# First Records of *Tracheliastes sachalinensis* (Copepoda: Lernaeopodidae), a Fin Parasite of Cyprinids, from Japan

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The lernaeopodid copepod *Tracheliastes sachalinensis* Markevich, 1936 was found on the fins of three species of the subfamily Leuciscinae Bonaparte, 1846 (Cypriniformes: Cyprinidae): big-scaled redfin, *Tribolodon hakonensis* (Günther, 1877); Sakhalin redfin, *Tribolodon sachalinensis* (Nikolskii, 1899); and lake minnow *Rhynchocypris percnurus* (Pallas, 1814); collected in three lakes (Lake Tôro, Lake Shirarutoro, and Lake Abashiri) and two rivers (Mena River and Jirô-sawa River), Hokkaido, northern Japan. These findings represent the first records of *Tracheliastes sachalinensis* from Japan and also from outside of Russia, in which the copepod has hitherto been found. The species is specific to leuciscine fishes in the subarctic region of the Russian Far East and Japan. We also provide a review of parasitic copepods of freshwater fishes from Hokkaido.

Key Words: Tracheliastes sachalinensis, fish parasite, new country record, Hokkaido, Leuciscinae, Tribolodon hakonensis, Tribolodon sachalinensis, Rhynchocypris percnurus.

#### Introduction

While the fauna of parasitic copepods of freshwater fishes of the Japanese Archipelago has been well studied (see Nagasawa *et al.* 2007a, b; Nagasawa and Uyeno 2015), little has been published concerning the parasitic copepods of Hokkaido, the second largest island of Japan with an area of 77,984 km<sup>2</sup>. To date, 11 species of copepods belonging to four families have been reported from Hokkaido (Table 1, see also Nagasawa 1994). Among these species, *Lepeophtheirus salmonis* (Krøyer, 1837) and *Ergasilus wilsoni* Markevich, 1933, which are parasites of marine and brackish-water fishes, respectively, are transported to fresh waters by anadromous fishes (Urawa 1986, 2004; Nagasawa *et al.* 1994a).

During a study of the parasitic copepods of freshwater fishes of Hokkaido, we collected the lernaeopodid copepod *Tracheliastes sachalinensis* Markevich, 1936 (Siphonostomatoida) from the following three species of the subfamily Leuciscinae Bonaparte, 1846 (Cypriniformes: Cyprinidae): big-scaled redfin, *Tribolodon hakonensis* (Günther, 1877); Sakhalin redfin, *Tribolodon sachalinensis* (Nikolskii, 1889); and lake minnow *Rhynchocypris percnurus* (Pallas, 1814). These collections constitute the first records of *Tracheliastes sachalinensis* in Japan. This copepod was insufficiently described by Markevich (1936) based on the material from Sakhalin, the Soviet Union (now Russia), and it has since been poorly reported for its morphology (Markevich 1937, 1956; Gusev 1962, 1987). This paper deals with the morphology of the species based on the specimens from Hokkaido, Japan. The paper also discusses the geographical distribution and host specificity of the species.

## **Materials and Methods**

The host fishes were collected in five localities, Hokkaido, from 1981 to 1988: Lake Abashiri (43°57'49"N, 144°10′19″E, locality 1 in Fig. 1), Abashiri; Lake Shirarutoro (43°10'39"N, 144°30'7"E, locality 2 in Fig. 1), Shibecha; Lake Tôro (43°8'42"N, 144°32'26"E, locality 3 in Fig. 1), Shibecha; the Mena River (42°44'59"N, 140°27'7"E, locality 4 in Fig. 1), a tributary of the Shiribetsu River, Rankoshi; and the Jirô-sawa River (41°50'43"N, 140°20'27"E, locality 5 in Fig. 1), a tributary of the Assabu River, Assabu. The fishes were fixed in 10% formalin immediately after capture, brought to the laboratory, and examined for the presence of parasitic copepods. When copepods were found, they were removed carefully, preserved in 70% ethanol, subsequently cleared, and dissected in 85% lactic acid by the wooden slide procedure of Humes and Gooding (1964). Drawings were made with the aid of a drawing tube. Morphological terminology follows Kabata (1979). Two infection parameters, the prevalence and the mean intensity, were calculated based on the formulae and definitions provided by Bush et al. (1997). The scientific and common names of fishes follow Froese and Pauly (2016), while the common name of Tribolodon sachalinensis follows Nagasawa and Katahira (2013). Vouch-

