ISSN 0032-9452, Journal of Ichthyology, 2017, Vol. 57, No. 4, pp. 569–579. © Pleiades Publishing, Ltd., 2017.
Original Russian Text © O.Yu. Busarova, E.V. Esin, T.E. Butorina, A.V. Esipov, G.N. Markevich, 2017, published in Voprosy Ikhtiologii, 2017, Vol. 57, No. 4, pp. 424–434.

Ecological Differentiation of Resident Dolly Varden *Salvelinus malma* (Salmonidae) from Lake Dal'nee, Kamchatka

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Received April 28, 2016

Abstract—Resident Dolly Varden *Salvelinus malma* of Lake Dal'nee (Paratunka River basin) is represented by two stable trophic groups: one group feeds on mainly amphipods while another on gastropods. The former group is dominantly infected by *Cyathocephalus truncatus* and *Crepidostomum metoecus*, whereas the latter group is infected with *Crepidostomum farionis*, *Ichthyocotylurus erraticus*, and *Diplostomum* spp. The fishes of the former group grow faster and defined by higher fat content of muscular tissue. In addition, they accumulate monoenic fatty acids in the muscles. The fishes of the latter group differ in a high content of omega-3 and omega-6 fatty acids in the muscles. The amphipod foragers are characterized by a larger head with elongated upper jaw and comparatively short fins. A similar ecological differentiation is observed in the littoral benthivorous charrs from Lake Kronotskoe. The group feeding on amphipods was found in both lakes. In Lake Kronotskoe, the second group consumes the most abundant sedentary benthos, mollusks and chironomids.

Keywords: Dolly Varden *Salvelinus malma*, trophic groups, benthivorous fishes, parasites-indicators, fatty acids, growth rate, Lake Dal'nee, Kamchatka

DOI: 10.1134/S0032945217040026

INTRODUCTION

The charrs of the genus *Salvelinus* distributed in numerous lakes of the Holarctic exhibits a specialization in the types of feeding that often leads to the sympatric morphs originating with different biology (Behnke, 1980; Savvaitova, 1989; Hindar and Jonsson, 1993; Klemetsen, 2013). The main direction of the divergence is the speciation along pelagic-benthic resource axis . It results in diversification of planktivorous fishes and predators feed in the water column, and benthivorous fishes feed near the bottom (Jonsson and Jonsson, 2001; Adams et al., 2003; Wilson et al., 2004; Klemetsen, 2013). Another direction of the divergence is an originating of several benthivorous forms foraging in different depths. Both mechanisms of the divergence represent a present mosaic of intralacustrine variability of the charrs along the depth gradient. In particular, they are observed in the water bodies of Scandinavia, Iceland, Transbaikalia, and Kamchatka (Skulason et al., 1989; Klemetsen et al., 1997; Gordeeva et al., 2015; Praebel et al., 2015; Saltykova et al., 2015).

In Fjellfrøsvatn lakes (Norway) and Kronotskoe Lake (Kamchatka), the coastal benthivorous morph of charrs is additionally separated into two stable groups: one group feeds on amphipods (Amphipoda) and another group feeds on sedentary benthos (chironomid larvae (Chironomidae) and mollusks) that leads to different growth rates and condition factors (Busarova et al., 2015, 2016b, 2017; Knudsen et al., 2010). The published data on a similar differentiation in other lakes inhabited by charrs are absent, and, therefore, the mechanisms of diversification, reproductive relationships of the groups, and frequency of occurrence of such differentiation remain unclear.

The mechanisms of ecological differentiation of landlocked littoral charrs can be clarified based on the analysis of a polymorphism of a single taxonomic group (species) in the ecosystems of different types. In particular, northern Dolly Varden *S. malma* of Kamchatka is distributed in numerous lakes with different features in both the presence and absence of other fish species. In the case of a specialization occurrence in the littoral benthivorous Dolly Varden in the ecosystems of different types, an existence of a distinct universal (and poorly described) diversification pathway in lacustrine charrs can be approved. This study is devoted to the ecological differentiation of landlocked Dolly Varden from Lake Dal'nee (Paratunka River basin).

The aim of the study is to describe two stable littoral groups of resident Dolly Varden with different feeding strategies.

MATERIALS AND METHODS

Lake Dal'nee with the area of 1.4 km^2 is located on the right bank of the Paratunka River, and a meandering tributary connects the lake and the river. Thespawning tributaries are lucking in the lake basin, its transversal profile is trough-shaped, the southern and northern banks are steeply cut up to the flattened bottom, the littoral zone is developed in the western and eastern parts of the water body only. The maximum depth is 60 m, and the average depth is 31.5 m (Krogius et al., 1987; Kurenkov, 2005). The fish community of Lake Dal'nee includes anadromous sockeye salmon *Oncorhynchus nerka* and coho salmon *O. kisutch* as well as resident sticklebacks *Gasterosteus aculeatus* and *Pungitius pungitius*, anadromous northern Dolly Varden *S. malma*, and reproductively isolated resident Dolly Varden (Konovalov, 1971; Krogius et al., 1987). Until present, the endemic predator phylogenetically similar to *S. taranetzi* from Chukotka inhabited the lake (Chereshnev et al., 2002; Oleinik and Skurikhina, 2007). This species had been presumably exterminated because of anthropogenic pressure (Esin et al., 2015).

Anadromous Dolly Varden spawns in the main riverbed of the Paratunka River, in numerous tributaries of the river, and, most likely, in the channel flowing from the lake. The juveniles and maturing individuals of anadromous Dolly Varden migrate to forage into the lake, but the lacustrine spawning of this form is not observed. However, a distinct resident group of the fish spawns in the lake.

The fishes were collected (in August 2014) with gill nets, mesh size 20–40 mm, in various parts of the lake at a depth between 5 and 50 m and in the main riverbed of the Paratunka River 1 km from the mouth of the channel flowing from the lake. The composition of the catches conducted during the day and night and at different depths (littoral, slope, and profundal zones) was registered. In total, 100 and 25 individuals of Dolly Varden were collected in the lake and river, respectively. In 60 fishes from the lake and in all exemplars from the river, the following parameters were determined: fork length (*FL*), body weight, sex, and qualitative stomach content composition (presence or absence of amphipods and mollusks). In addition, the absence or presence of the parasites-indicators (*Cyatocephalus truncatus* and *Crepidostomum* spp.) was assessed. Remaining 40 exemplars of the fish from the lake were photographed according to the requirements recommended for morphometric analysis of images (Rohlf, 2000; Mandritsa, 2007). Then the fishes were frozen, and their subsequent investigation was conducted in the laboratory.

In the frozen fishes, in addition to the measurements of body length and weight, maturity stages of the gonads and age (based on otoliths) were determined. In 20 exemplars from the lake and 15 exemplars from the river, the otoliths were grinded to primordiums, and the width of interannual increments was determined. The measurements were conducted with a TPS package (Rohlf, 2010) on the images obtained with a Leica DMLS light microscope and Leica DC100 digital camera. For the standardization of the measurements, they were made along the line directed at an angle of 60° to the longitudinal axis of each otolith. The edge of the opaque zone was interpreted as the annual ring.

