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Salmincola edwardsii (Copepoda: Lernaeopodidae) Parasitic on Southern Asian Dolly Varden, *Salvelinus malma krascheninnikova*, from Hokkaido Island, Japan, with the Southernmost Distribution Record of the Copepod in Asia

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Females of the lernaeopodid copepod *Salmincola edwardsii* (Olsson, 1869) were found parasitizing the gill area of southern Asian Dolly Varden, *Salvelinus malma krascheninnikova* Taranetz, 1933, from four rivers (Rusha River, Rausu River, Shari River, Shibetsu River) in and near the Shiretoko Peninsula, eastern Hokkaido Island, Japan. The females are briefly described as the first record of *S. edwardsii* from Hokkaido Island and the southernmost distribution record for the species in Asia. The branchial chamber was the most frequently used site for attachment by the females, followed by the gill filaments and the inner surface of the operculum. The overall prevalence of infection was 42.1%, and intensity ranged from 1 to 6 (mostly 1 or 2). The species was not collected from the central and western regions of Hokkaido Island, and the restriction of its distribution to eastern Hokkaido Island is discussed in terms of anadromy of the host species. The impact of global climatic warming on the Hokkaido populations of *S. edwardsii* is also discussed.

Key Words: Parasitic copepod, freshwater fish parasite, new locality record.

Introduction

Salmincola edwardsii (Olsson, 1869) is a lernaeopodid copepod parasitic on chars (the salmonid genus *Salvelinus* Richardson, 1836) in the Northern Hemisphere (Kabata 1969). Little information is available on the species in Japan, where it has been reported from Kunashir Island and Iturup Island, the southern Kuril Islands, east of Hokkaido Island, one of the four major islands of the country (Shedko and Shedko 2002). Specimens of *S. edwardsii* were collected from southern Asian Dolly Varden, *Salvelinus malma krascheninnikova* Taranetz, 1933 (Salmoniformes: Salmonidae), caught in 1993 on Hokkaido Island. This represents the first record of *S. edwardsii* from Hokkaido Island and the southernmost distribution record for the species in Asia. This paper briefly describes *S. edwardsii* using the specimens collected and reports on its attachment sites, distribution on Hokkaido Island, and prevalence and intensity of infection on southern Asian Dolly Varden.

Materials and Methods

Southern Asian Dolly Varden were caught by electrofishing by the staff of the Hokkaido Fish Hatchery from August to November 1993 during a survey of the distribution and abundance of the species on Hokkaido Island (Takami *et al.* 1995). Most of the fish caught were released back into each collection site not to reduce the population size of the species after they were counted, whereas others were fixed in 10% formalin for subsequent examination of stomach contents. In June 2006, some of the latter fish from nine rivers (Table 1) were sent to the laboratory of Hiroshima University, where they were measured for fork length (FL, mm) and examined for endo- and ectoparasitic metazoan parasites. When ectoparasitic copepods were found, they were carefully removed and preserved in 70% ethanol after their attachment sites were recorded. The copepods were examined for their morphology using an Olympus SZX10 stereo microscope and an Olympus BX51 compound microscope. Two specimens from the Shari River were soaked in lactophenol for 2–3 h, and dissected and observed using the wooden slide method of Humes and Gooding (1964). Drawings were made with the aid of drawing tubes fitted on the stereo microscope (for the habitus) and the compound microscope (for the second antenna, mandible, first maxilla, and maxilliped). Morphological terminology follows Kabata (1979) and that for the armature of the endopod of the second antenna is based on Kabata (1969). Voucher specimens of *S. edwardsii* (five and four females from the Shari and Shibetsu rivers, respectively) have been deposited in the Crustacea collection of the National Museum of Nature and Science, Tsukuba, Ibaraki Prefecture (NSMT-Cr 28183 and 28184), and the remaining specimens are retained by the author for a taxonomic study of *Salmincola* spp. from fresh-

Table 1. Occurrence of *Salmincola edwardsii* on southern Asian Dolly Varden in nine rivers, Hokkaido.

Collection locality			Collection date	Fork length (mean) in mm	Percent prevalence (infected/examined)	Intensity (mean)	Total number of copepods found	No. of copepods per attachment site		
River	Site	No. in Fig. 3						Branchial chamber	Gill filaments	Operculum
Rusha River	Lower reaches of the main stream	5	6 October 1993	62–174 (118)	36.4 (4/11)	1 (1.0)	4	2	0	2
Rausu River	Lower reaches near the river mouth	6	5 October 1993	72–182 (127)	33.3 (1/3)	2 (2.0)	2	2	0	0
Shari River	Sattsuru Stream	7	5 October 1993	110–145 (128)	41.7 (5/12)	2–6 (3.2)	16	9	5	2
Shibetsu River	Upper reaches of the main stream	8	7 October 1993	88–198 (143)	50.0 (6/12)	1–4 (1.7)	10	6	3	1
Saru River	Uenzaru Stream	9	8 October 1993	103–173 (138)	0 (0/3)	0 (—)	0	0	0	0
Yoichi River	Miginomata Stream	10	15 October 1993	105–159 (117)	0 (0/7)	0 (—)	0	0	0	0
Shiribetsu River	Makkari Stream	11	25 August 1993	90–129 (110)	0 (0/10)	0 (—)	0	0	0	0
	Pēpenai Stream	11	2 November 1993	53–131 (96)	0 (0/6)	0 (—)	0	0	0	0
Notto River	Upper reaches of the main stream	12	21 August 1993	118–162 (141)	0 (0/5)	0 (—)	0	0	0	0
Chihase River	Nagumo Stream	13	13 October 1993	83–141 (112)	0 (0/10)	0 (—)	0	0	0	0
							Grand total: 32	19	8	5

