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1 **Size-dependent growth tactics of a partially migratory fish before migration**

2

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17

18

19 **Authors' contributions**

20 RF, KM, YK and OK conceived the ideas. All authors designed the methodology and  
21 collected the data. RF and OK analyzed the data and led the writing of the manuscript.  
22 All authors contributed critically to the drafts and gave final approval for publication.

23

24 **ABSTRACT**

25 In many migratory species, smaller migrants suffer higher mortality rates during the  
26 risky migration. To minimize the size-selective mortality, migrants with smaller body  
27 sizes would need to accelerate growth rates or delay migration timing to attain a large  
28 enough body size prior to migration. To test these predictions, we investigated size-  
29 dependent patterns of growth rates and migration timing of juvenile masu salmon  
30 (*Oncorhynchus masou*) before their oceanic migration. We tracked uniquely marked  
31 individuals in a study population consisted of oceanic migrants and river-dwelling  
32 residents using mark-recapture surveys and PIT-tag antenna-reader system. Data  
33 supported our predictions about size-dependent growth rates and migration timing. For  
34 approximately 6 months before outmigration (i.e., between the decision of migration  
35 and the start of migration), eventual migrants grew more than residents if their initial  
36 size was smaller, but such a difference in growth rate diminished for fish with larger  
37 initial sizes. In addition, smaller eventual migrants delayed the timing of outmigration  
38 compared to larger individuals, to attain a larger body size in the river prior to  
39 migration. These results suggest that size-selective mortality during migration has  
40 shaped size-dependent patterns of the pre-migration growth in migratory masu salmon.  
41 Size-conditional changes in growth rate and duration of pre-migration period may be an  
42 adaptive tactic for the migratory animals.

43 **Keywords:**

44 anadromous fish, growth period, growth rate, life history, *Oncorhynchus masou*

45

## 46 INTRODUCTION

47           Some animals compulsory or conditionally migrate between different habitats in  
48 particular life stages to improve their fitness (Dingle & Drake, 2007; Gross et al., 1988;  
49 Newton, 2010). Despite the apparent benefits of migration such as fast growth and high  
50 reproductive success (Chapman et al., 2012; McKinnon et al., 2010; Nøttestad et al.,  
51 1999), migration is not a universal behavior across species and individuals because it  
52 also incurs costs (Chapman et al., 2011). During the long trip, migrants are exposed to  
53 various biotic and abiotic stressors that lead to high mortality rates (Alerstam et al.,  
54 2003; Lok et al., 2015; Osterback et al., 2013; Sillett et al., 2002). Migratory species  
55 have evolved life history strategies to cope with the risk of migration (Furey et al.,  
56 2016; Roff, 1991).

57           Migratory animals suffer varying degrees of mortality en route due to energetic  
58 demands and risk of predation. Migrants begin their preparations for the long journey  
59 well before migration by adopting strategies to cope with the costs of migration. In  
60 particular, attaining sufficiently large body size prior to migration is critical for  
61 completing the risky migration because smaller individuals are more vulnerable to a  
62 multitude of stressors during migration (Koenings et al., 1993; Sogard, 1997; Zabel et  
63 al., 2002). This suggests that pre-migration growth is under natural selection, and hence  
64 it leads us to expect different growth patterns between migrants and non-migrants  
65 (Gillanders et al., 2015). In fact, average growth rates prior to migration are higher in  
66 migratory species compared to their non-migratory congeners (Chaplin & Chaplin,  
67 1981) and in migratory individuals compared to non-migratory conspecifics (Olsson &  
68 Greenberg, 2004; Palmer & Dingle, 1986; Snyder, 1991). Because rapid growth inflicts  
69 physiological and ecological costs (Hector & Nakagawa, 2012), the faster growth of

70 migrants before migration compared to residents represents an adaptive tactic of  
71 migratory individuals (Arendt, 1997; Roff, 1991).

72         However, growth tactics before migration may not be uniform among migratory  
73 individuals (i.e., eventual migrants) because ecological demands vary according to their  
74 status. In particular, growth tactics before migration may depend on body size of  
75 eventual migrants. Because mortality is size-dependent and smaller migrants suffer  
76 higher risk of mortality en route (Alerstam et al., 2003), smaller eventual migrants  
77 should enhance their growth rate before migration. However, accelerated growth may  
78 incur behavioral and physiological costs (Arendt, 1997; Dmitriew, 2011 Metcalfe &  
79 Monaghan 2001). For example, more foraging activities needed for faster growth are  
80 intimately associated with increased risk of predation and competition (Nicieza &  
81 Metcalfe, 1999; Stoks et al., 2005). Furthermore, faster growth negatively affects  
82 physiological conditions such as fat storage and immune function (Stoks et al, 2006).  
83 Thus, larger eventual migrants may be less incentivized to invest in body growth to  
84 ensure survival until migration commences. Alternatively, smaller eventual migrants  
85 may delay migration until they attain sufficiently large body size. Again, larger eventual  
86 migrants may be less incentivized to delay migration, since later-arriving migrants may  
87 have more limited access to resources at the new habitat. Despite these plausible  
88 expectations, only a few studies have investigated individual variation in the pre-  
89 migration growth tactics within populations (but see Bohlin et al., 1996; Metcalfe et al.,  
90 1998). Filling this knowledge gap should contribute to the mechanistic understanding of  
91 tradeoffs that shape intraspecific variation in life history tactics. Furthermore, these can  
92 also provide insights into variation in ecological roles of eventual migrants since the  
93 distinctive growth tactics are realized by different behaviors (e.g., active or non-active

94 foraging and early or late start of migration) with profound ecological consequences via  
95 altered predator–prey interactions (Bolker et al., 2003; Rohr et al., 2015; Schmitz et al.,  
96 2004).

