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Author(s)	Yamada, Hiroyuki; Wada, Satoshi
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Original Article

Phenotype-dependent downstream dispersal under ordinary flow conditions in juvenile white-spotted char

Authors and affiliations

Hiroyuki Yamada (ORCID iD: 0000-0002-8034-5687)

Satoshi Wada (ORCID iD: 0000-0002-5316-8048)

Laboratory of Marine Biology, Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1, Minato-cho, Hakodate, Hokkaido 041-8611, Japan.

Corresponding author

Hiroyuki Yamada

Tel: 0138-40-5547

Email: kosame107@gmail.com

Abstract

Animal dispersal is often phenotype-dependent and can exert evolutionary pressures on populations in which it occurs. The evolutionary pressure arising from phenotype-dependent dispersal is called spatial sorting. We examined the evolutionary pressure arising from spatial sorting (sorting pressure) caused by downstream dispersal in juvenile white-spotted char *Salvelinus leucomaenis* under ordinary flow conditions. We conducted outdoor experiments using an artificial channel with ten steps to investigate the relationship between phenotypic characteristics and the occurrence or distance of downstream dispersal during five daytime hours. Six experiments were conducted using young-of-the-year juveniles collected early in the morning of each experimental day. We focused on two phenotypes, fork length (body size) and station-holding (SH) behavior, where juveniles remain sedentary on the substrate. Juveniles were assigned to the "SH group" if they exhibited SH behavior for more than 10 s during a 540-s observation period, and to the "swimming group" if they exhibited SH behavior for less than 10 s. Juveniles in the swimming group had a higher occurrence of downstream dispersal than in the SH group. In addition, large juveniles in the SH group and small juveniles in the swimming group tended to show long dispersal distances. These results suggest an effective sorting pressure against juveniles with active swimming behavior. This sorting pressure may accumulate in isolated char populations located above a tall migration barrier and contribute to the creation and maintenance of the reported interpopulation variation in SH behavior.

Keywords:

39 adaptation to flow, downstream movement, downstream drift, juvenile fish, salmonid

40

1 Introduction

Numerous phenotypes can affect the occurrence and distance of organism dispersal (Edelaar et al., 2008; Shine et al., 2011a; Bonte et al., 2012; Edelaar & Bolnick, 2012; Bonte & Dahirel, 2017; Holtmann et al., 2017). One phenotype that is particularly important for dispersal is body size. Jenkins et al. (2007), in a meta-analysis of species ranging from bacteria to mammals, demonstrated that large organisms generally disperse over greater distances than small organisms. Conversely, however, larger individuals are less likely to demonstrate downstream dispersal in riverine vertebrates such as fishes (Meffe, 1984; Chapman & Kramer, 1991; Blondel et al., 2021) and larval salamanders (Petranka et al., 1987; Thiesmeier & Schuhmacher, 1990; Veith et al., 2019). Physiological and behavioral phenotypes can also affect dispersal. Metabolic rates and boldness are associated with dispersal tendency in the round goby *Neogobius melanostomus* (Myles-Gonzalez et al., 2015) and the brown trout *Salmo trutta* (Jones et al., 2021). Individuals with poor nutritional status tend to disperse downstream in the larval European fire salamander *Salamandra salamandra* (Schafft et al., 2022), and bold dunnock *Prunella modularis* with short flight initiation distances disperse into urban habitats, whereas shy individuals remain in rural habitats (Holtmann et al., 2017).

Phenotype-dependent dispersal can in turn generate variations in phenotype among local populations (Phillips et al., 2006; Bolnick et al., 2009; Holtmann et al., 2017; Yamada & Wada, 2021). For instance, in species undergoing range expansion, individuals with high dispersal ability are more likely to reach and persist in local populations at the edge of the range (Phillips et al., 2006, 2008; Shine et al., 2011a). In fact, differences in dispersal

63 phenotypes between local populations in the core and edge of the range have been reported
64 in many range-expanding animals including insects (Berggren et al., 2012; Ochocki &
65 Miller, 2017; Weiss-Lehman et al., 2017), mammals (Forsman et al., 2011), birds
66 (Berthouly-Salazar et al., 2012), amphibians (Phillips et al., 2006; Pelletier & Carstens,
67 2016; Louppe et al., 2017), and fishes (Myles-Gonzalez et al., 2015; Aulus-Giacosa et al.,
68 2021).

69 When a dispersal phenotype has a genetic basis (Ronce, 2007; Bonte & Dahirel,
70 2017), variations in the phenotype among individuals can give rise to microevolutionary
71 changes (reviewed in Edelaar & Bolnick, 2012; see also Kawecki & Ebert, 2004; Shine et
72 al., 2011a). For example, the occurrence of dispersal is affected by body morphology, a
73 genetically determined trait, in the three-spined stickleback *Gasterosteus aculeatus*, and
74 this could contribute to the adaptive divergence of this species, with shallower bodies
75 becoming predominant in lakes and deeper bodies in inlet streams (Bolnick et al., 2009).
76 Consequently, phenotype-dependent dispersal has recently gained recognition as an
77 evolutionary pressure caused by gene flow (Edelaar et al., 2008; Shine et al., 2011a;
78 Edelaar & Bolnick, 2012). Shine et al. (2011a) defined this evolutionary pressure as
79 "spatial sorting" arising from differential dispersal rates and distinguished it from natural
80 selection, which arises from differential fitness. In this paper, we therefore refer to the
81 evolutionary pressure from spatial sorting as "sorting pressure."

