

Trophic Relations between Native *Salvelinus malma* Walb. and Introduced *Oncorhynchus nerka* Walb. in the Landlocked Lake Sevo, Kamchatka

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Abstract—Fish introductions are known to be dangerous due to the unexpected spread of diseases and disorganization of the food web. In 1986, the resident sockeye salmon *Oncorhynchus nerka* from Kronotskoye Lake was introduced into an isolated lake in Kamchatka inhabited by the native lacustrine Dolly Varden charr *Salvelinus malma*. Thirty years later, we analyzed the stomach content, stable isotope ratio and lipid fractions in muscles, as well as the parasite fauna of fish to assess the trophic relationships between the two species. It has been found that the sockeye salmon has occupied the planktivorous niche; no diversification into trophic forms depending on the number of gill rakers, like in the ancestral population, was detected. The indigenous benthivorous *S. malma* is represented by three trophic groups. Mature dwarf individuals, as well as the juveniles, mainly consume insect larvae on the lake slope; large fish feed on amphipods in the same habitats; and 10% of the large Dolly Varden switches to facultative piscivory. Predators die as a result of *Diphyllbothrium* sp. hyper invasion, which infects fish when feeding on the sockeye salmon. The diversity of parasite fauna is 3/4 poorer in the introduced sockeye in comparison with the donor population; part of the parasite species is obtained by the sockeye from the Dolly Varden.

Keywords: introduced species, native species, ecological diversification, feeding patterns, trophic niche, stable isotope composition, lipid content, parasite fauna, salmonids, Kamchatka

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INTRODUCTION

In the 1970s–1980s, large-scale introducing of the sockeye salmon *Oncorhynchus nerka* Walb. from Kronotskoye Lake into the non-fisheries lakes was carried out in Kamchatka in order to increase the fish productivity of the water bodies (Pogodaev and Kurenkov, 2007). The naturalization of residential sockeye was successful in small lakes such as Klyuchevoye, Sevo, and Demidovskoye, as well as in Tolmachevo Reservoir, the largest reservoir on the peninsula (Bugayev and Kirichenko, 2008; Markevich, 2008). Interrogatory data also confirm the naturalization of the sockeye in Khangar Lake.

However, Lake Sevo turned out to be different from other water bodies with successful sockeye introduction because before the sockeye was introduced in 1986 and 1987, it had already been populated by a residential Dolly Varden charr *Salvelinus malma* Walb.

(Pogodaev and Kurenkov, 2007). According to the data from 2007, the sockeye population of Lake Sevo increased significantly. The abundant food supply and the presence of predatory charrs were considered factors that determined successful naturalization (Pogodaev and Kurenkov, 2007). The influence of the sockeye salmon itself on the ecosystem of Lake Sevo was not considered. No study of the parasite fauna of the reservoir was carried before or after the experiment, either. However, the introduction is considered one of the most important reasons for the decline in biological diversity (Vitousek et al., 1997; Olden et al., 2004), since dangerous parasites are introduced into lakes and rivers along with introduced species, which promotes epizootic spread (Johnsen and Jensen, 2006; Boys et al., 2012; Lymbery et al., 2014), resource redistribution, and changes in the trophic structure of ecosystems (Baxter et al., 2004; Eby et al., 2006; Amundsen et al., 2013; Stolbunov et al., 2021). The fauna of small inland water bodies is considered especially vul-

Abbreviations: MS, maturity stage; FL, Smith's body length (Fork length); Q, body weight.

nerable to the introduction of alien species (Gherardi, 2007; Vitule et al., 2009).

The history of salmonid fish introductions (Aprahamian et al., 2003; Crawford and Muir, 2008; Markevich and Esin, 2019) is full of cases ending in disaster for the recipient ecosystems and native species (Buoro et al., 2016). The introduction of *Salmo* spp. in the rivers of the Pacific coast of America led to a large-scale death of native *Oncorhynchus* spp. from vibriosis (Ginetz, 2002). Attempts to reintroduce *Salmo salar* L. into the Scandinavian rivers led to the death of local populations due to the parasite *Gyrodactylus salaris* epizooty (Bakkel et al., 1992). In other cases, introduced species displaced native salmon species from their food niches (Eloranta et al., 2015; Nasegava, 2020). The introduction of salmonids into isolated ecosystems with specific endemic fauna most often led to the extinction of the latter (Markevich et al., 2019).

Thus, the purpose of this study was to determine the trophic relationships between the native Dolly Varden and the introduced sockeye salmon in terms of their food composition, stable isotope and lipid ration, and parasite fauna.

