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Relative importance of host dependent vs. physical environmental characteristics affecting the distribution of an ectoparasitic copepod infecting to the mouth cavity of stream salmonid

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Abstract

Understanding parasite distributional patterns is fundamental for elucidating host-parasite relationships. The genus *Salmincola* is an ectoparasitic copepod group specifically infecting freshwater salmonids. Considering their strong association with their hosts, we can predict that the distribution and prevalence (analogues to abundance) of *Salmincola* reflect host salmonids. An alternative hypothesis is that their distribution will be strongly affected by environmental factors like stream drift because they have a free-living stage with low swimming ability. If this is the case, we predict a longitudinal gradient with higher occurrence or infection levels in downstream areas. To estimate the relative strength among factors affecting infection levels, we investigated the distribution pattern of *Salmincola* sp. on wild white-spotted charr *Salvelinus leucomaenis* in a southern Hokkaido river system. Based on data from 19 sites across three seasons, we found that host density and flow velocity affected the prevalence of *Salmincola*. On the other hand, no longitudinal gradient was observed and the prevalence was extremely low in some fragmented habitats (i.e., above dams and waterfalls). This indicates some compensation mechanisms against unidirectional downstream dispersal. We found that parasite prevalence and intensity were much higher in large migratory (anadromous) fish and, therefore, hypothesize that long-distance upstream migration helps the redistribution and population persistence of parasites in upstream areas.

KEYWORDS

ectoparasites, parasitic copepod, *Salmincola,* stream-drift paradox

1 | INTRODUCTION

Parasites account for a large proportion of biomass of living organisms (Dobson et al., 2008; Kuris et al., 2008) and play many important roles in natural systems, such as ecosystem functioning and host population dynamics (Anaya-Rojas et al., 2019; Hudson, Dobson & Newborn, 1998; Lafferty, Dobson & Kuris, 2006; Lafferty et al., 2008; Morton & Silliman, 2020; Sato et al., 2012). Despite their potential impacts, however, most parasites have been neglected in ecological studies (Gordy, Koprivnikar, McPhail & Hanington, 2020; Poulin, 2011), which is partly due to difficulty in finding and identifying them. Accordingly, we have lacked even general patterns for the distribution and abundance of parasites until recently (e.g. Berkhout et al., 2020; Blasco-Costa, Koehler, Martin & Poulin, 2013).

Compared to free-living organisms, parasite distribution can be either simple or complex. For example, some parasites merely follow their host distribution (Arneberg, 2002; Hansen & Poulin, 2006), resulting in simple distribution patterns. In addition, since parasites *per se* have low mobilities (Poulin, 2011), their dispersal and genetic structure mirrors their hosts (Blasco-Costa & Poulin, 2013; Criscione & Blouin, 2004). However, complex distribution patterns are also expected, because many parasites are affected not only by their hosts but also the external physical environment, that also mediates host abundance and distribution (Berkhout et al., 2020; Grunberg, 2021). Physical factors such as temperature, flow velocity and pH level generally affect life-history and transmission of parasites, especially during infectious stages (Baker & Cone, 2000; Johnston & Dykeman, 1987; Mouritsen, 2002; Pietrock & Marcogolies, 2003; Thieltges, Jensen & Poulin, 2008). Although disentangling the factors affecting their distribution is a critical issue in ecology, only a few studies have evaluated the

69 relative importance of ecological factors including host characteristics and external
70 environments affecting parasites (Berkhout et al., 2020; Poulin, 1995).
71 Lotic ecosystems provide a good opportunity to elucidate the relative importance of
72 host characteristics and other external environmental factors on parasite distribution and
73 abundance. This is because unidirectional water flow should be the major physical
74 determinant, especially for parasites that have free-swimming infectious stages
75 (Blasco-Costa, Waters & Poulin, 2012; Blasco-Costa et al., 2013). Passive dispersal by
76 constant stream drift (Müller, 1982) generates an infection gradient from upstream to
77 downstream along the river, which may be a common pattern in aquatic parasites
78 (Blasco-Costa et al., 2013). Alternatively, when the influence of host dependency is
79 stronger than stream drift, we will not detect a distributional gradient. This could occur
80 either when host transmission occurs via direct host physical contact, when the
81 transmission window is short, or when host upstream movement compensates for
82 stream drift (e.g. Blasco-Costa et al., 2012).
83 The genus *Salmincola* (Family Lernaeopodidae), ectoparasitic copepods, and their
84 host salmonids are ideal to evaluate the relative importance of factors affecting parasite
85 distributions in lotic systems. *Salmincola* spp. complete a direct life cycle without
86 intermediate hosts (Kabata & Cousens, 1973) and have a short lived (only a few days)
87 free-living stage. Because the infectious copepodids are tiny (i.e. 0.6-0.7 mm; Kabata &
88 Cousens, 1973) and seem to have a low swimming ability (Friend, 1941; McGladdery &
89 Johnston, 1988), they should be strongly affected by stream drift. On the other hand,
90 considering their strong association with their hosts (Kabata, 1969), we can also predict
91 that their distribution should be strongly affected by host distribution and dispersal.
92 Salmonids often prefer upstream areas, resulting in high densities (Imanishi, 1996;

