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Specific Features of Ecology of Chars of the Genus *Salvelinus* (Salmonidae) from the Basin of Lake Kronotskoe (Kamchatka) According to Parasitological Data

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Abstract—A parasitological study was performed of chars of the genus *Salvelinus* inhabiting Lake Kronotskoe (Kamchatka Peninsula)—*S. malma*, *S. albus*, *S. schmidtii*, and *S. kronocius*, as well as of juvenile *Salvelinus* spp. Twenty-three species of parasites, including six species new for the lake, *Hennequya zschokkei*, *Protteocephalus longicollis*, *Diphyllobothrium dendriticum*, *Crepidostomum* sp., *Echinorhynchus salmonis*, and *Paracanthobdella livanowi*, were found. With consideration of published data, in chars of this water body, 28 species of parasites were recorded, including seven species (*N.* cf. *pungitius*, *B. luciopercae*, *Crepidostomum* sp., *Cr. fausti*, *Cr.* cf. *cooperi*, *Eubothrium crassium*, and *Proteocephalus* sp.), whose presence or species identification in the lake ecosystem need confirmation. Two species (*N. rutili* and *Diphyllobothrium* sp.) are removed from the list. Parasites common for all species of chars were revealed. They include *Myxobolus arcticus*, *E. salvelini*, *D. ditretum*, *Crepidostotum* sp., *Cr. farionis*, *Cr. metoecus*, *Cystidicola farionis*, *Cucullanus truttae*, *Philonema oncorhynchi*, and *Salmincola carpionis*. Cluster analysis of the fauna of parasites of different species of chars demonstrated considerable differences in infestation, which indicates differences between them in preference for food items and occupied biotopes and thereby supports the ecological differentiation of chars in the basin of Lake Kronotskoe. *S. albus* and *S. kronocius* are most similar in parasitofauna, which is determined by their predation; *S. malma* as a benthophage is infected by the same species of parasites, but considerably less intensively. Extremely high indices of population numbers of some parasite species are considered as a manifestation of the Krebs cycle in parasites under the conditions of an isolated lake.

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Kronotskoe Lake is located on the territory of the Kronotskii State Nature Biosphere Reserve in the eastern part of Kamchatka Peninsula. It is 370 m asl and is the largest freshwater water body of the peninsula, reaching a length of 29 km and a width of 18 km. The age of the lake is about 14000–15000 years. The runoff of water from the lake to Kronotskii Bay is exercised via Kronotskaya River, having a length of about 40 km, whose upper reaches are difficult to pass by fish because of rapids (Kurenkov, 1977; Viktorovskii, 1978). Only chars of the genus *Salvelinus* can overcome waterfalls of Kronotskaya River and arrive to the lake (Krokhin and Kurenkov, 1964). Ichthyofauna of the lake is represented by the resident form of sockeyed salmon (kokanee) *Oncorhynchus nerka* and four species of chars: Dolly Varden trout *S. malma*, *S. albus*, and endemic chars—*S. kronocius* and *S. schmidti*. In Kronotskaya River, downstream rapids, of salmonids, only the riverine form of *S. malma* dwells. In the spawning period, anadromous *S. malma*, East Siberian char *S. leucomaenis*, pink salmon *O. gorbusha*, coho salmon *O. kisutch*, chum salmon *O. keta*, king salmon *O. tschawytscha*, and sock-eyed salmon *O. nerka* enter the river; smelt of the genus *Osmerus* and stickleback of the genera *Pungitius* and *Gasterosteus* have also been recorded here (Viktorovskii, 1978; Chereshnev et al., 2002; Reshetnikov, 2003; Frolov et al., 2005). Note that, with respect to the species composition of Lake Kronotskoe chars, there is also another point of view (Savvaitova, 1989; Reshetnikov et al., 1997; Reshetnikov, 1998), according to which all chars are considered as different ecomorphs in the composition of a fully complex species, the *Salvelinus malma* complex.

Fish ecology is in many respects determined by the pattern of their parasitofauna. At the same time, the qualitative and quantitative composition of parasites provides information on specific ecological features of their hosts—pattern of fish feeding and its changes, distribution in a water body, migrations, etc. (Polyanskii and Shul'man, 1969). Parasitological data were successfully applied to elucidate specific features of ecology and differentiation of chars of different species or ecotypes of the same species coinhabiting the same water body (Konovalov, 1971; Butorina et al., 1980; Atrashkevich and Orlovskaya, 1993; Atrashkevich et al., 1993). However, chars from Lake Kronotskoe have been almost unstudied in this respect.

The first data on char parasites from Lake Kronotskoe were cited by Zschokke and Heitz (1914) on the basis of materials collected by the expedition of Ryabushinskii that worked in Kamchatka from 1908 to 1909 under the supervision of Schmidt. In *S. malma* (at that time, only this species and *S. leucomaenis* were recorded for Kamchatka), cestodes *Eubothrium crassum* [=*Abothrium crassum*][1] and *Cyathocephalus truncatus*, nematodes *Cucullanus truttae* [=*Dacnitis laevis* n. sp.], *Cystidicola farionis* [=*Ancyracanthus impar]*, and unidentified nematodes. In 1973, one of the authors of the present paper performed a parasitological examination of several individuals of *S. albus* and *S. schmidti* preserved in formalin. As a result (Butorina et al., 1980; Butorina and Kuperman, 1981; Butorina, 2003), *C. truttae* and still another 12 species of parasites were reported for the lake: myxosporidians *Myxidium salvelini*, *Zschokkella orientalis*, and *Myxobolus arcticus*; infusorian *Capriniana piscium* [=*Trichophrya piscium*]; cestodes *Eubothrium salvelini* and *Diphyllobothrium* sp.; trematodes *Crepidostomum farionis* and *Phyllodistomum umblae* [=*Phyllodistomum conostomum*]; nematodes *Cystidicoloides ephemeridarum* and *Philonema oncorhynchi*; proboscis worm *Neochinorhynchus rutili*; as well as copepod *Salmincola carpionis*.

A new stage of parasitological study of chars from Lake Kronotskoe has started since 2003. Pavlov et al. (2003) found differences in infestation of different forms of chars in the lake by nematodes, cestodes, proboscis worms, and cestodes (without indication of systematic status). As a result of study of species composition and occurrence of parasitic copepods in fish of the lake, besides *S. carpionis*, still another species—*S. edwardsii*—was found (Shed'ko et al., 2004; Shed'ko, 2005, 2006). According to preliminary results of studying helminthofauna of chars and resident sockeyed salmon *O. nerka* of this water body based on collections in 2003 (Atrashkevich et al., 2005a), the following species of parasites have been first recorded for the lake fauna: proboscis worms *Neoechinorhynchus salmonis* and *N.* cf. *pungitius*, trematodes *Crepidostomum metoecus*, *C. fausti*, *C.* cf. *cooperi* and *Bunodera luceopecae*, and cestodes *Diphyllobothrium ditremum* and *Proteocephalus* sp. Thus, according to published data, 24 species of parasites and unidentified nematodes were found in Lake Kronotskoe chars.

Our study continues parasitological studies of chars from the basin of Lake Kronotskoe. The task of the work was to study specific ecological features of each char species from Lake Kronotskoe and reveal differences between them on the basis of parasitofauna analysis.

[1] Synonyms under which these species of parasites were indicated for chars from the given water body previously are listed in square brackets.

MATERIALS AND METHODS

The paper is based on collections of parasites from 300 individuals of chars of four species and juvenile *Salvelinus* spp. unidentified up to species and caught in March and October 2003 and from August to September 2004 in the basin of Lake Kronotskoe: in Bay Krodagyk (estuary of Kronotskaya River) and Kronotskaya River downstream rapids (16 and 26 km from the estuary). Fish were caught with fixed nets and vertical spooning. In all fish, fork length was measured; chars or their separate organs were preserved in 4% formaldehyde.

