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Helminths of epipelagic fish in the western Bering Sea and southern Sea of Okhotsk

I.I. Gordeev[1,2,*], S.G. Sokolov[3]

[1] Lomonosov Moscow State University, Leninskiye Gory 1/12, Moscow, 119234, Russia.
[2] Russian Federal Research Institute of Fisheries and Oceanography, Okruzhnoy Proezd 19, Moscow, 105187, Russia. E-mail: gordeev_ilya@bk.ru
[3] A.N. Severtsov Institute of Ecology and Evolution of the RAS, Leninskij pr. 33, Moscow, 119071, Russia. E-mail: sokolovsg@mail.ru
I.I. Gordeev ORCID: 0000-0002-6650-9120
S.G. Sokolov ORCID: 0000-0002-4822-966X
** Corresponding author*

ABSTRACT: During the parasitological survey on the research vessel *Professor Kaganovsky*, the western part of the Bering Sea and the southern part of the Sea of Okhotsk was investigated for fish infection by parasites. In total, 1083 specimens of 17 species of teleosts and salmon shark *Lamna ditropis* were dissected, in which 32 species of parasites were found. The plerocercoids *Pelichnibothrium speciosum s. lato* prevailed in the Bering Sea. In the Sea of Okhotsk, the maximum intensity and prevalence of infection were noted for *P. specioum s. lato*, *Anisakis* sp. and *Echinorhynchus gadi s. lato*. The difference in the number of studied fish species in the Bering and Okhotsk Seas (14 *vs* 9) significantly affected the species diversity of noted parasites (28 *vs* 18). Teleosts caught in the coastal area and the ones performing vertical migrations to some degree differed in terms of infection pattern, primarily due to digeneans component. Macroparasites of the crested sculpin *Blepsias bilobus* were studied for the first time, and 20 new records were made on the infection of previously studied fish species. Parasite fauna of fish in the epipelagic zone of the western part of the Bering Sea and the southern part of the Sea of Okhotsk is characterized by significant intensity, however, relatively poor species diversity.
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KEY WORDS: helminths, Pacific Ocean, fish parasites, marine biology, parasitology.

Гельминты эпипелагических рыб западной части Берингова моря и южной части Охотского моря

И.И. Гордеев[1,2], С.Г. Соколов[3]

[1] Московский государственный университет им. М.В. Ломоносова, Ленинские горы, д. 1/12, Москва, 119234, Россия. E-mail: gordeev_ilya@bk.ru
[2] Всероссийский научно-исследовательский институт рыбного хозяйства и океанографии, Окружной проезд, д. 19, Москва 105187, Russia.
[3] Институт проблем экологии и эволюции им. А.Н. Северцова РАН, Ленинский пр. 33, Москва 119071, Россия. E-mail: gordeev_ilya@bk.ru

РЕЗЮМЕ: В ходе исследований на НИС «Профессор Кагановский» на предмет зараженности рыб паразитами в западной части Берингова моря и южной части Охотского моря было вскрыто 1083 экз. 17 видов костистых рыб и одна особь

лососевой акулы *Lamna ditropis*, в которых обнаружено 32 вида паразитов. В Беринговом море преобладали плероцеркоиды *Pelichnibothrium speciosum s. lato*. В Охотском море максимальная интенсивность и экстенсивность инвазии была отмечена для *P. specioum s. lato*, *Anisakis* sp. и *Echinorhynchus gadi s. lato*. Разница в количестве исследованных видов рыб в Беринговом и Охотском морях (14 *vs* 9) существенно повлияла на видовое разнообразие отмеченных паразитов (28 *vs* 18). Костистые рыбы, пойманные в прибрежной зоне, и те, что совершают вертикальные миграции, несколько различались по картине заражения, в первую очередь за счет наличия трематод. Впервые изучены макропаразиты двухлопастного бычка *Blepsias bilobus* и в целом сделано 20 новых записей о наличии тех или иных видов паразитов у ранее изученных видов рыб. Паразитофауна рыб эпипелагиали западной части Берингова моря и южной части Охотского моря характеризуется значительной интенсивностью, однако относительно бедным видовым разнообразием.
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КЛЮЧЕВЫЕ СЛОВА: гельминты, Тихий океан, Pisces, паразиты рыб, морская биология, паразитология.

Introduction

The Bering Sea, a marginal sea of the northern Pacific Ocean, separates Eurasia from the Americas. Despite direct contact with the Arctic waters, the Bering Sea is ice-free for most of the year and plays an important role in the marine ecosystems of the North Pacific. The Sea of Okhotsk is located between the Kamchatka Peninsula, the Kuril Islands, Hokkaido Island, and Sakhalin Island. Due to a high solubility of oxygen in cold water the sub-polar regions are very productive. This is one of the reasons why salmon and other anadromous fish feed in this area during the marine period of their life (Gritsenko, 2002; Gordeev, Klovach, 2019). Extensive fishing is going on in the Bering Sea and the Sea of Okhotsk for valuable fish such as salmon, *Oncorhynchus* spp. (Salmonidae) (Klovach *et al.*, 2021), walleye pollock, *Gadus chalcogrammus* Pallas, 1814 (Gadidae), Pacific herring, *Clupea pallasii* Valenciennes, 1847 (Clupeidae), Pacific saury, *Cololabis saira* (Brevoort, 1856) (Scomberesocidae), chub mackerel, *Scomber japonicus* (Houttuyn, 1782) (Scombridae), and halibuts, *Hippoglossus* spp. and *Atheresthes* spp. (Pleuronectidae) (Antonov *et al.*, 2016).

