

## Macroparasites of epipelagic and eurybathic fishes in the north-western Pacific

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**ABSTRACT:** A total of 25 parasitic species were found to infect 23 species of teleost and two species of cartilaginous fish in the north-western Pacific. Known generalists, anisakid and raphidascaridid juveniles (Nematoda), plerocercoids of *Nybelinia surmenicola* (Cestoda), and acanthocephalan *Echinorhynchus gadi* (Acanthocephala) were prevalent; however, plerocercoids of *Pelichnibothrium speciosum* were the most common parasites of epipelagic and eurybathic fish, infecting 16 out of 23 examined teleost species. Digenean infection of eurybathic species *Aptocyclus ventricosus* (Cyclopteridae), *Zaprora silenus* (Zaproridae), *Leuroglossus schmidti* (Bathylagidae), and *Icichthys lockingtoni* (Centrolophidae) differ from other teleost fish in their parasite fauna. The present study is the first report of macroparasites from *Magnisudis atlantica* (Paralepididae) and *I. lockingtoni*. In addition, this is the first data on the infection of *Gasterosteus aculeatus* (Gasterosteidae) far into the open ocean. Macroparasite infection of fish in the epipelagic layer of the north-western Pacific Ocean is characterised by high infection rates and low species diversity of parasites.

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**KEY WORDS:** helminths, Pacific Ocean, fish parasites, marine biology, parasitology.

## Макропаразиты эпипелагических и эврибатных рыб северо-западной части Тихого океана

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**РЕЗЮМЕ:** В ходе паразитологического исследования рыб в северо-западной части Тихого океана было обследовано 23 вида костистых и 2 вида хрящевых рыб, в которых обнаружено 25 видов паразитов. Известные генералисты, такие как личинки

анизакидных и рафидаскаридных нематод, плероцеркоиды *Nybelinia surmenicola* и скребень *Echinorhynchus gadi* встречались часто, однако, наиболее массовыми были плероцеркоиды *Pelichnibothrium speciosum*, найденные в 16 из 23 обследованных видов костистых рыб. Трематоды были обнаружены в эврибатных видах рыб — *Aptocyclus ventricosus* (Cyclopteridae), *Zaprora silenus* (Zaproridae), *Leuroglossus schmidti* (Bathylagidae) и *Icichthys lockingtoni* (Centrolophidae), что заметно отличало их от других обследованных видов. Макропаразиты рыб *Magnisudis atlantica* (Paralepididae) и *I. lockingtoni* исследованы впервые, также впервые получены данные о зараженности трехиглой колюшки *Gasterosteus aculeatus* (Gasterosteidae) в открытых водах Тихого океана на значительном удалении от берега. В целом, инвазия рыб макропаразитами в эпипелагиали северо-западной части Тихого океана характеризуется значительной интенсивностью инвазии, однако бедным видовым составом.

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КЛЮЧЕВЫЕ СЛОВА: гельминты, Тихий океан, паразиты рыб, морская среда, паразитология.

## Introduction

The study of the open ocean is a hard task, due to its depth, size, and distance from the centres of civilisation. The Pacific Ocean, occupying half the globe, can compete with the Southern Ocean in its degree of unexploredness (Rhode, 2005). In the polar and circumpolar, the most productive regions of the Pacific Ocean, there is a large number of concentrated fisheries, aimed at such valuable fish species as salmon, *Oncorhynchus* spp. (Salmonidae) (Gordeev, Klovach, 2019), 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).

The main reason to study the biodiversity and biology of parasites is their role in ecosystem functioning. There is increasing evidence that parasite-mediated effects could be significant. They shape host population dynamics, alter interspecific competition, influence energy flow, and appear to be important drivers of biodiversity (Hudson *et al.*, 2006). Also, para-

sites appear to have an important role in influencing organisation within communities via reducing host fitness, modifying competitive and trophic interactions among species, altering the behaviour of the host and in other ways (Hudson *et al.*, 2006). The role of parasites and their hosts in marine invasions, when invaders directly or indirectly affect parasite and host populations and communities, is an actively studied area of fish parasitology (Goedknecht *et al.*, 2016). Undoubtedly, data on the infection of wild fish populations are the primary data to elucidate the fundamental role of parasites in marine ecosystem functioning. Moreover, parasites are of undoubted importance for the economy, since they not only cause significant damage to a fishery product's marketable condition, but also sometimes make it unsafe to use it for food (e.g. Quiazon, 2015). While the knowledge of parasites is sufficient for commercially important fish species, the great majority of other fish have never been investigated in this respect (Klimpel *et al.*, 2009). There are many species that inhabit the same water horizon (0–50 m) as salmon during their period in the marine environment (Gordeev *et al.*, 2018), and parasitological examination of these species is interesting in terms of broadening our understanding of helminth infection in the open ocean.