93 Morita, Sahashi & Tsuboi, 2016) and they also exhibit long-distanced upstream
94 migration for spawning (Solomon & Templeton, 1976). Therefore, we can evaluate the
95 relative strength of host characteristics and the physical environment. That is, if stream
96 drift dominates the parasite distribution, an increase of abundance or occurrence is
97 expected in lower altitude (Blasco-Costa et al., 2012, 2013). Alternatively, if host
98 characteristics mainly govern parasites distribution, we will observe the opposite pattern
99 because of high host density at higher altitude, as well as upstream host migration.
100 We tested these predictions by examining the basin-wide distribution pattern of
101 *Salmincola* sp. on wild white-spotted charr (*Salvelinus leucomaenis*) in the Shiodomari
102 River system, southern Hokkaido, Japan. We particularly focused on how host
103 characteristics (density and dispersal) and stream drift (water velocity and altitudinal
104 distribution) affect the infection level of these parasite (i.e. prevalence and intensity).
105 The role of host dispersal can be inferred from the infection level of the migratory
106 (anadromous) form because such individuals are known to undertake long-distance
107 upstream migration before spawning (Quinn, 2018). Because *Salmincola* spp. tend to
108 infect larger host individuals (Kabata & Cousens, 1977; Bowen & Stedman, 1990;
109 Nagasawa, Yamamoto, Sakurai & Kumagai, 1995), large anadromous fish can carry the
110 parasites in upstream areas effectively. We also evaluated the effects of stream drift and
111 host migration compensation by examining the populations above physical barriers,
112 such as dams and waterfalls. If stream drift and host upstream migration are crucial for
113 the parasite's distribution, we can expect low infection levels in such isolated
114 populations. This is plausible given that even host white-spotted charr often go extinct
115 after dam constructions or show reduced density above dams (Morita & Yamamoto,
116 2002; Morita et al., 2019). Finally, we also examined the effects of other environmental

117 factors, such as water temperature and stream size, which might have affected parasite
118 distributions.
119
120 **2 | METHODS**

121 **2.1 | Study area and species**

122 We conducted our field survey in the Shiodomari River in 2019 (Figure 1). The
123 Shiodomari River system has been designated as a protected freshwater area and is
124 closed to recreational fishing year-round for all species (Tsuboi & Morita, 2004). The
125 upstream areas of this river system are dominated by white-spotted charr, whereas
126 downstream and mainstem are dominated by masu salmon (*Oncorhynchus masou*),
127 freshwater sculpin (*Cottus nozawae*), Siberian stone loach (*Noemacheilus barbatulus*),
128 Japanese dace (*Pseudaspius hakonensis*) and a small number of invasive rainbow trout
129 (*Oncorhynchus mykiss*).

130 In the Shiodomari River system, white-spotted charr are frequently infected with
131 *Salmincola* sp. (but not other salmonids) and their infections commonly occur in the
132 mouth cavity but not in the gill tissue or on the body surface. To date, five species of the
133 genus *Salmincola* have been recorded from Japan; *S. californiensis* (reported as *S.*
134 *yamame* in Hoshina & Suenaga, 1954; Hoshina & Nishimura, 1976; Nagasawa &
135 Urawa, 2002), *S. carpionis* (reported as *S. falculata* in Yamaguti, 1939; Nagasawa et al.,
136 1995; Nagasawa & Urawa, 2002; Nagasawa & Sakaki, 2020), *S. stellata* (Nagasawa &
137 Urawa,1991; Nagasawa, Watanabe, Kimura & Hara, 1994; Hiramatsu et al., 2001), *S.*
138 *edwardsii* (Nagasawa, 2020a, b; Nagasawa & Kawai, 2020) and *S. markewitschi*
139 (Nagasawa, 2020c; Nagasawa & Ishiyama, 2021). *S. carpionis* and *S. markewitschi*

140 mainly infect the mouth cavity of the genus *Salvelinus* (Kabata, 1969; Nagasawa et al.,
141 1995; Shedko & Shedko, 2002). Based on the taxonomic studies proceeded by the first
142 author (R. Hasegawa), we confirmed by genetic analysis that only a single species was
143 present in the river system. However, since morphological variation was quite large,
144 possessing the characteristics of both *S. carpionis* and *S. markewitschi* (Hasegawa
145 unpublished data), we could not conclude which scientific names should be applied
146 without analyzing additional specimens from other areas. Thus, we treated the tentative
147 species as *Salmincola* sp. Heavy infections of *Salmincola* spp. can cause various
148 impacts on host fish in hatchery environments (Herron, Kent & Schreck, 2018; Kabata
149 & Cousens, 1977; Nagasawa et al., 1998; Sutherland & Wittrock, 1985), whereas the
150 impacts on wild fishes have rarely been reported or may be negligible, possibly due to
151 the low prevalence and intensity in natural conditions (e.g. Amundsen, Kristoffersen,
152 Knudsen & Klemetsen et al., 1997; Ayer, Morita, Fukui & Koizumi, 2021; but see
153 Mitro, 2016).