82 The evolutionary effects of sorting pressures are often considered transient
83 because the biased phenotypic distributions created by sorting pressures tend to dissolve
84 once range expansion abates (e.g., Lee, 2011; Shine et al., 2011b). Lee (2011) suggested

85 that individuals with high dispersal ability along the edge of an expanding range will
86 eventually disperse back into the core population, homogenizing the phenotypic
87 distribution. For this reason, sorting pressures are generally not regarded to have a
88 cumulative effect (Lee, 2011). However, in riverine systems, recent studies have shown that
89 sorting pressures caused by downstream dispersal can be cumulative (Allgayer et al., 2021).
90 Allgayer et al. (2021) examined individual-based evolutionary models that included
91 selection pressures from natural selection and sorting pressure and found that cumulative
92 sorting pressure can swamp natural selection and drive evolutionary changes that reduce
93 dispersal tendencies in upstream populations. Therefore, knowledge of sorting pressures
94 caused by downstream dispersal should be important for gaining a better understanding of
95 the evolution of riverine organisms. Despite this, few studies to date have regarded
96 downstream dispersal as an evolutionary pressure (but see Bolnick et al., 2009; Jiang et al.,
97 2015; Blondel et al., 2020; Yamada & Wada, 2021).
98 The occurrence of phenotype-dependent downstream dispersal is well
99 documented for dispersal caused by pulse flooding events, which cause strong flows that
100 greatly exceed the coping capacity of the organisms (e.g., Meffe, 1984; Chapman &
101 Kramer, 1991; Parkyn & Colier, 2004; Clark & Kershner, 2011; Blondel et al., 2020;
102 Yamada & Wada, 2021; Schafft et al., 2022). However, phenotype-dependent downstream
103 dispersal can occur even in constant flows under non-flooding conditions that organisms
104 can potentially cope with (i.e., “ordinary” flows) (Petranka et al., 1987; Thiesmeier &
105 Schuhmacher, 1990; Bolnick et al., 2009; Jiang et al., 2015). Sorting pressure from ordinary
106 downstream dispersal can be an important evolutionary force because it is more stable and

more frequent than flood conditions. This study aims to evaluate the sorting pressures arising from downstream dispersal under ordinary flow conditions in juvenile white-spotted char *Salvelinus leucomaenis*.

2 Materials and methods

2.1 Study species

White-spotted char is a stream-dwelling salmonid with life-history polymorphism (i.e., it is found in anadromous and resident forms). In this study, we focused on young-of-the-year juveniles. Salmonid juveniles are generally observed to be stationary on the substrate when they are inactive (Arnold et al., 1991; Yamada et al., 2019; Hasegawa et al., 2020). Here, we define station-holding (SH) behavior as a benthic behavior in which juveniles settle to the substrate and maintain their position (Yamada & Wada, 2023a, 2023b), and use the occurrence of this behavior as an index of behavioral activity. The genetic basis of SH behavior has not been studied, but that of metabolic rates (Kendall et al., 2015) and freezing behavior (Kortet et al., 2014; Ågren et al., 2019), which are likely associated with SH behavior, have been demonstrated repeatedly in salmonids. Therefore, we can expect a genetic component for SH behavior (see Yamada & Wada, 2023b).

2.2 Evaluation of sorting pressure from ordinary downstream dispersal

We conducted outdoor experiments from late June to early July 2019 to examine the relationships between body size or SH behavior and downstream dispersal under ordinary flow conditions. We collected 25, 24, 27, 25, 24, and 26 young-of-the-year

129 juvenile white-spotted char using hand nets during the early mornings of 19 June and 1, 3,
130 8, 10, and 12 July 2019, respectively, from the Kurohajiri River, southern Hokkaido, Japan
131 (lat 41°59′38″N, long 140°52′16″E). There were no migration barriers around the sampling
132 site. We distinguished young-of-the-year juveniles by their body size and color pattern, as
133 they were clearly smaller than the other cohorts in this season and lacked white spots. The
134 juveniles were brought back to the laboratory of the Nanae Fresh-Water Station, Northern
135 Biosphere Field Science Center, Hokkaido University (lat 41°54′04″N, long 140°41′25″E).
136 An artificial narrow channel (58 cm in width) at the Nanae Fresh-Water Station was used
137 for the outdoor experiments (Figure 1). The channel flows a mix of river water from the
138 neighboring Kunebetsu River and groundwater. There were ten steps (elevation changes) at
139 1.8-m intervals in the channel (Figure 1).
140 To evaluate phenotype-dependent dispersal, juveniles were gently released into the
141 uppermost step section of the experimental channel (step section 0 in Figure 1) about an
142 hour after they were collected. The mean water flows on the six experimental dates were
143 3.316, 3.424, 2.980, 3.136, 2.944, and 3.096 L s^{-1}, respectively. The flow rate per unit
144 width (0.0054 ± 0.0003 $m^3 s^{-1} m^{-1}$, mean ± SD) was comparable to that of ordinary river
145 conditions in the wild habitat of white-spotted char (see Yamamoto et al., 2006). The
146 channel depth was about 10 cm, shallower than reported for the natural habitat of this
147 species (Morita et al., 2000), but not extreme, as juveniles inhabit shallower water than
148 adults (see also Yamamoto et al., 2006). Although juvenile densities in the initial release
149 section were higher than in the natural habitats (Morita et al., 2000), previous studies on
150 salmonid juveniles have conducted similar channel experiments at even higher densities