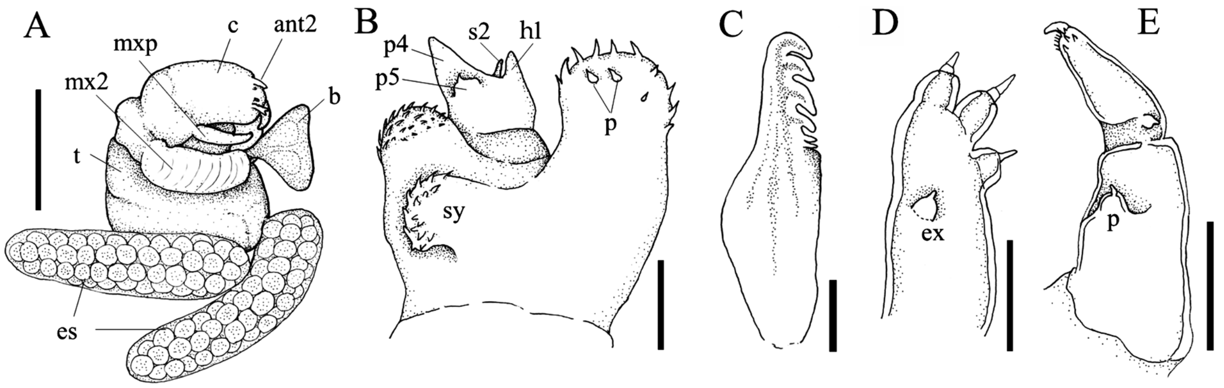

Fig. 1. *Salmincola edwardsii*, female, from southern Asian Dolly Varden, *Salvelinus malma krascheninnikova*, from the Shari River, Hokkaido Island. A, habitus, anterolateral view; B, second antenna, lateral view; C, mandible, lateral view; D, first maxilla, lateral view; E, maxilliped, lateral view. Abbreviations: ant2, second antenna; b, bulla; c, cephalothorax; es, egg sac; ex, exopod; h1, hook 1; mx2, second maxilla; mxp, maxilliped; p, palp; p4, process 4; p5, process 5; s2, spine 2; sy, sympod; t, trunk. Scale bars: A, 1 mm; B, 50 µm; C, 20 µm; D, 100 µm; E, 200 µm.

water salmonids of Japan. Prevalence, intensity, and mean intensity follow the definitions of Bush *et al.* (1997).

In the past parasitological papers, several scientific names were used for southern Asian Dolly Varden from Japan [*Salvelinus malma* (Walbaum, 1792) (Seki 1975; Ito *et al.* 1987; Shedko and Shedko 2002); *S. m. krascheninnikovi* (Katahira *et al.* 2017)] and the Russian Far East [*S. malma* (Shedko and Shedko 2002); *S. curilus* (Pallas, 1814) (Shedko *et al.* 2005)], but *S. m. krascheninnikova* is herein used based on WoRMS Editorial Board (2020). Following Dunham *et al.* (2008: 539), "southern Asian Dolly Varden" is used as the common name of *S. malma krascheninnikova*. The scientific and common names of other fishes mentioned in this paper follow Froese and Pauly (2019).

Results

Adult females of *S. edwardsii* were collected from southern Asian Dolly Varden from four of the nine rivers surveyed on Hokkaido Island (Table 1).

Description of adult female. Cephalothorax (Figs 1A, 2) subtriangular, shorter than trunk, slightly swollen in posterolateral portions, and separated from trunk by shallow constriction. Trunk (Figs 1A, 2) from orbicular to suboval with rounded margins, 1.3–1.7 (mean=1.5) mm long (n=17). Total body length (excluding egg sacs) 2.1–2.9 (2.5) mm (n=17).

Second antenna (Fig. 1B) biramous with spiny pad on sympod; exopod slightly bulbous, unsegmented, equipped with scattered spines and two papillae; endopod two-segmented; basal segment with spiny pad; distal segment with armature comprising prominent process 4, smaller process 5, projecting hook 1, and small spine 2. Mandible (Fig. 1C) with six teeth; first and second distal teeth slightly smaller than third tooth being largest; two proximal teeth small. First maxilla (Fig. 1D) uniramous with three papillae on endopod; exopod lateral. Second maxilla (Figs 1A, 2) cylindrical, originating from base of cephalothorax at junction with trunk; bulla (Fig. 1A) with subconical anchor and short manubrium. Maxilliped (Figs 1E, 2) positioned in ventrolateral region of cephalothorax, tapering to its tip; corpus with prominent conical palp; subchela with small seta near base and patch of denticles near base of claw, ending in small claw.

Attachment sites. All specimens (*n*=32) of *S. edwardsii* were found attached to the gill area of the fish. The wall of the branchial chamber was the most common attachment site (59.4%), followed by the gill filaments (25.0%) and the inner surface of the operculum (15.6%) (Table 1). Infected gill filaments were often abbreviated in length, and the host tissue enveloping the bulla was bulbously enlarged (Fig. 2).

Distribution on Hokkaido Island. *Salmincola edwardsii* was collected from four rivers (Rusha, Rausu, Shari, and Shibetsu rivers) in and near the Shiretoko Peninsula, eastern Hokkaido Island (localities 5–8 in Fig. 3; Table 1). The species, however, was not found from five rivers [Saru, Yoichi, Shiribetsu (two sites), Notto, and Chihase rivers] in the central and western regions of the inland (localities 9–13 in Fig. 3; Table 1).