154 White-spotted charr in the Shiodomari River have two types of life-history: some
155 individuals remain in rivers and reproduce as residents, whereas other individuals
156 migrate to the sea or lakes and return to their natal rivers to spawn as migrants
157 (Yamamoto, Nakano & Tokuda, 1992; Morita, 2001; Morita et al., 2019). Sea-run or
158 anadromous forms can be infected by *Salmincola* sp. because salinity tolerance is often
159 reported in other members of the genus (Black, Montogomery & Whoriskey, 1983;
160 Friend, 1941; Nagasawa, 1998). Above natural waterfalls and man-made dams (i.e.,
161 closed-populations), white-spotted charr have a non-anadromous life history (residents;
162 Morita, Yamamoto & Hoshino, 2000).

163

164 **2.2 | Fish collection and measurement**

165 Sampling was carried out at 17, 15 and 14 sites during three separated seasons
166 (May, July, October), respectively (i.e., 19 sites in total) (Figure 1, Table 1, Supporting
167 Information). Two sampling tributaries have natural waterfalls (head water area of Ito
168 River; Figure 1) and three tributaries have impassable dams installed to control erosion
169 (Sasagoya Stream, Nishimata Stream, Sentarosawa Stream; Figure 1). A high-dam
170 (Yabetsu reservoir) was constructed in the upper area of the main stem (Figure 1).
171 While no fish can access upstream areas above impassable dams from downstream areas,
172 a few fish, including anadromous forms (migrants), can pass some small waterfalls (i.e.
173 Site 16, 18, R. Hasegawa, unpublished data).

174 In May and October, fish were collected within 100-300 m reaches using a
175 backpack electro-fisher (model 12B; Smith-Root, Inc.) in each site. At each site, we
176 tried to collect at least 30 host individuals to estimate reliable parasite abundance data.
177 In addition, at the sites where dams or waterfalls were present, we started sampling
178 within 150 m from above or below the barrier to compare the infection levels between
179 them, although we could not catch fish in these areas at two sites (Site 17, 19) due to the
180 difficulty of the approach. During July sampling, we estimated host density (see 2.4
181 Host density estimation) and measured physical environmental variables at 11 sites
182 within a 100 m area as described in the next section. If we could not collect more than
183 10 fish in a reach, we sampled for additional fish outside of the sampling area (but
184 within the same reach as May and October).
185 In May, we captured age-1 and older individuals, whereas we did not capture newly

186 emerged fries (age-0) because the average fork length of fries was less than 50 mm in
187 May (Yamamoto & Kato, 1984) and a previous study showed that fish less than 50 mm
188 were rarely infected with *Salmincola* sp. (Barndt & Stone, 2003). In July, to check the
189 infection pattern, captured fish were categorized into two age classes; age-0 (ca., less
190 than 78 mm) and age-1 and older, based on visual observation and bimodal frequency in
191 a histogram. During the breeding season (October), in addition to the classification of
192 age-0 (ca., less than 89 mm), the age-1 and older individuals were categorized into two
193 life history types: resident and migrant, determined according to their body size and
194 coloration as follows (Ishigaki, 1984; Yamamoto, Morita & Goto, 1999). (i) *Residents*
195 were usually brownish and had many small white spots on the sides of the body. The
196 abdomen had a characteristic yellow tinge. (ii) *Migrants* showed silver body color with
197 relatively large white spots on the sides of the body. Some migrants were captured from
198 additional reaches because it was difficult to collect enough samples at each site. In
199 addition, we also captured masu salmon (in July and October) and rainbow trout (in
200 May and October) to confirm whether infection had occurred or not. Captured fish were
201 anesthetized with FA100 (DS Pharma Animal Health Co., Ltd.) and measured for fork
202 length (FL) to the nearest 1 mm. Since the main attachment sites of *Salmincola* sp.
203 parasitic on white-spotted charr are the body surfaces and buccal cavities (Nagasawa et
204 al. 1995; Nagasawa 2020c), we examined fish body surfaces and buccal cavities for the
205 presence of copepods. When found, we counted the number of individuals and recorded
206 their attachment sites. All the copepods detected were considered as females, because
207 the males are dwarf, attaching to females, and difficult to observe by the naked eye
208 (Kabata & Cousens, 1973). As no copepods were found on newly emerged
209 white-spotted charr fries (age-0), we excluded these hosts from all calculations and

analyses. In addition, migrants were also excluded from calculations and analyses because of their high infection levels and significant body size differences as discussed below.

2.3 | Measurements of the physical environment

Physical environmental factors such as water temperature and flow velocity can influence the development, infection and abundance of *Salmincola* spp. (Conley & Cutis, 1993; Mitro & Griffin, 2018; Monzyk, Friesen & Romer, 2015; Vigil, Christianson, Lepak & Williams, 2016). Therefore, we measured multiple physical environmental factors (water temperature, stream width, stream depth, substrate score, flow velocity) at 11 sites in July (Figure 1; Supporting Information). We established seven measurement points on 11 transects per 100 m reach (i.e., 77 measurement points in total), which were equally spaced longitudinally along each of the sites. Only the flow velocity was measured in the middle of each measurement point (6 points per 1 transect), resulting in a total of 66 measurement points. Water temperatures were recorded with HOBO data loggers (Onset Computer Corporation, Bourne, MA) from July to October. We set each logger near the riverbed (about 0.3-1.0 m depth) and measured temperature at 1h intervals beginning on the 24th to 31st of July and until the 19th to 24th of October. Stream widths were measured on each transect (i.e., 11 measurement transects). Stream depths were measured on each measurement point. The dominant substrate was visually classified into seven categories and scored as follows: 1, silt and sand (< 2 mm); 2, gravel (2-16 mm); 3, pebble (16-64 mm); 4, cobble (64-256 mm); 5, boulder (> 256 mm); 6, bedrock, a system modified from Bain et al. (1985).