151 and provided biologically interpretable results (e.g., Crisp, 1991; Nagata et al., 1994;
152 Nagata & Irvine, 1997; see also Crisp & Hurley, 1991a, 1991b). After the juveniles were
153 released, the channel was left flowing for 5 h in the daytime to allow them to disperse. At
154 the end of the experiment, the water flow was stopped, and the juveniles in each step
155 section were collected by using a small hand net. To prevent the escape of juveniles, the
156 lowest section (i.e., section 8 in Figure 1) was monitored during the experiments, and
157 individuals reaching that step section were gently collected with a hand net and stored in an
158 aerated container with water from the same source as the experimental channel.
159 The juveniles used in the outdoor experiments were then brought to the
160 thermostatic chamber (15 °C) of the Controlled Environment Rooms on the Hakodate
161 campus of Hokkaido University (lat 41°48′34″N, long 140°43′09″E). The juveniles from
162 each step group were kept separately in small holding tanks (30 × 18 × 24 cm, water depth,
163 10 cm) in the thermostatic chamber until the next procedure.
164 We observed juvenile behavior on the day after each outdoor experiment. To
165 quantify SH behavior, juveniles were individually placed in an observation tank in the
166 thermostatic chamber (Figure 2). The observation side of the tank was covered with an
167 opaque gray sheet to ensure that the juveniles would not be disturbed by the activities of the
168 researcher conducting the experiments. The water in the observation tank was circulated by
169 a submersible pump (e-ROKA PF701; GEX Co. Ltd., Osaka, Japan) at a flow rate of 0.16 L
170 s^{-1} (Figure 2). The inside of the tank was lit by an LED light with sufficient intensity for the
171 behavioral observations. Behaviors were recorded by using a digital camera (TG-4;
172 Olympus Co. Ltd., Tokyo, Japan) fixed inside the opaque sheet. We observed whether an

individual showed SH behavior at 1-s intervals from 0 to 540 s after a 60-s acclimation period immediately after the introduction of the fish, and the sum of the intervals during which SH behavior was observed was recorded as the SH behavior time for the individual.

The SH behavior in the observation tank was expected to reflect the behavior in the experimental channel since sedentary behavior is repeatable in juveniles of the genus *Salvelinus* (Wilson & McLaughlin, 2007; Biro & Ridgway, 2008). For instance, Wilson and McLaughlin (2007) found that juvenile brook trout *Salvelinus fontinalis* that were sedentary in the field were also sedentary in an experimental tank and tended to remain at the bottom of the tank.

On the basis of a histogram of the time spent in SH behavior (Figure 3), we classified individuals with an SH behavior time of less than 10 s as belonging to the "swimming group" and the other individuals as belonging to the "SH group." Although this classification results in the loss of some information about behavior, it allows for the proper construction of a statistical model and facilitates a clear biological interpretation of the results of the analysis (see below).

After behavioral observations, the left side of each juvenile was photographed by using a digital camera (TG-4; Olympus Co. Ltd.) fixed on a camera stand. We used these photographs and image analysis software (ImageJ; National Institutes of Health, Bethesda, MD, USA) to measure fork length (FL) in millimeters as an index of body size. Subject juveniles were returned to their original habitat after all outdoor experiments had been completed.

195 *2.3 Data analysis*

196 We used a hurdle model with random effects to analyze the occurrence of
197 downstream dispersal and the dispersal distance (the number of steps over which juveniles
198 dispersed) in the outdoor experiments by using the *glmmTMB* function in the package
199 "glmmTMB" (Brooks et al., 2017). We used a binomial distribution with a logit link
200 function for the zero versus non-zero component of the model (i.e., the occurrence of
201 downstream dispersal), and a truncated Poisson distribution with a log link function for the
202 zero-truncated component (i.e., the number of steps over which juveniles dispersed). For
203 both model components, the explanatory variables were FL, behavioral group (SH group =
204 1, swimming group = 0), and their interaction. A random factor was included to allow each
205 behavioral group to have a separate random slope for each experimental day to properly
206 evaluate the interaction term (i.e., [1 + FL | experimental day:behavioral group]; see
207 Arnqvist, 2020). The interaction terms were removed from the model if they did not have a
208 significant effect at $\alpha = 0.05$, and a random factor for the reduced model was modeled so
209 that each behavioral group had separate random intercepts for each experimental day (i.e.,
210 [1 | experimental day:behavioral group]). We used R version 4.1.0 (R Core Team, 2021) for
211 all statistical analyses.

212

213 **3 Results**

214 A total of 151 juveniles were examined in the outdoor experiments (FL, 46.9 ± 7.4 mm). A
215 total of 21 juveniles dispersed downstream from the release section over six experiments.
216 Based on histograms of SH behavior time, 130 individuals (FL, 47.5 ± 7.0 mm) were

217 classified as belonging to the SH group and 21 individuals (FL, 43.1 ± 8.5 mm) to the
218 swimming group (Figure 4). The fork length of juveniles in the swimming group was
219 significantly smaller than in the SH group (Welch's *t*-test, $t = -2.27$, $df = 24.65$, $P = 0.032$;
220 Figure 4).

221 Eight juveniles (FL, 60.3 ± 2.9 mm) were collected in the upstream section above
222 the uppermost step, with a height of 20 cm (see Figure 1) and their FLs were significantly
223 larger than those of the other juveniles (Welch's *t*-test, $t = -12.18$, $df = 12.01$, $P < 0.001$;
224 Figure 5). However, there were no differences between this group and the other juveniles
225 either in the time spent in SH behavior (Wilcoxon rank sum test, $W = 653.5$, $P = 0.501$) or
226 in the proportion of juveniles assigned to the two behavioral groups (Fisher's exact test, $P =$
227 0.308). These eight juveniles did not pass into any downstream steps and were therefore
228 treated as juveniles without downstream dispersal.

229 The hurdle model for the zero versus non-zero component revealed that the
230 occurrence of downstream dispersal was significantly lower in the SH group than in the
231 swimming group (zero versus non-zero model: $n = 151$; $z = -2.276$, $P = 0.023$; Figure 6a,
232 Table 1), but FL had no effect (Table 1). The hurdle model for non-zero components
233 detected a significant interaction (zero-truncated model: $n = 21$; $z = 2.328$, $P = 0.020$; Table
234 1), indicating a negative relationship between dispersal distance and size (FL) in the
235 swimming group, but a positive relationship in the SH group (Figure 6b).

