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

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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

INTRODUCTION

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

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

DISCUSSION

262

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 ± 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 (Metcalfe & 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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357

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

FIGURE LEGENDS

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

Fig. 2 Relationship between initial and final size (fork length) of masu salmon juveniles in the pre-migration periods. Shaded and open circles represent eventual migrants and residents, respectively. Regression lines are estimated after natural logarithmic transformation (i.e., $\ln(Y) = a \times \ln(X) + b \leftrightarrow Y = X^a \times e^b$). **a** Size relationship between previous autumn and early spring (winter period, 2018–2019); **b** size relationship between previous autumn and early spring (winter period, 2019–2020); **c** size relationship between early spring and migration season (spring period, 2020). Regression lines: **a** $Y = X^{0.50} \times e^{2.44}$, p < 0.001, adjusted $R^2 = 0.62$, for eventual migrants (N = 60); $Y = X^{0.81} \times e^{0.96}$, p < 0.001 adjusted $R^2 = 0.81$, for residents (N = 41); **b** $Y = X^{0.72} \times e^{1.38}$, p < 0.001, adjusted $R^2 = 0.83$, for eventual migrants (N = 72); $Y = X^{0.96} \times e^{0.21}$, p <0.001, adjusted $R^2 = 0.94$, for residents (N = 74); **c** $Y = X^{0.52} \times e^{2.43}$, p < 0.001, adjusted $R^2 = 0.49$, for eventual migrants (N = 117); $Y = X^{0.82} \times e^{1.02}$, p < 0.001, 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: $Y = 0.18X + 123.87$, $p = 0.003$,
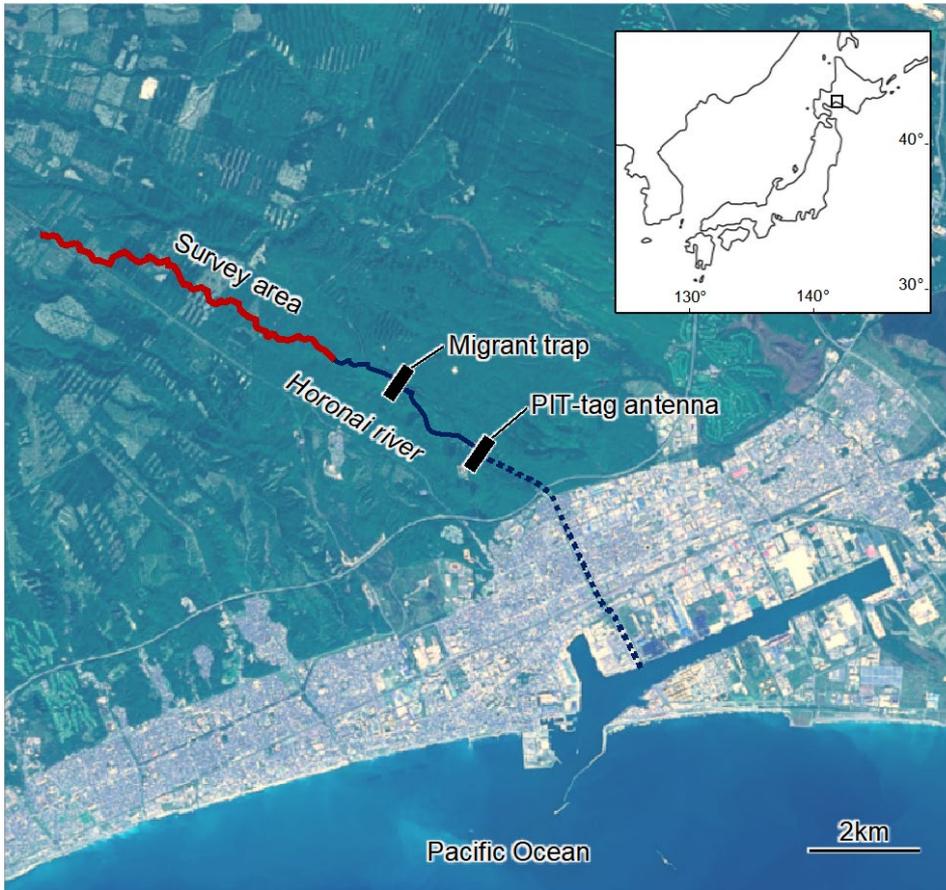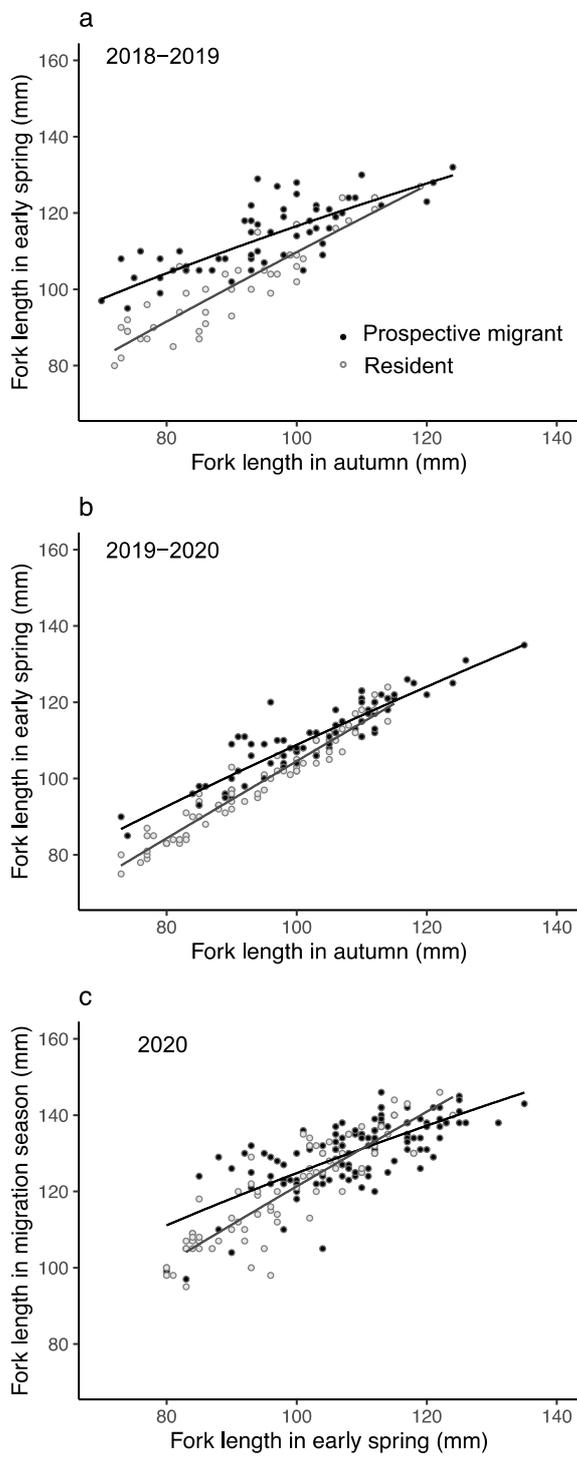
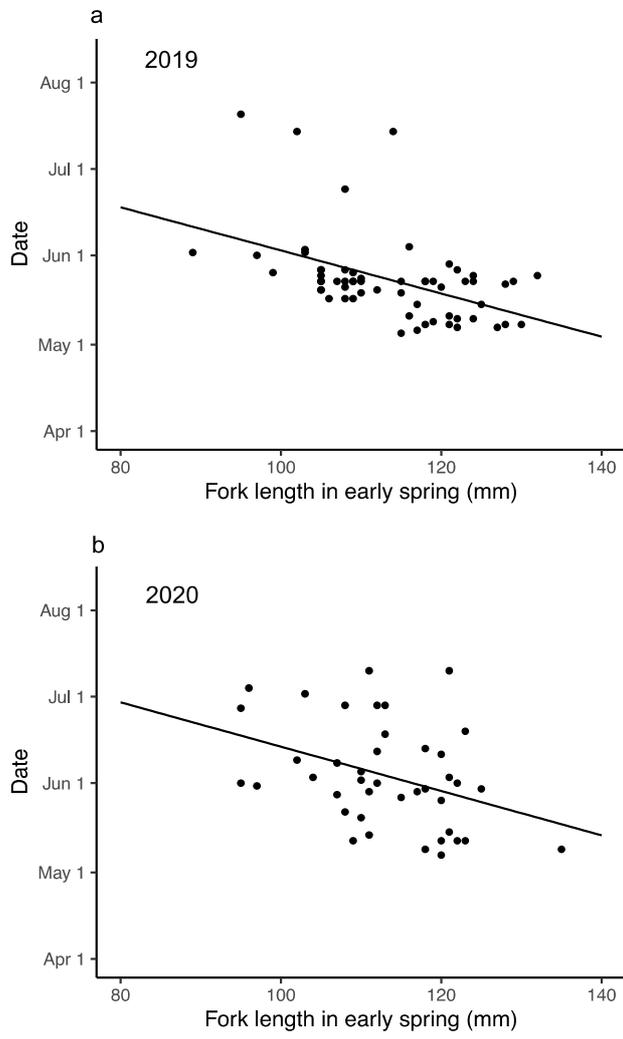622 adjusted $R^2 = 0.05$) (N = 170)

Fig. 1

Fig. 2

a

2018−2019

y-axis: Fork length in early spring (mm)
x-axis: Fork length in autumn (mm)

- Prospective migrant
○ Resident

b

2019−2020

y-axis: Fork length in early spring (mm)
x-axis: Fork length in autumn (mm)

c

2020

y-axis: Fork length in migration season (mm)
x-axis: Fork length in early spring (mm)

Fig. 3

Fig. 4

Fig.1

Fig.2

a

2018–2019

Fork length in early spring (mm)

● Eventual migrant
○ Resident

Fork length in autumn (mm)

b

2019–2020

Fork length in early spring (mm)

Fork length in autumn (mm)

c

2020

Fork length in migration season (mm)

Fork length in early spring (mm)