The quantitative analysis of the stomach content included a calculation of the average number of food items of each group consumed by a fish in the sample (n) and the frequency of occurrence of food items (FO, %), the ratio between the number of fishes with a certain food items and the number of feeding fishes of a certain group. The following food was registered: amphipods *Gammarus lacustris*, snails *Valvata* (*Cincinna*) sp. and *Lymnaea* sp., larvae and pupae of chironomids, mayfly (Ephemeroptera) and caddis fly (Trichoptera) larvae, and imago of insects. A degree of overlapping of foraging niches was assessed with C_λ index (Horn, 1966).

A parasitological analysis of 40 lacustrine fishes was conducted by the method of total parasitological dissection (Bykhovskaya-Pavlovskaya, 1985) with identification of the parasites to the species (*Opredelitel' parazitov* ..., 1984, 1987). The following invasion parameters of each parasitic species were used: invasion extensiveness (IE, %) (proportion of invaded fishes in the sample), confidence interval of the occurrence (d) at $p = 0.05$ (Roitman and Lobanov, 1985), and index of parasite abundance (IA, no.) (number of parasites of a fish in the sample). The average conditional biomass of helminthes was calculated according to the recommendations of Dorovskikh and Stepanova (2009).

The body proportions of 40 fishes from the lake were assessed based on 15 linear measurements of the head, trunk, and fins according to a scheme of Pravdin (1966). The groups used for the comparison had a narrow range of body length (20–31 cm *FL*). Therefore, the indices (in % *FL*) were applied, and allometric component of variation was not considered. The sexual morphometric differences were not revealed. Therefore, the analysis was conducted on the joint samples including the representatives of both sexes.

In 20 fishes from the lake, lipids were extracted based on the method of Bligh and Dayer (1959). The analysis of fatty acids (FA) was conducted with the method of gas-liquid chromatography after their methylation (Carreau and Dubacq, 1978). A Shimadzu GC-2010 chromatograph with flame ionization detector (Supelcowax 10 capillary GC column 30 m in length with internal diameter 0.25 mm, phase width 0.25 μm, and at injector temperature 250°C). A preliminary purification of methyl ethers of fatty acids was conducted with the method of thin-layer chromatography in benzol-hexane mixture (5 : 3 by volume) (Kates, 1972). Fatty acids were identified based on

Table 1. Food composition of two trophic groups of Dolly Varden *Salvelinus malma* from Lake Dal'nee in August

Feeding organisms	Group A ($n = 23$)		Group G ($n = 17$)		Mann–Whitney test	
	FO, %	no. of items	FO, %	no. of items	*U*	*p*
Gammarus lacustris	0	0	100	36.00 (130)	57.5	<0.001
Valvata (Cincinna) sp.	66.67	16.87 (228)	36.36	0.56 (4)	121.0	0.040
Lymnaea sp.	22.22	0.87 (15)	0	0	152.0	0.079
Chironomidae:						
– pupae	5.56	0.17 (4)	0	0	176.0	0.401
– larvae	11.11	0.09 (1)	0	0	168.0	0.233
Ephemeroptera (larvae)	5.56	0.57 (13)	0	0	176.0	0.400
Trichoptera (larvae)	5.56	0.78 (17)	9.09	0.13 (2)	179.5	0.779
Insecta (imago)	11.11	0.09 (1)	0	0	168.0	0.231

Trophic groups (here and in Tables 2–6): A, feeding on benthos excluding amphipods; G, feeding on mainly amphipods; FO, frequency of occurrence of a food item; no. of items, mean value and (in the parentheses) maximum value.

comparative time of retention and the values of equivalent chain length (Ackman, 1969; Stransky et al., 1997).

For the classification of fishes by the foraging type, a stepwise discriminant analysis was performed. The differences between the groups based on morphometric measurements were assessed with Student's *t*-test. The frequency distributions of the values of other parameters of the groups were statistically different from normal distributions (χ^2 tests, $p \le 0.05$). Therefore, nonparametric statistics in Statsoft Statistica 13.0 program were used to determine significant differences between the groups in the size-age composition, foraging parameters, parasitic fauna, and lipid composition of muscles.

RESULTS

Feeding and groups identification in resident Dolly Varden. Eight groups of food objects were identified in the stomachs in Dolly Varden from Lake Dal'nee. All organisms were captured by the fish at shallow waters. Oligochaetes (Oligochaeta), freshwater clams of the genus *Pisidium*, planktonic crustaceans, and remains of fish were not found in the stomachs. The fishes fed actively, and the proportion of individuals with empty stomachs was less than 5% of the sample.

Based on the stomach content, the fishes represented two groups (Table 1). Mainly amphipods were found in the stomachs of a part of the fish. In addition, snails and caddis fly larvae were registered, and other benthic organisms were absent. In the stomachs of another part of the fish, amphipods were not observed, and these fishes fed on snails (*Valvata*), chironomid larvae, and imago of insects, as well as snails (*Lymnaea*), chironomid pupae, and mayfly and caddis fly larvae. In the sample, the ratio between the representatives of the two groups was 2 : 3, respectively. A classification of the sample including 40 fishes based on the proportion of food components using a step-

Table 2. Body length and body weight parameters of Dolly Varden *Salvelinus malma* with the gonads at maturity stage III–IV in August (Lake Dal'nee and lower reaches of the Paratunka River)

Parameter	Lacustrine		Anadromous from the river ($n = 25$)	Kruskal–Wallis test	
	group A ($n = 59$)	group G ($n = 39$)		*H*	*p*
Length (*FL*), cm	$\frac{22.3 \pm 0.52}{19.8–30.7}$	$\frac{23.3 \pm 0.75}{20.3–31.8}$	$\frac{39.9 \pm 0.79}{27.4–53.0}$	16.5	0.363
Weight, g	$\frac{103.1 \pm 1.97}{53–197}$	$\frac{112.0 \pm 2.33}{99–226}$	$\frac{643.8 \pm 3.79}{120.4–1280}$	11.0	0.150
Age, years:					
mean	6.9	7.2	7.5	14.5	0.285
maximum	8	9	10		

Here and in Table 4: above the line, mean value and standard error; below the line, range of the values.

