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

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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 (3rd–18th Sep-2018), (2) early spring 2019 (1st–5th Apr-
138 2019), (3) autumn 2019 (7th–11th Oct-2019), (4) early spring 2020 (18th–26th Mar-2020),
139 and (5) summer 2020 (25th–26th 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 23rd, 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 ± 9.1 , 129.4 ± 9.20 , 133.5 ± 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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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

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

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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

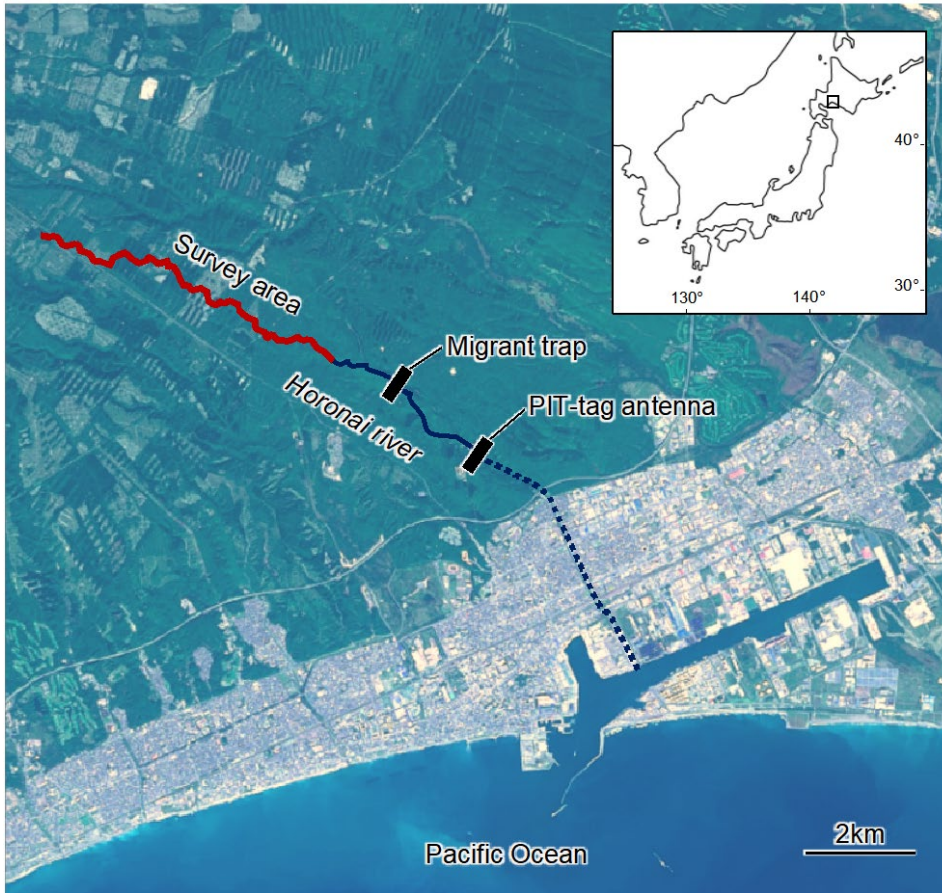


Fig. 2

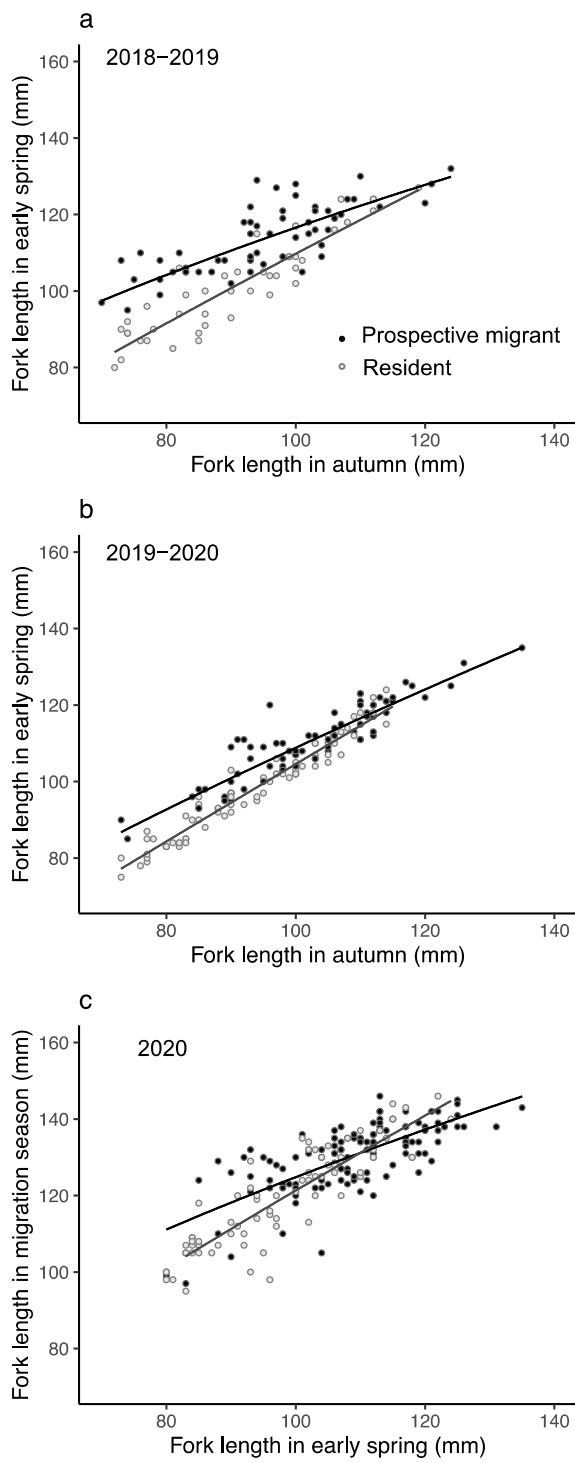


Fig. 3

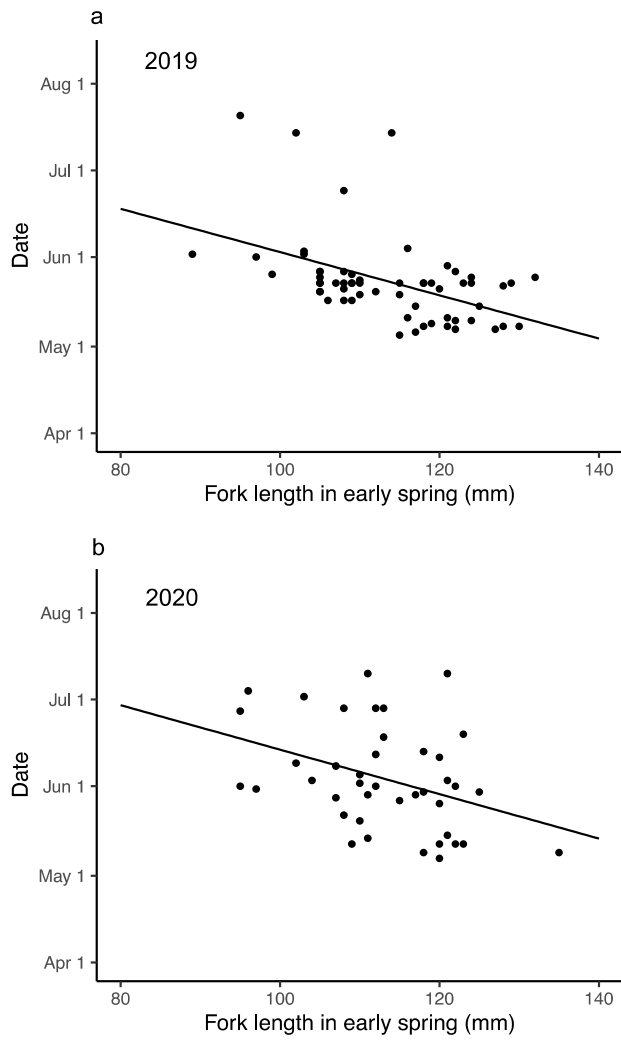


Fig. 4

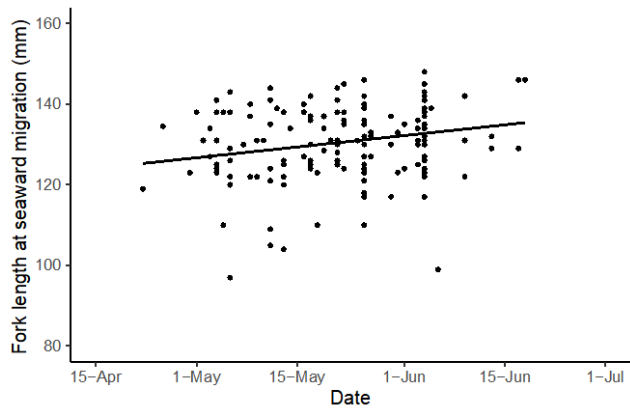


Fig.1

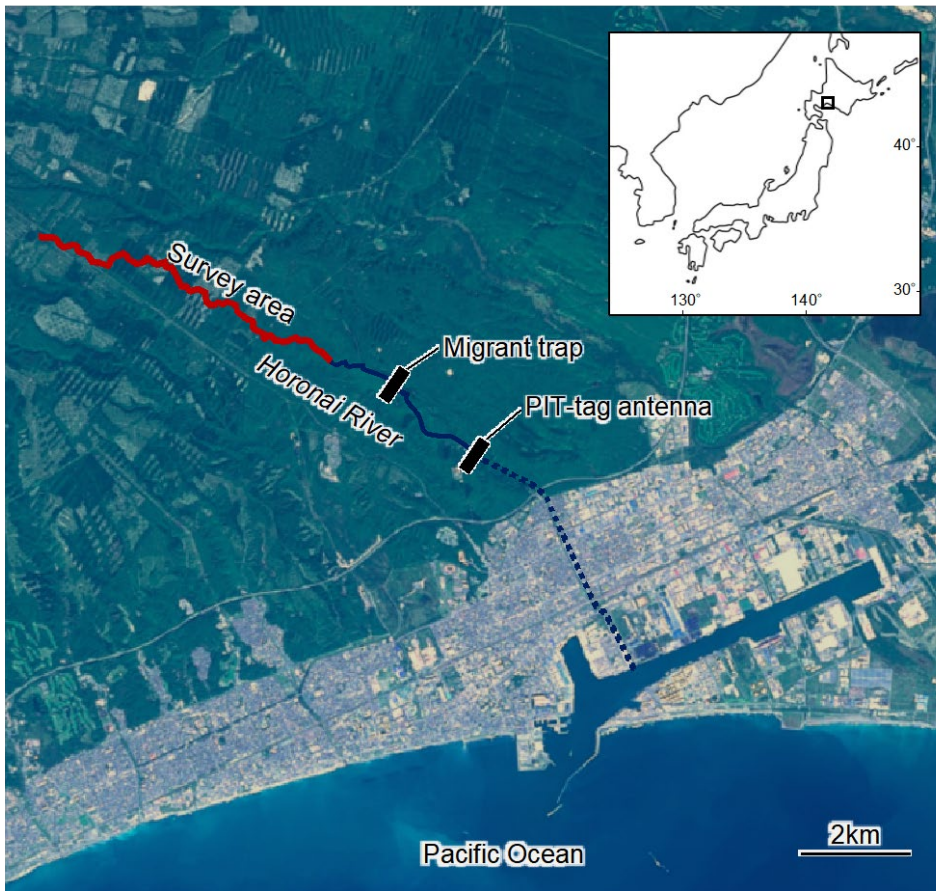


Fig.2

