54.9 ± 1.46</u> 48.6–67.4 (12)	<u>57.6 ± 1.35</u> 52.5–61.8 (6)	<u>53.2 ± 1.66</u> 46.2–60.4 (7)
hXi, mm	<u>16.2 ± 0.21</u> 15.2–17.4 (10)	<u>15.7 ± 0.14</u> 15.4–16.2 (6)	<u>16.4 ± 0.25</u> 15.3–17.6 (12)	<u>17.0 ± 0.34</u> 16.1–18.4 (6)	<u>16.3 ± 0.33</u> 15.4–17.6 (7)
aAXi, mm	<u>163.7 ± 0.67</u> 160.0–166.8 (10)	<u>165.6 ± 0.78</u> 163.4–168.2 (6)	<u>166.7 ± 0.76</u> 162.0–170.3 (12)	<u>166.7 ± 0.76</u> 162.0–170.3 (6)	<u>166.7 ± 0.69</u> 163.8–169.0 (7)
aVXi, mm	<u>109.5 ± 0.53</u> 106.2–112.7 (10)	<u>113.4 ± 1.51</u> 106.9–118.1 (6)	<u>113.2 ± 0.87</u> 109.1–119.2 (12)	<u>112.5 ± 1.33</u> 107.9–116.1 (6)	<u>111.9 ± 1.33</u> 108.8–120.6 (7)
aDXi, mm	<u>105.7 ± 0.72</u> 102.0–108.5 (10)	<u>105.5 ± 1.10</u> 102.2–108.9 (6)	<u>104.0 ± 0.89</u> 99.1–107.3 (12)	<u>103.4 ± 0.83</u> 101.1–105.9 (6)	<u>103.4 ± 0.76</u> 100.8–105.9 (7)
aPXi, mm	<u>43.9 ± 0.43</u> 41.6–45.4 (10)	<u>47.2 ± 0.54</u> 45.5–49.2 (6)	<u>44.4 ± 0.48</u> 42.2–47.4 (12)	<u>44.1 ± 0.74</u> 41.9–46.4 (6)	<u>44.1 ± 0.85</u> 41.0–46.8 (7)
DCXi, mm	<u>121.5 ± 0.59</u> 117.9–124.2 (10)	<u>118.3 ± 0.62</u> 116.8–120.6 (6)	<u>119.9 ± 1.24</u> 114.3–129.5 (12)	<u>120.6 ± 1.27</u> 116.4–124.6 (6)	<u>122.1 ± 1.45</u> 115.5–125.7 (7)
ACXi, mm	<u>57.3 ± 0.63</u> 54.0–60.0 (10)	<u>57.0 ± 0.71</u> 55.3–60.0 (6)	<u>55.4 ± 0.47</u> 53.7–58.5 (12)	<u>56.8 ± 0.68</u> 55.1–59.1 (6)	<u>56.3 ± 1.03</u> 51.9–59.8 (7)
PAXi, mm	<u>120.4 ± 0.85</u> 116.2–123.8 (10)	<u>119.6 ± 0.71</u> 117.3–122.1 (6)	<u>124.4 ± 0.66</u> 121.6–128.6 (12)	<u>123.4 ± 0.90</u> 120.9–126.7 (6)	<u>123.4 ± 0.80</u> 120.8–127.3 (7)
PVXi, mm	<u>65.8 ± 0.60</u> 61.3–67.9 (10)	<u>66.4 ± 0.96</u> 62.3–69.6 (6)	<u>69.8 ± 0.89</u> 67.1–76.9 (12)	<u>68.6 ± 1.36</u> 65.3–73.5 (6)	<u>67.7 ± 1.31</u> 64.9–75.0 (7)
VAXi, mm	<u>56.2 ± 0.77</u> 50.6–59.2 (10)	<u>54.9 ± 1.15</u> 51.3–58.1 (6)	<u>56.3 ± 0.58</u> 52.8–60.5 (12)	<u>57.8 ± 0.97</u> 54.2–61.1 (6)	<u>57.3 ± 0.48</u> 56.0–60.0 (7)
pAXi, mm	<u>29.2 ± 0.73</u> 25.4–33.2 (10)	<u>28.9 ± 0.60</u> 27.0–30.8 (6)	<u>27.7 ± 0.54</u> 25.4–31.3 (12)	<u>28.6 ± 0.93</u> 24.7–31.4 (6)	<u>28.9 ± 0.81</u> 26.6–32.1 (7)
pDXi, mm	<u>90.4 ± 1.02</u> 85.3–94.8 (10)	<u>90.3 ± 1.10</u> 85.3–92.6 (6)	<u>89.3 ± 0.64</u> 86.0–92.6 (12)	<u>91.5 ± 1.32</u> 88.4–96.0 (6)	<u>91.3 ± 1.39</u> 86.0–96.1 (7)
lDXi, mm	<u>37.6 ± 0.84</u> 32.2–42.5 (10)	<u>36.6 ± 0.58</u> 34.7–38.1 (6)	<u>38.0 ± 0.69</u> 34.5–41.5 (12)	<u>39.2 ± 0.90</u> 35.3–41.4 (6)	<u>39.2 ± 0.59</u> 36.7–41.0 (7)
lAXi, mm	<u>23.1 ± 0.39</u> 21.1–25.0 (10)	<u>23.3 ± 0.56</u> 21.9–25.9 (6)	<u>22.6 ± 0.41</u> 20.5–26.1 (12)	<u>23.4 ± 0.76</u> 20.4–25.7 (6)	<u>22.8 ± 0.29</u> 21.7–23.9 (7)
lVXi, mm	<u>30.9 ± 0.35</u> 29.3–32.7 (10)	<u>30.6 ± 0.82</u> 27.2–32.6 (6)	<u>30.8 ± 0.69</u> 27.3–35.2 (12)	<u>31.3 ± 0.52</u> 29.7–32.7 (6)	<u>31.4 ± 0.42</u> 29.7–32.7 (7)
lPXi, mm	<u>34.5 ± 0.85</u> 29.5–38.8 (10)	<u>35.2 ± 0.90</u> 33.0–38.8 (6)	<u>33.3 ± 0.81</u> 29.3–40.3 (12)	<u>35.2 ± 1.04</u> 30.9–38.6 (6)	<u>33.9 ± 0.66</u> 32.3–37.5 (7)
hDXi, mm	<u>27.7 ± 0.84</u> 24.4–32.0 (10)	<u>25.9 ± 0.76</u> 23.4–28.9 (6)	<u>27.9 ± 0.97</u> 23.6–32.7 (12)	<u>27.0 ± 0.86</u> 23.2–29.2 (6)	<u>27.6 ± 0.77</u> 25.4–30.4 (7)
hAXi, mm	<u>26.7 ± 0.81</u> 22.7–30.6 (10)	<u>26.3 ± 0.84</u> 24.3–29.4 (6)	<u>26.7 ± 0.41</u> 24.5–28.4 (12)	<u>25.7 ± 1.11</u> 22.8–28.6 (6)	<u>25.5 ± 0.78</u> 23.2–28.6 (7)

