Highly threatened status for the relict populations of ectoparasitic copepod *Salmincola californiensis* in Japan

Ryota Hasegawa[1, 2] (ORCID: https://orcid.org/0000-0002-3563-7031)

Yohsuke Uemura[1] (ORCID: https://orcid.org/0000-0002-7703-9857)

Yasunori Yamashita[3, 4] (ORCID: https://orcid.org/0009-0001-8475-3733)

Makoto Inoshita[3]

Itsuro Koizumi[1,5] (ORCID: https://orcid.org/0000-0001-8934-8561)

Affiliations:

[1]Graduate School of Environmental Science, Hokkaido University, N10W5 Sapporo, Hokkaido 060-0810, Japan

[2]Department of Zoology, University of Otago, P.O. Box 56, Dunedin, 9054, New Zealand

[3]Gunma Prefectural Fisheries Experiment Station, 13, Shikishima, Maebashi, Gunma 371-0036, Japan

[4]Fisheries Technology Institute, Japan Fisheries Research and Education Agency, 2482-3, Chugushi, Nikko, Tochigi 321-1661, Japan

[5]Faculty of Environmental Earth Science, Hokkaido University, N10W5 Sapporo 060-0810, Hokkaido, Japan

Contact details for corresponding author:

Ryota Hasegawa, Department of Zoology, University of Otago, 340 Great King St, Dunedin, 9016, New Zealand

Email: ryotahase344922@gmail.com

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Abstract

Many species have been threatened over the past century because of anthropogenic disturbances. Parasites are among the most vulnerable groups because they rely on host organisms, many of which are now endangered. While many studies have argued and evaluated the risk of parasite's extinction, empirical evidence is still lacking, especially from aquatic ecosystems. Here, we show the highly threatened status of the relict populations of the ectoparasitic copepod *Salmincola californiensis* in Japan. *S. californiensis* attaches to the branchial cavities of freshwater salmonids of the genus *Oncorhynchus* spp., and only four local populations have been reported from separated regions of Japan, probably due to range contractions after glacial periods. Through intensive field surveys, we found no copepod infections in half of the populations despite high prevalence and intensity reported in the past literature, suggesting that local extinction has occurred within the last 50–60 years. Our citizen science approach identified that the upstream reaches of the Kiso River and the Naka River harbor the only sustained populations, though the former population may also have experienced population decline. Our results indicate that parasites can quickly decline over a large geographic scale, especially at range margins. When focal parasites are visible, citizen science would be an effective approach for identifying the distributional range of rare parasites and aiding their conservation.

1. Introduction

Parasites are ubiquitous in natural systems, compose a large amount of biomass, and play many pivotal roles in ecosystems (Hudson et al., 2006; Dobson et al., 2008; Lafferty et al., 2008; Kuris et al., 2008; Sato et al., 2012; Wood & Johnson, 2015). Despite their prevalence and ecological importance, they are highly vulnerable to environmental changes including host and habitat loss, and consequently face extinction threats (Koh et al., 2004; Strona, 2013; Carlson et al., 2020; Brian & Aldridge, 2022; Wood et al., 2023). In fact, several studies have estimated that many parasite species have gone extinct or will go extinct in the near future due to climate change, anthropogenic environmental changes, and host conservation strategies (Dobson et al., 2008; Carlson et al., 2017; Milotic et al., 2020; Brian, 2023; Wood et al., 2023). Therefore, the momentum for parasite conservation has been increasing recently (Windsor, 1995; Carlson et al., 2020; Lymbery & Smit, 2023).

Although studies have pointed out that parasites' extinction has already been occurred worldwide (Carlson et al., 2020; Lymbery & Smit, 2023), empirical evidence of parasites' extinction at both population and species levels is still limited (e.g. Black, 1983; Rózsa & Vas, 2015; Kwak, 2018; MacKenzie & Pert, 2018). Furthermore, most previous studies have focused on fleas and ticks that infect endangered mammals and birds, facing co-extinction risk (Durden & Keirans, 1996; Rózsa & Vas, 2015; Kwak,

68 2018; Carlson & Phillips, 2020). Other parasites, especially aquatic parasites have been
69 understudied, even though these parasites should face extinction risk because aquatic
70 ecosystems are highly vulnerable throughout the world (Dudgeon et al., 2006; Reid et
71 al., 2019). Additional case studies are required to identify the mechanisms and
72 processes leading to parasite extinction in the wild (Carlson et al., 2020).
73 Here, we report the population decline and possible local extinctions of the
74 freshwater parasitic copepod *Salmincola californiensis* throughout Japan. The copepods
75 have a simple direct life cycle and exhibit genus-level host specificity, mainly infecting
76 salmonids of the genus *Oncorhynchus* (Kabata, 1969). They are distributed along the
77 northern Pacific Ocean rim (Kabata, 1969) and have historically been known as
78 notorious “gill lice” or “gill maggots” that cause damage to host health (e.g. Gall et al.,
79 1972; Sutherland &Wittrock, 1985; Ruiz et al., 2017; Neal et al., 2021). Their
80 distribution records in Japan are highly limited, with only four populations have been
81 known (Hoshina & Suenaga, 1954; Hoshina & Nishimura, 1976; Nagasawa & Urawa,
82 2002; Nagasawa et al., 2018; Hasegawa et al., 2025). Japan is the southern margin of
83 their native distributional range, as well as that of the host (Nagasawa et al., 2018;
84 Nagasawa, 2020), and repeated range expansions and contractions of host salmonids
85 during glacial periods (Yamamoto et al., 2014, 2020, 2023) might have caused the
86 highly limited and fragmented local populations of the parasite (i.e. relict populations).

87 Recently, Nagasawa et al. (2018) re-examined the current infection status of the
88 copepods in a known population (Ôtaki River, Kiso River system, central Honshu), but
89 they could not find the copepods at several sites, suggesting that the population has
90 declined over the past 60 years. In this paper, we re-examine the current population
91 status of *S. californiensis* in most of the populations in Japan. Additionally, taking
92 advantage of vicinity of the parasitic copepods to fishermen (Mitro, 2016; Hasegawa &
93 Koizumi, 2023), we also examined distributional data collected from citizens (mainly
94 fishermen) to infer the current distributional range of the copepods in Japan. Citizen
95 science approach, defined as public engagement in research projects (e.g. Bonney et al.,
96 2014), could be a powerful method for identifying parasite distributions. However, the
97 application of this approach in parasitology remains limited (e.g. Elmer et al., 2019;
98 Doherty et al., 2021; Poulin et al., 2021). Following intensive and extensive surveys
99 employing several methods, we found that half of the known populations have
100 potentially been extirpated, with only two populations remaining in Japan.
101
102 ## 2. Methods
103 ### 2.1. Target parasite and host species
104 The freshwater parasitic copepods *Salmincola californiensis* have simple direct life
105 cycle utilizing only a host individual during their life-time (Kabata, 1969; Kabata &
106 Cousens, 1973). Their life cycle was composed of seven separated stages; nauplius,