Family	Species	Host	Reference
Ergas	silidae Burmesiter, 1835		
	Ergasilus auritus Markevich, 1940	Hypomesus nipponensis McAllister, 1963	Urawa (2004)
	Ergasilus briani Markevich, 1933	Hypomesus nipponensis	Urawa (2004)
	Ergasilus hypomesi Yamaguti, 1936	Gymnogobius casteneus (O'Shaugnessy, 1875) [as Chaenogobius laevis (O'Steindachner, 1875)], Gymnogobius urotaenia (Hilgendorf, 1879) [as Chaenogobius urotaenia (Hilgendorf, 1879)], Hypomeus nipponensis, Tribolodon hakonensis	Nagasawa <i>et al.</i> (1989)
	Ergasilus wilsoni Markevich, 1933*	Hypomesus nipponensis	Urawa (2004)
	Neoergasilus japonicus (Harada, 1930)	<i>Carassius</i> sp. (as <i>C. auratus langsdorfii</i> Temminck et Schlegel, 1846), <i>Tribolodon hakonensis</i>	Nagasawa et al. (1989)
	Thersitina gasterostei (Pagenstecher, 1861)	Gasterosteus aculeatus Linnaeus, 1758	Ohtsuka et al. (2004)
Lerna	aeidae Cobbold, 1879		
	<i>Lernaea cyprinacea</i> Linnaeus, 1758	Gymnogobius casteneus (as Chaenogobius laevis), Cyprinus carpio Linnaeus, 1758, Pungitius pungitius (Linnaeus, 1758) [as P. p. pungitius], Tribolodon hakonensis	Hokkaido Salmon Hatchery (1937, as <i>L. elegans</i> Leigh-Sharpe, 1925), Nagasawa <i>et al.</i> (1989)
Calig	idae Burmeister, 1835		
	Lepeophtheirus salmonis (Krøyer, 1837)**	Oncorhynchus keta (Walbaum, 1792), Salvelinus leucomaenis leucomaenis (Pallas, 1814) (as S. leucomaenis), Tribolodon hakonensis	Urawa (1986), Nagasawa <i>et al.</i> (1994a)
Lerna	aeopodidae Milne Edwards, 1840		
	Salmincola californiensis (Dana, 1852)	Oncorhynchus masou masou (Brevoort, 1856)	Nagasawa and Urawa (2002)
	Salmincola carpionis (Krøyer, 1837)	Oncorhynchus nerka (Walbaum, 1792), Salvelinus leucomaenis leucomaenis (as S. leucomaenis)	Yamaguti [1939, as S. <i>falculata</i> (Wilson, 1908)]***, Nagasawa and Urawa (2002: 12, footnote)
	Salmincola stellatus Markevich, 1936	Hucho perryi (Brevoort, 1856)	Kabata (1986), Nagasawa and Urawa (1991), Nagasawa <i>et al.</i> (1994b), Hiramatsu <i>et al.</i> (2001)
	Tracheliastes sachalinensis Markevich, 1936	Rhynchocypris percnurus, Tribolodon hakonensis, Tribolodon sachalinensis	this study

Table 1. Parasitic copepods of freshwater fishes of Hokkaido, Japan, based on the previous and present studies. The scientific names of hosts are adopted from Froese and Pauly (2016).