MATERIALS AND METHODS

Lake Sevo is located in the spurs of the Valagin Range in central Kamchatka (54.479372' N, 158.673444' E) at an altitude of 620 m above sea level. It is a dammed lake, drainless; length of 3.5 km, average width 0.7 km, maximum depth 100 m (Esin and Markevich, 2017).

The study material was collected in August 2015. Fish were caught with gillnets (mesh pitch 20–35 mm) throughout the lake littoral; two large dying Dolly Varden charrs were sampled from the surface of the water. In total, 65 Dolly Varden specimens and 52 specimens of the sockeye salmon were studied according to the standard protocol (45% of fish catches were the Dolly Varden). For each freshly caught fish, *FL* (cm), *Q* (g), and maturity stage (MS, points) were determined (Murza and Khristoforov, 1991). In the sockeye salmon, the number of gill rakers on the first gill arch was also counted.

The fish feeding strategy was analyzed from stomach contents (Amundsen et al., 1996). We calculated the frequency of occurrence of various food object groups, i.e., the ratio of the number of fish with a given type of food to the number of fish in the sample (%), as well as the average number of food objects of each group per one fish in the sample (ind.). The commonality of food niches was assessed using the Morisita index modified by Horn (Horn, 1966); the proportion of groups in the diet was determined by the number of victims.

Since a rapid shift to feeding on mass prey is possible for charrs in summer (Tveiten et al., 1996; Jorgensen and Johnsen, 2014), a retrospective assessment

of trophic niches was additionally carried out. For this, fish at the 3–4 MS were compared by the ratio of stable isotopes of $^{14}\text{N}/^{15}\text{N}$ nitrogen and $^{12}\text{C}/^{13}\text{C}$ carbon in muscle tissue (Peterson and Fry, 1987), by the lipid composition of muscles (Bogdan et al., 2001), and by the composition of parasite fauna (Knudsen et al., 2004).

For isotope analysis, samples of muscle tissue were cut out from under the posterior edge of the dorsal fin and dried to constant weight. Mass spectrometric analysis of the samples was carried out at the Instrumental Methods in Ecology Shared Use Center at the Severtsov Institute for Ecology and Evolution of the Russian Academy of Sciences on a Thermo Finnigan Delta V Plus device equipped with a Flash 1112 analyzer. The isotopic composition is presented in pro mille of a deviation (‰) from the standards (atmospheric nitrogen and belemnite sample). Since the $\delta^{13}\text{C}$ values varied within 10‰, normalization by lipid composition was not performed (Post et al., 2007).

The content of the main lipid fractions in the muscles was assessed spectrophotometrically using a Hatch DR2400 device. Extraction (Folch et al., 1957) was performed from tissue fragments weighing 0.4 ± 0.001 g, followed by washing in 1% KCl solution. The gross lipid concentration was determined by reaction with phosphoric vanillin in 10% H_2SO_4 ; optical density was determined at a wavelength of 520 nm (Knight et al., 1972). The content of triacylglycerides and phospholipids was determined by enzyme-photometric approach at a wavelength of 505 nm using commercial Spinreact kits in accordance with the manufacturer's instructions. The values were expressed as % by weight of the tissue samples.

A parasitological analysis of fish was carried out using an incomplete parasitological dissection (Bykhovskaya-Pavlovskaya, 1985). The fish were examined for the presence of parasites on the body surface, in the oral and gill cavities, in the eyes (in the internal environment and lenses), in the body cavity, on the surface of the heart, in the swim bladder, in the ureters, and on the walls and in the cavity of the stomach and intestines. The fish were not examined for the presence of protozoa, myxosporidium (except for *Henneguya zschokkei* (Gurley, 1894)), or monogeneans. Most of the parasites were identified up to the species level (*Opredelitel'...*, 1985, 1987). Traditional indicators of infestation were used: extensiveness of invasion is the proportion of infected fish in the sample, %; the abundance index is the average number of parasites per fish in the sample, ind.

To determine the statistical significance of differences between groups of fish in their feeding strategies, isotopic and lipid composition, and parasite infestation, the nonparametric Mann–Whitney test was used after the presence of differences was confirmed by the Kruskal–Wallis test (Conover, 1999). The significance of size trends in changes in the proportion of

food objects in the stomachs, the ratio of isotopes and lipids in muscles, and infestation with parasites was determined by the method of least squares (Plokhinskii, 1970). Mathematical data processing was carried out using the StatSoft Statistica v.13 software.