236

237 **4 Discussion**

238 Downstream dispersal was phenotype-dependent under ordinary flow conditions in juvenile

239 white-spotted char. Juveniles in the swimming group moved downstream from the initial
240 release section more frequently than those in the SH group. This result is consistent with
241 the general understanding of displacement in other flow-sensitive species, such as larval
242 salamanders (Schafft et al., 2022), aquatic invertebrates (Brittain & Eikeland, 1988; Naman
243 et al., 2016), and small fishes (Lechner et al., 2016), where active individuals are more
244 likely to encounter fast currents and thus are at higher risk of downstream displacement.
245 The occurrence of downstream dispersal, on the other hand, could also have been
246 affected by competitive interactions among juveniles because all fish were initially released
247 into the single upstream section of the experimental channel, where the high density of
248 juveniles may have fostered competition. In this case, large and active juveniles would be
249 expected to avoid downstream dispersal most successfully since they would generally have
250 an advantage in competitive interactions (Näslund & Johnsson, 2016; Church & Grant,
251 2018). However, our results show that downstream dispersal occurred more often in the
252 active swimming group than in the sedentary SH group and was not affected by body size.
253 This suggests that competitive interactions did not drive the occurrence of downstream
254 dispersal identified in our results.
255 Alternatively, the initial high density in the release section may have caused active
256 downstream dispersal of juveniles seeking downstream habitats with lower densities.
257 Juveniles in the swimming group actively swam in the experimental tank and showed only
258 short SH behavior time (i.e., less than 10 s out of 540 s), and they likely had high metabolic
259 rates that led to high dispersal tendencies (e.g., Myles-Gonzalez et al., 2015). We did not,
260 however, find a trend toward higher dispersal occurrence in larger individuals, which have

261 a greater physical advantage in dispersal (Jenkins et al., 2007; Jones et al., 2021). In
262 addition, although the outdoor experiments were conducted during the daytime, juvenile
263 salmonids generally exhibit active downstream dispersal during the nighttime to avoid
264 predation risk (e.g., Northcote, 1981; Crisp, 1991; Crisp & Hurley, 1991b; Nagata et al.,
265 1994; Riley et al., 2013, 2015). We therefore suggest that the occurrence of downstream
266 dispersal observed in this study is mainly initiated by downstream displacement.
267 The relationship between dispersal distance and body size differed between the
268 two behavioral groups. In the SH group, smaller individuals had shorter dispersal distances.
269 Smaller individuals are generally better able to avoid downstream displacement in benthic
270 animals, including gastropods (Moore, 1964; see also Le Pennec et al., 2017), aquatic
271 insects (Poff et al., 1991), crayfish (Parkyn & Collier, 2004; Clark & Kershner, 2011), and
272 salmonid juveniles (Good et al., 2001; see also Heggenes et al., 2013), and this pattern is
273 thought to be due to small individuals having less hydrodynamic stress and better access to
274 a wide range of benthic shelters (Clark & Kershner, 2011). The small juveniles in the SH
275 group may have had this small-size advantage because they likely spent a lot of time in the
276 benthic area of the experimental channel. On the other hand, large juveniles in the SH
277 group may have engaged in active downstream dispersal. In fact, some large juveniles in
278 the SH group reached the lowest section of the experimental channel, as did small juveniles
279 in the swimming group. Given that larger fish generally have better swimming ability (e.g.,
280 Chapman & Kramer, 1991; Blondel et al., 2021; Jones et al., 2021), it would be difficult to
281 explain the dispersal distances of the large SH juveniles by downstream displacement alone.
282 In the swimming group, by contrast, dispersal distances became slightly shorter with

283 increasing body size. This trend is consistent with the pattern of downstream displacement
284 reported for non-benthic fishes (Chapman & Kramer, 1991; Blondel et al., 2021).
285 Additionally, small juveniles in the swimming group were estimated to have longer
286 dispersal distances than those in the SH group. Juveniles in the swimming group would not
287 have experienced the small-size advantage related to the use of benthic shelter (e.g., Clark
288 et al., 2008) because they frequently leave the benthic area. However, caution should be
289 exercised in inferring the cause of this weak trend because of the small sample size.
290 There are some limitations to our inferences regarding the mechanisms that
291 produced the observed patterns of downstream dispersal. Eight large juveniles swam over
292 the uppermost step in the experimental channel, which was 20 cm in height, suggesting that
293 large juveniles with strong swimming ability could ascend the channel (see also Johnson et
294 al., 2012; Jones et al., 2021). Therefore, the observed dispersal distance and dispersal
295 occurrence of large juveniles may have been lessened by their return to upstream steps. For
296 example, the lack of an observed effect of body size on dispersal occurrence in the present
297 study could be attributed to the return of large juveniles from downstream sections.
298 Although it is unlikely that dispersed individuals would be motivated to return to the high-
299 density initial section, caution should be exercised in interpreting the relationship between
300 body size and downstream dispersal in particular.
301 The observed trends in downstream dispersal suggest that several sorting pressures
302 acted on the juvenile white-spotted char. Specifically, we can infer the existence of sorting
303 pressures against small juveniles in the swimming group and large juveniles in the SH
304 group. The occurrence of downstream dispersal, in addition, was higher for the swimming

group than for the SH group, suggesting the importance of sorting pressures against the swimming juveniles. On the other hand, sorting pressures might not be cumulative for the SH group, because large juveniles have a strong ability to swim against a current and return upstream (see also Johnson et al., 2012; Jones et al., 2021). Overall, the present study highlights the sorting pressure against swimming juveniles of white-spotted char. The sorting pressure against swimming juveniles is likely to have been flow-driven as described above. Therefore, this sorting pressure could act even more strongly under high flow conditions, such as during snowmelt floods that coincide with the early part of the juvenile growing season (Fausch et al., 2001), because the occurrence and the distance of downstream displacement would be increased by strong water flow. Although the results of our study are preliminary, this inference leads us to expect that the sorting pressure creates and or maintains functional traits reducing downstream displacement in wild populations.

