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Diversity and distribution of European whitefish (*Coregonus lavaretus*) in watercourses of Murmansk region

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Abstract: European whitefish (*Coregonus lavaretus*) is a highly polymorphic species, but the wider scale diversity and distribution of sympatric morphs in subarctic lakes of northwestern Russia has not been recently studied and analyzed. The aim of the present study was to investigate diversity and distribution of whitefish morphs in different sized lakes and watercourses of Murmansk region. Our study of the water bodies in four major river basins of Murmansk region revealed the presence of two whitefish morphs: sparsely rakered (*sr*) and medium rakered (*mr*). The *mr* morph is less common and observed only alongside the *sr* whitefish. In general, in *sr* whitefish the number of gill rakers ranges between 15 and 31, and in *mr* whitefish between 27 and 44. Among whitefishes with 27 to 31 gill rakers, both *sr* and *mr* morphs were observed and distinguishable by the shape of the rakers. In the studied *sr* whitefish populations, relatively long and short rakered whitefish morphs were found. In Lake Kuetsyarvi (Pasvik River basin), the *sr* and *mr* whitefish formed additional slow- and fast-growing ecological morphs. The four whitefish morphs in Lake Kuetsyarvi specialize to different ecological niches correlating with morphological and behavioral differences. The observed diversity and distribution of whitefish in the Murmansk region requires genetic studies of the population to assess the origins of divergence.

Keywords: Arctic, NW Russia, sparsely rakered, medium rakered, sympatric morphs.

Introduction

In Arctic fresh water bodies, the formation of sympatric morphs in dominant fish species (such as European whitefish *Coregonus lavaretus*, Arctic charr *Salvelinus alpinus*, brown trout *Salmo trutta*) is a mechanism for compensating for the low species diversity of the fish communities. That allows the species efficiently use available resources and determines the stability of water ecosystems as a whole (Reshetnikov 1980; Moiseenko 1983; Kashulin *et al.* 1999; Amundsen *et al*. 2004 a; Kahilainen and Østbye 2006; Siwertsson *et al.* 2008, 2010; Laske *et al.* 2019; Skulason *et al.* 2019; Zubova *et al*. 2019). The related polymorphism arises through the divergence of the original nonspecialized populations into several specialized morphs along the resource availability gradient, usually in response to reduced competition under rapid changes in environmental conditions (Lundsgaard-Hansen *et al.* 2013). Such resource-based divergence can lead to phenotypic segregation of subpopulations (Thomas *et al.* 2019).

Whitefish, hereinafter this species name is only used in regard to the European whitefish, is a fish species found in Northern Europe that has multiple allopatric and sympatric morphs and populations (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; Zubova *et al.* 2019). The whitefish divergence is particularly pronounced in Northern Fennoscandia, where polymorphic populations (between two to four morphs) are found in many lakes. This polymorphism correlates well with the size of the water body and how well the main limnological zones are defined (Kahilainen *et al.* 2004, 2007, 2009, 2014; Siwertsson *et al.* 2010; Præbel *et al.* 2013). In general, it is assumed that the divergence in whitefish is a form of a specialization in the use of the resources (including food) of the main limnological zones – pelagial (plankton), littoral (benthos, plankton), profundal (benthos) – and the morphological adaptations of the shape of the body and head simultaneously determine the direction of the process (Klemetsen *et al.* 2002; Kahilainen *et al.* 2003, 2005, 2011; Amundsen *et al.* 2004 a,b; Bernatchez 2004; Knudsen *et al.* 2006). Such morphological adaptations, usually associated with the shape of the head, jaws, and gill rakers, control the efficient use of food (Schluter 1996; Zuikova and Bochkarev 2008). At the same time, the shape and number of gill rakers, which are responsible in whitefish for prey retention, are considered the most important adaptive trait and are most often used to distinguish between its sympatric morphs or ecotypes (Reshetnikov 1980; Amundsen *et al.* 2004b; Bernatchez 2004; Kahilainen and Østbye 2006; Siwertsson *et al.* 2010; Kahilainen *et al.* 2011, 2014). However, the “evolutionary fate” of young sympatric species or morphs largely depends on the maintenance of divergent natural and/or sexual selection and the effectiveness of prezygotic isolation mechanisms to maintain the differences until permanent reproductive isolation barriers evolve. This dependence on environmental conditions makes many morphs resulting from ecological speciation vulnerable to changes in habitat, including, in the most severe cases, a reversal of the speciation process (Feulner and Seehausen 2019).

The whitefish of Murmansk region in the northwestern of Russia is of particular interest because the Barents Sea, White Sea, and Baltic populations inhabited that region (Pravdin 1954), which in turn could form local morphs, both in the hybridization of different phylogenetic lineages and in the physical and geographical features of the region's rivers and lakes (Lundsgaard-Hansen *et al.* 2013; Rougeux *et al.* 2019; Thomas *et al.* 2019). The Murmansk Region is characterized by an extraordinary diversity of natural conditions governed by both natural and anthropogenic factors that modify habitats (Moiseenko and Yakovlev 1990; Kashulin *et al.* 1999, 2007, 2009, 2012). These include the diversity of natural landscapes and climatic zones, changes in the hydrology, industrial pollution, eutrophication, introduction of alien species, and more, and this causes differences in the evolution of local whitefish populations. Despite the existing fairly extensive literature on the biological properties of the whitefish and its life strategies in anthropogenically modified water bodies of Russia's Murmansk region (Moiseenko 1991, 1997, 2000; Moiseenko and Yakovlev 1990; Moiseenko and Lukin 1999; Kashulin *et al.* 1999; Sharova and Lukin 2000; Kashulin 2004), the diversity of the ecological morphs of this species, the mechanisms of morphogenesis and spatial-functional differentiation of its populations remain poorly understood. A general description of the ecological morphs of whitefish based on the number of rakers on the first branchial arch in the water bodies of the Murmansk region was provided by Reshetnikov (1980). He described single individual from the Zoological Institute of the Russian Academy of Sciences collection (without specifying the exact date of catch) and presented the most complete data on the lakes of the Lapland Nature Reserve (Lake Imandra basin) for the 1960s.

The aim of the present study was to investigate of the current diversity and distribution of whitefish morphs in different watercourses and lake sizes of Murmansk region.

Study area

Whitefish populations were studied in water bodies of various origins and morphology belonging to the four largest lacustrine-river systems of the Murmansk region. Our study area covered the Pasvik River ($S_{catchment\ area\ (ca)}$ = 18300 km^2), the Tuloma River (S_{ca}= 21500 km^2), Imandra Lake – the Niva River (S_{ca}= 12830 km^2), Umbozero Lake-the Umba River (S_{ca}= 6250 km^2). The Pasvik and Tuloma rivers drain into the Barents Sea, and the Niva and Umba rivers drain into the White Sea (Fig. 1a).

The lacustrine-river system of the Pasvik River is regulated by a chain of hydroelectric dams (Fig. 1b). Here, the study of whitefish here we carried out in different types of water bodies. In addition to changes in the hydrology and the relative isolation of individual reaches by dams, powerful additional factors modifying the whitefish habitat include the industrial pollution spreading from the Pechenganickel smelter (Nickel, Murmansk region) (Kashulin *et al.* 1999; Ylikörkkö *et al.* 2015) and the invasive dispersal of the introduced vendace *Coregonus albula* (L., 1785) (Amundsen *et al.* 1999). In the upper reaches of the Pasvik River, we studied three minor riverbed reservoirs: Kaytakoski, Yaniskoski and Rayakoski (Table 1, Fig. 1b).

Lakes of the Nautsiyoki River basin, which flows into the Pasvik River downstream of the village of Rayakoski, are a series of small, flowing, shallow lakes of glacial origin – Riuttikyaure, Virtuovoshyaur, Ilya-Nautsiyarvi and Ala-Nautsiyarvi (Table 1, Fig. 1b). The most studied is Lake Virtuovoshyaur, and the greatest depths are found in the northern and southern parts of the lake (Ylikörkkö *et al.* 2015). The lake is shallow in its center area – not deeper than 2.5 m. A separate stretch adjoining the southern part of the lake via a rocky channel is also shallow (1 to 2 m) and is 1.2 km long. Lake Virtuovoshyaur

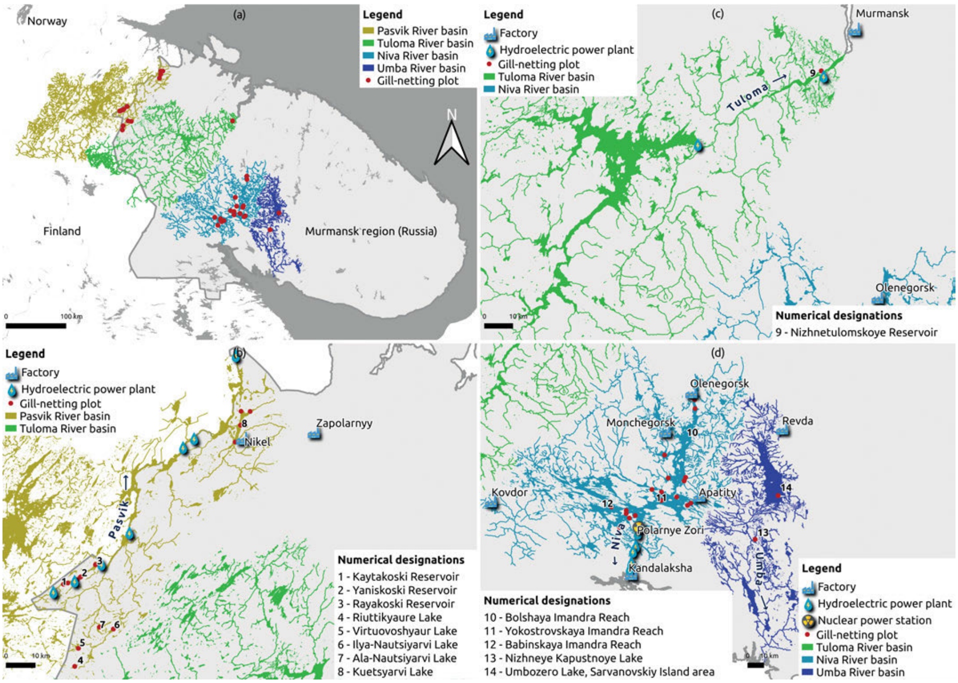

Fig. 1. Map of the study areaand sampling locations, 2011–2021: **a** – position of the four studied river basins in the Murmansk region and sampling locations; **b** – studied water bodies in the Pasvik River basin and sampling locations; **c** – studied water bodies in the Tuloma River basin and sampling locations; **d** – studied water bodies in the Niva and Umba River basins and sampling locations.