Table 3. Parasites of two trophic groups of Dolly Varden *Salvelinus malma* from Lake Dal'nee in August

Parasitic species (location)	Group A (n = 23)			Group G (n = 17)			Mann–Whitney test	
	IE, %	d	IA, no. of exemplars	IE, %	d	IA, no. of exemplars	U	p
Myxidium salvelini	43.5	20.7–57.9		37.5	15.8–62.2		173.0	0.710
Myxobolus arcticus	87.0	59.1–92.5		83.3	58.7–96.1		178.5	0.820
Crepidostomum farionis	95.6	83.5–100.0	54.2	68.8	44.2–88.7	3.2	42.0	<0.001
C. metoecus	<0.1	0–12.2	0.0	100	82.0–100.0	268.2	0	<0.001
Diplostomum sp. 1 (internal medium of the eye)	100	87.8–100.0	6.2	87.5	67.1–98.8	4.1	121.0	0.070
Diplostomum sp. 2 (lens of the eye)	13.0	2.6–29.0	0.2	<0.1	12.5	0.3	183.5	0.980
Ichthyocotylurus erraticus	100	87.8–100.0	30.4	93.8	81.9–100.0	18.9	136.5	0.180
Cyathocephalus truncatus	4.4	0–16.5	0.04	100	82.9–100.0	37.8	0	<0.001
Proteocephalus longicollis	21.7	7.5–40.9	0.8	25.0	7.3–48.8	1.8	173.0	0.670
Cucullanus truttae	17.4	4.8–35.5	0.4	12.5	1.2–32.9	0.1	172.0	0.590
All species			92.2 (10.0–273.0)			334.4 (88.0–689.0)	24.0	<0.001
Conditional biomass of helminthes, mg	110.1 (12.6–422.5)			614.8 (137.0–1221.0)			12.0	<0.001

IE, invasion extensiveness; d, confidence interval of occurrence; IA, index of abundance; before the parentheses, mean value; in the parentheses, range of the values; IA was not calculated for Myxosporidia.

wise discriminant analysis showed a significant distinctions between two groups with 95% probability ($F_{1.25} = 39.05$, $p < 0.001$, tolerance = 0.001). A classification error was connected with the presence of a low number of mollusks in the diet of amphipod foragers. The main loading of the classification was associated with two components: amphipods and snails (*Valvata*). The differences connected with other food objects had a substantially lower (at an order of magnitude) loading in the classification. In the stomachs of mollusk foragers (25% of individuals), inedible objects (vegetation remains, detritus, and sand) were observed. However, their proportion in the food composition was low. In the stomachs of amphipod foragers, such components were not observed. In the two groups of resident Dolly Varden, the index of niche overlap of food resources (C_λ) was 0.0001.

In anadromous Dolly Varden collected in the Paratunka River downstream from the mouth of the channel, the stomachs were empty (90%) or they included a small number of salmonid eggs and riverine benthos.

Thus, in the catches conducted in Lake Dal'nee, the fishes were referred to two trophic groups based on stomach content. Similar to the trophic groups of a littoral benthivorous charr from Lake Kronotskoe (Busarova et al., 2015, 2016b, 2017), these groups were designated as G (amphipod foragers) and A (fishes feeding on benthos excluding amphipods).

Distribution. Based on the catches conducted with gill nets in the late summer, the trophic groups of lacustrine Dolly Varden were foraging within the same biotopes, but in the different proportion. Group G comprised 60–70% of the catches on the slopes of the basin near the southern and northern banks of the lake both within the border of the photic zone (at a depth of 10–12 m and at water transparency by Secchi disk 3.7 m) and at larger depths, . In the profundal zone at a depth of 40–50 m, single exemplars of Dolly Varden were collected. However, in the littoral zone at a depth of 5–12 m, the proportion of fishes of group A was larger reaching approximately 60% of the catches near the eastern bank and 70% near the western bank in the vicinity of the river head. It is important to note that the area of a larger abundance of the mollusk foragers coincided with the appearance of a turbidity zone determined by breeze fetch.

The maximum catch of the charrs (0.06–0.07 fishes/m^2 of a net per hour) was registered at the

Table 4. Body proportions in two trophic groups of Dolly Varden *Salvelinus malma* from Lake Dal'nee, *% FL*

Character	Group A ($n = 26$)	Group G ($n = 16$)	Student's *t*-test	
			t	*p*
Head length	18.8 ± 0.24 17.5–20.6	20.1 ± 0.20 18.7–22.0	–4.292	<0.001
Snout length	3.4 ± 0.11 2.9–4.4	4.1 ± 0.10 3.2–5.0	–4.239	<0.001
Eye diameter	4.1 ± 0.05 3.6–4.5	3.8 ± 0.04 3.4–4.2	3.914	<0.001
Upper jaw length	8.7 ± 0.19 7.5–10.5	9.6 ± 0.14 8.4–11.3	–3.947	<0.001
Upper jaw width	1.6 ± 0.04 1.3–1.8	1.7 ± 0.04 1.4–2.1	–1.609	0.116
Lower jaw length	11.1 ± 0.11 10.4–11.8	11.2 ± 0.12 10.0 – 12.2	–0.740	0.464
Head depth near the occiput	14.3 ± 0.14 13.5–15.3	14.3 ± 0.14 13.0–15.9	0.277	0.783
Fin length:				
pectoral	14.4 ± 0.19 13.1–15.7	14.0 ± 0.11 13.0–15.6	2.055	0.047
pelvic	11.2 ± 0.21 10.2–13.0	10.7 ± 0.11 9.7–11.7	2.419	0.020
dorsal	13.2 ± 0.18 12.0–14.9	12.8 ± 0.15 11.9–14.7	2.069	0.045
Anal fin length	12.3 ± 0.13 11.0–13.5	12.0 ± 0.12 10.8–13.2	2.010	0.054
Distance:				
pectroventral	29.8 ± 0.28 28.3–31.9	29.3 ± 0.18 27.0–30.9	1.725	0.092
antedorsal	44.0 ± 0.20 42.5–45.3	43.7 ± 0.18 42.2–45.5	1.007	0.320
anteventral	49.5 ± 0.22 47.8–51.0	49.4 ± 0.20 47.5–51.2	0.291	0.772
anteanal	67.9 ± 0.20 66.6–69.7	67.9 ± 0.17 66.8–69.7	0.144	0.887

border of the photic zone on the steep coastal slopes. At the depths exceeding 10–12 m, the catching efficiency was low during both the day and night. The average catching efficiency in the littoral zone at night was 0.05 fishes/m^2 per net per hour. During the day, the catches in shallow sites were low.

Size-age characteristics. The body size of resident Dolly Varden collected in Lake Dal'nee was substantially lower than the body size of anadromous Dolly Varden from the Paratunka River (Table 2). The lacustrine representatives of group A used in the analysis were slightly smaller than the fishes of group G in body length (Mann-Whitney test, $p = 0.06$) and body weight ($p = 0.01$). In addition, the groups differed in the average and maximum age. In group A, the females prevailed, while the sex ratio was similar in group G and anadromous Dolly Varden from the river.