233 Flow velocity was measured with a propeller-type meter (CR-11; Cosmo-Riken, Osaka,
234 Japan) at about 60 % of the depth from the surface to the bed. All variables were
235 calculated in averages for each site and used for the principal components analysis
236 (PCA) and a generalized linear mixed models (GLMMs) as described below. Elevation
237 (m) for each site was determined using 1:25000 scale topographic maps
238 (http://maps.gsi.go.jp) and also included PCA analysis.

239

240 **2.4 | Host density estimation**

241 In general, host density can be a strong predictor of parasite abundance (Anderson &
242 May, 1978; Hansen & Poulin, 2006). Thus, we estimated charr density in the same
243 reaches as used for environmental factor measurements in July as described above.
244 Charr abundance was estimated by a two-pass removal method (e.g., Riley & Fausch,
245 1992). We set block nets at both ends of the reach to prevent fish from entering or
246 leaving during the sampling. White-spotted charr abundance was calculated by using the
247 model M (bh) in program CAPTURE (White, Burnham, Otis & Anderson, 1978).
248 Reach wide density of charr (number / m^2) was calculated by dividing the estimated
249 number of charr by the reach area (m^2) (Supporting Information).

250 **2.5 | Statistical analysis**

251 We calculated prevalence (percentage of individuals infected), intensity (the
252 number of individual parasites in a single infected fish) and mean intensity (the average
253 number of parasites among the infected fish) following Bush et al. (1997).

To summarize physical environmental factors (elevation, water temperature, stream width, stream depth, substrate score, flow velocity), we used a principal component analysis (PCA). Only principal components (PC) showing eigenvalue greater than one (Kaiser–Guttman criterion) were selected for further analysis. This resulted in two principal components describing all factors (Table 2).

During the population level analysis, we examined if the prevalence was affected by each principal component, host density (calculated from age-1 and older individuals) and habitat types (i.e., closed or open) by using GLMM with a binomial error distribution and logit link function. The response variable, prevalence, was the binary variable defined as (n, N-n), where n and N indicate number of infected individuals and number of all individuals at each population (i.e., N-n indicates numbers of uninfected individuals), respectively. Explanatory variables were PC1 (continuous variable), PC2 (continuous variable), host density (continuous variable) and habitat type (categorical variable; closed, open). Sampling sites and season (May, July, October) were treated as random effects. Statistical significance ($p \leq 0.05$) was evaluated by likelihood ratio test between the full model and reduced model. We did not include the interaction terms between habitat type and other variables, because preliminary analysis showed any significant effects. Thus, the full model as follows:

(n, N-n) ~ PC1 + PC2 + host density + habitat type (closed, open) + (1 | sites) + (1 | seasons).

Of the 19 sites we captured fish from, for only 11 sites physical environment measurements and charr abundance estimations were conducted. In addition, because we lost water temperature loggers at 3 sites, we conducted PCA analysis using the data of 8 sites. To minimize the effect of this smaller sample size, we firstly conducted

GLMM only with elevation and habitat type (closed, open), but without PCs and host density (i.e., 19 sites) and subsequently included all the variables into the analysis (i.e., 8 sites).

To consider the effects of host body size on infection, we also performed an individual level analysis. In this analysis, we constructed GLMM with a binomial error distribution to examine if the probability of infection was affected by fish size and population type (closed or open). The response variable was the binary variable that defined infected or uninfected (infected = 1, uninfected = 0) and explanatory variables were FL and habitat type (closed, open). Sampling sites and season were treated as random effects. Statistical significance ($p \leq 0.05$) was evaluated by likelihood ratio test between the full model and reduced model. Finally, we compared the infection prevalence and mean intensity between residents and migrants in October by Fisher's exact test and Wilcoxon rank-sum test, respectively. We used the package lme4 (Bates et al., 2011) for the mixed model procedures. All the statistical analyses were conducted using R version 3.5.2 (R Core Team, 2018).

3 | RESULTS

3.1 | Basin-wide distribution of *Salmincola* sp.

Salmincola sp. infections on white-spotted charr were present in 15 sites and absent in 4 sites (Table 1). Average prevalence was 26.4 % (0.00–53.6 %) in May, 19.4 % (0.00–38.9 %) in July and 14.3 % (0.00–46.7 %) in October. Average mean intensity was 1.95 (1.00–4.46) in May, 1.54 (1.00–2.50) in July and 1.70 (1.00–2.17) in October. All individual copepods were found from the buccal cavities of age-1 and older

white-spotted charr, whereas no copepods were found from newly emerged fries (mean FL: 63.3 mm [39–89 mm]; n = 384), nor other salmonid fishes such as rainbow trout (mean FL: 152.2 mm [90–327 mm]; n = 40) and masu salmon (mean FL: 98.0 mm [49–223 mm]; n = 353).