Table 1.

Hydrological and hydrochemical characteristics of the studied water body

Studied area	Coordinates	Water body type	Reservoir area, km^2	Average depth, m	Maximum depth, m	Total phosphorus, µg/l / total nitrogen, µg/l*	Eutrophy status of the water body**
Pasvik River basin							
Pasvik River upper course:							
Kaytakoski reservoir	68.952 N, 28.633 E	Artificial	8.0	4.0	10.0	–	–
Yaniskoski reservoir	68.983 N, 28.828 E	Artificial	5.0	–	21.5	–	–
Rayakoski reservoir	69.021 N, 28.956 E	Artificial	8.0	–	20.0	7 / 166	ultraoligotrophic
Tributary Pasvik River upper course, the Nautsiyoki River system:							
Riuttikyaure Lake	68.712 N, 28.781 E	Natural	< 5.0	–	–	7 / 143	ultraoligotrophic
Virtuovoshyaur Lake	68.767 N, 28.812 E	Natural	1.25	2.5	13.0	9 / 217	ultraoligotrophic
Ilya-Nautsiyarvi Lake	68.826 N, 29.107 E	Natural	3.32	–	–	/ 195	-
Ala-Nautsiyarvi Lake	68.832 N, 28.988 E	Natural	4.64	–	–	3 / 160	ultraoligotrophic
Pasvik River lower course: Kuetsyarvi Lake	69.439 N, 30.179 E	Natural	17.0	–	37.0	20 / 291	mesotrophic with signs of eutrophicity
Tuloma River basin							
Nizhnetulomskoye reservoir	68.833 N, 32.806 E	Artificial	38.5	–	20.0	16 / 288	mesotrophic with signs of eutrophicity
Niva River basin							
Imandra Lake i Bolshaya Imandra Reach	67.815 N, 33.129 E	Artificial	327.5	14.7	67.0	55 / 396	mesotrophic with signs of eutrophicity
Yokostrovskaya Imandra Reach	67.559 N, 32.914 E		361.9	10.9	42.0	19 / 183	mesotrophic with signs of eutrophicity

Studied area	Coordinates	Water body type	Reservoir area, km^2	Average depth, m	Maximum depth, m	Total phosphorus, µg/l / total nitrogen, µg/l*	Eutrophy status of the water body**
Babinskaya Imandra Reach	67.507 N, 32.151 E		191.0	16.3	43.5	6 / 147	oligotrophic with signs of mesotrophy
Umba River basin							
Nizhneye Kapustnoye Lake	67.352 N, 34.175 E	Natural	8.04	0.7	3.2	–	–
Umbozero Lake, Sarvanovskiy Island area	67.581 N, 34.484 E	Natural	319.4	15.0	115.0	–	–

* – based on the literature and own unpublished data: Pasvik River basin – along Ylikörkkö et al., 2015, Niva River basin – Zubova et al., 2018, Tuloma River basin – own unpublished data. ** – along Likens, 1975.

connects with Lake Puldshekyarvi via a small stream flowing from its northern end. Dark greenish silty sediment predominates from depths of approximately 1.5–2.0 m. The studied reservoirs and lakes belonging to the upper reaches of the Pasvik River were ultraoligotrophic water bodies in terms of biogenic elements (total phosphorus and nitrogen) content in the water (Table 1).

In the lower reaches of the Pasvik River, material was collected from Lake Kuetsyarvi (Table 1, Fig. 1b), which is the most industrially polluted natural water body in the entire European Arctic (Kashulin *et al.* 1999; Zubova *et al.* 2020). The lake is one of the largest in Russia's borderlands. It is a relatively deepwater, elongated lake of glacial origin (Table 1). The greatest depths are found in the northern part of the lake with steep shores. The lake is shallow in its center area and is not deeper than 10 m. The southern part of the lake is also shallow with maximum depths that do not exceed 12 m. Lake Kuetsyarvi connects with the Pasvik River via a small channel (Fig. 1b).

In the Tuloma River basin, whitefish was studied in Nizhnetulomskoye reservoir (Table 1, Fig. 1c). This is a moderately large riverbed reservoir created by one of Russia's oldest hydroelectric dams (Bydin 1962). In terms of the content of total phosphorus and nitrogen in the water, the Nizhnetulomskoye reservoir is close to the highly polluted Lake Kuetsyarvi and belongs to a mesotrophic water body with signs of eutrophication (Table 1), what can be connected by the work of the trout farm.

In the Niva River basin, detailed data was collected on Lake Imandra (Table 1, Fig. 1d). Lake Imandra is the largest water body in the Murmansk region and is exposed to a variety of anthropogenic effects (Moiseenko *et al.* 2002). It consists of three independent reaches – Bolshaya, Yokostrovskaya and Babinskaya Imandra – connected by narrow straits and differing in hydrology and environmental factors controlling water quality (Moiseenko and Yakovlev 1990; Moiseenko *et al.* 2002; Zubova *et al*. 2016a, 2018). There is substantial content of total phosphorus and nitrogen in the Bolshaya and Yokostrovskaya Imandra reaches (Table 1). Their trophic status was assessed as mesotrophic. Based on these parameters, the Babinskaya Imandra reach is remote from pollution sources and is referred to as an oligotrophic area.

Lake Umbozero is the second largest and deepest natural water body in the Murmansk region (Table 1, Fig. 1d). At present, the northeastern part (mine water and Lovozero Concentrator process effluents) and the southwestern part (mine water from Apatit Joint Stock Company and SZFK Joint Stock Company, municipal sewage from the town of Koashva) of Lake Umbozero are most exposed to anthropogenic impacts (Dauvalter and Kashulin 2010). Lake Nizhneye Kapustnoye, located 15.4 km south-west of the Oktyabrskiy town, is essentially a stretch of the Umba River (Table 1, Fig. 1d). It has an oval elongated shape, shallow with a winding, often swampy shoreline. Birch and pine forests are common in the catchment area (Kashulin *et al.* 2012).

Material and Methods

We combined the data for the three reservoirs of Pasvik River upper course (Kaytakoski,Yaniskoski, Rayakoski) into a single dataset and studied together (Table 2). The data collected for the lakes belonging to the Nautsiyoki River system (Lakes Riuttikyaure, Virtuovoshyaur, Ilya-Nautsiyarvi, Ala-Nautsiyarvi) was combined and studied together. Despite the different living conditions in the three reaches of Lake Imandra (Bolshaya, Yokostrovskaya and Babinskaya Imandra), are connected. Therefore, we think that the collected ichthyological material from different reaches of Lake Imandra should be combined and studied together.

The fish were collected using gillnets in all three sampled habitats of the lakes (littoral, pelagic, and profundal). In the littoral zone (at a depth of 1.5–3 m), 25-m-long nets 1.5 m high, with a mesh size of 10, 12, 16, 18, 20, 30, 35, 40, 45, 50, 55, and 60 mm (to capture fish ≥ 5 cm long), were set. The nets were set in groups of 1 to 2 perpendicular to the shore on sites with sand and gravel banks and large boulder deposits. In the profundal zone with depths of more than 18 m, up to 10 nets were set with various mesh-size combinations in the same group. In the pelagic zone of the water body, we used Nordic multi-mesh gillnets with a height of 3 m and a length of 30 m, consisting of 2.5 m sections with mesh sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, and 55 mm. We also used ichthyological materials transferred by the fish protection inspectorate to the Institute of Industrial Ecology of the North of the Kola Scientific Center of the Russian Academy of Sciences for for study (Umba River basin). Detailed information on the sample sizes, catch times and fish species composition in gillnets catches is presented in Table 2. The study of the biological characteristics of whitefish was carried out after the killing of animals. The body weight of the fish was measured within accuracy 1 g, and the fork length was measured within accuracy 1 mm. The fish sex was determined at autopsy. The maturity stage of the gonads was determined using a six-point scale (I – VI) by Lapnitsky (Pravdin 1966). We assigned fish to those taking part in spawning if their gonads were in sexual maturity stage III to IV (Reshetnikov and Bogdanov 2011). The age of the fish was determined by scales using commonly accepted methods (Van Oosten 1928; Reshetnikov 1966). The study of the back-calculated whitefish length on scales was conducted according to the method of Zubova *et al.* (2016 b). To study and compare the branchial apparatus of whitefishes, the following properties of the first branchial arch were taken into consideration: total number of rakers, total length of the branchial arch (from the outmost raker of the upper arch to the outmost raker of the lower arch), relative length of the central gill raker (as a percentage of the branchial arch length) (Reshetnikov 1980; Zuikova and Bochkarev 2008). Whitefish morphs, namely sparsely rakered (*sr*) and medium rakered (*mr*), were identified based on the number of rakers on the 1st branchial arch: 16 to 30 in *sr* whitefish, 31 to 42 in

Table 2.