97       Some animal populations consist of both migratory and non-migratory (i.e.,  
98 resident) individuals, and such partially migratory populations provide an ideal  
99 opportunity to test intraspecific variation in growth tactics in relation to the migration  
100 strategy. Masu salmon (*Oncorhynchus masou*) exhibits partial migration commonly in  
101 northern Japan (Kato 1991; Morita 2018). Adults spawn eggs in rivers, and some  
102 individuals complete their life entirely in the freshwater environment, but others migrate  
103 to the ocean after spending one or two years in the freshwater environment. Migrants  
104 descend the river to the ocean (i.e., seaward migration) in spring, but juveniles make  
105 decisions to migrate or not by the previous autumn (Nagae et al., 1994; Tamate &  
106 Maekawa, 2002). This has been evidenced by the physiological studies (i.e., the  
107 eventual migrants increase the concentration of smoltification-related hormone thyroxin  
108 by the previous autumn [e.g., Nagae et al., 1994]). Migrants achieve considerably  
109 higher growth rates in the resource-rich ocean, compared to freshwater residents. Upon  
110 return to the river for reproduction, body length of migrants is several times larger than  
111 that of mature residents (Morita, 2018; Tamate, 2012), and migrants that have returned  
112 to the river are more reproductively successful than mature residents. However, the  
113 migrants suffer high mortality rates during migration (Miyakoshi et al., 2001; Morita et  
114 al., 2014). Importantly, mortality during migration is typically size-selective where  
115 survival increases with body size until it reaches an asymptote at certain body size  
116 (Shimoda et al., 2003). Therefore, the ecological demands of smaller eventual migrants  
117 to grow are substantial. This allows us to make the following two predictions on size-

118 dependent growth patterns of eventual migrants. First smaller eventual migrants  
119 accelerate growth rates in the pre-migration period but larger ones don't. Second  
120 migration timing depends on body size of eventual migrants, where smaller individuals  
121 delay migration to attain a larger body size in the river before the ocean entry. To test  
122 these operational predictions, (1) we compared size-dependent patterns of growth rates  
123 between eventual migrants and residents during 6 months leading up to migration (i.e.,  
124 fall to spring), and (2) we investigated whether body size of eventual migrants in early  
125 spring just prior to migration explained their timing of seaward migration.

126

## 127 **METHODS**

### 128 **Study system**

129 Our study was conducted in the Horonai River, a small spring-fed stream (2–5 m  
130 wide) located in Hokkaido, Japan. The river is approximately 12 km long from its  
131 headwaters to the ocean, and our study area was established in the uppermost 5.32 km  
132 part (hereafter called the survey area) (Fig. 1). We marked the 5.32 km survey area by  
133 10 m increments to record fish locations. Our survey area was established to encompass  
134 the portion of the river occupied by juvenile masu salmon (Fig. 1).

### 135 **Capture-mark-recapture survey**

136 We conducted a capture-mark-recapture survey throughout the survey area on  
137 five occasions; (1) autumn 2018 (3<sup>rd</sup>–18<sup>th</sup> Sep-2018), (2) early spring 2019 (1<sup>st</sup>–5<sup>th</sup> Apr-  
138 2019), (3) autumn 2019 (7<sup>th</sup>–11<sup>th</sup> Oct-2019), (4) early spring 2020 (18<sup>th</sup>–26<sup>th</sup> Mar-2020),  
139 and (5) summer 2020 (25<sup>th</sup>–26<sup>th</sup> Jun-2020). On each survey occasion, we collected fish  
140 and recorded the section of capture (10-m scale) using a backpack electrofishing unit  
141 (300–400 V DC, model 12B, Smith-Root, Inc., Vancouver, WA, USA) and 3-mm mesh

142 dipnets (30 cm wide). Captured fish were anesthetized with eugenol (FA-100 DS  
143 Pharma Animal Health Co., Ltd.) to measure their fork length (nearest 1 mm) and body  
144 weight (nearest 0.1 g). We examined whether fish had been previously marked by  
145 checking for and recording a PIT tag (12.0 mm × 2.12 mm, Oregon RFID, Inc). Up to  
146 12 individuals (> 50 mm fork length) without PIT tags were randomly tagged in each  
147 10-m section on each sampling occasion. We inserted a tag in abdominal cavity of the  
148 fish through a small hole made by a clean scalpel. Fish were then allowed to recover  
149 from anesthesia in a bucket with fresh river water, and were released to the section of  
150 capture alive. We tagged a total of 3513 individuals (680 in 2018 autumn, 695 in 2019  
151 early spring, 1325 in 2019 autumn, and 813 in 2020 early spring).