In the present paper, we summarise the results of the parasitological examination of 25 species of teleost and cartilaginous, epipelagic and eurybathic fishes in the north-western Pacific Ocean performed aboard the *RV Professor Kaganovsky* in June–July 2018 (Gordeev *et al.*, 2018).

## Material and Methods

All specimens were caught between 31 May and 9 July 2018 by the research vessel *Professor Kaganovsky* during a survey of Pacific salmon (stock assessment), using midwater net trawl RT/TM 80/396, with a 10 mm mesh insert in the

Table 1. Length, weight and locations of catches of fish examined during the parasitological survey on the *RV Professor Kaganovsky*.

Таблица 1. Длина, вес и координаты вылова особей, исследованных в ходе паразитологического исследования на НИС «Профессор Кагановский».

Species / total length range, weight range	Total no. examined	Localities (no. examined)
1	2	3
<b>Salmoniformes</b>		
<i>Oncorhynchus gorbuscha</i> (Walbaum, 1792) / 42.0–46.2 cm, 717–959 g	15	45°06'N&149°39'E (1); 49°59'N&156°16'E (2); 50°45'N&159°57'E (1); 46°09'N&155°49'E (1); 43°58'N&152°16'E (1); 43°14'N&148°28'E (2); 46°00'N&157°46'E (1); 46°55'N&158°22'E (2); 49°06'N&161°58'E (4)
<i>Oncorhynchus keta</i> (Walbaum, 1792) / 42.9–56.0 cm, 902–1966 g	15	49°59'2&156°16'E (3); 49°24'N&159°56'E (2); 46°27'N&161°53'E (5); 43°57'N&149°31'E (5);
<i>Oncorhynchus kisutch</i> (Walbaum, 1792) / 44.6–53.6 cm, 1072–1908 g	3	46°27'N&166°21'E (3)
<b>Perciformes</b>		
<i>Brama japonica</i> Hilgendorf, 1878 / 40.8–45.2 cm, 1217–1833 g	13	42°41'N&154°38'E (13)
<i>Hyperoglyphe japonica</i> (Döderlein, 1884) / 21.0–38.7 cm, 267–469 g	2	42°18'N&146°31'E (1); 41°48'N&150°41'E (1)
<i>Icichthys lockingtoni</i> Jordan et Gilbert, 1880 / 37.0 cm, 398 g	2	41°50'N&148°45'E (1); 43°26'N&155°56'E (1)
<i>Zaprora silenus</i> Jordan, 1896 / 23.0–31.0 cm, 90–471 g	6	47°31'N&155°31'E (1); 44°41'N&153°48'E (1); 46°00'N&157°46'E (1); 49°02'N&163°27'E (1); 49°58'N&167°45'E (2);
<b>Aulopiformes</b>		
<i>Lestidiops ringens</i> (Jordan et Gilbert, 1880) / 17.0–21.0 cm, 8–12 g	30	48°11'N&166°10'E (30)
<i>Magnisudis atlantica</i> (Krøyer, 1868) / 38.0 cm, 185 g	1	45°09'N&152°18'E (1)
<i>Alepisaurus ferox</i> Lowe, 1833 / 100.2–133.0 cm, 1057–4016 g	4	50°06'N&158°50'E (1); 46°58'N&156°56'E (1); 46°37'N&159°56'E (1); 50°33'N&165°30'E (1)

Table 1 (continued).  
Таблица 1 (продолжение).