Characteristics of the used ichthyological material

Fishing area	Research period	Whitefish with the investigated branchial arch, n	Whitefish with the studied size and age characteristics, n	Species fish composition in gill-nets catches
Pasvik River basin				
Pasvik River upper course: Kaytakoski reservoir	VIII.2019	6	6	Whitefish, brown trout, perch *Perca fluviatilis*, pike *Esox lucius*
Yaniskoski reservoir	VIII.2019	27	27	Whitefish, brown trout, grayling *Thymallus thymallus*, perch, pike
Rayakoski reservoir	VIII.2012, IX.2013	58	66	Whitefish, vendace, brown trout, grayling, perch, pike, burbot *Lota lota*
Tributary Pasvik River upper course, the Nautsiyoki River system: Riuttikyaure Lake	VIII.2013	6	6	Whitefish, brown trout, perch
Virtuovoshyaur Lake	VIII.2013	103	102	Whitefish, grayling, perch, pike
Ilya-Nautsiyarvi Lake	VIII.2013	21	23	Whitefish, brown trout, perch, pike, minnow *Phoxinus phoxinus*
Ala-Nautsiyarvi Lake	VIII.2012	6	6	Whitefish, brown trout, perch, pike
Pasvik River lower course: Kuetsyarvi Lake	VII–VIII.2012, VII–IX.2013, IX.2015, IX.2020	660	689	Whitefish, vendace, brown trout, grayling, perch, pike, burbot
Tuloma River basin				
Nizhnetulomskoye reservoir	XII.2018, monthly from V. to XII.2019–2020, V–VI.2021	207	235	Whitefish, vendace, salmon *Salmo salar* , brown trout, grayling, rainbow trout *Oncorhynchus mykiss* ,smelt *Osmerus eperlanus*, perch, pike, burbot

Fishing area	Research period	Whitefish with the investigated branchial arch, n	Whitefish with the studied size and age characteristics, n	Species fish composition in gill-nets catches
Niva River basin				
Imandra Lake:				
Bolshaya Imandra Reach	VIII–IX.2012, X.2013, IX.2017, VIII–IX.2018	174	174	Whitefish, vendace, Arctic char, grayling, smelt, perch, ruffe *Gymnocephalus cernua*, pike
Yokostrovskaya Imandra Reach	VIII.2011, VI.2012, monthly from IX. to XII.2012, from I. to V.2013, VI.2013, IX.2013, X.2014, X., XII.2015,VIII.2016, VIII.2018	421	421	Whitefish, vendace, brown trout, grayling, smelt, perch, ruffe, pike
Babinskaya Imandra Reach	VIII–IX.2011, VIII.2018	179	179	Whitefish, vendace, Arctic char, grayling, smelt, perch, ruffe, pike, burbot
Umba River basin				
Nizhneye Kapustnoye Lake	IX.2018, X.2020	28	19	–
Umbozero Lake, Sarvanovskiy Island area	VI.2005, IX.2017	26	33	–

mr whitefish, 43 to 65 in densely rakered (*dr*) whitefish (Pravdin 1954; Reshetnikov 1980).

For every trait (length and weight values, total number of rakers and relative length of the central gill raker), the mean and standard error were calculated. Normal distribution of the traits was tested in Statistica 10 (asymmetry and kurtosis, Kolmogorov-Smirnov, Shapiro-Wilk tests, two normal probability plots). 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 $p \leq 0.05$.

Results

Pasvik River basin. — Whitefish and perch dominated in the catches, 45% and 35%, respectively, in the upper reservoirs of the Pasvik River. The whitefish was represented by individuals with 19 to 34 rakers (Table 3), which formally corresponds to *sr* and *mr* whitefish morphs. Using the number of rakers on the first branchial arch, the fish individuals were distributed into heterogeneous groups (Fig. $2a_1$), and the statistical analysis showed that the distribution is significantly different from normal in 3 tests out of 6. However, in our studies, it was difficult to classify a specific individual in one group or another based on the number of rakers on the first branchial arch (Fig. $3a_1$-a_2). The relative length of the central gill raker in the sample as a whole varied within 8.9–18.8% (Table 3, Fig. $2a_2$). The average and extreme linear-weight and age characteristics for the whole whitefish sample are presented in Table 3. The fish individuals had relatively high rates of observed and back-calculated linear and weight growth (Fig. 4a–c). The whitefish began to mature at the age of 4+ years, at a length of 295 mm, and at a mass of 351 g, and the majority were mature by the age of 6+ to 9+ years (67% of the mature fish sample), at an average length of 362 mm, and an average weight of 632 g (Table 3).

In the lacustrine-river system of the Nautsiyoki River, perch dominated in catches (74%), and whitefish was a subdominant species (22%). The whitefish in that system was represented by the *sr* morph with elongated gill rakers (Fig. $3b_1$). The number of gill rakers in the whitefish found was 19 to 31 (Table 3), and the normal distribution curve by the number of rakers showed one pronounced peak (Fig. $2b_1$). The relative length of the central branchial raker varied within 7.8–18.2% (Table 3, Fig. $2b_2$). The minimum and maximum number of rakers and the relative length of the central raker in the whitefish from the lakes of the Nautsiyoki River system are close to the values found in the whitefish from the reservoirs (Table 3). The linear-weight and age characteristics for the whole whitefish sample are presented in Table 3. The fish individuals had lower average values of observed-back-calculated body length and mass ($p = 0.001$) compared

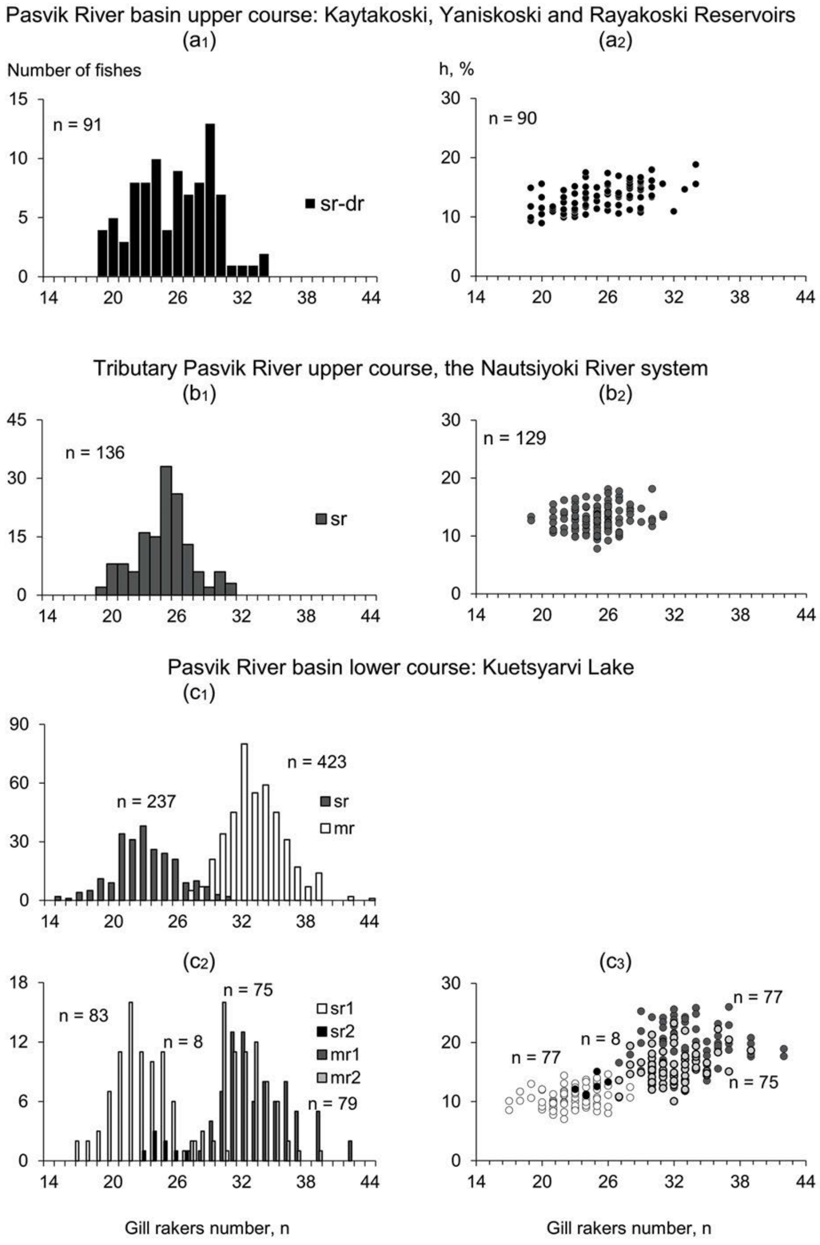

Fig. 2. Whitefish distribution by the number of gill rakers on the first branchial arch (a_1, b_1, c_1, c_2) and the ratio of the relative length of the central gill raker (h) % and the number of gill rakers on the first branchial arch (a_2, b_2, c_3) in the whitefish from the water bodies in the Pasvik River basin (Murmansk region), 2012–2020; here and in Figs. 3, 4, 5, 6 and 7: *sr* – sparsely rakered whitefish morph, *mr* – medium rakered whitefish morph, *sr-mr* – whitefish morph falling between the sparsely and medium rakered morphs, *sr1* – slow-growing sparsely rakered whitefish morph, *sr2* – fast-growing sparsely rakered whitefish morph, *mr1* – slow-growing medium rakered whitefish morph, *mr2* – fast-growing medium rakered whitefish morph.

Table 3.

