ISSN 0032-9452, Journal of Ichthyology, 2022, Vol. 62, No. 5, pp. 797–811. © Pleiades Publishing, Ltd., 2022.
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"Freshwater Components" in the Populations of Whitespotted Char *Salvelinus leucomaenis* (Salmonidae) in the North of the Species Range (Kamchatka)

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Received May 13, 2022; revised May 17, 2022; accepted May 18, 2022

Abstract—The variety of types of life strategy and the structure of the populations of whitespotted char *Salvelinus leucomaenis* (Pallas, 1814) are considered at Kamchatka. At the north of the species range, the populations of whitespotted char are heterogeneous. The main role in reproduction belongs to anadromous whitespotted char, but there are also the groups in the populations that realize their life cycle exclusively in fresh waters. Dwarf males are common in the rivers of different types. In the geomorphologically complex river (Kol), there is also the river populations of rheodromous whitespotted char, represented by males and females. Favorite biotopes (blockages and creases of woody material on deep reaches, found only in foothill rivers) are key parameters predetermining the presence of a river population of rheodromous whitespotted char. At the north of the species range, the variety of individuals with different types of life strategy in whitespotted char is comparable to that observed in the southern parts, in particular, in the basin of the Sea of Japan, which is considered the zone of the ecological optimum of the species.

Key words: whitespotted char, life strategy, anadromy, residence, dwarf males, river-resident rheodromous fish, population structure, geomorphology, Kamchatka

DOI: 10.1134/S0032945222050083

INTRODUCTION

Whitespotted char *Salvelinus leucomaenis* is a salmonid confined to the Asian coast of the Pacific Ocean. Its range covers the basins of the Sea of Japan, the Sea of Okhotsk, and the southwestern part of the Bering Sea. Comparing to other char species of the genus *Salvelinus,* whitespotted char remains a poorly studied species (Kawanabe, 1989; Yamamoto et al., 1999; Gritsenko, 2002; Hosoya, 2002; Nakamura, 2003; Dunham et al., 2008; Ryby..., 2012; Yamaguchi et al., 2016). The greatest diversity of whitespotted char is observed on the Japanese islands of Hokkaido and Honshu, which are the southern part of its range. In addition to the nominal subspecies *S. l. leucomaenis,* confined to the water bodies of Hokkaido, three more subspecies inhabit Honshu (*S. l. imbrius, S. l. pluvius / pluvicus,* and *S. l. japonicus*), leading a freshwater lifestyle and differing in color and some morphological and genetic features (Kawanabe 1989; Nakajima, Fujio, 1995; Hosoya, 2002; Yamamoto et al., 2004; Yamaguchi et al., 2010, 2016). Sympatric and allopatric ecological groupings of whitespotted char with varying anadromy and residence parameters are described in different rivers of Hokkaido as part of the subspecies *S. l. leucomaenis*. In some cases, resident and anadromous individuals are the interacting elements of the same population; in other cases, they may be isolated from each other by physical barriers (Yamamoto et al., 1999, 2004; Morita and Yamamoto, 2002; Kikko et al., 2009; Morita et al., 2013). Therefore, a wide range of intraspecific groupings of whitespotted char is currently observed in the south of the species range; the detailed descriptions of various cases of coexistence and relationships between resident and anadromous fish are provided in the literature.

At the same time, there are few data on whitespotted char of the northern part of the range (Kawanabe 1989; Yamamoto et al., 1999; Yamamoto and Morita, 2002; Chereshnev et al., 2002; Dunham et al., 2008; Morita et al., 2013). In the available literature, there is a description of the structure of populations of anadromous whitespotted char and scarce data about lake-riverine and riverine groups from some rivers of the mainland coast of the Sea of Okhotsk (Volobuev and Nikulin, 1975; Volobuev et al., 1985; Volobuev, 1987; Gudkov, 1991; Gudkov et al., 1991; Chereshnev et al., 2002). Whitespotted char from the rivers of Kamchatka remains the least studied (Chereshnev et al., 2002; Savvaitova et al., 2007). There are only a few ref-

Table 1. Geomorphological parameters of the basins of the Kol and Kekhta rivers (according to: *Resursy*..., 1973; Pavlov et al., 2008, 2009; with additions and modifications)

Parameter	Basin of the Kol River	Basin of the Kekhta River
River length, km	~130	~60
Catchment area, km^2	1580	657
Riverbed slope, m/km	>5	<3
River type	Forked channel, mountainous and foothill type	Straight channel, tundra type along entire river
Tributaries	Many; tundra and mountain types, the latter prevail; tributary length 5–30 km, most of tributaries are 5–10 km	Solitary, only tundra type; short (1–3 km) and narrow (about 1 m)
Occurrence of woody material in the channel	Everywhere, a lot of blockages and creases	Solitary
The presence of deep pits	Single	Numerous in the lower and middle reaches of the river
Reach characteristics	Length 100–300 m, depth down to 3 m, flow velocity 0.6–0.7 m/s, pebbles and gravel at the bottom, there are always blockages of trees	Length 200–400 m, depth down to 2 m, current velocity ~0.3 m/s, bottom composed of sand, almost no woody material
The presence of a brackish estuary at the confluence of the river into the sea	No brackish estuary. The river flows into the sea at a single mouth, the depth at the mouth is 1.2–2.1 m; there is only fresh water in the river before flowing into the sea	Present. Length 1.0–1.3 km, width ~40–45 m, depth down to 4 m at high tide, salinity 5–12‰

erences to the "river whitespotted char in the basin of large Kamchatka rivers" regarding the freshwater groupings of this species in Kamchatka (Chereshnev et al., 2002; Esin and Markevich, 2017). The only description of a bisexual stream population refers to one thermal stream at the eastern coast of Kamchatka (Esin, Sorokin, 2012).

In this regard, our study aims to analyze the structure of the local populations of whitespotted char in Kamchatka rivers with different geomorphology and to identify freshwater groups in their composition.

MATERIALS AND METHODS

The material was collected in the field according to a single scheme using the same approaches and methods in the Kol River in 2002–2008 and the Kekhta River in 2003–2008, at the western coast of the Kamchatka Peninsula. In 2003–2006, the studied at both rivers were carried out continuously from May through October from the source to estuary.

Despite their close location (the distance between the river estuaries is about 8 km), the Kol and Kekhta rivers differ greatly in their structure (Table 1, Fig. 1). The Kol River is a foothill river with a branched channel, a large slope of the bed, and a fast current; the Kekhta River belongs to the tundra type with a straight channel and a weak current (Pavlov et al., 2008, 2009; Kuzishchin, 2010).

Fishing was carried out in the main river channel, their tributaries of the tundra and mountain types, in the reservoirs of the accessory system, in the estuary of the Kekhta River, and in the sea close by the estuary zone. Sampling was performed with cast nets, gill nets included in the standard set (mesh size from 20 to 75 mm), and fishing gear. Juveniles, dwarf males, and breeders were caught on spawning grounds using electric fishing Smith-Root 24L (Smith-Root, USA) in sparing mode (Bird, Cowx, 1993) with alternating pulsed current (voltage 350–400 V, frequency 40–60 Hz, pulse duration 2 ms). After capture, all individuals were immobilized with solutions of MS-222 or clove oil (Kouřil et al., 2009; Mikodina et al., 2011). The method of three-time fishing was applied to assess the population density of juveniles (Zippin, 1956), the density and biomass of juvenile fish were determined for the plots of at least 150 m^2 each. The material was collected at more than 50 sites in the Kol River and more than 25 sections in the Kekhta River (Fig. 1). In total, more than 50000 specimens were analyzed. juveniles of different ages. The behavior of fish during spawning was studied by visual underwater observations and using a GoPro camera (GoPro, Inc, USA) (Kuzishchin et al., 2008; Gruzdeva et al., 2013, 2017).

More than 600 sexually mature fish and 10000 juveniles were biologically analyzed (Pravdin, 1966). In all fish, the sex and maturity stage of the gonads were determined (Murza and Khristoforov, 1991). For some fish, morphometric analysis was performed