1	2	3
<b>Aulopiformes</b>		
<i>Scopelosaurus harryi</i> (Mead, 1953) / 11.5–22.0 cm, 5–49 g	2	42°55'N&153°03'E (1); 42°41'N&154°38'E (1)
<i>Anotopterus nikparini</i> Kukuev, 1998 / 43.0–114.0 cm, 62–1778 g	9	50°06'N&158°50'E (1); 47°48'N&157°56'E (1); 46°58'N&156°56'E (1); 50°45'N&159°57'E (1); 46°55'N&158°22'E (1); 49°02'N&163°27'E (1); 45°02'N&161°53'E (1); 45°09'N&152°18'E (2)
<b>Myctophiformes</b>		
<i>Diaphus theta</i> Eigenmann et Eigenmann, 1890 / 4.1–7.5 cm, 2.6–3.2 g	25	45°39'N&160°57'E (25)
<i>Notoscopelus japonicus</i> (Tanaka, 1908) / 11.5–14.0 cm, 11.9–12.8 g	35	43°14'N&148°28'E (10); 42°55'N&153°03'E (1); 42°55'N&153°03'E (24);
<i>Stenobranchius leucopsarus</i> (Eigenmann et Eigenmann, 1890) / 6.4–8.5 cm, 4.3–6.5 g	14	44°41'N&153°48'E (12); 42°55'N&153°03'E (2)
<i>Tarletonbeania crenularis</i> (Jordan et Gilbert, 1880) / 6.5 cm, 4 g	1	42°41'N&154°38'E (1)
<b>Scorpaeniformes</b>		
<i>Aptocyclus ventricosus</i> (Pallas, 1769) / 3.0–29.0 cm, 1.12–1385 g	15	50°06'N&158°50'E (2); 47°31'N&155°31'E (3); 45°56'N&153°20'E (1); 45°20'N&154°51'E (2); 45°09'N&152°18'E (2); 44°58'N&158°12'E (2); 48°13'N&162°26'E (2); 47°20'N&167°07'E (1)
<b>Scombriformes</b>		
<i>Scomber japonicus</i> Houttuyn, 1782 / 19.9–40.2 cm, 77–529 g	25	43°58'N&152°16'E (5); 42°35'N&148°50'E (5); 40°26'N&147°51'E (5); 43°26'N&155°56'E (10)
<b>Beloniformes</b>		
<i>Cololabis saira</i> (Brevoort, 1856) / 26.8–39.5 cm, 11–154 g	52	43°26'N&155°56'E (1); 45°39'N&160°57'E (27); 45°02'N&161°53'E (24)
<b>Argentiniformes</b>		
<i>Leuroglossus schmidti</i> Rass, 1955 / 11.1–17.2 cm, 38.2–43.1 g	16	50°06'N&158°50'E (16)
<b>Clupeiformes</b>		
<i>Sardinops sagax melanosticta</i> (Temminck et Schlegel, 1846) / 16.2–22.6 cm, 39–114 g	10	40°26'N&147°51'E (10)

Table 1 (continued).  
Таблица 1 (продолжение).

1	2	3
<b>Lampriformes</b>		
<i>Desmodema lorum</i> Rosenblatt et Butler, 1977 / 113.0 cm, 640 g	1	41°29'N&147°16'E (1)
<b>Gasterosteiformes</b>		
<i>Gasterosteus aculeatus</i> Linnaeus, 1758 / 4.5–8.7 cm, 2.16–4.17 g	214	50°43'N&164°05'E (14); 48°53'N&165°07'E (100); 47°12'N&165°29'E (100)
<b>Lamniformes</b>		
<i>Lamna ditropis</i> Hubbs et Follett, 1947 / 131.0 cm, 24.56 kg	1	42°35'N&148°50'E (1)
<b>Carcharhiniformes</b>		
<i>Prionace glauca</i> (Linnaeus, 1758) / 140.0 cm, 42 kg	1	41°29'N&147°16'E (1)

net bag. Locations of the trawls are given in Table 1.

All specimens were examined macroscopically for the presence of ectoparasites immediately after capture and then dissected and studied for endoparasitic helminths and other metazoan parasites using a standard method of parasitological examination (Bykhovskaya-Pavlovskaya, 1985). All sharks caught alive were released after measuring. Only two specimens were hauled, already dead, and subsequently included in the parasitological survey. Prefixation treatment of trematodes and cestodes included cleaning and straightening for better identification. Acanthocephala were transferred to fresh water until the proboscis everted prior to fixation. All parasites except nematodes were preserved in 70% and 96% ethanol. Nematodes were preserved in 4% formaldehyde, and three days later, transferred to 70% ethanol for long-term storage. Subsequently, temporary glycerol preparations of acanthocephalans and nematodes were made. Digenea were stained with acetic carmine, dehydrated, contrasted (cleared) with dimethyl phthalate, and finally mounted in Canada balsam. Cestoda 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).

In consideration of how to present our findings, we faced difficulties due to the fact that specimens of some species were caught with a significant difference in time and location. However, taking into account that almost all captures occurred within one month and the fact that in the open ocean environment, millions of square kilometres can be regarded as homogeneous from a biological point of view, in Table 2 we have provided the infection indices all together (all specimens of one species were pooled together to count parasitological indices), calculated in accordance with Bush *et al.* (1999). However, in Table 1, we have provided a list of the examined species and the exact catch locations, with the number of specimens caught.

## Results

Helminths were found in all studied fish species except slender barracudina, *Lestidiops ringens* (Jordan, Gilbert, 1880), and scaly paperbone, *Scopelosaurus harryi* (Mead, 1953). Most species were infected by the larvae of *P. speciosum* and *Anisakis* sp. juveniles (Tables 2–8). Unlike all other bony fishes studied by us, *M. atlantica* and long snouted lancetfish, *Alepisaurus ferox* Lowe, 1833, had in their intestines both undeveloped (normal) plerocercoids *P. speciosum*, up to 3 cm long, and large plero-

Table 2. Infection of Pacific salmon.  
Таблица 2. Паразиты тихоокеанских лососей.