Prevalence and intensity. The overall prevalence of *S. edwardsii* on southern Asian Dolly Varden [62–198 (mean=117) mm FL, *n*=38] from the four rivers was 42.1%: prevalence in each river ranged from 33.3–50.0% (Table 1). The overall mean intensity was 2.6 copepods, and mean intensity in each river was 1.0–3.2 copepods (Table 1). One copepod (50.0%) was most commonly found per infected host, followed by 2 (31.3%), 4 (12.5%), and 6 (6.2%) copepods. The smallest infected fish was 71 mm FL from the Rusha River, and 6 copepods were found on a fish of 123 mm FL from the Shari River.

Remarks. The morphology of the copepod specimens from southern Asian Dolly Varden from Hokkaido Island corresponds well to the diagnosis of *S. edwardsii* reported by Kabata (1969) based on his revision of the genus *Salmincola* C. B. Wilson, 1915. The most important key to separate *S. edwardsii* from its congeners is the presence of a large process on the endopod of the second antenna (Kabata 1969), which is confirmed in the present study (p4 in Fig. 1B). Other morphological characters of the specimens also fit those of *S. edwardsii* reported before (Kabata 1969; Fryer 1981; Shedko and Shedko 2002; Ruiz *et al.* 2017). Therefore, the specimens collected in this study are considered conspecific with *S. edwardsii.*

The trunk length of *S. edwardsii* is known to differ between the Nearctic and Palearctic regions: individuals from the former region were reported to have shorter trunks (1.60–2.00 mm) than those from the latter region (2.96–3.00 mm) (Kabata 1969). Actually, the trunks of specimens from North Carolina, U.S.A., in the Nearctic region are similarly short [1.6–2.1 (mean=1.9, *n*=16) mm] (Ruiz *et al.* 2017). However, those of specimens from Far East Asia in the Palearctic region are unexpectedly as short as 1.50–2.25 (2.05, *n*=40) mm (Shedko and Shedko 2002) and 1.3–1.7 (1.5) mm (this paper), which suggests that regional variations in trunk length of *S. edwardsii* are more complicated than those indicated by Kabata (1969). In the present study, 10% formalin used to fix the host fish might have caused a considerable reduction in trunk length of the specimens of *S. edwardsii.*

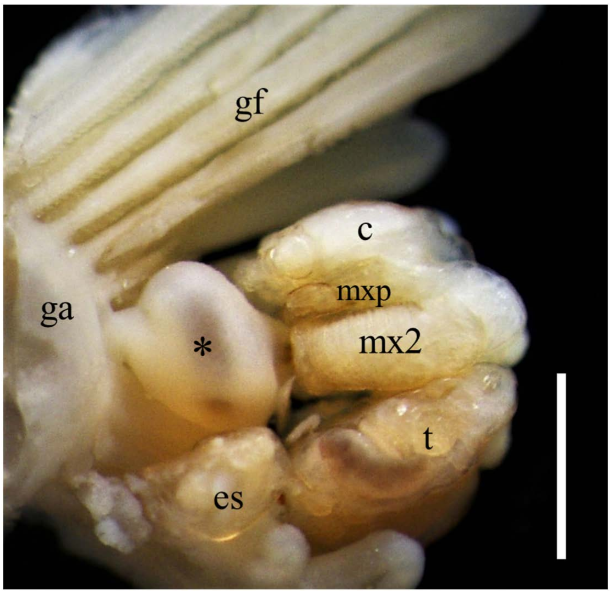

Fig. 2. Female of *Salmincola edwardsii* attached to the base of gill filament of southern Asian Dolly Varden, *Salvelinus malma krascheninnikova*, from the Shari River, Hokkaido Island. Formalin-fixed and later ethanol-preserved specimen, lateral view. Abbreviations: c, cephalothorax; es, egg sac; ga, gill arch; gf, gill filament; mx2, second maxilla; mxp, maxilliped; t, trunk. Scale bar: 1 mm. Note most portions of the infected gill filament lost, and a bulbous swelling (*) enveloping the bulla.

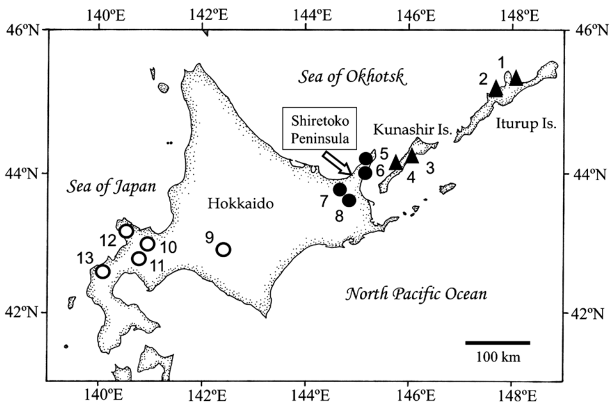

Fig. 3. Map of Hokkaido Island and the southern Kuril Islands, showing the collection localities of *Salmincola edwardsii* in the previous (closed triangles, Shedko and Shedko, 2002) and present (closed circles) studies. Open circles show no copepod infection on southern Asian Dolly Varden. 1, Olya Inlet (Prostor Bay), Iturup Island; 2, Kuibyshev Bay, Iturup Island; 3, Petrova River, Kunashir Island; 4, a nameless creek, Kunashir Island; 5, Rusha River; 6, Rausu River; 7, Shari River; 8, Shibetsu River; 9, Saru River; 10, Yoichi River; 11, Shiribetsu River; 12, Notto River; 13, Chihase River.