For determining infestation with parasitic copepods, 250 individuals of different species were examined, and with microsporidia of the genus *Henneguya* and leeches, 102 individuals. For determining the presence of helminths, analysis was made of gastrointestinal tracts and swimming bladders from 70 chars caught in 2004, among them were the following: in Bay Krodagyk, 43 individuals of *S. malma* (AC 23.5–45.0 cm), 11 individuals of *S. kronocius* (19.0–67.0 cm), six individuals of *S. schmidti* (31.0–46.0 cm), and seven individuals of *S. albus* (39.0–60.0 cm); in the river downstream rapids, three individuals of *S. malma* (39.0–46.0 cm). In 17 individuals of these fish (14 individuals of *S. albus* and 3 individuals of *S. schmidti*), brain was examined for the presence of infestation with microsporidia of the genus *Myxobolus*. For the presence of trematodes of the genus *Phyllodistomum*, kidneys from 19 individuals of *S. malma* from Kronotskaya River were examined (such material was not collected for other species of chars). No examination was made of the heart and eyes of fish; therefore, parasites common for these organs (trematodes of the families Diplostomidae and Strigeidae) are lacking in our material; no study was made of the inner organs for the presence of Protozoa either.

Fish or their organs before study were kept in water during several days with the replacement of water. For finding ectoparasites, body surface and mouth and gill cavities of fish were examined, recording the exact place of fixation of copepods and leeches and the localization of cysts of myxosporidians. A parasitological study of inner organs of fish was performed using standard methods with consideration of specific features of work with a preserved material.

Traditional indices of infestation were used in the paper: invasion extensity (IE)—the proportion of infected fish in a sample, in %; invasion intensity (II)—number of parasite individuals in a separate infected fish; average invasion intensity (I_{av})—sum of all individuals of parasites of one species divided by the number of infected individuals of the host; index of abundance (IA)—the average number of parasites per one individual in the studied host sample.

Mathematical data processing was performed using the Statistica 6.0 software package on the basis of the Institute of Marine Biology, RAS (Vladivostok). To reveal ecological inhomogeneity of chars, all fish in the total sample were compared without separating them into species. For this purpose, cluster analysis was used in which invasion intensity was used as a character. The Euclidean distance served as a measure of similarity; for plotting clusters, a method of complete relation was used. For comparison of different species of chars from Lake Kronotskoe by indices—invasion extensity, average invasion intensity, and index of abundance—we applied the Ward method similar to discriminant analysis (it minimizes dispersion within clusters and maximizes dispersion between clusters) and Pearson coefficient of correlation (for assessing conjugation of correlation pleiads of characters).

RESULTS AND DISCUSSION

Data on Biology of Parasites of Chars from Lake Kronotskoe

In chars from Lake Kronotskoe, we found 23 parasite species, including six species new for the fauna of the lake; no marine parasites were found. Most detected species were helminths (Table 1), mostly cestodes, trematodes, and nematodes. We found no helminths recorded by other authors: *B. luciopercae*, *Cr. fausti*, *Cr.* cf. *cooperi*, *N.* cf. *Pungitius*, *E. crassum*, *Diphyllobothrium* sp., and *Proteocephalus* sp. (Zschokke and Heitz, 1914; Butorina, 2003; Atrashkevich et al., 2005a).

Of five species of cestodes, *Eubothrium salvelini* is the most widespread (Table 1); its pleurocercoids and adult individuals were found in the intestine and pyloric caeca of all studied by us char species. Another species of this genus—*E. crassum*—was found by Zschokke and Heitz (1914) in *S. malma*. Up to the recent time, these species were difficult to distinguish, and they were often attributed to *E. crassum*, which is noted, for instance, by Konovalov (1971). Kuperman (1978) stressed differences between these two species and demonstrated experimentally that *E. crassum* cannot exercise its cycle in fresh water and is an estuary parasite often brought by anadromous salmon to fresh waters. As a result of recent morphoecological studies of both species (Hanzelová et al., 2002), it was shown nevertheless that *E. crassum* develops also under freshwater conditions. However, we have not found it in Kronotskoe Lake fish. Pleurocercoids and adult individuals of cestode *Proteocephalus longicollis**[2] were found by us in the intestine of all species of chars from Lake Kronotskoe, except *S. schmidti*. Possibly, *Proteocephalus* sp. recorded here by Atrashkevich et al. (2005a) also belongs to this species. Cestodes of the genus *Diphyllobothrium* are found in fish only at the stage of pleurocercoid. In chars of the lake, they were found in capsules localized at inner organs and were represented by two types that correspond to species typical of Salmonidei—*D. dendriticum** and *D. ditremum*, clearly distinguishable in the body shape, especially of its anterior end. Previously these species were reported as *Diphyllobothrium* sp. (Butorina et al., 1980). In *S. kronocius* and *S. albus*, both species were recorded in approximately equal ratio (according to our observations, in *S. kronocius* of 50 pleurocercoids, 24 and 26 individuals, respectively). In *S. malma* and *S. schmidti*, only *D. ditretum* was recorded. For some individuals, the number of helminths of each species was not always counted; therefore, Tables 1 and 4 list generalized data on the infestation of fish with cestodes of the given genus designated as *Diphyllobothrium* spp. Copepods act as the first intermediate hosts of all aforementioned species of cestodes (*Identification Key to…*, 1987); a large factual material indicates the possibility of reinvasion of these fish with parasites as a result of predation (for instance, Konovalov, 1971; *Identification Key to…*, 1987).

Still another species of cestodes *Cyathocephalus truncatus* was found in *S. malma* from Kronotskaya River and most frequently in *S. schmidti* from the lake. The life cycle of this parasite proceeds with the participation of one intermediate host—Amphipoda; under conditions of the lake, of *Gammarus lacustris* (Atrashkevich et al., 2005a).

Trematodes are represented by four species, of which three species (*Crepidostomum farionis*, *C. metoecus*, and *Crepidostomum* sp.*) belong to the family Allocreadiidae (cited from Caira, 1989). They very intensively infect chars of all species (Table 1). Atrashkevich et al. (2005a) state still another two species of this genus—*Cr. fausti* and *Cr.* cf. *cooperi*—that were not previously mentioned for Asia. According to several researchers (Hoffman, 1999; et al.), *Cr. fausti* is identical to *Cr. cooperi*. It is likely that trematode individuals designated by us as *Crepidostomum* sp. belong to *Cr. cooperi*; however, additional studies are needed to clarify which species they belong in. We have not found a representative of this family *Bunodera lucioprcae* stated for the fish of the lake (Atrashkevich et al., 2005a). Its species identification is doubted (Sokolov et al., 2006) because of the absence in the region of obligate hosts—Percidae. The first intermediate hosts of representatives of the genus *Crepidostomum* for a rare exception are small bivalves from the families Sphaeriidae and Euglesidae (Caira, 1989), including

[2] Species of parasites first recorded by us for Lake Kronotskoe were marked by an asterisk.

Table 1. Data on invasion with helminths of chars of the genus *Salvelinus* from Lake Kronotskoe, 2003–2004

