



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

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## Abstract

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

**Keywords** Anadromous fish · Growth period · Growth rate · Life history · *Oncorhynchus masou*

## Introduction

Some animals compulsory or conditionally migrate between different habitats in particular life stages to improve their fitness (Dingle and 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

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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 congeners (Chaplin and Chaplin 1981) and in migratory individuals compared to non-migratory conspecifics (Olsson and Greenberg 2004; Palmer and Dingle 1986; Snyder 1991). Because rapid growth inflicts physiological and ecological costs (Hector and Nakagawa 2012), the faster growth of migrants before migration compared to residents represents an adaptive tactic of migratory individuals (Arendt 1997; Roff 1991).

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

predator–prey interactions (Bolker et al. 2003; Rohr et al. 2015; Schmitz et al. 2004).

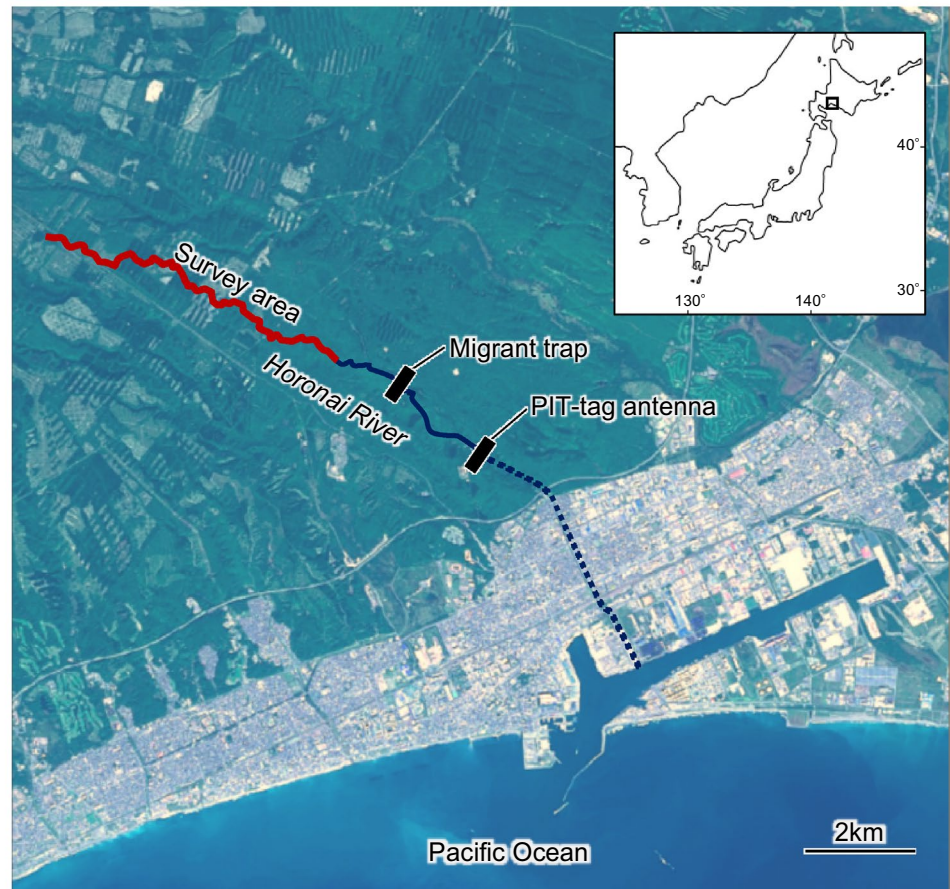
Some animal populations consist of both migratory and non-migratory (i.e., resident) individuals, and such partially migratory populations provide an ideal opportunity to test intraspecific variation in growth tactics in relation to the migration strategy. Masu salmon (*Oncorhynchus masou*) exhibits partial migration commonly in northern Japan (Kato 1991; Morita 2018). Adults spawn eggs in rivers, and some individuals complete their life entirely in the freshwater environment, but others migrate to the ocean after spending one or two years in the freshwater environment. Migrants descend the river to the ocean (i.e., seaward migration) in spring, but juveniles make decisions to migrate or not by the previous autumn (Nagae et al. 1994; Tamate and Maekawa 2002). This has been evidenced by the physiological studies (i.e., the eventual migrants increase the concentration of smoltification-related hormone thyroxin by the previous autumn [e.g., Nagae et al. 1994]). Migrants achieve considerably higher growth rates in the resource-rich ocean, compared to freshwater residents. Upon return to the river for reproduction, body length of migrants is several times larger than that of mature residents (Morita 2018; Tamate, 2012), and migrants that have returned to the river are more reproductively successful than mature residents. However, the migrants suffer high mortality rates during migration (Miyakoshi et al. 2001; Morita et al. 2014). Importantly, mortality during migration is typically size-selective where survival increases with body size until it reaches an asymptote at certain body size (Shimoda et al. 2003). Therefore, the ecological demands of smaller eventual migrants to grow are substantial. This allows us to make the following two predictions on size-dependent growth patterns of eventual migrants. First smaller eventual migrants accelerate growth rates in the pre-migration period but larger ones don't. Second migration timing depends on body size of eventual migrants, where smaller individuals delay migration to attain a larger body size in the river before the ocean entry. To test these operational predictions, (1) we compared size-dependent patterns of growth rates between eventual migrants and residents during 6 months leading up to migration (i.e., fall to spring), and (2) we investigated whether body size of eventual migrants in early spring just prior to migration explained their timing of seaward migration.