The gill rakers number, n (*gr*, n) and the relative length of the central gill raker, % (*h*, %) on the first branchial arch; linear, weight and age values for whole sample (*FL*(ws), mm, *W*(ws), g and Age(ws), respectively) and for mature individuals (*FL*(mf), mm, *W*(mf), g and Age(mf), respectively) in whitefish morphs from the water bodies in the Pasvik, Tuloma, Niva and Umba River basins (Murmansk region)

Study area	Whitefish morph	*gr*, n	*h*, %	*FL*(ws), mm	*W*(ws), g	Age (ws)	*FL* (mf), mm	*W* (mf), g	Age (mf)
Pasvik River basin									
Pasvik River upper course: Kaytakoski, Yaniskoski and Rayakoski reservoirs	*sr-mr*	**25.7 ± 0.38** 19–34 (91)	**13.4 ± 0.24** 8.9–19.8 (90)	**342 ± 5.7** 127–485 (99)	**535 ± 24.0** 19–1470 (99)	**6+–9+** 1+–14+ (99)	**362 ± 4.9** 295–485 (54)	**632 ± 29.7** 351–1470 (54)	**6+–9+** 4+–14+ (54)
Tributary Pasvik River upper course, the Nautsiyoki River: Riuttikyaure, Virtuovoshyaur, Ilya-Nautsiyarvi, Ala – Nautsiyarvi Lakes	*sr*	**25.2 ± 0.20** 19–31 (136)	**13.1 ± 0.18** 7.8–18.2 (129)	**214 ± 5.4** 92–410 (137)	**140 ± 13.9** 7–976 (137)	**3+–4+** 0+–14+ (137)	**291 ± 13.0** 183–410 (22)	**329 ± 50.3** 57–976 (22)	**4+, 6+–9+** 3+–14+ (22)
Pasvik River lower course: Kuetsyarvi Lake	*sr*	**23.3 ± 0.20** 17–31 (237)	**10.9 ± 0.19** 7.0–15.1 (85)	–	–	–	–	–	–
	mr	**33.1 ± 0.12** 27–44 (423)	**17.9 ± 0.30** 10.0–26.0 (152)	–	–	–	–	–	–
	sr1	**22.7 ± 0.28** 17–31 (83)	**10.8 ± 0.20** 7.0–14.6 (77)	**168 ± 3.5** 62–238 (84)	**53 ± 3.4** 2–146 (84)	**2+, 5+– 6+** 0+–9+ (84)	**177 ± 3.4** 116–238 (62)	**60 ± 3.8** 14–146 (62)	**2+, 5+–6+** 2+–9+ (62)
	sr2	**24.8 ± 0.45** 23–27 (8)	**12.1 ± 0.53** 10.6–15.1 (8)	**243 ± 19.0** 166–326 (8)	**187 ± 45.6** 47–405 (8)	**–** 2+–6+ (8)	–	–	–
	mr1	**33.3 ± 0.35** 27–42 (79)	**20.0 ± 0.37** 12.3–26.0 (77)	**116 ± 1.7** 83–174 (82)	**15 ± 0.9** 4–49 (82)	**2+–4+** 1+–10+ (82)	**118 ± 1.5** 100–164 (57)	**15 ± 0.8** 7–45 (57)	**2+–4+** 2+–7+ (57)
	mr2	**31.9 ± 0.27** 27–39 (75)	**15.8 ± 0.31** 10.0–23.3 (75)	**205 ± 5.3** 100–325 (75)	**110 ± 10.9** 6–403 (75)	**2+–5+** 1+–9+ (75)	**242 ± 9.6** 160–325 (25)	**185 ± 23.6** 41–403 (25)	**4+–6+** 2+–9+ (25)

Study area	Whitefish morph	*gr*, n	*h*, %	*FL*(ws), mm	*W*(ws), g	Age (ws)	*FL* (mf), mm	*W* (mf), g	Age (mf)
Tuloma River basin									
Nizhnetulomskoye reservoir	*sr*	**20.8 ± 0.14** 17–28 (206)	**11.8 ± 0.16** 6.7–18.2 (151)	**219 ± 2.9** 104–333 (235)	**154 ± 6.6** 9–505 (235)	**3+–5+** 0+–8+ (217)	**232 ± 3.4** 170–333 (95)	**174 ± 9.6** 51–505 (95)	**4+–6+** 2+–8+ (95)
	mr	**39** (1)	**11.9** (1)	**158** (1)	**42** (1)	**2+** (1)	–	–	–
Niva River basin									
Imandra Lake: Bolshaya, Yokostrovskaya and Babinskaya Imandra Reaches	*sr*	**23.4 ± 0.09** 15–31 (750)	**10.1 ± 0.16** 5.2–15.6 (595)	**287 ± 1.8** 113–464 (772)	**318 ± 7.3** 29–1660 (772)	**3+–5+** 0+–9+ (772)	**324 ± 3.4** 228–464 (176)	**470 ± 19.7** 151–464 (176)	**4+–6+** 3+–9+ (176)
	mr	**38.5 ± 0.67** 32–43 (24)	**16.0 ± 0.60** 9.8–20.2 (24)	**301 ± 7.1** 250–382 (24)	**391 ± 31.4** 186–784 (24)	**3+–5+** 2+–7+ (24)	–	–	–
Umba River basin:									
Nizhneye Kapustnoye Lake	*sr*	**21.5 ± 0.39** 17–25 (28)	**11.2 ± 0.38** 9.4–15.9 (19)	**326 ± 4.2** 285–400 (28)	**439 ± 17.1** 295–772 (28)	**4+–6+(89** 4+–7+ (19)	**331 ± 5.5** 305–400 (18)	**468 ± 22.4** 363–772 (18)	**4+–6+** 4+–7+ (18)
Umbozero Lake, Sarvanovskiy Island area	*sr*	**26.3 ± 0.46** 23–29 (26)	**12.5 ± 0.46** 9.3–15.6 (26)	**349 ± 6.2** 292–450 (33)	**600 ± 43.5** 280–1115 (33)	**4+–6+** 4+–10+ (33)	**363 ± 7.0** 315–450 (22)	**694 ± 50.1** 408–1115 (22)	**4+–7+** 4+–10+ (22)

Note. Above the line – the average value and its error (in bold), below the line – the limits of variation of the indicator, in brackets – the number of fish, specimens; *sr* – sparsely rakered whitefish morph, *mr* – medium rakered whitefish morph, *sr-mr* – whitefish morph falling between the sparsely and medium rakered morphs, *sr1* – slowgrowing sparsely rakered whitefish morph, *sr2* – fastgrowing sparsely rakered whitefish morph, *mr1* – slowgrowing medium rakered whitefish morph, *mr2* – fastgrowing medium rakered whitefish morph.

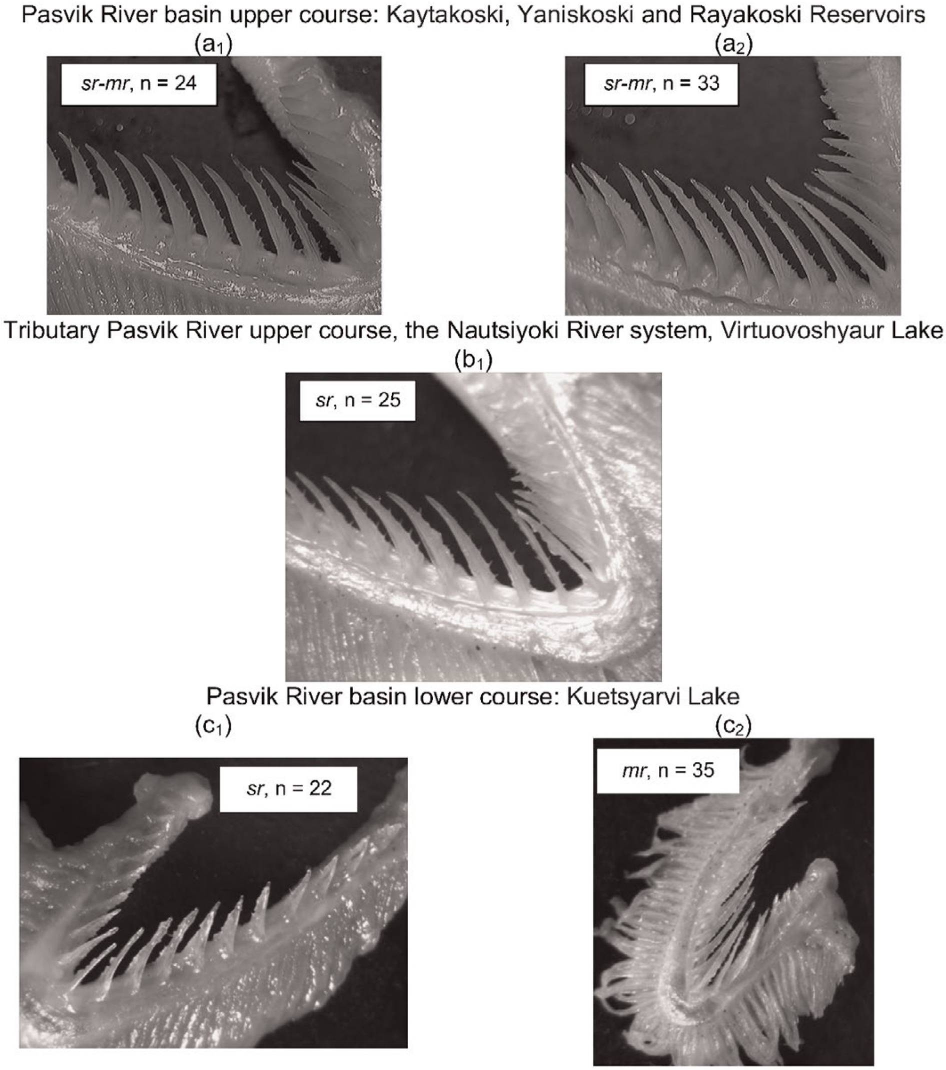

Fig. 3. Photographs of the first branchial arch of the whitefish morphs from the water bodies in the Pasvik River basins (Murmansk region) in 2012–2021.

to whitefish of the same age from the reservoirs of the Pasvik River (Fig. 4a–c). Whitefish began to mature at the age of 3+ years, and the majority were mature by the age of 4+ years and 6+ to 9+ years (68%) with significantly smaller values (p = 0.001) for the average length and mass (291 mm and 329 g, respectively) than in whitefish from the reservoirs of the Pasvik River (Table 3).