Parasite species	*S. malma* (*n* = 45)			*S. albus* (*n* = 7)			*S. schmidti* (*n* = 6)			*S. kronocius* (*n* = 12)		
	EI, %	II, individuals / I_{av}	IO	Number of fish: studied/infected	II, individuals / I_{av}	IO	Number of fish: studied/infected	II, individuals / I_{av}	IO	EI, %	II, individuals	IO
Eubothrium salvelini	33.3	$\frac{1–13}{3.1}$	1.0	7/6	$\frac{8–271}{71.0}$	60.9	6/1	$\frac{5}{5.0}$	0.8	100.0	$\frac{3–863}{131.9}$	131.9
Diphyllobothrium spp.	4.4	$\frac{1–3}{2.0}$	0.1	7/3	$\frac{8–21}{13.0}$	5.6	6/1	$\frac{1}{1.0}$	0.2	83.3	$\frac{1–89}{29.1}$	24.3
Proteocephalus longicollis	8.9	$\frac{1–7}{3.0}$	0.3	7/1	$\frac{229}{229.0}$	32.7	0	$\frac{0}{0}$	0	8.3	$\frac{1}{1.0}$	0.1
Cyathocephalus truncates	2.2	$\frac{4}{4.0}$	0.1	0	0	0	6/3	$\frac{19–83}{43.0}$	21.5	0	0	0
Crepidostomum farionis	37.8	$\frac{1–2.4}{4.0}$	1.5	7/7	$\frac{25–782}{323.3}$	323.3	6/3	$\frac{11–37}{25.7}$	12.8	91.7	$\frac{2–88}{18.0}$	16.5
C. metoecus	13.3	$\frac{1–6}{2.5}$	0.3	7/7	$\frac{22–2937}{514.1}$	514.1	6/4	$\frac{1–29}{11.5}$	7.7	75.0	$\frac{2–22}{8.0}$	6.0
Crepidostomum sp.	8.9	$\frac{1}{1.0}$	0.1	7/7	$\frac{6–39}{21.6}$	21.6	6/6	$\frac{20–1240}{405.8}$	405.7	75.0	$\frac{1–42}{11.0}$	8.3
Phyllodistomum umblae	0	0	0	+[1]	+	+	+[2]	+	+	–	–	–
Cystidicola farionis	6.7	$\frac{1–30}{10.7}$	0.7	7/3	$\frac{9–35}{25.3}$	10.9	6/6	$\frac{27–296}{142.4}$	142.4	8.3	$\frac{11}{11.0}$	0.9
Cystidicoloides ephemeridarum	8.9	$\frac{1–8}{3.8}$	0.3	7/2	$\frac{1–185}{93.0}$	26.6	6/1	$\frac{2}{2.0}$	0.3	0	0	0
Philonema oncorhynchi	42.2	$\frac{1–36}{4.5}$	1.9	7/6	$\frac{5–161}{54.2}$	46.5	6/2	$\frac{3–8}{5.5}$	1.8	91.7	$\frac{2–290}{119.4}$	109.4
Cucullanus truttae	66.7	$\frac{1–23}{4.6}$	3.1	7/6	$\frac{3–239}{72.3}$	62.0	6/3	$\frac{1–9}{3.7}$	1.8	41.7	$\frac{1–33}{10.0}$	4.2
Neoechinorhynchus salmonis	13.3	$\frac{1–19}{5.0}$	0.7	7/5	$\frac{32–516}{226.2}$	161.6	6/1	$\frac{1}{1.0}$	0.1	91.7	$\frac{12–960}{121.2}$	111.1
Echinorhynchus salmonis	2.2	$\frac{3}{3.0}$	0.1	0	0	0	0	0	0	0	0	0

Note: EI, invasion extensity; II, invasion intensity; I_{av}, average invasion intensity; IO, abundance index; (1) according to data by Atrahkevich et al. (2005a); (2) according to data by Butorina (2003).

those on Kamchatka (Butorina and Sinebokova, 1987; Prozorova and Shed'ko, 2003). Infestation of fish with suckers *Cr. farionis* and *Cr. metoecus* is related to feeding on gammarids and larval mayflies (*Identification Key to*…, 1987; Caira, 1989). In addition, in the cycle of *Cr. metoecus*, small fish species can also be involved as paratenic hosts (Moravec, 1982).

The fourth species of trematodes, *Phyllodistomum umblae*, was found by us only in the examined in 1973 *S. schmidti* (Butorina, 2003) and by Atrashekevich et al. (2005a) in *S. albus*. The first intermediate hosts of trematodes of this genus are bivalves from the families Sphaeriidae and Euglesidae. Infestation of fish with these parasites takes place either during feeding on mollusks from the same families or on larval chironomids and dragon flies acting as secondary intermediate hosts (Butorina and Sinebokova, 1987; Prozorova and Shed'ko, 2003; Atrashkevich et al., 2005b) or during eating directly free-swimming cercariae imitating larval mites (Pronin et al., 1991).

Among nematodes, *Cucullanus truttae*, *Philonema oncorhynchi*, and *Cystidicola farionis* turned out most common (Table 1). Intermediate hosts of *C. truttae* are larval lampreys (Petromyzontidae) that are the source of infestation of salmonids, parallel to reinvasion, as a result of eating already infected small fish (Moravec, 1994). In the basin of Kamchatka River, larvae of these nematodes were found by Butorina (1988) in ammocete larvae and adult lampreys *Lenthenteron reissneri* and *L. camtschaticum* [are indicated as *Lampetra japonica*]. *C. truttae* belongs to rheophilic species, like its hosts—lampreys. This is indicated, in particular, by a higher infestation with this species of nematodes of brook chars as compared to lake chars (Butorina, 1988). Butorina considers (1988) that, after spawning and death, lampreys pass *C. truttae* to young immature chars that concentrate not far from their spawning grounds. Fish eat drifted by the current weakened or dead lampreys (*L. reissneri*) with a length smaller than 13–18 cm that contain larval nematodes at developmental stage III. However, lampreys have been recorded in Lake Kronotskoe up to the present time (Chereshnev, 1996; personal communication by S.V. Frolov). Therefore, it is not excluded that, in water bodies of Kamchatka, another course of the life cycle of *C truttae* is possible that proceeds without the participation of lampreys.

The infestation of salmonids with nematode *P. oncorhynchi*, a parasite of the body cavity and connective tissue, occurs during feeding on freshwater copepods (*Identification Key to*…, 1987). The distribution of *P. oncorhynchi* in Lake Kronotskoe is related to habitation here of the obligate host of nematode—*O. nerka*—in which this parasite was found (Atrashkevich et al., 2005a; our unpublished data). Its main food in Lake Kronotskoe (Krokhin and Kurenkov, 1964; Kurenkov, 1977), as in other water bodies of Kamchatka (Konovalov, 1971; Butorina and Shed'ko, 1989), are plankton organisms. Although there is no experimental proof for the possibility of transmission of phylonemes from fish to fish (Moravec, 1994), it is not excluded that *O. nerka* may serve as a constant source of invasion for predatory chars (*S. albus* and *S. kronocius* in Lake Kronotskoe).

The life cycle of nematode of the swimming bladder of *Cystidicola farionis* proceeds with the participation of relic crustaceans *Pontoporeia affinis* (Amphipoda) and *Mysis relicta* (Mysidae), as well as of some representatives of the genus *Gammarus* (*Identification Key to …,* 1987; Butorina and Shed'ko, 1989; Moravec, 1994). In Lake Kronotskoe, larvae of this nematode were found in *G. lacustris* (Atrashkevich et al., 2005a). Note that there is no convincing proof for the possibility of reinvasion of fish with nematodes of the swimming bladder as a result of predation (Moravec, 1994). The parasite was found in all species of Lake Kronotskoe chars, among which *S. schmidti* was the most intensively infected (Table 1).

Infestation of fish with nematode *Cystidicoloides ephemeridarum* is related to feeding on mayflies (Ephemeroptera); however, the participation in the cycle of paratenic hosts—small fish species—is also possible (Moravec, 1994). This parasite was found in 1973 in *S. schmidti* (Butorina, 2003), and in 2004, in all species of chars, except *S. kronocius* (Table 1).

Proboscis worms are represented in our material by two species, among which *Neoechinorhynchus salmonis* dominates. Previously, *N. rutili* was also recorded in this lake (Butorina et al., 1980; Butorina, 2003). However, the findings of this species caused a justified doubt in relation to finding here of closely related to it species *N. salmonis* (Atrashkevich et al., 2995a). Moreover, as a result of the last revision of the genus, it was established that, in the northeast of the Asian part of Russia, *N. rutili* occurs extremely rarely and was recorded only in lake minnow *Phoxinus perecnurus* in the basin of Verkhyaya Kolyma (Atrashkevich and Mikhailova, 2006), while *N. salmonis* is widely spread in lake systems (Mikhailova, 2003). In connection with this, we reexamined individuals of proboscis worms from chars collected in 1973, paying attention to differential characters of *N. rutili* and *N. salmonis*—sizes of the body and hooks, proboscis proportions, and vagina structure (Ching, 1984; Mikhailova et al., 2004)—and came to the conclusion that we actually deal with *N. salmonis*. Therefore, we remove *N. rutili* from the list of fish parasites in this water body. As intermediate hosts for *N. salmonis* in Lake Kronotskoe, plankton ostracods of the genus *Cypria* were revealed (Atrashkevich et al., 2005a). Our material lacked still another form of proboscis worms of this genus—*N.* cf. *pungitius* reported by Atrashkevich et al. (2005a) only as one individual in two *S. albus* each. In the Far East of Russia, this parasite, as a rule, is an obligate intestinal parasite of smelts of the genus *Pungitius*. Another species of proboscis worms, *Echinorhynchus salmonis**, was found only in

Table 2. Data on the invasion by microsporidia, infusorians, and leeches of chars of the genus *Salvelinus* from Lake Kronotskoe in 1973 and 2003 (the number of fish: studied/infected)