RESULTS

Biological characteristics of fish. In our catches, the Dolly Varden was represented by juveniles with gonads of the second MS (17 specimens, FL 10–20 cm, Q 10–70 g), adults of both sexes at MS 4+ (11 specimens), so-called “dwarfs” with FL 14–20 (on average 17.2 ± 4.28) cm and Q 32–60 (43.7 ± 3.01) g, and large adults of both sexes on the third–fourth MS (37 specimens) with FL 20–42 (27.3 ± 8.90) cm and Q 68–580 (208.9 ± 19.94) g.

The sockeye salmon with FL 14–29 (19.9 ± 3.36) cm and Q 20–110 (53.3 ± 2.40) g had gonads on the fourth MS. In the ancestral (donor) resident population of Kronotskoye Lake, there are two groups in the sockeye salmon population: the one of benthivorous sockeye with few gill rakers (<39) and the other of planktivorous sockeye with dense gill rakers (≥ 39), which differ in body size (Kurenkov, 1977). In Lake Sevo (as well as in other Kamchatka lakes), the planktivorous densely-rakered sockeye salmon was introduced. In 2015, a sample from Lake Sevo included fish with few (<39) and many (≥ 39) gill rakers (11 ind. and 41 ind., respectively). These individuals did not differ in body size (t -test $p = 0.281$).

Differences in fish nutrition. Eight groups of food objects were distinguished in the stomachs of the studied fish (Table 1). Juveniles and dwarfs of the Dolly Varden predominately fed on chironomid larvae and did not differ in the number of victims of all groups in the stomachs (U -tests $p > 0.05$). According to the feeding strategy, large Dolly Varden was divided into benthivorous (58 ind.) and piscivorous (7 ind.). In the stomachs of the first group, besides gammarids (amphipods), chironomid larvae and mollusks were also noted. Fish and benthos were present in the stomachs of the predatory Dolly Varden. Predators were larger than “large” benthophages: FL 31–42 (on average 35.1) cm and Q 215–580 (386.8) g, versus FL 20–39 (26.1) cm and Q 68–480 (181.3) g (t -tests $p = 0.009$ and $p = 0.004$ for FL and Q , respectively).

The Sockeye salmon with different number of gill rakers (more or less than 39) did not differ in regards to stomach contents (U -tests, $p > 0.05$ for all groups of objects). In August, it fed on planktonic crustaceans, gammarids, and insect imagoes. The Sockeye salmon significantly differed from the dwarf, large benthivorous, or predatory Dolly Varden by the high content of planktonic crustaceans in the stomachs ($p < 0.001$); it differed from the dwarf and benthivorous Dolly Varden by a smaller number of gammarids and mollusks ($p < 0.001$); insect imagoes ($p = 0.010$); and chirono-

mid larvae, mayflies, and caddisflies ($p < 0.001$). The Sockeye salmon had a higher stomach fullness compared to the Dolly Varden ($p = 0.006$).

The food niches of the Dolly Varden and the sockeye salmon did not overlap. The Morisita index in pairs of sockeye salmon–dwarf Dolly Varden, sockeye salmon–large benthivorous Dolly Varden, and sockeye salmon–predatory Dolly Varden was less than 0.1; in the pair of piscivorous–benthivorous Dolly Varden it was 0.5. The biological significance of the Morisita index was 0.6 (Horn, 1966).

The increase in the size of the benthivorous Dolly Varden coincides with a decrease in the proportion of insect larvae in diet and an increase in the proportion of gammarids. The value of the linear approximation R of the relation FL –the number of chironomid larvae in the stomach reached 0.66 ($p = 0.037$); for FL –gammarids it was 0.57 ($p = 0.043$). The Sockeye salmon did not show any change in food composition associated with an increase of FL , $R < 0.30$ ($p > 0.05$).

Ratio of stable isotopes in the muscle tissue of fish.

The Adult benthivorous Dolly Varden, piscivorous Dolly Varden, and sockeye salmon formed nonoverlapping areas in the $\delta^{13}C$ – $\delta^{15}N$ space (Fig. 1). The benthivorous Dolly Varden differed from predators of this species, as well as from the sockeye salmon, by a higher $\delta^{13}C$ ($H_{2,48} = 36.22$, $p < 0.001$; U -tests $p = 0.041$ and $p < 0.001$, respectively). Dwarfs differed from adult large benthivorous fish by a reduced $\delta^{15}N$ ($p = 0.045$). The predatory Dolly Varden has higher $\delta^{15}N$ in comparison to the benthivorous Dolly Varden and the sockeye salmon ($H_{2,48} = 16.67$, $p = 0.002$; U -tests $p < 0.001$). The Sockeye salmon did not differ significantly in nitrogen signature from benthivorous Dolly Varden ($p = 0.322$) or in carbon signature from the predatory Dolly Varden ($p = 0.287$).