Based on the increments on otoliths, anadromous Dolly Varden at the age exceeding 4 years differed from resident fishes (Kruskal–Wallis test, $H = 18.55$, $p = 0.001$; based on the increments of the fifth year). Therefore, the patterns of somatic growth rate in these forms were different. The individuals collected in the river, most likely, began to migrate into the sea on the fourth or fifth year of life. Based on the increment width on otoliths, lacustrine Dolly Varden of group G at the age older than 4 years had a higher growth rate than the fishes of group A (Mann–Whitney test,

Table 5. Fatty acids muscle composition in two trophic groups of Dolly Varden *Salvelinus malma* from Lake Dal'nee in August, % total fatty acids

Fatty acids	Group A ($n = 8$)	Group G ($n = 10$)	Mann–Whitney test	
			U	p
Saturated including:	38.00 (30.4–48.0)	37.45 (32.7–46.8)	49.0	0.969
C12–20 : 0	37.64 (30.1–47.7)	37.02 (32.2–46.3)	49.0	0.969
C21–23 : 0	0.37 (0.2–0.6)	0.44 (0.2–1.0)	43.0	0.648
Monoenic including:	24.29 (9.2–37.5)	35.63 (28.4–43.2)	10.0	0.003
C14–20 : 1	22.05 (8.6–36.6)	33.79 (26.8–41.2)	11.0	0.005
C22–24 : 1	1.54 (0.7–2.4)	1.84 (1.01–2.53)	34.0	0.369
Dienoic including:	10.52 (7.9–12.3)	10.65 (8.7–11.4)	48.0	0.909
C20 : 2	1.43 (0.8–1.9)	1.50 (0.8–2.0)	28.0	0.111
Polyenoic including:	27.19 (13.2–55.2)	16.27 (8.0–26.3)	21.0	0.030
C20–24 : 5–6	20.79 (9.3–49.4)	11.86 (5.4–20.3)	23.0	0.049
omega-3 including:	23.27 (10.9–51.0)	13.76 (6.2–22.0)	20.0	0.025
C18–20	9.02 (4.1–12.3)	6.02 (2.3–9.4)	18.0	0.015
C22–24	14.25 (5.7–39.1)	7.73 (3.4–13.6)	24.0	0.053
omega-6	3.93 (1.9–8.3)	2.52 (1.5–4.3)	30.0	0.138
General lipids, % dry weight	12.24 (8.6–18.8)	14.86 (10.1–20.9)	20.0	0.011

Mean values and (in the parentheses) ranges of the values are indicated.

$p = 0.030$; based on the increments of the fifth year). The logarithmic trends of the linear growth increments in the three groups showed a difference registered from the fifth year of life (figure 1).

Composition of parasites. In resident Dolly Varden, 12 parasitic species were identified, and parasitic composition was different in the two trophic groups (Table 3). The largest differences were observed in the infection with trematodes, *Crepidostomum metoecus* (Mann–Whitney test, $p < 0.001$) and *C. farionis* ($p < 0.001$), and cestode *Cyathocephalus truncatus* ($p < 0.001$). The amphipod foragers showed a large invasion of *C. metoecus* (IA = 268.2) and *C. truncatus* (IA = 38.7). In the representatives of group A, these parasites were almost absent. However, the fishes of group A were infected with *C. farionis* (IA = 54.2), and they were infected more intensively with *Ichthyocotylurus erraticus* (IA = 30.4) and *Diplostomum* sp. 1 (IA = 6.2). In addition to the parasites mentioned above, the following parasites were found in Dolly Varden of Lake Dal'nee: *Myxidium salvelini*, *Myxobolus arcticus*, *M. neurobius, Diplostomum* sp. 2, *Proteocephalus longicollis*, *Cucullanus truttae* as well as glochidia of mollusk *Beringiana beringiana*. Nevertheless, the level of invasion of these parasites was low, and it was statistically insignificant in both groups of fish.

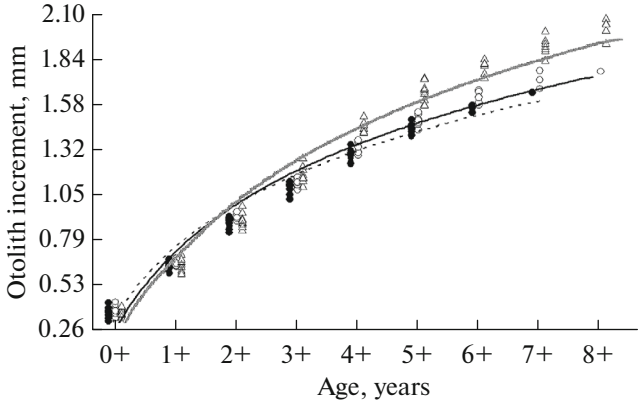

Fig. 1. Absolute postrostral annual increments of the otoliths of Dolly Varden *Salvelinus malma* from Lake Dal'nee (···●···) group A and (—○—) group G) and (—△—) lower reaches of the Paratunka River.

The fishes with two types of infection were significantly different in the total number of individuals of all parasites ($p < 0.001$) and conditional biomass of parasites ($p < 0.001$) per fish (Table 3). The average values of these two parameters were larger in group G than in group A at 3.6 and 5.6 times, respectively.

Anadromous Dolly Varden was not infected with *C. truncatus*, but larvae of nematodes *Anisakis* sp. were found in the body cavity and on the internal organs that is usual for anadromous charrs of Kamchatka (Konovalov, 1971).

Morphology. The visual differences in the exterior or body coloration between the representatives of two groups of resident Dolly Varden were not registered. However, a statistical analysis of the indices of morphological characters showed that amphipod foragers

Table 6. Several parameters of two trophic groups of littoral benthivorous charrs *Salvelinus malma* from lakes Dal'nee and Kronotskoe

Parameter	Lake Dal'nee		Lake Kronotskoe[1]	
	A	G	A	G
Mean body length (*FL*), mm	223.0	233.0	285.0	344.0
Mean body weight, g	103.1	112.0	206.0	409.0
Maximum age, years	8	9	11	15
Mean number of prey in the stomachs, exemplars:				
Gammarus lacustris	0	36.0	1.5	37.0
Chironomidae (larvae)	0.1	0	20.4	0.6
Lymnaea sp.	0.9	0	0	<0.1
Valvata sp.	16.9	0.6	0	0
Pisidium sp.	0	0	1.0	0.2
Mean number of parasites, exemplars	92.2	334.4	115.6	4093.0
Average conditional biomass of parasites, mg	110.1	614.8	103.9	9751.6
Index of abundance, exemplars:				
Cyathocephalus truncatus	<0.1	37.8	0.4	237.3
Crepidostomum metoecus	0	268.2	11.8[2]	1082.3
Cystidicola farionis	0	0	0.1	183.4

[1] Based on the published data (Busarova et al., 2015); [2] because of a great abundance of trematodes, the species *C. metoecus* and *C. farionis* were not identified, and they were designated as *Crepidostomum* spp.

differed significantly from the fishes of group A in a larger head with a longer snout and longer upper jaw, lower eye diameter, and shorter fins (Table 4). The representatives of the two trophic groups did not differ in the position of the fins, head depth, length of the lower jaw, and width of the upper jaw.