Parasite	Dev. stage	Prevalence (%)	Intensity (mean)	Site of infection	
<b><i>Oncorhynchus gorbuscha</i> (n=15)</b>					
Cestoda	<i>Pelichnibothrium speciosum</i>	larva	100.00	1–36 (10.07)	guts
Copepoda	<i>Lepeophtheirus salmonis salmonis</i>	ad.	26.67	1–5 (2.25)	body surface
Chromadorea	<i>Anisakis</i> sp.	juv. III	33.33	1–13 (4.40)	guts
	<i>Hysterothylacium</i> sp.	juv. III	6.66	1 (1.00)	guts
	<i>Ascarophis</i> sp.	subad.	6.66	1 (1.00)	guts
Palaeacanthocephala	<i>Echinorhynchus salmonis</i>	ad.	6.66	1 (1.00)	intestine
<b><i>Oncorhynchus keta</i> (n=15)</b>					
Copepoda	<i>Lepeophtheirus salmonis salmonis</i>	ad.	20.00	1–3 (2.00)	body surface
Cestoda	<i>Eubothrium salvelini</i>	ad.	26.67	1 (1.00)	guts
	<i>Pelichnibothrium speciosum</i>	larva	100.00	4–56 (26.47)	guts
	<i>Nybelinia surmenicola</i>	larva	6.67	2 (2.00)	stomach wall
Chromadorea	<i>Anisakis</i> sp.	juv. III	20.00	2–10 (5.67)	guts
<b><i>Oncorhynchus kisutch</i> (n=3)</b>					
Cestoda	<i>Pelichnibothrium speciosum</i>	ad.	100.00	4–56 (26.47)	guts

cercoids, up to 15cm long with undeveloped sexual complexes (Fig. 1).

## Discussion

As can be seen in Tables 2–8, species richness of macroparasites in pelagic fish in the north-western Pacific is quite poor, but studied specimens are highly infected. Well-known generalists in the area (Volkov *et al.*, 1999), anisakid and raphidascaridid juveniles, plerocercoids of *N. surmenicola*, and *E. gadi* made up 13% of the total number of parasites found in bony fishes and 22.2% of all species. Another common tapeworm, *P. speciosum*, could be labelled

as a generalist because plerocercoids of this species made up 64% of the total number of parasites and were found infecting 16 out of 23 examined teleost fish. Klimpel *et al.* (2006) studied the infection of bony fishes and revealed that in the Greenland Sea and in the Irminger Sea, the diversity of parasites in pelagic fish species was poor, while the parasite load in demersal fishes was heavy. Species diversity of marine fish parasites depends on the specific feeding behaviour of the hosts, the availability of intermediate and final hosts, depth distribution and host migration. Similarities in diet and habitat of potential host species often result in a similar or even identical parasite fauna (Dogiel,

Table 3. Infection of Perciformes fish examined.  
Таблица 3. Зараженность представителей отряда Perciformes.

Parasite		Dev. stage	Prevalence (%)	Intensity (mean)	Site of infection
<b><i>Hyperoglyphe japonica</i> (n=2)</b>					
Cestoda	<i>Glossobothrium nipponicum</i>	adult	100.00	10.07 (1–36)	intestine
<b><i>Brama japonica</i> (n=13)</b>					
Cestoda	<i>Nybelinia surmenicola</i>	larva	7.69	1 (1.00)	stomach wall
	<i>Pelichnibothrium speciosum</i>	larva	69.32	3–14 (6.67)	intestine
Chromadorea	<i>Hysterothylacium</i> sp.	juv. III	7.69	1 (1.00)	guts
<b><i>Icichthys lockingtoni</i> (n=2)</b>					
Trematoda	<i>Licithophyllum botryoporon</i>	ad.	50.00	1 (1.00)	guts
	<i>Paracaccladium</i> cf. <i>jamiesoni</i>	ad.	50.00	1 (1.00)	guts
Cestoda	<i>Pelichnibothrium speciosum</i>	larva	50.00	1 (1.00)	guts
<b><i>Zaprora silenus</i> (n=6)</b>					
Trematoda	<i>Prodistomum alaskense</i>	ad.	66.67	5–94 (42.50)	intestine
Cestoda	<i>Pelichnibothrium speciosum</i>	larva	66.67	2–9 (5.50)	intestine
Chromadorea	<i>Hysterothylacium</i> sp.	juv. III	16.67	1 (1.00)	guts

1962). In contrast, hosts with different food preferences may have large differences in their parasite fauna (Klimpel *et al.*, 2006). Within the north-western Pacific, a combination of different factors, especially the availability of intermediate hosts and the habitat preferences of the fish, can be seen as the main reason for the observed infection.

All studied species of bony fish could be divided into two unequal groups: eurybathic species that perform significant vertical migrations (lumpfish *Aptocyclus ventricosus*, prowlfish *Zaprora silenus*, northern smoothtongue *Leuroglossus schmidti*, and medusafish *Icichthys lockingtoni*) and epipelagic anadromous and non-anadromous species that inhabit cold

and moderate waters of the north-western Pacific Ocean (all other species). Infection of eurybathic species differs from that of other fish due to the presence of trematodes.