Salmincola edwardsii is the fourth species of the genus found on Hokkaido Island. To date, three species of the genus have been reported from salmonids of this island: *Salmincola californiensis* (Dana, 1852) from masu salmon, *Oncorhynchus masou* (Brevoort, 1856) (Nagasawa and Urawa 2002); *Salmincola carpionis* (Krøyer, 1837) from whitespotted char, *Salvelinus leucomaenis* (Pallas, 1814) [as *Salmin-*

cola falculata (C. B. Wilson, 1908) (Yamaguti 1939), see Nagasawa *et al.* (1995) for copepod and host identification; Nagasawa and Urawa 2002: appendix, footnote]; and *Salmincola stellata* Markewitsch, 1936 from Japanese huchen, *Parahucho perryi* (Brevoort, 1856) (Kabata 1986; Nagasawa and Urawa 1991; Nagasawa *et al.* 1994; Hiramatsu *et al.* 2001). As stated above, *S. edwardsii* is easily differentiated from these congeners by having a large ventral process on the endopod of the second antenna. Both *S. edwardsii* and *S. carpionis* parasitize chars (the genus *Salvelinus*), but their attachment sites are different from each other: *S. edwardsii* is found on the branchial cavity, gill filaments, and the inner wall of the operculum (this paper), whereas *S. carpionis* in the buccal cavity (Yamaguti 1939; see Nagasawa *et al.* 1995, 1997).

Discussion

Salmincola edwardsii has a holarctic distribution and occurs in the U.K. (Fryer 1981), Greenland (Due and Curtis 1995), Iceland (Kristmundsson and Richter 2009), Norway (*e.g.*, Stańkowska-Radziun and Radziun 1993; Amundsen *et al.* 1997; Paterson *et al.* 2019), Finland (Boxshall 2020), Sweden (Boxshall 2020), Germany (Boxshall 2020), Poland (Boxshall 2020), Russia (*e.g.*, Gussev 1962, 1987; Pugachev 1984; Shedko and Shedko 2002), Canada (*e.g.*, Kabata 1988; White *et al.* 2020), and the U.S.A. (*e.g.*, Hoffman 1999; Ruiz *et al.* 2017). In Japan, the species is known from the southern Kuril Islands (Shedko and Shedko 2002) and eastern Hokkaido Island (this paper). To date, two sites on Kunashir Island (the Petrova River and a nameless creek: localities 3 and 4 in Fig. 3 respectively; Marina B. Shedko, personal communication) have been recognized as the southernmost localities of *S. edwardsii* in Asia. However, the Shibetsu River (locality 8 in Fig. 3), from which the species was collected in this study, is more southerly located than the two sites and represents a new southernmost locality for *S. edwardsii* in Asia.

Southern Asian Dolly Varden are distributed in Sakhalin, Primorye, Hokkaido, and the Kuril Islands (Shedko *et al.* 2007; Osinov and Mugue 2008), and Hokkaido Island is located at the southernmost limit of their distribution (Morita *et al.* 2005; Yamamoto *et al.* 2014). According to Nakano *et al.* (1996: fig. 4), the Hokkaido populations of the species would be seriously affected by global climatic warming: they would begin reductions with an increase of 1°C in mean annual air temperature and become extinct on eastern Hokkaido Island with an increase of 3°C. This could happen to *S. edwardsii* as well.

In the present study, *S. edwardsii* was collected from the four rivers of eastern Hokkaido Island, but not from the rivers of the central and western regions of the island (Fig. 3). In the latter regions, southern Asian Dolly Varden are land-locked in the upper reaches of the rivers (Fausch *et al.* 1994; Takami *et al.* 1995). However, in the rivers of eastern Hokkaido Island, some individuals of the fish exhibit anadromy (Hikita 1962; Ishigaki 1967; Maekawa 1973; Komiyama *et al.* 1982; Morita *et al.* 2005; Kasugai *et al.* 2016; Umatani *et al.* 2018), and there are records of *S. edwardsii* from the same fish species caught in the coastal sea (Olya Inlet and Kuibyshev Bay) of Iturup Island (localities 1 and 2 in Fig. 3) (Shedko and Shedko 2002). The copepod is also known to survive on brook trout, *Salvelinus fontinalis* (Mitchill, 1814), in saline conditions in eastern Canada (Black *et al.* 1983). Based on these facts, *S. edwardsii* is a freshwater parasite but euryhaline and might have expanded its distribution range southward to and established its populations in the rivers of eastern Hokkaido Island together with anadromous southern Asian Dolly Varden.

Like on Hokkaido Island, *S. edwardsii* parasitizes southern Asian Dolly Varden on Kunashir and Iturup islands (Shedko and Shedko 2002). The copepod uses the same host in the Russian Far East, including Kamchatka (Shedko and Shedko 2002) and Sakhalin (Shedko *et al.* 2005; Sokolov *et al.* 2012). Nonetheless, whitespotted char have also been recorded as a host for the copepod on Paramushir Island and in Sakhalin and Primorye (Shedko and Shedko 2002; Shedko *et al.* 2005). On eastern Hokkaido Island, whitespotted char are found with southern Asian Dolly Varden in the same rivers with some segregations (Komiyama 1982; Ishigaki 1984; Fausch *et al.* 1994). It is thus desirable to examine whitespotted char from eastern Hokkaido Island for the infection of *S. edwardsii*.