The importance of parasitic surveys of marine fish cannot be underestimated. Helminths and crustaceans cause significant damage to their fish and invertebrate hosts, and may make the fishery product unmarketable (e.g. Quiazon, 2015). Studies of drift net catches in the Russian exclusive economic zone have shown that infection with cestodes *Eubothrium* spp. results in a significant decrease of the Fulton condition index of the chum salmon *Oncorhynchus keta* (Walbaum, 1792) during the marine period of life (Yarzhombek, Klovach, 2002). Fish infected with nematodes can be the source of human diseases such as anisakiasis (Rahmati *et al.*, 2020).

While the parasites of commercially important fish species are described fairly well, most other fish have never been investigated in this respect (Klimpel *et al.*, 2006; Klimpel *et al.*, 2009). At the same time, small fishes, which serve as intermediate or paratenic hosts to parasites of larger predators and as definitive hosts to some other parasites, may be excellent indicators of food web structure (Marcogliese, 2005). A comprehensive inventory of the fish parasite fauna would not only update the information about the parasites of valuable commercial fish but also provide new data for an analysis of the spatial and the vertical distribution of fish parasites and their host specificity and expand our knowledge about the distribution and transmission of the parasitic larvae in the marine environment.

In this paper, we summarise the results of the parasitological examination of 18 species of elasmobranch and teleost fish caught in the epipelagic layer in the western Bering Sea and

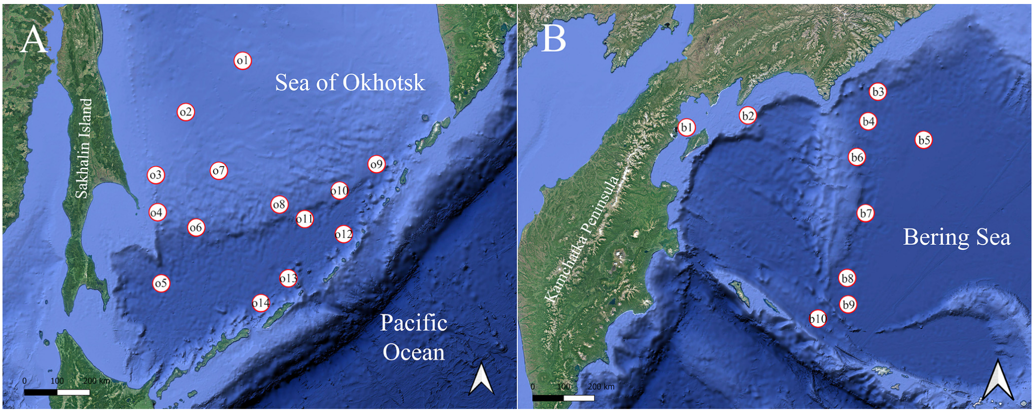

Fig. 1. Map of trawl stations in the Sea of Okhotsk (A) and in the Bering Sea (B). Station numbers are shown as o1–o14 in the Sea of Okhotsk and b1–b10 in the Bering Sea.
Рис. 1. Карта траловых станций в Охотском (A) и Беринговом (B) морях. Номера станций показаны как o1–o14 в Охотском море и b1–b10 в Беринговом море.

the southern Sea of Okhotsk in September–October 2019.

Material and Methods

Fish specimens were caught between 26 September and 6 October 2019 in the Bering Sea and between 11 October and 21 October 2019 in the Sea of Okhotsk from the research vessel *Professor Kaganovsky* during the survey (stock assessment) of the Pacific salmon. Midwater net trawl RT/TÌ 80/396 was used, with a 10 mm mesh insert in the net bag (Gordeev *et al.*, 2019). Locations of the trawl stations are given in Table 1 and shown in Figure 1. We dissected 601 individuals of teleosts caught in the Bering Sea and 481 caught in the Sea of Okhotsk (Tables 1–2). An individual of the salmon shark *Lamna ditropis* Hubbs et Follett, 1947, the only elasmobranch in our study, was caught in the Sea of Okhotsk.