Fatty acid composition of muscular tissue. Dolly Varden of group G differed from the fishes of group A in a significantly higher fat content of muscular tissue (Table 5). In the two groups, 47 remains of different fatty acids were registered among muscular lipids. In addition, the fishes of group G were characterized by a significantly higher content of monoenic acids (due to shorter chains) and a lower content of polyenoic acids (mainly because of the presence of omega-3 group with short chains and, in addition, because of the presence of essential fatty acids with five or six unsaturated connections, including docosahexaenoic acid (22:6n-3)). At a similar content of saturated fatty acids in muscles of the two ecological groups of Dolly Varden, the content of the shortest dodecanoic and tetradecanoic acids (Mann–Whitney test, $p = 0.001$), as well as dienoic fatty acids, was higher in amphipod foragers than in mollusk foragers (Table 5).

DISCUSSION

Resident Dolly Varden from Lake Dal'nee is represented by two ecological groups. The fishes of the first group feed on amphipods while the individuals of the second group prefer snails (*Valvata*) and at a lower degree benthos, and they do not consume mobile amphipods. In these groups, the foraging niches do not overlap, which is supported by an extremely low value of C_λ index (0.0001). A substantially larger value (0.6) is applied for the designation of biologically significant overlapping of foraging niches (Wallace, 1981). Within each group, similar types of feeding and similar parasite composition were revealed.

Both groups of Dolly Varden differ from anadromous fishes of the same species from the river (showing an upstream migration from the sea to the lake in late summer) in body size, growth rate, and parasitic fauna. The resident Dolly Varden differs from the predatory charr that recently disappeared from the lake in the total absence of *Diphyllobothrium* plerocercoids (Konovalov, 1971; Gorovaya and Butorina, 2007). Because of this feature, the absence of juvenile salmonids in the food composition of the resident fish is supported.

Resident Dolly Varden represented by two trophic groups is distributed over the entire water area at a depth between 5–50 m. However, the spatial occurrence of the groups is different. In the littoral zone exposed to the wind and characterized by a high turbidity due to wave action, the mollusk foragers prevail. In the lee side of the lake along a steep slope, the

amphipod foragers are a dominant group. The representatives of both groups explore the feeding resources of the photic zone.

The stability of the feeding segregation can be supported by the infection with parasites–indicators (Konovalov, 1971; Knudsenetal, 2004). In Lake Dal'nee, an intensive invasion with *C. truncates* and *C. metoecus* (amphipods are intermediate hosts of the parasites) is registered in the fishes of group G. The former parasite lives in the fish for 20–55 days, and the latter one lives during a year (Vik, 1958; Awachie, 1968). In the Dolly Varden of group A, these parasites are absent. However, the representatives of this group are infected with *C. farionis*, a parasite living in the fish for approximately a year; and mayfly larvae are intermediate hosts (Crawford, 1943). A larger invasion of the fish of group A with metacercaria of *I. erraticus* and *Diplostomum* spp. (Stregiidae) is connected with the close contact of the fish with the first intermediate host of these helminthes, snails of the genera *Valvata* and *Lymnaea* (Prozorova and Shed'ko, 2003). The duration of life of *I. erraticus* in the fish is more than 5 months, most likely, up to several years (Olson, 1970), and *Diplostomum* spp. lives in the fish for more than 5–6 years (Shigin, 1986). A parasite–indicator, which can be used for the reliable identification of the trophic groups of Dolly Varden from Lake Dal'nee, is cestode *C. truncatus*. This parasite is numerous in the pyloric part of the intestine of the fishes of group G (IA = 37.8.), and it is absent in the representatives of group A. The type of feeding of the charrs does not change at least within the range of 20–30 cm *FL*.

The fishes of group G are subjected to a substantially larger parasitic pressure in comparison to the charrs of group A: the average number and biomass of parasites is several times larger in the former group. At the same time, the amphipod foragers reach a larger body weight and grow faster at older age. This feature indirectly supports the following assumption: energetic expenses used for a struggle against stress caused by a negative effect of parasitic invasion are compensated by a high feeding value of amphipods. The average caloric content of amphipods is 10.49–23.03 kJ/g (2.5–5.5 kcal/g) of the dry mass, and the average caloric content of snails is 7.12–14.24 kJ/g (1.7–3.4 kcal/g) (Greze, 1977).

A part of revealed morphometric differences between the ecological groups of the fish, most likely, is connected with the different rates of somatic growth. In the charrs, a faster growth rate is associated with a relative decrease of the length of fins and eye diameter (Savvaitova, 1989). A similar pattern is found in group G. Nevertheless, observed elongation of the head (in particular, the snout) and elongation of the upper jaw in amphipod foragers, most likely, are connected with the change of the habitus because of feeding specialization.

The functional differences between the trophic groups are also revealed in muscle fatty acid composition. The differences in lipids content are connected with fish metabolic conditions. At a high fat content in the muscles of the fish from group G, the ratio between unsaturated fatty acids is deviated from essential polyenoic acids to reserved monoenic acids and dienoic chains. Polyenoic fatty acids determine viscosity of membranes increasing their fluidity and modulating activity of membrane-bound enzymes (Sidorov, 1983; Bogdan et al., 2001). We suppose that the metabolism is deviated to the storage of biopolymers in Dolly Varden of group G. In Dolly Varden of group A, intensification of the metabolism is required for the assimilation of food with low caloric values. In the fish of the latter group, the resources for the storage of triacilglicerids are more restricted.

A similar differentiation of the littoral benthivorous charr into two trophic groups has been described before in Lake Kronotskoe, Kamchatka (Busarova et al., 2015a, 2015b, 2017). However, several differences are observed between the similar trophic groups of the charrs from lakes Dal'nee and Kronotskoe (Table 6). In Lake Dal'nee, Dolly Varden of group A feeds mainly on snails of the genera *Valvata* and *Lymnaea*; in Lake Kronotskoe, the littoral charr of a similar trophic group feeds on larvae and pupae of chironomids and (at a lower degree) mollusks of the genus *Pisidium*. Therefore, the parasitic fauna of these groups is also different. In Lake Dal'nee, an intensive invasion with metacercaria of *I. erraticus* and *Diplostomum* spp. is observed. These parasites are transmitted to the host through the snails *Valvata* and *Lymnaea*. In Lake Kronotskoe, the fishes are intensively infected with a trematode of the ureter *Phyllodistomum umblae*. This parasite infects the fish during feeding on freshwater clams of the genus *Pisidium* (Prozorova and Shed'ko, 2003). The Dolly Varden of Lake Dal'nee is not infected with *P. umblae*, because this parasite is not distributed in the lake (Konovalov, 1971). The similar features of the analogous groups A from the two lakes are the absence of amphipods in the food and absence of related parasites (using amphipods as intermediate hosts). In both lakes, the charrs of group A prefer different food objects. However, the pattern of choosing of the food is the same: the fishes prefer the most abundant and available sedentary benthos. The difference in the diet is in agreement with the data on the composition of benthic communities in the littoral zones of the lakes. In the littoral zone of Lake Kronotskoe, chironomid larvae prevail, the abundance and biomass of mollusks are very low, and the most abundant mollusks are freshwater clams (Izvekova, 2012). In the littoral zone of Lake Dal'nee, the main part of benthic biomass is represented by gastropods (Sorokin and Pavel'eva, 1977; Krogius et al., 1987).