\*Brackish-water species. \*\*Marine species. Currently, based on molecular analysis, the specimens of the species originally from British Columbia, Canada, were described as *L. salmonis oncorhynchi* by Skern-Mauritzen et al. (2014). \*\*\*Although Kabata (1969) synonymized *S. falculata* with *S. californiensis*, Nagasawa *et al.* (1995: 182) suggested that the specimens of *S. faculata* reported by Yamaguti (1939) were not *S. californiensis* but *S. carpionis*.

er specimens of the copepods found were deposited in the Crustacea (Cr) collection of the National Museum of Nature and Science, Tsukuba, Japan (NSMT-Cr 24303 [n=5] from *Tribolodon hakonensis* in Lake Tôro on 21 August 1981; NSMT-Cr 24304 [n=5] from *T. hakonensis* in Lake Abashiri on 20 July 1984; NSMT-Cr 24305 [n=6] from *Tribolodon sachalinensis* from Lake Tôro on 21 August 1981; NSMT-Cr 24306 [n=5] from *Rhynchocypris percnurus* in Lake Shirarutoro on 19 September 1981; and NSMT-Cr 24607 [n=1] from *T. hakonensis* in the Mena River on 30 June 1988).

Family **Lernaeopodidae** Milne Edwards, 1840 [Japanese name: Nagakubi-mushi-ka] Genus *Tracheliastes* Nordmann, 1832 [Japanese name: Ugui-nagakubi-mushi-zoku] *Tracheliastes sachalinensis* Markevich, 1936 [Japanese name: Ugui-nagakubi-mushi] (Figs 2, 3)

*Tracheliastes sachalinensis* Markevich, 1936: 106; Markevich 1937: 145–146, 188–189, 221–222, fig. 25; Markevich 1976 (originally in 1956): 379–381, figs 138–139; Do-

giel and Akhmerov 1952: 287; Gusev 1964 (originally in 1962): 795, 797, fig. 1617; Yamaguti 1963: 265, pl. 304, fig. 4; Smirnova 1971: 192; Gusev 1987: 506, fig. 578; Shedko *et al.* 2005: 60–61; Sokolov *et al.* 2012: 208.

**Material examined.** The following description is based on four ovigerous females from *Tribolodon hakonensis* (Lake Abashiri) and two ovigerous females from *Tribolodon sachalinensis* (Jirô-sawa River).

**Description of adult female.** Cephalothorax (Fig. 2A–F) cylindrical, 2.2–2.9 mm long (n=6), about half or slightly longer than half length of trunk, shorter than second maxillae, uniform diameter but sometimes slightly swollen near its base; usually deflected dorsally; broad shoulder-like structure (Fig. 2G) formed at base of cephalothorax and second maxillae and separated from trunk by deep narrow constriction. Trunk (Fig. 2A–F) dorsoventrally flattened, 3.7–4.3 mm long (n=6), about 2.5–3.4 times longer than wide (1.1–1.7 mm, n=6); lateral margins nearly parallel but sometimes slightly uneven; posterolateral lobes (Fig. 2H) present; center of posterior margin with genital process protruding in posterior direction.

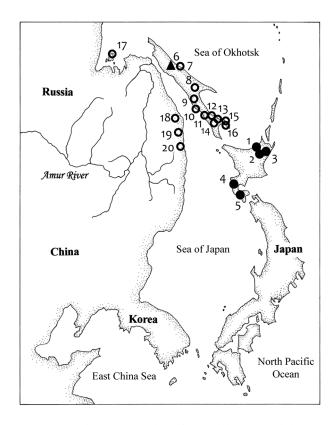


Fig. 1. Distribution records of Tracheliastes sachalinensis Markevich, 1936 in Far East Asia. Collection localities (solid circles) in this study (Hokkaido: 1, Lake Abashiri; 2, Lake Shirarutoro; 3, Lake Tôro; 4, Mena River; 5, Jirô-sawa River); type locality of Tra. sachalinensis (solid triangle) (Sakhalin: 6, Tym River [Markevich 1936]); collection localities (open circles) in the previous studies (Sakhalin: 7, Aslanbekova Passage; 8, Poronai River (including the Leonidovka River); 9. Uglegorka River; 10. Tatar Strait at Lomonon Cape; 11, Ainskoye Lake; 12, Naiva River; 13. Mal Takoy River; 14. Lake Tunaycha; 15, Vavaiskoe Lake; 16, Lebyazh'ye Lake [Shedko et al. 2005; Sokolov et al. 2012]; the Shantar Islands: 17, Bol'shoye Lake [Shedko et al. 2005]; the Primorsky Krai: 18, Koppi River; 19, Samarga River; 20, Amgu River [Shedko et al. 2005]). The species was also reported from the Amur River basin (Dogiel and Akhmerov 1952) including Lake Khivanda (Smirnova 1971), but this lake is not shown herein because its location was not determined.