Contrary to the initial prediction, elevation positively affected the prevalence in the population level analysis (i.e. 19 sites; Table 3a), whereas the significant effect disappeared in the additional analysis (i.e. 8 sites, Table 3b). Differences of prevalence between above and below dam sites were evident even in the same stream (Figure 2, Table 1): GLMM showed that prevalence in closed populations were significantly lower than those of open populations (Table 3a, b), consistent with the second prediction. In two out of three above dam areas (Site 4, 10), no copepods were found across all seasons (Table 1). Although we found two individual copepods at the other closed population above a dam in May (Site 1; Table 1a), the prevalence was evidently low and no copepods were found in July and October (Table 1b, c). The individual level analysis also showed that hosts caught in closed populations showed significantly lower probability of infection (Likelihood-ratio test; $G^2 = 5.20$, $p = 0.02$; Figure 3), as well as a positive effect of fork length on the probability of infection ($G^2 = 186.44$, $p < 0.01$; Figure 3).

3.2 | Environmental factors affecting the abundance of *Salmincola* sp.

PCA compressed the environmental data into two principal components (PCs) (Table 2). PC1 and PC2 covered 84 % of the total variance (Table 2). Water

323 temperature, stream depth and stream width loaded positively on PC1, whereas
324 elevation and substrate score loaded negatively (Table 2). Flow velocity loaded
325 negatively on PC2 (Table 2).
326 While PC1 had no significant effect on prevalence, PC2 had a significant negative
327 effect on prevalence, meaning that higher prevalence was detected at sites with higher
328 flow velocity (Table 3b). Also, host density had a significant positive effect on
329 prevalence (Table 3b).
330

331 **3.3 | Comparison of infection level between resident and migratory host fish**

332 Migrant white-spotted charr (n = 21; mean ± SD FL: 358.33 ± 93.07 mm) showed
333 higher prevalence and mean intensity compared to residents (n = 439; mean ± SD FL:
334 161.34 ± 43.87 mm) (Figure 4). While 15.0 % of residents (n = 66) were infected with
335 *Salmincola* sp., 76.2 % of migrants (n = 16) were infected (Fisher's exact test; $p < 0.01$).
336 Mean intensity of migrants (3.56 parasites per infected fish) were more than two times
337 higher than that of residents (1.59 parasites per infected fish, Wilcoxon rank-sum test;
338 W = 3232.5, $p < 0.01$; Figure 4).
339

340 **4 | DISCUSSION**

341 This is one of few studies demonstrating the relative importance of host characteristics
342 and other external factors affecting parasite distribution and/or abundance. We found
343 that host density positively affects parasite prevalence and large migratory fish had
344 much higher prevalence and intensity. No altitudinal distribution was detected, but the

345 prevalence was extremely low in stream reaches above physical barriers. Together, our
346 results suggest that while stream drift is acting in the study system as inferred from low
347 prevalence above barriers, that effect is compensated by high host density in upstream
348 areas and also by upstream migration of large anadromous individuals. This contradicts
349 the presumed “general" pattern of stream parasites (Blasco-Costa et al., 2013) and the
350 ecological mechanisms against the pattern are proposed as below.
351
352 **4.1 | Basin-wide distribution pattern of *Salmincola* sp.**
353 According to previous studies on other aquatic parasites, an infection gradient from
354 upstream to downstream along a river might be a common distribution pattern
355 (Blasco-Costa et al., 2013). Unexpectedly, prevalence for *Salmincola* sp. exhibited
356 positive or no trend with elevation in the present study, suggesting that populations of
357 *Salmincola* sp. can persist in upstream areas even though the swimming ability of the
358 free-living infective stage is low (Friend, 1941; Monzyk et al., 2015). A similar
359 phenomenon is known as the “stream drift paradox” where populations of drift-affected
360 aquatic species remain in upstream areas despite the tendency for larvae to drift
361 downstream (e.g., Müller, 1982). Some studies have reported that upstream movements
362 by adult aquatic insects may compensate downstream drift of the larvae (see Brittain &
363 Eikeland, 1988). The fact that no negative trend was observed in the present study,
364 implies that other factors compensating for their downstream dispersal may exist in this
365 system.

366 One of the possible explanations is the spawning migration of host fish. Salmonids,
367 including white-spotted charr, generally move upstream to spawn (Nakamura, 1999;
368 Solomon & Templeton, 1976). Through this process, *Salmincola* sp. can be transferred

by host fishes to upstream areas and among open populations, resulting in population persistence in upstream reaches. Similarly, other studies have already shown that some parasites had no gradient in their abundance along rivers, suggesting that the dispersal abilities of their definitive hosts altered the gradient (Blasco-Costa et al., 2013; Paterson et al., 2019). In particular, migrants may play an important role in the recruitment of copepods during spawning. We found that migrants showed a much higher infection level than residents, which was probably due to their larger body size (Kabata & Cousen, 1977; Bowen & Stedman, 1990). Migrants return to rivers from the sea during the summer and move upstream to spawn during the autumn (Morita, 2001). This long-distance movement from downstream to upstream by highly infected migrants may markedly compensate the copepod's drift from upstream to downstream. However, although some species of the genus *Salmincola* have salinity tolerance (Black et al., 1983; Nagasawa, 1998), it remains unclear if this species can survive in saltwater while migrant charrs live in the ocean. It is also unclear during what period migrants are most likely to be infected. More studies are needed to prove this hypothesis.