**Note:** *Sr* – sparsely rakered whitefish morph, *FL* – Smith length, *sp.br.* – number of rakers on the first branchial arch, *ll* – number of perforated scales in the lateral line, *H* – highest body height, *h* – caudal peduncle height, *aA*, *aV*, *aD*, *aP* – anteanal, anteventral, antedorsal, antepectral distances, respectively, *DC*, *VC*, *AC* – dorsocaudal, ventrocaudal and analcaudal distances, respectively, *PA*, *PV*, *VA* – pectroanal, pectroventral, ventroanal distances, respectively, *pA* – caudal peduncle length, *pD* – post-dorsal distance, *ID*, *IA*, *IV*, *IP* – the length of the dorsal, anal, ventral and pectoral fins, respectively, *hD*, *hA* – length of the bases of the dorsal and anal fins, respectively, *C* – head length, *r* – snout length, *o* – eye diameter, *b* – pupil diameter, *po* – postorbital distance, *Ch1* and *Ch2* – head height at the level of the eye and the back of the head, respectively, *lmax* and *hmax* – length and height of the upper jaw respectively, *lmd* – lower jaw length, *Xi* – is the size-adjusted plastic measurement. Above the line is the average value of the characteristics and its error, below the line is the minimum and maximum value of the characteristics. The number of whitefish specimens is shown in parentheses, *n*.



the back of the head was greater ( $p = 0.05-0.001$ ) in “wide-bodied” and “dolphin-snouted” whitefish morphotypes. The “high-bodied” whitefish morphotype were characterized by the lowest ( $p = 0.05-0.001$ ) values of head parameters (Table 3). Thus, extreme values of head parameters were mainly characteristic of “humpbacked” and “low-bodied” whitefish morphotypes (highest values) and “high-bodied” whitefish morphotype (lowest values) (Table 3).

The average length in the sample for the “high-bodied” whitefish morphotype was greater ( $p = 0.05-0.001$ ) than for other whitefish morphotypes (Table 3). When studying the body morphology of the identified groups of whitefish, the values of the size-adjusted parameters overlapped (Table 3). Differences in body structure were minor and were mainly observed only in “humpback” whitefish. They had the lowest values ( $p = 0.05-0.001$ ) of the traits  $aA$ ,  $aV$ , and  $PA$  compared to the other morphotypes (Table 3).

Thus, we can observe diversity in some meristic traits and morphometric head characteristics in the *sr* whitefish morph from the NTR in the absence of hiatus. In a series of changes in the head morphometric and meristic characteristics of the five identified whitefish morphotypes, the extreme average values are typical for “humpbacked” and “short-bodied” whitefish (highest values of head parameters and lowest values of meristic parameters) and for “high-bodied” whitefish (the lowest values of head parameters and the highest values of meristic parameters). The values for these parameters in “wide-bodied” and “dolphin-snouted” whitefish are often intermediate.

Based on the analysis results of the contribution of the size-adjusted morphometric characteristics to the principal components (PCs), only the graph of  $PC2$  against  $PC1$  is worth considering;  $PC3$  and  $PC4$  have low factorial loadings (Table 4). Figure 5 clearly distinguishes the group of “high-bodied” whitefish. The whitefish closest to the “high-bodied” whitefish morphotype are those belonging to the “dolphin-snouted” morphotype, the furthest from them are the “humpbacked” and “low-bodied” whitefish, and the intermediate position is occupied by the “wide-bodied” whitefish morphotype. The main positive contribution to  $PC1$  was made by body shape parameters (the greatest ( $H$ ) and smallest ( $h$ ) body heights, the length of the dorsal ( $LD$ ) and anal ( $LA$ ) fins), and the main negative contribution was made by head shape parameters (the eye diameter ( $o$ ) and pupil diameter ( $b$ ), and the length of the upper jaw ( $lmax$ )) (Table 4). In the  $PC2$ , the main positive contribution was made by the body parameter



**Fig.4.** The appearance of sparsely rakered whitefish morph (a –  $FL = 161$  mm, aged 2+,  $sp.br. = 20$ ,  $ll = 81$ ; b –  $FL = 249$  mm, aged 5+,  $sp.br. = 20$ ,  $ll = 89$ ; c –  $FL = 229$  mm, aged 6+,  $sp.br. = 21$ ,  $ll = 89$ ; d –  $FL = 296$  mm, aged 3+,  $sp.br. = 27$ ,  $ll = 92$ ; e –  $FL = 203$  mm, aged 4+,  $sp.br. = 18$ ,  $ll = 87$ ; f –  $FL = 257$  mm, aged 4+,  $sp.br. = 22$ ,  $ll = 93$ ) in the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022.  $Sp.br.$  – the number of gill rakers on the first branchial arch,  $n$ ,  $ll$  – the number of perforated scales in the lateral line,  $n$ .

(caudal peduncle length (*pA*)), the main negative contribution was made by the head parameter – the upper jaw height (*hmax*) (Table 4).

Summarizing the above, we can talk about the presence of individuals of the *sr* whitefish morph in the NTR with such morphotypes as “humpbacked”, “low-bodied”, “wide-bodied”, “dolphin-snouted”, “high-bodied”, that is, the presence of a polymorphic population of the *sr* whitefish morph in the NTR, for which generalized biological characteristics will be given below.

The generalized table with meristic and the size-adjusted morphometric characteristics of the *sr* whitefish morph from the NTR is presented in Table 5.

The *lsp.br.* in the *sr* whitefish morph varied from 1.7 to 4.6 ( $2.9 \pm 0.03$ ) mm, while in *mr* whitefish morph it was 2.5 and 3.8 mm (Table 5). The *ssp.br.* in *sr* whitefish varied from 0.6 to 2.1 ( $1.2 \pm 0.01$ ), in *mr* – from 0.5 to 0.7 mm (Table 5). The distribution of the *sr* whitefish morph from NTR according to the *ll* is formed by heterogeneous groups (Fig. 6) (statistical analysis showed a significant difference in this distribution from the normal one in 3 out of 6 tests). Given the range of numbers of *ll* in *sr* whitefish in the reservoir (Table 5), it included both small scaled, medium scaled and multi scaled whitefish.

3.4. Age and sex composition of whitefish

According to our data, in the NTR the *sr* whitefish morph is represented by 10 (from 0+ to 9+ years) age groups (Table 6), fish aged 3+, 4+ and 5+ years predominated (63% of the whitefish sample) (Table 6). The *mr* whitefish morph in the NTR were represented by individuals aged 2+ years. The sex ratio of the *sr* whitefish in the NTR corresponded to an average of 1:1 (Table 6).

3.5. Length-weight characteristics of whitefish

The distribution of whitefish from the NTR by length and weight is presented in Figures 7a, b. In terms of length, *sr* whitefish morph have a normal distribution; the most common are individuals with a length from 181 to 240 mm (Fig. 7a). The weight distribution of the *sr* whitefish is formed by heterogeneous groups (Fig. 7b).