#### 152 **Defining life history types and identifying migrants at seaward migration**

153 Juvenile masu salmon decide whether they migrate or not approximately half a  
154 year before descending the river (Nagae et al. 1994). However, identifying the life  
155 history types of individuals at this point is difficult visually in the field. Although an  
156 increase in concentration of smoltification-related hormone in the previous autumn is an  
157 indicator of eventual migrants, monitoring the physiological changes is logistically  
158 unrealistic when handling many individuals. In the present study, we identified the life  
159 history type of each individual based on behavioral evidence of outmigration. **The**  
160 **criteria we used is outlined below.**

161 In the Horonai River, masu salmon migrate to the sea from late April to early  
162 July. During the migration season of 2019 and 2020, we recorded individual fish  
163 descending the river (i.e., migrants) using two types of devices installed downstream of  
164 the survey area (Fig. 1). A pair of PIT antennas operated in 2019 and 2020 to  
165 automatically detect individuals descending the river and their migration timing (i.e.,

166 hereafter, river-descending timing). In addition, a fyke-net type trap was installed in  
167 2020 to capture river-descending fish (hereafter called the migrant trap).

168         The PIT antenna system was installed 4.6 km upstream from the river mouth, or  
169 2.3 km downstream from the lowermost boundary of the survey area. A pair of antennas  
170 was installed to determine the direction of fish passage. We detected 157 individuals in  
171 2019 and 256 individuals in 2020, and considered them migrants descending the river  
172 for the following reasons. First, the antennas were installed in a habitat not occupied by  
173 resident masu salmon, thus this is a transient movement in a corridor to the sea. Second,  
174 none of the individuals that passed the antennas in a downstream direction were  
175 detected again by the antennas system within the same year. Third, in an additional  
176 survey using a mobile PIT antenna (Oregon RFID, ORSR Single Antenna Reader)  
177 conducted just after the migration season of 2019 (July 23<sup>rd</sup>, 2019), we did not detect  
178 any fish with PIT tags between the antenna location and river mouth downstream.  
179 Fourth, all fish collected by the migrant trap showed external morphological features of  
180 migrants (see below).

181         The migrant trap was set at 5.7 km upstream from the river mouth (i.e., 1.2 km  
182 downstream of the survey area). The trap was placed where the river narrows (50 cm  
183 wide) just below a cascade (70 cm high). The trap operated from 04-Apr-2020 to 24-  
184 Jul-2020. The trap was checked three times daily (i.e., morning [4:00], evening [16:00],  
185 night [22:00]). Once anesthetized, fish were checked for PIT tags, and their fork length  
186 and weight were measured. In addition, we examined morphological signs of migration  
187 (i.e., smoltification), including silver-colored body and an accumulation of black  
188 pigments along the outer edges of the dorsal and caudal fins (Quinn, 2018). Migrants  
189 differed markedly in their external appearances from residents. When fish have

190 recovered from anesthesia, they were released to the pool habitat just below the trap. In  
191 2020, we trapped a total of 579 fish, among which 179 individuals had PIT tags (i.e.,  
192 recaptured individuals). All of the trapped fish were identified as migrants based on the  
193 external morphological characteristics.

194 We defined residents as individuals never detected by the antennas or captured  
195 by the trap. For analysis of body growth, we excluded individuals that had already  
196 matured in the autumn because maturity status may affect somatic growth rates (Rowe  
197 & Thorpe, 1990). However, our preliminary analyses showed that including mature  
198 individuals did not affect results.

#### 199 **Statistical analysis**

200 Our first prediction is that smaller eventual migrants accelerate their growth  
201 rates in the pre-migration period, but larger ones don't. To test this prediction, we  
202 compared size-dependent patterns of individual growth between eventual migrants and  
203 residents. Using residents as a control group allowed us to investigate growth patterns  
204 specific to the eventual migrants. If smaller eventual migrants accelerate their growth  
205 rates, eventual migrants with smaller size should grow more or faster than similar-sized  
206 residents in the pre-migration period but the growth difference between life history  
207 types should diminish as body size increases. The analysis of pre-migration growth was  
208 conducted in the following two pre-migration periods: (1) winter period and (2) spring  
209 period. Here, winter period was defined as the period between autumn and the next  
210 early spring, while spring period was defined as the period between early spring and the  
211 onset of seaward migration for the eventual migrants (i.e., between the mark-recapture  
212 survey in early spring and the trap survey in the river-descending season in 2020) and as  
213 the period between early spring and summer for the residents (i.e., between the mark-