Parasite species	*S. albus*		*S. schmidti*		*S. kronocius*	*S. malma*	*Salvelinus* spp., juv.
	1973	2004	1973	2003	2004	2003	2004
Myxidium salvelini	4/0	–	6/2	–	–	–	–
Zschokkella orientalis	4/1	–	6/0	–	–	–	–
Myxobolus arcticus	4/4	14/14	6/5	3/3	–	–	–
Henneguya zschokkei	–	10/3	–	25/8	7/2	2/0	58/0
Capriniana piscium	4/3	–	6/3	–	–	–	–
Paracanthobdella livanowi	–	10/0	–	25/1	7/2	2/0	58/0

Table 3. Data on invasion of chars of the genus *Salvelinus* from Lake Kronotskoe with copepods of the genus *Salmincola*

Fish species (water body)	Fish length, cm	Number of fish, individuals (EI, %)	Number of copepods	II (I_{av})	IO
Salvelinus spp.	3.0–13.2 (6.5)	58 (0)	0	0	0
Salmincola edwardsii					
S. kronocius	17.7–80.3 (46.9) / 46.3–60.0 (53.2)	32 (18.75)	22	1–8 (3.67)	0.69
S. albus	25.0–67.5 (51.4) / 41.0–59.0 (52.6)	57 (7.01)	15	3–5 (3.75)	0.26
Salmincola carpionis					
S. albus	25.0–67.5 (51.4) / 25.0–67.5 (52.0)	57 (92.98)	358	1–53 (6.76)	6.28
S. kronocius	17.7–80.3 (46.9) / 22.5–80.3 (51.5)	32 (81.25)	257	1–45 (9.89)	8.03
S. malma (Bay Krodagyk)	13.6–58.3 (33.0) / 27.0–58.3 (37.6)	40 (60.0)	121	1–21 (5.04)	3.03
S. malma (the Kronotskaya River)	23.5–46.0 (31.9) / 41.0	13 (7.69)	37	37 (37.0)	2.85
S. schmidti immature	19.0–29.0 (24.6) / –	30 (0)	0	0	0
S. schmidti mature	30.0–42.7 (34.9) / 30.0–42.7 (36.1)	43 (46.51)	33	1–3 (1.65)	0.77

Note: Beyond the parentheses are limits of fish length variation; in parentheses, average value; above the line, studied individuals; below the line, infected. The remaining designations are the same as in Table 1.

one *S. malma* from Kronotskaya River (Table 1). The causes of the rare occurrence of this species are unclear so far. Its intermediate hosts are relic amphipods *Pontoporeia affinis* and *Hyalella azteca*, as well as lake amphipod *Gammarus lacustris* (*Identification Key to*…, 1987; Atrashkevich et al., 1993).

Microsporidia are represented in Kronotskie chars by species typical for salmonids of Kamchatka—*Myxidium salvelini* from the urinary bladder, *Zschokkella orientalis* from the gall bladder, *Myxobolus arcticus* from the brain, and *Henneguya zschokkei** (Table 2). Cysts with spores of *H. zschokkei* localized under skin on the body of fish near fin insertions (mainly of dorsal, pectoral, and ventral fins) and in one case at the gill arch. This parasite causes a tubercular (on Kamchatka, “saranic”) disease in salmonids. Of the aforementioned myxosporidians, the most frequently recorded species in the fish of the lake is *M. arcticus*, a species of the arctic freshwater complex occurring almost throughout northern water bodies, including those on Kamchatka

(Butorina et al., 1980; Pugachev, 2001). Infusorians *Capriniana piscium* were found on gills of *S. albus* and *S. schmidti*. Leeches *Paracanthobdella livanowi** were singly recorded on fins of *S. schmidti* and *S. kronocius*.

Crustaceans *Salmincola carpionis* were found in the buccopharyngeal cavity of all species of chars, and *S. edwardsii*, in the gill cavity and at gill filaments of only *S. kronocius* and *S. albus* (Table 3). The development of copepods of this family (Lernaeopodidae) proceeds without the participation of intermediate hosts; a copepodite larva hatches from an egg thanks to which the period of a free life of crustaceans is strongly decreased (*Identification Key to…*, 1987); therefore, the search for a host and fixation to it is realized most successfully under conditions of fish aggregations.

Thus, with consideration of the aforementioned remarks, in chars of the lake, 28 species of parasites were found, including seven species (*N.* cf. *pungitius*, *B. luciopercae*, *Crepidostomum* sp., *Cr. fausti*, *Cr.* cf. *cooperi*, *E. crassum*, and *Proteocephalus* sp.), whose presence or species identification in the lake ecosystem require confirmation. Two species (*N. rutili* and *Diphyllobothrium* sp.) are removed from the list.

Ecological Characteristic of Chars from Lake Kronotskoe According to Parasitological Data

S. schmidti is an endemic of Lake Kronotskoe. It occurs in the lake in inflowing streams and small rivers, occupies the niche of a costal benthophage, performs no long migrations, and reproduces in the lake and in Listvennichnaya River (Viktorovskii, 1978; Savvaitova, 1989). We found in this species 18 species of parasites, including 12 species of helminths (Tables 1–3). *S. schmidti* differs from other species of chars in an extremely intense infestation with *Crepidostomum* sp.; it is characterized by a high invasion with *C. farionis* and *C. truncatus*. We found *P. umblae* only in this species [Atrashkevich et al. (2005a) note it also in *S. albus*]. All of these data, as well as findings of other trematodes of the genus *Crepidostomum* and nematodes *C. ephemeridarum*, indicate that these chars feed mainly on benthic organisms—crustaceans (in the first turn, gammarids), larvae of mayflies and other amphibiotic insects, and small mollusks inhabiting the littoral, as a rule. The infestation of fish with infusorians, microsporidia, and leeches (Table 2) also occurs more frequently in the coastal zone of the lake. Plankton is also present in the diet of this char species, which is evidenced by findings in it of nematode *P. oncorhynchi*, juvenile and young immature individuals of *E. salvelini*, and singly of *D. ditretum* and proboscis worm *N. salmonis*. For this species, the lowest infestation with copepod *S. carpionis* was found among other chars of the lake. Copepods were lacking in fish with a length less than 29 cm and were found only in mature individuals (Table 3). In all probability, the infestation of *S. schmidti* with crustaceans occurs in the Listvennichnaya River, where it spawns simultaneously with *S. kronocius*—one of the main hosts of the parasite in the lake. The invasion of *S. schmidti* with rheophilic nematode *Cucullanus truttae* at low invasion intensity also testifies to its migration to flow-through water bodies (streams and rivers) (Table 1). Thus, parasitological data provide us an idea of *S. schmidti* as a benthophage with a wide spectrum of feeding on invertebrates that inhabits the littoral zone of the lake, but performs migrations also to rivers.

S. kronocius is an endemic of Lake Kronotskoe. This most isolated and specialized species stays in the lake pelagial over large depths, where it occupies a dominant position and spawns in the Listvennichnaya River. Juveniles feed on zooplankton and larvae of amphibiotic insects; on reaching body length of 30–35 cm, it passes to feeding on exclusively resident *O. nerka* (Viktorovskii, 1978). We found in *S. kronocius* 11 species of helminths, both species of parasitic copepods, microsporidia *H. zschokkei*, and leeches (Tables 1–3). Regrettably, this char species has not been examined for the presence of other, typical for *S. albus* and *S. schmidti*, representatives of microsporidia and infusorians that, most likely, will be detected in it at additional study.

The qualitative and quantitative composition of helminths of all studied large (AC > 40 cm) individuals of *S. kronocius* is rather uniform. They are especially intensively infected with *E. salvelini*, *N. salmonis*, *P. oncorhynchi*, and *D. ditretum* (Table 1). In a single examined juvenile of this char species (AC 19 cm), only three species of parasites were found (three individuals of *E. salvelini*, 15 individuals of *N. salmonis*, and 33 individuals of *C. truttae*). In large fish, maximal invasion intensity with *C. truttae* does not exceed seven (I_{av} = 4.3), i.e., it is almost five times lower than in the juvenile individual. Findings of *C. truttae* in adult individuals are apparently related to predation, while the young char became infected most likely with larvae, which was stated above.