In whitefish from the NTR, the measured length and weight of males and females at different ages did not differ significantly (Table 7); therefore, below we will present generalized length-weight characteristics of fish (Table 7). We observed significant differences in the measured length and especially the weight of fish of the same age (min.-max. values), with some fish being up to thirteen times larger than others (weight 46-615 g, age 4+ years) (Table 7). The *mr* whitefish morph at the age of 2+ years had a length of 178-183 mm and a weight of 40-42 g. Linear growth rates were calculated using the scale back-calculation method only for *sr* whitefish morph from the NTR due to the large sample size. The relationship between the measured length of

Table 4. Contributions of plastic characteristics to principal components (PCs) 1-4 in the morphotypes of sparsely rakered whitefish from the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022

Parameters	PCs			
	1	2	3	4
<i>FL</i>	0.02	0.08	-0.04	0.07
<i>H</i>	<b>0.25</b>	-0.08	-0.27	-0.33
<i>h</i>	<b>0.18</b>	0.02	-0.03	-0.06
<i>aA</i>	0.05	0.02	-0.09	0.003
<i>aV</i>	0.03	-0.04	-0.07	0.03
<i>aD</i>	-0.02	0.07	-0.07	-0.02
<i>aP</i>	-0.16	0.01	0.02	-0.02
<i>DC</i>	0.08	0.17	-0.09	0.09
<i>VC</i>	0.07	0.09	-0.05	-0.01
<i>AC</i>	0.05	0.10	0.09	0.05
<i>PA</i>	0.12	0.02	-0.12	-0.01
<i>PV</i>	0.13	-0.07	-0.13	0.08
<i>VA</i>	0.11	0.08	-0.18	-0.12
<i>pA</i>	0.03	<b>0.38</b>	0.06	0.12
<i>pD</i>	0.05	0.15	0.04	-0.02
<i>ID</i>	0.11	0.09	0.17	0.17
<i>IA</i>	<b>0.22</b>	-0.01	0.42	0.02
<i>IV</i>	0.11	-0.06	0.27	0.18
<i>IP</i>	0.10	-0.03	0.56	0.07
<i>hD</i>	<b>0.20</b>	0.06	-0.30	0.42
<i>hA</i>	0.07	-0.17	0.07	0.12
<i>C</i>	-0.15	0.07	-0.02	-0.09
<i>r</i>	-0.07	0.09	0.10	-0.46
<i>o</i>	<b>-0.47</b>	0.01	-0.003	0.09
<i>b</i>	<b>-0.62</b>	0.12	-0.01	0.24
<i>po</i>	-0.04	0.09	-0.17	0.02
<i>Ch1</i>	-0.11	-0.13	-0.16	-0.12
<i>Ch2</i>	0.03	-0.17	-0.15	-0.06
<i>lmax</i>	<b>-0.18</b>	-0.10	0.19	-0.44
<i>hmax</i>	-0.06	<b>-0.79</b>	-0.01	0.18
<i>lmd</i>	-0.04	-0.01	0.002	-0.21
Eigenvalue, %	37.46	13.28	7.60	6.57

**Note:** The maximum contributions of parameters are highlighted in bold. The length of the eigenvector is 1. *FL* – Smith length, *sp.br.* – number of rakers on the first branchial arch, *ll* – number of perforated scales in the lateral line, *H* – highest body height, *h* – caudal peduncle height, *aA*, *aV*, *aD*, *aP* – anteanal, anteventral, antedorsal, antepectral distances, respectively, *DC*, *VC*, *AC* – dorsocaudal, ventrocaudal and analcaudal distances, respectively, *PA*, *PV*, *VA* – pectroanal, pectroventral, ventroanal distances, respectively, *pA* – caudal peduncle length, *pD* – post-dorsal distance, *ID*, *IA*, *IV*, *IP* – the length of the dorsal, anal, ventral and pectoral fins, respectively, *hD*, *hA* – length of the bases of the dorsal and anal fins, respectively, *C* – head length, *r* – snout length, *o* – eye diameter, *b* – pupil diameter, *po* – postorbital distance, *Ch1* and *Ch2* – head height at the level of the eye and the back of the head, respectively, *lmax* and *hmax* – length and height of the upper jaw respectively, *lmd* – lower jaw length.

**Table 5.** Some meristic and size-adjusted plastic characteristics of the sparsely rakered whitefish morph from the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022

Parameters	$M \pm m$	$S$	$cv$	$min-max$
$FL$ , mm	$231 \pm 5.5$ (55)	40.9	17.7	133 – 338
$sp.br.$ , $n$	$20.7 \pm 0.10$ (377)	2.01	9.71	16 – 28
$lsp.br.Xi$ , mm	$2.9 \pm 0.03$ (201)	0.45	15.65	1.7 – 4.6
$ssp.br.Xi$ , mm	$1.2 \pm 0.02$ (201)	0.14	12.14	0.6 – 2.1
$ll$ , $n$	$87.6 \pm 0.58$ (50)	4.12	4.70	80 – 98
$CXi$ , mm	$44.9 \pm 0.26$ (55)	1.89	4.22	40.7 – 49.9
$rXi$ , mm	$11.0 \pm 0.13$ (55)	0.94	8.51	8.7 – 13.0
$oXi$ , mm	$11.7 \pm 0.13$ (55)	0.93	7.98	9.5 – 13.1
$bXi$ , mm	$5.3 \pm 0.08$ (55)	0.59	11.20	4.3 – 6.5
$poXi$ , mm	$23.0 \pm 0.08$ (55)	1.21	5.29	20.4 – 26.2
$Ch1Xi$ , mm	$21.6 \pm 0.19$ (55)	1.38	6.41	17.7 – 25.3
$Ch2Xi$ , mm	$32.7 \pm 0.25$ (55)	1.88	5.74	29.0 – 36.6
$lmaxXi$ , mm	$13.2 \pm 0.14$ (55)	1.07	8.11	10.1 – 15.4
$lmdXi$ , mm	$18.0 \pm 0.18$ (55)	1.31	7.31	15.6 – 21.0
$HXi$ , mm	$54.1 \pm 0.58$ (55)	4.34	8.01	45.1 – 67.4
$hXi$ , mm	$16.3 \pm 0.12$ (55)	0.88	5.40	14.0 – 18.4
$aAXi$ , mm	$166.1 \pm 0.37$ (55)	2.74	1.65	160.0 – 173.0
$aVXi$ , mm	$112.5 \pm 0.42$ (55)	3.15	2.80	106.2 – 120.6
$aDXi$ , mm	$104.0 \pm 0.35$ (55)	2.56	2.47	99.1 – 108.9
$aPXi$ , mm	$44.9 \pm 0.27$ (55)	2.02	4.52	41.0 – 49.5
$DCXi$ , mm	$120.1 \pm 0.43$ (55)	3.18	2.64	114.3 – 129.5
$VCXi$ , mm	$112.2 \pm 0.34$ (55)	2.49	2.22	107.0 – 117.3
$ACXi$ , mm	$56.3 \pm 0.28$ (55)	2.11	3.74	51.9 – 60.7
$PAXi$ , mm	$122.6 \pm 0.45$ (55)	3.35	2.74	114.7 – 132.0
$PVXi$ , mm	$67.9 \pm 0.40$ (55)	2.97	4.37	61.3 – 76.9
$VAXi$ , mm	$56.6 \pm 0.34$ (55)	2.54	4.48	50.6 – 62.9
$pAXi$ , mm	$28.2 \pm 0.29$ (55)	2.17	7.70	24.1 – 33.2
$pDXi$ , mm	$90.4 \pm 0.38$ (55)	2.84	3.15	85.3 – 96.5
$lDXi$ , mm	$38.1 \pm 0.30$ (55)	2.24	5.90	32.2 – 43.6
$lAXi$ , mm	$23.0 \pm 0.18$ (55)	1.36	5.90	20.4 – 26.6
$lVXi$ , mm	$31.1 \pm 0.22$ (55)	1.66	5.35	27.2 – 35.2
$lPXi$ , mm	$34.6 \pm 0.32$ (55)	2.38	6.89	29.3 – 40.3
$hDXi$ , mm	$27.2 \pm 0.31$ (55)	2.28	8.39	23.1 – 32.7
$hAXi$ , mm	$26.4 \pm 0.25$ (55)	1.83	6.93	22.7 – 30.6