Our data on the infection of the poorly studied lumpfish, *Aptocyclus ventricosus*, is similar to the data of Machida (1985) who performed a targeted study on this species off northern Japan. However, our specimens were collected to the north closer to the Bering Sea, so in our study infection by digenean species is presented by more polar species, like *Prodistomum alaskense* (Ward et Fillingham, 1934). *Proisorhynchus mizellei* Kruse, 1977 was described from *A. ventricosus* caught in the Bering Sea (Kruse, 1977), but that seems to be the only record of *P.*

Table 4. Infection of Aulopiformes.  
Таблица 4. Зараженность представителей отряда Aulopiformes.

Parasite		Dev. stage	Prevalence (%)	Intensity (mean)	Site of infection
<b><i>Alepisaurus ferox</i> (n=4)</b>					
Cestoda	<i>Pelichnibothrium speciosum</i>	larva	100.00	60–211 (122.75)	guts
	<i>Nybelinia surmenicola</i>	larva	50.00	16–28 (22.00)	stomach wall
Chromadorea	<i>Anisakis</i> sp.	juv. III	50.00	4–7 (5.50)	guts
	<i>Hysterothylacium</i> sp.	juv. III	25.00	2 (2.00)	guts
<b><i>Anotopterus nikparini</i> (n=9)</b>					
Cestoda	<i>Pelichnibothrium speciosum</i>	larva	11.00	4 (4.00)	guts
<b><i>Magnisudis atlantica</i> (n=1)</b>					
Cestoda	<i>Pelichnibothrium speciosum</i>	larva	in 1 of 1	26 (26.00)	guts

Table 5. Infection of Myctophiformes.  
Таблица 5. Зараженность представителей отряда Myctophiformes.

Parasite		Dev. stage	Prevalence (%)	Intensity (mean)	Site of infection
<b><i>Diaphus theta</i> (n=25)</b>					
Cestoda	<i>Hysterothylacium</i> sp.	larva	4.00	1 (1.00)	guts
Chromadorea	<i>Anisakis</i> sp.	juv. III	4.00	1 (1.00)	guts
<b><i>Notoscopelus japonicus</i> (n=34)</b>					
Chromadorea	<i>Anisakis</i> sp.	larva	14.71	1–2 (1.20)	guts
	<i>Ascarophis</i> sp.	subad.	2.94	1 (1.00)	guts
<b><i>Stenobranchius leucopsarus</i> (n=14)</b>					
Chromadorea	<i>Anisakis</i> sp.	juv. III	14.29	1 (1.00)	guts
<b><i>Tarletonbeania crenularis</i> (n=1)</b>					
Cestoda	<i>Pelichnibothrium speciosum</i>	larva	in 1 of 1	1 (1.00)	guts

*mizellei*. Prowfish *Z. silenus* has never been studied for parasitic infection, so all three common species are recorded for the first time. Northern smoothtongue *L. schmidtii* has been

studied, but quite fragmentarily. It was recorded as a host of *Anisakis* sp. (Solovyova, 1999), *Steringophorus congeri* Shen, 1987, and *Aponurus argentini* Polyanski, 1952 (see



Table 6. Infection of Scorpaeniformes, Scombriformes, and Beloniformes.  
 Таблица 6. Зараженность представителей отрядов Scorpaeniformes, Scombriformes и Beloniformes.

Parasite	Dev. stage	Prevalence (%)	Intensity (mean)	Site of infection	
1	2	3	4	5	
<b><i>Scomber japonicus</i> (n=25)</b>					
Chromadoreia	<i>Anisakis</i> sp.	juv. III	64.00	1–21 (7.25)	guts
	<i>Hysterothylacium</i> sp.	juv. III	20.00	1–35 (8.20)	guts
Trematoda	<i>Prodistomum orientale</i>	ad.	12.00	5–67 (32.00)	intestine
	<i>Opechona olssoni</i>	ad.	4.00	1 (1.00)	intestine
	<i>Lecithocladium excisum</i>	ad.	44.00	1–5 (1.82)	intestine
Palaeacanthocephala	<i>Rhadinorhynchus trachuri</i>	ad.	12.00	1 (1.00)	intestine
	<i>Rh. cololabis</i>	ad.	32.00	1–2 (1.14)	intestine
	<i>Rh. selkirki</i>	ad.	4.00	1 (1.00)	intestine
Cestoda	<i>Pelichnibothrium speciosum</i>	larva	16.00	1–2 (1.50)	guts
<b><i>Aptocyclus ventricosus</i> (n=15)</b>					
Trematoda	<i>Prodistomum alaskense</i>	ad.	26.67	3–11 (6.00)	intestine
	<i>Paraccacladium</i> cf. <i>jamiesoni</i>	ad.	73.33	1–15 (5.54)	intestine
Chromadoreia	<i>Ascarophis</i> sp.	subad.	26.67	1–2 (1.50)	guts
	<i>Anisakis</i> sp.	juv. III	6.67	1 (1.00)	guts
	<i>Hysterothylacium</i> sp.	juv. III	6.67	1 (1.00)	guts
Acanth.	<i>Echinorhynchus gadi</i>	ad.	6.67	1 (1.00)	intestine
Cestoda	<i>Nybelinia surmenicola</i>	larva	6.67	1 (1.00)	stomach wall
	<i>Pelichnibothrium speciosum</i>	larva	6.67	1 (1.00)	guts
<b><i>Cololabis saira</i> (n=52)</b>					
Chromadoreia	<i>Anisakis</i> sp.	juv. III	7.69	1–7 (2.50)	guts
Copepoda	<i>Penella</i> sp.	ad.	23.08	1–4 (1.75)	body surface, musculature