For the benthivorous and predatory Dolly Varden, there was a positive correlation between an increase in $\delta^{15}N$ and body size ($R = 0.72$, $p = 0.035$).

Lipid composition of fish muscle tissue. The sockeye salmon differed from the adult Dolly Varden in a reduced fat content of the muscle tissue ($H_{2,48} = 26.05$, $p < 0.001$; U -tests, $p < 0.001$); no significant differences in the total lipid concentration were obtained for the various trophic groups of the Dolly Varden ($p = 0.174$) (Fig. 2a). According to the content of triacylglycerides, dwarfs differed from large benthivorous fish ($p = 0.039$) and predators ($p = 0.003$), while large benthophages and predators did not differ significantly ($p > 0.05$) (Fig. 2b). The sockeye salmon differed by a reduced phospholipid content from the dwarf large benthic, and predatory Dolly Varden ($p = 0.021$, 0.004, 0.001, respectively), while in both groups of benthivorous Dolly Varden this lipid fraction was lower than in predators ($p = 0.049$) (Fig. 2c).

Table 1. Feeding of *Salvelinus malma* and *Oncorhynchus nerka* in Lake Sevo, Kamchatka (August 2015)

Food object	<i>O. nerka</i> (52 ind.)		<i>S. malma</i>				<i>H</i> -test	<i>U</i> -test		
			predators (7 ind.)		benthophages (58 ind.)					
	OF	<i>n</i>	OF	<i>n</i>	OF	<i>n</i>		<i>O. nerka</i> – <i>S. malma</i> , predators	<i>O. nerka</i> – <i>S. malma</i> , benthophages	<i>S. malma</i> , predators– <i>S. malma</i> , benthophages
Chironomidae, larvae	17	0.4 (5)	14	0.3 (2)	38	17.8 (205)	$\frac{9.52}{0.009}$	$\frac{152}{0.945}$	$\frac{845}{0.020}$	$\frac{144}{0.182}$
Ephemeroptera, larvae	0	0.0 (0)	0	0.0	11	0.8 (27)	$\frac{6.61}{0.037}$	–	$\frac{175}{0.016}$	$\frac{85}{0.379}$
Trichoptera, larvae	0	0.0 (0)	14	0.2 (1)	9	0.9 (31)	$\frac{5.46}{0.065}$	$\frac{182}{0.393}$	$\frac{1326}{0.029}$	$\frac{179}{0.043}$
Insecta, imago	31	10.2 (300)	14	0.7 (5)	13	0.2 (5)	$\frac{6.75}{0.034}$	$\frac{153}{0.403}$	$\frac{1158}{0.010}$	$\frac{190}{0.820}$
Amphipoda	10	10.8 (285)	14	0.9 (6)	41	15.8 (158)	$\frac{13.58}{0.001}$	$\frac{175}{0.754}$	$\frac{1012}{<0.001}$	$\frac{138}{0.150}$
Copepoda and Ostracoda	92	167.6 (590)	0	0.0 (0)	2	0.1 (3)	$\frac{80.77}{<0.001}$	$\frac{21}{<0.001}$	$\frac{177}{<0.001}$	$\frac{186}{0.553}$
<i>Pisidium</i> sp.	6	0.1 (2)	0	0.0 (0)	36	3.5 (51)	$\frac{18.22}{<0.001}$	$\frac{172}{0.538}$	$\frac{995}{<0.001}$	$\frac{126}{0.066}$
Fishes (<i>S. malma</i> and <i>O. nerka</i>)	0	0.0 (0)	100	1.0 (2)	0	0.0 (0)	$\frac{113.88}{0.000}$	$\frac{950}{<0.001}$	–	$\frac{1456}{<0.001}$
Stomach fullness, %	45.0		34.4		28.4		$\frac{7.66}{0.022}$	$\frac{139}{0.316}$	$\frac{1011}{0.006}$	$\frac{196}{0.991}$

OF, frequency of occurrence of the food object groups in the stomachs of fish, %; *n*, average number of victims per one fish in the sample (the maximum number of victims, ind., is in parentheses). A dash indicates the absence of the food object.

The growth of the large benthivorous Dolly Varden was associated with a trend towards an increase in the fat content of its muscle tissue ($R = 48$, $p = 0.05$).