107 free-living copepodid, 1–4 chalimus, mature adult (Kabata & Cousens, 1973
108 Stankowska-Radziun & Radziun, 1993; Murphy et al., 2020a). This species has been
109 recorded from Pacific salmons (i.e. fishes of the genus *Oncorhynchus*) such as chinook
110 salmon *O. tshawytscha*, rainbow trout *O. mykiss* and masu salmon *O. masou masou*
111 (Kabata, 1969; Nagasawa & Urawa, 2002; Monzyk et al., 2015, Vigil et al., 2016;
112 Shedko et al., 2023). Their range extends across freshwater systems along the northern
113 Pacific Rim, coinciding the distribution of Pacific salmons (Kabata, 1969). In North
114 America, their native range extends from Alaska (Moles, 2007) to California (Wilson,
115 1915; Kabata, 1969). In Asia and Russia, *S. californiensis* has been recorded in
116 Kamchatka (Shedko et al., 2023), Sakhalin (Shedko et al., 2005), Primorye (Shedko et
117 al., 2023), Hokkaido, and Honshu Island, Japan (Hoshina & Suenaga, 1954; Nagasawa
118 & Urawa, 2002, see specific river systems below). Recently, however, the species has
119 successfully invaded several watersheds both within and outside of its native
120 distribution (e.g. Kamerath et al., 2009; Ruiz et al., 2017; Mullin & Reyda, 2020). These
121 invasions were primarily driven by fish stocking (e.g. Ruiz et al., 2017; Mullin &
122 Reyda, 2020).
123 In Japan, the only known wild host species are masu salmon and red-spotted
124 masu salmon *O. m. ishikawae*, a subspecies of masu salmon in the western Japanese
125 region (Hosoya, 2013). Both host species have two types of life history: residents and

126 migrants (Kato, 1991; Kiso, 1995; Tamate & Maekawa, 2000). After spending juvenile
127 stages in rivers for 1–2 years, some fish mature as migrants, descending to the sea or
128 lakes during spring to fall (Tamate & Maekawa, 2000), whereas others mature as
129 residents and remain rivers (Kiso, 1995).

130 The following four river systems were designated as habitats of the copepod:
131 the Bekanbeushi River system in eastern Hokkaido (Nagasawa & Urawa, 2002; Figure
132 1), the Agatsuma River in the Tone River system in Gunma Prefecture, central Honshu
133 (Hoshina & Nishimura, 1976; Figure 1), the upstream reaches of the Kiso River system
134 in Nagano Prefecture, central Honshu (Hoshina & Suenaga, 1954; Nagasawa et al.,
135 2018; Figure 1), and the upstream reaches of the Naka River system in Tochigi
136 Prefecture, central Honshu (Hasegawa et al., 2025; Figure 1).
137

138 **2.1. Intensive and extensive surveys in Hokkaido**

139 To examine the current population status of *S. californiensis*, we first
140 conducted intensive field surveys in the Bekanbeushi River system (Figure 1b), the only
141 known population of *S. californiensis* in Hokkaido (Nagasawa & Urawa, 2002), and
142 then conducted extensive field surveys in 17 other river systems in Hokkaido to confirm
143 the occurrence of the species (Supplementary material 1).

144 The Bekanbeushi River system (Figure 1b), located in eastern Hokkaido,
145 flows within the Bekanbeushi Wetlands, which are registered under the Ramsar

146 Convention. This river system largely maintains pristine conditions. The upstream
147 reaches are almost intact, but the downstream reaches flow through farmlands (Miura et
148 al., 2023). A few dams for erosion control exist only at the most upstream reaches, but
149 no other significant artificial structures have been installed (Ishigaki, 1975), and no
150 masu salmon stocking has ever been conducted in the river system (Salmon Research
151 Department, Fisheries Resource Institute, Japan Fisheries Research and Education
152 Agency, 2024).

153 Nagasawa & Urawa (2002) reported high infection levels of *S. californiensis*
154 on masu salmon in the river system during 1982–1983, with a prevalence of 94.7% (18
155 of 19 fish were infected) and a mean intensity of 10.3 (range: 1–26) across two studied
156 tributaries (i.e. Toraibetsu and Chiraikaribetsu Streams; Figures 1b, 2). They also
157 examined white-spotted charr *Salvelinus leucomaenis* and Sakhalin taimen *Parahucho*
158 *perryi*, but the authors did not find *S. californiensis* on these salmonid species
159 (Nagasawa & Urawa, 2002).

160 In the Bekanbeushi River system, we conducted field surveys several times at
161 9 sites, including the two previously investigated sites (i.e. Toraibetsu and
162 Chiraikaribetsu Streams; Nagasawa & Urawa, 2002), from 2020 to 2022 (Figure 1b;
163 Table 1). We captured fish by angling and 2-pass electrofishing (Model 12B; Smith-
164 Root, Inc., Vancouver, Washington, USA). At each site, we aimed to capture as many

165 fish (i.e. masu salmon) as possible for the reliable calculation of infection levels. All
166 captured masu salmon were anesthetized using the anesthetic agent FA100 (Bussan
167 Animal Health Co., Ltd., Osaka, Japan), and their body length (fork length: FL) was
168 measured to the nearest 1 mm. We carefully examined fish body surfaces, with special
169 attention to branchial cavities, fins, and fin bases for the presence of copepods because
170 these areas are the main attachment sites of the copepod species (Kabata, 1969;
171 Nagasawa & Urawa, 2002; Ruiz et al., 2017). Subsamples ($N = 36$) were brought back
172 to the laboratory for the careful examinations of their infection status under the
173 microscope, which avoid the possibility of overlooking copepods, especially small
174 chalimus stages (e.g. Kabata & Cousens, 1973).

175 We also carried out field surveys in 17 river systems in eastern and southern
176 Hokkaido from 2019 to 2023 (Supplementary material 1). We captured masu salmon
177 and rainbow trout by electrofishing and angling, and examined for copepod infections in
178 the same manner as described above.

179

180 **2.2. Field survey in Gunma Prefecture**

181 We additionally examined the current population status of *S. californiensis* in
182 the Agatsuma River, within the Tone River system in Gunma Prefecture, central Japan
183 (Figure 1c; Table 1). The copepod naturally occurred on masu salmon in the upstream

184 area of the Agatsuma River (Hoshina & Nishimura, 1976) and was abundant in some of
185 the streams (Kiyoshi Tobe, Tsumagoi Trout and Charr Culture Production Association;
186 Kin-ei Takizawa, Agatsuma Inland Fisheries Cooperative Association, personal
187 communications). Outbreaks of the copepod occurred at the Masuya Trout Culture Farm
188 (Figure 1c) from 1970 to 1972 when infected masu salmon were introduced from the
189 Agatsuma River (Hoshina & Nishimura, 1976). No copepod infections have been
190 observed in this trout farm (Kiyoshi Tobe, personal communication), or the upper
191 Agatsuma River recently (Kin-ei Takizawa, personal communication).
192 During October to November 2023, we sampled masu salmon by
193 electrofishing (Model 20B; Smith-Root, Inc.) at three sites where *S. californiensis* had
194 been observed until the 1970s (Kiyoshi Tobe and Kin-ei Takizawa, personal
195 communications). We aimed to capture at least 30 fish at each site. Fish were killed by
196 an overdose of FA100, and then transported to the laboratory on ice. In the laboratory,
197 we measured the fish FL and carefully examined fish body surfaces as described above.
198
199 **2.3. Citizen science approach for inferring current distribution of *Salmincola* spp.**
200 **in Japan**
201 To infer the current distribution of the genus *Salmincola* throughout Japan,
202 we gathered distributional records from citizens, mainly from fishermen. In May 2020,
203 we posted information about *Salmincola* spp. on social networking services (SNS, e.g.