Table 6 (continued).  
Таблица 6 (продолжение).

	1	2	3	4	5
Palaeacanthocephala	<i>Rhadinorhynchus cololabis</i>	ad.	98.08	1–8 (3.07)	intestine
	<i>Rh. selkirki</i>	ad.	3.85	1 (1.00)	intestine
	<i>Rh. trachuri</i>	ad.	5.77	1 (1.00)	intestine
Cestoda	<i>Pelichnibothrium speciosum</i>	larva	26.92	1–3 (1.71)	guts

Table 7. Infection of other species of bony fishes.  
Таблица 7. Зараженность представителей других отрядов костистых рыб.

Parasite	Dev. stage	Prevalence (%)	Intensity (mean)	Site of infection	
<b><i>Sardinops sagax melanostictus</i> (n=10)</b>					
Chromadorea	<i>Anisakis</i> sp.	juv. III	10.00	1 (1.00)	guts
<b><i>Leuroglossus schmidti</i> (n=16)</b>					
Cestoda	<i>Pelichnibothrium speciosum</i>	larva	6.25	1 (1.00)	guts
Trematoda	<i>Licithophyllum botryoporon</i>	ad.	6.25	1 (1.00)	intestine
	<i>Paracaecladium jamiesoni</i>	ad.	12.50	1–2 (1.50)	intestine
<b><i>Desmodema lorum</i> (n=1)</b>					
Chromadorea	<i>Hysterothylacium</i> sp.	juv. III	in 1 of 1	1 (1.00)	guts
	<i>Anisakis</i> sp.	juv. III	in 1 of 1	6 (6.00)	guts
Cestoda	<i>Pelichnibothrium speciosum</i>	larva	in 1 of 1	10 (10.00)	guts
<b><i>Gasterosteus aculeatus</i> (n=214)</b>					
Chromadorea	<i>Anisakis</i> sp.	juv. III	2.34	1–2 (1.40)	guts
Cestoda	<i>Pelichnibothrium speciosum</i>	larva	7.01	1 (1.00)	guts
	<i>Bothriocephalus scorpii</i>	larva	7.01	1–3 (1.25)	guts
Trematoda	<i>Bunodera mediovitellata</i>	ad.	12.62	1–3 (1.13)	intestine

Kuramochi, 2009). All three species mentioned in Table 7 are noted for *L. schmidti* for the first time. The same is true for the three parasitic

species that we found in medusafish *I. lockingtoni*, which seems to have never been checked for infection before.

Table 8. Infection of cartilaginous fish.  
Таблица 8. Зараженность хрящевых рыб.

Parasite		Dev. stage	Prevalence (%)	Intensity (mean)	Site of infection
<b><i>Lamna ditrops</i> (n=1)</b>					
Chromadorea	<i>Anisakis</i> sp.	juv. III	in 1 of 1	7 (7.00)	stomach
Trematoda	<i>Lecithocladium excisum</i>	ad.	in 1 of 1	1 (1.00)	stomach
Cestoda	<i>Nybelinia surmenicola</i>	ad.	in 1 of 1	27 (27.00)	spiral valve
Cestoda	<i>Dinobothrium</i> sp.	ad.	in 1 of 1	2 (2.00)	spiral valve
<b><i>Prionace glauca</i> (n=1)</b>					
Chromadorea	<i>Anisakis</i> sp.	juv. III	in 1 of 1	6 (6.00)	stomach
Cestoda	<i>Platybothrium auriculatum</i>	ad.	in 1 of 1	323 (323.00)	spiral valve
	<i>Anthobothrium caseyi</i>	ad.	in 1 of 1	120 (120.00)	spiral valve
	<i>Scyphophyllidium exiguum</i>	ad.	in 1 of 1	155 (155.00)	spiral valve



Fig. 1. Dissected intestine of *Alepisaurus ferox*, infected by plerocercoids of *Pelichnibothrium speciosum*.  
Рис. 1. Вскрытый кишечник *Alepisaurus ferox*, зараженного плероцеркоидами *Pelichnibothrium speciosum*.