Hokkaido Island is one of the regions whose parasite fauna of freshwater fishes has been well studied in Japan (Nagasawa *et al.* 1989; Nagasawa 1994; Nagasawa and Urawa 2017: table 1). However, the finding of *S. edwardsii* in this study indicates that previous works were insufficient and further research is necessary to clarify the parasite fauna of freshwater fishes of Hokkaido Island. The parasite fauna of wild southern Asian Dolly Varden from this island remains poorly known, being composed of nematodes—*Pseudocapillaria* (*Ichthyocapillaria*) *salvelini* (Polyanski, 1952) (as *Capillaria* sp.), *Salmonema ephemeridarum* (von Linstow, 1872) (as *Cystidicoloides ephemeridarum*), *Rhabdochona oncorhynchi* (Fujita, 1921), and *Rhabdochona* sp. (Seki 1975; Ito *et al.* 1987)—and a leech *Taimenobdella amurensis* (Epshtein, 1964) (Katahira *et al.* 2017). Another subspecies of Dolly Varden, Miyabe charr, *Salvelinus malma miyabei* Oshima, 1938, also occurs on Hokkaido Island and is endemic to Lake Shikaribetsu (Maekawa 1984; Dunham *et al.* 2008: 539). The known parasite fauna of Miyabe charr from the lake consists of trematodes—*Crepidostomum metoecus* (Braun, 1900) and *Crepidostomum* sp.—and nematodes—*P. salvelini* (as *Capillaria* sp.), *S. ephemeridarum* [as *Metabronema salvelini* (Fujita, 1920)], and *Cucullanus* sp.—(Seki 1975).

The attachment sites of *S. edwardsii* on host fish have been reported to be the fins, gills, and branchial (as gill) chamber (Kabata 1969), and Black (1982) observed that the species more frequently used the gills than the fins and opercula with an increase in length of brook trout in Ontario, Canada. Based on a recent observation using brook trout in North Carolina, U.S.A., the species infected mainly the gills but rarely the gill arches, buccal cavity, and fins (Ruiz *et* *al.* 2017). However, in Ennerdale Water, U.K., it was found only on the fins of Arctic char, *Salvelinus alpinus* (Linnaeus, 1758) (Fryer 1981). In the present study, *S. edwardsii* was most frequently found in the branchial chamber, but the specimens on the gills and the operculum were not common (Table 1). The results of these studies indicate that the major attachment site of the species may be different between host species and between locations, and further research is needed on the attachment sites of *S. edwardsii.*

The gill filaments of brook trout infected by *S. edwardsii* have been reported to manifest clubbing and crypting and to develop a bulbous swelling at an insertion site of the bulla (Ruiz *et al.* 2017). A similar bulbous swelling was observed in the infected gill filament of southern Asian Dolly Varden in this study (Fig. 2). The copepod is also known to reduce the resistance of brook trout to high water temperature (Vaughan and Coble 1975).

In North America, *S. edwardsii* has been studied for its taxonomy and morphology (Wilson 1915; Fasten 1920; Kabata 1969; Ruiz *et al.* 2017), attachment sites (Black 1982), reproduction (Fasten 1914), hatching, larval development and growth (Fasten 1920; Poulin *et al.* 1990a; Conley and Curtis 1993, 1994), larval ecology (Fasten 1913; Poulin *et al.* 1990b, 1991a, b), occurrence on wild hosts (Black *et al.* 1983; Bertrand *et al.* 2008; Mitro 2016; Mitro and Griffin 2018; White *et al.* 2020) and hatchery hosts (Hare and Frantsi 1974; Duston and Cusack 2002), impact on host (Vaughan and Coble 1975; Ruiz *et al.* 2017), and treatment (Duston and Cusack 2002). In contrast, much remains unstudied about the biology of *S. edwardsii* in East Asia: the species was examined only in taxonomic and faunal research in the Russian Far East (Markewitsch 1937, 1956; Gussev 1962, 1987; Pugachev 1984; Shedko and Shedko 2002; Shedko *et al.* 2005; Sokolov *et al.* 2012; Busarova *et al.* 2017) and Japan (Shedko and Shedko 2002; this paper). We need to study various aspects of the biology of *S. edwardsii* in East Asia.

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References

Amundsen, P. A., Kristoffersen, R., Knudsen, R., and Klemetsen, A. 1997. Infection of *Salmincola edwardsii* (Copepoda: Lernaeopodidae) in an age-structured population of Arctic charr—a long-term study. Journal of Fish Biology 51: 1033–1046.

Bertrand, M., Marcogliese, D. J., and Magnan, P. 2008. Trophic polymorphism in brook charr revealed by diet, parasites and morphometrics. Journal of Fish Biology 72: 555–572.

Black, G. A. 1982. Gills as an attachment site for *Salmincola edwardsii* (Copepoda: Lernaeopodidae). Journal of Parasitology 68: 1172–1173.

Black, G. A., Montgomery, W. L., and Whoriskey, F. G. 1983. Abundance and distribution of *Salmincola edwardsii* (Copepoda) on anadromous brook trout, *Salvelinus fontinalis*, [*sic*] (Mitchill) in the Moisie River system, Quebec. Journal of Fish Biology 22: 567–575.

Boxshall, G. 2020. Fauna Europaea: *Salmincola edwardsii* (Olsson, 1869). Available at https://fauna-eu.org/cdm_dataportal/taxon/b8394e29-8c8b-4f21-857e-612fb331885c (4 May 2020).

Busarova, O. Y., Markevich, G. N., Knudsen, R., and Esin, E. V. 2017. Trophic differentiation of the nosed charr *Salvelinus schmidti* Viktorovsky, 1978 in Lake Kronotskoe (Kamchatka). Russian Journal of Marine Biology 43: 57–64.

Bush, A. O., Lafferty, K. D., Lotz, J. M., and Shostak, A. W. 1997. Parasitology meets ecology on its own terms: Margolis *et al.* revised. Journal of Parasitology 83: 575–583.

Conley, D. C. and Curtis, M. A. 1993. Effects of temperature and photoperiod on the duration of hatching, swimming, and copepodid survival of the parasitic copepod *Salmincola edwardsii*. Canadian Journal of Zoology 71: 972–976.