X, originally known as Twitter) and web communities (e.g. Japanese fish image database: https://zukan.com/fish/ and our laboratory HP: https://noah.ees.hokudai.ac.jp/envmi/koizumilab/) to encourage fishermen to share information about the copepods. When receiving information, we mainly asked citizens to provide us with (1) when and where fish parasitized with *Salmincola* copepods were captured, (2) the attachment sites of the copepods, and (3) photos of fish and parasites whenever possible. We received information via X/Twitter, email, telephone, and other methods. Five species of the genus *Salmincola* have been reported in Japan (Hasegawa et al., 2022b; Nagasawa & Urawa, 2022), and all these species exhibit strong host specificity and preferred attachment sites (Hasegawa et al., 2022b; Nagasawa & Urawa, 2022). Except for *S. californiensis*, there are no congeneric copepod species attaching to the branchial cavities and fins of the genus *Oncorhynchus* in Japan (Hasegawa et al., 2022b). Therefore, we could confidently identify the copepod species from the received information, especially when the information contained photos and samples. We analyzed datasets collected from May 2020 to May 2024 (i.e. four years).

During this process, we also received several samples of red-spotted masu salmon infected with parasitic copepods from fishermen. These fish samples were examined in the laboratory as described above. We recovered copepod samples from fish bodies, and then stored them in 70% ethanol. We calculated infection indices

223 defined by Bush et al. (1997) as following; prevalence (percentage of fish individuals
224 infected), intensity (the number of individual parasites in a single infected fish),
225 abundance (the number of individual parasites in a single examined fish), mean
226 intensity (the average number of parasites among the infected fish), and mean
227 abundance (the average number of parasites among the all examined fish).
228

229 # 3. Results

230 ## 3.1. No presence records in Hokkaido and Gunma Prefecture

231 In total, 164 and 123 resident masu salmon were captured from the Bekanbeushi River
232 in Hokkaido and the Agatsuma River in central Honshu region, respectively (Table 1).
233 No *Salmincola californiensis* were found in these two river systems (Figure 2). We also
234 examined 2,913 masu salmon and 452 rainbow trout collected in 17 river systems in
235 Hokkaido but again no infections were found in these study sites either (Supplementary
236 material 1).
237

238 ## 3.2. Citizen science approach revealed only two sustained populations in Japan

239 In total, 173 data points were collected from citizens from May 2020 to May 2024
240 (Figure 3; Table 2). Of these, only 13 data points (7.5%) were identified as *S.*
241 *californiensis*, whereas 153 (88.4%), 6 (3.5%), 1 (0.6%) datapoints were potentially
242 identified as *S. markewitschi*, *S. stellata*, and *S. edwardsii*, respectively (Figure 3; Table

243 2). Data points for *S. californiensis* were exclusively collected from the gill cavities or
244 fins of either masu salmon or red-spotted masu salmon (Table 3). Data points for *S.*
245 *markewitschi* were mostly collected from the buccal cavities of white-spotted charr
246 (93.5%, $N = 143$), but were also reported from the buccal cavities of Miyabe charr
247 (0.7%, $N = 1$), brook trout (1.3%, $N = 2$), hybrids of white-spotted charr and rainbow
248 trout (2.6%, $N = 4$), hybrids of white-spotted charr and masu salmon (0.7%, $N = 1$), and
249 unidentified fish (0.7%, $N = 1$). Data points for *S. stellata* and *S. edwardsii* were
250 exclusively reported from the buccal cavities of Sakhalin taimen and the gill cavities of
251 southern Asian Dolly Varden, respectively.
252 The most frequently reported species, *S. markewitschi*, was found not only
253 in fields (129 data points, 84.3%), but also in aquariums, fish farms, and fishing ponds
254 (24 data points, 15.7%; Figure 3; Table 2). In contrast, *S. californiensis* was exclusively
255 reported from fields (Figure 3; Table 2). Of these data points potentially indicating *S.*
256 *californiensis*, two did not contain photos or samples, whereas the other 11 contained
257 reliable photos or samples (Tables 2, 3), allowing us to identify the copepods as *S.*
258 *californiensis* based on host species and attachment sites. These data points were
259 reported from the Ôtaki River, a tributary of the Kiso River system in Nagano
260 Prefecture ($N = 10$, Table 3), and from the upstream reaches of the Naka River in
261 Tochigi Prefecture ($N = 1$, Table 3; Hasegawa et al., 2025).

In total, we got 12 resident (FL, 146–196 mm, mean, 172.2 mm) and one lake-migrant (FL, 411 mm) red-spotted masu salmon parasitized with *S. californiensis*, and all these fish were captured by citizens at the Ôtaki River, Kiso River system (Figure 1d). The mean intensity of resident was 4.2 (range 1–9) and intensity of a migrant form was 93. In resident fish, the main attachment sites of the copepods were branchial cavities (N = 36, 72%), including the inner surface of operculum (N = 18, 36%) and the inner wall of branchial cavities (N = 18, 36%). Other copepods attached to pectoral fins and fin bases (N = 14, 28%). In the lake-migrant form, most copepod individuals were recovered from the branchial cavity (N = 80, 86.0%) including gill filaments and gill arches (N = 60, 64.5%), inner wall of branchial cavity (N = 12, 12.9%) and inner surface of operculum (N = 8, 8.6%). Others found from fish surfaces including pectoral and pelvic fins and fin bases (N = 13, 13.9%), and one copepod found from the buccal cavity floor (N = 1, 1.1%).

4. Discussion

Even though many studies have pointed out that parasite extinction has occurred worldwide (Koh et al., 2004; Dobson et al., 2008; Strona, 2013; Carlson et al., 2020; Wood et al., 2023), evidence for local extinction of parasites in the wild has been limited (Black, 1983; Rózsa & Vas, 2015; Kwak, 2018; MacKenzie & Pert, 2018; Brian, 2023), especially in aquatic ecosystems. Here, we report the highly threatened

282 status of the parasitic copepod *S. californiensis* in Japan. Our intensive field surveys
283 found that no infections occurred in two known populations (i.e. Bekanbeushi and
284 Agatsuma Rivers) and 17 river systems in Hokkaido. Based on our citizen science data
285 widely collected from the host salmonid distributional range in Japan, only two river
286 systems may harbor sustained populations (i.e. Kiso and Naka River systems), whereas
287 congeneric copepod species *S. markewitschi*, mainly infecting white-spotted charr, was
288 frequently and widely reported from both fields and artificial facilities, such as fish
289 farms. Masu salmon and red-spotted masu salmon are widely distributed throughout in
290 Japan (Hosoya, 2013). They are popular fishing targets amongst the Japanese fishermen,
291 as well as white-spotted charr (Nakamura, 2020) and reared in many fish farms,
292 fisheries stations and fishing ponds. Further, since *S. californiensis* mainly attaches to
293 host gills and fins, fishermen and fisheries managers could easily notice the parasite, as
294 indicated by other gill-and fin-attaching congeneric copepods (Mitro & Griffin, 2018),
295 and hence overlooking this parasite species should be unlikely. Therefore, the
296 distributional range of *S. californiensis* in Japan is originally highly limited and the
297 likelihood that other local populations existing in Japan is very low. Nonetheless, our
298 study suggest that parasite abundance has dramatically declined in at least two known
299 populations within the past 60 years (i.e. Bekanbeushi and Agatsuma River systems).