The infection of Pacific salmon is a well-studied issue. Many publications dedicated to the parasites of salmon at different developing stages are available (e.g. Kononov, 1971; Karmanova, 1998; Vyalova, 2002; Posphehov et

al., 2014). *Pelichnibothrium speciosum* (Monticelli, 1889) was the most abundant species in our samples. For the first time, phyllobothriidean plerocercoids were found in Pacific salmon by F. Zschokke and described as *Pelichniboth-*

*rium caudatum* Zschokke in Zschokke and Heitz, 1914 (see Zschokke & Heitz, 1914). Zmeev (1936) moved this species to the genus *Phyllobothrium* Van Beneden, 1850. Dubinina (1971) considered *P. caudatum* as conspecific with *P. speciosum*. However, Szholz *et al.* (1998) disagreed with this, based on the presence in the zone of proglottis differentiation situated far posterior to the scolex of *P. speciosum* sensu Dubinina, 1971. Most authors indicate the common plerocercoids from Pacific salmon as *P. speciosum* (Vyalova, 2002; Karmanova, 1998; Pospehov *et al.*, 2014). The type host of *P. speciosum* is *A. ferox* (see Monticelli, 1889). In our materials collected from nine examined specimens of *A. ferox*, we found both small plerocercoids (2–3 cm, matching the description of *P. caudatum*) and large (up to 15 cm), as described by Szholtz *et al.* (1998). Since we could observe gradual change in the scolex morphology and were convinced that the large plerocercoids processed are conspecific with the small ones we found in 16 out of 23 examined teleost species, including *A. ferox*, all of them in Tables 2–8 are indicated as *P. speciosum*.

In the works of Mamaev *et al.* (1959) and Margolis (1963) were records of Pacific salmon species in the open ocean being heavily infected by marine digenean species (*Brachyphallus crenatus* (Rudolphi, 1802) and others), but in our research, we found none of them. It can be assumed that this is a consequence of the wave-like change in the number of both parasites and their hosts. In 1958, when Mamaev and his colleagues collected their samples, only 39 tons of pink salmon were caught in the Russian Far East, while in 2018, it was the historical maximum of the pink salmon fishing season, and more than 511 tons were caught (Gordeev *et al.*, 2018). Undoubtedly, the 13-fold difference in the number of hosts that did not form shoals during the feeding migration could affect the dynamics of parasitic cycles.

Pacific barrelfish, *Hyperoglyphe japonica* (Döderlein, 1884), was heavily infected solely by a cestode *Glossobothrium nipponicum* Yamaguti, 1952 (Table 3). Taking into account

that this fish feeds on Japanese anchovy, *Engraulis japonicas* Temminck et Schlegel, 1846, euphysiids, hyperiids, and squid, as do many other teleost fish (Chuchukalo, 2006), host specificity of this tapeworm seems to be limited to a small number of fish hosts, including *Seriolella brama* (Günther, 1860) (see Gulyaev, Korotava, 1989) and *Schedophilus velaini* (Sauvage, 1879) (see Brabec *et al.*, 2015). Another representative of the order Perciformes — Pacific pomfret, *Brama japonica* Hilgendorf, 1878, is well studied in terms of parasitic infection by: copepods (McDonald, Margolis, 1995), digeneans (Love, Moser, 1983; Moles, 2007), cestodes (Iannacone, Alvarino, 2013), and acanthocephalans (Didenko, Shevshenko, 1999) throughout its wide habitat range. However, *P. speciosum* and *Hysterothylacium* sp. are recorded as infecting for the first time.

Two species of Aulopiformes — North Pacific daggertooth, *Anotopterus nikparini* Kukev, 1998, and *A. ferox* — are similar both in appearance and in the structure of the jaw apparatus. However, *A. nikparini* bites pieces of flesh from its victims, while *A. ferox* swallows its prey whole. This dissimilarity in the feeding method is reflected in the dramatic difference in the helminth infection: only one out of the nine examined specimens of *A. nikparini* was infected by four plerocercoids of *P. speciosum*, while *A. ferox* was heavily infected by generalist nematodes and especially cestodes (Table 4, Fig. 1). The reason why *P. speciosum* develops into a large plerocercoid only in *A. ferox* and *M. atlantica* among fish species remains unclear. *M. atlantica* was studied for infection for the first time.