Composition of fish parasites. Nine species of parasites were found in the examined fish of both species (Table 2). *Salmincola edwardsii* Olsson, 1869 from the gill cavity and *Paracanthobdella livanowi* (Epstein, 1966) from the body surface have direct development. The rest of the parasites marked various food preferences of fish, as they were associated with the consumption of different groups of invertebrates. On the surface of the fish body, cysts of the myxosporidium *Henneguya zschokkei* (Gurley, 1894), whose main hosts are benthic annelids (Okamura et al., 2015), were noted. In the fish eyes, there were metacercarids *Diplostomum* sp., which infect fish upon contact with lung mollusks (Sudarikov et al., 2002). *Crepidostomum farionis* Muller, 1874 was determined in the intestines of fish. Its intermediate host is mayfly larvae (Crawford, 1943). *Cystidicola farionis* Fisher, 1798 was noted in the swim bladder and *Echinorhynchus salmonis* Muller, 1780, in the intestine. Both of these parasites

are associated with amphipods as intermediate hosts (Black and Lankester, 1980; Measures and Bosse, 1993). Plerocercoids of *Diphyllbothrium* sp., whose intermediate hosts are planktonic crustaceans, were present in the walls of the stomach and on the surface of the internal organs of fish (Delyamure et al., 1985). *Proteocephalus longicollis* Zeder, 1800 was found in the intestines of fish; its intermediate hosts are cyclops and diaptomuses (Willemsse, 1969).

The Benthivorous Dolly Varden, piscivorous Dolly Varden, and sockeye salmon differed in parasite infestation. The first differed from the predatory Dolly Varden and the sockeye salmon by the low abundance of *Diphyllbothrium* sp. (*U*-tests, $p < 0.001$). At the same time, dwarfs differed from large benthivorous fish by a greater abundance of *Proteocephalus longicollis* ($p = 0.008$) and a lower invasion of *Echinorhynchus salmonis* and *Cystidicola farionis* ($p < 0.001$). The predatory Dolly Varden differed by an extremely high infestation with *Diphyllbothrium* sp. (up to 524 ind./fish). The Sockeye salmon was characterized by significantly low invasion of *Diplostomum* sp., *Cystidicola far-*

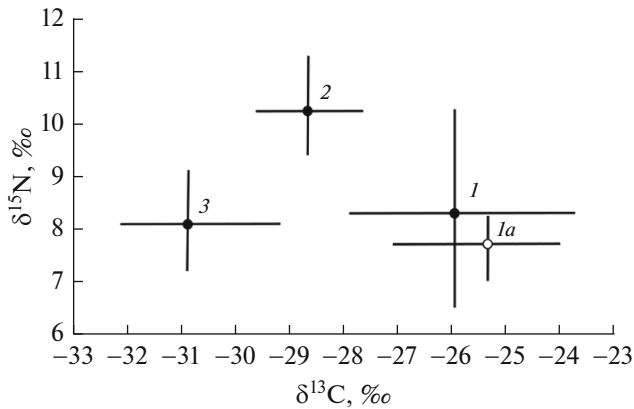


Fig. 1. Carbon and nitrogen isotope composition in the muscle tissue of the benthivorous Dolly Varden (1) ((1a) early maturing individuals), piscivorous Dolly Varden (2), and the planktivorous sockeye salmon (3) from Lake Sevo. Average values (points) and variation limits (lines) are given.

ionis, and *Echinorhynchus salmonis* ($p < 0.001$), as well as the absence of *Salmincola edwardsii*.

The growth of the Dolly Varden of all trophic groups was characterized by an increase in the number of *Echinorhynchus salmonis* ($R = 0.87$, $p = 0.001$) and *Cystidicola farionis* ($R = 0.77$, $p = 0.003$) against the background of a decrease in the number of *Proteocephalus longicollis* ($R = 0.65$, $p = 0.013$).

DISCUSSION

Our study showed that Dolly Varden from Lake Sevo is polymorphic in its ecology. Juveniles mainly

feed on insect larvae. With age, the food spectrum expands: gammarids and mollusks are included in the diet. Adults >20 cm feed almost exclusively on gammarids. At the same time, some fish ($\sim 10\%$) matured in the size range of juveniles (males at $FL \geq 13$ cm, females at $FL \geq 15$ cm) continue feeding on insect larvae without switching to gammarids. Such fish differ from gammarid-consumers in their low nitrogen signature, since amphipods themselves are benthos consumers and enrich large Dolly Varden with heavy isotopes (MacNeil et al., 1997). Despite the obviously higher calorie content of gammarus compared to chironomid larvae, dwarfs store lipids more efficiently than large benthivorous fish.

The composition of Dolly Varden parasites indicates that it feeds on benthos near the lake bottom. Five of the seven parasite species infect fish either by eating benthic organisms (*Crepidostomum farionis*, *Cystidicola farionis*, and *Echinorhynchus salmonis*) or by contact with them (*Diplostomum* spp., *Henneguya zschokkei*). Only *Proteocephalus longicollis* and *Diphyllobothrium* sp. infect Dolly Varden when feeding on plankton. The large benthivorous Dolly Varden is heavily infested with *Cystidicola farionis* and *Echinorhynchus salmonis*, which is associated with its feeding on gammarids.