In both lakes, the groups of amphipod foragers are infected with helminthes *C. truncates* and *C. metoecus*. In Lake Kronotskoe (but not in Lake Dal'nee), the

charrs are infected with *Cystidicola farionis*, which remains within the fish for at least 2 years (Black and Lankester, 1980). This nematode is a reliable indicator of regular feeding on amphipods, but it is absent in the fauna of Lake Dal'nee (Konovalov, 1971; Gorovaya and Butorina, 2007). In Dolly Varden of group G of Lake Dal'nee, all parasites-indicators have a short life cycle: from several weeks (*C. truncatus*) to a year (trematodes). Formally, these parasites support a feeding specialization only during a year. However, it seems obvious that the trophic niches of the charrs of group G in the two lakes are similar.

The amphipod foragers, most likely, are characterized by a specific feeding behavior, which is different from that in benthivorous collectors, predators, and euryphages. The prey (amphipods) hide under stones in the coastal zone in daytime and are distributed in the near-bottom water layers during twilight and at night (Wilhelmetal, 2000). In the stomachs of the fish of group G, inedible objects and sedentary benthos are hardly ever found, and, therefore, a selective feeding type should be supposed. A visual searching of amphipods moving under the bottom, most likely, occurs.

A degree of the difference of parasitic invasion between the trophic groups of the charrs in lakes Dal'nee and Kronotskoe is various (Table 6). In Lake Dal'nee, the abundance of parasites of the fish in group G is larger than that in group A at 3.6 times. In Lake Kronotskoe, this difference reaches 35 times. In addition, the average conditional biomass of parasites is larger (in group G in comparison to group A) at 5.6 and 93 times in both lakes, respectively. In Lake Kronotskoe, group G is infected with *C. truncatus* and *C. metoecus* substantially more intensively than in Lake Dal'nee. The differences reach six and four times for two parasitic species, respectively. Moreover, the fishes from Lake Kronotskoe are strongly infected with nematode of swimming bladder *Cystidicola farionis*. A substantially higher parasitic invasion of the fish of group G in Lake Kronotskoe is connected with two main reasons: (1) larger body size of the fishes and (2) very high intensity of parasitic invasion usual for the ecosystem of Lake Kronotskoe (Butorina et al., 2008; Pavlov et al., 2013; Busarova et al., 2016a, 2016b).

Thus, the pairs of trophic groups have originated convergently in the resident littoral benthivorous charrs from lakes Dal'nee and Kronotskoe with different ecosystems structure.

A part of the charrs feeds on almost exclusively amphipods, and other fishes prefer the most abundant groups of sedentary benthic organisms. In both lakes, the littoral charrs evolved in the conditions of sympatry with other closely related groups: in Lake Dal'nee, with predatory lacustrine charr and omnivorous anadromous Dolly Varden (Savvaitova, 1989); in Lake Kronotskoe, with the predatory and omnivorous morphs (Viktorovskii, 1978). In addition, the other competitors of the benthivorous charrs are represented by sticklebacks of the family Gasterosteidae (Lake Dal'nee) or kokanee *Oncorhynchus nerka* (Lake Kronotskoe). These conditions could facilitate ecological differentiation of the littoral benthivorous charrs.

The results of this study indicate a possibility of the occurrence of a universal base of a trophic diversification of the charrs in the coastal ecosystems of oligotrophic lakes. A similar pathway of the trophic groups separation can be expected in other water bodies inhabited by resident charrs. The trophic specialization of the littoral charrs, most likely, appears de novo in each generation and it is connected with a variability of the progeny. A separation of the young salmonids into the pelagic and demersal groups with different growth rates in the conditions of a strong feeding competition is well known (Thorpe, 1977; Metcalfeetal, 1989; Pavlov et al., 2010). The fast-growing aggressive juveniles, most likely, begin to feed on amphipods, and the slow-growing fishes continue to feed on smaller benthic organisms. Moreover, this ecological diversification maintains partly due to f the appearance of the areas with turbid waters in the shallow zones of lee banks during the summer (for example, due to breeze action). The fishes of group A exposed to the wind in the littoral zone, most likely, have an advantage in feeding because of their restricted requirements to a good visibility. Another possibility cannot be excluded: a part of the charrs does not feed on amphipods representing an avoidance of parasitic hyperinvasion (Mikheev at al., 2013).

ACKNOWLEDGMENTS

We thank N.G. Busarova (Pacific Institute of Bioorganic Chemistry, Far Eastern Branch, Russian Academy of Sciences) and S.V. Ramus' (Primorskaya State Academy of Agriculture, Ussuriisk) for help in the treatment of the material.

This work was supported by the Russian Foundation for Basic Research, project no. 16-04-01687.

REFERENCES

Ackman, R.G., Gas-liquid chromatography of fatty acids and esters, *Methods Enzymol.*, 1969, vol. 14, pp. 329–381.

Adams, C.E., Fraser, D., McCarthy, I., et al., Stable isotope analysis reveals ecological segregation in a bimodal size polymorphism in Arctic charr from Loch Tay, *Scotland J. Fish Biol.*, 2003, vol. 62, pp. 474–481.

Awachie, J.B.E., On the bionomics of *Crepidostomum metoecus* (Braun, 1900) and *Crepidostomum farionis* (Müller, 1784) (Trematoda, Allocreadiidae), *J. Parasitol.*, 1968, vol. 58, no. 2, pp. 307–324.

Behnke, R.J., A systematic review of the genus *Salvelinus*, in *Charrs Salmonid Fishes of the Genus Salvelinus*, Balon, E.K., Ed., Hague: Junk, 1980, pp. 441–480.

Black, G.A. and Lankester, M.W., Migration and development of swim-bladder nematodes, *Cystidicola* spp. (Habronematoidea), in their definitive hosts, *Can. J. Zool.*, 1980, vol. 58, no. 11, pp. 1997–2005.

Bligh, E.G. and Dyer, W.J., A rapid method for total lipid extraction and purification, *Can. J. Biochem. Physiol.*, 1959, vol. 37, pp. 911–917.

Bogdan, V.V., Sidorov, V.S., and Zekina, L.M., Role of fish lipids in adaptation to the different ecological conditions, in *Ekologicheskie problemy obtogeneza ryb: fiziologo-biokhimicheskie aspekty* (Ecological Problems of Fish Ontogenesis: Physiological and Biochemical Aspects), Moscow: Mosk. Gos. Univ., 2001, pp. 188–202.