A considerable invasion intensity of *S. kronocius* with helminths typical also for *O. nerka* (Konovalov, 1971; Kurenkov, 1977; Atrashkevich et al., 2005a) supports its ichthyophagy, as a result of which parasite accumulation occurs. This can be illustrated by comparison of invasion indices of predatory *S. kronocium* and benthophagous *S. malma* with common for them helminth species (Table 1). It is seen from these data that the extensity of infestation of *S. kronocius* with diphylobothriids is 20 times higher, and the average intensity, 16 times higher, than in *S. malma*. The difference in the invasion intensity for *N. salmonis*, *P. oncorhynchi*, and *E. salvelini* is more drastically pronounced (25.0, 27.0, and 46.0, times). *S. kronocius* is infected far more intensively than *S. malma*, with trematodes of the family Allocreadiidae (Table 1) that also accumulate in it; however, in this case, differences in infestation are no more than 2.4–5.3-fold, and only for *Crepidostomum* sp., 8–12-fold. An additional confirmation of reinvasion is the absence of these trematodes in the juvenile individual of *S. kronocius* feeding on copepods and ostracods. Thus, parasitological data support the preference of mature *S. kronocius* to lake biotopes, as was noted by ichthyologists (Viktorovskii, 1978).

S. albus is an endemic of Kamchatka Peninsula. In Lake Kronotskoe it is represented by only a resident lake form. Juveniles live for a long time in streams and small rivers, feed on benthos, and, at a body length of 30–35 cm, migrate down to the lake and pass to feeding on resident sock-eyed salmon and small char, actively consuming insects and benthos. Spawning takes place in rivers or in shallow waters of the lake (Viktorovskii, 1978; Savvaitova, 1989).

In *S. albus*, 18 helminths were found; among them, 12 species of helminths (Table 1). It acquires some of them as a result of reinvasion at ichthyophagy; the infestation with others is related to consumption of invertebrates—intermediate hosts of helminths. On the whole, species composition of parasites of *S. albus* is similar to that of *S. kronocius*; however, despite a limited size of material available to us, several differences can be seen between them. On the basis of data in Table 1, a tendency for a weaker infestation of *S. albus* is traced as compared to *S. kronocius* with indicator parasites of predators such as *E. salvelini*, *P. oncorhynchi*, and *Diphyllobothrium* spp. We obtained still lower values of invasion with these parasites previously (Butorina et al., 1980) for *S. albus* from Lake Kronotskoe, i.e., the found differences are not accidental. In addition, the indices of infestation of *S. albula* with nematode *C. truttae* considerably exceed those of *S. kronocius* (Table 1), which can be explained by periodic and relatively long staying of *S. albus* in rivers or their estuary sections. It is noteworthy that the highest indices of invasion with nematode *C. ephemeridarum*, whose intermediate hosts inhabit mainly estuaries of rivers and streams, were recorded namely for *S. albus*. Atrashkevich et al. (2005a) note in *S. albus* trematodes *P. umblae*, the infestation with which apparently occurs in the coastal zone of the lake, where *S. schmidti*, infested with these trematodes, also stays. All this testifies to a high migration capacity of *S. albus* as compared to *S. kronocius* and *S. schmidti*, as well as to the absence in it of food specialization. The intensity of invasion of *S. albus* with trematodes *Cr. farionis* and *Cr. metoecus* is higher by factors of 18 to 64 than in *S. kronocius* (Table 1), which more likely reflects different ways of infestation of fish with them. On the one hand, it may proceed during feeding on intermediate hosts of trematodes, and, on the other, as a result of ichthyophagy. Findings in considerable amounts of nematode *C. farionis* also indicate feeding on benthos. A 100% infestation of *S. albus* with microsporidia *M. arcticus* is also related to feeding near bottom. However, besides fish and bottom invertebrates, *S. albus* sometimes also consumes plankton crustaceans in considerable amounts. This is evidenced by findings of juvenile immature and even juvenile individuals of *P. longicollis* (up to 229 individuals in one fish) and of *E. salvelini* (Table 1). Parasitological data testify to the feeding of *S. albus*, as of *S. schmidti* also, on amphipods *G. lacustris* in the littoral zone of the lake. However, if for *S. schmidti*, amphipods are more likely one of the main food items, for *S. albus*, they are only additional. Table 1 shows that the limits of invasion intensity with nematode *C. farionis* in *S. albus* and *S. schmidti* do not overlap in fact. Differences in the pattern of their feeding are evidenced also by the fact that, at an equal size of samples of these char species, we failed to find in *S. albus* any individual of cestode *C. truncatus*, while the intensity of invasion with this parasite of *S. schmidti* averaged 43 individuals per fish, and maximal was 83.

Our data expand our concept of the ecology of *S. albus*. In Lake Kronotskoe it occupies the niche of an euryphage using as food, not only fish and benthic invertebrates, but also plankton crustaceans. Its diet is far more diverse than in *S. kronocius* and *S. schmidti*. The capacity of *S. albus* for occupying different biotopes can also be noted. It inhabits flow-through water bodies and in the littoral zone of the lake together with *S. schmidti*; in common with *S. kronocius*, occurs in the pelagial and periodically even in the benthal zone of the lake.

S. malma in the lake basin is represented by a river form inhabiting Listvennichnaya and Unana rivers and the upper reaches of Kronotskaya River (Viktorovskii, 1978; Pavlov et al., 2003). In this species, 13 species of helminths and one species of crustaceans was found (Tables 1 and 3). Parasitofauna of *S. malma* caught in different sections of Kronotskaya River is rather uniform in composition and invasion indices, except the fact that *S. malma* from Bay Krodagyk is considerably more intensively infected with small crustaceans *S. carpionis* than from the river sections downstream rapids (Table 3). Rheophylic nematodes *C. truttae* were most frequently recorded in these fish, which reflects the preference of *S. malma* for flow-through water bodies. Parallel to mature parasites, it often contained juvenile individuals (up to 15 individuals/fish), which testifies to a recent fish invasion; *S. malma*, as a species is not characterized by ichthyophagy (Chereshnev et al., 2002). *S. malma* is considerably infected (EI = 40.9%) with young nematodes *P. oncorhynchi*, which indicates its feeding on copepods, components of plankton of most lakes. The inclusion into its diet of plankton ostracods is proven by the presence of proboscis worms *N. salmonis*. Related to feeding on plankton are also invasion with cestodes *P. longicollis*, single findings of *D. ditretum*, and low indices of invasion with *E. salvelini*. These facts also indicate that *S. malma* visits river sections with a relatively slow current. Benthos is also included into the diet of *S. malma*, however, in small amounts. This is also indicated by a low invasion of *S. malma* with *C. ephemeridarum* (feeding on larval mayflies), *C. farionis*, and *S. truncatus* (use amphipods *G. lacustris* as food). During consumption of crustaceans and larval mayflies, *S. malma* is infected with trematodes of the family Allocreadiidae common for the lake fauna. A lower intensity of invasion with them, as compared to lake chars, is possibly explained by low numbers in the mouth of Kronotskaya River of intermediate hosts of these trematodes. No *P. umblae* was found in *S. malma*, although a special examination of kidneys from 19 individuals of *S. malma* caught 16 km apart from the effluent was performed. In all likelihood, *S. malma* constantly stays in rivers and performs no long migrations to the lake. This also proves indirectly that some species of small bivalves from the families Sphaeriidae and Euglesidae that are intermediate hosts of *P. umblae* inhabit the lake and are lacking or extremely rare in Kronotskaya River. We found *E. salmonis* only in one specimen from the Kronotskaya source and did not find it in other species. The list of *S. malma* parasites will be undoubtedly extended at the expense of myxosporidians and infusorians. Thus, according to parasitological data, *S. malma* is attributed to the river system; plankton and benthos play almost an equal role in its feeding.

The analysis performed shows that, of lake chars, *S. albus* has the most diverse ichthyofauna: besides parasites background for the lake, it is invaded with the highest number of helminths (Table 1), which emphasizes the diversity of its diet. It is noteworthy that river *S. malma* to a greater or smaller degree is infected with almost all helminths (except *P. umblae*) recorded in lake chars.