The most probable mechanism of population decline in the Bekanbeushi River system is the decline of definitive host. In Hokkaido, masu salmon dramatically declined around the 1970s to 1980s (Tamate, 2008; Tamate & Hayajiri, 2008) and low abundance continued until around the 2000s (Hasegawa et al., 2022), mainly due to dam constructions and forest conversion (Tamate, 2008; Tamate & Hayajiri, 2008; Ishiyama et al., 2021). We could infer the decline in host populations in the river system from previous fish faunal studies. Ishigaki (1975) reported that masu salmon were abundant and widely distributed within the river system in 1974 and 1975. Later, several studies re-examined fish fauna in the same river system (in 1997 by Kuwahara, 1997; in 2000 by Shimoda et al., 2003; in 2003–2005 by Kume & Torii, 2009). However, these studies rarely captured masu salmon, even at sites where previous studies and we sampled masu salmon. These host declines were also inferred by studying other parasites in the same river system, such as freshwater pearl mussel *Margaritifera laevis* (Miura et al., 2024), which infects to masu salmon as temporary hosts (Kondo, 2008; Miura et al., 2024). The freshwater mussel's population in this river system were mostly composed of 40 to 50 year-old individuals (Miura et al., 2024). No recently recruited individuals were found (Miura et al., 2024), suggesting that reproduction stopped during around 1980 due to the loss of host masu salmon (Miura et al., 2024). Since *S. californiensis* is specific to the genus *Oncorhynchus* and there were no potential host except for masu

319 salmon (Ishigaki, 1975; Kuwahara, 1997; Shimoda et al., 2003; Kume & Torii, 2009),
320 the population would have rapidly decreased due to the temporal host decline within 50
321 years. The decline of hosts had also been indicated as a main driver for the extinction of
322 other parasites (e.g. Black, 1983; Rózsa & Vas, 2015; Kwak, 2018; MacKenzie & Pert,
323 2018).
324 Habitat fragmentation by damming might have directly and indirectly caused
325 local extinction in the Agatsuma River. In some studied tributaries, many dams for
326 erosion control were constructed. Such habitat fragmentation directly affects parasite
327 populations (Resasco et al., 2019; Hasegawa & Koizumi, 2021; Hasegawa et al.,
328 2022a). Once erosion control dams are constructed, infected hosts and parasites in the
329 downstream could not access to above-dam sites (Morita et al., 2000; Hasegawa &
330 Koizumi, 2021). In addition, since free-swimming copepodids have low swimming
331 ability (Monzyk et al., 2015; Hasegawa & Koizumi, 2021), they would be washed away
332 from above-dam areas by stream drift (Hasegawa & Koizumi, 2021). Under these
333 processes, parasite populations above dams could easily go extinct. Habitat
334 fragmentation also negatively affect host salmonid populations (Morita & Yamamoto,
335 2002; Pépino et al., 2012; Nathan et al., 2018). Many studies have reported that local
336 population extinction of salmonids in fragmented habitats due to declines in population
337 size and genetic diversity (Morita & Yamamoto, 2002; Pépino et al., 2012; Nathan et

338 al., 2018). These local extinctions of host populations might have induced subsequent
339 local extinctions of parasites.
340 Another potential mechanism of the parasite loss in the Agatsuma River is
341 eradication control. After the outbreaks of *S. californiensis* (Hoshina & Nishimura,
342 1976), it was said that a trout farm distributed massive amounts of salt in the upstream
343 reaches to control the parasite (Kiyoshi Tobe, personal communication). Because *S.*
344 *californiensis* could survive in salt water (Bailey et al., 1989; Nagasawa, 2023), it is
345 questionable if that control method was effective in reducing parasite population.
346 However, we could not deny the possibility of loss of salinity tolerance in Japanese
347 populations due to long-term isolation from the sea. Further studies are required if
348 ecological characteristics of this copepod species differ among regions.
349 Our citizen science data suggested that only two river systems (Ôtaki River
350 and the upstream reach of the Naka River) harbor the remaining population of *S.*
351 *californiensis* in Japan. Since most of the data points of *S. californiensis* were reported
352 from Ôtaki River, this river system may harbor a relatively large population. However,
353 given the distributional records reported in previous studies, this population might also
354 have shrunk within about 60 years (Figures 1d, 2). Hoshina & Suenaga (1954) indicated
355 that *S. californiensis* was widely distributed in the Ôtaki River in 1952 (Figure 1d). On
356 the other hand, Nagasawa et al. (2018) found the copepod only in the Kami-Kurosawa

357 Stream in 2017, and they did not find any copepods in other three sites located in the
358 middle and downstream areas of the tributary (main stem of Ôtaki River, Nishino River,
359 Nakazawa River; Figures 1d, 2, Nagasawa et al., 2018). These results suggest that the
360 current distributional range of the parasites in this river system is restricted to the
361 uppermost reaches of each stream. In fact, citizen (mainly fishermen) reported *S.*
362 *californiensis* only from the upstream reaches in each stream (Figure 1d; Table 3).
363 Because the life cycle of *Salmincola* spp. is strongly affected by water temperature
364 (Yamamoto & Nagasawa, 2001; Murphy et al., 2020a; Neal et al., 2021), increased
365 water temperature by climate change might have caused population decline (cf. Carlson
366 et al., 2017). Consequently, the copepods would be currently restricted to upstream
367 reaches where water temperature is still cold. Given that *S. californiensis* has only been
368 recorded from high elevation areas (both Ôtaki River and Agatsuma River are located at
369 elevations over 1,000 m, and the upstream of Naka River is located at elevations over
370 600 m and characterized as cool temperature throughout the year) or northern area
371 (Bekanbeushi River, Hokkaido), it is highly possible that the Japanese populations are
372 vulnerable to high water temperatures.
373 Even though we discussed possible copepod's population declines in the
374 Ôtaki River, this population could still persistent. The upstream reaches of the Ôtaki
375 River have limited access by fishermen, and fish exploitation restricted (Kitano et al.,

2005). Moreover, no fish stocking has occurred (Kitano et al., 2005), and the numbers of dams for erosion control are limited. These intact natural environments may allow host fish and copepods to sustain their populations. Another potential key for the persistence of the parasite population is the migrant form of host red-spotted masu salmon. In this tributary, lake-run migrants occur that may descend to the Miura Reservoir and the Ontake Lake (Figure 1d). Since migrant salmon apparently had higher infection levels (intensity = 93), possibly due to their larger body size and high infection levels in low-flow reservoir (e.g. Monzyk et al., 2015; Hasegawa & Koizumi, 2021), they could be a source of infections. In other words, massive supply of infectious copepodids by their migration from downstream to upstream may largely contribute to population persistence. Hasegawa & Koizumi (2021) also hypothesize that heavy infections of *Salmincola* sp. (later identified as *S. markewitschi*; Hasegawa et al., 2022b; Shedko et al., 2023) on migrant white-spotted charr played pivotal roles in population persistence of the copepod.