Among the older and already mature fish $\sim 10\%$ become piscivorous and accelerate in growth. This phenomenon is typical for charrs in isolated lakes of Kamchatka (Esin and Markevich, 2019) and throughout the range of the genus (Reist et al., 2013; Esin and Markevich, 2017). Feeding on their own juveniles and sockeye salmon, the predatory Dolly Varden is reinvaded by *Cystidicola farionis*, *Echinorhynchus salmonis*, and *Diphyllobothrium* sp., and also acquires higher

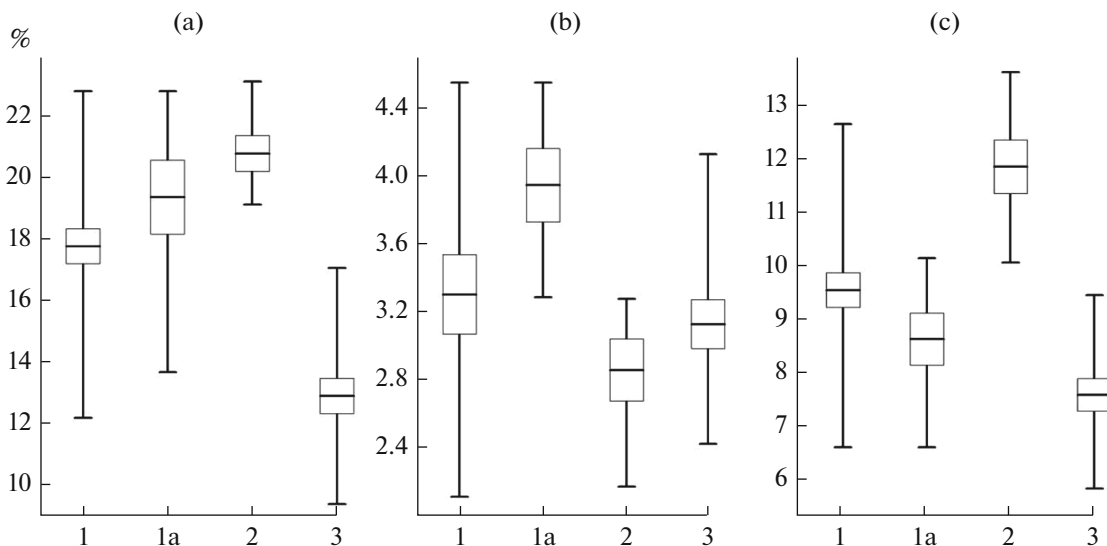


Fig. 2. Lipid composition in the muscle tissue of the Dolly Varden and the planktivorous sockeye salmon from Lake Sevo: (a) gross concentration of lipids, (b) triacylglycerides, and (c) phospholipids. Mean values (transverse lines), standard errors (rectangles), and limits of variation (vertical lines) are given. Designations of fish groups are same as in Fig. 1.

Table 2. *Salvelinus malma* and *Oncorhynchus nerka* parasites in Lake Sevo, Kamchatka (August 2015)

Parasites	<i>O. nerka</i> (52 ind.)		<i>S. malma</i>				<i>H</i> -test	<i>U</i> -test		
			predators (7 ind.)		benthophages (58 ind.)					
	EI	AI	EI	AI	EI	AI		<i>O. nerka</i> – <i>S. malma</i> , predators	<i>O. nerka</i> – <i>S. malma</i> , benthophages	<i>S. malma</i> , predators– <i>S. malma</i> , benthophages
Myxosporea										
<i>Henneguya zschokkei</i>	+	–	+	–	+	–	–	–	–	–
Trematoda										
<i>Diplostomum</i> sp.	50.0	0.9	7 from 7	13.1	100.0	30.0	$\frac{77.62}{<0.001}$	$\frac{11}{<0.001}$	$\frac{77}{<0.001}$	$\frac{140}{0.220}$
<i>Crepidostomum farionis</i>	36.5	0.6	6 from 7	0.4	32.1	10.1	$\frac{1.56}{0.450}$	$\frac{156}{0.751}$	$\frac{349}{0.432}$	$\frac{155}{0.45}$
Cestoda										
<i>Diphyllobothrium</i> sp.	94.2	8.1	6 from 7	119.1	7.1	0.1	$\frac{75.85}{<0.001}$	$\frac{103}{0.070}$	$\frac{143}{<0.001}$	$\frac{60}{<0.001}$
<i>Proteocephalus longicollis</i>	3.9	0.04	1 from 7	1.1	30.4	3.6	$\frac{14.05}{<0.001}$	$\frac{162}{0.23}$	$\frac{1054}{<0.001}$	$\frac{164}{0.38}$
Chromadorea										
<i>Cystidicola farionis</i>	34.6	0.7	6 from 7	119.0	91.1	80.7	$\frac{56.82}{<0.001}$	$\frac{41}{<0.001}$	$\frac{292}{<0.001}$	$\frac{169}{0.552}$
Acantocephala										
<i>Echinorhynchus salmonis</i>	88.5	30.0	6 from 7	845.6	94.6	420.8	$\frac{25.57}{<0.001}$	$\frac{71}{0.009}$	$\frac{686}{<0.001}$	$\frac{128}{0.140}$
Crustacea										
<i>Salmincola edwardsii</i>	0.0	–	6 from 7	3.4	14.3	1.2	16.07	$\frac{104}{<0.001}$	$\frac{1248}{0.005}$	$\frac{137}{0.053}$
Hirudinea										
<i>Paracanthobdella livanowi</i>	+	–	+	–	+	–	–	–	–	–