In Lake Kuetsyarvi, whitefish dominated in catches from 2012 to 2015, from 70 to 82%. In 2020, the share of whitefish in catches was only 35%, while the number of perch increased significantly and its share in catches began to reach

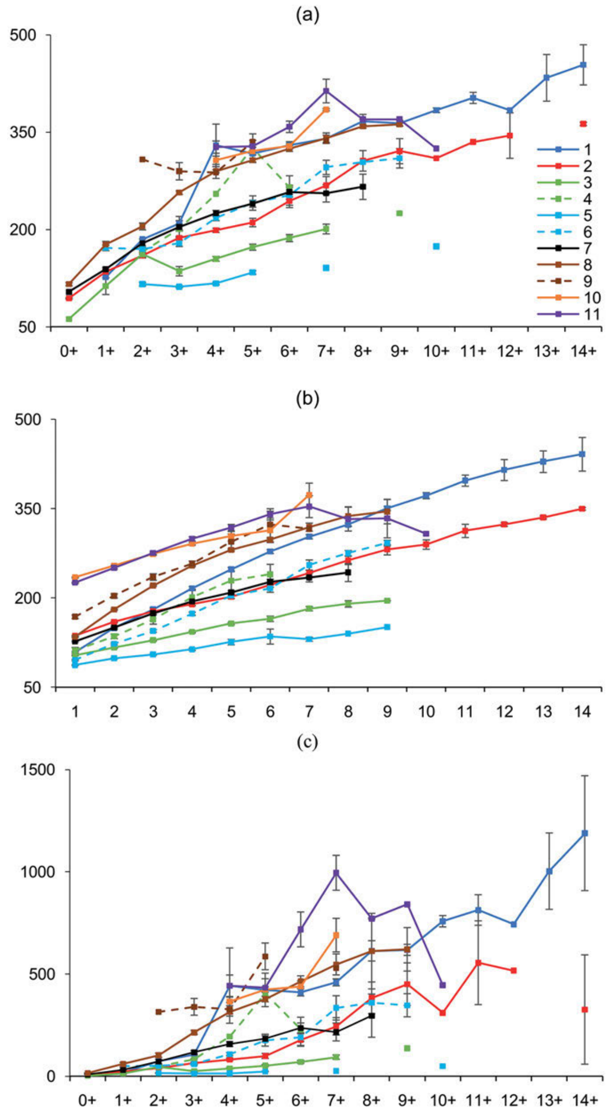

Fig. 4. Curves of observed linear (**a**), back-calculated linear (**b**) and weight (**c**) growth of the whitefish morphs from the water bodies in the Pasvik, Tuloma, Niva and Umba River basins, 2011–2021: 1 – *sr-mr* whitefish morph of Pasvik River basin upper course: Kaytakoski, Yaniskoski and Rayakoski reservoirs, 2 – *sr* whitefish morph of tributary Pasvik River upper course, the Nautsiyoki River system, 3 – *sr1* whitefish morph of Pasvik River basin lower course: Lake Kuetsyarvi, 4 – *sr2* whitefish morph of Pasvik River basin lower course: Lake Kuetsyarvi, 5 – *mr1* whitefish morph of Pasvik River basin lower course: Lake Kuetsyarvi, 6 – *mr2* whitefish morph of Pasvik River basin lower course: Lake Kuetsyarvi, 7 – *sr* whitefish morph of Tuloma River basin, Nizhnetulomskoye reservoir, 8 – *sr* whitefish morph of Niva River basin, Lake Imandra, 9 – *mr* whitefish morph of Niva River basin, Lake Imandra 10 – *sr* whitefish morph of Umba River basin, Lake Nizhnee Kapustnoe, 11 – *sr* whitefish morph of Umba River basin, Lake Umba. Abbreviations as in Fig. 2.

37%. In Lake Kuetsyarvi the whitefish distribution by the number of rakes on the first branchial arch is clearly bimodal (Fig. $2c_1$). Modes with an average value of 23.3 ± 0.20 (range from 17 to 31) and 33.1 ± 0.12 (range from 27 to 44) can be considered the *sr* and *mr* morphs, respectively (Table 3). The rakers in these morphs also differ in appearance. The *sr* whitefish had thickened and short rakers, *mr* whitefish had thin and elongated rakers (Fig. $3c_1$, c_2). The ratio of whitefish morphs in the samples averaged 2:1 with the *mr* morph dominating. Our study of the external structure of whitefishes in 2015 and 2020 made it possible to identify additional groups of whitefish, differing in the structure of the head. Among *sr* whitefish, individuals were found: 1) with large eyes, pronounced subterminal mouth, blunt snout (*sr1*) (Fig. 5a); 2) with smaller eyes, subterminal or terminal mouth, sharp snout (*sr2*) (Fig. 5b). Among *mr* whitefish, individuals were found: 1) with pronounced large eyes, superior mouth (*mr1*) (Fig. 5c); 2) with smaller eyes, subterminal or terminal mouth, sharp snout (*mr2*) (Fig. 5d). However, the *sr2* and *mr2* groups practically did not differ in terms of their morphology of parts of the head, and their identification was based only on the structure of the branchial apparatus. The percentages of the four whitefish groups were as follows: *sr1* 33.7% (84 individuals): *sr2* 3.3% (8 individuals): *mr1* 32.9% (82 individuals): *mr2* 30.1% (75 individuals). The majority of the *sr1* (74%) whitefish were caught in the profundal zone of the lake, *sr2* were equally represented both in the littoral and in the profundal zone (50% each); 61% of *mr1* was caught in the pelagic zone, 63% of *mr2* in the littoral zone of the lake. The structure of the branchial apparatus (gill rakers number on the first branchial arch, the relative lengths of the central gill rakers) in the four whitefish groups differed (p = 0.05) and decreased as follows: *mr1* > *mr2* > *sr2* > *sr1* (Table 3). The frequency distribution diagrams of four whitefish groups according to the number of gill rakers and the relative length of the central gill raker are shown in Fig. $2c_2$ and $2Ac_3$. The identified whitefish groups had different (p = 0.01) average linear-weight indicators: *sr1* > *mr2* > *sr1* > *mr1* (Table 3). Groups *sr1* and *sr2* were represented by individuals aged 0+ to 9+ and 2+ to 6+ years, respectively (Table 3). In the former, fish aged 2+ years and 5+ to 6+ years prevailed (69%), and in the latter, the predominant age is unknown because of the small number of fish. The observed length and mass of the *sr2* whitefishes were significantly higher (p = 0.001) at all ages compared to *sr1* (Fig. 4a, c). Additionally, *mr1* and *mr2* were represented by individuals aged from 1+ to 10+ and 1+ to 9+ years, respectively (Table 3). In the former, fishes aged 2+ to 4+ years prevailed in catches (91%), in the latter those aged 2+ to 5+ years (82%). Similarly, to *sr* whitefish, the size and weight indicators of the *mr2* whitefish were higher (p = 0.001) in all age groups compared to *mr1* (Fig. 4a, c). When studying the "individual" rates of linear growth in *sr* and *mr* whitefish, starting from the second or third year of life, slow-growing (*sr1* and *mr1*) and fast-growing (*sr2* and *mr2)* groupings were found (Fig. 4b). Compared to other intraspecific groups of the Kuetsyarvi whitefish, the slowest-growing

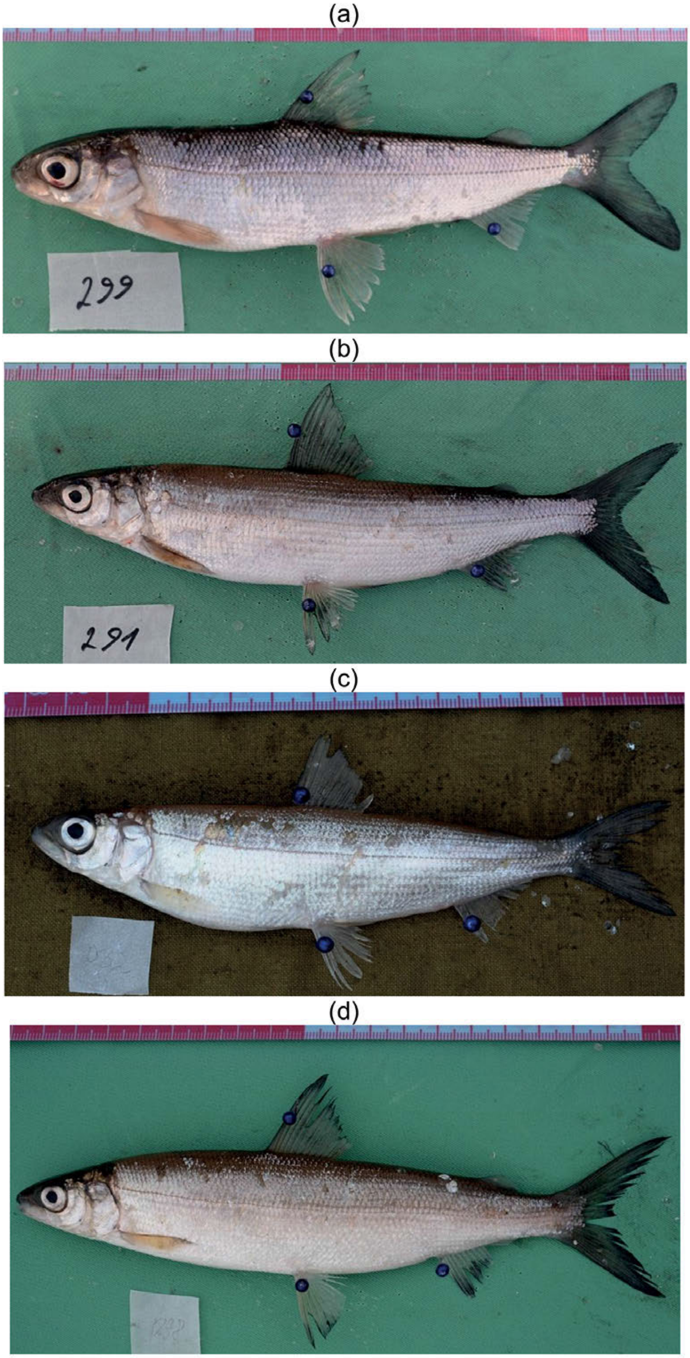

Fig. 5. The appearance of *sr1* whitefish morph, body length 184 mm, age 5+ (**a**); *sr2* whitefish morph, body length 166 mm, age 2+ (**b**); *mr1* whitefish morph, body length 143 mm, age 5+ (**c**); *mr2* whitefish morph, body length 179 mm, age 2+ (**d**) of Pasvik River basin lower course: Lake Kuetsyarvi in 2015.

mr1 whitefish begin to mature at the smallest size and weight, at a body length of 100–104 mm and a weight of 7–8 g at an age of 2+ years (Table 3), with an average length of 118 mm and a weight of 15 g at an age of 2+ to 4+ years. Fast-growing *mr2* individuals matured at large body sizes: at a length of 160–325 mm and a weight of 41–403 g at an age of 2+ to 3+ years and at an average length of 242 mm and a weight of 185 g at an age of 4+ to 6+ years (Table 3). Slow-growing *sr1* begin to mature at a length and weight of 116–135 mm and 14–22 g, respectively, at an age of 2+ to 3+ years, and at an average length of 177 mm and a weight of 60 g at an age of 2+ years and 5+ to 6+ years (Table 3). Among the fast-growing *sr2,* no sexually mature individuals were found.