First antenna (Fig. 3A) reduced and unsegmented; at least two setae seen as apical armature. Second antenna (Fig. 3B) biramous with long sympod; exopod almost as long as endopod, unsegmented, equipped with two papillae, one near apex and another subapical, with tip covered by fine spinules; basal segment of endopod with batch of spinules on ventral wall; terminal segment of endopod (Fig. 3C) armed with large strong hook, with short spiniform seta and conical papilla near dorsal side of apex; ventral bulbous swelling covered with many denticles; setiform process arising from medial side of swelling. Mandible (Fig. 3D) with nine teeth; second distal tooth largest; third from tip small; fourth and fifth from tip slightly larger than four proximal teeth. First maxilla (Fig. 3E) uniramous with two setae of unequal size at tip; papillae absent. Second maxilla (Fig. 2A-F) cylindrical, slightly tapering towards tip; bulla (Fig. 3F) with suborbicular anchor and short manubrium. Maxilliped (Fig. 3G)

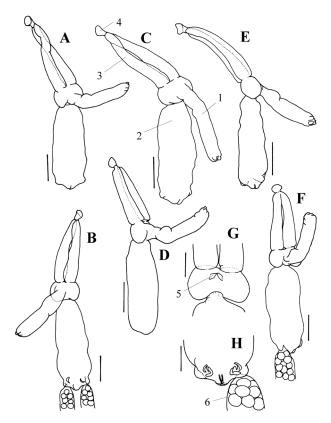


Fig. 2. *Tracheliastes sachalinensis* Markevich, 1936, adult females from *Tribolodon hakonensis* in Lake Abashiri (A–D) and *Tribolodon sachalinensis* in the Jirô-sawa River (E–H), Hokkaido. A–F, variation in shape of habitus (A, C, D, dorsolateral; B, F, dorsal; E, lateral); G, base of second maxillae, ventral; H, posterior extremity of trunk, ventral. 1, cephalothorax; 2, trunk; 3, second maxilla; 4, bulla; 5, maxilliped; 6, egg sac. Scale bars: A–F, 1 mm; G, H, 0.5 mm.

positioned near bases of second maxillae, tapering to its tip; subchela short with small claw.

Hosts and localities. *Tracheliastes sachalinensis* was found on the following three cyprinid species from the following localities in Hokkaido: *Tribolodon hakonensis* from Lake Tôro, Shibecha, Lake Abashiri, Abashiri, and the Mena River, Rankoshi; *Tribolodon sachalinensis* from Lake Tôro, Shibecha and the Jirô-sawa River, Assabu; and *Rhynchocypris percnurus* from Lake Shirarutoro, Shibecha.

**Prevalence and intensity.** Prevalence ranged from 8.7% in *Tribolodon sachalinensis* from the Jirô-sawa River to 13.2% in *T. hakonensis* from Lake Tôro (Table 2). Up to four copepods occurred on a single infected fish (Table 2), but one copepod per fish was most commonly found (42.8, 50.0, and 68.4% in *T. hakonensis* from Lake Tôro [3 fish with one copepod/7 fish infected], *T. sachalinensis* [2/4] combined from Lake Tôro and the Jirô-sawa River, and *R. percnurus* from Lake Shirarutoro [13/19], respectively), followed by two and three copepods per fish.

**Site of infection.** All fins, except the dorsal fin, were infected: the pelvic-, caudal-, and anal fins, especially the first two, were more abundantly infected than the pectoral fin (Table 3).