Fishes were was examined for the presence of helminths and other macroparasites by total necropsy. This included examination of the skin, fins, and gills, and then examination of individual visceral organs and musculature using a stereomicroscope (Bykhovskaya-Pavlovskaya, 1985; Klimpel *et al.*, 2019). Prefixation treatment of trematodes and cestodes included cleaning and straightening for better identification. Acanthocephalans were transferred to fresh water until the proboscis everted and then fixed. All parasites except nematodes were preserved in 70% and 96% ethanol. Nematodes were fixed in 4% formaldehyde and three days later transferred to 70% ethanol for long-term storage. Temporary glycerol preparations of acanthocephalans and nematodes were made (Klimpel *et al.*, 2019). Digeneans were stained with acetic carmine, dehydrated, contrasted (cleared) with dimethyl phthalate, and finally mounted in Canada balsam (Bykhovskaya-Pavlovskaya, 1985). Cestodes were hydrated, stained with Harris's hematoxylin, differentiated in tap water, de-stained in ethanol, dehydrated, cleaned in methyl salicylate, and finally mounted in Canada balsam (Jensen *et al.*, 2011).

The captures in each of the two seas were made within a very small time frame. Moreover, they were made in an open ocean environment, where millions of square kilometres can be regarded as homogeneous from a biological viewpoint. Therefore, we present our data only in two blocks: the Bering Sea (Suppl. Table 1) and the Sea of Okhotsk (Suppl. Table 2).

Parasitological indices were calculated after Bush *et al.* (1999).

Results

All the fish species examined in our study were infected with parasites. The number of parasite species recorded in the Bering Sea and the Sea of Okhotsk was 28 and 18, respectively (Suppl. Tables 1, 2). Most of them were endohelminths (Suppl. Table 1). The most common generalists were *Pelichnibothrium speciosum* Monticelli, 1889 *s. lato* and *Anisakis* sp. (in both seas) and, in addition to that, *Echinorhynchus gadi* Zoega in Müller, 1776 *sensu lato* in the Sea of Okhotsk.

Table 1. Length, weight and locations of catches of fish examined during parasitological survey on the RV *Professor Kaganovsky* in the Bering Sea.
Таблица 1. Длина, вес и места поимок рыб, исследованных в ходе паразитологических работ на НИС «Профессор Кагановский» в Беринговом море.

Species / total length range, weight range	Total number examined	[station number] Localities (number examined)
Salmoniformes		
Oncorhynchus gorbuscha (Walbaum, 1792) / 20.8–26.3 cm, 64–161 g	20	[b7] 57°08'N&172°09'E (10); [b5] 58°58'N&174°54'E (10)
Oncorhynchus keta (Walbaum, 1792) / 35.4–41.7 cm, 444–661 g	5	[b7] 57°08'N&172°09'E (4); [b3] 60°07'N&172°45'E (1)
Perciformes		
Brama japonica Hilgendorf, 1878 / 37.7–47.0 cm, 1086–1327 g	5	[b9] 54°44'N&171°21'E (5)
Anarrhichthys ocellatus Ayres, 1855 / 46 cm, 132 g	1	[b8] 55°27'N& 171°19'E (1)
Trichodon trichodon (Tilesius, 1813) / 9.6–19.0 cm, 10–76 g	7	[b1] 59°16'N&163°44'E (7)
Scorpaeniformes		
Aptocyclus ventricosus (Pallas, 1769) / 2.0–14.0 cm, 122–400 g	5	[b5] 58°58'N&174°54'E (1); [b3] 60°07'N&172°45'E (1); [b6] 58°34'N&171°46'E (1);
Blepsias bilobus Cuvier, 1829 / 14.0–20.7 cm, 51–168 g	12	[b10] 54°21'N&169°56'E (3); [b2] 59°34'N&166°37'E (8); [b1] 59°16'N&163°44'E (1)
Anoplopoma fimbria (Pallas, 1814) / 16.3–17.3 cm, 29–38 g	2	[b7] 57°08'N&172°09'E (2)
Hemitripterus villosus (Pallas, 1814) / 46.5 cm, 1995 g	1	[b1] 59°16'N&163°44'E (1)
Eumicrotremus orbis (Günther, 1861) / 5.7–8.3 cm, 9–42 g	16	[b1] 59°16'N&163°44'E (16)
Clupeiformes		
Clupea pallasii pallasii Valenciennes, 1847 / 16.2–22.6 cm, 39–114 g	30	[b1] 59°16'N&163°44'E (30)
Gasterosteiformes		
Gasterosteus aculeatus Linnaeus, 1758 / 5.9–10.4 cm, 2.83–8.03 g	600	[b8] 55°27'N&171°19'E (200); [b4] 59°25'N&172°18'E (200); [b2] 59°33'N&166°37'E (200)

In the Bering Sea *P. speciosum sensu lato* infected 10 out of the 14 examined fish species and amounted to 19.78% of the total number of worms found (Table 3). *Anisakis* sp. was found only in 5 out of 14 fish species. Infection with this nematode was usually represented by one or two worms per a host individual. *Hemitripterus villosus* (Pallas, 1814) was the only fish in which *Anisakis* sp. was abundant.