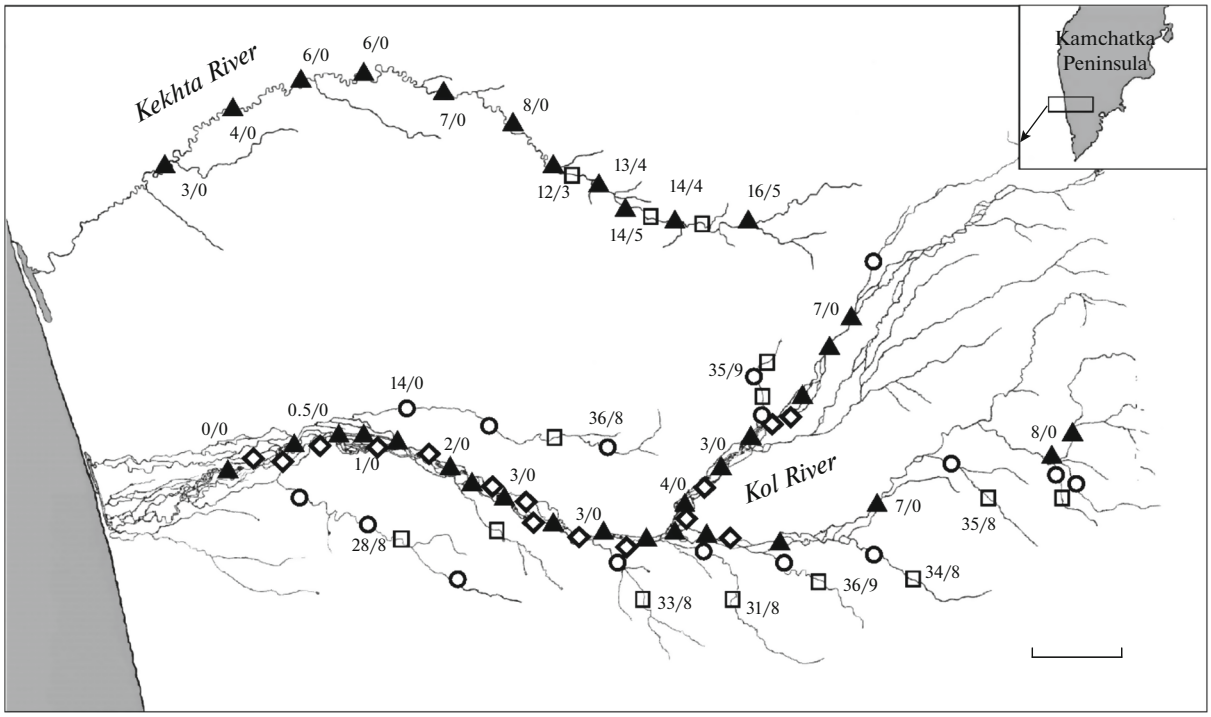

Fig. 1. Schematic map of the study, sampling sites: (▲)—main channel, (◇)—side channels, (○)—tributaries, (□) —identified spawning grounds of whitespotted char *Salvelinus leucomaenis*. Numerals, %: left to the slash—the number of whitespotted char in relation to the total number of individuals of all other salmon species, values right to the slash—the number of dwarf males in relation to the total number of young whitespotted char. Scale: 4 km.

according to a modified scheme for salmon fish (Pavlov et al., 2001), namely, 25 plastic signs and 10 meristic signs were evaluated. The age of fish was determined by otolith analysis (sagitta). The recommendations of Gudkov (1991), Gudkov et al. (1991), and Tiller (2007) were taken into account when assessing age and identifying freshwater and marine periods of life. The ratio of strontium and calcium ions on thin sections of otoliths was simultaneously estimated using X-ray fluorescence analysis to clarify the periodization of the freshwater and marine periods of life; the most important results were presented earlier (Pavlov et al., 2013, 2016; Pavlov and Skorobogatov, 2014). The composition of the food bolus was studied by the counting-weight method to assess the nutritional characteristics (Shorygin, 1952; *Rukovodstvo*..., 1961). Specific sample sizes for different types of analysis are indicated in the relevant sections of the article. Statistical analysis of the data was carried out using the standard methods of univariate analysis (Lakin, 1990).

RESULTS

Population structure of whitespotted char in the rivers Kol and Kekhta is described considering the fish size, fish age, sex composition, fish abundance, and seasonal distribution of fish in the river system, the estuary (for the Kekhta River), and the estuarine part of the sea (for both rivers).

In the Kol River, population of whitespotted char comprises anadromous and resident (freshwater) components. The first one is represented by individuals that migrate to the sea in summer to feed, the second one, by river-resident juveniles of different ages (parrs) and downstream juveniles migrating to the sea at different stages of smoltification (smolts). In the river basin, there are also individuals that reach sexual maturity in the river, namely, these are dwarf males, similar in appearance and color to immature juveniles, and river-resident rheodromous individuals, which have a number of differences in body proportions, body size, and coloration from juveniles, dwarf males, and anadromous fish (Table 2, Fig. 2). The fish is considered "river-resident rheodromous" (according to: Pavlov, Skorobogatov, 2014) if its life cycle is realized within the river, where it migrates from spawning tributaries to the main channel and back, the length of such migrations is dozens of kilometers. Population of whitespotted char in the Kekhta River also consists of anadromous and resident components. Parr, smolts, and dwarf males are found in the composition of the resident herd.

In the Kol River basin, undifferentiated juveniles of whitespotted char (parrs) are found mainly in tributaries of mountain and tundra types, where their abun-

Table 2. Morphometric characteristics of whitespotted char *Salvelinus leucomaenis* belonging to different groups, the Kol River

Sign	Parrs, 3+ ($n = 25$)	Smolts, 3+ ($n = 25$)	Dwarf males ($n = 25$)	River-resident rheodromous ($n = 31$)	Anadromous ($n = 50$)
FL mm	172.1 (128–192)	212.3 (201–221)	219.6 (196–229)	355.5 (324–427)	516.8 (497–603)
			In % *FL*		
c	22.49 ± 0.18 (21.2–23.5)	21.30 ± 0.17 (18.9–22.3)	23.53 ± 0.39 (22.4–24.6)	23.87 ± 0.31 (21.8–24.9)	21.42 ± 0.24 (20.2–23.2)
ao	5.44 ± 0.12 (4.4–6.2)	5.14 ± 0.13 (4.3–6.1)	6.64 ± 0.16 (5.3–7.0)	5.98 ± 0.17 (5.5–7.3)	7.01 ± 0.12 (6.4–8.2)
o	5.31 ± 0.10 (4.5–5.8)	4.32 ± 0.12 (3.9–5.0)	4.87 ± 0.13 (4.1–5.1)	5.16 ± 0.12 (4.5–6.0)	2.61 ± 0.14 (2.1–3.8)
op	12.42 ± 0.15 (11.8–13.5)	12.65 ± 0.13 (11.3–13.1)	13.29 ± 0.16 (12.3–14.3)	14.37 ± 0.13 (12.7–15.1)	12.39 ± 0.15 (11.5–12.8)
io	6.48 ± 0.14 (5.6–7.4)	6.18 ± 0.11 (5.3–7.0)	6.88 ± 0.14 (6.1–7.7)	7.42 ± 0.14 (6.9–8.1)	7.45 ± 0.13 (6.7–8.3)
hcz	14.56 ± 0.21 (12.8–16.0)	13.04 ± 0.13 (12.4–14.6)	16.42 ± 0.19 (16.1–17.9)	15.26 ± 0.15 (13.2–17.3)	13.15 ± 0.18 (12.0–14.7)
lm	11.46 ± 0.19 (10.4–12.6)	10.88 ± 0.12 (9.9–11.7)	13.72 ± 0.18 (12.6–14.1)	13.88 ± 0.17 (12.1–15.3)	12.21 ± 0.13 (11.4–13.9)
hm	2.26 ± 0.05 (1.9–2.6)	1.76 ± 0.09 (1.5–1.9)	2.79 ± 0.11 (2.3–3.2)	2.33 ± 0.12 (2.1–2.7)	2.01 ± 0.09 (1.6–2.3)
lmd	13.17 ± 0.17 (12.5–14.3)	12.87 ± 0.12 (11.6–13.7)	13.55 ± 0.18 (12.9–14.8)	15.06 ± 0.15 (13.2–16.8)	13.85 ± 0.18 (12.4–16.2)
H	19.78 ± 0.48 (17.0–22.1)	17.33 ± 0.20 (16.2–18.8)	24.37 ± 0.32 (22.9–25.8)	20.06 ± 0.21 (17.8–22.3)	21.55 ± 0.20 (19.5–22.9)
h	8.63 ± 0.14 (7.8–9.4)	8.23 ± 0.17 (7.3–9.0)	9.17 ± 0.16 (8.4–9.5)	9.05 ± 0.18 (7.9–10.1)	8.63 ± 0.12 (7.8–9.2)
pl	17.71 ± 0.21 (17.2–18.9)	18.22 ± 0.19 (17.3–20.1)	17.13 ± 0.21 (16.1–17.5)	16.56 ± 0.19 (15.7–17.2)	16.81 ± 0.14 (15.9–18.1)
lD	12.68 ± 0.29 (11.2–13.9)	12.32 ± 0.12 (10.9–13.5)	15.74 ± 0.25 (14.8–16.8)	14.23 ± 0.18 (12.9–15.4)	11.07 ± 0.13 (9.7–12.2)
hd	16.25 ± 0.41 (13.5–18.0)	13.12 ± 0.13 (12.0–14.0)	17.04 ± 0.33 (14.2–18.7)	16.76 ± 0.22 (15.3–17.7)	11.14 ± 0.12 (9.6–13.6)
la	9.14 ± 0.15 (8.1–10.0)	9.16 ± 0.11 (8.2–10.0)	9.18 ± 0.16 (8.3–10.1)	8.98 ± 0.17 (8.0–10.0)	7.98 ± 0.10 (6.9–8.8)
hA	14.51 ± 0.23 (13.1–16.2)	12.11 ± 0.13 (11.7–13.8)	14.77 ± 0.21 (13.6–16.2)	13.71 ± 0.18 (11.9–14.3)	11.85 ± 0.11 (10.5–13.1)
LP	16.08 ± 0.33 (14.2–18.3)	14.51 ± 0.14 (13.2–15.4)	17.30 ± 0.35 (15.5–18.2)	16.79 ± 0.16 (15.3–18.4)	12.38 ± 0.13 (11.8–14.2)
LV	12.73 ± 0.24 (10.5–13.6)	11.46 ± 0.12 (10.9–12.6)	12.05 ± 0.21 (11.0–13.8)	12.57 ± 0.18 (11.3–14.2)	11.56 ± 0.13 (10.7–12.6)
aD	42.43 ± 0.48 (39.6–43.5)	41.77 ± 0.19 (39.4–42.8)	42.72 ± 0.52 (39.8–44.6)	40.11 ± 0.23 (38.5–43.1)	43.89 ± 0.22 (41.2–45.7)
PD	38.65 ± 0.37 (36.7–40.9)	39.37 ± 0.18 (37.2–41.8)	36.75 ± 0.44 (35.0–38.2)	38.72 ± 0.24 (36.5–40.8)	41.18 ± 0.20 (39.6–42.5)
aV	48.50 ± 0.42 (45.7–51.4)	49.02 ± 0.22 (46.7–50.8)	49.36 ± 0.52 (47.7–52.1)	48.54 ± 0.25 (45.4–50.8)	51.23 ± 0.25 (49.2–54.2)
aA	67.22 ± 0.65 (65.4–69.3)	69.37 ± 0.25 (66.9–71.2)	64.55 ± 0.74 (63.3–68.9)	64.67 ± 0.30 (62.3–68.2)	70.14 ± 0.33 (68.1–72.2)
P–V	30.08 ± 0.31 (25.8–35.0)	30.29 ± 0.23 (26.1–33.6)	30.37 ± 0.35 (26.3–34.5)	27.54 ± 0.22 (25.3–29.2)	29.53 ± 0.23 (26.7–31.6)
V–A	20.07 ± 0.29 (18.4–23.1)	21.42 ± 0.21 (18.9–23.8)	19.65 ± 0.28 (18.6–21.4)	17.66 ± 0.18 (15.3–20.3)	19.69 ± 0.21 (18.9–21.9)