Mictophids California headlightfish, *Diaphus theta* Eigenmann et Eigenmann, 1890, Japanese lanternfish *Notoscopelus japonicus* (Tanaka, 1908), northern lampfish, *Stenobrachius leucopsarus* (Eigenmann et Eigenmann, 1890), and blue lanternfish, *Tarletonbeania crenularis* (Jordan et Gilbert, 1880), showed weak involvement in the parasitic life cycles. Only 10 out of 74 fishes were infected by generalists — *Anisakis* sp., *Ascarophis* sp., and by *P. speciosum* (Table 5).

Chub mackerel, *Scomber japonicus* Houttuyn, 1782, is well studied for parasitic infection in the north-western Pacific Ocean (Ishihara, 1968; Kovalenko, 1986) and the biological diversity of its infection is the greatest among epipelagic species covered in this research, due to its significant migrations from the areas of spawning (Japanese archipelago) to the feeding area in the more productive north areas. All parasitic species found by us were previously recorded repeatedly in chub mackerel (Volkov *et al.*, 1999).

Infection of the Pacific saury, *Cololabis saira* (Brevoort, 1856), is well studied in the area under consideration (Kurochkin *et al.*, 1987; Gordeev *et al.*, 2017; Suyama *et al.*, 2019). Our findings are broadly consistent with the available information on infection of *C. saira*, in the northern part of the Pacific Ocean (Table 6). Total infection by acanthocephalans of the genus *Rhadinorhynchus* Lühe, 1911 was characterised by higher prevalence of *Rhadinorhynchus cololabis* Laurs et McCauley, 1964, while in more southerly waters, *Rhadinorhynchus trachuri* Harada, 1935 prevailed in the Pacific saury's intestine.

Japanese pilchard, *Sardinops sagax melanosticta* (Temminck et Schlegel, 1846), and whiptail ribbonfish, *Desmodema lorum* Rosenblatt et Butler, 1977, were poorly observed in this work. However, in the latter fish species, we have found *Hysterothylacium* sp., *Anisakis* sp., and *P. speciosum* (Table 7). This is the first study of whiptail ribbonfish infection.

Threespine stickleback, *G. aculeatus*, an anadromous species in the Pacific Ocean, performs significant migrations from its spawning grounds to the open waters. Our specimens were caught at a distance of 500–600 km from the shore and were infected only by *Anisakis* sp., *P. speciosum*, *Bothriocephalus scorpii* (Müller, 1776) and *Bunodera mediovitellata* Zymbaluk et Roitman, 1966. Among the listed parasites, only *B. mediovitellata* remained in the examined sticklebacks from the fresh waters since its first intermediate hosts are insects (Trichoptera) (Caira, 1981). Our study showed that *G. aculeatus*'s infection significantly differs from all oth-

er studied species of bony fish. The stickleback feeds in the sea; however, the parasitological examination of more than 200 specimens revealed the prevalence of coastal (*B. scorpii*) and freshwater (*B. mediovitellata*) parasites. This is the first data on *G. aculeatus* infection so far in the open ocean.

The salmon shark, *Lamna ditropis* Hubbs et Follett, 1947, was studied in a single specimen and comparatively little infection was found in the form of the adult stages of *N. surmenicola* and *Dinobothrium* sp. (Table 8). *Anisakis* sp. and *Lecithocladium excisum* (Rudolphi, 1819) were found in the stomach. *Lamna ditropis* is a paratenic host of *Anisakis* sp., while for *L. excisum* it is a postcyclic host. Both cestodes were previously recorded in the salmon shark by Palm (2004). Two specimens of *Dinobothrium* found by us do not fit the morphological description of any of the six known species and probably belong to a new species. The blue shark, *Prionace glauca* (Linnaeus, 1758), was studied in a single specimen too and was not much older than the salmon shark specimen, but was much more heavily infected. All three species of cestodes recorded from the spiral valve were already recorded in *P. glauca* (Merlo-Serna, Garcia-Prieto, 2016; Alves *et al.*, 2017).

Both species of sharks studied feed on fish. However, the blue sharks mostly feed on *Leuroglossus schmidti*, *Cololabis saira*, and myctophids with sea elephants, planktonic crustaceans, thaliaceans, chum salmon, and coho salmon being found occasionally. In the feeding of the salmon shark, pink salmon, and other salmon, *Engraulis japonicus*, *Sardinops sagax melanostictus*, *Clupea pallasii*, and squid prevail (Chuchukalo, 2006). Despite their generally different feeding habits, both species of shark share the same feeding base, so in our opinion, the clear distinction between infections by cestodes arose due to the significant difference in the morphology of the spiral valve (Leigh *et al.*, 2019). The blue shark is a representative of the order Carcharhiniformes and has a cylindrical spiral in the valve, while the salmon shark belongs to the order Lamniformes and has a vertical spiral in the valve.

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### Compliance with ethical standards

**Conflict of Interest:** The authors declare that they have no conflict of interest.

**Ethical approval:** This article does not contain any studies with animals performed by any of the authors.

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