Because only one data point was collected in the upstream reaches of the Naka River system, the current population status in this river system is uncertain. However, our previous study suggests that both prevalence and intensity were relatively high in this area (Hasegawa et al., 2025), indicating that the parasite population status is relatively healthy. The Naka River flows through Nikko National Park (Miyata et al.,

2022), and this region is characterized as cool temperature throughout the year (mean annual temperature 9.3℃; Japan Meteorological Agency, 2024). These persisted natural environments may contribute to the high density of masu salmon population and their parasites. Further population censuses are required in this region.

Although two data points were collected from unreported study sites through a citizen science approach (Table 3), these data points did not contain any photos or parasite samples, and no specific information was available. Hence, we could not exclude the possibility that people misjudged this finding and confidential identifications were impossible. Additional fieldwork is required to identify whether these study sites were real localities of this copepod species. Nonetheless, these results suggest that a citizen science approach is effective in identifying novel distributional ranges of rare parasites.

Given their highly fragmented populations mostly at high-altitudinal areas, *S. californiensis* are apparently glacial relict populations (Hasegawa et al., 2025). Like their host salmonids, Japan represents the southernmost margin of the distributional range of *Salmincola* spp. (Nagasawa et al., 2018; Nagasawa, 2020). *Salmincola* spp. have extended their distribution with their host salmonids (Nagasawa, 2020). Their host salmonids are also regarded as relict species that experienced repeated range expansions and contractions during the glacial period (Yamamoto et al., 2014, 2020, 2023).

414 Therefore, the copepod species also experienced the similar population processes during
415 the glacial periods with their hosts, consequently creating their current fragmented
416 distributions. In general, glacial relict populations are vulnerable to environmental
417 changes, particularly global warming (Booher & Walters, 2022; Audzijonyte et al.,
418 2023). Indeed, as discussed above, our distributional data suggest that increased water
419 temperature driven by climate change may be the possible reason of population
420 shrinkages in Japanese populations. The Ôtaki River system is a particularly important
421 site because it is the type locality of *S. yamame*, a junior synonym of *S. californiensis*
422 (Hoshina & Suenaga, 1954; Nagasawa et al., 2018), which has yet to be genetically
423 evaluated but is crucial for future taxonomic research within the genus *Salmincola*. This
424 locality represents the southernmost margin of their distributional range in East Asia
425 (Hoshina & Suenaga, 1954; Nagasawa et al., 2018). Therefore, urgent conservation
426 actions are necessary for this parasite species in Japan.
427 *S. californiensis* has been rapidly increasing and expanding its distributional
428 range within and outside of its native range (Monzyk et al., 2015; Ruiz et al., 2017;
429 Mullin & Reyda, 2020; Lepak et al., 2022). Its invasions and epizootics are mostly
430 accompanied by fish stocking (Ruiz et al., 2017; Mullin & Reyda, 2020). Despite the
431 potential local extinction in Japan, this parasite can still successfully invade or increase
432 in some regions due to several factors. In North America, reservoirs are the main sites

where epizootics occur (Hargis et al., 2014; Lepak et al., 2022), and such novel environmental changes can significantly contribute to its population maintenance, as low-flow environments facilitate copepodid transmission (Monzyk et al., 2015; Murphy et al., 2020b). High host abundance in reservoirs or lakes also leads to elevated infection levels, as some fish, especially chinook salmon, stay longer in reservoirs (Monzyk et al., 2015) and continuous fish stocking also occurs in these environments. Moreover, prolonged drought conditions, which force fish into confined spaces, further enhance copepodid transmission and contribute to high infection levels in certain areas (Hargis et al., 2014). In contrast, such extensive environmental changes have rarely occurred in Japan, limiting the maintenance of copepod populations (but see discussions on reservoir construction in the Ôtaki River).

While *S. californiensis* appear to expand its distribution and increase in North America by invasion, native populations may also be declining because they are believed to be glacial relict. Indeed, Murphy et al. (2020b) showed that the infection levels and distribution of this species were historically highly limited, as indicated by museum ichthyology collections from around 1950s, while infections increased rapidly in the same watersheds following reservoir constructions (Monzyk et al., 2015). In other words, their infection levels are naturally maintained at low levels in the wild, as suggested by other *Salmincola* spp. (Amundsen et al., 1997), and epizootics generally

452 do not occur unless triggered by specific environmental changes (e.g. reservoir
453 constructions or drought). Native populations of fishes of the genus *Oncorhynchus* are
454 declining in many areas due to habitat fragmentation and climate change (e.g.
455 Ruckelshaus et al., 2002; Ward et al., 2015). Therefore, population declines of the
456 copepod species may occur through similar mechanisms in both North America and
457 Japan. Researchers should evaluate the original native ranges of this species through
458 genetic analysis.

459 Finally, our study provides important insights into parasite conservation;
460 problematic parasites in some regions can be targets for conservation in other regions.
461 Recently in North America, populations of *S. californiensis* has been rapidly increasing,
462 and its distribution range has also been expanding, possibly due to the reservoir
463 construction and fish introduction (Monzyk et al., 2015; Ruiz et al., 2017; Lepak et al.,
464 2022). Since their infections cause harmful impacts on native host fishes (Gall et al.,
465 1972; Kabata & Cousens, 1977; Sutherland & Wittrock, 1985; Neal et al., 2021), they
466 are the targets for elimination (Roberts et al., 2004; Murphy et al., 2022). On the
467 contrary, we showed that the same copepod species are highly threatened in Japan.
468 Similar scenarios may also arise in other host-parasite systems. For instance, freshwater
469 mussels of the genus *Sinanodonta* are endangered in some native ranges (Liu et al.,
470 2014; Kuwahara et al., 2017), but recently they invaded other regions (Kondakov et al.,

2020; Douda et al., 2024) and pose major threats to native biodiversity (Douda et al., 2017, 2024). Their parasitic larvae (i.e. glochidia), which infect fishes, have harmful impacts on native host health (Douda et al., 2017; Reichard et al., 2023). The glochidia also compete with the glochidia of endangered native freshwater mussel on host fish, resulting in the decline of native mussels (Donrovich et al., 2017; Douda et al., 2024). These dilemmas in parasite conservation, that is, endangered parasites in one region (environment) can be problematic mainly as invasive species in other regions (environments) may be prevail across other host-parasite systems. Parasites can have large impacts on endangered or economically important host species, but they form a fundamental part of ecosystems and are biologically significant. Thus, we should carefully consider their population control, depending on the status of both parasites and hosts.