214 recapture surveys in early spring and summer in 2020). We analyzed the effects of  
215 individual size in fork length and body mass in the beginning of each period (i.e., initial  
216 size), life history types (i.e., eventual migrants and residents) and their interactions on  
217 the individual size in the end of each period (i.e., final size). Natural log-transformation  
218 was applied to the data before analyses to assume non-linearity of size-dependent  
219 growth (Lugert et al. 2016), and linear regression models were used on the transformed  
220 values. In the model analyses, we additionally considered the effects of duration of the  
221 pre-migration period (i.e., number of days in each pre-migration period), survey year,  
222 habitat (i.e., spatial variation in growth rates) and their interactions with other factors  
223 (Table S1). The habitat effects (i.e., spatial variation in growth rates) were considered in  
224 two ways. First, we tested if individual growth depended on the longitudinal position of  
225 the individuals along the river by using the section of initial capture as a continuous  
226 covariate. Except for the seaward migration, our additional surveys using portable PIT  
227 antennas showed a majority of individuals stayed in the same 10-m section over several  
228 months (*unpublished data*) and territoriality is common in stream-dwelling salmonids  
229 (e.g., Rodriguez, 2002). Second, we incorporated ‘Section’ as a random effect in a  
230 mixed model to account for spatial variation, independent of the longitudinal position.  
231 A total of eight models used in this analysis are in Online Resource 1: Table S1 (i.e.,  
232 two size traits [fork length or mass] × two periods [winter or spring] × two types of  
233 habitat effects [stream-position dependent or independent]). To test the second  
234 prediction that smaller eventual migrants descend the river later than larger ones, we  
235 investigated whether individual size at the capture survey in early spring explained the  
236 river-descending timing. We used a linear model with the river-descending timing as a  
237 response variable, and body size (fork length or body mass), year and section of capture

238 as fixed predictor variables. We included section of capture in early spring as a  
239 covariate to account for varying distances of individuals to the PIT antenna system. We  
240 didn't consider the interactive effects among body size, habitat section and year because  
241 our preliminary analysis using a full model showed non-significant effects of their  
242 interactions. All statistical analyses were conducted in R version 3.6.1 using package  
243 "lme4".

244

## 245 **RESULTS**

246 Analyses of final size in the two pre-migration periods (i.e., winter and spring  
247 periods) supported the first prediction (i.e., accelerated growth of smaller eventual  
248 migrants in the pre-migration period). The interaction between initial body size and life  
249 history types was consistently significant across the eight models ( $p < 0.01$ ; see Table  
250 S2 in Online Resource 1). Specifically, compared to the residents with smaller initial  
251 size, the eventual migrants with smaller initial size exhibited larger final size in the pre-  
252 migration periods, but such a final size difference between the life history types  
253 diminished for larger fish (Fig. 2; Online Resource 1: Fig. S1). This indicated that the  
254 eventual migrants exhibited higher growth rates than residents in the pre-migration  
255 periods, only among smaller individuals. Other main and interaction terms were also  
256 statistically significant (Online Resource 1: Table S2).

257 River-descending timing was influenced significantly by body size in early  
258 spring ( $p < 0.001$ ), habitat section captured in early spring ( $p < 0.05$ ) and year ( $p <$   
259  $0.001$ ) (see Online Resource 2: Table S3). As predicted, among the eventual migrants  
260 captured in early spring, smaller fish descended the river later than larger fish (Fig. 3;  
261 Online Resource 2: Fig. S2).

262 **DISCUSSION**

263           Although size-selective mortality during migration selects for larger body size,  
264 the costs associated with growth require individuals to optimize but not maximize  
265 growth before migration (Arendt, 1997; Dmitriew, 2011). The trade-off is expected to  
266 shape size-dependent growth in the pre-migration period, but it has not been  
267 documented to our knowledge. Our study revealed that smaller eventual migrants grew  
268 more rapidly than smaller residents **before migration** but larger eventual migrants and  
269 residents grew similarly. **This pattern was consistently observed in the two**  
270 **measurements (i.e., fork length and body mass) across the two pre-migration periods**  
271 **(i.e., winter period and spring period) (Fig. 2 and Fig. S1). The results implies** that the  
272 eventual migrants change their growth rates, according to their ecological demands for  
273 attaining a sufficiently large body size. In addition, migration timing also depended on  
274 body size in early spring just before the migration season. As we expected, smaller  
275 eventual migrants descended the river later than larger ones to increase river residency  
276 time for growth prior to migration. As a result, body size at the time of seaward  
277 migration was remarkably constant throughout the river-descending season (i.e., fork  
278 length [mean  $\pm$  1SD] in April, May, June are  $128.6 \pm 9.1$ ,  $129.4 \pm 9.20$ ,  $133.5 \pm 8.6$  mm,  
279 respectively; Fig. 4). This suggests a size threshold, above which migrants can better  
280 survive during the migration. In fact, our additional investigation showed that the  
281 smallest 10% among the migrants (i.e., <121 mm in fork length) suffered a 1.5 times  
282 higher mortality rate than that of larger migrants when they passed through the area  
283 downstream which is inhabited by large piscivorous salmonids (*unpublished data*).  
284 Hence, our results strongly suggest that the smaller eventual migrants need to accelerate  
285 growth or extend their growth period before migration to attain a sufficiently large size

286 for successful migration. In contrast, larger eventual migrants closer to the threshold  
287 body size do not need to invest in growth in the pre-migration period and may opt to  
288 avoid the costs of growth. Therefore, the size-dependent growth patterns likely  
289 represent the life history tactics shaped by current and future needs that varies by  
290 individuals based on body size and life history.