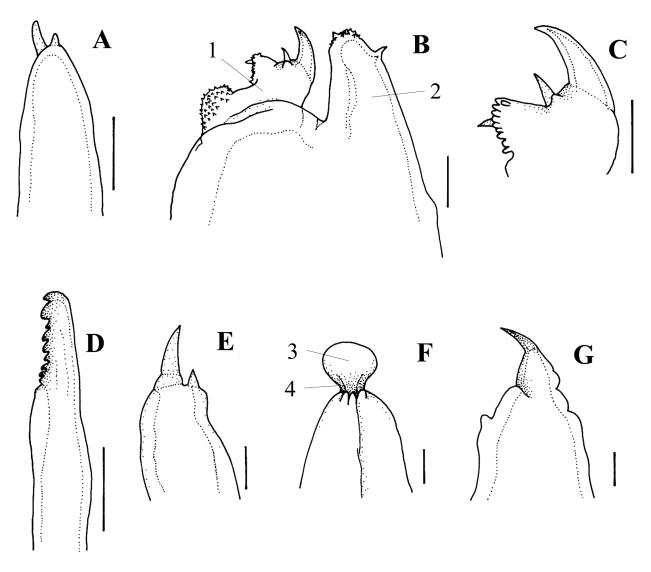


Fig. 3. *Tracheliastes sachalinensis* Markevich, 1936, adult female from *Tribolodon sachalinensis* in the Jirô-sawa River, Hokkaido. A, first antenna, medial; B, second antenna, lateral; C, same, tip of endopod, lateral; D, mandible, lateral; E, first maxilla, lateral; F, bulla and tips of second maxillae, dorsal; G, maxilliped, dorsal. 1, endopod of second antenna; 2, exopod of second antenna; 3, anchor; 4, manubrium. Scale bars: A–D, G, 20 µm; E, 10 µm; F, 0.2 mm.

Table 2. Occurrence of Tracheliastes sachalinensis on three species of leuciscine fishes collected in four localities, Hokkaido\*.

Species	Collection locality	Collection date	Standard length (mean) in mm	Percent prevalence (infected/examined)	Mean intensity (range)
Tribolodon hakonensis	Lake Tôro	21 Aug., 1981	63-138 (83)	13.2 (7/53)	1.7 (1-3)
	Mena River	30 Jun., 1988	105 (105)	— (1/—)	1.0 (1)
Tribolodon sachalinensis	Lake Tôro	21 Aug., 1981	77-143 (101)	10.5 (2/19)	2.5 (1-4)
	Jirô-sawa River	1 Jun., 1986	70-145 (103)	8.7 (2/23)	1.5 (1-2)
Rhynchocypris percnurus	Lake Shirarutoro	19 Sep., 1981	67–100 (84)	— (19/—)	1.3 (1–3)

\* No data were taken for the sample from Lake Abashiri.

## Discussion

The genus *Tracheliastes* von Nordmann, 1832 currently consists of eight valid species: *Tra. polycolpus* Nordmann, 1832; *Tra. maculatus* Kollar, 1835; *Tra. mourkii* Hoffman, 1881; *Tra. sachalinensis*; *Tra. longicollis* Markevich, 1940; *Tra. tibetanus* Kuang, 1964; *Tra. chondrostomi* Hanek, 1969; and *Tra. brevicorpus* Kuang, 1980 (see Boxshall and Walter 2016). Previously, however, Kabata (1979: 357) regarded *Tra. mourkii* as a *species inquirenda* because it had been not adequately established, and also suggested to re-examine *Tra. chondrostomi* because of its poor description. Moreover, a closely related genus, *Pseudotracheliastes* Markevich, 1956 contains three freshwater species that were originally placed in *Tracheliastes*: *P. stellatus* (Mayor, 1824) (originally as *Tra.* 

C	Collection locality	Number of copepods on each fin				Total number of	
Species		Pectoral fin	Dorsal fin	Pelvic fin	Anal fin	Caudal fin	copepods found
Tribolodon hakonensis	Lake Tôro	1	0	7	1	3	12
	Mena River	0	0	1	0	0	1
Tribolodon sachalinensis	Lake Tôro	0	0	1	3	1	5
	Jirô-sawa River	0	0	3	0	0	3
Rhynchocypris percnurus	Lake Shirarutoro	2	0	5	6	12	25
		3	0	17	10	16	46

Table 3. Distribution of Tracheliastes sachalinensis on the fins of leuciscine fishes collected in four localities, Hokkaido\*.