Tuloma River basin. — In Nizhnetulomskoye Reservoir, the whitefish dominated in catches by 45%. European smelt was in second place in terms of number, and its share was 23%. In that reservoir, catches mainly contained *sr* whitefish with 17 to 28 rakers (20.8 ± 0.14) (Table 3, Figs. $6a_1$ and $7a_1$). Throughout the entire study period, only one individual was captured with 39 rakers, which can be classified as the *mr* morph (Table 3, Figs. $6a_1$ and $7a_1$). The relative length of the central gill raker in *sr* whitefish varied 6.7 to 18.2 (11.8 ± 0.16)%, while in *mr* whitefish it was 11.9% (Table 3, Fig. $6a_1$). The average values of body length and mass in *sr* whitefish – both in the sample as a whole and at different ages – are close to those observed in the *sr* whitefish from the Nautsiyoki River system (Pasvik River basin) (Table 3, Fig. 4a–c). The *sr* whitefish is represented by individuals aged 0+ to 8+ years, with the 3+ to 5+ years group dominating (67%). Sexually mature individuals aged 2+ to 8+ years were observed, with the majority maturing at the age of 4+ to 6+ (77%). The average length and weight of sexually mature fish were 232 mm and 174 g, respectively (Table 3).

Niva River basin. — One of the important aspects of the functioning of the modern ecosystem of Lake Imandra is a significant increase in the role of the European smelt in the structure of the fish community. At present, its share in the lake catches can vary from 30 to 36%. At the same time, a relatively high share of whitefish (up to 30%) remains only in the water area of the Babinskaya Imandra reach. The whitefish in catches from Lake Imandra are represented by both morphs, *i.e.*, *sr* and *mr*. The number of rakers varied from 15 to 43 (Table 3, Fig. $6b_1$, $7b_1$-b_2). The *sr* whitefish is common throughout the lake, while *mr* whitefish is rare, and its distribution across the lake is extremely uneven. Most of the *mr* whitefish catch came from the Bolshaya Imandra reach (17 individuals). Six and one individuals, respectively, were caught in the Yokostrovskaya and Babinskaya Imandra reaches during the entire study period. The number of rakers in the *sr* whitefish from Lake Imandra varied from 15 to 31 (23.4 ± 0.09) (Table 3, Fig. $6b_1$). The average value of the relative length of the central raker in *sr* whitefish was 10.1 ± 0.16. The minimum and maximum values of this indicator were 5.2 and 15.6%, respectively (Table 3, Fig. $6b_2$).

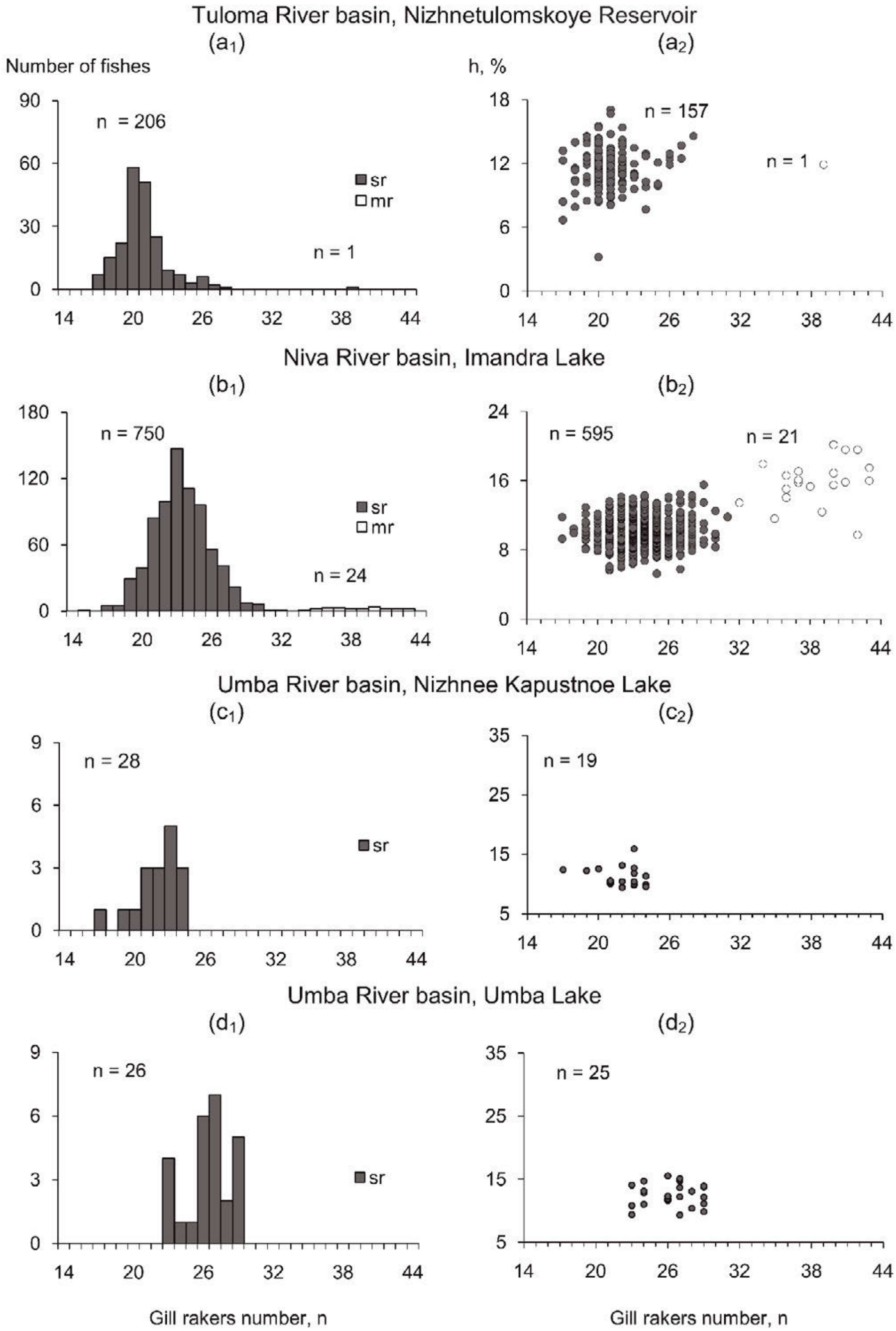

Fig. 6. Whitefish distribution by the number of gill rakers on the first branchial arch (a_1, b_1, c_1, d_1) and the ratio of the relative length of the central gill raker (h) % and the number of gill rakers on the first branchial arch (a_2, b_2, c_2, d_2) in the whitefish from the water bodies in the Tuloma, Niva and Umba Rivers basins (Murmansk region) in 2011–2021.

The number of rakers in the *mr* whitefish in Imandra reaches varied from 32 to 43 (38.5 ± 0.67) (Table 3, Fig. 6b_1). The relative length of the central gill raker in the *mr* whitefish varied 9.8–20.2%, averaged 16.0 ± 0.60 (Table 3, Fig. 6b_2). The structural values of the first branchial arch in the *mr* whitefish significantly differed from the values found in the *sr* whitefish from the studied reaches of Lake Imandra (p = 0.001), and *sr* whitefish had fewer rakers on the first branchial arch and the relative length of the central gill raker was lower (Table 3). The