291         The non-exclusive nature of the effects of growth rate and duration on pre-  
292 migration growth allows us to expect that these alternative growth mechanisms operate  
293 complementarily. Eventual migrants may not delay the start of migration, if they grow  
294 well in winter. This hypothesis was supported by our additional analysis of the river-  
295 descending timing. Analysis using a linear model considering daily growth rate during  
296 the winter period, fork length in previous autumn and year as predictor variables  
297 showed significant negative effects of daily growth on the river-descending timing  
298 (Online Resource 3: Fig. S3; Table S4), indicating that eventual migrants with faster  
299 growth during the winter period descended the river earlier. Such a growth-dependent  
300 pattern of the migration timing can represent adaptive phenotypic plasticity (sensu Via  
301 et al. 1995) under unpredictable growth conditions (e.g., resource availability and  
302 temperature) in the pre-migration period, which allows individuals to take full  
303 advantage of migration. If so, it should shape annual covariation between growth in  
304 winter and river-descending timing of migrants. Our two-year data support this idea.  
305 The significant effects of year and its interactions with initial size on the final size  
306 (Online Resource 1: Table S2) suggest that the eventual migrants plastically change  
307 their pre-migration growth rates according to a combination of their own size and year-  
308 specific conditions such as resource availability. The annual variation in winter growth  
309 rates might affect migration timing (Online Resource 1: Table S2). The eventual

310 migrants that grew better in winter (i.e., 2019–2020) started their migration earlier than  
311 those that grew less (i.e., 2018–2019) (Fig. 3, Online resource Fig S2). Future long-term  
312 monitoring is required to rigorously test whether annual variation in the winter growth  
313 rate predicts the river-descending timing of the eventual migrants, which is critical in  
314 advancing our understanding of life history strategies under the variable environment.

315         Intraspecific variation in life history sometimes provides profound impacts in  
316 population and community processes as well as ecosystem functions through significant  
317 behavioral variation among individuals (Bassar et al., 2010; Takatsu & Kishida, 2015).  
318 Individuals can achieve higher growth rates by increasing foraging activities (Damsgird  
319 & Dill, 1998; Sundström & Devlin, 2011). Increased foraging may lead to more  
320 profound ecological consequences by consuming more prey and also increasing the  
321 likelihood of encounter with predators (Biro et al., 2004; Kishida et al., 2011). Here, we  
322 found that smaller eventual migrants stay longer in the river and grow faster than larger  
323 ones. This suggests that the former has a potential to influence the stream community  
324 during the pre-migration period (i.e., autumn to spring) more strongly than the latter  
325 through more intensive and prolonged foraging in the river. Since juveniles of migratory  
326 salmonids often dominate in boreal streams, size distributions of eventual migrants may  
327 drive the abundance and individual growth of predators and prey. Hence, unravelling  
328 the behavioral mechanisms shaping size-dependent growth is critical to identify the role  
329 of intraspecific growth variation in the dynamics of ecological communities in the river  
330 and even in adjacent ecosystems such as riparian forests (Baxter et al., 2004, Nakano &  
331 Murakami, 2001).

332         The size-conditional changes in growth rates and timing of migration of the  
333 eventual migrants may be adaptive tactics common in other migratory species. A

334 comparative study of milkweed bugs reported that average growth rates of migratory  
335 species before migration are higher than those of non-migratory species (Chaplin &  
336 Chaplin, 1981). This suggests that migrating milkweed bugs are exposed to the size-  
337 dependent selection during the migration and, thus, similar size-dependent growth  
338 patterns are expected. Many species of migratory birds accumulate lipids before  
339 migration (Metcalf & Furness, 1984; Rubolini et al., 2002; Skrip et al., 2015). In these  
340 species, lighter individuals may accumulate lipids more rapidly before migration and  
341 they may start migration later than heavier ones. Future research investigating the  
342 prevalence of size-dependent growth tactics across migratory species can reveal a  
343 common mechanism maintaining individual growth variation and provide an insight  
344 into the evolution of migration.

345

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359

360 **DECLARATIONS**

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365

366 **Conflicts of interest**

367 The authors declare that they have no conflict of interest.

368

369 **Ethics approval**

370 Our work conforms to the guidelines for the proper conduct of animal experiments in  
371 Japan and was approved by the committee for animal experiments in FSC of Hokkaido  
372 University (ID2-6).