The sorting pressure identified in this study operates most strongly against small swimming juveniles. Therefore, juvenile white-spotted char would be expected to exhibit behavioral plasticity, with smaller individuals being more sedentary. However, in this study, juveniles of the swimming group were smaller than those of the SH group, which is the opposite of the expected pattern. This suggests that the sorting pressure was overridden by other factors. The juveniles used in this study were collected from anadromous populations, in which anadromous and resident individuals coexist (Morita et al., 2000; Yamada & Wada, 2023b). In such populations, the sorting pressure acting on juveniles can be diluted by the upstream migration of anadromous parents. Anadromous populations, in addition, generally contribute to high juvenile density due to the greater fecundity of anadromous females than

resident females (Morita et al., 2000), which would lead to increased competition among juveniles. The abundance of small swimming juveniles might reflect the need for increased behavioral activity among small subordinate juveniles to support compensatory growth (Yamada & Wada, 2023b).

However, stream fishes also persist in habitats where fish cannot return to their original habitat once they have dispersed downstream (reviewed by Northcote, 2010; Zarri et al., 2022). For instance, white-spotted char populations often persist in river sections above tall impassable barriers such as artificial check dams (Morita et al., 2000; Sato, 2006; Yamada et al., 2019; Hasegawa et al., 2020; Yamada & Wada, 2023b). In these above-dam populations, fish cannot return to their original habitat once they are dispersed downstream of the dam (Morita & Yamamoto, 2001; Yamada & Wada, 2023b), and thus the sorting pressure caused by downstream dispersal should not be diluted by upstream migration from the downstream side of the dam. As a result, sorting pressures of the type found in the present study would accumulate in above-dam populations and lead to more sedentary behavior over time. Consistent with this expectation, Yamada and Wada (2023b), who conducted a comparative study of juveniles of this species in southern Hokkaido, Japan, found that juveniles in above-dam populations spent more time on SH behavior than those of populations in river sections without dams. Although it is unclear to what extent the sorting pressure found in this study contributes to interpopulation variation in the field, this consistency supports the notion that this type of sorting pressure can give rise to and maintain functional behaviors.

However, at this stage, the strength of our inferences is limited by several factors.

First, our study did not examine the genetic basis of SH behavior. Second, the experimental channel used in this study did not fully simulate the natural environment, such as patterns in juvenile density and water depth, due to equipment limitations. These challenges make it difficult at this stage to apply the inferred sorting pressures to field conditions or to conclude that sorting pressures actually drive evolutionary change. Therefore, further studies, including common-garden experiments and field experiments using natural streams, are needed to validate our evolutionary hypothesis. Despite these limitations, the present study is a pioneering attempt to consider the downstream dispersal of riverine organisms as a sorting pressure (see also Allgayer et al., 2021; Yamada & Wada, 2021). This perspective could contribute to a better understanding of the evolution of riverine organisms in future studies.

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Data availability statement

Data are available from the authors upon reasonable request.

Conflict of interest

The authors declare that they have no conflicts of interest.

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Table 1

Results from a hurdle model with a random factor for outdoor experiments with juvenile white-spotted char *Salvelinus leucomaenis* in an artificial channel. "Zero vs. non-zero component" indicates the analysis of the occurrence of downstream dispersal from the release section (i.e., section 0 in Figure 1) and "zero-truncated component" indicates the analysis of the number of steps traversed by dispersed individuals (i.e., the distance of downstream dispersal). "Behavioral group" refers to the results for juveniles with more than 10 s of station-holding behavior (i.e., the SH group). Significant *P* values are shown in bold. Random intercepts and slopes were modeled and estimated as varying among the 12 subgroups (i.e., 6 experimental days × 2 behavioral groups) to facilitate model convergence.

Fixed effects	Estimate	SE	*z*	*P*
Zero vs. non-zero component (binomial error distribution with logit link)				
Intercept	0.740	1.505	0.492	0.623
Fork length	−0.034	0.034	−0.991	0.322
Behavioral group (SH group)	−1.281	0.563	−2.276	**0.023**
Zero-truncated component (truncated Poisson error distribution with log link)				
Intercept	2.880	3.988	0.722	0.470
Fork length	−0.059	0.097	−0.610	0.542
Behavioral group (SH group)	−11.505	4.683	−2.457	**0.014**
Interaction	0.253	0.109	2.328	**0.020**

Random factors	SD	Correlation
Zero vs. non-zero component		
Random intercept	0.00014	-

Zero-truncated component		
Random intercept	2.55681	-
Random slope	0.04058	−0.95

649

650

651 **Figure legends**

652 **Figure 1**

653 Schematic cross-sectional view of the experimental channel with small steps (gray
654 rectangles) for the outdoor experiments conducted at the Nanae Fresh-Water Station, Field
655 Science Center for Northern Biosphere, Hokkaido University. The height of the top step
656 was double that of the other steps. Fabric was placed under each step to lessen the shock
657 when juveniles fell from the step above. Riverine substrate was placed in each section of
658 the channel (mean substrate diameter based on mass: 15.0 mm). The mean slope of the
659 channel was 3.3°. The open arrow indicates the direction of flow.

660

661 **Figure 2**

662 Schematic of the observation tank. For simplicity, the opaque sheet covering the front of the
663 tank has been omitted from the illustration.

664

665 **Figure 3**

666 Histogram of station-holding (SH) behavior time for juvenile white-spotted char *Salvelinus*
667 *leucomaenis* in outdoor experiments. Individuals with less than 10 s of SH behavior (gray
668 bar) were assigned to the "swimming group," and the remaining juveniles (open bars) were
669 assigned to the "SH group"; "behavioral group" was used as a categorical variable in a
670 hurdle model for the outdoor experiments.