Busarova, O.Yu., Butorina, T.E., Markevich, G.N., and Anisimova, L.A., Parasite fauna of the kokanee salmon *Oncorhynchus nerka* of Kronotskoe Lake (Kamchatka), *Parazitologiya*, 2016, vol. 50, no. 3, pp. 212–224.

Busarova, O.Yu., Knudsen, R., and Markevich, G.N., Parasite fauna of the charrs (*Salvelinus*) of Kronotskoe Lake, Kamchatka, *Parazitologiya*, 2016, vol. 50, no. 6, pp. 409–425.

Busarova, O.Yu., Markevich, G.N., Esin, E.V., et al., Possible reasons for charr microspecialization in littoral zone of Lake Kronotskoe, *8th Int. Charr Symp., Abstracts of Papers*, Tromsø, 2015, p. 91.

Busarova, O.Yu., Markevich, G.N., and Knudsen, R., Differentiation of the Schmidt's charr (Salvelinus schmidti) of the Kronotskoe Lake (Kamchatka) according to parasitological data, *Issled. Vodn. Biol. Resur. Kamchat. Sev.-Zap. Chasti Tikhogo Okeana*, 2015, no. 39, pp. 5–13.

Busarova, O.Yu., Markevich, G.N., Knudsen, R., and Esin, E.V., Trophic differentiation of the nosed charr *Salvelinus schmidti* Viktorovsky, 1978 in Lake Kronotskoe (Kamchatka), *Russ. J. Mar. Biol.*, 2017, vol. 43, no. 1, pp. 57–64.

Butorina, T.E., Shed'ko, M.B., and Gorovaya, O.Yu., Specific features of ecology of chars of the genus *Salvelinus* (Salmonidae) from the basin of Lake Kronotskoe (Kamchatka) according to parasitological data, *J. Ichthyol.*, 2008, vol. 48, no. 8, pp. 622–636.

Bykhovskaya-Pavlovskaya, I.E., *Parazity ryb. Rukovodstvo po izucheniyu* (Fish Parasites: Manual), Leningrad: Nauka, 1985.

Carreau, J.P. and Dubacq, J.P., Adaptation of macro-scale method to the micro-scale for fatty acid methyl transesterification of biological lipid extracts, *J. Chromatogr.*, 1978, vol. 151, no. 3, pp. 384–390.

Chereshnev, I.A., Volobuev, V.V., Shestakov, A.V., and Frolov, S.V., *Lososevidnye ryby Severo-Vostoka Rossii* (Salmoniformes of the Northeast of Russia), Vladivostok: Dal'nauka, 2002.

Crawford, W.W., Colorado trematodes studies. I. A further contribution to the life history of *Crepidostomum farionis* (Muller), *J. Parasitol.*, 1943, vol. 29, no. 6, pp. 379–384.

Dorovskikh, G.N. and Stepanov, V.G., *Metody sbora i obrabotki ikhtioparazitologicheskikh materialov* (Methods for Sampling and Processing of Ichthyo-Parasitological Materials), Syktyvkar: Syktyvkar. Gos. Univ., 2009.

Esin, E.V., Markevich, G.N., Bocharova, E.S., and Saltykova, E.A., Living chars (*Salvelinus*, Salmonidae) in the glacial lakes of Kamchatka: endemic relict species or forms of the Arctic char? *Mater. XV mezhdunarodnoi konferentsii "Sokhranenie bioraznoobraziya Kamchatki i prilegayushchikh morei"* (Proc. XV Int. Conf. "Conservation of Biological Diversity of Kamchatka and Adjacent Seas"), Petropavlovsk-Kamchatskii: Kamchatpress, 2015, pp. 32–46.

Gordeeva, N.V., Alekseyev, S.S., Matveev, A.N., and Samusenok, V.P., Parallel evolutionary divergence in Arctic char *Salvelinus alpinus* complex from Transbaikalia: variation in differentiation degree and segregation of genetic diversity among sympatric forms, *Can. J. Fish. Aquat. Sci.*, 2015, vol. 72, pp. 96–115.

Gorovaya, O.Yu. and Butorina, T.E., Parasitological fauna of freshwater Dolly Varden trout (*Salvelinus malma*) from the Dal'nee Lake (Kamchatka), *Nauch. Tr. Dal'rybvtuza*, 2007, no. 19, pp. 174–181.

Greze, I.I., *Amfipody Chernogo morya i ikh biologiya* (Amphipods of the Black Sea and Their Biology), Kiev: Naukova Dumka, 1977.

Hindar, K. and Jonsson, B., Ecological polymorphism in Arctic charr, *Biol. J. Linn. Soc.*, 1993, vol. 48, pp. 63–47.

Horn, H.S., Measurement of "overlap" in comparative ecological studies, *Am. Nat.*, 1966, vol. 100, pp. 419–424.

Izvekova, E.I., Bottom species of the Kronotskoe Lake (summer 2010), *Tr. Kronotskogo Gos. Prirod. Biosfernogo Zapoved.*, 2012, no. 2, pp. 194–197.

Jonsson, B. and Jonsson, N., Polymorphism and speciation in Arctic charr, *J. Fish Biol.*, 2001, vol. 58, pp. 605–638.

Kates, M., *Techniques of Lipidology: Isolation, Analysis and Identification of Lipids*, Amsterdam: North Holland, 1972.

Klemetsen, A., The most variable vertebrate on Earth, *J. Ichthyol.*, 2013, vol. 53, no. 10, pp. 781–791.

Klemetsen, A., Amundsen, P.-A., Knudsen, R., and Hermansen, B., A profundal winter-spawning morph of Arctic charr *Salvelinus alpinus* (L.) in Lake Fjellfrøsvatn, Northern Norway, *Nord. J. Freshwater Res.*, 1997, vol. 73, pp. 13–23.

Knudsen, R., Curtis, M.A., and Kristoffersen, R., Aggregation of helminthes: the role of feeding behavior of fish hosts, *J. Parasitol.*, 2004, vol. 90, pp. 1–7.

Knudsen, R., Siwertsson, A., Adams, C., et al., Temporal stability of niche use exposes sympatric Arctic charr to alternative selection pressures, *Evol. Ecol.*, 2010, vol. 25, pp. 589–604.

Konovalov, S.M., *Differentsiatsiya lokal'nykh stad nerki Oncorhynchus nerka* (Differentiation of Local Herds of Sockeye Salmon Oncorhynchus nerka), Leningrad: Nauka, 1971.

Krogius, F.V., Krokhin, E.M., and Menshutkin, V.V., *Tikhookeanskii losos'—nerka (krasnaya) v ekonomike ozera Dal'nego (Kamchatka)* (The Pacific Salmon—Red Sockeye salmon in the Ecosystem of Dal'nee Lake (Kamchatka)), Leningrad: Nauka, 1987.

Kurenkov, I.I., *Zooplankton ozer Kamchatki* (Zooplankton of the Kamchatka Lakes), Petropavlovsk-Kamchatskii: Kamchat. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr., 2005.