373

374 **Consent to participate**

375 Not applicable

376

377 **Consent for publication**

378 Not applicable

379

380 **Availability of data and material**

381 All of the data analyzed in this study are available in the following site.

382 [https://www.dropbox.com/sh/hlukeab2sk7za5l/AADjtYSO\\_8YLY3H4eJfO-YVba?dl=0](https://www.dropbox.com/sh/hlukeab2sk7za5l/AADjtYSO_8YLY3H4eJfO-YVba?dl=0)

383

384 **Code availability**

385 All of the R scripts are available in the following site.

386 [https://www.dropbox.com/sh/hlukeab2sk7za5l/AADjtYSO\\_8YLY3H4eJfO-YVba?dl=0](https://www.dropbox.com/sh/hlukeab2sk7za5l/AADjtYSO_8YLY3H4eJfO-YVba?dl=0)

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582

### 583 **SUPPORTING INFORMATION**

584 **Online Resource 1:** Detailed information of the statistical analyses for the first  
585 prediction (i.e., smaller eventual migrants accelerated pre-migration periods).

586 **Online Resource 2:** Detailed information of the statistical analyses for the second  
587 prediction (i.e., smaller eventual migrants descend the river later than larger ones).

588 **Online Resource 3:** Statistical analysis of the complementary relationship between the  
589 effects of growth rate and period.

590

591

## 592 FIGURE LEGENDS

593 **Fig. 1** The location of our survey area. This study was conducted at 5.3 km reach (as  
594 shown in red line) which corresponds to the primary distribution area of juvenile masu  
595 salmon in the Horonai River. The further downstream areas consist of the slow-flowing  
596 reaches where brown trout (*Salmo trutta*) dominate (as shown in blue lines) and the  
597 fast-flowing reaches due to the past straitened river modification with concrete  
598 revetment, in which very few fish inhabit (as shown in dotted blue lines). The migrant  
599 trap and PIT-tag antenna was installed 1.2 km and 2.3 km downstream from the survey  
600 area, respectively. This map is based on the Digital Map (Aerial image map) published  
601 by Geospatial Information Authority of Japan

602 **Fig. 2** Relationship between initial and final size (fork length) of masu salmon juveniles  
603 in the pre-migration periods. **Shaded** and **open** circles represent eventual migrants and  
604 residents, respectively. Regression lines are estimated after natural logarithmic  
605 transformation (i.e.,  $\ln(Y) = a \times \ln(X) + b \leftrightarrow Y = X^a \times e^b$ ). **a** Size relationship between  
606 previous autumn and early spring (winter period, 2018–2019); **b** size relationship  
607 between previous autumn and early spring (winter period, 2019–2020); **c** size  
608 relationship between early spring and migration season (spring period, 2020).

609 Regression lines: **a**  $Y = X^{0.50} \times e^{2.44}$ ,  $p < 0.001$ , adjusted  $R^2 = 0.62$ , for eventual migrants  
610 ( $N = 60$ );  $Y = X^{0.81} \times e^{0.96}$ ,  $p < 0.001$  adjusted  $R^2 = 0.81$ , for residents ( $N = 41$ ); **b**  $Y =$   
611  $X^{0.72} \times e^{1.38}$ ,  $p < 0.001$ , adjusted  $R^2 = 0.83$ , for eventual migrants ( $N = 72$ );  $Y = X^{0.96} \times$   
612  $e^{0.21}$ ,  $p < 0.001$ , adjusted  $R^2 = 0.94$ , for residents ( $N = 74$ ); **c**  $Y = X^{0.52} \times e^{2.43}$ ,  $p < 0.001$ ,  
613 adjusted  $R^2 = 0.49$ , for eventual migrants ( $N = 117$ );  $Y = X^{0.82} \times e^{1.02}$ ,  $p < 0.001$ ,  
614 adjusted  $R^2 = 0.77$ , for residents ( $N = 74$ )

615 **Fig. 3** Relation between the river-descending timing (date) and fork length at the early  
616 spring of the eventual migrants of **masu salmon** in **a** 2019 and **b** 2020. Regression lines:  
617 **a**  $Y = -0.75X + 134.54$ ,  $p < 0.001$ , adjusted  $R^2 = 0.20$  ( $N = 60$ ); **b**  $Y = -0.77X + 150.60$ ,  
618  $p = 0.015$ , adjusted  $R^2 = 0.12$  ( $N = 41$ )

619 **Fig. 4** Fork length at seaward migration in relation to date (i.e., timing of being captured  
620 by the migrant trap in the river-descending season of 2020). Slope of the regression line  
621 is significant but relatively weak (regression line:  $Y = 0.18X + 123.87$ ,  $p = 0.003$ ,  
622 adjusted  $R^2 = 0.05$ ) ( $N = 170$ )