Here and in Table 3: EI, extensity of invasion, %; AI, abundance index, ind. A plus/minus sign indicates only the presence/absence of *H. zschokkei* and *P. livanowi*; for *H. zschokkei* and *P. livanowi*, EI and AI were not calculated.

$\delta^{15}\text{N}$ values (Minagawa and Wada, 1984). The specific lipid composition of predators indicates a good food supply and an increased level of metabolism compared to benthivorous individuals (Houlihan et al., 1993).

Sockeye salmon in Lake Sevo is uniform in nutrition; fish with different numbers of gill rakers (<39 and ≥ 39) mainly feed on planktonic crustaceans (average 168 ind./fish). The composition of parasites confirms the preferential feeding of sockeye salmon on plankton. Compared to the benthivorous Dolly Varden, sockeye salmon is invaded more by *Diphyllobothrium* sp., which infects fish when feeding on cyclops, and less by *Diplostomum* sp., *Cystidicola farionis*, and *Echi-*

norhynchus salmonis, which are transmitted to fish through mollusks and amphipods.

Thus, 30 years after the introduction of the sockeye salmon (about eight generations) in the ecosystem of Lake Sevo, there is stable food segregation between the native Dolly Varden and the introduced species. In contrast to other salmon lakes, such as Inari Lake in Finland, the native species was not displaced from its trophic niche (Eloranta et al., 2015). The food niches of the Dolly Varden and sockeye salmon, according to the results of the Morisita index, do not overlap. Species are separated by isotopic signature, showing segregation of trophic niches over several months, i.e., throughout the spring–summer feeding period (Peter-

Table 3. Comparative characteristics of the resident *Oncorhynchus nerka* from water bodies of Kamchatka

Features	Kronotskoye Lake		Lake Sevo	Tolmachevo Reservoir
	29–38 rakers, benthophages	39–47 rakers, planktophages	36–46 rakers, planktophages	35–45 rakers, benthophages
<i>FL</i> , average (min–max), mm	253 (205–313)	233 (215–250)	199 (140–290)	189.5 (161–270)
<i>Q</i> , average (min–max), g	185 (83–350)	125 (63–236)	53.3 (20–110)	82.8 (56–158)
♀ : ♂	1 : 1.5	1 : 2.6	1 : 1	1 : 1.6
Dominant food objects	Chironomid larvae and pupae	Zooplankton	Zooplankton, adult insects	Gammarids, chironomid larvae and pupae
Number of parasite species	16	16	8 (incomplete dissection)	2
Predominant types of helminths (EI, AI)	<i>Crepidostomum metoecus</i> (93.3, 146.5); <i>Crepidostomum farionis</i> (96.7, 23.9)	<i>Neoechinorhynchus salmonis</i> (100, 306); <i>Proteocephalus longicollis</i> (90, 60.5); <i>Eubothrium salvelini</i> (76.7, 19); <i>Diphyllobothrium</i> sp. (96.7, 14.6)	<i>Echinorhynchus salmonis</i> (88.5, 30); <i>Diphyllobothrium</i> sp. (94.2, 8.1)	<i>Diplostomum</i> sp. (100, 23.7)

son and Fry, 1987) and, judging by the difference in infestation of *Cystidicola farionis* and *Echinorhynchus salmonis*, for at least the last two years (Black and Lankester, 1980; Mikhailova, 2015). The reduced $\delta^{13}\text{C}$ of the sockeye salmon is associated with its involvement in the secondary cycle of organic matter in the hypolimnion (Wada, 2009). Despite more actively feeding in August, sockeye salmon is characterized by a lower fat content, which may indicate worse feeding conditions when compared with benthivorous Dolly Varden (Bogdan et al., 2001; Houlihan et al., 1993).