In the Sea of Okhotsk *P. speciosum sensu lato*, *Anisakis* sp., and *E. gadi sensu lato* were the most common generalists, infecting 9, 7, and 6 out of the 9 fish species, respectively (Suppl. Table 2). The single specimen of the shark

Table 2. Length, weight and locations of catches of fish examined during parasitological survey on the RV *Professor Kaganovsky* in the Okhotsk Sea.
Таблица 2. Длина, вес и места поимок рыб, исследованных в ходе паразитологических работ на НИС «Профессор Кагановский» в Охотском море.

Species / total length range, weight range	Total number examined	[station number] Localities (number examined)
Salmoniformes		
Oncorhynchus gorbuscha (Walbaum, 1792) / 16.8–29.6 cm, 82–222 g	15	[o10] 49°06'N&152°21'E (8); [o8] 48°45'N&150°04'E (10); [o1] 52°12'N&148°40'E (10); [o2] 51°00'N&146°31'E (10);
Oncorhynchus keta (Walbaum, 1792) / 20.0–28.8 cm, 73–222 g	40	[o7] 49°35'N&147°46'E (20); [o1] 52°12'N&148°40'E (9); [o2] 51°00'N&146°31'E (11)
Perciformes		
Zaprora silenus Jordan, 1896 / 16.7 cm, 74 g	1	[o12] 48°00'N&152°32'E (1)
Myctophiformes		
Stenobrachius leucopsarus (Eigenmann et Eigenmann, 1890) / 11.6–12.0 cm, 14–17 g	3	[o13] 46°52'N&150°23'E (3)
Scorpaeniformes		
Aptocyclus ventricosus (Pallas, 1769) / 13.2 cm, 99–623 g	4	[o12] 48°00'N&152°32'E (1)
Blepsias bilobus Cuvier, 1829 / 14.4–25.6 cm, 54–298 g	13	[o11] 48°23'N&151°01'E (2); [o13] 46°52'N&150°23'E (2); [o6] 48°10'N&146°55'E (1); [o3] 49°28'N&145°22'E (2); [o5] 46°44'N&145°35'E (6);
Pleurogrammus azonus Jordan et Metz, 1913 / 17.5–22.3 cm, 43–92 g	101	[o14] 46°13'N&149°21'E (50); [o3] 49°28'N&145°22'E (51)
Argentiniformes		
Lipolagus ochotensis (Schmidt, 1938) / 7.2–11.2 cm, 2–8 g	69	[o6] 48°10'N&146°55'E (40); [o4] 48°33'N&145°27'E (29)
Clupeiformes		
Clupea pallasii pallasii Valenciennes, 1847 / 16.2–22.6 cm, 39–114 g	18	[o2] 51°00'N&146°31'E (4); [o3] 49°28'N&145°22'E (14)
Argentiniformes		
Leuroglossus schmidti Rass, 1955 / 7.6–13.6 cm, 3–19 g	201	[o13] 46°52'N&150°23'E (1); [o4] 48°33'N&145°27'E (200);
Lamniformes		
Lamna ditropis Hubbs et Follett, 1947 / 164.0 cm, 55.8 kg	1	[o9] 49°44'N&153°46'E (1)

Table 3. Infection of elasmobranchs.
Таблица 3. Зараженность паразитами хрящевых рыб.

Parasite		Dev. stage	Prevalence (%)	Intensity (mean)	Site of infection
Lamna ditrops (n=1)					
Cestoda	*Dinobothrium* sp.	ad.	in 1 of 1	1 (1.00)	spiral valve
	Nybelinia surmenicola	ad.	in 1 of 1	267 (267.00)	spiral valve
Chromadorea	*Anisakis* sp.	juv. III	in 1 of 1	13 (13.00)	stomach

examined in the Sea of Okhotsk was infected by three parasites: adults and undeveloped plerocercoids of *Nybelinia surmenicola* Okada in Dollfus, 1929 and a single gravid *Dinobothrium* sp. in the spiral valve and *Anisakis* sp. larvae in stomach (Table 3).

Discussion

Pacific salmons *Oncorhynchus gorbuscha* (Walbaum, 1792) and *O. keta* play a paramount role in the fisheries of the Russian Far East and the entire North Pacific. Food safety is an important issue since these salmons are involved into life cycles of helminthiasis agents such as *Anisakis* spp. and *Corynosoma* spp. Parasitic fauna of Pacific salmons is studied fairly well throughout its range (Mamaev *et al.*, 1959; Konovalov, 1971; Pospehov *et al.*, 2014; Byrne *et al.*, 2018). Parasites registered in our study were typical of *O. gorbuscha*. However, there were some differences in the infection of this fish in the Bering Sea and the Sea of Okhotsk. In the former digeneans were represented by a greater number of species than in the latter (4 *vs* 2). However, no acanthocephalans were found in the Bering Sea, while in the Sea of Okhotsk, the infection was mostly represented by cestodes and acanthocephalans (Suppl. Tables 1, 2). The absence of *Brachyphallus crenatus* (Rudolphi, 1802) in the guts of chum and pink salmon in our previous parasitological study in the open water of north-western Pacific (Gordeev, Sokolov, 2020b) was strikingly different from the data collected by Mamaev *et al.* (1959), who showed a heavy infection with this parasite (up to 750 worms per fish). In our research *B. crenatus* was present in the stomachs of both salmon species, but the value of infection never exceeded five worms per fish (Suppl. Tables 1, 2). This observation indirectly confirms our earlier ideas about the presence of waves of infection with *B. crenatus* (Gordeev, Sokolov, 2020b).