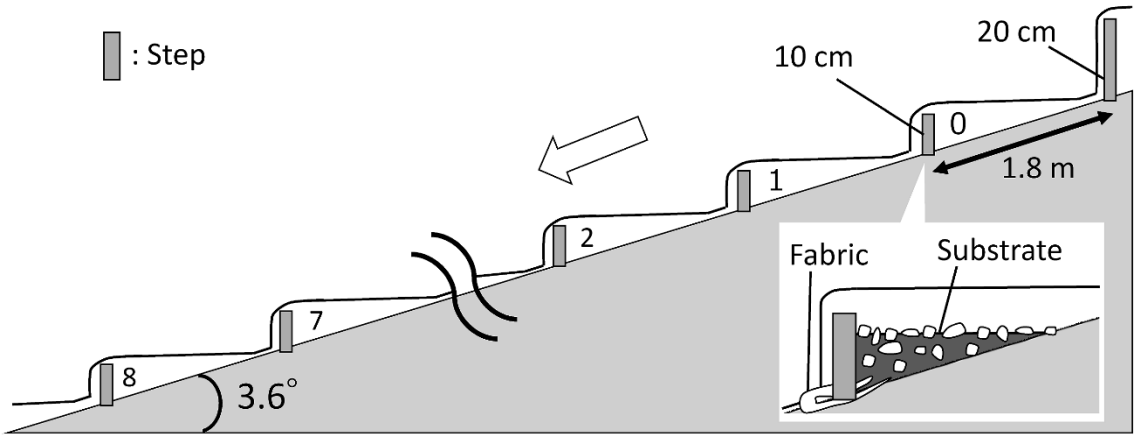
671

672 **Figure 4**

673 Stacked size–frequency distribution of juvenile white-spotted char *Salvelinus leucomaenis*
674 belonging to two behavioral groups. Juveniles with less than 10 s of station-holding (SH)
675 behavior were assigned to the "swimming group," and the remaining juveniles were
676 assigned to the "SH group."
677
678 **Figure 5**
679 Comparison of fork length between juvenile white-spotted char *Salvelinus leucomaenis* that
680 ascended above the uppermost step of the experimental channel and those that did not.
681 Whiskers indicate the maximum and minimum values of non-outlier data. The bottom and
682 top edges of each box indicate the first and third quartiles, respectively. Thick horizontal
683 lines indicate the medians. Gray points indicate the raw data.
684
685 **Figure 6**
686 Results of a hurdle model for the outdoor experiments with juvenile white-spotted char
687 *Salvelinus leucomaenis* (Table 1). Relationship between fork length and the occurrence of
688 downstream dispersal from the release site (i.e., section 0 in Figure 1) (0 = not dispersed; 1
689 = dispersed) **(a)**, and the distance of downstream dispersal (number of steps dispersed) **(b)**.
690 Filled black and open circles indicate juveniles with less than 10 s of station-holding (SH)
691 behavior (i.e., the swimming group) and the remaining juveniles (i.e., the SH group),
692 respectively. Black dashed lines and solid gray lines show estimates of the zero versus non-
693 zero component **(a)** and the zero-truncated component **(b)** of the hurdle model for the
694 swimming and SH juveniles, respectively. In panel **(b)**, the zero data not subjected to

695 analysis are plotted in a lighter shade of gray.