**Note:**  $M \pm m$  – mean value and standard error,  $S$  – standard deviation,  $cv$  – coefficient of variation,  $min-max$  – minimum and maximum value of the characteristic,  $FL$  – Smith length,  $sp.br.$  – number of rakers on the first branchial arch,  $lsp.br.$  – central gill raker length,  $ssp.br.$  – distance between the gill rakers,  $ll$  – number of perforated scales in the lateral line,  $H$  – highest body height,  $h$  – caudal peduncle height,  $aA$ ,  $aV$ ,  $aD$ ,  $aP$  – anteanal, anteventral, antedorsal, antepectral distances, respectively,  $DC$ ,  $VC$ ,  $AC$  – dorsocaudal, ventrocaudal and analcaudal distances, respectively,  $PA$ ,  $PV$ ,  $VA$  – pectroanal, pectroventral, ventroanal distances, respectively,  $pA$  – caudal peduncle length,  $pD$  – postdorsal distance,  $lD$ ,  $lA$ ,  $lV$ ,  $lP$  – the length of the dorsal, anal, ventral and pectoral fins, respectively,  $hD$ ,  $hA$  – length of the bases of the dorsal and anal fins, respectively,  $C$  – head length,  $r$  – snout length,  $o$  – eye diameter,  $b$  – pupil diameter,  $po$  – postorbital distance,  $Ch1$  and  $Ch2$  – head height at the level of the eye and the back of the head, respectively,  $lmax$  and  $hmax$  – length and height of the upper jaw respectively,  $lmd$  – lower jaw length,  $Xi$  – is the size-adjusted plastic measurement. Above the line is the average value of the characteristics and its error, below the line is the minimum and maximum value of the characteristics. The number of whitefish specimens is shown in parentheses,  $n$ .



*sr* whitefish and their anterior diagonal radius of scales is presented in Figure 8 and is well described by both the linear regression formula and the power regression formula. The regression line does not pass through the origin, hence, we find the formula for back-calculation length for *sr* whitefish from the NTR:  $\ln L_i = \ln 37.53 + \ln R_i / \ln R_n \times (\ln L_n - \ln 37.53)$  (Fig. 8). Based on the generalized results, the Rosa Lee “phenomenon” is absent in reverse growth calculations, which indicates the correctness of our chosen methodology (Chugunova, 1959; Bryuzgin, 1969; Mina, 1981; Khurshut, 2000; 2003). The *sr* whitefish morph from the NTR were caught

throughout the year, but 83% of the fish in the sample were caught in the summer-autumn-winter period (August-December), that is, the fish had almost completed their full growth of the current year. Therefore, the best agreement between the measured and back-calculated lengths is obtained by comparing the average measured length estimates of whitefish with the average back-calculated lengths at the time of the current annual ring formation (Fig. 9). The variability of the back-calculated length of *sr* whitefish, based on the analysis of the values of the coefficient of variation (cv), gradually increases from the first to the sixth year

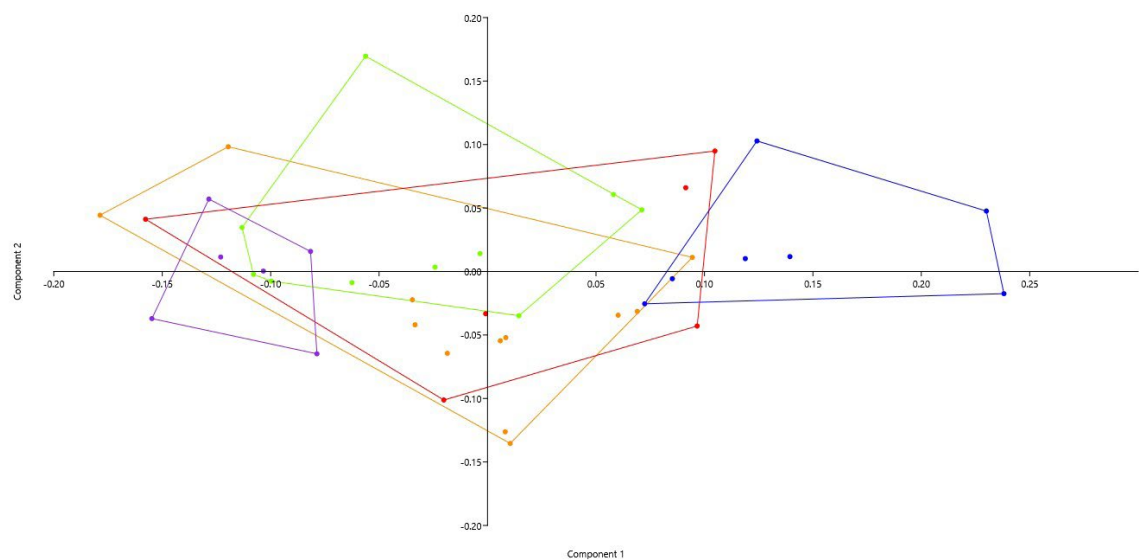
**Table 6.** Age and sex composition of the sparsely rakered whitefish morph in the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022

Age										In whole for the sample <i>juv</i> / males / females, n
0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	
<i>juv</i> / males / females, n (share of age group from the whole sample size, %)										
<u>1/0/0</u> (0.2)	<u>5/4/14</u> (5.7)	<u>4/19/22</u> (11.2)	<u>0/41/44</u> (21.1)	<u>0/43/47</u> (22.3)	<u>0/31/48</u> (19.6)	<u>0/32/21</u> (13.2)	<u>0/9/10</u> (4.7)	<u>0/3/3</u> (1.5)	<u>0/1/1</u> (0.5)	<u>10/183/210</u>

**Table 7.** Length (*FL*), mm and weight (*W*), g of the sparsely rakered whitefish morph the Nizhnetulomskoye Reservoir (Tuloma River basin) at different ages, 2018-2022