We dissected only four individuals of *O. keta* from the Bering Sea, which is not enough for any conclusions. In the Sea of Okhotsk, where the number of dissected individuals was ten times greater, the usual helminth fauna was registered in this fish (Suppl. Table 2), the dominant species being *E. gadi sensu lato*, *Anisakis* sp., and *P. speciosum sensu lato*.

We examined one individual of the wolf-eel, *Anarrhichthys ocellatus* Ayres, 1855, from the Bering Sea. This species has been previously recorded as a host of ectoparasites, the leech *Mabniana* spp. (McDonald, Margolis, 1995) and the monogenean *Gyrodactylus corti* Mizelle et Kritsky, 1967 (see Love, Moser, 1983; King *et al.*, 2014). We did not find any ectoparasites, probably because they were lost during trawling, or the examined specimen was not infected. We found five helminths in the wolf-eel (*Lecithaster gibbosus* (Rudolphi, 1802), *B. crenatus*, *Tubulovesicula lindbergi* (Layman, 1930), *Eubothrium* sp. and *P. speciosum sensu lato*), all of which were recorded in this fish for the first time. Note that the results of the study by Atopkin *et al.* (2020) do not support the well-known concept of Zhukov (1960) about the presence of *L. gibbosus* in the North Pacific. According to Atopkin *et al.* (2020) *L. gibbosus* of Zhukov (1960) is actually *Lecithaster salmonis* Yamaguti, 1934. Krupenko *et al.* (2022) reported the registration of *L. salmonis* in the White Sea and do not confirm the previous data on the registration of *L. gibbosus* in this water area. The question of the species identity of *Lecithaster* specimens from different hosts in the water area of the North Pacific requires further investigation. In this study, we adhere to the concept of Zhukov (1960).

The sablefish, *Anoplopoma fimbria* (Pallas, 1814), has been previously recorded as a host of various helminths such as cestode plerocercoids (*Scolex pleuronectis*), *N. surmenicola*, digeneans (*Stephanostomum* Looss, 1899, *Steringophorus* Odhner, 1905, *Derogenes* Lühe, 1900, *Dinosoma* Manter, 1934, *Podocotyle* Dujardin, 1845), acanthocephalans (*Corynosoma* Lühe, 1904) and anisakids (Volkov *et al.*, 1999). We also registered *Anisakis* sp. in our two specimens caught in the Bering Sea (Suppl. Table 1).

Smooth lumpsucker, *Aptocyclus ventricosus* (Pallas, 1769), has been examined for infection in several studies (Machida, 1985; Volkov *et al.*, 1999). The two trematode species, *Paraccacladium* sp. and *Prodistomum alaskense* (Ward et Fillingham, 1934) found by us (Table 3, 4), were also recorded from the same host in the open waters of north-western Pacific in 2018 with similar indices of prevalence and intensity (Gordeev, Sokolov, 2020b; Sokolov *et al.*, 2020, 2021).

Pacific pomfret, *Brama japonica* Hilgendorf, 1878, has been studied quite thoroughly throughout its range (Love, Moser, 1983; Moles, 2007; Iannacone, Flores, 2013; Sokolov *et al.*, 2021). Nevertheless, the digenean *L. gibbosus* found by us in specimens from the Bering Sea (Suppl. Table 1) was recorded in this fish for the first time.

Rested sculpin, *Blepsias bilobus* Cuvier, 1829, is common in by-catches of trawl fisheries in north-western Pacific (Gordeev *et al.*, 2019), but we failed to find a single record of its helminths. In this study we provide the first parasitological information on this fish species. It was infected only by generalists such as *Anisakis* sp., *Contracaecum osculatum* (Rudolphi, 1802) *sensu lato*, *E. gadi sensu lato*, and *P. speciosum sensu lato* (Suppl. Tables 1, 2). Its only congener, silverspotted sculpin, *Blepsias cirrhosus* (Pallas, 1814), inhabiting shallower waters of the North Pacific (Fedorov *et al.*, 2003), hosts at least 14 parasitic species including an ultra-specialist *Hysterolecitha blepsiae* Layman, 1930 (Volkov *et al.*, 1999; Gibson, 1996; Love, Moser, 1976).