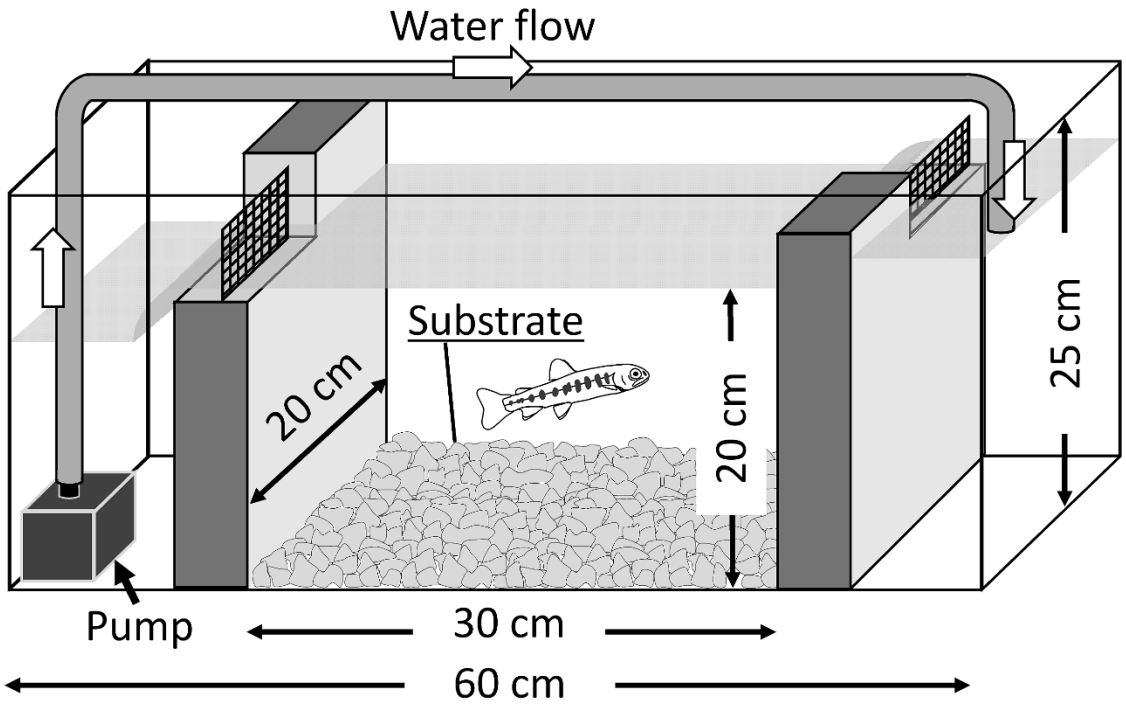
696



697

698 **Figure 1**

699



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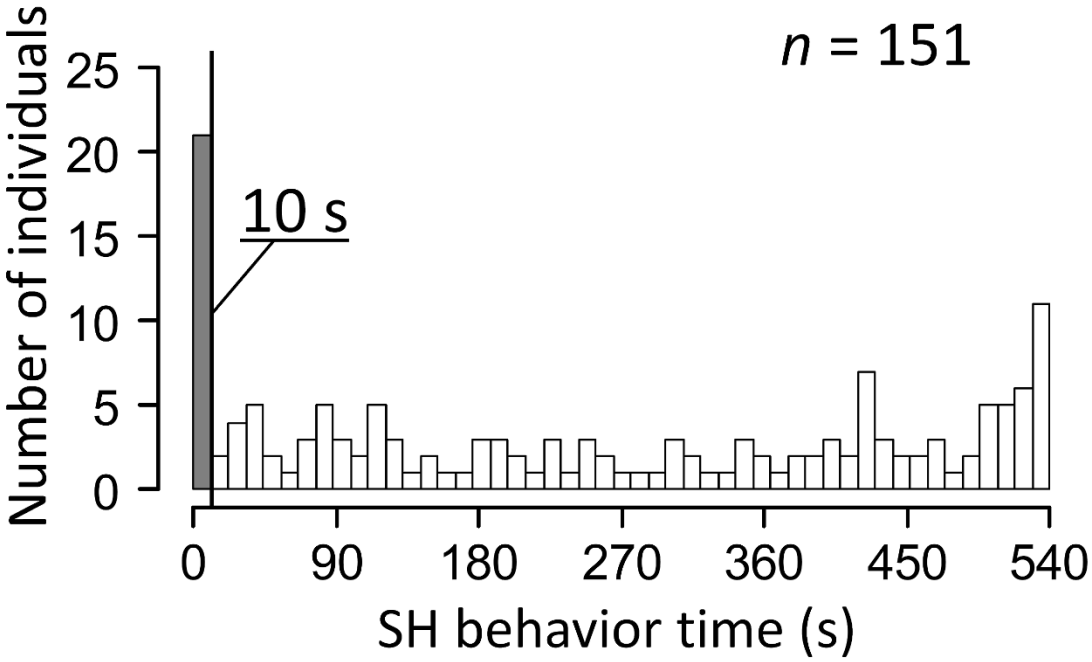
701 **Figure 2**

702



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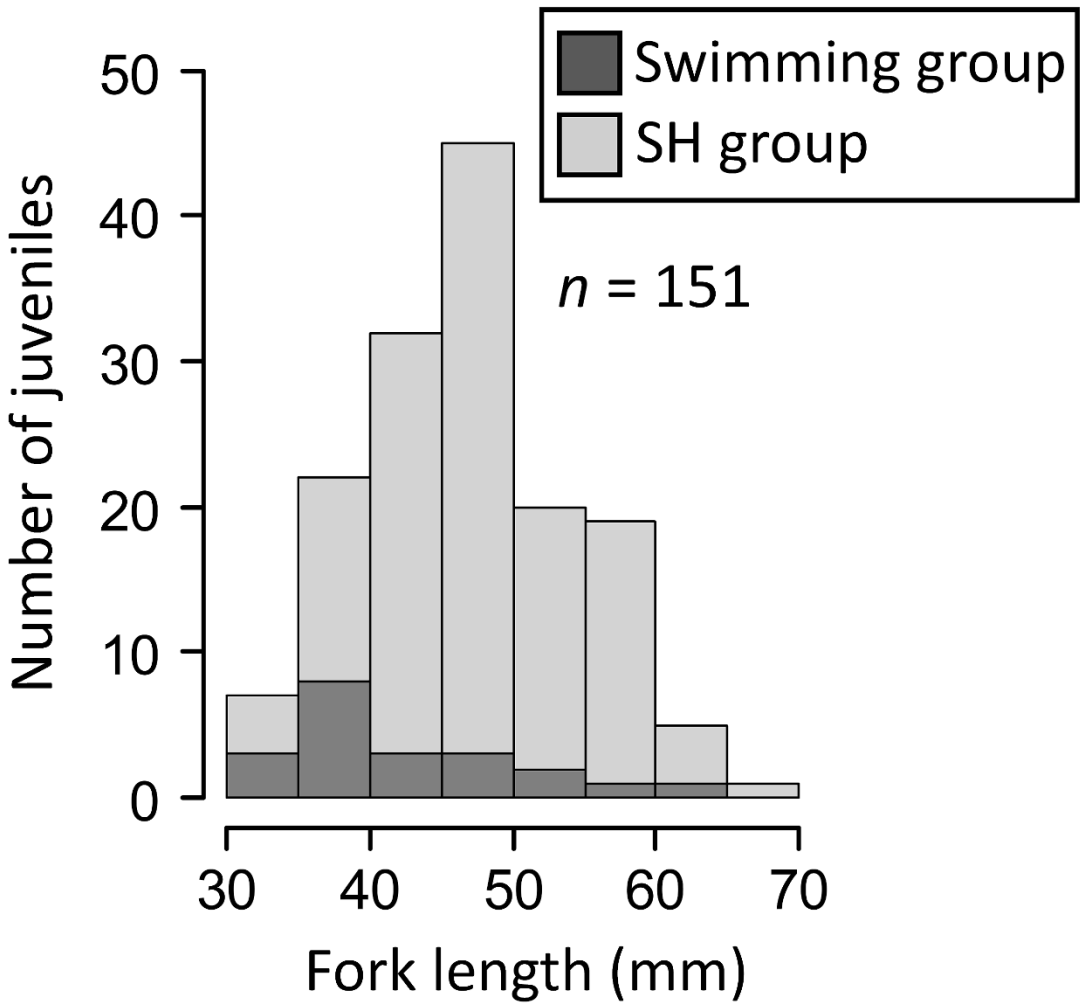
704 **Figure 3**