Sex	Age									
	0 +	1 +	2 +	3 +	4 +	5 +	6 +	7 +	8 +	9 +
<i>FL</i>										
male <sup>1</sup>	-	<u>138 ± 6.7</u>	<u>181 ± 7.7</u>	<u>205 ± 4.8</u>	<u>215 ± 5.4</u>	<u>235 ± 4.2</u>	<u>252 ± 7.0</u>	<u>239 ± 9.0</u>	<u>247 ± 0.9</u>	<u>270</u>
	-	128–157 (4)	142–253 (19)	162–277 (41)	162–335 (43)	196–272 (31)	192–333 (32)	201–286 (9)	245–248 (3)	(1)
female <sup>2</sup>	-	<u>148 ± 3.1</u>	<u>176 ± 6.1</u>	<u>205 ± 3.5</u>	<u>224 ± 4.5</u>	<u>240 ± 4.9</u>	<u>237 ± 7.2</u>	<u>252 ± 13.2</u>	<u>279 ± 15.0</u>	<u>256</u>
	-	133–177 (14)	135–250 (22)	148–293 (44)	170–280 (47)	182–293 (48)	189–318 (21)	197–320 (10)	253–305 (3)	(1)
<i>t</i> 1-2	-	1.60	0.58	0.00	1.37	0.67	1.37	0.78	2.17	-
common	104	<u>145 ± 2.3</u>	<u>176 ± 4.4</u>	<u>205 ± 3.5</u>	<u>220 ± 3.5</u>	<u>238 ± 3.4</u>	<u>246 ± 5.1</u>	<u>246 ± 8.1</u>	<u>263 ± 9.9</u>	<u>263 ± 7.0</u>
	(1)	128–177 (23)	135–253 (45)	148–293 (85)	162–335 (90)	182–293 (79)	189–333 (53)	197–320 (19)	245–305 (6)	256–270 (2)
<i>W</i>										
male <sup>1</sup>	-	<u>30 ± 4.4</u>	<u>82 ± 12.6</u>	<u>112 ± 9.3</u>	<u>137 ± 15.4</u>	<u>172 ± 12.4</u>	<u>226 ± 20.3</u>	<u>157 ± 22.7</u>	<u>193 ± 14.6</u>	<u>230</u>
	-	25–43 (4)	20–199 (19)	48–271 (41)	46–615 (43)	74–336 (31)	80–405 (32)	74–306 (9)	166–216 (3)	(1)
female <sup>2</sup>	-	<u>38 ± 4.4</u>	<u>67 ± 9.1</u>	<u>125 ± 10.1</u>	<u>155 ± 11.2</u>	<u>201 ± 14.1</u>	<u>192 ± 24.5</u>	<u>228 ± 38.6</u>	<u>348 ± 79.2</u>	<u>245</u>
	-	24–59 (14)	24–188 (22)	30–277 (44)	59–364 (47)	62–401 (48)	78–492 (21)	80–408 (10)	251–505 (3)	(1)
<i>t</i> 1-2	-	1.46	0.97	0.94	0.97	1.42	1.06	1.54	1.92	-
common	9	<u>34 ± 1.9</u>	<u>69 ± 6.8</u>	<u>118 ± 6.9</u>	<u>147 ± 9.4</u>	<u>189 ± 9.9</u>	<u>213 ± 15.7</u>	<u>195 ± 23.9</u>	<u>271 ± 49.9</u>	<u>238 ± 7.5</u>
	(1)	22–59 (23)	20–199 (45)	30–277 (85)	46–615 (90)	62–401 (79)	78–492 (53)	74–408 (19)	166–505 (6)	230–245 (2)

**Note:** Student’s *t*-test. Differences were considered statistically significant at  $p \leq 0.05$ .

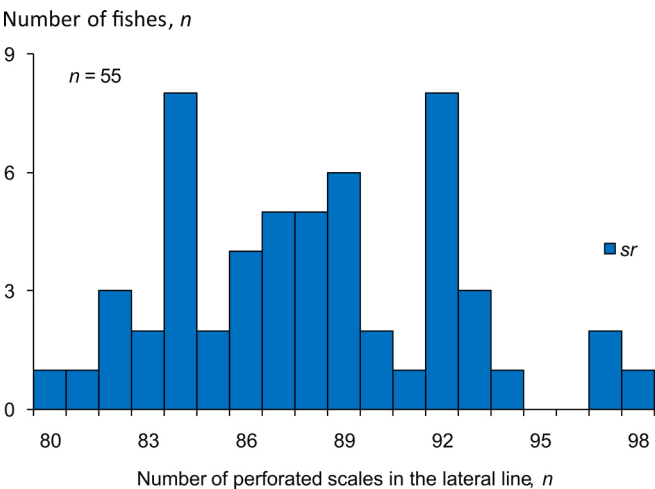


**Fig.5.** Arrangement of individuals of sparsely rakered whitefish morph in the space of 1-2 main components according to morphometric characteristics in the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022: – “humpbacked” whitefish morphotype, – “low-bodied” whitefish morphotype, – “wide-bodied” whitefish morphotype, – “dolphin-snouted” whitefish morphotype, – “high-bodied” whitefish morphotype.

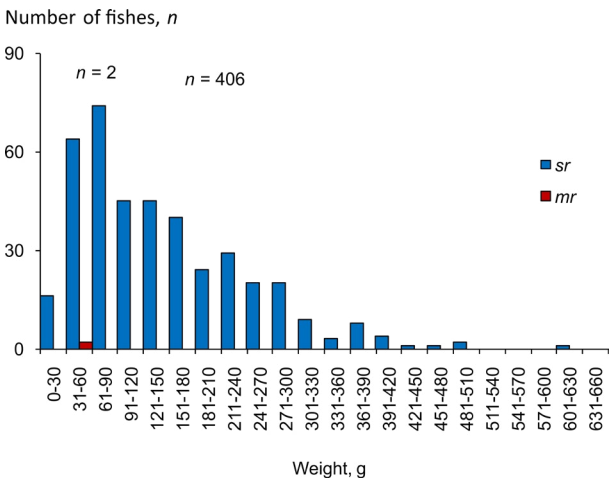
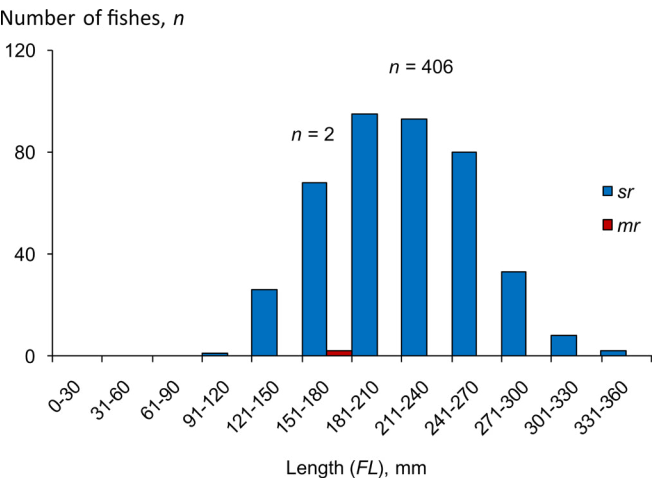
of life and reaches a maximum value of 13.5% (average), after which it gradually decreases again (Table 8). The absolute linear increments in *sr* whitefish morph in the first year of life are maximum, then, they gradually decrease until the age of seven years (Table 8). From the age of eight, there is an alternation of larger and smaller increments (Table 8). Starting from the second year of life, estimates of back-calculated lengths made on the basis of relative increments are generally similar to estimates made on the basis of absolute increments (Table 8).