Pacific herring, *Clupea pallasii* Valenciennes, 1847, was represented in our material by specimens caught in the Bering Sea in the shallow area (<250 m) of the Karaginsky Gulf (mostly near Karaginsky Island) and specimens caught in midwaters of the Sea of Okhotsk. A comparison of these samples highlights parasitological differences between the coastal zone and the open sea above the abyssal depths (Suppl. Tables 1, 2). In the coastal area, trematodes (*B. crenatus*, *Pronoprymna petrowi* (Layman, 1930)) and the coastal cestode *Bothriocephalus scorpii* (Müller, 1776) *sensu lato* prevailed, while in the Sea of Okhotsk only generalists typical of the pelagic fish (*Anisakis* sp., *E. gadi sensu lato*, *P. speciosum sensu lato*) were registered, and their infection intensity was rather high. A recent survey of *C. pallasii* in the north-western Pacific focussed on the Taui population (Tauiskaya Guba Bay, Okhotsk Sea) near Magadan (Pospekhov, 2021). In our study, the Pacific herring was infected by 17 helminth species (six trematodes, five cestodes, four nematodes, and two acanthocephalans). All these species except *B. scorpii* were also recorded in Tauiskaya Guba Bay. Nevertheless, *B. scorpii sensu lato* has also been reported from the Pacific herring in north-western Pacific (Volkov *et al.*, 1999). Preliminary data on the infection of *C. pallasii* examined in this survey were earlier published by us together with a phylogenetic assessment of *Pronoprymna* spp. (Sokolov *et al.*, 2021).

The Pacific saury, *Cololabis saira* (Brevoort, 1856), has been studied in parasitological respect fairly well (Kurochkin *et al.*, 1987; Gordeev *et al.*, 2017; Gordeev, Sokolov, 2020b; Suyama *et al.*, 2019). In this study, we examined only eight individuals of *C. saira* from the Bering Sea. However, we registered the trematode *L. gibbosus*, which has not been found in *C. saira* in our previous study of epipelagic fish parasites to the north of the research area of this study (Gordeev, Sokolov, 2020b). The finding of numerous acanthocephalans *Rhadinorhynchus cololabis* Laurs et McCauley, 1964 (Suppl. Table 1) agrees with the previous studies.

A total of 600 individuals of the three-spined stickleback, *Gasterosteus aculeatus* Linnaeus, 1758, from the Bering Sea were dissected, providing good statistical support of the results. In general, our findings agree with our earlier data on the infection of three-spined stickleback in the open waters of the north-western Pacific Ocean further south (Gordeev, Sokolov, 2020b). Freshwater digenean *Bunodera mediovitellata* Tsimbalyuk et Roitman, 1966 and cestode *Dibothriocephalus dendriticus* (Nitzsch, 1824) were found in the guts of 0.8% and 3.40% of dissected individuals, correspondingly. These prevalence values found in fish at a distance of 121–498 km away from the nearest continental shore show that some freshwater parasites persist after the catadromous migration of the host. Plerocercoids of *D. dendriticus* were located mainly in the connective tissue capsules in the liver, while the adults of *B. mediovitellata* were found in the intestine. Different levels of contact with the external environment may be a reason behind the differences in the prevalence of these parasites. A common near-shore cestode *B. scorpii sensu lato* was the most prevalent (4.00%) in the three-spined stickleback, while a "truly oceanic" cestode *P. speciosum sensu lato* infected four times fewer individuals (Suppl. Table 1), which is in agreement with our earlier research (Gordeev, Sokolov, 2020b). *Hysterothylacium aduncum* (Rudolphi, 1802) and *D. dendriticus* were recorded in the three-spined stickleback in the open ocean for the first time.

Pacific spiny lumpsucker, *Eumicrotremus orbis* (Günther, 1861), is a rarely studied cyclopterid fish. There is only one record on its infection by the juveniles of *A. simplex sensu lato* and *C. osculatum sensu lato* in the Pacific Ocean (Solovyova, 1999). Pacific spiny lumpsucker is a demersal fish, inhabiting the depths of up to 575 m (Allen, Smith, 1988). However, all 16 specimens examined in this study were caught in the waters to the north of the Litke Strait. The maximum depth there is 80-90 m, so the distance between the footrope of the fully opened trawl and the seabed was only 30-40 meters. This means that the catch could include epipelagic, demersal and shallow-water near-shore fish that are included in the life cycles of coastal parasites. This is probably the reason why *E. orbis* examined in our study was infected by *B. scorpii sensu lato* and *Prosorhynchus* cf. *mizellei* Kruse, 1977, which were not found in any other fish in the Bering Sea (except *B. scorpii sensu lato* in *G. aculeatus*, see above). About a half of the parasites from *E. orbis* were trematodes, which is characteristic of other eurybathic or vertically migrating species such as *A. ventricosus* and *Zaprora silenus* Jordan, 1896 (see Gordeev, Sokolov, 2020b) and not characteristic of truly epipelagic species, whose parasitic fauna is dominated by cestodes and nematodes, which are transmitted through planktonic crustaceans.