\* No data were taken for the sample from Lake Abashiri.

*stellatus* and *Tra. gigas* Richardi, 1881), *P. stellifer* (Kollar, 1835) (originally as *Tra. stellifer*), and *P. soldatovi* (Markevich, 1933) (originally as *Tra. soldatovi*) (Gusev 1987; Piasecki 1993; Boxshall and Walter 2016).

The copepod specimens examined in this study correspond to the morphology of Tra. sachalinensis (see Markevich 1937, 1956; Gusev 1962, 1987). In particular, the proportion of the cephalothorax length and the trunk length is important in identification, and the specimens are differentiated from other congeners by their short cephalothorax, which is nearly or slightly longer than half of the trunk length (Fig. 2A-F). The species was originally described based on adult females from Pacific redfin, Tribolodon brandtii (Dybowski, 1872) (as "Leuciscus brandti"), in the Tym River (locality 6 in Fig. 1), Sakhalin (Markevich 1936). As the original description was insufficient, the copepod was later redescribed using the same material (Markevich 1937). However, this redescription was still superficial, and the subsequent publications (Markevich 1956; Gusev 1962, 1987) of the morphology of the species were not based on original works but copied from the redescription. Therefore, the present paper attempts to provide new information on the morphology of Tra. sachalinensis.

*Tracheliastes polycolpus* is known to occur in Sakhalin (Yamaguti 1940; Shedko *et al.* 2005; Sokolov *et al.* 2012), which is close to our sampling area (Hokkaido). This species, however, differs from *Tra. sachalinensis* in having a longer cephalothorax (*i.e.*, about two-thirds of trunk length) and a trunk with uneven lateral margins, and lacking fine spinules at the tip of exopod of the second antenna (see Kabata 1979; Gusev 1987).

The geographical distribution of *Tra. sachalinensis* has hitherto been restricted to the Russian Far East, including Sakhalin (Markevich 1936, 1937; Shedko *et al.* 2005; So-kolov *et al.* 2012; localities 6–16 in Fig. 1), the Amur River basin (Dogiel and Akhmerov 1952; Gusev 1962, 1987; Smirnova 1971; Fig. 1), the Shantar Islands (Shedko *et al.* 2005; locality 17 in Fig. 1), and the Primorsky Krai (Maritime Province) (Shedko *et al.* 2005; localities 18–20 in Fig. 1). The species was collected for the first time from outside of Russia in this study (localities 1–5 in Fig. 1). The past and present distribution records of the species demonstrate that the species occurs in the subarctic region of the Russian Far East and Japan (Fig. 1)

In this study, Tra. sachalinensis was discovered in Hok-

kaido, which is geographically close to Sakhalin and the Eurasian continent. This is interesting because there is a suggestion that the ancestors of some freshwater fishes, including cyprinids, colonized Hokkaido from Far Eastern Siberia via Sakhalin about two to five million years ago (Goto 1982). Actually, the parasite occurs in the Amur River basin, the Shantar Islands, the Primorsky Krai, and Sakhalin, and might have been brought to Hokkaido by the ancestral stocks of cyprinids and then established in Hokkaido.