**3.6. Feeding of whitefish**

The share of feeding individuals of the *sr* whitefish morph from the NTR in different months ranged from 80 to 100% (Table 9). The highest degree of stomach fullness in whitefish was observed in the spring-summer months (May-August) and averaged 2.9-3.4 points



**Fig.6.** The sparsely rakered whitefish distribution by the number of perforated scales in the lateral line in the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022. *Sr* – sparsely rakered whitefish morph.



**Fig.7.** The European whitefish distribution by the measured length (a), mm and weight (b), g in the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022. *Sr* – sparsely rakered whitefish morph, *mr* – medium rakered whitefish morph.



**Table 8.** Back-calculated length (FL), mm and absolute increments, mm/ relative growth rate according to Schmalhausen-Brody of the sparsely rakered whitefish morph in the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022

Age								
1	2	3	4	5	6	7	8	9
Back-calculated length (FL), mm								
105 ± 0.6; 11.1	140 ± 0.8; 11.0	171 ± 1.2; 12.8	191 ± 1.5; 12.3	209 ± 2.0; 13.2	221 ± 3.3; 13.5	228 ± 5.0; 11.7	240 ± 8.1; 10.1	244 ± 7.8; 4.5
72-159	104-230	125-294	145-278	152-299	170-295	188-290	208-292	236-252
(404)	(384)	(343)	(253)	(159)	(80)	(28)	(9)	(2)
Absolute increments, mm								
105	35	31	20	18	12	7	12	4
Relative growth rate according to Schmalhausen-Brody								
-	0.43	0.50	0.39	0.41	0.31	0.20	0.38	0.14

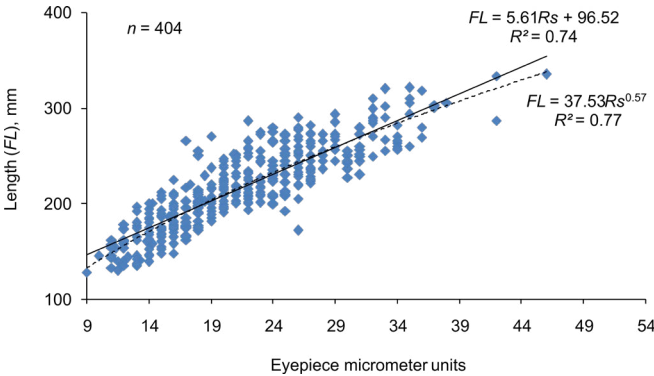
**Note:** Above the line is the average value of the characteristic, its error and coefficient of variation, %, below the line is the minimum and maximum value of the characteristic. The number of specimens of the whitefish, n, is presented in parentheses.

(on a scale of 0-4 points); in the autumn-winter months, it gradually decreased and reached an average of 1.9-2.1 points.

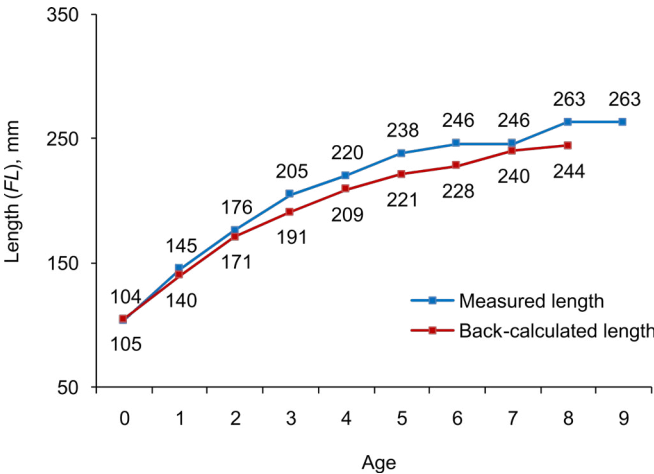
In 31 individuals of *sr* whitefish morph (33% of the sample of *sr* whitefish with examined stomachs) ranging from 207 to 318 mm in length; only pelleted feeds were found, which were used to feed rainbow trout at fish hatcheries in this reservoir. In the remaining 62 whitefish (67%) with a length of 130 to 333 mm, only natural food was found in the stomachs, which consisted of representatives of 6 invertebrate animals' taxonomic groups and fish eggs (Table 10). Bivalve mollusks of the genera *Euglesa* and *Sphaerium* play a greater role ( $IR = 59.7\%$ ) in the natural diet of the NTR whitefish (Table 10). Gastropods of the genera *Limnea* and *Valvata* were less common in the food bolus, in contrast to bivalves (8.6%). Chironomid larvae (*Chironomus*, *Procladius*, *Prodiamesa*, *Psectrocladius*, *Sergentia*) (Table 10) are the second most important in the diet of *sr* whitefish morph (up to 16.7%  $IR$ ). For zooplankton organisms, this index was only 3.9% (Table 10). Zooplankton was represented by large predatory cladocerans and copepods belonging to the genera *Acanthocyclops* and *Eurycercus*. The stomachs of two *mr* whitefish morph, caught in the NTR were empty.

3.7. Maturation of whitefish

The *sr* whitefish morph with a juvenile stage of gonad development (with poorly developed gonads) in the NTR was found in age groups of 0+ -2+ years (Table 6). Sexually mature males and females of the *sr* whitefish were found at ages from 2+ years to 9+ years (Table 11). The modal age of maturation in both sexes was 4+ -5+ years (on average, 50-60% of the sample of sexually mature whitefish of different ages) (Table 11). The average observed length-weight characteristics of mature males and females of *sr* whitefish morph at different ages did not differ significantly (Table 11): fish began to mature at a length of 162-173 mm and a weight of 45-56 g, the average length of



**Fig.8.** The ratio of the measured length (FL), mm and the anterior diagonal radius of the scales (Rs), eyepiece micrometer units of sparsely rakered whitefish morph in the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022.



**Fig.9.** Comparison of the measured length (FL), mm with the back-calculated length (FL), mm of sparsely rakered whitefish morph in the different ages in the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022.

**Table 9.** The share of the feeding sparsely rakered whitefish morph in different months, % from the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022

Date of catching (month, year)										
January, 2021	February, 2021	March, 2019 2022	May, 2019 2020 2021	June, 2019 2020 2021	July, 2022	August, 2019 2020 2021 2022	September, 2019 2020 2021 2022	October, 2019 2020 2021 2022	November, 2019 2020 2021 2022	December, 2018 2019 2020 2021 2022
-	-	-	100 (24)	91 (11)	80 (25)	97 (103)	99 (67)	81 (72)	91 (35)	94 (17)

**Note:** “-” – absence from the sample; the number of studied fish is presented in parentheses.

mature fish was 225-226 mm, weight was 158-165 g. The only sexually mature female *mr* whitefish morph from the NTR at the age of 2+ years had length-weight characteristics of 168 mm and 40 g.

Whitefish with flowing reproductive products (stage V of gonad development) in the NTR began to be found in catches in the first ten days of October and were found until mid-November.