Another fish from the same genus, *Eumicrotremus fedorovi* Mandrytsa, 1991, has been recently studied parasitologically near Simushir Island (Kuril Islands, Russia) and found to be infected by various helminths, the most prevalent being *N. surmenicola*, *Ascarophis pacifica* Zhukov in Spassky et Rakova, 1960 and *H. aduncum* (Gordeev, Sokolov, 2020a). This is quite different from the infection of *E. orbis* (Suppl. Table 1), which was not infected by nematodes at all. This difference could be associated with the differences in the diet: *E. fedorovi* feeds mainly on the fish young, while *E. orbis* readily consumes juveniles of hyperiids, euphausiids and squids (Chuchukalo, 2006; Antonenko *et al.*, 2009; Gordeev *et al.*, 2021).

Shaggy sculpin, *H. villosus*, has been repeatedly examined for infection in the Russian Far East, and at least 30 parasites have been recorded (Volkov *et al.*, 1999; Markevich, Butorina, 2005; Motora, 2019). We examined a single specimen of this fish caught in Litke Strait in the same trawl as *E. orbis*. Based on the information obtained from this specimen, the infection of *H. villosus* in the Bering Sea (Suppl. Table 1) did not seem to be much different from that in the north-western part of the Sea of Japan.

Pacific sandfish, *Trichodon trichodon* (Tilesius, 1813), which was also caught in the Litke Strait, was infected by plerocercoids of *P. speciosum sensu lato* and *Eubothrium crassum* (Bloch, 1779). In the area near the Kamchatka Peninsula this fish is known as a host of two *Eubothrium* spp.: *E. arcticum* Nybelin, 1922 (Strelkov, 1960) and *E. vittevitellatus* Mamaev, 1968 (Mamaev, 1968; Kennedy, Andersen, 1988). This may mean that we registered the third species in this fish, though it cannot be ruled out that the cestodes found by Strelkov (1960) also belonged to *E. crassum*. Strelkov *et al*. (1960) also noted the infection of *T. trichodon* by '*Scolex pleuronectis*' (prev. 54.5%, intensity 2-9), which is consistent with the prevalence values of *P. speciosum sensu lato* plerocercoids registered in our study (Suppl. Table 1).

In this work we dissected 201 specimens of northern smoothtongue, *Leuroglossus schmidti* Rass, 1955, which is considerably more than 16 specimens dissected in our previous study (Gordeev, Sokolov, 2020b; Sokolov *et al.*, 2021a,b). The history of parasitological research on this fish species is fragmentary. Solovyova (1999) noted *A. simplex sensu lato* in an unnamed *Leuroglossus* sp. in 'Aleuto-Kamchatka and North Japanese provinces' but no further data could be extracted from this source. Kuramochi (2009) noted *Steringophorus congeri* Shen, 1987 off the Pacific coast of Northern Japan, but there are reasons to believe that he actually dealt with *Steringophorus occidentalipacificus* Sokolov, Shchenkov et Gordeev, 2021 (see Sokolov *et al.*, 2021). In this study, we found that *L. schmidti* was infected with *P. speciosum*, *Lecithophyllum botryophoron* (Olsson, 1868), *S. occidentalipacificus*, *Paraccladium* sp., *A. pacifica*, and *N. surmenicola*. The latter two parasites were recorded in this host for the first time. High values of infection with *L. botryophoron* and *A. pacifica* (see Suppl. Table 2) are striking. Nothing like this has ever been noted before. These high prevalence values may be due to the large sample size or the new locality. There are some limited data on the infection of the congeneric California smoothtongue, *Leuroglossus stilbius* Gilbert, 1890, which was found to be infected by *Aponurus californicus* Noble et Orias, 1970 (see Noble, Orias, 1970; Cailliet, Grego, 1990) in the stomach and by the ectoparasite *Cardiodectes bellottii* (Richiardi, 1882) (as *C. medusaeus*) (Love, Moser, 1983).

Eared blacksmelt, *Lipolagus ochotensis* (Schmidt, 1938), has previously been found to be infected only by *Paraccladium* sp. (Kuramochi, 2009). The five species of parasites (Suppl. Table 2) and an unidentified plerocercoid were recorded in *L. ochotensis* for the first time in our study.

Northern lampfish, *Stenobrachius leucopsarus* (Eigenmann, Eigenmann, 1890), was another myctophid fish involved in our study though a much more modest number of specimens (3) were examined. The only parasite found in this fish was *P. speciosum sensu lato*, which was registered in the Sea of Okhotsk (Suppl. Table 2). Earlier, we found *Anisakis* sp. in *S. leucopsarus* caught in the open waters of the north-western Pacific (Gordeev, Sokolov, 2020b). A fairly heavy infection has been registered in *S. leucopsarus* from the north-eastern Pacific (Collard, 1970; Moles, 2007). Therefore, we expect that more extensive studies in other areas would reveal a more abundant parasitic fauna in this fish.

Myctophids are thought to play an important role in the transfer of the parasitic larvae from bathypelagic to epipelagic habitats (Collard, 1970). They perform daily vertical migrations from mesopelagic to epipelagic layer, which leads to a more uniform distribution of the parasitic larvae at shallow depths (up to 500). However, one may expect a complete disruption of larval transmission between demersal and epipelagic hosts at greater depths.