1. Ethics and Integrity statements

Data availability statements:

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Ethics and permit approval statements:

Field surveys were conducted with the permission of the governor of Hokkaido, Japan, and the Agriculture, Sericulture, and Horticulture Promotion Division, Department of Agriculture, Gunma Prefecture, Japan. Our work did not require special permissions on animal welfare; however, all procedures were conducted according to Hokkaido University's animal experiments regulations.

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Conflict of interest disclosure:

The authors declare that they have no potential conflicts of interest, financial or otherwise, associated with this work.

Permission to reproduce material from other sources

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Author's contributions

Ryota Hasegawa: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; software; validation; visualization; writing—original draft preparation; writing—review and editing.

Yohsuke Uemura: Conceptualization; data curation: funding acquisition; investigation; methodology; writing—review and editing.

Yasunori Yamashita: Conceptualization; data curation; investigation; writing—review and editing.

Makoto Inoshita: Conceptualization; data curation; investigation; writing—review and editing.

Itsuro Koizumi: Conceptualization; methodology; project administration; supervision; writing—review and editing.

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Figures

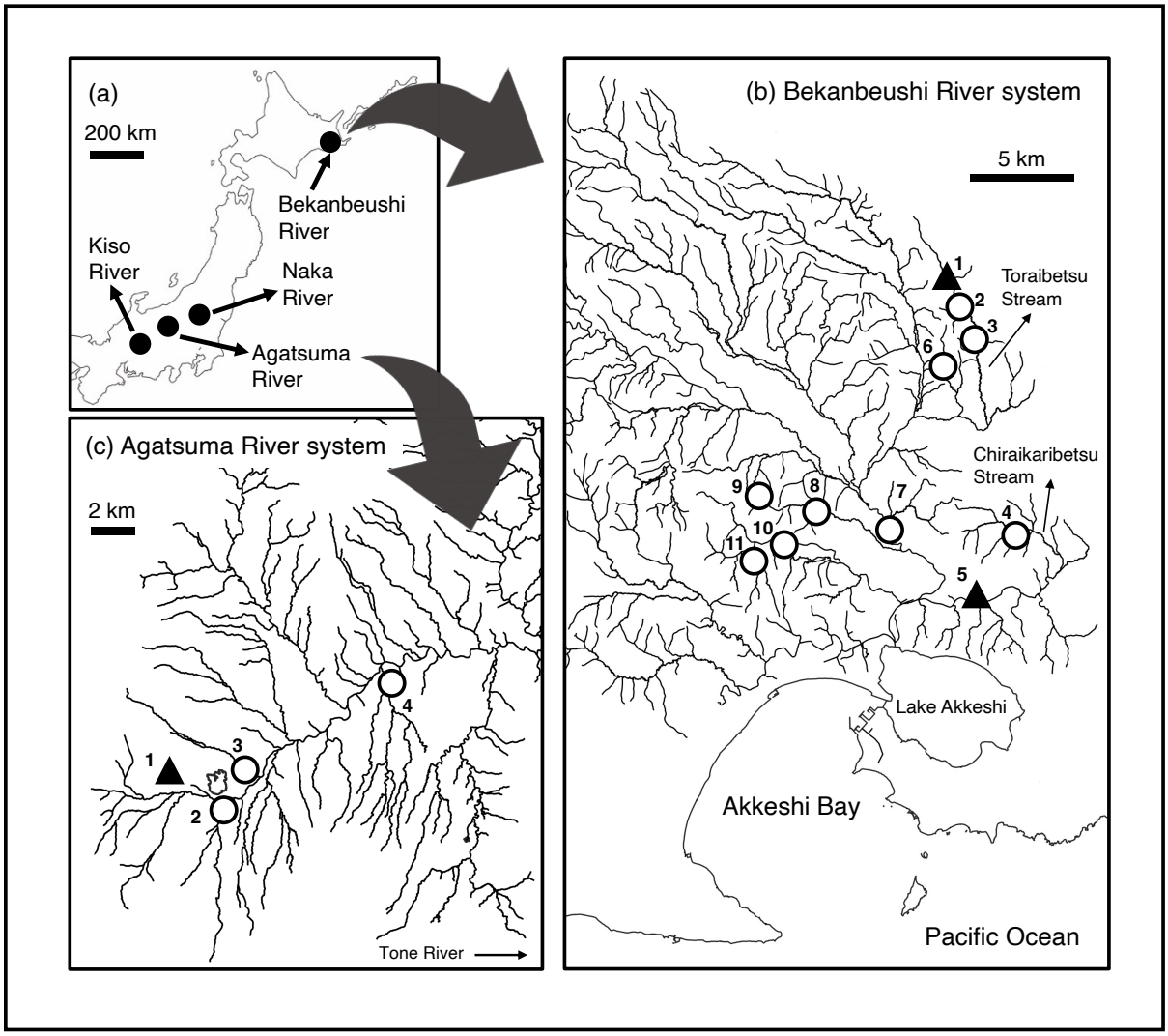

Figure 1. Maps of the known localities of *Salmincola californiensis* in Japan (a) and specific sampling sites in this study (b, c, d). (b) Bekanbeushi River system in eastern Hokkaido; 1–3. Toraibetsu Stream, 4–5. Chiraikaribetsu Stream, 6. Shimo-Fuppoushi Stream, 7. Unbekan Stream, 8. Sattebetsu Stream, 9. Katamusari Stream, 10–11. Oobetsu Stream. (c) Agatsuma River, Tone River system in central Honshu; 1. Masuya