Cluster analysis of the generalized sample of chars based on comparison of individuals by the intensity of invasion with parasites indicated (Fig. 1) that chars form several groups differing in invasion pattern. The most numerous and compact group of fish close in invasion is formed by *S. malma*, except one individual—M1A from the lower reaches of the Kronotskaya River. Unlike the remaining individuals of *S. malma*, this individual is intensively infected with *S. carpionis* (II = 37) and *C. farionis* (II = 30). The remaining lake chars form groups smaller by size; *S. schmidti* (cluster from N2, N51, N53, and NF6) turned out the closest to *S. malma*. *S. albus* are less similar between themselves in indices of invasion with parasites as compared to individuals of other species. Among *S. kronocius*, one individual (D4) not accidentally turned out at the dendrogram to be closer to *S. malma* than to individuals of its species. This is the smallest immature individual with a length of only 19 cm that, as *S. malma*, continues to feed on invertebrates and has not passed to predation. Thus, according to the invasion pattern, the char sample separated into four groups corresponding to four char species distinguished by exterior characters. It is of interest that three individuals identified by ichthyologists from characters of external morphology as *S. malma* (individuals M4 and M59) and *S. schmidti* (N8) from the results of parasitological analysis turned out to belong to other species (Fig. 2). The assessment of species composition of parasites in these fish and comparison of intensity of their invasion with parasites with average values (I_{av}) for each species of Lake Kronotskoe chars served the basis for assigning individual M4 to *S. schmidti*; M59, to *S. kronocius*; and N8, to *S. malma*. On the whole, the results of the analysis indicate that parasites as indicators of the feeding pattern in different char species with a high degree of reliability can be used for their identification.

Species diversity of parasites in chars from Lake Kronotskoe is reflected in Fig. 3. It is represented by species widely distributed in all lake–river systems of Kamchatka Peninsula, except trematode *Crepidostomum* sp. recorded until presently only in fish of Lake Kronotskoe. Common for all char species are the following: *Eubothrium salvelini*, *Crepidostomum* sp., *Cr. farionis*, *Cr. metoecus*, *Cucullanus truttae, Cystidicola farionis*, *Philonema oncorhynchi*, as well as copepod *Salmincola carpionis*, and more likely myxosporidium *Myxobolus arcticus*. *Cyathocephalus truncatus* was found only in benthophages (*S. schmidti* and *S. malma*), and *Echinorhynchus salmonis*, only in *S. malma* from Kronotskaya River.

Cluster analysis of four studied char species from Lake Kronotskoe based on comparison of fish by all invasion parameters (EI, I_{av}, IO) indicate (Fig. 4) the greatest similarity of *S. albus* and *S. kronocius* in parasitofauna, which is determined by their predation. *S. malma*, as a bentho-planktophage, is infected with the same parasite species, but noticeably less. The most original parasite composition is typical of *S. schmidti*, whose specificity is determined by maximal numbers of *Crepidostomum* sp. and invasion with *P. umblae*, as well as by weak invasion with cestodes *E. salvelini* and *D. ditretum*.

The data we obtained on invasion of different char species from Lake Kronotskoe with nematode *C. farionis* (Table 1) testify to the different importance of amphipods in their feeding. The highest invasion indices were recorded for *S. schmidti* (I_{av} and IO are 142.4); further, in decreasing order, follow *S. albus*, *S. malma*, and *S. kronocius*; in the last char, the parasite occurs singly. A reverse pattern is exhibited by another species of nematodes—*P. oncorhynchi*: maximum invasion intensity was recorded in predators—*S. kronocius* (I_{av} = 54.2) and *S. albus* (119.4)—while in benthophages, it turned out to be lower by an order of magnitude—in *A. malma* and *S. schmidti*, 4.6 and 5.5, respectively.

All char species in Lake Kronotskoe are infected with copepods *S. carpionis*, however, to a different degree (Table 3). The most intensively infected predators are *S. kronocius* and *S. albus* (EI, 81.3 and 93.0%, respectively; IO, 8.0 and 6.3); to a smaller degree, *S. malma* and *S. schmidti* were characterized by a mixed type of feeding. The second copepod species *S. edwardsii* was singly recorded only in large (AC < 40 cm) individuals of *S. kronocius* and *S. albus*. These crustaceans were not found in juvenile chars; although

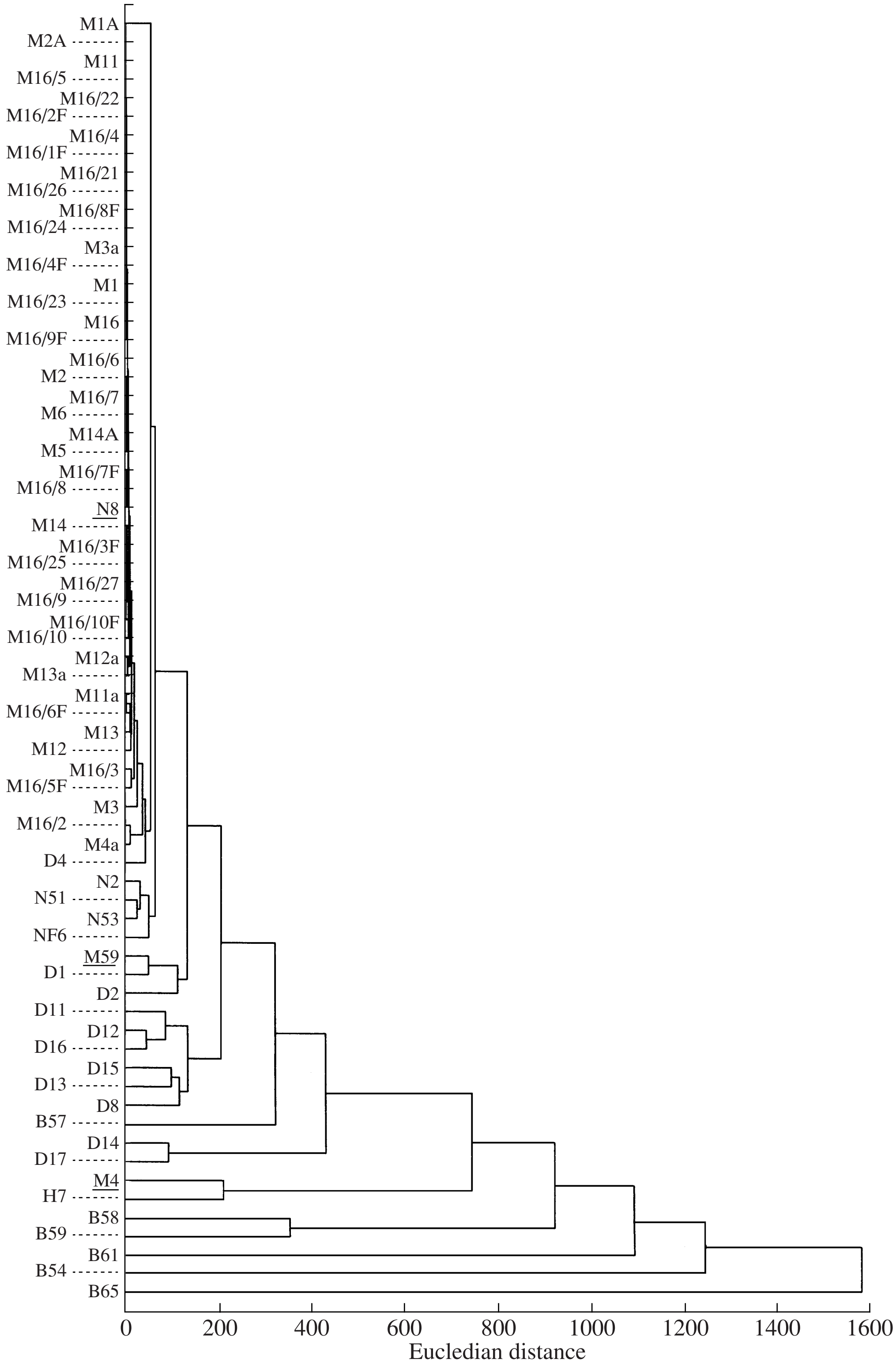

Fig. 1. Dendrogram of similarity of chars of the genus *Salvelinus* from the basin of Lake Kronotskoe by the intensity of invasion with parasites plotted by the method of complete relation. M, *S. malma*; N, *S. schmidti*; D, *S. kronocius*. Figures and letters following them in some cases denote ordinal numbers of fish assigned to them during catch.