Okhotsk atka mackerel, *Pleurogrammus azonus* Jordan et Metz, 1913, has been thoroughly studied (Solovyeva, Motora, 2014; Motora, 2019). It harbours at least 38 species of parasites (Volkov *et al.*, 1999). The six species of parasites registered in this fish in our study (Suppl. Table 2), including the prevailing *L. gibbosus*, *Anisakis* sp., and *E. gadi sensu lato*, are typical for *P. azonus* in the study area.

Cartilaginous fish was represented in our study by a single individual of salmon shark, *Lamna ditropis* Hubbs et Follett, 1947 (Table 3). It was infected with parasites typical for the species. The most abundant helminth, *N. surmenicola*, has been repeatedly recorded in the area. Nematodes *Anisakis* sp. were found only in the stomach. This is unsurprising because salmon shark is not the definitive host of these nematodes, this role being played by marine mammals.

Pelichnibothrium speciosum sensu lato is a dominant parasite in the epipelagic fish of the north-western Pacific. Fishes become infected with this cestode by feeding on planktonic organisms that serve as its first intermediate hosts and by preying on smaller fish infected by *P. speciosum sensu lato* larvae (post-cyclic transmission). Note that in recent years, new data have appeared that indicate the fallacy of the *P. speciosum sensu lato* concept. Molecular studies by Kurashima (2016) confirm the opinion of Scholz (1998) about *P. speciosum* and *Phyllobothrium caudatum* (Zschokke et Heitz, 1914) as different species. The idea of synonymizing *P. speciosum* and *P. caudatum* was suggested by Dubinina (1971). Before this author's conclusions, the name *P. caudatum* was used for "tetraphyllid" plerocercoids parasitizing Pacific salmon *Oncorhynchus* spp. According to Caira`s *et al*. (2021) phylogenetic data, *P. speciosum* branches within the *Clistobothrium* clade, so the genus of this species needs clarification. Caira *et al*. (2020) found *Clistobothrium* sp. in sockeye salmon, *Oncorhynchus nerka* (Walbaum, 1792), spawning in the rivers of Alaska. We do not exclude the conspecificity of *P. caudatum* with *Clistobothrium* sp. of Caira *et al*. (2020). In general, the question of the true species identity of *P. speciosum sensu lato* isolates from different hosts requires further investigation. Pending further data, we continue to consider all *P. speciosum*-like plerocercoids within the concept of *P. speciosum sensu lato*. Some epipelagic fish are also heavily infected by acanthocephalans *Echinorhynchus* spp., whose transmission involves amphipods. Post-cyclic transmission of acanthocephalans was experimentally shown for *Pomphorhynchus laevis* (Zoega in Müller, 1776) Porta, 1908 (see Kennedy, 1999) and *Acanthocephalus tumescens* (von Linstow, 1896) Porta, 1905 (see Rauque *et al.*, 2002), which successfully infected rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792). In our opinion, post-cyclic transmission is the best explanation of the high infection rates of fish with acanthocephalans registered in our study.

The marine ecosystem includes a huge number of organisms that harbour parasites. These organisms belong to various systematic groups and differ in the complexity of organization. Distribution patterns of the parasites in the marine environment are determined by the migration and the food chains of their hosts. At the same time, the functioning of the marine community of nekton, plankton, and benthos is greatly influenced by more or less unpredictable environmental factors of non-biological nature such as currents, weather, and solar radiation.

One of the adaptations of parasites that inhabit pelagic hosts is a low host specificity. For example, many parasites that use planktonic organisms as intermediate hosts show a broad host specificity. Similarly, many parasites that have life cycles implemented mostly in the benthic layer demonstrate a low specificity for their invertebrate intermediate hosts (Marcogliese, 2002). There are also vertical gradients in the diversity of parasites: there are more species in shallow waters because a wider range of intermediate hosts is available there (Marcogliese, 2002). On the other hand, the diversity of parasites is higher in benthic organisms than in pelagic ones, because benthic invertebrates are more diverse and live longer (Campbell *et al.*, 1980; Marcogliese, 2005).

Differences in the species diversity of the parasites registered in our study in fish from the Bering Sea and the Sea of Okhotsk (28 *vs* 18) were probably due to the different number of studied fish species (14 vs 9). Teleosts caught in the coastal area and those performing vertical migrations showed somewhat different infection patterns, mostly due to the digenean component. We made 20 new records on the infection of previously studied fish species and described the parasites of the crested sculpin *Blepsias bilobus* for the first time. To sum up, the parasitic infection of fish in the epipelagic zone of the western Bering Sea and the southern Sea of Okhotsk is characterised by a considerable intensity but a relatively low species diversity.

Supplementary data. The following Supplementary Tables are available online.

Supplementary Table 1. Infection of teleost fish in the Bering Sea.

Supplementary Table 2. Infection of teleost fish in the Sea of Okhotsk.

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