The values outside the brackets are the mean value and its error, in brackets, limits of variation (min–max). *FL*—length by Smith, *c*—head length, *ao*—snout length, *o*—horizontal diameter of the eye, *op*—postorbital distance, *io*—interorbital distance, *hcz*—head height at the occiput level, *lm*—maxillary length, *Hm*—upper jaw width, *lmd*—lower jaw length, *H*—maximum body height, *h*—caudal peduncle height, *pl*—caudal peduncle length, *lD*—length of the dorsal fin base, *hD*—dorsal fin height, *lA*—length of the anal fin base, *hA*—anal fin height, *lP*—pectoral fin length, *lV*—pelvic fin length; distances: *aD*—antedorsal, *pD*—postdorsal, *aV*—anteventral, *aA*—anteanal, *P–V*—pectoventral, and *V–A*—ventroanal.

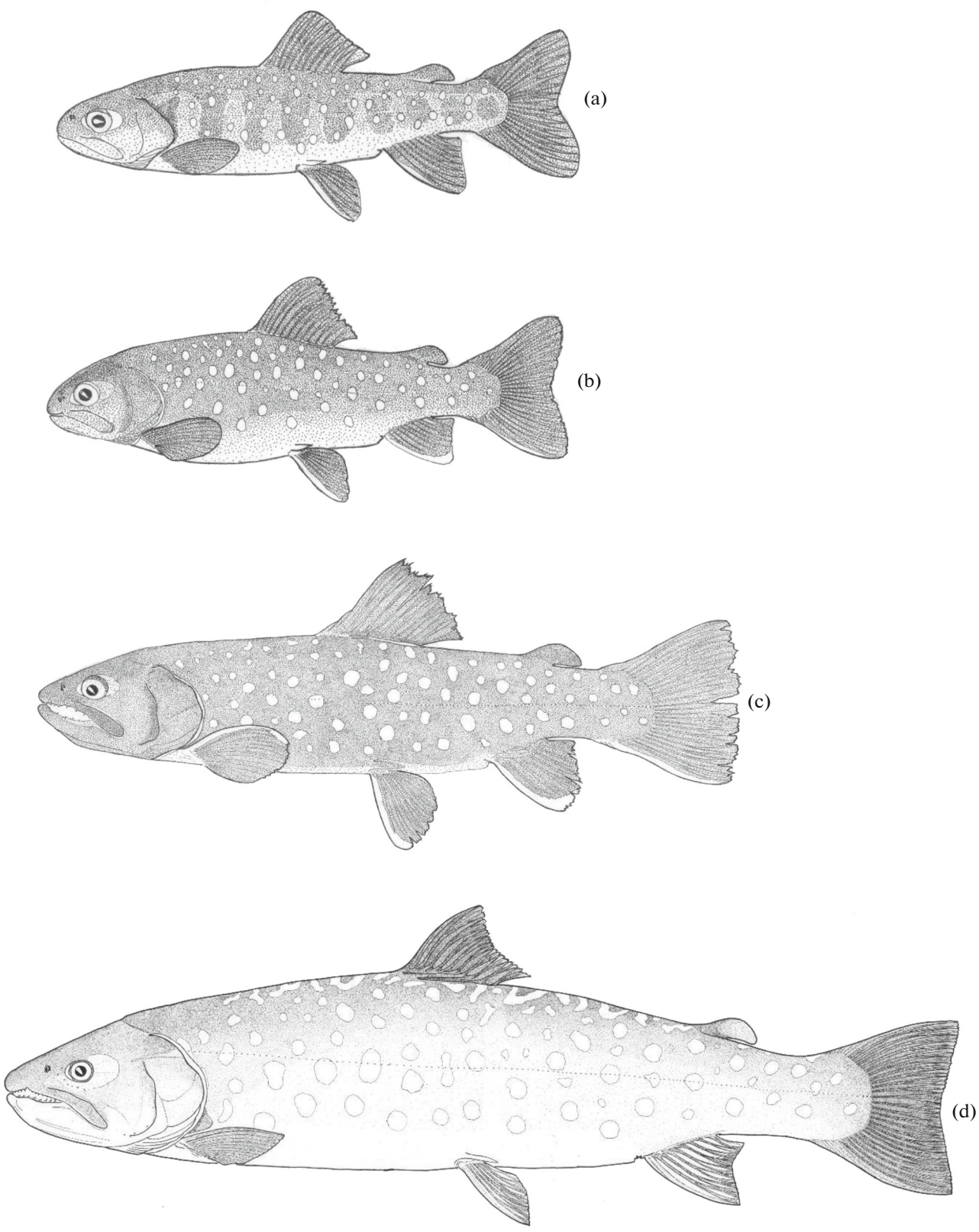

Fig. 2. Appearance of whitespotted char *Salvelinus leucomaenis* from the Kol River basin, Western Kamchatka: (a) parr *FL* 134 mm, age 2+, female, II stage of gonad maturity (Simovy brook, September 3, 2004); (b) dwarf male *FL* 194 mm, 3+, V stage of gonad maturity (Simovy Brook, whitespotted char spawning grounds, September 3, 2004); (c) river-resident rheodromous individual *FL* 329 mm, 6+, male, IV stage of gonad maturity (main channel of the Kol River, 35 km from the mouth, August 18, 2007); (d) anadromous individual *FL* 636 mm, 9+, female, IV stage of gonad maturity (mouth of the Kol River, August 28, 2006).

dance may exceed 30% of the total number of juveniles of all other salmon species (Fig. 1). In the tributaries, parrs of whitespotted char consume a wide range of prey; from the first summer of life, they become predators and prey on the juvenile Dolly Varden *S. malma;* at the age of 1+ and older, fish food makes up more than 30% of their diet (Table 3). In the main channel and side channels, juveniles of whitespotted salmon are found singly.

In the Kekhta River, parrs of whitespotted char live over a considerable distance, from the zone of influence of the sea tide up to the sources of the river and tributaries (Fig. 1). The largest concentrations and the most complex age composition of juveniles of whitespotted char are found in the middle and upper reaches. Underyearlings of whitespotted char live throughout the entire section of the river, hiding in crevices of boulders and large pebbles; older parrs locate under steep banks or among placers of large boulders, as well as in small pits in the areas of the gate current. In the main riverbed of the Kekhta River, whitespotted char occupies the 4th place by abundance after juvenile Dolly Varden, rainbow trout *Parasalmo* (=*Oncorhynchus*) *mykiss,* and coho salmon *Oncorhynchus kisutch* (36 control catches at 8 plots). Juvenile whitespotted char in the Kekhta River begins to consume fish food as they become yearlings, similarly to those in the Kol River; from the age of 1+, more than 30% of their diet is made up of juveniles of other salmonids; fish food becomes dominant as they grow further on (Table 3).

Dwarf males of whitespotted char in the Kol River basin differ from immature fish by a massive head, the upper jaw is slightly curved upwards (straight in immature fish), the profile of the back between the head and the beginning of the dorsal fin is steeper, the body height is greater (23.1–24.3 versus 20.4–21.8% *FL* in immature juveniles), the body and caudal peduncle are almost round in cross section (in immature fish they are distinctly laterally compressed), the caudal peduncle is shorter (16.2–17.1 versus 17.3–18.2% *FL* in juveniles) and high (8.4–9.5 versus 7.4–8.5% *FL*), the pectoral fins of dwarf males are wide, fan-shaped, and the caudal fin is weakly emarginated with rounded lobes (Table 2, Fig. 2).

In immature fish, 9–10 fry spots-stripes are always clearly visible on the body sides; in dwarf males, they have the blurred edges and become visible only in side light; during spawning, they merge with the background of the body. In dwarf males, the first rays of the ventral and anal fins are milky white, contrasting sharply with the dark background of the rest of the fin; the abdomen has a well-defined orange or reddish color, which never occurs in immature individuals; spots on the body sides are light or with a slight yellow tint throughout the year. During spawning, dwarf males become darker; their pectoral, ventral, and anal fins are orange; the abdomen is less bright and is covered with a black pigmented reticulum; the color of the spots on the body sides does not change.