Fig. 1

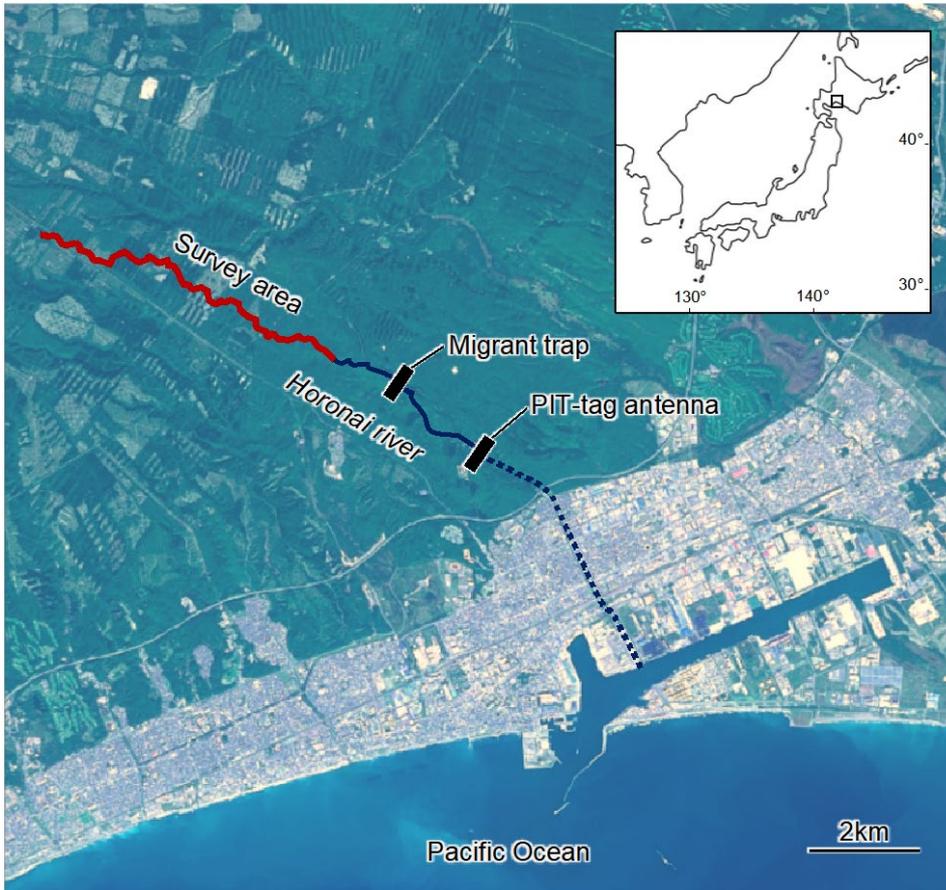


Fig. 2

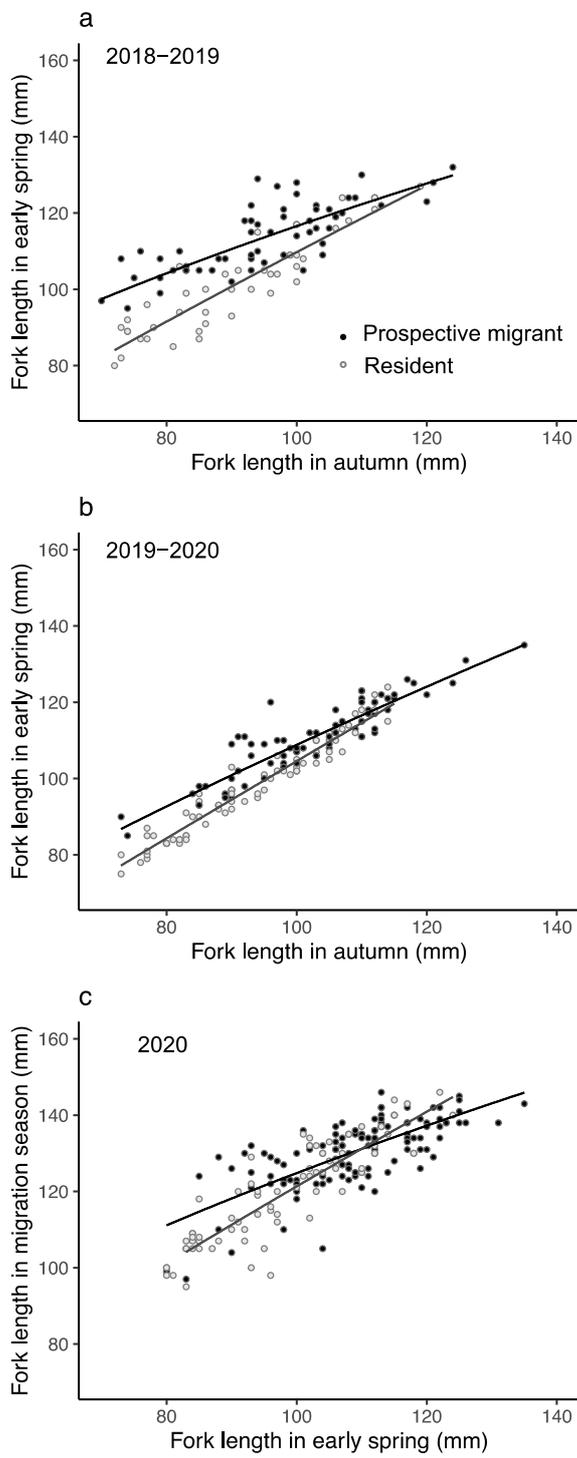