## 4. Discussion

Our research enabled to identify the peculiarities of the functioning of the NTR ecosystem. Currently, we observe the process of eutrophication in the reservoir. High concentrations of total phosphorus and nitrogen are recorded in the water, the sources of which are cage farms for growing rainbow trout. It is considered that cage farming significantly exceeds all other types of aquaculture in terms of negative impact on the environment (Duktov and Lavushev, 2022). Besides, in the reservoir's catchment area, there are large agricultural areas of the "Tuloma" enterprise, large settlements (Tuloma, Murmashi, Prichalnoe), and intensively developing dacha and villa communities, which also make a significant contribution to the processes of anthropogenic eutrophication. In addition to the pollution of water bodies with biogenic and organic compounds, one of the factors contributing to the negative impact of cage aquaculture is the entry into the ecosystem in large quantities of a new type of food for autochthonous aquatic organisms. Despite the high content of biogenic elements in the NTR water, the average quantitative parameters of planktonic communities and chlorophyll *a* correspond to the oligotrophic status. In addition to the development of eutrophication processes, regulation of the flow regime at the spillway of the Nizhnetulomskaya HPP (the reservoir remains a lotic system, where the flow is maintained and planktonic organisms are carried away), as well as temperature conditions are the most significant factors determining the seasonal dynamics of plankton. According to ecological characteristics, the bulk of phyto- and zooplankton communities were representatives typical of subarctic reservoirs of the northern taiga zone, as well as cosmopolitans with a wide biogeography. The consequences of anthropogenic eutrophication of the NTR waters are manifested in the development of cyanoprokaryotes in phytoplankton communities, mainly in the autumn (up to 85%), including potentially toxic species that can cause water blooms.

Macrozoobenthos of the NTR littoral zone is represented by groups that are typical and widespread in freshwater bodies of the Murmansk region (Yakovlev, 2005; Valkova, 2020). High quantitative parameters (abundance and biomass) of macrozoobenthos with the dominance of a limited number of species in the macrozoobenthos of the littoral zone are possible response of the community to reservoir water eutrophication (Yakovlev, 2005; Kashulin et al., 2012; 2018; Valkova, 2020; Lukin et al., 2003; Mousavi et al., 2003; Denisov et al., 2020; Zubova et al., 2020a). The seasonal dynamics of zoobenthos abundance and biomass were closely related to the life cycle of chironomids, which were the dominant group of benthic fauna throughout the entire observation period. The maximum average abundance and biomass of macrozoobenthos in the littoral zone was observed in summer, and the minimum – in autumn.

It is known that 17 species of fish live in the Tuloma River basin (Berg and Pravdin, 1948; Galkin et al., 1966; Nelichik, 2005): Arctic lamprey *Lethenteron camtschaticum* (Tilesius), Atlantic salmon (salmon), brown trout, Arctic char *Salvelinus alpinus* (Linnaeus), European vendace, European whitefish, European grayling, northern pike, common minnow *Phoxinus phoxi-*

**Table 10.** Feeding according to the index of relative importance (*IR*), % of the sparsely rakered whitefish morph in the Nizhnetuloma Reservoir (Tuloma River basin), 2018-2022

Characteristics	IR, %
Min.-max. length ( <i>FL</i> ), mm of whitefish with an examined stomach	130-333
Zooplankton	3.9
Macrozoobenthos:	87.6
chironomids	16.7
caddisflies	2.2
alderflies	0.4
bivalves	59.7
gastropods	8.6
Fish caviar	0.2
Uncertain mass	8.3
Number of fish with examined stomach, <i>n</i>	62

**Table 11.** Measured length (FL), mm and weight (W), g in mature males and females of sparsely rakered whitefish morph from the Nizhnetulomskoye Reservoir (Tuloma River basin), 2018-2022

Sex	Age										In whole for the sample
	0 +	1 +	2 +	3 +	4 +	5 +	6 +	7 +	8 +	9 +	
FL											
male	-	-	<u>200 ± 26.7</u>	<u>204 ± 7.1</u>	<u>211 ± 6.3</u>	<u>238 ± 4.7</u>	<u>248 ± 7.8</u>	<u>235 ± 12.2</u>	<u>247 ± 1.5</u>	<u>270</u>	<u>225 ± 3.5</u>
	-	-	173–253	165–266	162–335	197–271	200–333	201–286	245–248	-	162–335
			(3; 16)	(18; 43)	(32; 68)	(22; 65)	(22; 69)	(6; 78)	(2; 67)	(1;100)	(107)
female	-	-	<u>180 ± 11.7</u>	<u>212 ± 7.7</u>	<u>218 ± 5.3</u>	<u>236 ± 5.6</u>	<u>228 ± 5.4</u>	<u>242 ± 10.3</u>	<u>279 ± 15.0</u>	<u>256</u>	<u>226 ± 3.0</u>
	-	-	162–202	158–265	170–280	182–290	189–260	200–273	253–305	-	158–305
			(3; 14)	(14; 30)	(33; 69)	(34; 71)	(16; 73)	(7; 64)	(3; 100)	(1; 100)	(112)
W											
male	-	-	<u>104 ± 47.3</u>	<u>116 ± 16.3</u>	<u>131 ± 19.5</u>	<u>177 ± 14.1</u>	<u>212 ± 23.2</u>	<u>157 ± 33.5</u>	<u>191 ± 25.0</u>	<u>230</u>	<u>158 ± 9.7</u>
	-	-	56–199	48–271	46–615	74–319	82–435	74–306	166–216	-	46–615
female	-	-	<u>66 ± 14.7</u>	<u>138 ± 137.7</u>	<u>142 ± 14.0</u>	<u>188 ± 16.9</u>	<u>155 ± 14.9</u>	<u>196 ± 32.5</u>	<u>348 ± 79.2</u>	<u>245</u>	<u>165 ± 8.6</u>
	-	-	45–94	46–239	59–364	62–401	78–271	80–296	251–505	-	45–505

**Note:** Above the line is the average value of the parameter and its error, below the line is the minimum and maximum value of the parameter. The number of whitefish specimens, n and % of sexually mature individuals within the age group are presented in parentheses.

nus (Linnaeus), burbot, European perch, three-spined stickleback *Gasterosteus aculeatus* Linnaeus, nine-spined stickleback, fourhorn sculpin *Myoxocephalus quadricornis* (Linnaeus) \*, European flounder *Platichthys flesus* (Linnaeus)\* (\* – species that live only in the estuarine zone of the river).

Before the construction of hydroelectric dams, the Tuloma River was characterized by the dominance of salmonids in the ichthyofauna. Since 1960, pink salmon *Oncorhynchus gorbuscha* (Walbaum) acclimated in the seas of the North, began to enter the fish passage of the Nizhnetulomskaya HPP. From 1979 to 1985, 258.8 million larvae of small European smelt were released from Lake Onega in order to reproduce the food supply for salmon predators in the VTR (Tuloma River basin). In the reservoir, smelt adapted well (gave numerous offspring) and in terms of growth rate significantly surpassed its relative from Lake Onega (Nelichik, 1998; Mitenev et al., 2007). It is currently distributed throughout the Tuloma River system.