Conley, D. C. and Curtis, M. A. 1994. Larval development of the parasitic copepod *Salmincola edwardsii* on brook trout (*Salvelinus fontinalis*). Canadian Journal of Zoology 72: 154–159.

Due, T. T. and Curtis, M. A. 1995. Parasites of freshwater resident and anadromous Arctic charr (*Salvelinus alpinus*) in Greenland. Journal of Fish Biology 46: 578–592.

Dunham, J., Baxter, C., Fausch, K., Fredenberg, W., Kitano, S., Koizumi, I., Morita, K., Nakamura, T., Rieman, B., Savvaitova, K., Stanford, J., Taylor, E., and Yamamoto, S. 2008. Evolution, ecology, and conservation of Dolly Varden, white-spotted char, and bull trout. Fisheries 33: 537–550.

Duston, J. and Cusack, R. R. 2002. Emamectin benzoate: an effective in-feed treatment against the gill parasite *Salmincola edwardsii* on brook trout. Aquaculture 207: 1–9.

Fasten, N. 1913. The behavior of a parasitic copepod, *Lernaeopoda edwardsii* Olsson. Journal of Animal Behavior 3: 36–60.

Fasten, N. 1914. Fertilization in the parasitic copepod, *Lernaeopoda edwardsii* Olsson. The Biological Bulletin 27: 115–126.

Fasten, N. 1920. Morphology and attached stages of first copepodid larva of *Salmincola edwardsii* (Olsson) Wilson. Publications —Puget Sound Biological Station 2: 153–181.

Fausch, K. D., Nakano, S., and Ishigaki, K. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. Oecologia 100: 1–12.

Froese, R. and Pauly, D. (Eds) 2019. FishBase. World Wide Web electronic publication, version (12/2019). Available at http://www.fishbase.org (4 May 2020).

Fryer, G. 1981. The copepod *Salmincola edwardsii* as a parasite of *Salvelinus alpinus* in Britain, and a consideration of the so-called relict fauna of Ennerdale Water. Journal of Zoology 193: 253–268.

Gussev, A. V. [transliterated as Gusev, A. V.] 1962. Phylum Arthropoda. Pp. 630–683. *In*: Bikhovskaya-Pavlovskaya, I. E. (Ed.) *Key to Parasites of Freshwater Fish of the U.S.S.R.* Academy of Sciences of the U.S.S.R., Zoological Institute, Leningrad. [Pp. 745–806. Translated from Russian, by the Israel Program for Scientific Translations, Jerusalem, 1964]

Gussev, A. V. 1987. Phylum Arthropoda. Pp. 378–524. *In*: Bauer, O. N.

(Ed.) *Key to Parasites of Freshwater Fishes of the U.S.S.R., Volume 3*. Nauka, Leningrad. [In Russian]

Hare, G. M. and Frantsi, C. 1974. Abundance and potential pathology of parasites infecting salmonids in Canadian Maritime hatcheries. Journal of the Fisheries Board of Canada 31: 1031–1036.

Hikita, T. 1962. On the sea-run char *Salvelinus malma* (Walbaum), taken from an eastern stream of Hokkaido Island. Scientific Reports of the Hokkaido Fish Hatchery 17: 59–63. [In Japanese]

Hiramatsu, N., Fukada, H., Kirtamura, M., Shimizu, M., Fuda, H., Kobayashi, K., and Hara, A. 2001. Serum immunoglobulin M (IgM) in Sakhalin taimen (*Hucho perryi*): purification, characterization, circulating levels, and specific IgM production by the parasite *Salmincola stellatus*. Suisanzoshoku 49: 347–355.

Hoffman, G. L. 1999. *Parasites of North American Freshwater Fishes. Second Edition*. Cornell University Press, Ithaca, New York, 539 pp.

Humes, A. G. and Gooding, R. U. 1964. A method for studying the external anatomy of copepods. Crustaceana 6: 238–240.

Ishigaki, K. 1967. On an anadromous specimen of the Dolly Varden char, *Salvelinus malma* (Walbaum), from the Ichani River, eastern Hokkaido. Bulletin of the Biogeographical Society of Japan 24: 37–43. [In Japanese]

Ishigaki, K. 1984. *Iwana no Nazo wo Ou* [*Exploring the Mystery of Chars*]. Iwanami Shoten, Tokyo, 216 pp. [In Japanese]

Ito, M., Nagasawa, K., Kamiya, H., and Ohbayashi, M. 1987. Morphological variation in teeth of *Rhabdochona oncorhynchi* (Fujita, 1921) from Japanese freshwater salmonids. Folia Parasitologica 34: 287–288, pls I–II.

Kabata, Z. 1969. Revision of the genus *Salmincola* Wilson, 1915 (Copepoda: Lernaeopodidae). Journal of the Fisheries Research Board of Canada 26: 2987–3041.

Kabata, Z. 1979. *Parasitic Copepoda of British Fishes*. The Ray Society, London, 468 pp.

Kabata, Z. 1986. Redescriptions of and comments on four little-known Lernaeopodidae (Copepoda). Canadian Journal of Zoology 64: 1852–1859.

Kabata, Z. 1988. Copepoda and Branchiura. Pp. 3–127. *In*: Margolis, L. and Kabata, Z. (Eds) *Guide to the Parasites of Fishes of Canada, Part II—Crustacea*. *Canadian Special Publication of Fisheries and Aquatic Sciences 101*. Department of Fisheries and Oceans, Ottawa.

Kasugai, K., Nagata, M., Takeuchi, K., Torao, M., Murakami, Y., Sasaki, Y., Miyakoshi, Y., and Irvine, J. R. 2016. Migratory timing of masu salmon and Dolly Varden smolts exiting the Uebetsu River near the Shiretoko World Heritage Site, Hokkaido, Japan, and potential angling effects. Ichthyological Research 63: 181–186.