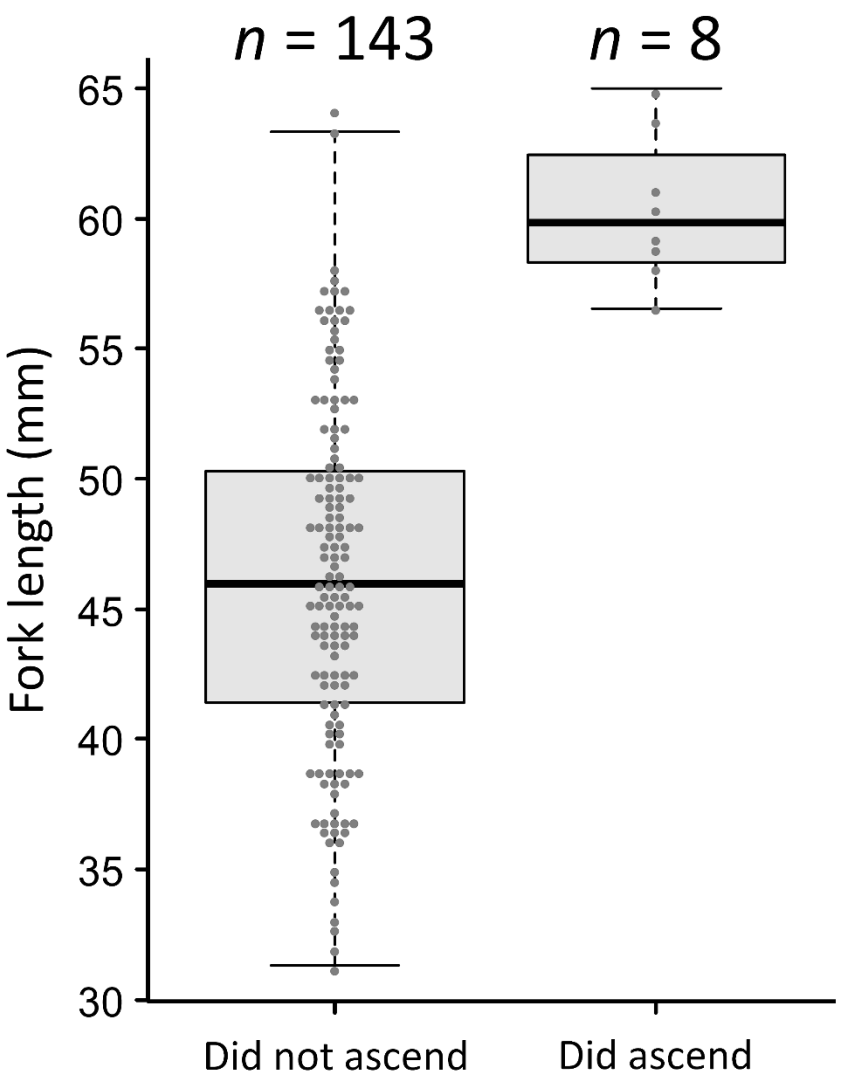
705



706

707 **Figure 4**

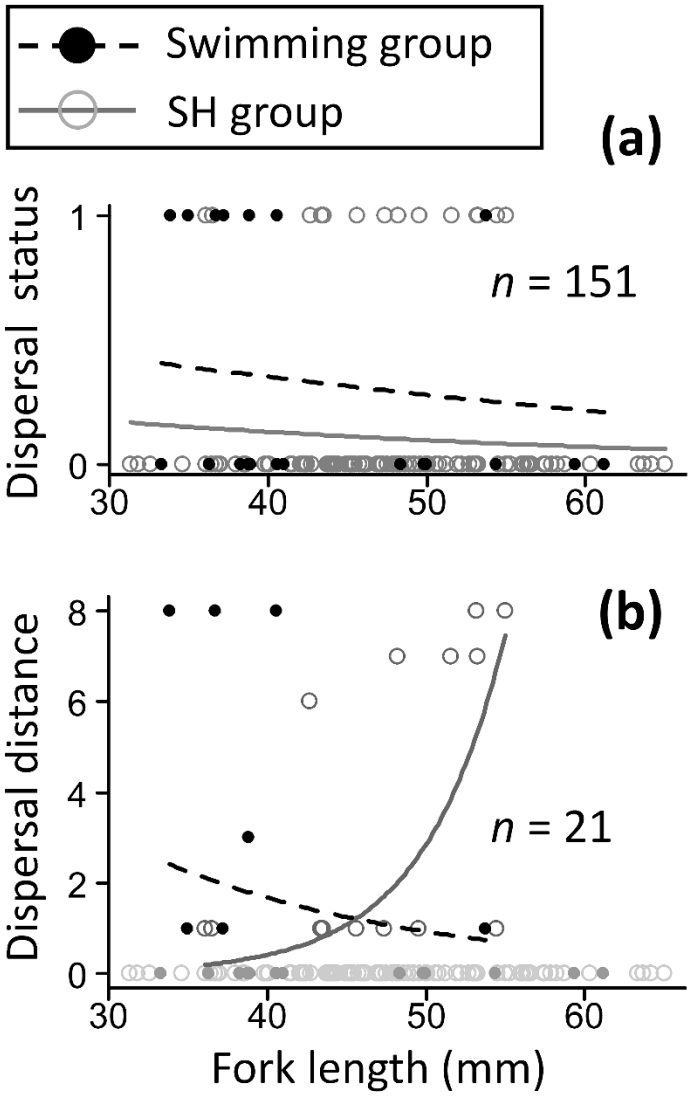
708



709

710 **Figure 5**

711



712

713 **Figure 6**