948 Trout Culture Farm, 2. Main stem of Agatsuma River, 3. Ooyoko River, 4. Koyado

949 River.

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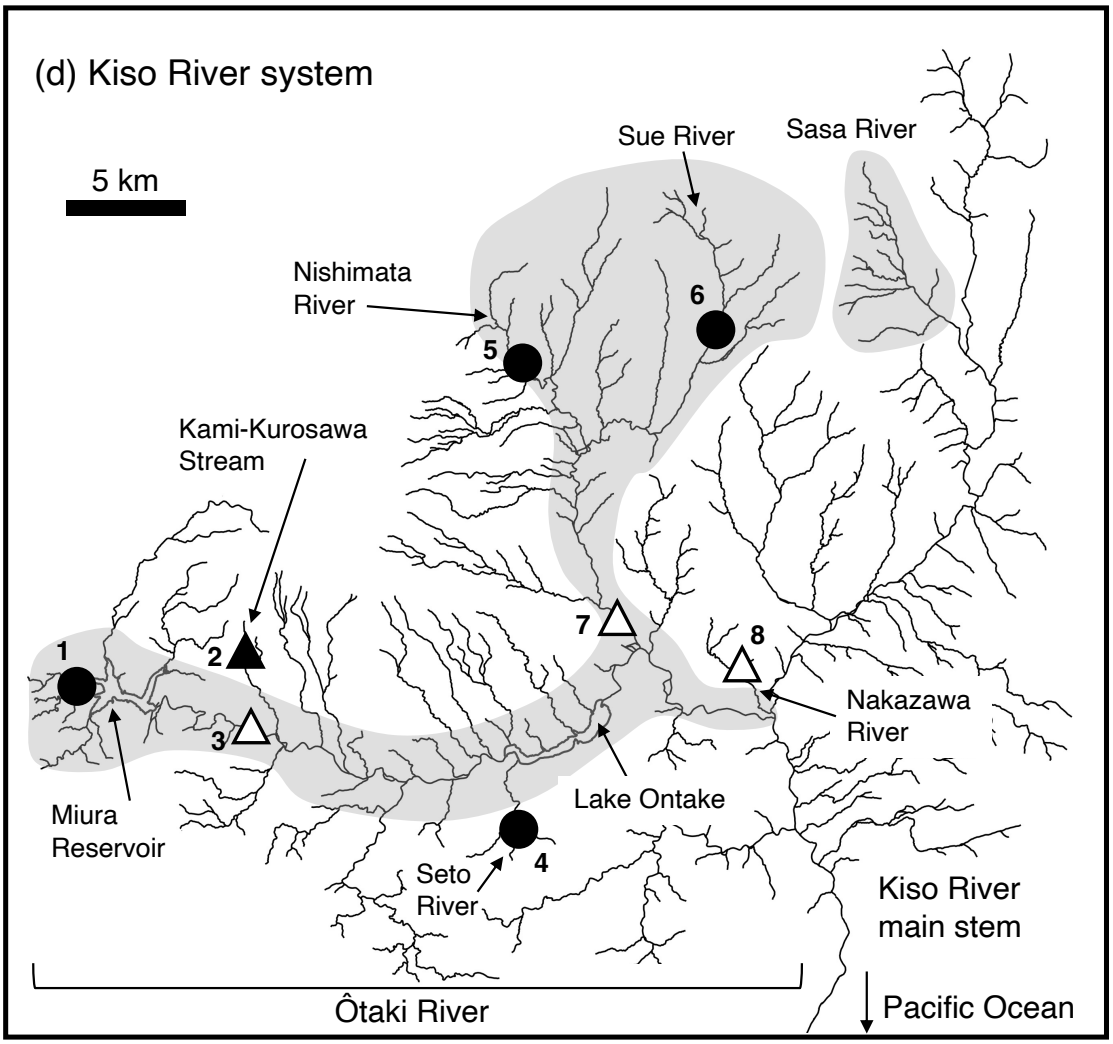


951

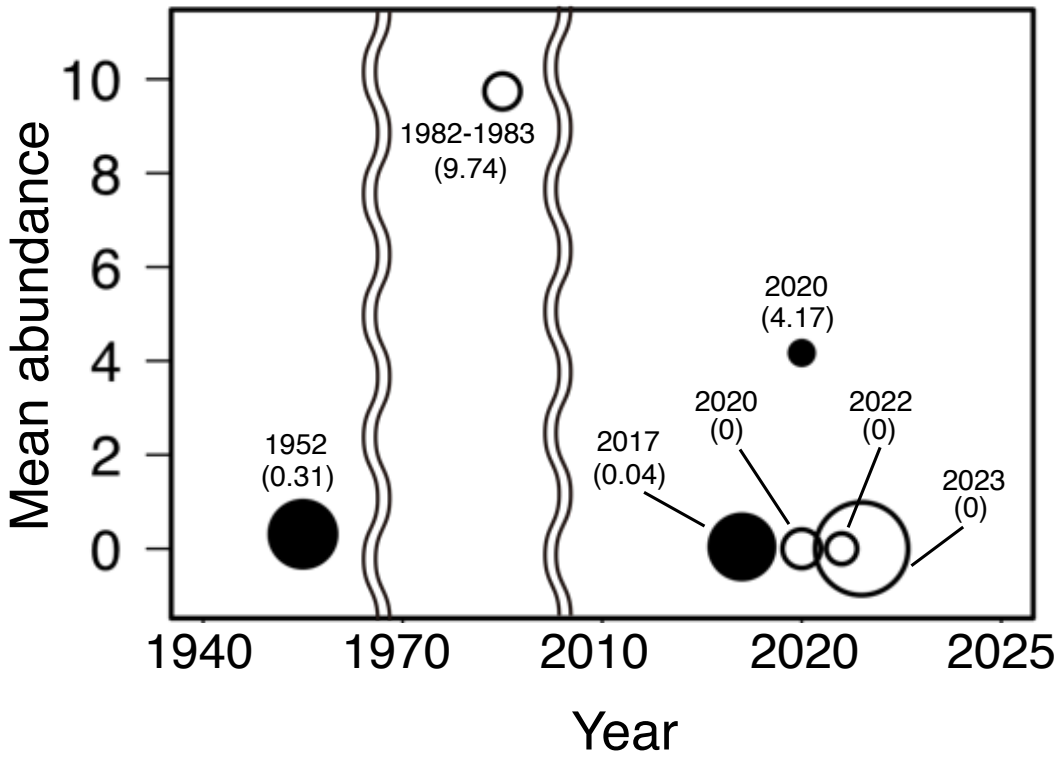
952 (d) Kiso River system in central Honshu; 1, 3. Upstream of main stem of the Ôtaki