Katahira, H., Yamazaki, C., Fukui, S., Ayer, C. G., and Koizumi, I. 2017. Spatial aggregation in small spring-fed tributaries leads to a potential metapopulation structure in a parasitic fish leech. Parasitology Open 3: e11.

Komiyama, E. 1982. [Freshwater fish fauna in the Shari River system]. Bulletin of the Shiretoko Museum 4: 29–36. [In Japanese]

Komiyama, E., Ohtaishi, N., and Maekawa, K. 1982. Occurrence of a sea-run type of the Dolly Varden in the Shiretoko Peninsula, Hokkaido. Japanese Journal of Ichthyology 29: 298–302.

Kristmundsson, Á. and Richter, S. H. 2009. Parasites of resident arctic charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta,* in two lakes in Iceland. Icelandic Agricultural Sciences 22: 5–18.

Maekawa, K. 1973. On a silvery smolt of the Dolly Varden, *Salvelinus malma*, collected from the Shiretoko Peninsula, Hokkaido. Japanese Journal of Ichthyology 20: 245–247. [In Japanese]

Maekawa, K. 1984. Life history patterns of the Miyabe charr in Shikaribetsu Lake, Japan. Pp. 233–250. *In*: Johnson, L. and Burns, B. L. (Eds) *Biology of the Arctic Charr, Proceedings of the International Symposium on Arctic Charr*. University of Manitoba Press, Winnipeg.

Markewitsch, A. P. 1937. *Copepoda Parasitica of the Fresh Waters of the USSR*. Akademia Nauk Ukrainskoi SSR, Kiev, 223 pp. [In Ukrainian]

Markewitsch, A. P. 1956. *Parasitic Copepods of Fishes of the USSR*. Akademia Nauk Ukrainskoi SSR, Kiev, 259 pp. [Translated from Russian, published by National Scientific Documentation Centre, New Delhi, 1976, 445 pp.]

Mitro, M. G. 2016. Brook trout, Brown trout, and ectoparasitic copepods *Salmincola edwardsii*: species interactions as a proximate cause of brook trout loss under changing environmental conditions. Transactions of the American Fisheries Society 145: 1223–1233.

Mitro, M. G. and Griffin, J. D. 2018. Distribution, prevalence, and maximum intensity of the ectoparasitic copepod *Salmincola* cf. *edwardsii* in brook trout in Wisconsin streams. Journal of Parasitology 104: 628–638.

Morita, K., Arai, T., Kishi, D., and Tsuboi, J. 2005. Small anadromous *Salvelinus malma* at the southern limits of its distribution. Journal of Fish Biology 66: 1187–1192.

Nagasawa, K. 1994. Parasitic Copepoda and Branchiura of freshwater fishes of Hokkaido. Scientific Reports of the Hokkaido Fish Hatchery 48: 83–85.

Nagasawa, K. and Urawa, S. 1991. New records of the parasitic copepod *Salmincola stellatus* from Sakhalin taimen (*Hucho perryi*) in Hokkaido, with a note on its attachment site. Scientific Reports of the Hokkaido Salmon Hatchery 45: 57–59.

Nagasawa, K. and Urawa, S. 2002. Infection of *Salmincola californiensis* (Copepoda: Lernaeopodidae) on juvenile masu salmon (*Oncorhynchus masou*) from a stream in Hokkaido. Bulletin of the National Salmon Resources Center 5: 7–12.

Nagasawa, K. and Urawa, S. 2017. First records of *Tracheliastes sachalinensis* (Copepoda: Lernaeopodidae), a fin parasite of cyprinids, from Japan. Species Diversity 22: 167–173.

Nagasawa, K., Awakura, T., and Urawa, S. 1989. A checklist and bibliography of parasites of freshwater fishes of Hokkaido. Scientific Reports of the Hokkaido Fish Hatchery 44: 1–49.

Nagasawa, K., Watanabe, J. R., Kimura, S., and Hara, A. 1994. Infection of *Salmincola stellatus* (Copepoda: Lernaeopodidae) on Sakhalin taimen *Hucho perryi* reared in Hokkaido. Bulletin of the Faculty of Fisheries, Hokkaido University 45: 109–112.

Nagasawa, K., Yamamoto, M., Sakurai, Y., and Kumagai, A. 1995. Rediscovery in Japan and host association of *Salmincola carpionis* (Copepoda: Lernaeopodidae), a parasite of wild and reared freshwater salmonids. Canadian Journal of Fisheries and Aquatic Sciences 52 (supplement 1): 178–185.

Nagasawa, K., Ikuta, K., and Kitamura, S. 1997. Distribution of *Salmincola carpionis* (Copepoda: Lernaeopodidae) in the buccal cavity of salmonids. Bulletin of the National Research Institute of Aquaculture 26: 35–39.

Nakano, S., Kitano, F., and Maekawa, K. 1996. Potential fragmentation and loss of thermal habitats for charrs in the Japanese archipelago due to climatic warming. Freshwater Biology 36: 711–722.

Osinov, A. G. and Mugue, N. S. 2008. Variation of the mitochondrial DNA control region in the populations of southern form of Dolly Varden (*Salvelinus malma krascheninnikovi*) from Sakhalin. Russian Journal of Genetics 44: 1446–1453.

Paterson, R. A., Knudsen, R., Blasco-Costa, I., Dunn, A. M., Hytterød, S., and Hansen, H. 2019. Determinants of parasite distribution in Arctic charr populations: catchment structure versus dispersal potential. Journal of Helminthology 93: 559–566.