Tracheliastes sachalinensis has been reported from four species of cyprinid fishes: Tribolodon brandtii (as "L. brandti" in Markevich 1936, 1937), T. hakonensis (as "T. hakuensis" in Shedko et al. 2005), and T. sachalinensis (as "T. ezoe Okada et Ikeda, 1937" in Shedko et al. 2005) in Sakhalin (Markevich 1936, 1937; Gusev 1962, 1987; Shedko et al. 2005; Sokolov et al. 2012); and T. brandtii (as "L. brandti") and R. percnurus (as "Phoxinus percnurus") in the Amur River basin (Dogiel and Akhmerov 1952; Gusev 1962, 1987; Smirnova 1971), although the Smirnova's (1971) identification of the species from R. percnurus in the Amur River basin was considered doubtful by Shedko et al. (2005). These four cyprinids all belong to the subfamily Leuciscinae, and Tra. sachalinensis is thus specific to the fishes of this subfamily.

Among the three cyprinids examined in this study, *Tribolodon hakonensis* has the widest geographical distribution in Japan, ranging from Hokkaido in the north to Kyushu in the south (Kurawaka 1977; Sakai 1995), and it is desirable to clarify, by investigating populations of the fish from various localities, whether *Tra. sachalinensis* has remained in Hokkaido or has expanded its distribution range to more southern, temperate regions in Japan.

Tribolodon hakonensis is one of the most-extensively studied freshwater fishes in Japan in terms of its parasite fauna. To date, 43 species of protistan and metazoan parasites, including six species of copepods: Caligus orientalis Gusev, 1951; C. punctatus Shiino, 1955; Ergasilus hypomesi Yamaguti, 1936; Lepeophtheirus salmonis; Lernaea cyprinacea Linnaeus, 1758; and Neoergasilus japonicus (Harada, 1930), have been reported from this fish in Japan (Nagasawa and Katahira 2013). Nevertheless, the finding of Tra. sachalinensis from the fish in this study indicates that some parasites may still be undiscovered and we need more study to understand the parasite fauna of this fish. In addition, Tra. sachalinensis is the first species of parasitic copepod from *Tribolodon sachalinensis* and *R. percnurus* in Japan (see Nagasawa *et al.* 1989; Nagasawa and Katahira 2013).

Based on the fact that Tra. sachalinensis infected Tribolodon hakonensis (as "T. hakuensis") in the Tatar Strait (the Sea of Japan, locality 10 in Fig. 1), Sakhalin, Shedko et al. (2005) suggested that this copepod is euryhaline. Sokolov et al. (2012) also collected Tra. sachalinensis from the same fish species caught in Aslanbekova Passage (locality 7 in Fig. 1) into the Sea of Okhotsk, Sakhalin. In this study, we collected the copepod from the three species of leuciscine fishes caught in fresh waters. It should be emphasized, however, that T. hakonensis can also inhabit brackish and marine waters (Sakai 1995). Thus, further study is needed to examine whether the copepod occurs in such saline waters in Japan as well. In particular, Lake Abashiri (locality 1 in Fig. 1), one of the sampling localities in this study, is located on the Okhotsk-Sea coast of Hokkaido and is composed of freshwater and brackish-water regions (Motoda 1950), which may be suitable to examine the occurrence of Tra. sachalinensis on T. hakonensis from different sites differing in salinity.

This study shows that the leuciscine fishes from Hokkaido harboured the copepod mostly abundantly on the pelvic and caudal fins (Table 3). In Sakhalin near Hokkaido, the copepod was found most abundantly on the caudal fin, followed by the pectoral-, anal-, and pelvic fins (Shedko *et al.* 2005). These results indicate that the caudal fin is commonly used by *Tra. sachalinensis* as its site of infection. The dorsal fin was the least abundantly infected in both Sakhalin (Shedko *et al.* 2005) and Hokkaido (Table 3).

Recently, a significant progress has been made in research on the ecology of a closely related congener *Tra. polycolpus* (*e.g.*, Loot *et al.* 2004, 2011; Blanchet *et al.* 2009a, b; Cardon *et al.* 2011; Lootvoet *et al.* 2013; Mazé-Guilmo *et al.* 2014). In contrast to it, almost nothing is known about the host-parasite relationship between *Tra. sachalinensis* and its hosts. Further studies are needed on various aspects of the biology of the species.

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