In the Kol River, dwarf males are found only in spawning tributaries, where they occupy sections of the middle and upper reaches. Their numbers are low: generally, only one dwarf male is found on a 20–30-m long reach in July–August (data for 237 reaches of six tributaries). In spawning tributaries, the number of dwarf males in relation to the total number of immature juveniles of all age classes is the smallest compared to other salmon species (Table 4). Within the reach, dwarf males choose specific biotopes: they are located in places with the greatest depth (on average 0.73 ± 0.10 m, but not less than 0.65 m, $n = 38$) with various shelters. Most often, these are the sections of turf hanging over the water or the roots of near-water trees, less often, a tree trunk fallen into the stream. Usually, dwarf males live in niches under washed-out banks, thereby they choose a site with shelters, resembling the roof, in most cases. As a rule, at the location of a dwarf male, the current velocity is 0.53 ± 0.11 m/s ($n = 44$). The bottom substrate is not a limiting factor for choosing a biotope; in approximately 60% of cases, the bottom is composed of sand and gravel, less often, of large pebbles (~35%) or boulders at the bottom. Dwarf males stay almost always in the middle layer of water between the bottom and the surface. In the tributaries of the Kol River, dwarf males of whitespotted char are solitary predators; >70% of their diet consists of juveniles of Dolly Varden and coho salmon (Table 3). Based on observations and targeted fishing with fishing gear, dwarf males grab their prey near the coast, making throws from their shelter; after a successful hunt, they seek to immediately return back under the overhanging coast. Dwarf males actively feed in the summer, but stop feeding during the spawning period.

In the Kekhta River, dwarf males of whitespotted char are found in areas of the middle and upper reaches. Due to the complex structure and large size of the main channel of the river, their biotope is somewhat different than in the tributaries of the Kol River. In the upper reaches of the Kekhta River, where the bottom is composed of coarse-grained material (boulders up to 60 cm in size and blocks with sharp edges), dwarf males are located in depressions ("circuses") between large boulders on rifts, being covered from all sides. However, here dwarf males do not have a "roof over their heads", but there is always a local water vortex above the upper boundary of the boulders. Usually, the depth above the biotope is 0.3–0.5 m (0.39 m on average), the flow velocity over the upper edge of boulders is 0.6–0.8 m/s (0.73 m/s on average). Two or three dwarf males whitespotted char may locate at one rift 15–17-m wide and 10–12-m long, in a distance of 8–10 m from each other. In the Kekhta River, dwarf males are not found at the sites where small tree trunks fallen into the water or washed banks are present. The number of dwarf males of whitespotted char is significantly lower than those of Dolly Varden and masu

Table 3. Characteristics of nutrition of intrapopulation groups of whitespotted char *Salvelinus leucomaenis* (share of the component, % of food mass) in the basins of the Kol and Kekhta rivers (values to the left and to the right of the slash, respectively)

Index	Underyearlings 0+	Parrs		Dwarf males*	River-resident rheodromous **	Anadromous***
		1+	2+			
Chironomidae larvae and Simuliidae midges	23/22	9/6	7/1	1/–		
Larvae of Ephemeroptera, Plecoptera, Trichoptera	34/25	21/20	16/14	9/5	7	
Eggs of Pacific salmon *Oncorhynchus* spp.	27/27	27/21	22/18	11/10	12	
Imago and larvae of terrestrial insects	12/21	14/20	13/21	8/5	<1	
Underyearlings of Dolly Varden *Salvelinus malma FL* < 50 mm	4/5	16/18	21/20	23/26	15	
Underyearlings of coho salmon *O. kisutch FL* < 70 mm		13/15	18/18	18/23	11	
Dolly Varden *FL* > 50 mm			2/6	18/19	26	
Parrs of coho salmon *FL* > 70 mm			1/1	12/12	23	
Downstream juveniles of pink salmon *O. gorbuscha* and chum salmon *O. keta*			–/1		5	11/18
Marine mysids (Mysidae)						12/27
Juveniles of starry flounder *Platichthys stellatus FL* 70–130 mm						56/43
Juveniles of yellowfin sole *Limanda aspera FL* 80–90 mm						<1/–
Juveniles of sculpins (Cottidae) *FL* 80–110 mm						8/10
Juveniles of saffron cod *Eleginus gracilis FL* 100–150 mm						4/–
Capelin *Mallotus villosus catervarius FL* 120–190 mm						3/–
Three-spined stickleback *Gasterosteus aculeatus FL* 60–90 mm						3/<1
Nine-spined stickleback *Pungitius pungitius FL* 40–60 mm						<1/<1
Pighead prickleback *Acantholumpenus mackayi FL* 200–250 mm						<1/–
Number of fish, ind.	88/30	124/50	35/30	21/15	23/–	28/30

* August, individuals of two age classes (3+ and 4+); ** only for the Kol River: summer period, July–August, for entire group, fish age 4+–8+, *FL* 270–430 mm; *** marine feeding period–late June–August, in general for the group, 5+–8+, *FL* 400–650 mm.

Table 4. Parameters of particular sites at spawning tributaries of the Kol River and the relative abundance of dwarf males (values left to the slash) and parrs (values right to the slash) in whitespotted char *Salvelinus leucomaenis*, Dolly Varden *S. malma*, and masu *Oncorhynchus masou*

Tributary	Length	Width	Depth, average	Area, m^2	Number of fish, ind.		
	m				white-spotted char	dolly varden	masu
Krasnaya River	271.8	3.6	0.33	993.6	3/583	72/825	24/552
Stream:							
— Glinisty	188.5	2.6	0.30	511.4	2/301	41/637	8/279
— Skvichik	201.5	3.5	0.36	734.8	2/469	55/751	11/412
— Simovy	233.5	2.6	0.32	642.6	4/388	48/722	22/433

O. masou. Usually, there are 15–20 dwarf males of Dolly Varden and up to ten dwarf males of masu per one dwarf male of whitespotted char. Similar to the tributaries of the Kol River, dwarf males of whitespotted char consume mainly fish food in the Kekhta River. Upper reaches of the Kekhta River, composed of boulders, are also inhabits by juveniles of various salmon species (primarily, juveniles of Dolly Varden and coho salmon), which are the main food for dwarf males of whitespotted char. Noteworthy, no cases of feeding of dwarf males of whitespotted char on the underyearlings and parrs of rainbow trout have been yet reported, which are comparable in number to juveniles of Dolly Varden and coho salmon.

River-resident rheodromous individuals are found only in the basin of the Kol River. They have a flat massive head (23–24% *FL)*, an upwardly curved upper jaw, a cylindrical body, an oval caudal peduncle, a truncated or even slightly oval caudal fin, wide fan-shaped pectoral fins; dorsal and anal fins have a convex, uneven outer edge. The coloration is protective: the fish body has a grayish-olive background, the belly is gray; spots on the sides of the body are light or light gray, weakly contrasting; worm-like light spots on the back (a characteristic feature of anadromous individuals) are weakly expressed, slightly elongated spots with an uneven edge are more common (Fig. 2). During spawning, the body of river-resident rheodromous fish becomes dark gray; head, including lower jaw, is black; all fins are almost black with a bluish tint; the first rays of the pectoral, ventral, and anal, as well as the lower unbranched rays of the caudal fins, become milky white and contrast sharply with the rest of them. The spots on the body sides become light pink. River-resident rheodromous males have a darker coloration during the spawning period compared to females.

River-resident rheodromous individuals of whitespotted char live mostly in the main channel of the river and very rarely, in large side channels. Their typical biotope is a deep laminar section of a large pool (depth 1.3–3.0 m, on average 1.7 ± 0.2 m), where the flow velocity is 0.5–0.6 m/s at low water (July–September); the presence of trees or blockages of trees fallen into the water is obligatory. In such areas, more than 95% catches of river-resident rheodromous whitespotted char are registered. The fish locate in the near-bottom water layer under fallen trunks or in submerged trees among their branches and trunks; almost always there is a "roof", as observed for dwarf males in tributaries. River-resident rheodromous whitespotted char leads a solitary and secretive way of life, rarely two or three individuals stay together in large creases. This is a predator that makes exits from shelters towards the high coast, where it consumes during the low season juvenile Dolly Varden (~40% of the diet), less often, coho salmon (~30%) (Table 3), and singly the juveniles of other salmon species (Chinook salmon *O. tshawytscha,* sockeye salmon *O. nerka)*, trying to keep in the deep-water zone. Unlike Dolly Varden, river-resident rheodromous whitespotted char in the riverbed feeds on the eggs of Pacific salmon species only in the years of the prolific generation of pink salmon, the share of eggs in the food bolus is ~12% (on average for the study period, data for mid-late August).

River-resident rheodromous whitespotted char is confined mainly to the middle course of the river, about 80% of non-zero catches belong to the main channel, in 20–80-km distance from the mouth. It is rare in the foothill zone, where few wide and calm reaches prevail. In all the years of observations, river-resident rheodromous individuals of whitespotted char have not been found either at the lower reaches. In summer, they do not make significant migrations along the river; in almost 100% of cases, after catching an individual in a particular habitat, another individual has not appeared at the site until the autumn flood or it appeared there only the next year. The redistribution of river-resident rheodromous fish in the river is associated with floods or spawning. Mature breeders enter the tributaries in late August–early September; in mid-September, after spawning, they migrate back to the main channel and occupy new channel biotopes. Therefore, river-resident rheodromous whitespotted char in the basin of the Kol River is a typical demersal predator confined to relatively spacious (wide and deep) sections of the riverbed.