953 River, 2. Kami-Kurosawa Stream, 4. Seto River, 5. Upstream of Nishimata River, 6.

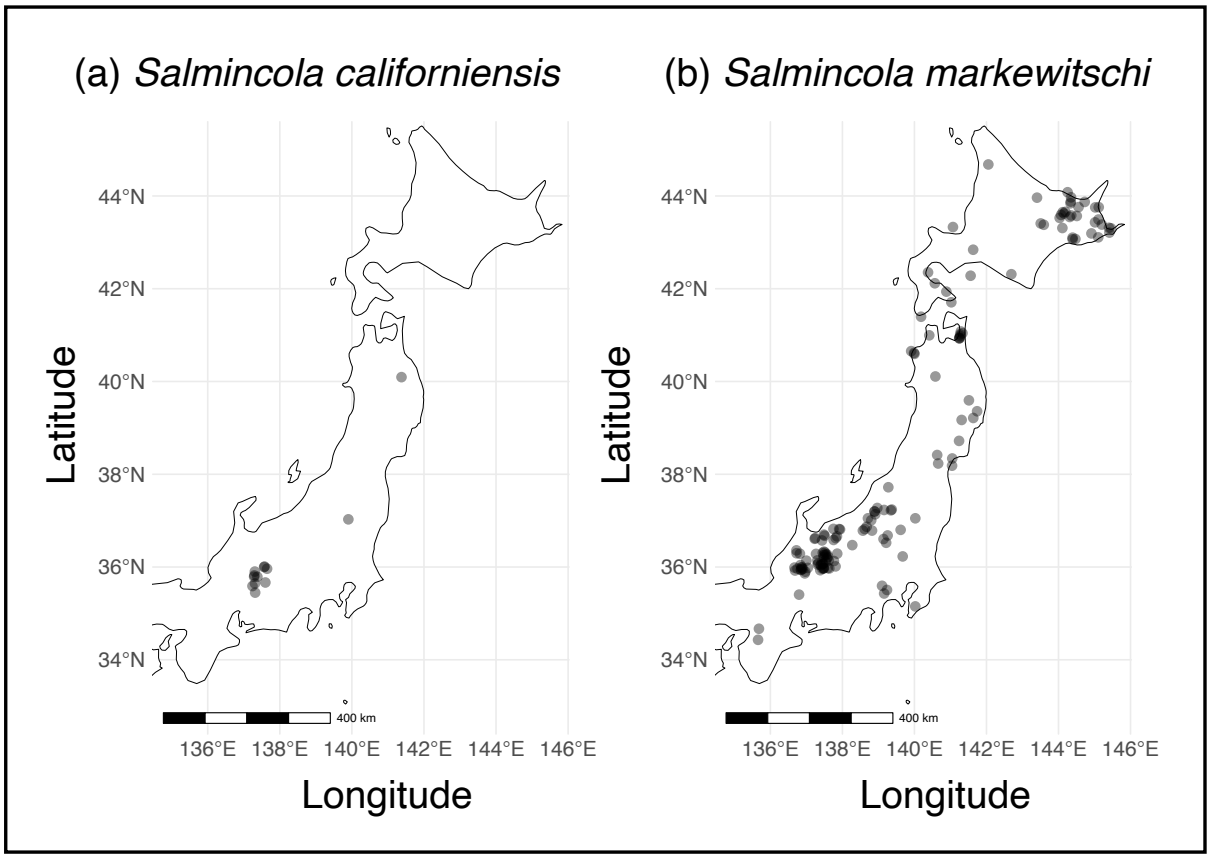
954 Sue River, 7. Downstream of Nishimata River, 8. Nakazawa River. The gray area in (d)

indicates the distributional area of *S. californiensis* in 1952 (see text-figure 4 in Hoshina & Suenaga, 1954).

In panels (b) to (d), white circles indicate the sites where host fish were sampled but no copepods were detected in the current study and black triangles mark the sites where previous studies reported *S. californiensis.* In panel (d), black circles represent the sites where host fish were sampled and copepods were detected in the current study and white triangles represent the sites where Nagasawa et al. (2018) did not find the copepod species.



964 **Figure 2.** Temporal changes in the mean abundance of *Salmincola californiensis* in two
965 river systems. White and black circles represent the Bekanbeushi and Kiso River
966 systems, respectively. The size of the plots indicates the number of hosts examined.
967 Numbers in parentheses indicate mean abundance (average numbers of parasites per all
968 examined hosts). Note that the mean abundance in the Kiso River system in 2020 was
969 calculated only from resident red-spotted masu salmon (due to the high infection levels
970 of the migrant type, we did not include this fish in the calculation). The period between
971 1970 and 2010 is indicated by two vertical dashed lines with a wave pattern, which
972 interval is visually compressed to avoid excessive blank space.



973

974 **Figure 3.** Maps of the reported localities of (a) *Salmincola californiensis* and (b) *S.*

975 *markewitschi* from citizens from May 2020 to May 2024. Points were jittered to

976 minimize overlapping.

977 # Tables

978

979 **Table 1.** Summary of sampled masu salmon *Oncorhynchus masou masou* in the

980 Bekanbeushi River and the Agatsuma River.

Sampling date	River system	Tributary	Sample size	FL range (mean) in mm	No. in Figure 1
September, 2020	Bekanbeushi River	Toraibetsu	22	81–160 (108.8)	b2, 3
July, 2022	Bekanbeushi River	Toraibetsu	14	74–188 (116.9)	b2, 3
July, 2022	Bekanbeushi River	Chiraikaribetsu	0	-	b4
August, 2023	Bekanbeushi River	Toraibetsu	99	59–212 (97.7)	b2, 3
August, 2023	Bekanbeushi River	Chiraikaribetsu	0	-	b4
August, 2023	Bekanbeushi River	Shimo-Fuppoushi	5	72–154 (93.4)	b6
August, 2023	Bekanbeushi River	Unbekan	3	82–101 (91.7)	b7
August, 2023	Bekanbeushi River	Sattebetsu	17	79–212 (132.9)	b8
August, 2023	Bekanbeushi River	Katamusari	0	-	b9
August, 2023	Bekanbeushi River	Obetsu	4	98–109 (103.8)	b10, 11
November, 2023	Agatsuma River	Main	51	87–133 (104.8)	c2
November, 2023	Agatsuma River	Ooyoko	30	89–165 (109.0)	c3
October & November, 2023	Agatsuma River	Koyado	42	107–173 (126.7)	c4

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984

985 **Table 2.** Summary of reported localities of *Salmincola* spp. from citizen science

986 approaches.

987

Potential parasite species	Total datapoints	Field (%)	Aquariums & fish farms
Salmincola californiensis	13	13 (100)	0
Salmincola markewitschi	153	129 (84.3)	24
Salmincola stellata	6	6 (100)	0
Salmincola edwardsii	1	1 (100)	0
Total	173	149 (86.1)	24

988

989

990 **Table 3.** Collected distributional records of *Salmincola californiensis* through citizen

991 science approach.

Date when	Host	Attachment sites	Prefecture	River system	Tributary	Photo or sample	No. in Figure 1
August 2010	Red-spotted masu salmon	gills	Nagano	Kiso River	Ôtaki River (Seto Stream)	Yes	d4
August 2011	Red-spotted masu salmon	fins	Nagano	Kiso River	Ôtaki River (Nishimata River)	Yes	d5
September 2019	Masu salmon	gills	Iwate	Mabuchi River	Hiranuka River	No	NA
September 2020	Red-spotted masu salmon	gills and fins	Nagano	Kiso River	Ôtaki River (upstream of main stem)	Yes	d1
September 2020	Red-spotted masu salmon	gills and fins	Nagano	Kiso River	Ôtaki River (Nishimata River)	Yes	d5
June 2021	Red-spotted masu salmon	unknown	Nagano	Kiso River	Atera River	No	NA
July 2022	Red-spotted masu salmon	gills and fins	Nagano	Kiso River	Ôtaki River (Nishimata River)	Yes	d5
September 2022	Red-spotted masu salmon	gills	Nagano	Kiso River	Ôtaki River (Nishimata River)	Yes	d5
September 2022	Red-spotted masu salmon	gills and fins	Nagano	Kiso River	Ôtaki River (Nishimata River)	Yes	d5
September 2023	Red-spotted masu salmon	gills and fins	Nagano	Kiso River	Ôtaki River (upstream of main stem)	Yes	d1
September 2023	Red-spotted masu salmon	gills	Nagano	Kiso River	Ôtaki River (Sue River)	Yes	d6
October 2023	Red-spotted masu salmon	gills and fins	Nagano	Kiso River	Ôtaki River (upstream of main stem)	Yes	d1
April 2024	Masu salmon	gills and fins	Tochigi	Naka River	Mainstem	Yes	NA

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