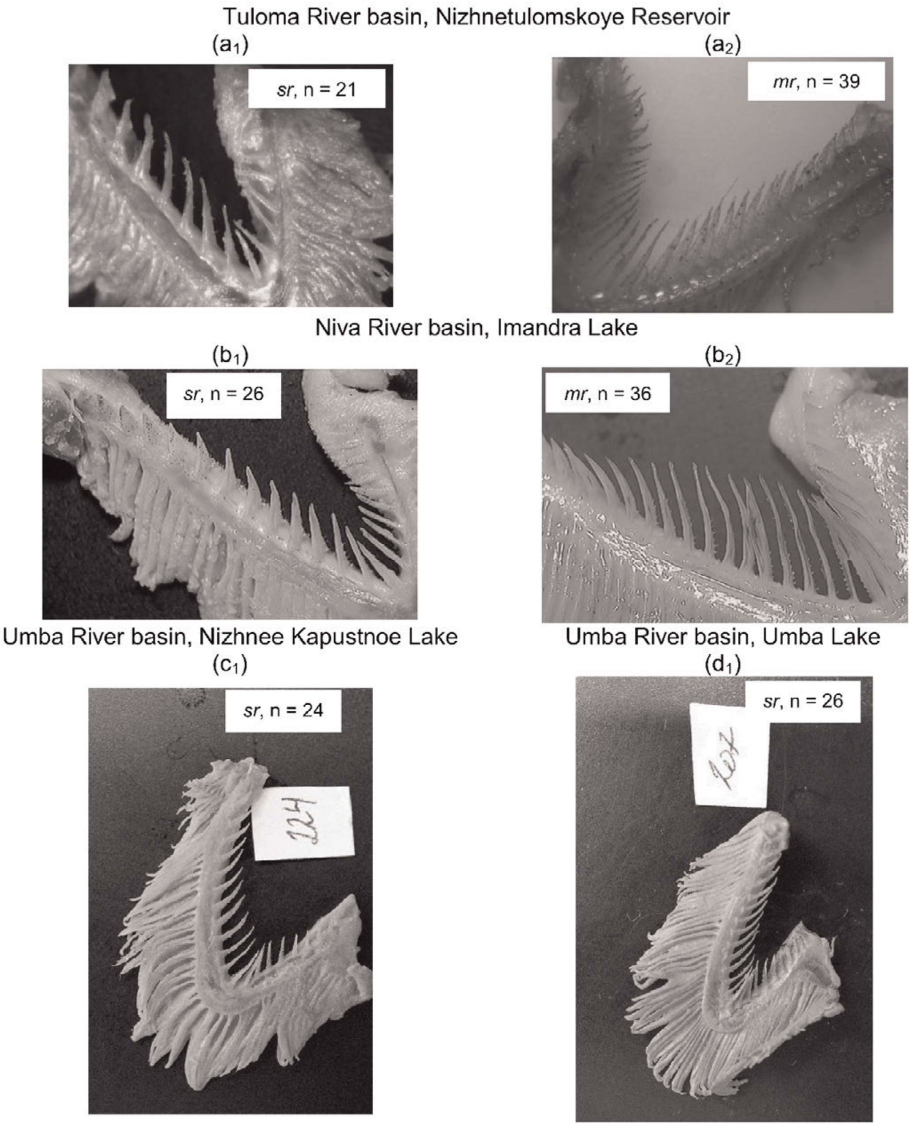

Fig. 7. Photographs of the first branchial arch of the whitefish morphs from the water bodies in the Tuloma, Niva and Umba River basins (Murmansk region) in 2011–2020.

average body length and weight values in both morphs are presented in Table 3. The *sr* whitefish in Lake Imandra were represented by 10 age groups: 0+ to 9+ years (individuals aged 3+ to 5+ years dominated at 77%), and *mr* whitefish were represented by 6 age groups: 2+ to 7+ years (3+ to 5+ years dominated at 92%). The observed and back-calculated average body length and weight values of the *mr* whitefish at different ages are closest to those of the *sr* whitefish (Fig. 4a–c). Sexually mature *sr* whitefish individuals in Lake Imandra were aged 3+ to 9+ years with a modal value of 4+ to 6+ years (88%). The *sr* whitefish begin to mature, reaching a length of 228 mm and a weight of 151 g, average values of length and mass of sexually mature fish were 324 mm and 470 g, respectively (Table 3). In the collected samples of *mr* whitefish from Lake Imandra, no mature individuals were found.

Umba River basin. — In our catches from Lake Nizhneye Kapustnoyein the Umba River basin, the whitefish was represented by the *sr* morph with 21.5 ± 0.39 rakers on average (the value varied 17 to 25) (Table 3, Figs. $6c_1$ and $7c_1$). In the area around Sarvanovskiy Island in Lake Umbozero, a *sr* whitefish was captured with a higher (p = 0.001) number of rakers on the branchial arch: 26.3 ± 0.46 (23–29) (Table 3; Figs. $6d_1$ and $7d_1$). The whitefish distribution by the number of rakers in Lake Umbozero also shows heterogeneity (Fig. $6d_1$), which potentially indicates the coexistence of several whitefish morphs in this area. The average relative length of the central raker in the whitefish from Lake Umbozero was 12.5 ± 0.46 (9.3–15.6)% and was higher (p = 0.01) compared to Lake Nizhneye Kapustnoye – 11.2 ± 0.38 (9.4–15.9)% (Table 3, Fig. $6c_2$, d_2). The *sr* whitefish from Lakes Umbozero and Nizhneye Kapustnoye were represented by individuals aged 4+ to 10+ years, individuals aged 4+ to 6+ years dominated at 77–89% (Table 3). In terms of the observed-back-calculated linear and weight growth, they were close to large whitefish individuals from water bodies in the upper reaches of the Pasvik River and Lake Imandra (Table 3, Fig. 4a–c). Sexually mature individuals were 4+ to 10+ years old. The average length and weight of sexually mature fish in Lake NizhneeKapustnoe was 331 mm and 468 g, respectively, in Lake Umbozero it was 363 mm and 694 g (Table 3).

Discussion

Features and patterns of distribution of ecological whitefish morphs. — Our investigation ofdiversity and distribution of whitefish morphs in different watercourses and lakes sizes in four major river basins in Russia's Murmansk Region (the Pasvik, Tuloma, Niva, and Umba rivers) revealed the presence of two whitefish morphs: *sr* whitefish and *mr* whitefish. The *sr* whitefish morph is the most common and can be found in water bodies on its own, while the *mr* morph is less common and is observed only alongside the *sr* morph. This pattern is generally characteristic of the lakes of Northern Fennoscandia and served as the basis for a hypothesis that the larger *sr* whitefish (or *LSR* whitefish) served as the original ancestral morph for the other whitefish morphs (Ostbye *et al.* 2005; Harrod *et al.* 2010; Siwertsson *et al.* 2010; Præbel *et al.* 2013). Moreover, according to our data, cohabitation *sr* and *mr* morphs of whitefish were found in large and medium-sized lakes with relatively significant depths (presence of pelagic biotopes) and a high content of nutrients (Imandra Lake, Niva River basin and Kuetsyarvi Lake, Pasvik River basin). Lake Kuetsyarvi is a natural open body of water, while Lake Imandra has been an artificial body of water since 1976. At the same time, a large number of rivers and streams flow into Lake Imandra. The hydrographic network of Lake Imandra is represented by 1379 watercourses and 2495 lakes (Moiseenko *et al.* 2002). The low abundance of the *mr* whitefish morph in Lake Imandra (3% of whitefish catches) most likely indicate that, at the present time, *mr* whitefish in the lake is represented by migrants from the connected lacustrine systems of the basin. In particular, in the Yokostrovskaya Imandra basin (Chinglsyavr, Kenzisyavr and Okhtozero lakes) Reshetnikov (1980) observed *mr* whitefish with 31 to 41 rakers (on average 32.7–39.6). In 2020, we observed two *mr* whitefish individuals in Lake Zayachye (basin of the Bolshaya Imandra reach) with 29 and 31 rakers. The combination of such factors in the northern reach of Lake Imandra (in Bolshaya Imandra), as the presence of a pronounced pelagic zone, a high nutrient level, and the highest biomass of zooplankton for the reservoir (Zubova *et al.* 2018), which plays an important role in the nutrition of the *mr* whitefish (Reshetnikov 1980; Kahilainen *et al.* 2004, 2006, 2014; Siwertsson *et al.* 2010) also creates the most favorable conditions for the habitat of the *mr* whitefish and determines its confinement to this area.

In Lake Kuetsyarvi, lower reaches of the Pasvik River, *sr* and *mr* whitefish formed additional ecological morphs: *sr1*, *sr2*, *dr1*, *dr2*. The four identified whitefish groups differ in the set of plastic and meristic features, size and weight indicators and, accordingly, in the rate of linear growth, *e.i.*: *sr1* – slow-growing sparsely rakered whitefish with large eyes, pronounced subterminal mouth, blunt snout and *sr2* – fast-growing sparsely rakered whitefish with smaller eyes, subterminal or terminal mouth, sharp snout; *mr1* – slow-growing medium rakered whitefish with pronounced large eyes, superior mouth, and *mr2* – fast-growing medium rakered whitefish with small eyes, subterminal or terminal mouth. *Sr1* predominantly inhabits the profundal zone of the lake, *mr1* the pelagic zone. The externally similar *sr2* and *mr2* inhabit in the littoral zone of the lake. Our findings on the whitefish from Lake Kuetsyarvi are close to the earlier ones on the whitefish from lakes in the upper and middle reaches of the Pasvik River (Bjørnvatn, Inari, Skrukkebukta, Vaggarem, Muddusjärvi, Paadar, Langfjord-vatn): slow-growing sparsely rakered whitefish (*sr1*) of Lake Kuetsyarvi corresponds to small sparsely rakered (*SSR*) whitefish, fast-growing sparsely rakered whitefish (*sr2*) *to* large sparsely rakered (*LSR*); slow-growing medium rakered whitefish (*mr1*) to *DR* (densely rakered), fast-growing medium rakered whitefish (*mr2*) to *LDR* (large densely rakered) (Østbye *et al.* 2005; Kahilainen and Østbye 2006; Kahilainen *et al.* 2004, 2006, 2007, 2009, 2014, 2017; Siwertsson *et al.* 2008, 2010; Harrod *et al.* 2010; Præbel *et al.* 2013; Thomas *et al.* 2019). Moreover, the average number of rakers on the first branchial arch in *sr1* (*SSR*) increases from the upper reaches of the Pasvik to the lower reaches: from 17 (Lake Muddusjärvi) to 23 rakers (Lake Kuetsjyarvi). In other whitefish groups from different parts of the system, the number of rakers on the first branchial arch varies insignificantly: in *sr2* (*LSR*) it averages from 23 to 25, in *mr1* (*DR*) from 33 to 36, in *mr2* (*LDR*) from 32 to 34. This leads to the fact that the four identified whitefish groups from Lake Kuetsyarvi are the closest in the number of rakers on the first branchial arch than those from other stretches of the Pasvik River. Thus, the described four whitefish groups are found in all the major lakes of the Pasvik River basin from the upper to the lower reaches.