The abundance of river-resident rheodromous whitespotted char in the Kol River is low. According to

estimates of spawning associations in various tributaries in different years, the share of river-resident rheodromous individuals is only 3–5% of total herd of spawners. According to the data of target fishing on blockages in the reaches, there are 1–2 specimens of river-resident rheodromous form at a 120–170-m long reach.

Anadromous whitespotted char is confined during the feeding to the seaward estuary zone of the Kol River. In the first half of summer, the smolts of this species migrate downstream to feed in the river-sea frontal zone and return back. They make periodic migrations towards the river and towards the sea, depending on weather conditions and the tide level. During calm weather, when a plume of fresh water is formed in the sea over denser and colder sea waters, whitespotted char may be found at a 3.5-km distance from the river mouth, most of the fish feed in about 1-km distance from the mouth. At the same time, whitespotted char prefers more saline (18–22‰) near-bottom zone under a layer of fresh water, where it feeds on marine organisms; the most important food items are juvenile flounders (Pleuronectidae) and large mysids (Mysidae) (Table 3). In case of strong waves or storms, whitespotted char goes into the river estuary and concentrates mainly in the estuarine zone of the river. A somewhat different distribution is observed in late June–early July. During this short period of time, fish accumulate in the estuarine zone of the river, where it feeds on juveniles of Pacific salmon species migrating downstream. However, whitespotted char starts feeding on larger objects (starry flounder *Platichthys stellatus,* yellowfin sole *Limanda aspera,* and saffron cod *Eleginus gracilis*) much earlier compared to other char species (estuary and river-estuarine rainbow trout and Dolly Varden).

Anadromous whitespotted char in the Kekhta River is confined mainly to the brackish estuary, along which it migrates in the near-bottom water layer. Rarely, it may be observed near the shore; in summer, it prefers the depths exceeding 1 m; the largest individuals locate in the deepest parts of the estuary at a depth of 3–5 m, when the migration of juveniles of Pacific salmons takes place. Most likely, anadromous whitespotted char leaves the estuary, pursuing flocks of juveniles of chum salmon *O. keta* and of other salmon species migrating downstream. Although whitespotted char leads a vagrant lifestyle in the estuary, there is still no evidence that during the summer it leaves the estuary and lives in the river. The near-bottom water layer of the estuary (salinity of 12–18‰ depending on the tide phase) is the habitat zone of anadromous whitespotted char, the salinity of the surface water layer (0–1 m) here varies from 1.5‰ at low tide to 23‰ at high tide. In the estuary of the Kekhta River, whitespotted char feeds mainly on sculpins (Cottidae) and starry flounder, as well as on marine mysids (Table 3). In the second half of June and until the end of the first decade of July, anadromous whitespotted char actively feeds on juveniles of Pacific salmons migrating downstream. No food selectivity is observed; ration consists of the most abundant species at the moment, mainly chum salmon. Marine mysids bring a significant share of the diet, since they form significant accumulations in the estuary in the summer. At the same time, large individuals of anadromous whitespotted char *FL* > 400 mm consume almost fish only, and mysids are found extremely rare in their stomachs.

Anadromous migration of whitespotted char from the sea to spawning grounds takes place in August in both rivers. Unlike other species of anadromous salmon fish, a pronounced spawning run in whitespotted char in the Kol River is not observed. Anadromous individuals of whitespotted char go singly or in groups of 2–4, as a rule, along a steep bank, trying to move away from the migrating individuals of pink salmon and chum salmon. Most often, anadromous whitespotted char migrating upstream may be found along steep banks heavily littered with woody material; it avoids shallow waters along a gently sloping coast or channel shallows near river midline. For a short period, anadromous specimens may concentrate in large deep and wide pits, but only if they are not occupied by Pacific salmons. In general, anadromous whitespotted char migrating upstream in the Kol River leads a very secretive life. According to the data of underwater observations, individuals of whitespotted char are very closely associated with the river bottom, especially if there is low illumination due to blockages or tree branches hanging over the water. Often, individuals of anadromous whitespotted char locates on the reaches among the rubble of trees, in the same places where river-resident rheodromous whitespotted char stays. There also cases, when anadromous whitespotted char moves from the blockages upstream and the individuals of river-resident rheodromous whitespotted char begin to migrate behind them, forming joint flocks. In conditions of underwater twilight, coloring provides them with highly effective camouflage. Whitespotted char rises into the middle water layer very rarely. When overcoming shallow rifts, it almost always tends to stay among the boulders close to the bottom. At the end of August, in the Kol River, anadromous and river-resident rheodromous whitespotted char concentrate near the mouths of spawning tributaries, both forms enter the tributaries simultaneously. When entering the spawning tributary, both anadromous and river-resident rheodromous whitespotted char continue to lead a secretive lifestyle, using any shelters in the stream, such as washed banks, tree roots, blockages, overhanging turfs. Generally, it is very difficult to detect spawners entering spawning streams. In the Kol River and its tributaries, the nature of migrations and the biotopes chosen by whitespotted char similar are in many respects to those for masu, especially in the tributaries. However, by the time of anadromous migration of

Table 5. Age composition of the groups of whitespotted char *Salvelinus leucomaenis* from the Kol and Kekhta rivers (long-term average data, 2003–2008), %

Age	Kol River	Kekhta River
	Dwarf males	
3+	41.6	100
4+	58.4	
Number of fish, ind.	361	44
	River-resident rheodromous	
5+	43.5	
6+	48.2	
7+	8.3	
Number of fish, ind.	120	
	Anadromous	
5+	21.5	20.4
6+	28.8	23.3
7+	23.5	25.2
8+	14.3	15.7
9+	8.3	9.3
10+	3.6	3.9
11+		2.2
Number of fish, ind.	302	209

whitespotted char (mid-August), masu spawners are almost all dead after spawning.

In the Kekhta River, anadromous whitespotted char migrates towards spawning grounds throughout August. A pronounced spawner run has not been observed; whitespotted char forms groups of three to six individuals of different sizes, which move along the very middle of the river at the maximum depth in the near-bottom water layer. Fish rest under steep washed-out banks or in deep channel pits. In the Kekhta River, anadromous whitespotted char always uses any shelters: single tree trunks fallen into the water, a washed-out shore, large pieces of the shore slipped into the water, and others. Upon reaching the sections of the middle course, where spawning grounds are located, anadromous whitespotted char stay in the pits at the maximum depth. In the Kekhta River, which has shorter length and smaller depth compared to the Kol River, whitespotted char leads an even more secretive way of life.

Age, size-weight, and sex composition of whitespotted char. In Kol River, dwarf males of whitespotted char belong to two age classes 3+ and 4+, in the Kekhta River, only four-year old dwarf males are found. River-resident rheodromous fish enter the spawning herd at the age of six (5+), their maximum life expectancy does not exceed eight years, most of the group is represented by fish of the age class 6+. The age composition of anadromous fish is most complex, mature fish are represented by individuals of six-year-olds (the Kol River) and seven-year-olds (the Kekhta river). Anadromous males and females reach sexual maturity after two trips to the sea (biogeographic group R.2 +, where R is the number of full years in the river, 2+ is the next two years of life with trips to the sea in summer), live to the age of 10– 11 years (Table 5).

Dwarf males in both rivers have the smallest length and body weight among producers, while in the Kekhta River, their sizes are somewhat larger than in the Kol River. River body length rheodromous individuals from the Kol River varies from 257 to 436 mm (on average, 336 mm), body weight, from 250 to 850 g (on average, 443 g). Anadromous individuals in the same age classes are characterized by the largest body length and weight (Table 6).

According to estimates of breeder abundance in spawning grounds, the share of females among river-resident rheodromous fish varies from 28 to 36% in different years and in different tributaries. Among anadromous spawners, females somewhat predominate, their share varies from 58 to 63% in different years.

Female fecundity. In the Kol River, fecundity varies from 1472 to 3,256 eggs (on average, 2234.2 eggs) in females of anadromous whitespotted char (*FL* 410–613 mm; $n = 75$), in river-resident rheodromous females (*FL* 302–436 mm, $n = 25$), from 356 to 1,223 eggs (on average 802.4 eggs) (Fig. 3). Fecundity correlates with the body size: $r = 0.82 \pm 0.038$, $p < 0.01$ in river-resident rheodromous females; $r = 0.86 \pm 0.041$, $p < 0.01$ in anadromous. The individual fecundity of river-resident rheodromous females is significantly lower than that of anadromous females. The egg diameter in anadromous females varies from 4.61 to 5.32 mm (on average, 5.04 ± 0.08 mm); in river-resident rheodromous females, from 4.42 to 5.24 mm (on average, 4.92 ± 0.07 mm), the differences are insignificant ($t_{st} = 1.13$, $p > 0.95$). Anadromous and river-resident rheodromous females differ in the color of eggs, they are orange and pale yellow, respectively. In the Kekhta River, fecundity of anadromous whitespotted char (*FL* 465–690 mm) varies from 1,432 to 3,887 eggs (on average 2,763.3 eggs); it depends on body size ($r = 0.81 \pm 0.054$, $p < 0.01$). The egg diameter of anadromous females varies from 4.74 to 5.96 mm (on average, 5.76 ± 0.10 mm) in the Kekhta River; eggs have a more intense orange color compared to those of anadromous females from the Kol River. This may be due to the peculiarities of nutrition, since whitespotted char from the Kekhta River mostly consumes marine crustaceans (mysids) (Table 3).