Sockeye salmon of Lake Sevo differs from its parental multiraker population from Lake Kronotskoye: in Sevo, individuals with a number of gill rakers <39 appeared, which is typical for specimens with few rakers from Kronotskoye Lake (Markevich, 2008). At the same time, no differences in nutrition were found between the specimens with many and few rakers in Lake Sevo, as well as differences in their infestation with parasites, biological parameters, and stages of gonadal maturity. Thus, in Sevo, sockeye salmon did not follow the scenario of the formation of independent ecological forms.

In addition to Lake Sevo, we have studied the diet and parasite fauna of the sockeye salmon introduced into the Tolmachevo Reservoir (Busarova and Esin, 2017). This population also differs from the parental one (Table 3). Like sockeye salmon from Sevo, the fish has a relatively smaller size and body weight and does not differentiate in terms of nutrition, despite the fact

that a third of individuals have a number of gill rakers <39. At the same time, in the Tolmachevsky Reservoir, sockeye salmon occupied the niche of a benthivorous fish. In lake Sevo this did not happen, because the native Dolly Varden, which is characterized by feeding from the bottom (Esin and Markevich, 2017), has competitive advantages over the sockeye salmon when feeding on benthophages.

Both daughter populations of the sockeye salmon are characterized by a depleted composition of the parasite fauna. In Lake Kronotskoye, we noted 17 species of parasites in the sockeye salmon (Busarova et al., 2016), which, together with sockeye salmon spawners, should have entered the recipient lakes. However, by 2015, not all types of parasites were preserved in the daughter populations. Therefore, the sockeye salmon of Lake Sevo (taking into account the incomplete parasitological dissection) housed eight species of parasites, of which only five species are common for the sockeye salmon of Lake Kronotskoye (*Crepidostomum farionis*, *Diplostomum* sp., *Diphyllobothrium* sp., *Proteocephalus longicollis*, *Cystidicola farionis*), and three species (*Henneguya zschokkei*, *Echinorhynchus salmonis*, *Paracanthobdella livanowi*) were absent in the parental population, i.e. were purchased from the native Dolly Varden. In the sockeye salmon of the Tolmachevo Reservoir, we noted only two species of parasites; the sockeye salmon has lost over 90% of the diversity of its parasite fauna (Busarova and Esin, 2017). At the same time, both Sevo and the Tol-

machevskoye Reservoir are inhabited by invertebrates that could serve as links in parasitic cycles.

Among the consequences of the introduction of the sockeye salmon in Lake Sevo, the hyperinvasion of predatory Dolly Varden by *Diphyllbothrium* sp. should also be noted. It is known that the high infestation of *Diphyllbothrium* sp. leads to multiple functional disorders in fish and their death (Pronin et al., 1991; Knudsen and Klemetsen, 1994). The dead Dolly Varden that we found in Lake Sevo was extremely heavily infested with this parasite (200–524 ind./fish). The predatory Dolly Varden accumulates representatives of the genus *Diphyllbothrium* when feeding on the sockeye salmon; on average, one sockeye salmon in the sample contained 8.1 ind. of *Diphyllbothrium* sp. Juvenile Dolly Varden, which also serves as food for predators, is minimally infected with this parasite. Larvae of *Diphyllbothrium* sp. in predators were located not only in the walls of the stomach, but also on the intestines, the walls of the abdominal cavity, and on the liver and in its tissue. Other individuals of the predatory Dolly Varden also had a high invasion of *Diphyllbothrium* sp. (invasion intensity 19–56 ind./fish).

CONCLUSIONS

According to our data, the introduction of the resident planktivorous sockeye salmon into isolated Lake Sevo, already inhabited by the Dolly Varden, did not lead to a change in the feeding strategies of these species. Dolly Varden continued to use the benthic food web. This native species is not uniform in nutrition: small individuals mainly consume chironomid larvae; the large-sized individuals switch to feeding on gammarids, while minor number of the fish at an older age begin to search for fish prey, hunting their own juveniles and the sockeye salmon. The elimination of the predatory individuals as a result of the accumulation of *Diphyllbothrium* sp. obtained from the sockeye salmon was noted. The sockeye salmon of Lake Sevo differs from the ancestral population from Lake Kronotskoye by a smaller size. The diversity of its parasitic fauna has decreased in comparison with the ancestral population.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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