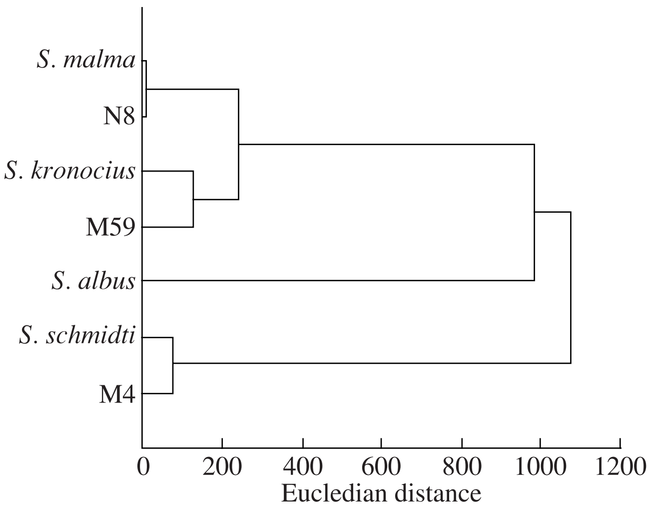

Fig. 2. Dendrogram of similarity of chars of the genus *Salvelinus* of Lake Kronotskoe basin by average intensity of infestation with parasites, constructed by the Ward method. Designations as in Fig. 1.

in the basin of Kamchatka River, namely this age group of chars is the main host for *S. edwardsii* (Shed'ko, 2005). At the same time, in Lake Kronotskoe, the atypical host—kokanee—is very intensively infected with this "char" species of copepods (EI = 90.2%, II = 1–22, IO = 5.1) (Shed'ko, 2005, 2006). In all probability, predatory chars have a possibility for being infected with the aforementioned parasite inhabiting areas where the sock-eyed salmon, their dominant food item, stays.

The basin of Lake Kronotskoe is one of the areas of sympatry of several species of chars. Another similar water body, the best studied in parasitological respect, is the basin of Lake Azabach'e (the lower reaches of the Kamchatka River). Here *S. leucomaenis*, *S. albus*, and *S. malma*, represented by different ecotypes, dwell in common (Konovalov, 1971; Glubokovskii, 1977; Butorina et al., 1980). We compared helminthofauna of nonmigratory forms of *S. malma* and *S. albus* from these lakes (Table 4) using data obtained previously from Lake Azabach'e (Butorina, 2003) and excluding from analysis parasites localized in fish organs not studied in this work. Besides species common for *S. albus* from two lakes, in char from Lake Azabach'e, *C. truncatus*, *Pseudocapillaria salvelini*, and *E. salmonis* not found in Lake Kronotskoe were discovered. The data obtained testify to noticeable differences in the invasion of *S. albus* from these lakes with background species of helminths—*P. oncorhynchi* and proboscis worms of the genus *Neoechinorhynchus*, as well as with cestode *E. salvelini*, even with correction for difference in the size of the samples. This is explained by the fact that, in Lake Kronotskoe, *S. albus* accumulates them when feeding on sock-eyed salmon, planktophage by the mode of feeding. In particular, a high invasion with pro-

Table 4. Data on invasion with helminths of nonmigratory chars of the genus *Salvelinus* in Lakes Azabach'e and Kronotskoe

Helminth species	*Salvelinus malma* (n = 113)						*Salvelinus albus* (n = 32)					
	Azabach'e[1] (n = 68)			Kronotskoe (n = 45)			Azabach'e[1] (n = 25)			Kronotskoe (n = 7)		
	number of infected fish	I_{av}	IO	number of infected fish	I_{av}	IO	number of infected fish	I_{av}	IO	number of infected fish	I_{av}	IO
Eubothrium salvelini	1	1.0	0.01	15	3.1	1.0	23	29.7	27.3	6	71.0	60.9
Proteocephalus longicollis	10	2.8	0.4	4	3.0	0.3	1	1.0	0.04	1	229.0	32.7
Diphyllobothrium spp.	0	0	0	2	2.0	0.1	21	9.5	8.0	3	13.0	5.6
Cyathocephalus truncatus	23	14.1	4.8	1	4.0	0.1	1	1.0	0.04	0	0	0
Phyllodistomum umblae	44	142.5	92.2	0	0	0	12	5.4	2.6	+[2]	+	+
Crepidostomum farionis	33	71.6	34.8	17	4.0	1.5	22	25.8	22.7	7	323.3	323.3
Cystidicola farionis	34	44.0	22.0	3	10.7	0.7	21	77.6	65.2	3	25.3	10.9
Cucullanus truttae	32	5.4	2.5	30	4.6	3.1	11	4.7	2.1	6	72.3	62.0
Philonema oncorhynchi	3	1.8	0.1	19	4.5	1.9	13	3.4	1.8	6	54.2	46.5
Cystidicoloides ephemeridarum	1	1.0	0.01	4	3.8	0.3	2	2.5	0.2	2	93.0	26.6
Pseudocapillaria salvelini	1	1.0	0.01	0	0	0	1	1.0	0.04	0	0	0
Neoechinorhynchus spp.	1	1.0	0.01	6	5.0	0.7	9	14.3	5.2	5	226.6	161.6
Echinorhynchus salmonis	35	43.8	22.5	1	3.0	0.1	17	5.6	3.8	0	0	0

Note: Designations are the same as in Table 1. Information sources: [1] Butorina, 2003; [2] Atrashkevich et al., 2005a.

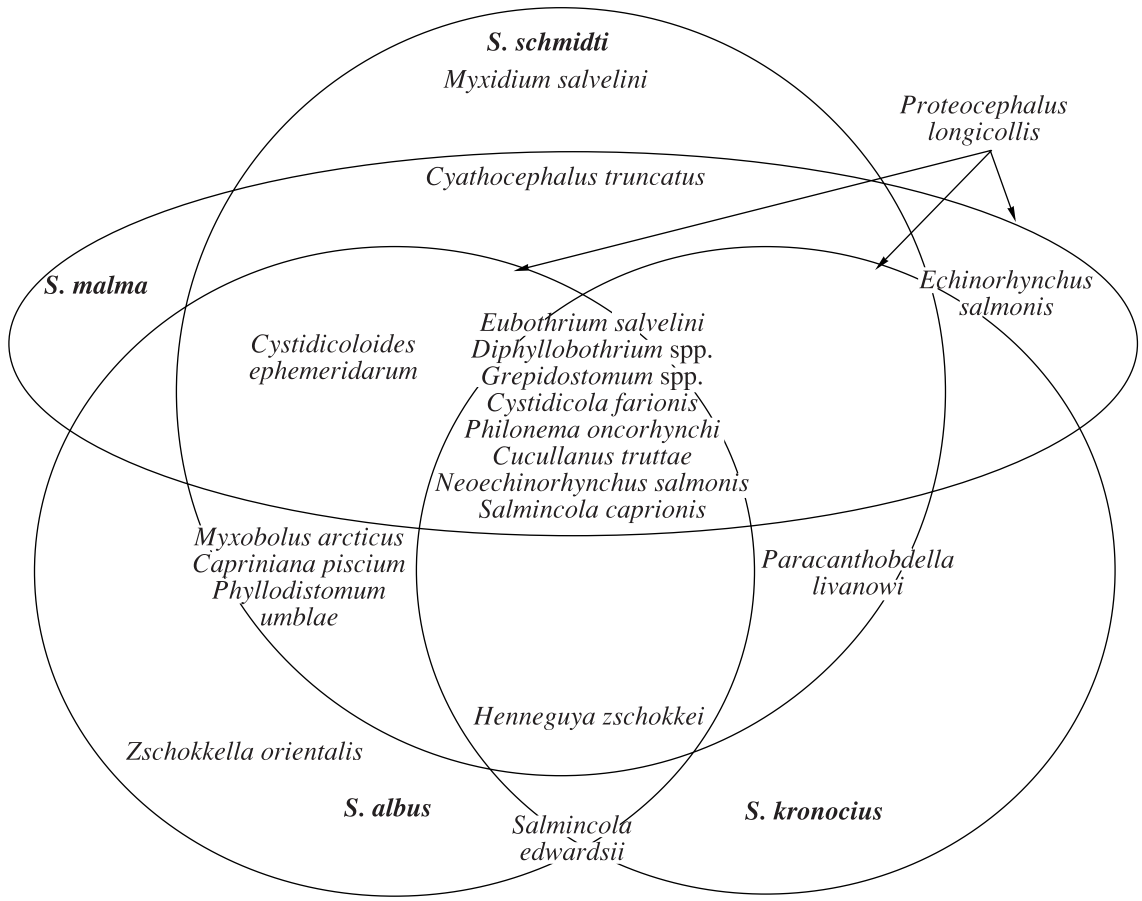

Fig. 3. Species diversity of parasites in different species of chars of the genus *Salvelinus* from the basin of Lake Kronotskoe.