Relationships between fish of different intrapopulation groups. In the summer, during the feeding period, anadromous, river-resident rheodromous and dwarf males are separated in river systems. However, during the spawning period, the formation of a single spawning population is observed. In the tributaries of the Kol

Table 6. Body length (*FL*) and body weight of mature specimens of whitespotted char *Salvelinus leucomaenis* from different groups in the Kol and Kekhta rivers

Age	Kol River			Kekhta River		
	FL mm	weight, g	number of fish, ind.	*FL* mm	weight, g	number of fish, ind.
	Dwarf males					
3+	198.5 (188–217)	103.6 (92–131)	179	207.3 (190–222)	122.3 (108–185)	38
4+	232.8 (223–247)	134.5 (105–155)	156			
	River-resident rheodromous					
5+	285.4 (257–374)	260.5 (250–500)	35			
6+	327.1 (285–400)	377.5 (284–704)	32			
7+	410.6 (380–436)	660.7 (455–850)	10			
	Anadromous					
5+	380.5 (298–486)	505.7 (304–1050)	65	401.8 (355–461)	661.0 (442–1000)	42
6+	461.1 (386–590)	902.8 (480–2000)	52	471.7 (431–528)	1063.4 (722–1631)	45
7+	522.8 (430–564)	1450.2 (933–2200)	73	533.5 (442–623)	1614.4 (720–2300)	49

The values outside the brackets are the mean value and its error, in brackets, limits of variation (min–max).

River, spawning of whitespotted char takes place in the second decade of September. In the areas, where the spawning grounds of whitespotted char are located, river-resident rheodromous and dwarf males breed together with a pair of anadromous spawners. Usually, one anadromous male, one river-resident rheodromous male, and one (very rarely, two) dwarf male breeds with one anadromous female. According to our observations (62 spawnings, 3 tributaries, 3 years), anadromous male spawns with only one female, while river-resident rheodromous and dwarf males may change female partners and breed with several anadromous females. River-resident rheodromous female breeds with the smallest anadromous males, river-resident rheodromous and dwarf males. Therefore, all components of the local population of whitespotted char constitute a single system.

DISCUSSION

According to the literature, it is believed that intraspecific diversity of whitespotted char is low, and the species is represented by an "anadromous form" with rare exceptions northwards off Hokkaido, in Kamchatka, and in the rivers of the continental coast of the Sea of Okhotsk (Fausch et al., 1994; Yamamoto et al., 1999, 2000; Hosoya, 2002; Morita et al., 2013).

Our results evidence that local populations of whitespotted char have a more complex structure in the north of the range (rivers of Kamchatka) than it has been proposed previously (Kawanabe, 1989; Chereshnev et al., 2002). In addition to anadromous individuals, the populations also contain dwarf males and river-resident rheodromous fish, which realize their life cycle in fresh waters. At the same time, dwarf males are found in both studied rivers, Kol and Kekhta, i.e., in mountain and tundra types. Dwarf males are also registered in other rivers of Kamchatka (Savvaitova et al., 2007; Pavlov et al., 2016). It is obvious that dwarf males are a universal freshwater component of the population structure of whitespotted chat in Kamchatka, in contrast to small "brook" females maturing in fresh waters in juvenile form, not found during our study. The only one "brook" population of whitespotted char, represented by mature males and females, has been found only in one thermal stream on the eastern coast of Kamchatka (Esin and Sorokin, 2012).

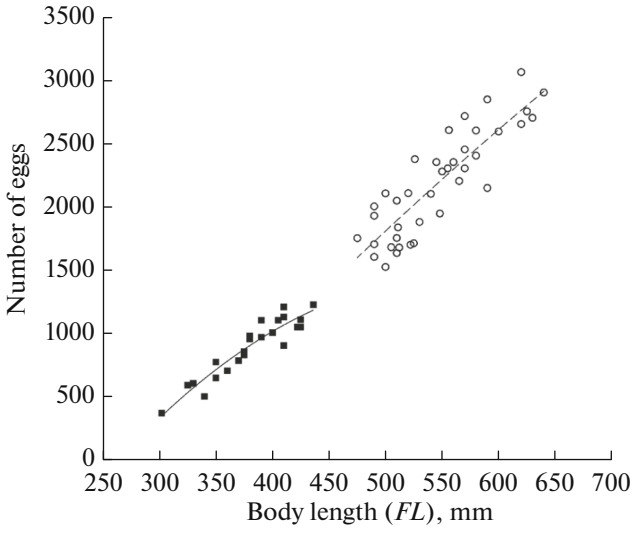

Fig. 3. Fecundity of female whitespotted char *Salvelinus leucomaenis* from the Kol River: (○) anadromous, $n = 75$; (■) river-resident rheodromous, $n = 25$.

An analysis of the occurrence of individuals of freshwater groups in the river system indicates a high degree of mosaicity in their distribution and confinement to specific biotopes. Thus, dwarf males are found only in spawning tributaries (Kol River) or in the immediate vicinity of spawning areas (Kehta River). River-resident rheodromous individuals are registered in the Kol River only, they exclusively occupy deep reaches with blockages and creases. The mouth zone of the river and the adjacent part of the sea is a habitat zone of anadromous fish. As a result, in summer, fish from different intrapopulation groups separate in space. Their joint spawning becomes an integrating factor: dwarf males, rheodromous and anadromous males and females form a single reproductive system, which ensures cross-breeding.

Noteworthy, relative abundance of fish realizing their life cycle in fresh waters is generally small compared to anadromous group, which mainly ensures the reproduction of the local population. At the same time, regard must be paid to large proportion of mature females (30% or more) in river-resident rheodromous grouping in the basin of the Kol River. Our data indicate that females with a resident type of life strategy can make a significant contribution to the reproduction of the local population in the north of the species range. Although the contribution of river-resident rheodromous females of whitespotted char, maturing in fresh waters, is significantly less in the reproduction of entire population than that of anadromous females, the former may be considered as an important reserve that provides the population with additional stability in the mosaic conditions of salmon river ecosystems.

Abundance of rheodromous whitespotted char is low in the Kol River; most likely, it is a consequence of the limited specific biotopes suitable for its habitation in the river basin. The Kol River is a small river, in which the biotopes suitable for habitation of the resident whitespotted char are concentrated only in a limited area of the middle course, where typical elements of the structure of the river channel are deep reaches with blockages of tree trunks that form shelters for fish. Therefore, it is every reason to believe that a limiting factor for existence of river-resident rheodromous fish in the Kol River is the presence of a specific biotope, "tree blockage at a deep reach". According to our data, river-resident rheodromous whitespotted char is characterized by the most pronounced confinement to strictly defined biotopes in comparison with all other salmon species in the Kol River (resident rainbow trout and Dolly Varden; dwarf males of Dolly Varden and masu). Previously, Japanese researchers have repeatedly pointed out a pronounced tendency to choose a biotope "with shelters", including "with a roof over their heads" for resident whitespotted char inhabiting the river ecosystem (Yagyu, 2009; Hasegawa and Yamamoto, 2009; Nakamura, 2011; Miyamoto and Araki, 2019). For some rivers of the islands of Hokkaido and Honshu, a high correlation has been found between the structure of the reaches and the number of river-resident individuals (Hasegawa and Maekawa, 2008; Kikko et al., 2011).

The "blockage on the reach" biotope as a limiting factor for the existence of river-resident rheodromous whitespotted char is confirmed by the absence of fish of this ecological group in the Kekhta River, where there are no such blockages. Weak development of woody vegetation on the banks, less pronounced processes of erosion of the banks due to the weak current, and lower slope of the bed are the possible reasons. Noteworthy, river-resident rheodromous whitespotted char has not been found in some other rivers of the tundra type, comparable in size and water content with the Kol River, for example, in the Utkholok River (Pavlov et al., 2016) and Sopochnaya River (our observations in 1997–2002). Probably, the absence of creases at deep reaches is the main reason for the absence of river-resident rheodromous whitespotted char in tundra-type rivers. Therefore, in whitespotted char, the diversity at the population level is predetermined by the geomorphological peculiarities of the rivers, inhabited by local populations. Similar patterns are observed for rainbow trout in the rivers of Kamchatka (Pavlov et al., 2008; Kuzishchin, 2010).

In this regard, there is every reason to believe that river-resident rheodromous group is present with high probability in the composition of local populations of whitespotted char in the foothill rivers, where the channel processes of bank erosion are well expressed and accompanied by blockages of woody material in the channel. Correspondingly, in the north of the range, the "channel" type of the life strategy of whitespotted char is found more widely than it has been previously proposed.