The exterior features of the identified four intraspecific whitefish groups in the lakes of the Pasvik River system play a functional role in the feeding and movement of the fish confined to certain zones of the lake (Kahilainen and Østbye 2006; Zubova *et al.* 2019). For instance, the largest eye diameter and the "large" superior mouth in *mr1 (DR)* are typical features of planktophages living in the water column, while the smallest body depth in *mr1* (*DR*) is energetically beneficial when searching for and feeding on zooplankton organisms in the pelagic zone. At the same time, the relatively large eye diameter in *sr1 (SSR)*, possibly facilitates the search for food in low light deep in the lake, and the inferior position of the mouth is effective when feeding on profundal macrozoobenthos. The subterminal or terminal mouth in the large whitefish from Lake Kuetsyarvi *sr2 (LSR) and mr2 (LDR)* is probably the most versatile and these whitefish groups can feed on different types of food or be better adapted to feeding on littoral benthos, as shown earlier by Zubova *et al.* (2019) and observed in large whitefish from other lakes of the Pasvik River system (Kahilainen and Østbye 2006). The intraspecific whitefish groups in Lake Kuetsyarvi can be characterized as a single whitefish population, including dissimilar individuals, where crossing between the two is highly probable, or a group of reproductively isolated populations, of which at least one is polymorphic (with the similarity of individual morphs in different populations) (Mina 1986). The likelihood of different scenarios of divergence origins in the whitefish in Lake Kuetsyarvi can be tested using various methods of genetics (*e.g.*, hybridological, ontogenetic, population) (*Griffiths et al.* 2000).

Despite the presence of pelagic biotopes in Lake Umbozero (Umba River basin), *mr* whitefish is not found here. For Lake Umbozero, a more detailed study of the hydrochemical characteristics and ichthyofauna is required.

In a small isolated run of the river reservoirs with relatively shallow depths, such as the Yaniskoski, Kaitakoski, and Rayakoski reservoirs in the upper reaches of the Pasvik River and the Nizhnetulomskoye Reservoir in the basin of the Tuloma, changes have apparently occurred or are going on in the intraspecific composition of whitefish toward its simplification, possibly as a result of a disturbance of the spawning grounds of the various whitefish morphs (damming, silting) or of a decrease in the diversity of ecological niches within the respective water bodies. The reason for the change in the intraspecific composition of the whitefish is the introduction of other fish species, for example, vendace in the Pasvik River system. That, in the early 1990s, before the invasion by vendace in the reservoirs of belonging to the Pasvik River basin, all water bodies were characterized by a clear division of whitefishes into two morphs – *sr* and *mr* (Lukin and Kashulin 1991; Amundsen *et al.* 1993, 1997, 1999; Bøhn and Amundsen 1998; Kashulin *et al.* 1999; Siwertsson *et al.* 2008). In addition to morphological features, they differed in size, growth rates, preferred habitats, and type of diet. The *sr* whitefish is a benthophage inhabiting mainly the littoral and profundal zones, while the *mr* whitefish is a plankton-feeder inhabiting the pelagic zone. Research in the Rayakoski reservoir in 2002 and 2004 showed a wider range in the distribution of whitefish rakers (16–44), which narrowed in 2012–2013 (20–34) (author’s unpublished data). It was shown previously that the introduction of vendace and its colonization of the upper reaches of the Pasvik River in the 1990s led to its domination in the pelagic zone and the displacement of the *mr* whitefish into the littoral and profundal zones with an overlap within the niches occupied by the *sr* whitefish (Kashulin *et al.* 1999; Reshetnikov *et al.* 2020; Amundsen *et al.* 1999). The absence of spatial segregation could have contributed to the hybridization of the *mr* and *sr* whitefish morphs and the convergence of traits (Bhat *et al.* 2014). However, the lack of evidence of reproductive isolation of the two whitefish morphs allows us to put forward a different hypothesis. The vendace in the upper reaches of the Pasvik River appears to be more competitive than the *mr* whitefish in the pelagic zone in the competition for resources (zooplankton). As a result, the population of *mr* whitefish decreases and it can face local extinction. Since there is insignificant competition between *sr* and *mr* whitefish morphs for the food resources they consume (Reshetnikov 1980), the niche occupied by *sr* whitefish expands and, accordingly, the population responds with morphological changes, which leads to the increase in the number of rakers to 34. This process can also be promoted by a decrease in the number of vendaces in catches from the upper reaches of the Pasvik River (author's unpublished data), in the Rayakoski reservoir, from 23% (2002) to 1% (2012-2013). In 2020, vendace was absent in catches from the Kaytakoski and Yaniskoski reservoirs. A decrease in the number of vendaces in catches is possibly associated with an increase in the number of perch in the water bodies of the Pasvik River, which began to feed on vendace. For instance, in the lower reaches of the Pasvik (Lake Kuetsyarvi), in the stomachs of perch with a body length of 128 mm or more, fish was found: perch, nine-spined stickleback, and vendace (author’s unpublished data from the 2020 catches).

According to our data, in small and shallow oligotrophic lakes, such as Riuttikyaure, Virtuovoshyaur, Ilya-Nautsiyarvi and Ala-Nautsiyarvithere is only *sr* whitefish morph. The gill structure of the *sr* whitefish the shallow lakes of the

Nautsiyoki River system, where there are no conditions for the segregation of sympatric morphs, is similar to the modern gill structure found in the whitefish from the above-described reservoirs Kaytakoski, Yaniskoski and Rayakoski. This suggests that they may represent the original morph. Neither is *mr* whitefish morph found in the shallow lake-reach stretches of the Umba River.

Structural features of the first branchial arch of ecological whitefish morphs. — In general, in the water bodies of the Murmansk region studied by us, in *sr* whitefish the number of gill rakers ranges between 15 and 31, in *mr* whitefish between 27 and 44. The *sr* whitefish, in the main, have rare short, thickened at the base of the rakers, while *mr* – elongated and thin rakers. Both morphs have thin outgrowths on the rakers – secondary gill rakers, but in the *mr* there are more of them. Among whitefishes with 27 to 31 gill rakers, both *sr* and *mr* morphs were observed, distinguishable by the shape of the rakers or by the structure of the head of fish in Lake Kuetsyarvi (the Pasvik River basin). In the *sr* whitefish, the relative length of the central gill raker ranges between 5.2 and 18.2%, in *mr* whitefish – between 9.8 and 26.0%. The *sr* whitefish with the largest average number of rakers on the first branchial arch inhabit the upper reaches of the Pasvik River and Lake Umbozero (the Umba River basin): 25 to 26 rakers. The lowest value of this indicator was found in the *sr* whitefish from the Nizhnetulomskoye reservoir (the Tuloma River basin) – 21 rakers. The average number of rakers on the first branchial arch in the *mr* whitefish from Lake Imandra (the Niva River basin) was higher than in the *mr* whitefish from Lake Kuetsyarvi: 39 *vs*. 32–33. Also, among the studied *sr* and *mr* whitefish morphs, relatively long- and short-rakered whitefish can be distinguished. For instance, the upper reaches of the Pasvik River and Lake Umba are inhabited by long-rakers, *sr* whitefish with an average length of the central branchial raker of 13%, Lake Imandra by short-rakers, *sr* whitefish with a relative length of the central raker of 10%. The central raker in the *mr* whitefish from Lake Kuetsyarvi (18%) is slightly longer than in Lake Imandra (16%).

Features of growth and maturation of ecological whitefish morphs. — Our studies demonstrated that the studied whitefish morphs in the water bodies of four river basins in Murmansk Region show differences not only in the structure of the gill apparatus and in the growth and maturation of fish individuals. The greatest diversity in the described biological indicators of fish can be observed in the water bodies of the Pasvik River system. Here one can distinguish relatively both fast-growing (or large) *sr* and *mr* whitefish, and slow-growing (small) whitefish belonging to these morphs. In the other river basins (Tuloma, Niva, Umba), only large *sr* and *mr* whitefish was observed. At the same time, the large whitefish from reservoirs in the upper reaches of the Pasvik River are the closest in terms of growth to the large whitefish from the Niva and Umba River basins, while the large *sr* and *mr* whitefish from the Tuloma River basin (Nizhnetulomskoye reservoir), the Nautsijoki River system (the upper reaches of the Pasvik River) and Lake Kuetsyarvi (the lower reaches of the Pasvik River) form an intermediate group in terms of growth between the large whitefish from the described water bodies and the small whitefish from Lake Kuetsyarvi. In general, the growth rate of the *mr* whitefish in Lake Imandra (the Niva River basin) did not differ significantly from the growth rate of the *sr* whitefish, while both large and small *mr* whitefish in Lake Kuetsyarvi grew more slowly than the large and small *sr* one. According Zubova *et al*. (2016a, 2018), the linear-growth rate in whitefish in the water bodies of the Murmansk region (especially in the first years of life) is closely related to the quantitative indicators of zooplankton and benthic organisms. Large *sr* whitefish begin to mature at the age of 2+ to 4+ years. The modal maturing age is 4+ to 7+ years or 6+ to 9+ years at a body length of 160–315 mm and a mass of 57–408 g. The sexual maturity age in *sr* and *mr* whitefish was 2+ years, while the modal value was 2+-6+ years. The former began to mature at a body length and weight of only 116 mm and 14 g, respectively, and the latter began to mature at a body length and weight of 100 mm and 7 g, respectively. The size at maturity of four whitefish morphs in Lake Kuetsyarvi correspond to the maturity size of similar morphs in other lakes of the Pasvik River system (Kahilainen *et al.* 2004).

The observed diversity and distribution of whitefish in the studied water bodies of the Murmansk region requires further study of its biological characteristics. There is almost no data on the morphological characteristics of the whitefish body and its nutrition. An assessment of the divergence origins of whitefish in the Murmansk region cannot be performed without modern genetic methods.

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