boscis worms *N. salmonis* was recorded for sock-eyed salmon (Atrashkevich et al., 2005a), and occurrence in it of *E. salvelini* in some spawning grounds reaches 100% at intensity of over 40 parasites per fish (Kurenkov, 1977). Meanwhile, in Lake Azabach'e, this char species consumes juveniles to a greater degree and mature smelt *Hypomesus olidus*, three-spined stickleback *Gasterosteus aculeatus*, and nine-spined stickleback *Pungitius pungitius* (Kohmenko, 1970), in which *E. salvelini* occurs singly (Kuperman, 1978). One may note also a weaker infestation of *S. albus* in Lake Kronotskoe with nematode *C. farionis* at higher indices of invasion with *C. truttae* and *P. longicollis*. These data show that, in both lakes, *S. albus* is not a specialized predator; however, in Lake Azabach'e, according to our observations, it occupies a dominant position, especially in the last years, while in Lake Kronotskoe it apparently undergoes a considerable pressure on the side of other char species. The result of it is its increased migration and adaptation capacity and maximal diversity of food items.

Both the Kronotskaya River and lake–river *S. malma* in Lake Azabach'e are noticeably infected with typical for dwellers of flow-through water bodies parasites *C. truttae* and *Cr. farionis* and, to a smaller degree, with cestodes and proboscis worms of the genus *Neoechinorhynchus* (Table 4). At the same time, in Lake Kronotskoe, *S. malma* is less intensively than in Lake Azabach'e infected with helminths related to

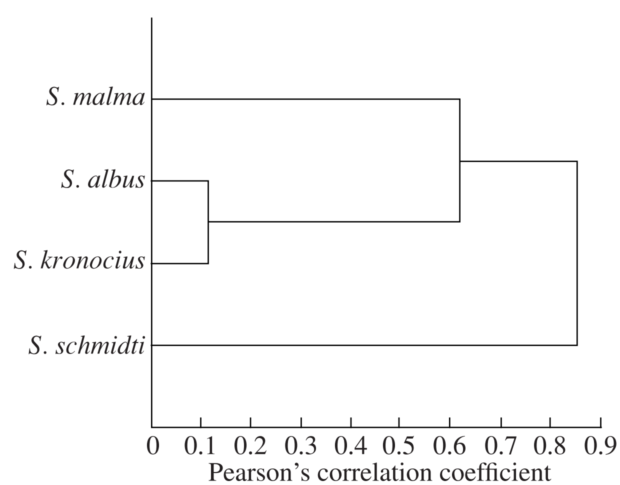

Fig. 4. Dendrogram of similarity of four species of chars of the genus *Salvelinus* from the basin of Lake Kronotskoe by the extensity of invasion, average intensity of invasion, and index of abundance of parasites plotted by the Ward method.

benthos (*C. truncatus*, *C. farionis*, and especially *E. salmonis*); however, the invasion of it with parasites whose development proceeds in plankton crustaceans (*P. oncorhynchi*, *E. salvelini*) turned out unexpectedly high. This suggests that, in Lake Kronotskoe, amphipods play a smaller role in the diet of *S. malma* than in mesotrophic Lake Azabach'e, where their average biomass in the littoral zone is 17 g/m^2 (Kurenkov, 2005), and of plankton, more considerable. Another difference of Kronotskoe Lake *S. malma* from *S. malma* from Azabach'e Lake is the absence in it of trematodes *P. umblae*, nevertheless recorded for the lake. All this indicates rather considerable differences in the diet of chars from the two lakes, which is evidently determined by specific features of species composition of invertebrates and their distribution in water bodies under comparison.

On the whole, chars from Lake Kronotskoe are characterized by a considerably more intense invasion with proboscis worms *N. salmonis* and a weak invasion with trematodes *P. umblae*, as compared to Lake Azabach'e. This may be explained by a wide distribution in the basin of Lake Kronotskoe of intermediate hosts of the first species (plankton ostracods) and a limited littoral of the lake—the zone of distribution of bivalves (intermediate hosts of trematodes). If in Lake Kronotskoe the background species of trematodes are all the three aforementioned species of the family Allocreadiidae, in Lake Azabach'e *Cr. farionis* and *P. umblae* dominate. Of proboscis worms in Lake Kronotskoe, the dominant position is occupied by *N. salmonis*, and in Lake Azabach'e, by *E. salmonis*.

In Lake Kronotskoe, we, following other authors (Pavlov et al., 2003; Atrashkevich et al., 2005a), observe an extremely intense invasion of chars with helminths (Table 1). In the first turn, it concerns the invasion of *S. schmidti* with trematode *Crepidostomum* sp., whose numbers in one fish reached 1240 individuals, as well as of *S. albus* with trematodes *Cr. farionis* and *Cr. metoecus* with maximal intensity of 782 and 2937 individuals, respectively. High values of intensity of invasion of fish were also recorded with cestodes (*E. salvelini*, 863 individuals in *S. kronocius*; *P. longicollis*, 229 individuals in *S. albus*); with nematodes (*C. farionis*, 296 individuals in *S. schmidti*; *C. ephemeridarum*, *P. oncorhynchi*, and *C. truttae*, 185, 290, and 239 individuals, respectively, in *S. albus*); and with proboscis worms (*N. salmonis*, 960 individuals in *S. kronocius*). These species of helminths reach extremely high numbers in the lake, as compared to other studied lake ecosystems of Kamchatka—Lakes Azabach'e, Dal'nee, and Kuril'skoe (Konovalov, 1971; Butorina et al., 1980). For Lake Kronotskoe, also very high indices of invasion of chars with copepod *S. carpionis* (Table 3)—a common parasite of the oral cavity of fish of the genus *Salvelinus* in water bodies of Far East of Russia were revealed. For instance, in some char samples from basins of the rivers Kamchatka, Ozernaya, Yama, Ola, Taui, Anadyr, and others, maximal values of II, EI, and IO of this parasite do not exceed, respectively, 16 individuals/fish, 53.3%, and 3.7 (Butorina et al., 1980; Nagasawa et al., 1994; Shed'ko, 2005; Shed'ko et al., 2005). The level of invasion of Lake Kronotskie chars with the listed parasite is comparable to only that cited by Japanese authors (Nagasawa et al., 1995) for chars in aquaculture.

We consider that a high invasion of chars with parasites is the manifestation of the Krebs cycle that is typical of insular biotas (Voronov, 1987). It involves the impossibility for young individuals to leave this territory and disperse, which leads to a rapid reproduction of some parasite species and reaching by them of extremely high numbers. We apparently observe the same picture in Lake Kronotskoe with respect to some parasites. Since in the lake basin almost only nonmigratory species of salmonids dwell (including kokanee), the entire cycle of their parasites is exercised over a limited area. This leads to the accumulation of parasites in this peculiar "aquarium" lake. Nothing of the kind occurs in lakes with an accessible exit to the sea and an entrance back. Among the lakes of this type is, for instance, the aforementioned Lake Azabach'e, in which most dwelling fish species, except typically freshwater, are represented by nonmigratory and migratory or only migratory ecotypes. Resident forms of fish periodically "take out" from the lake some parasites that perish during the period of the feeding migration, decreasing thus their numbers in the lake. This is evidenced by a lower invasion with such parasites of migratory forms of fish, as compared to nonmigratory (Butorina et al., 1980).

The high efficiency of plankton and benthos in Lake Kronotskoe (Kurenkov, 2005) and the diversity in its composition of invertebrates—intermediate hosts of helminthes—undoubtedly promote a successful circulation of parasites in the water body.

The data we obtained on parasitofauna of different char species from the basin of Lake Kronotskoe supplement and support facts of ecological divergence of lake chars recorded by ichthyologists (Viktorovskii, 1978; Savvaitova, 1989; Chereshnev et al., 2002; et al.). Differences in the pattern of feeding and mode of life of different char species formed as a result of long-term selection during common habitation in an isolated lake soften possible manifestations of competition between them. A similar distribution over ecological niches is typical of most lakes, where several species (or ecotypes) of chars coinhabit (Savvaitova, 1989).

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