Taking into account the presented literature and modern data, the structure of the fish community in the NTR is currently also undergoing significant changes. Smelt introduction into the Tuloma River system resulted in the development of a reservoir containing whitefish and salmon instead of a reservoir containing only whitefish and smelt within about half a century. The short life cycle of smelt, low abundance of predatory fish (northern pike, burbot) in the reservoir, inefficient commercial removals, and successful reproduction in tributary rivers make smelt a successful species in the NTR. Smelt can occupy different ecological niches throughout its life cycle leading to increased food competition with other fish species in the reservoir (Kashulin et al., 2012). In the water bodies of the Murmansk region, smelt under 100 mm in length is a typical planktonophages, while larger individuals feed on both benthic organisms and fish (mainly

vendace and nine-spined stickleback) (Zubova et al., 2020b; 2020c). Directly in the NTR, smelt feed on both artificial pelleted feed from fish nurseries and natural food. In smelt specimens 150-222 mm long, fish such as nine-spined stickleback and vendace had greater importance in their natural diet. Also, bivalves, chironomids, and cladocerans were found in the stomachs of smelt 150-188 mm long (own unpublished data). Thus, in conditions of intensification of water eutrophication processes and regional and climatic changes, including abnormal temperature deviations against the backdrop of a warming trend, advantages are gained by “universal species” of fish that are better adapted to high temperatures, such as perch and smelt, which have multichannel feeding and are capable of forming intraspecific groups within a reservoir (Zubova et al., 2020c; Kashulin and Bekkelund, 2022; Polyakov et al., 2002; McBean et al., 2005; ACIA, 2005; Ylikörkkö et al., 2015; Sa´nchez- Herna´ndez et al., 2021; Smalås et al., 2023).

Currently, whitefish remain the dominant species in the catches from the NTR. According to Reshetnikov (1980), the Tuloma River basin is mainly inhabited by the *sr* whitefish morph with the number of *sr.br.* 20-30 (on average 24-25) (58 specimens each). The author also described here the only *mr* whitefish morph with the number of *sr.br.* 33. In his work on the main areas of the VTR, the Note River, and the flooded Lake Katskim, Shuster (1985) notes the presence of multiple ecological morphs of whitefish and their “polymodality in the *sr.br.* number”. For the indicated areas, the average number of whitefish *sr.br.*, according to Shuster, was  $24.8 \pm 0.06$  (18-34) (1576 specimens each). In more recent works on the ichthyofauna of the VTR and NTR (Ilmast et al., 2018; 2019), only the *sr* whitefish morph is also described, but with a lower ( $p = 0.001$ ) average number of *sr.br.* –  $23.3 \pm 0.45$  (35 specimens each). In our catches from the NTR, whitefish had a wider range

of extreme values of *sr.br.* than indicated in the literature: 16-39 instead of 18-34. Mostly *sr* whitefish morph were also present (99.5% of the whitefish sample) with the *sr.br.* number from 16 to 28 ( $20.7 \pm 0.10$ ), the remaining percentage (0.5%) was *mr* whitefish morph with the *sr.br.* number 32 and 39. Taking into account the current literature data on the structure of the first whitefish gill arch from five large lake-river systems of the Murmansk region (basins of the Pasvik, Tuloma, Niva and Umba rivers), the *sr* whitefish morph with the lowest average *sr.br.* number inhabits the NTR ( $p = 0.05$ ) (Zubova et al., 2022; 2023): 21 gill rakers against 22-26 gill rakers. Among the *sr* whitefish morph of the NTR based on the structure of the head and body, up to 5 additional morphotypes are visually distinguished, the reasons for the differences of which we cannot know and are based on the available data. Also, given the range of the *ll* number (80-98) in the *sr* whitefish of the reservoir, it consists of both small-, medium- and multi scaled additional morphs of whitefish (Bochkarev, 2022). The coexistence of different whitefish morphs according to the *ll* number was observed by us in other studied water bodies of the Murmansk region, and the division into small, medium, and multi scaled morphs was characteristic of both *sr* whitefish and *mr* whitefish morphs (Zubova et al., 2019; 2022). It is believed that the *ll* number is an evolutionarily more neutral trait than *sr.br.* number, since a direct connection between the *ll* and the morphological characters and ecological preferences of whitefish has not yet been found (Bochkarev, 2022). Thus, the *ll* number may reflect phylogenetic relationships to a greater extent than the *sr.br.* number (Bochkarev, 2022).

Thus, the whitefish in the NTR is represented by a polymorphic population, which may be the result of a “mixing” in the Tuloma River of lake and lake-river whitefish from numerous subsidiary river systems of the basin and anadromous (“sea”) whitefish from the Barents Sea. Assessment of the origin of whitefish of the NTR polymorphism is impossible without modern genetic research methods.

Analysis of the modern age composition of the *sr* whitefish morph from the NTR, its length-weight characteristics, and sexual maturation relative to the literature data on the VTR whitefish for 1966-1984 revealed a number of changes (Shuster, 1985). In the NTR *sr* whitefish, the number of age groups decreases almost by half from 20+ years to 9+ years, the rate of linear and weight growth decreases, and maturation occurs earlier, at the age of 2+ years instead of 3-4+ years at lower length-weight characteristics of fish. The time of fish spawning (the first ten days of October to mid-November) corresponds to literature data (Shuster, 1985). We have not discovered mass spawning sites for the NTR whitefish. Possible spawning sites for the NTR whitefish can be considered tributaries (the rivers Pyaive, Sholgoch, Kercha, etc.), as well as their pre-estuary areas in the reservoir itself, where there is less siltation of the bottom and more favorable oxygen and hydrological regimes for the development of eggs.

Taking into account modern data on the biological characteristics of intraspecific groups of whitefish

from reservoirs of various river basins of the Murmansk region (Pasvik, Niva, Umba), *sr* whitefish morph from the NTR, according to length-weight characteristics, can be classified as a group of medium-sized whitefish with early maturation (Zubova et al., 2022; 2023). The *sr* whitefish morph with similar biological characteristics are also found in relatively clean (Lake Virtuvoshjaur) and heavily polluted (Lake Kuetsjarvi) water bodies of the Pasvik River basin (Zubova et al., 2022).

Based on the type of feeding, the *sr* whitefish morph from the NTR can be classified as benthophages with a wide range of consumption of food organisms. The stomach contents of *sr* whitefish morph in the summer-autumn period in water bodies of the Murmansk region usually correlate well with the hydrobiological characteristics of fish habitats (Reshetnikov, 1980; Zubova et al., 2023). The high content of bivalves in the stomachs of the *sr* whitefish from the NTR probably indicates that they were consumed from the profundal zone of the reservoir, since their numbers and biomass were insignificant in the littoral macrozoobenthos. The second most important food organisms, chironomids, could be consumed from both the littoral and profundal zones of the reservoir.

Additional artificial feed from numerous nurseries of trout farms in the reservoir is currently of great importance in the feeding of the NTR *sr* whitefish. Artificial pelleted feed was also found in the stomachs of smelt. Perhaps this is the main reason for the large differences in the minimum-maximum values of the measured length and especially the mass of the NTR *sr* whitefish morph of the same age.

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## Conflict of interest

The authors declare no conflict of interest.

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