Skewed distribution and abundance of host fish may also contribute to the population persistence of the copepods in upstream areas, because host density may be the strongest predictor for parasite abundance (Anderson & May, 1978; Hansen & Poulin, 2006). The density of white-spotted charr is generally higher in upstream reaches because they prefer cold water (Imanishi, 1996) and shelter such as rock interstices are abundant in upstream reaches (Morita et al., 2016). In addition, white-spotted charr tend to prefer upstream habitats when masu salmon co-occur because of interspecific competition (Miyasaka, Nakano & Furukawa-Tanaka, 2003; Nakano, 1995), which may be the case in the present study. In fact, host density had a

393 significant positive effect on prevalence and there was a significant positive relationship
394 between host density and elevation in the present study (Pearson's correlation: $r = 0.84$,
395 $p < 0.01$, $n = 11$). Therefore, unidirectional drift may be compensated by high host
396 density in upstream reaches.

397 Strikingly, we detected a significantly lower infection level in closed populations,
398 especially above dams, suggesting that some populations of *Salmincola* sp. (site 4, 10)
399 had already gone extinct as we predicted. While host fish and their parasites can access
400 open populations freely, they cannot access closed populations from downstream
401 (Morita et al., 2000; Yamamoto, Morita, Koizumi & Maekawa, 2004). In addition, the
402 copepods would be washed away from the above dam areas by stream drift. This
403 process may cause the extinction of the copepods in some closed populations. This
404 prediction does not contradict with the fact that extremely low prevalence was observed
405 above dams, where migrant forms cannot access.

406 Extinction of closed populations of copepods could also be accompanied by
407 extinction of the host. Since dams or waterfalls prevent fish from reaching upstream
408 habitats, once they emigrate to areas downstream from these barriers, they are unable to
409 return for reproduction, leading to gradual isolation or extirpation of the upstream
410 population (Morita et al., 2000; Morita & Morita, 2007; Yamamoto et al., 2004).
411 Therefore, habitat fragmentation by damming decreases the population size and genetic
412 diversity, and hence increases the extinction rate of freshwater fish (Morita &
413 Yamamoto, 2002; Yamamoto et al., 2004). In fact, Morita and Yamamoto (2002)
414 predicted that habitat fragmentation by damming decreases the population size of
415 white-spotted charr, and therefore cause local extinctions. Moreover, Morita et al.

(2019) re-investigated the same populations as the previous study and confirmed that extinction had already occurred in some of these populations. By these mechanisms, *Salmincola* sp. can easily go extinct when white-spotted charr populations are fragmented by dams, because local extinction of host-specific parasites is likely to occur faster than its hosts (Rózsa, 1992).

4.2 | Environmental factors affecting the infection level

Although there were no significant effects with PC1 (loaded with elevation, temperature, stream depth and width, substrate score), we found significant effects of PC2 (negatively correlated with flow velocity) on prevalence. This result is not consistent with previous studies that found fishes in streams having lower infection levels than lakes, where lower flow may contribute to their infection (Monzyk et al., 2015). As we discussed above, distribution and density of white-spotted charr were highly skewed toward upstream areas, where high water flow and low water temperature is generally observed. This skewed distribution of host fish may interact with other variables, and hence cause these unexpected results. Another possibility is the matter of scale. We measured the average water velocity at the reach level, but the velocity strongly varied at smaller scales, such as pools and riffles. For example, Morita et al. (2016) showed that the average water velocity was lower in upstream reaches compared to lower reaches in a high-gradient river and this was because there were more turbulent and slow flowing microhabitats in the upper reaches created by step-pool geomorphological structures. Therefore, to determine the limiting factors of

438 their distribution, we need to investigate the factors affecting their distribution across a
439 variety of scales (e.g., Fausch, Nakano & Ishigaki, 1994).

440

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721

Tables

Table 1. Prevalence and mean intensity of *Salmincola* sp. on white-spotted charr in each site and season in the Shiodomari River system. Prevalence (%) and mean intensity are given as the proportion of fish infected and the average number of parasites among infected fish in each population, respectively. "*n*" indicates the sample size of all inspected fish at each site. "NA" indicates that the variable was not applicable.

	May			July			October		
Site	*n*	Prevalence (%)	Mean Intensity	*n*	Prevalence (%)	Mean Intensity	*N*	Prevalence (%)	Mean Intensity
1	50	4.0	1.00	33	0.0	NA	31	0.0	NA
2	59	22.0	1.46	39	25.6	1.50	33	15.2	1.00
3	50	24.0	1.17	34	17.6	1.33	33	12.1	1.75
4	59	0.0	NA	44	0.0	NA	33	0.0	NA
5	28	53.6	1.93	36	38.9	1.71	40	10.0	1.00
6	0	NA	NA	11	27.3	1.33	0	NA	NA
7	2	0.0	NA	0	NA	NA	0	NA	NA
8	4	0.0	NA	0	NA	NA	0	NA	NA
9	23	34.8	2.38	25	16.0	1.00	20	5.0	1.00
10	0	NA	NA	8	0.0	NA	16	0.0	NA
11	4	50.0	1.50	18	27.8	1.00	22	4.5	4.00
12	4	25.0	1.00	0	NA	NA	0	NA	NA
13	25	28.0	2.29	22	27.3	2.00	26	26.9	1.71
14	5	40.0	2.00	0	NA	NA	0	NA	NA
15	29	48.3	2.21	30	26.7	2.50	30	46.7	1.50
16	55	16.4	1.44	89	27.0	1.25	31	16.1	1.20

17	54	24.1	4.46	51	21.6	1.18	43	25.6	1.64
18	63	33.3	2.10	120	15.8	1.89	51	11.8	2.17
19	53	45.3	2.42	46	19.6	1.78	30	26.7	1.75

726

Table 2. Results of principal component analysis (PCA) on physical environmental factors. Bold indicates variable that highly correlated with each PC.