Our data allow to expand the understanding of the intraspecific structure of whitespotted char within the species range. Earlier, it has been believed that various intrapopulation groups of whitespotted char (anadromous, river-resident rheodromous, dwarf bisexual brook forms, and dwarf males) are found only in water bodies of the Sea of Japan basin, which is considered an ecological optimum zone. In particular, it is emphasized that the greatest diversity of whitespotted char in the southern parts of the range is due to its preferences for the warmer environment (Kawanabe, 1989; Yamamoto et al., 1996; Morita et al., 2000; Morita and Morita, 2002; Morita and Yamamoto, 2002; Morita and Yokota, 2002; *Ryby*..., 2012; Morita et al., 2019). So far, the existence of the only brook bisexual population of whitespotted char in Kamchatka in a thermal stream is also due to stable high temperatures throughout the year (Esin and Sorokin, 2012). However, our data indicate that in the north of the range (in Kamchatka), the diversity of whitespotted char is comparable to that in the south of the range, despite a more severe climate here than in the

Sea of Japan basin. At the same time, it should be noted that the ratio of anadromous and resident fish in the composition of populations is shifted towards anadromous ones in the north of the range, In the south of the range of whitespotted char, the ratio of anadromous and resident individuals is either equal in the populations, or the resident ones predominate. Apparently, different ratio of anadromous and resident fish throughout of the range may be considered as a manifestation of clinal variability, expressed in an increase in the proportion of resident individuals in the ecological optimum zone of the species.

Therefore, local adaptations of whitespotted char in the north of the range are similar to those observed in the south (the Sea of Japan basin). Namely, there are anadromous and resident components, due to which the potential of the riverine species system is developed and polymorphism is maintained at the population level.

ACKNOWLEDGMENTS

The authors express their sincere gratitude to all participants of expeditions for invaluable help in collecting the material at the Kol and Kekhta rivers in 2002–2008.

FUNDING

The study was carried out within the framework of the State Task for Lomonosov Moscow State University (no. 121032300100-5), the project of the Lomonosov Moscow State University "Noah's Ark" (processing of materials, preparation of summary tables and figures), and with the support of the Russian Science Foundation (grant no. 19-14-00015-P, manuscript writing).

REFERENCES

Bird, D.J. and Cowx, I.G., The selection of suitable pulsed currents for electric fishing in fresh waters, *Fish. Res.*, 1993, vol. 18, nos. 3-4, pp. 363–376.
https://doi.org/10.1016/0165-7836(93)90163-2

Chereshnev, I.A., Volobuev, V.V., Shestakov, A.V., and Frolov, S.V., *Lososevidnye ryby severo-vostoka Rossii* (Salmonid Fish of the North-East of Russia), Vladivostok: Dal'nauka, 2002.

Dunham, J., Baxter, C., Fausch, K., et al., Evolution, ecology, and conservation of dolly varden, white-spotted char, and bull trout, *Fisheries*, 2008, vol. 33, no. 11, pp. 537–550.
https://doi.org/10.1577/1548-8446-33.11.537

Esin, E.V. and Markevich, G.N., *Gol'tsy roda Salvelinus Aziatskoi chasti Severnoi Patsifiki: proiskhozhdenie, evolyutsiya i sovremennoe raznoobrazie* (Charrs of the Genus *Salvelinus* in the Asian Part of the North Pacific: Origin, Evolution and Modern Diversity), Petropavlovsk-Kamchatsky: Kamchatpress, 2017.

Esin, E.V. and Sorokin, Yu.V., Residential form of white-spotted char *Salvelinus leucomaenis* inhabiting the warm stream discharging into Semlyachikskii Firth (Kronotskii natural reserve, Kamchatka), *J. Ichthyol.*, 2012, vol. 52, no. 2, pp. 172–179.

Fausch, K.D., Nakano, S., and Ishigaki, K., Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: Considering multiple factors across scales, *Oecologia*, 1994, vol. 100, nos. 1-2, pp. 1–12.
https://doi.org/10.1007/BF00317124

Gritsenko, O.F., *Prokhodnye ryby ostrova Sakhalin* (Anadromous Fishes of Sakhalin Island), Moscow: Vseross. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr., 2002.

Gruzdeva, M.A., Malyutina, A.M., Kuzishchin, K.V., et al., Regularities of the life history strategy adoption in masu salmon *Oncorhynchus masou* from the Kol River (Western Kamchatka) in regard to the processes of growth and sexual maturation, *J. Ichthyol.*, 2013, vol. 53, no. 8, pp. 585–599.
https://doi.org/10.1134/S0032945213050056

Gruzdeva, M.A., Kuzishchin, K.V., Pavlov, E.D., et al., Morphophysiological patterns of life history strategy adoption in Dolly Varden *Salvelinus malma* in Kamchatka, *J. Ichthyol.*, 2017, vol. 57, no. 5, pp. 688–705.
https://doi.org/10.1134/S0032945217050083

Gudkov, P.K., Materials on the biology of white-spotted charr *Salvelinus leucomaenis* of the Sea of Okhotsk, *Vopr. Ikhtiol.*, 1991, vol. 31, no. 6, pp. 898–909.

Gudkov, P.K., Skopets, M.B., and Chereshnev, I.A., On the biology of charrs of the genus *Salvelinus* (Salmonidae) in the Sea of Okhotsk basin. Characterization of the biological parameters of sympatric anadromous charrs from the rivers of Shelikhov Bay, in *Biologiya gol'tsov Dal'nego Vostoka* (Biology of Charrs of the Far East), Vladivostok: Dal'nevost. Otdel. Akad. Nauk SSSR, 1991, pp. 21–36.

Hasegawa, K. and Maekawa, K., Potential of habitat complexity for mitigating interference competition between native and non-native salmonid species, *Can. J. Zool.*, 2008, vol. 86, no. 5, pp. 386–393.
https://doi.org/10.1139/Z08-015

Hasegawa, K. and Yamamoto, S., Effects of competitor density and physical habitat structure on the competitive intensity of territorial white spotted charr *Salvelinus leucomaenis, J. Fish. Biol.*, 2009, vol. 74, no. 1, pp. 213–219.
https://doi.org/10.1111/j.1095-8649.2008.02133.x

Hosoya, K., Salmonidae, in *Fishes of Japan with Pictorial Keys to The Species*, Tokyo: Tokai Univ. Press, 2002, pp. 299–304.

Kawanabe, H., Japanese char(r)s and masu salmon problems: A review, *Physiol. Ecol. Japan. Spec.*, 1989, vol. 1, pp. 13–24.

Kikko, T., Kai, Y., and Nakayama, K., Relationships among tributary length, census population size and genetic variability of white-spotted charr (*Salvelinus leucomaenis*) in the Lake Biwa water system, *Ichthyol. Res.*, 2009, vol. 56, no. 1, pp. 100–104.
https://doi.org/10.1007/s10228-008-0063-0

Kikko, T., Kataoka, Y., Nishimori, K., et al., Size at maturity of fluvial white-spotted charr, *Salvelinus leucomaenis*, around the Lake Biwa water system varies with habitat size, *Ichthyol. Res.*, 2011, vol. 58, no. 4, pp. 370–376.
https://doi.org/10.1007/s10228-011-0229-z

Kouřil, J., Mikodina, E., Mikulin, A., et al., Different sensitivity between adult salmonids fish species and grayling to

an anaesthetic clove oil, *Abstr. Internat. Conf. "Aquaculture Europe 2009,"* Trondheim, 2009, p. 89.

Kuzishchin, K.V., Formation and adaptive significance of intraspecific ecological diversity in salmonids (family Salmonidae), *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Moskov. Gos. Univ., Moscow, 2010.

Kuzishchin, K.V., Mal'tsev, A.Yu., Gruzdeva, M.A., et al., Reproduction of mykiss *Parasalmo mykiss* in the Kol river (Western Kamchatka) and its controlling factors, *J. Ichthyol.*, 2008, vol. 48, no. 1, pp. 45–56.

Lakin, G.F., *Biometriya (Biometrics)*, Moscow: Vyssh. Shk., 1990.

Mikodina, E.V., Sedova, M.A., P'yanova, S.V., et al., *Rukovodstvo po primeneniyu anestetika "gvozdichnoe maslo" v akvakul'ture* (Guidelines for the Use of the Anesthetic "Clove Oil" in aquaculture), Moscow: Vseross. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr., 2011.

Miyamoto, K. and Araki, H., 2019. effects of water depth and structural complexity on survival and settlement of white-spotted charr (salvelinus leucomaenis), *J. High Resolut. Chromatogr. Chromatogr. Commun.*, vol. 840, no. 1, pp. 103–112.

Morita, K. and Morita, S.H.M., Rule of age and size at maturity: individual variation in the maturation history of resident white-spotted charr, *J. Fish. Biol.*, 2002, vol. 61, no. 5, pp. 1230–1238.
https://doi.org/10.1006/jfbi.2002.2138

Morita, K. and Yamamoto, S., Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations, *Conserv. Biol.*, 2002, vol. 16, no. 5, pp. 1318–1323.
https://doi.org/10.1046/j.1523-1739.2002.01476.x

Morita, K. and Yokota, A., Population viability of stream-resident salmonids after habitat fragmentation: A case study with white-spotted charr (*Salvelinus leucomaenis*) by an individual-based model, *Ecol. Modell.*, 2002, vol. 155, no. 1, pp. 85–94.
https://doi.org/10.1016/S0304-3800(02)00128-X

Morita, K., Yamamoto, S., and Hoshino, N., Extreme life history change of white-spotted char (*Salvelinus leucomaenis*) after damming, *Can. J. Fish. Aquat. Sci.*, 2000, vol. 57, no. 6, pp. 1300–1306.
https://doi.org/10.1139/f00-050

Morita, K., Morita, S.H., Nagasawa, T., and Kuroki, M., Migratory patterns of anadromous white-spotted charr *Salvelinus leucomaenis* in eastern Hokkaido, Japan: The solution to a mystery?, *J. Ichthyol.*, 2013, vol. 53, no. 10, pp. 809–819.
https://doi.org/10.1134/S0032945213100068

Morita, K., Sahashi, G., Miya, M., et al., Ongoing localized extinctions of stream-dwelling whitespotted charr populations in small dammed-off habitats of Hokkaido Island, Japan, *Hydrobiologia*, 2019, vol. 840, no. 1, pp. 207–213.
https://doi.org/10.1007/s10750-019-3891-1

Miyamoto, K. and Araki, H., Effects of water depth and structural complexity on survival and settlement of white-spotted charr (*Salvelinus leucomaenis*), *Hydrobiologia*, 2019, vol. 840, no. 1, pp. 103–112.
https://doi.org/10.1007/s10750-019-3887-x

Murza, I.G. and Khristoforov, O.L., *Opredelenie stepeni zrelosti gonad i prognozirovanie vozrasta dostizheniya polovoi zrelosti u atlanticheskogo lososya i kumzhi* (Determining the Degree of Maturity of the Gonads and Predicting the Age of Sexual Maturity in Atlantic Salmon and Brown Trout), Leningrad: Gos. Nauchno-Issled. Inst. Ozern. Rechn. Rybn. Khoz., 1991.