Mandritsa, S.A., Use of geometric morphometry in ichthyology, *Vestn. Permsk. Gos. Univ.*, 2007, vol. 5, no. 10, pp. 38–52.

Metcalfe, N.B., Huntingford, F.A., Graham, W.D., and Thorpe, J.E., Early social status and the development of life-history strategies in Atlantic salmon, *Proc. R. Soc., B*, 1989, vol. 236, pp. 7–19.

Mikheev, V.N., Zhokhov, A.E., and Slivko, M.E., Can the risk of parasite infection in fish cause the ecological differentiation in the population of roach *Rutilus rutilus* (Cyprinidae), *J. Ichthyol.*, 2013, vol. 53, no. 8, pp. 610–616.

Oleinik, A.G. and Skurikhina, L.A., Genetic divergence of sympatric chars of the genus *Salvelinus* from Nachikinskoe Lake (Kamchatka), *Russ. J. Genet.*, 2007, vol. 43, no. 8, pp. 910–917.

Olson, R.E., The life cycle of *Cotylurus erraticus* (Rudolphi, 1809) Szidat, 1928 (Trematoda: Strigeidae), *J. Parasitol.*, 1970, vol. 56, no. 1, pp. 55–63.

Opredelitel' parazitov presnovodnykh ryb fauny SSSR. Tom 1. Paraziticheskie prosteishie (Guide for Identification of Freshwater Fishes of Fauna of the Soviet Union, Vol. 1: Parasitic Protozoa), Leningrad: Nauka, 1984.

Opredelitel' parazitov presnovodnykh ryb fauny SSSR. Tom 3. Chast' 2. Paraziticheskie mnogokletochnye (Guide for Identification of Freshwater Fishes of Fauna of the Soviet Union, Vol. 3, Part 2: Parasitic Metazoa), Leningrad: Nauka, 1987.

Pavlov, D.S., Kostin, V.V., and Ponomareva, V.Yu., Behavioral differentiation of underyearlings of the Black Sea salmon *Salmo trutta labrax*: rheoreaction in the year preceding smoltification, *J. Ichthyol.*, 2010, vol. 50, no. 3, pp. 270–280.

Pavlov, D.S., Kuzishchin, K.V., Gruzdeva, M.A., et al., Phenetic diversity and spatial structure of chars (*Salvelinus*) of the Kronotskaya riverine-lacustrine system (Eastern Kamchatka), *J. Ichthyol.*, 2013, vol. 53, no. 9, pp. 662–686.

Pravdin, I.F., *Rukovodstvo po izucheniyu ryb* (Manual for Fish Analysis), Moscow: Pishchepromizdat, 1966.

Præbel, K., Østbye, K., Hassve, M., and Hagenlund, M., Into the Abyss II: evolutionary origin and temporal separation of the four sympatric Arctic char morphs in the deep lake Tinnsjøen, *8th Int. Charr Symp., Abstracts of Papers*, Tromsø, 2015, p. 17.

Prozorova, L.A. and Shed'ko, M.B., Mollusks from the Azabach'e Lake (Kamchatka) and their biocoenotic significance, *Tr. Kamchat. Fil., Tikhookean. Inst. Geogr., Dal'nevost. Otd., Ross. Akad. Nauk*, 2003, no. 4, pp. 120–151.

Rohlf, F.J., On the use of shape spaces to compare morphometric methods, *Hystrix*, 2000, vol. 11, pp. 9–25.

Rohlf, F.J., TpsDig, Version 2.16, 2010. http://life.bio.sunysb.edu/morph.

Roitman, V.A. and Lobanov, A.L., A method for estimating parasite hemopopulation numbers in host population, *Tr. Gel'mintol. Lab. Akad. Nauk*, 1985, vol. 23, pp. 102–123.

Saltykova, E., Markevich, G., and Kuzishchin, K., Divergent skull morphology between trophic separated lacustrine forms of Dolly Varden charr from Lake Kronotskoe, Kamchatka, Russia, *Environ. Biol. Fish*, 2015, vol. 98, no. 2, pp. 559–570.

Savvaitova, K.A., *Arkticheskie gol'tsy (struktura populyatsionnykh sistem, perspektivy khozyaistvennogo ispol'zovaniya),* (Arctic Chars: Structure of Population Systems and Perspective Economic Use), Moscow: Agropromizdat, 1989.

Shigin, A.A., *Trematody fauny SSSR. Rod Diplostomum. Metatserkarii* (Trematode Fauna of Soviet Union. Genus Diplostomum. Metacercaria), Moscow: Nauka, 1986.

Sidorov, V.S., *Ekologicheskaya biokhimiya ryb. Lipidy* (Ecological Biochemistry of Fishes. Lipids), Leningrad: Nauka, 1983.

Skulason S., Noakes D.L.G., and Snorrason S.S. Ontogeny of trophic morphology in four sympatric morphs of Arctic charr *Salvelinus alpinusin* Thingvallavatn, Iceland, *Biol. J. Linn. Soc.*, 1989, vol. 38, pp. 281–301.

Sorokin, Yu.N. and Pavel'eva, E.B., Energy of the ecosystem of salmon lake, *Zh. Obshch. Biol.*, 1977, vol. 38, no. 4, pp. 512–527.

Stransky, K., Jursik, T., and Vitek, A., Standard equivalent chain length values of monoenic and polyenic (methylene-interrupted) fatty acids, *J. High Resol. Chromatogr.*, 1997, vol. 20, no. 3, pp. 143–158.

Thorpe, J.E., Bimodal distribution of length of juvenile Atlantic salmon under artificial rearing conditions, *J. Fish. Biol.*, 1977, vol. 11, pp. 175–184.

Wallace, R.K., An assessment of diet-overlap indexes, *Trans. Am. Fish. Soc.*, 1981, vol. 110, pp. 2–76.

Wilhelm, F.M., Schindler, D.W., and McNaught, A.S., The influence of experimental scale on estimating the predation rate of *Gammarus lacustris* (Crustacea: Amphipoda) on Daphnia in an alpine lake, *J. Plankton Res.*, 2000, vol. 22, no. 9, pp. 1719–1734.

Wilson, A.J., Gislason, D., Skulason, S., et al., Population genetic structure of arctic charr, *Salvelinus alpinus* from northwest Europe on large and small spatial scales, *Mol. Ecol.*, 2004, vol. 13, pp. 1129–1142.

Vik, R., Studies of the helminth fauna of Norway. II. Distribution and life cycle of *Cyathocephalus truncates* (Pallas, 1781) (Cestoda), *Nytt Mag. Zool.*, 1958, vol. 6, pp. 97–110.

Viktorovskii, R.M., *Mekhanizmy vidoobrazovaniya u gol'tsov Kronotskogo ozera* (Mechanisms of Speciation in Chars of Kronotskoe Lake), Moscow: Nauka, 1978.

Translated by D.A. Pavlov