Variables	PC1	PC2
Elevation	**−0.741**	0.339
Water temperature	**0.917**	0.170
Stream width	**0.917**	−0.302
Stream depth	**0.805**	−0.357
Substrate Score	**−0.844**	−0.334
Flow velocity	−0.420	**−0.899**
Eigenvalue	3.769	1.280
Proportion of variance	0.628	0.213
Cumulative proportion of Variance	0.628	0.842

738 Table 3. Results of generalized linear mixed models (GLMMs) with binomial error
739 distributions to analyze whether environmental factors affect prevalence: (a) only
740 elevation and habitat type (closed vs. open) were included (i.e., 19 sites), (b) all the
741 variables were included (i.e., 8 sites). Bold indicates variable showing significant effect
742 on response variable. Closed populations were set as baseline for determination of any
743 significant differences between Open populations.

(a) 19 sites

	ln$L$	lnL_R	G^2	Coefficient	p-value
Elevation (m)	−112.69	−115.91	6.44	0.011	0.01
Closed vs Open		−120.44	15.5	2.387	< 0.001

(b) 8 sites

	ln$L$	lnL_R	G^2	Coefficient	p-value
PC1	−57.40	−58.30	1.79	0.128	0.181
PC2		−64.06	13.32	−0.650	< 0.001
Host density		−64.13	13.46	7.852	< 0.001
Closed vs Open		−68.65	22.50	2.742	< 0.001

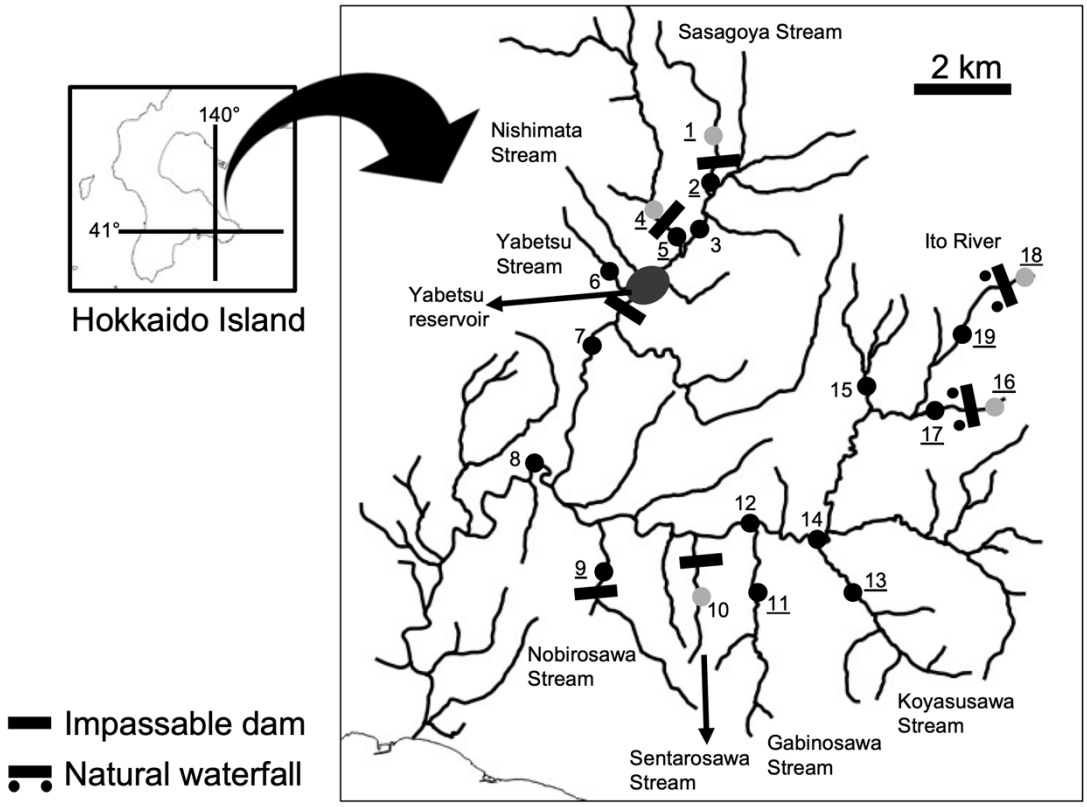
744

745 ln$L$: log likelihood for the full model; lnL_R: log likelihood for the model when the
746 variable is removed; G^2: statistics for the likelihood-ratio test calculated as follows; $G^2 =$
747 $-2\ (\ln L_R - \ln L)$

748
749

Fig. 1

Map of the sampling tributaries in the Shiodomari River system, southern Hokkaido, Japan. Detailed information on each tributary is shown in Supporting Information. Underlined site represents the sites where measurements of environmental factors and fish abundance estimation were conducted. Gray and black circles indicate closed and open populations, respectively.