Nakajima, M. and Fujio, Y., Genetic differentiation among local populations of Japanese char *Salvelinus leucomaenis, Fish. Sci.*, 1995, vol. 61, no. 1, pp. 11–15.
https://doi.org/10.2331/fishsci.61.11

Nakamura, T., Meristic and morphometric variations in fluvial Japanese charr between river systems and among tributaries of a river system, *Environ. Biol. Fish*, 2003, vol. 66, no. 2, pp. 133–141.
https://doi.org/10.1023/A:1023674523652

Nakamura, T., relationships between physical characteristics of pools and the residency of stream-dwelling white-spotted charr, *Aquac. Sci.*, 2011, vol. 59, no. 3, pp. 427–433.
https://doi.org/10.11233/aquaculturesci.59.427

Pavlov, D.S. and Skorobogatov, A.M., *Migratsii ryb v zaregulirovannykh rekakh* (Fish Migrations in Regulated Rivers), Moscow: T-vo Nauch. Izd. KMK, 2014.

Pavlov, D.S., Savvaitova, K.A., Kuzishchin, K.V., et al., *Tikhookeanskie blagorodnye lososi i foreli Azii* (Pacific True Salmon and Trout of Asia), Moscow: Nauchnyi Mir, 2001.

Pavlov, D.S., Savvaitova, K.A., Kuzishchin, K.V., et al., Diversity of life strategies and population structure of Kamchatka mykiss *Parasalmo mykiss* in the ecosystems of small salmon rivers of various types, *J. Ichthyol.*, 2008, vol. 48, no. 1, pp. 37–44.

Pavlov, D.S., Savvaitova, K.A., Kuzishchin, K.V., et al., *Sostoyanie i monitoring bioraznoobraziya lososevykh ryb i sredy ikh obitaniya na Kamchatke (na primere territorii zakaznika "Reka Kol'")* (Status and Monitoring of Biodiversity of Salmonids and Their Habitat in Kamchatka (on the Example of the Territory of the Kol River Reserve)), Moscow: T-vo Nauch. Izd. KMK, 2009.

Pavlov, D.S., Kuzishchin, K.V., Gruzdeva, M.A., et al., Life history strategy diversity in the Kamchatkan Dolly Varden char *Salvelinus malma* (Walbaum) (Salmonidae, Salmoniformes): Ontogenetic reconstructions based on the data of X-ray fluorescence analysis of the microchemistry of recording structures, *Dokl. Biol. Sci.*, 2013, vol. 450, no. 1, pp. 142–145.
https://doi.org/10.1134/S0012496613030071

Pavlov, D.S., Kirillova, E.A., Kirillov, P.I., et al., *Sostoyanie bioraznoobraziya lososevykh ryb i ryboobraznykh i sredy ikh obitaniya v basseine reki Utkholok* (State of Biodiversity of Salmonids and Pisciforms and Their Habitats in the Utkholok River Basin), Moscow: T-vo Nauch. Izd. KMK, 2016.

Pravdin, I.F., *Rukovodstvo po izucheniyu ryb* (Guide on Fish Study), Moscow: Pishchepromizdat, 1966.

Resursy poverkhnostnykh vod SSSR. T. 20. Kamchatka (Resources of Surface Waters of the USSR. Vol. 20. Kamchatka), Leningrad: Gidrometeoizdat, 1973.

Rukovodstvo po izucheniyu pitaniya ryb v estestvennykh usloviyakh (Guide on Study of Fish Nutrition in Natural Conditions), Moscow: Akad. Nauk SSSR, 1961.

Ryby Kuril'skikh ostrovov (Fishes of the Kuril Islands), Moscow: Vseross. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr., 2012.

Savvaitova, K.A., Kuzishchin, K.V., Pichugin, M.Yu., et al., Systematics and biology of the East Siberian char

Salvelinus leucomaenis, J. Ichthyol., 2007, vol. 47, no. 1, Article number: 53.

Shorygin, A.A., *Pitanie i pishchevye vzaimootnosheniya ryb Kaspiiskogo morya* (Nutrition and Nutritional Relationships of the Fish of the Caspian Sea), Moscow: Pishchepromizdat, 1952.

Tiller, I.V., Anadromous Dolly Varden (*Salvelinus malma*) of Kamchatka, *Issled. Vodn. Biol. Resur. Kamchatki Sev.-Zap. Ch. Tikh. Okeana*, 2007, no. 9, pp. 79–95.

Volobuev V.V., On the biology of white-spotted char *Salvelinus leucomaenis* (Pall.) of the continental coast of the Sea of Okhotsk, in *Biologiya presnovodnykh ryb Dal'nego Vostoka* (Biology of Freshwater Fishes of the Far East), Vladivostok: Dal'nevost. Otdel. Akad. Nauk SSSR, 1987, pp. 89–100.

Volobuev, V.V. and Nikulin, O.A., On the biology of white-spotted char *Salvelinus leucomaenis* (Pall.) from the Motykley Bay, in *Gidrobiologicheskie issledovaniya vnutrennikh vodoemov Severo-Vostoka SSSR* (Hydrobiological Studies of Internal Water Bodies of the North-East of the USSR), Vladivostok: Dal'nevost. Nauch. Tsentr Akad. Nauk SSSR, 1975, pp. 354–375.

Volobuev, V.V., Maksimov, V.A., and Rogatnykh, A.Yu., Residential white-spotted char *Salvelinus leucomaenis* (Pall.), *Vopr. Ikhtiol.*, 1985, vol. 25, no. 4, pp. 546–552.

Yagyu, M., Foraging microhabitat of Japanese charr, *Salvelinus leucomaenis*, in a mountain stream, *Jpn. J. Ichthyol.*, 2009, vol. 56, no. 2, pp. 111–118.
https://doi.org/10.11369/jji.56.111

Yamaguchi, K., Nakajima, M., and Taniguchi, N., Loss of genetic variation and increased population differentiation in geographically peripheral populations of Japanese char *Salvelinus leucomaenis, Aquaculture*, 2010, vol. 308, no. Suppl. 1, pp. S20–S27.
https://doi.org/10.1016/j.aquaculture.2010.07.032

Yamaguchi, K., Nakajima, M., and Taniguchi, N., Population structure and conservation genetics of anadromous white-spotted char (*Salvelinus leucomaenis*) on Hokkaido Island: Detection of isolation-by-distance, *Environ. Biol. Fish*, 2016, vol. 99, nos. 6–7, pp. 513–525.
https://doi.org/10.1007/s10641-016-0494-9

Yamamoto, S. and Morita, K., Interpopulation comparison of size and age at smolting of white-spotted charr, *Salvelinus leucomaenis, Ecol. Freshw. Fish*, 2002, vol. 11, no. 4, pp. 281–284.
https://doi.org/10.1034/j.1600-0633.2002.00021.x

Yamamoto, S., Takahashi, I., Kitano, S., and Goto, A., Residual female parr in an anadromous population of white-spotted char *Salvelinus leucomaenis* in southern Hokkaido, Japan, *Jpn. J. Ichthyol.*, 1996, vol. 43, no. 4, pp. 101–104.
https://doi.org/10.11369/jji1950.43.101

Yamamoto, S., Morita, K., and Goto, A., Geographic variations in life-history characteristics of white-spotted charr (*Salvelinus leucomaenis*), *Can. J. Zool.*, 1999, vol. 77, no. 6, pp. 871–878.
https://doi.org/10.1139/z99-055

Yamamoto, S., Kuhara, M., Sawamoto, Y., and Tsukisaka, M., Variation of spots in Japanese char *Salvelinus leucomaenis* in the rivers of Nagano prefecture, Japan, *Bull. Nagano Pref. Fish. Exp. Stn.*, 2000, no. 4, pp. 16–23.

Yamamoto, S., Morita, K., Koizumi, I., and Maekawa, K., Genetic differentiation of white-spotted charr (*Salvelinus leucomaenis*) populations after habitat fragmentation: Spatial-temporal changes in gene frequencies, *Conserv. Genet.*, 2004, vol. 5, no. 4, pp. 529–538.
https://doi.org/10.1023/B:COGE.0000041029.38961.a0

Zippin, C., An evaluation of the removal method of estimation animal populations, *Biometrics*, 1956, vol. 12, no. 2, pp. 163–189.
https://doi.org/10.2307/3001759

Translated by D. Martynova