Poulin, R., Conley, D. C., and Curtis, M. A. 1990a. Effects of temperature fluctuations and photoperiod on hatching in the parasitic copepod *Salmincola edwardsii*. Canadian Journal of Zoology 68:

1330–1332.

Poulin, R., Curtis, M. A., and Rau, M. E. 1990b. Responses of the fish ectoparasite *Salmincola edwardsii* (Copepoda) to stimulation, and their implication for host-finding. Parasitology 100: 417–421.

Poulin, R., Curtis, M. A., and Rau, M. E. 1991a. Size, behaviour, and acquisition of ectoparasitic copepods by brook trout, *Salvelinus fontinalis*. Oikos 61: 169–174.

Poulin, R., Rau, M. E., and Curtis, M. A. 1991b. Infection of brook trout fry, *Salvelinus fontinalis*, by ectoparasitic copepods: the role of host behaviour and initial parasite load. Animal Behaviour 41: 467–476.

Pugachev, O. N. 1984. *Parasites of Freshwater Fishes of North-East Asia*. USSR Academy of Sciences, Zoological Institute, Leningrad, 155 pp. [In Russian]

Ruiz, C. F., Rash, J. M., Besler, D. A., Roberts, J. R., Warren, M. B., Arias, C. R., and Bullard, S. A. 2017. Exotic "gill lice" species (Copepoda: Lernaeopodidae: *Salmincola* spp.) infect rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*) in the southeastern United States. Journal of Parasitology 103: 377–389.

Seki, N. 1975. [Helminth parasites of salmonids in Hokkaido, especially the plerocercoids of *Diphyllobothrium latum*]. Journal of the Hokkaido Veterinary Medical Association 19: 119–123. [In Japanese]

Shedko, M. B. and Shedko, S. V. [Shed'ko, M. B. and Shed'ko, S. V. in English abstract] 2002. Parasitic copepods of the genus *Salmincola* (Lernaeopodidae) from Far-Eastern chars *Salvelinus* (Salmonidae) with a description of the new species *S. markewitschi* sp. n. Zoologicheskii Zhurnal 81: 141–153. [In Russian with English abstract]

Shedko, M. B., Shedko, S. V., and Vinogradov, S. A. 2005. Fauna of the freshwater parasitic copepods of the family Lernaeopodidae (Crustacea: Copepoda) of fishes from Sakhalin Island. Pp. 52–63. *In*: Bogatov, V. V., Barkalov, V. Yu., Lelef, A. S., Makarchenko, E. A., and Storozhenko, S. Yu. (Eds) *Flora and Fauna of Sakhalin Island (Materials of International Sakhalin Island Project)*. Dalnauka, Vladivostok. [In Russian]

Shedko, S. V., Ginatulina, L. K., Miroshnichenko, I. L., and Nemkova, G. A. 2007. Phylogeography of mitochondrial DNA in south Asian dolly varden char *Salvelinus curilus* Pallas, 1814 (Salmoniformes, Salmonidae): mediated gene introgression? Russian Journal of Genetics 43: 165–176.

Sokolov, S. G., Shedko, M. B., Protasov, E. N., and Frolov, E. V. 2012. Parasites of the inland water fishes of Sakhalin Island. Pp. 179–216. *In*: Bogatov, V. V., Barkalov, V. Y., Lelef, A. S., Makarchenko, E. A., and Storozhenko, S. Y. (Eds) *Flora and Fauna of North-West Pacific Islands (Materials of International Kuril Island and International Sakhalin Island Projects)*. Dalnauka, Vladivostok. [In Russian]

Stańkowska-Radziun, M. and Radziun, K. 1993. Observations on the development of *Salmincola edwardsii* (Olsson, 1869) parasitizing the Arctic charr (*Salvelinus alpinus* (L.)) in the Hornsund region (Vest Spitsbergen). Acta Ichthyologica et Piscatoria 23 (Supplement): 107–114.

Takami, T., Araya, K., Sakamoto, H., and Tanaka, T. 1995. [Distribution of southern Asian Dolly Varden in Hokkaido]. Uo to Mizu 32: i–iii, 5–10. [In Japanese]

Umatani, Y., Arai, T., and Maekawa, K. 2018. Flexible seaward migration of Dolly Varden *Salvelinus malma* in the Shiretoko Peninsula, Hokkaido, Japan. Ichthyological Research 65: 202–209.

Vaughan, G. E. and Coble, D. W. 1975. Sublethal effects of three ectoparasites on fish. Journal of Fish Biology 7: 283–294.

White, C. F., Gray, M. A., Kidd, K. A., Duffy, M. S., Lento, J., and Monk, W. A. 2020. Prevalence and intensity of *Salmincola edwardsii* in brook trout in northwest New Brunswick, Canada. Journal of Aquatic Animal Health 32: 11–20.

Wilson, C. B. 1915. North American parasitic copepods belonging to the Lernaeopodidae, with a revision of the entire family. Proceedings of the United States National Museum 47: 565–729, pls 25–56.

WoRMS Editorial Board. 2020. *Salvelinus malma krascheninnikova* Taranetz, 1933. Available at: http://www.marinespecies.org/aphia.php?p= taxdetails&id=293727 (4 May 2020).

Yamaguti, S. 1939. Parasitic copepods from fishes of Japan. Part 6. Lernaeopodidae, I. Volumen Jubliare pro Professore Sadao Yoshida 2: 529–578, pls 34–58.

Yamamoto, S., Maekawa, K., Morita, K., Crane, P. A., and Oleinik, A. G. 2014. Phylogeography of the salmonid fish, Dolly Varden *Salvelinus malma*: multiple glacial refugia in the North Pacific Rim. Zoological Science 31: 660–670.