Fig. 3

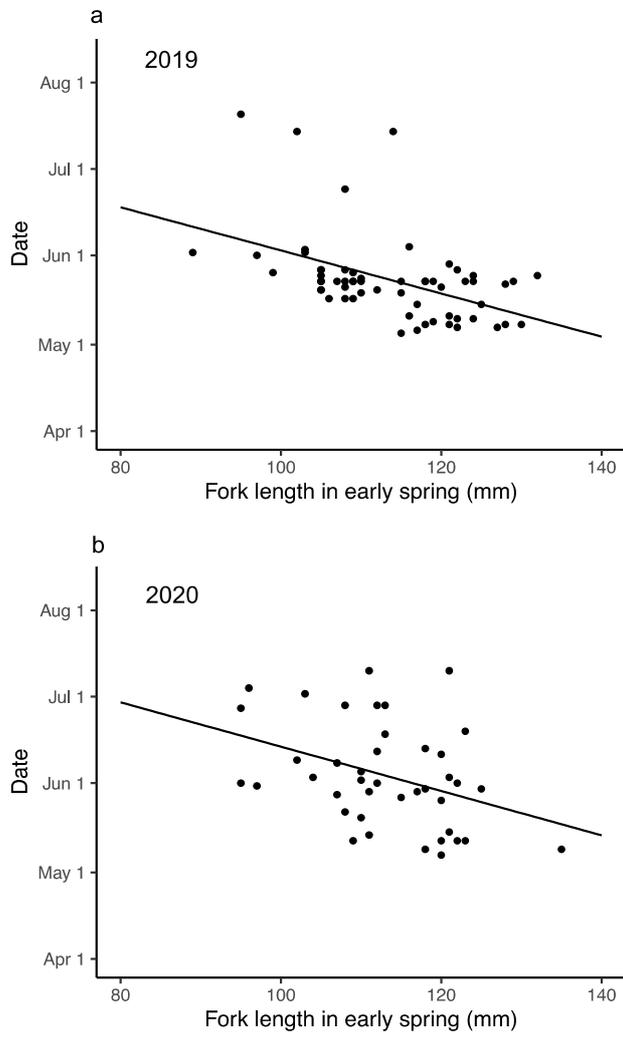




Fig.1

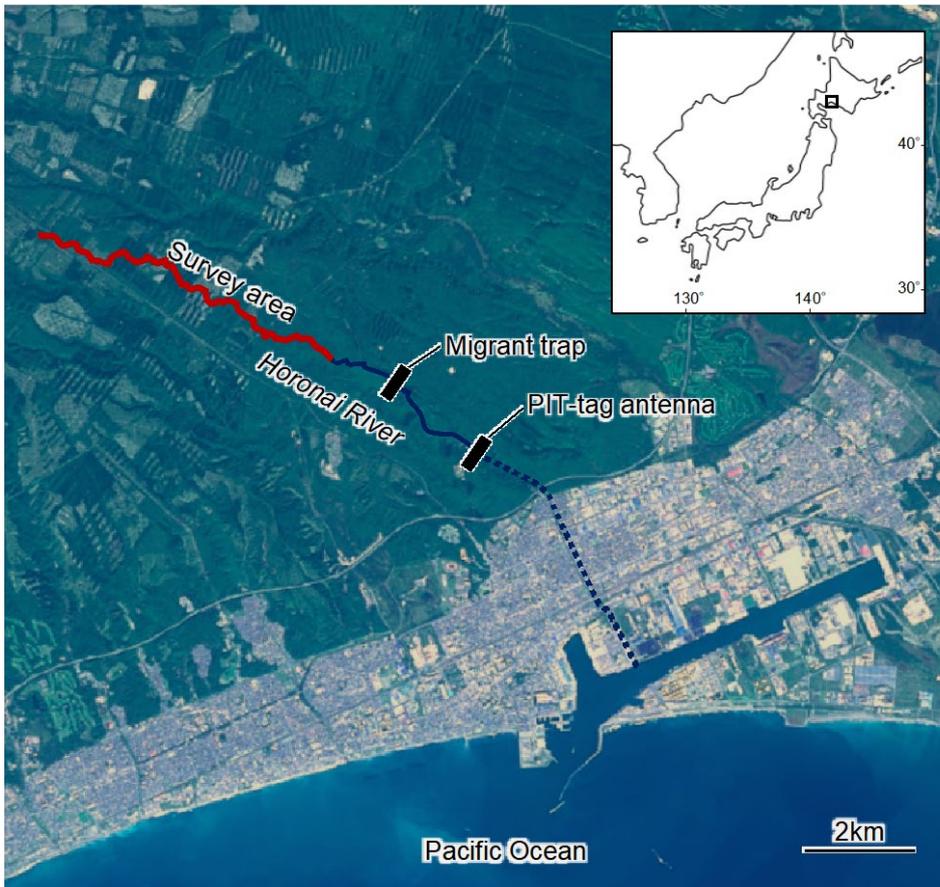


Fig.2