761 Fig. 2

762 Relationship between infection prevalence and elevation in each season. Open circles

763 and crosses indicate open and closed populations, respectively. Different plots scattered

764 at the same elevation indicate different season (May, July, October).

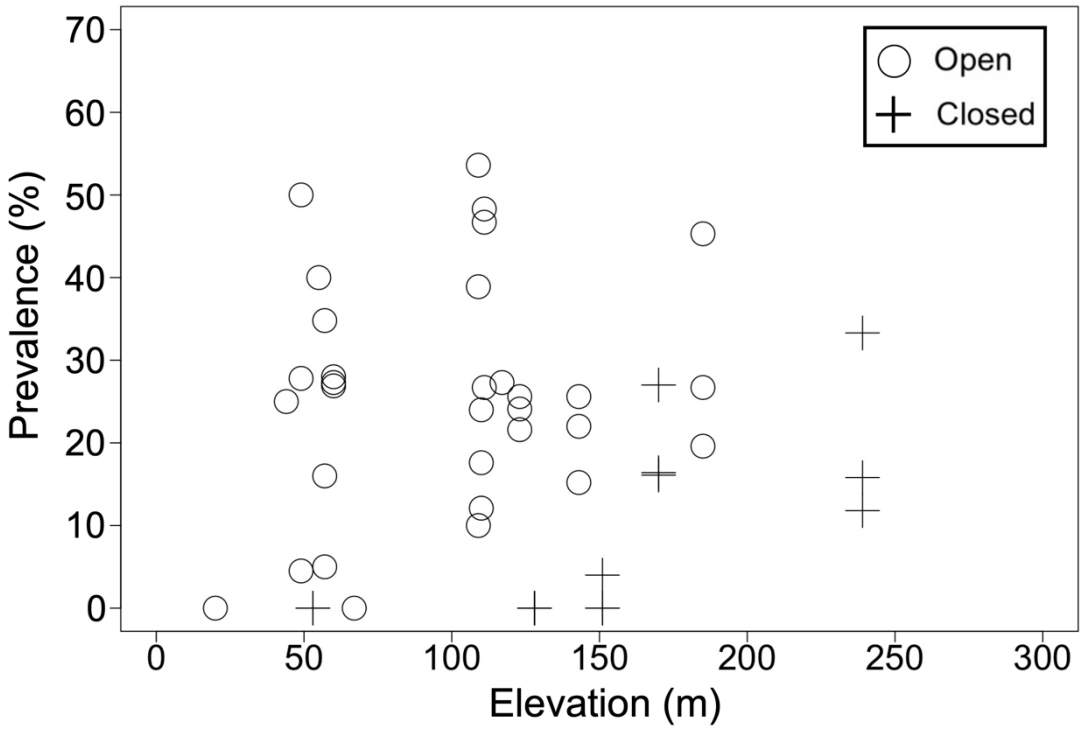


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Fig. 3

The relationships between parasite infections and host fork length. (a) Logistic relationships between infection probability and fork length. Open circles and crosses indicate open and closed populations, respectively. The curves were estimated by a generalized linear mixed model (GLMM) with binomial error distribution. Barplots indicate the ratio of infected fish for each fork length class. (b) open and (c) closed populations.

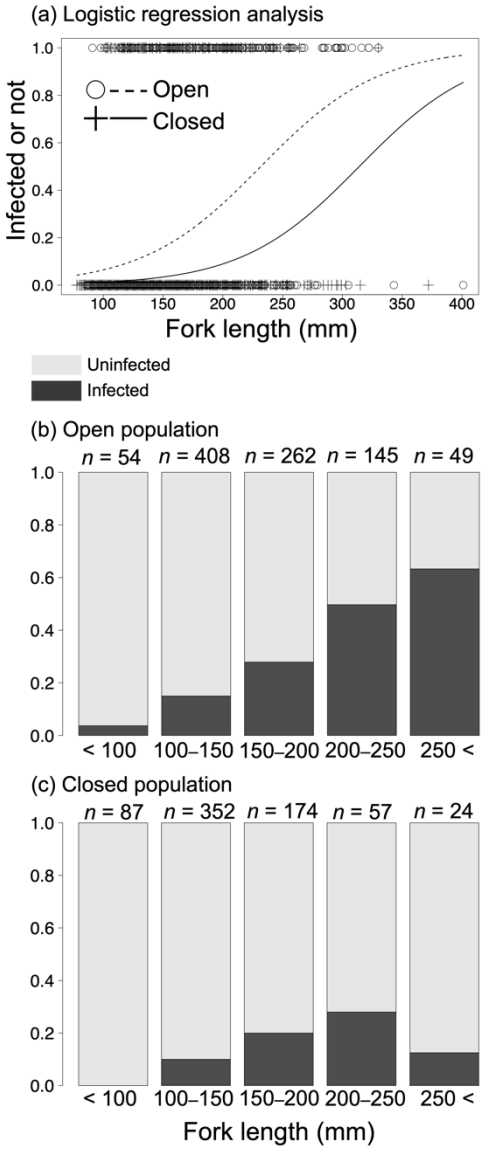

Fig. 4

Comparison of parasite number between (a) residents and (b) migrants of white-spotted charr during the spawning season (October).