## Methods

### Study system

Our study was conducted in the Horonai River, a small spring-fed stream (2–5 m wide) located in Hokkaido, Japan. The river is approximately 12 km long from its headwaters to

**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



the ocean, and our study area was established in the uppermost 5.32 km part (hereafter called the survey area) (Fig. 1). We marked the 5.32 km survey area by 10 m increments to record fish locations. Our survey area was established to encompass the portion of the river occupied by juvenile masu salmon (Fig. 1).

### Capture-mark-recapture survey

We conducted a capture-mark-recapture survey throughout the survey area on five occasions; (1) autumn 2018 (3rd–18th Sep-2018), (2) early spring 2019 (1st–5th Apr-2019), (3) autumn 2019 (7th–11th Oct-2019), (4) early spring 2020 (18th–26th Mar-2020), and (5) summer 2020 (25th–26th Jun-2020). On each survey occasion, we collected fish and recorded the section of capture (10-m scale) using a backpack electrofishing unit (300–400 V DC, model 12B, Smith-Root, Inc., Vancouver, WA, USA) and 3-mm mesh dipnets (30 cm wide). Captured fish were anesthetized with eugenol (FA-100 DS Pharma Animal Health Co., Ltd.) to measure their fork length (nearest 1 mm) and body weight (nearest 0.1 g). We examined whether fish had been previously marked by checking for and recording a PIT tag (12.0 mm × 2.12 mm, Oregon RFID, Inc). Up to 12

individuals (> 50 mm fork length) without PIT tags were randomly tagged in each 10-m section on each sampling occasion. We inserted a tag in abdominal cavity of the fish through a small hole made by a clean scalpel. Fish were then allowed to recover from anesthesia in a bucket with fresh river water, and were released to the section of capture alive. We tagged a total of 3513 individuals (680 in 2018 autumn, 695 in 2019 early spring, 1325 in 2019 autumn, and 813 in 2020 early spring).

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

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

In the Horonai River, masu salmon migrate to the sea from late April to early July. During the migration season of 2019 and 2020, we recorded individual fish descending the river (i.e., migrants) using two types of devices installed downstream of the survey area (Fig. 1). A pair of PIT antennas operated in 2019 and 2020 to automatically detect individuals descending the river and their migration timing (i.e., hereafter, river-descending timing). In addition, a fyke-net type trap was installed in 2020 to capture river-descending fish (hereafter called the migrant trap).

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

The migrant trap was set at 5.7 km upstream from the river mouth (i.e., 1.2 km downstream of the survey area). The trap was placed where the river narrows (50 cm wide) just below a cascade (70 cm high). The trap operated from 04-Apr-2020 to 24-Jul-2020. The trap was checked three times daily (i.e., morning [4:00], evening [16:00], night [22:00]). Once anesthetized, fish were checked for PIT tags, and their fork length and weight were measured. In addition, we examined morphological signs of migration (i.e., smoltification), including silver-colored body and an accumulation of black pigments along the outer edges of the dorsal and caudal fins (Quinn 2018). Migrants differed markedly in their external appearances from residents. When fish have recovered from anesthesia, they were released to the pool habitat just below the trap. In 2020, we trapped a total of 579 fish, among which 179 individuals had PIT tags (i.e., recaptured individuals). All of the trapped fish were identified as migrants based on the external morphological characteristics.

We defined residents as individuals never detected by the antennas or captured by the trap. For analysis of body growth, we excluded individuals that had already matured in the autumn because maturity status may affect somatic growth rates (Rowe and Thorpe 1990). However, our

preliminary analyses showed that including mature individuals did not affect results.

## Statistical analysis

Our first prediction is that smaller eventual migrants accelerate their growth rates in the pre-migration period, but larger ones do not. To test this prediction, we compared size-dependent patterns of individual growth between eventual migrants and residents. Using residents as a control group allowed us to investigate growth patterns specific to the eventual migrants. If smaller eventual migrants accelerate their growth rates, eventual migrants with smaller size should grow more or faster than similar-sized residents in the pre-migration period but the growth difference between life history types should diminish as body size increases. The analysis of pre-migration growth was conducted in the following two pre-migration periods: (1) winter period and (2) spring period. Here, winter period was defined as the period between autumn and the next early spring, while spring period was defined as the period between early spring and the onset of seaward migration for the eventual migrants (i.e., between the mark-recapture survey in early spring and the trap survey in the river-descending season in 2020) and as the period between early spring and summer for the residents (i.e., between the mark-recapture surveys in early spring and summer in 2020). We analyzed the effects of individual size in fork length and body mass in the beginning of each period (i.e., initial size), life history types (i.e., eventual migrants and residents) and their interactions on the individual size in the end of each period (i.e., final size). Natural log-transformation was applied to the data before analyses to assume non-linearity of size-dependent growth (Lugert et al. 2016), and linear regression models were used on the transformed values. In the model analyses, we additionally considered the effects of duration of the pre-migration period (i.e., number of days in each pre-migration period), survey year, habitat (i.e., spatial variation in growth rates) and their interactions with other factors (Table S1). The habitat effects (i.e., spatial variation in growth rates) were considered in two ways. First, we tested if individual growth depended on the longitudinal position of the individuals along the river by using the section of initial capture as a continuous covariate. Except for the seaward migration, our additional surveys using portable PIT antennas showed a majority of individuals stayed in the same 10-m section over several months (*unpublished data*) and territoriality is common in stream-dwelling salmonids (e.g., Rodriguez 2002). Second, we incorporated ‘Section’ as a random effect in a mixed model to account for spatial variation, independent of the longitudinal position. A total of eight models used in this analysis are in Online Resource 1: Table S1 (i.e., two size traits [fork length or mass] × two periods [winter

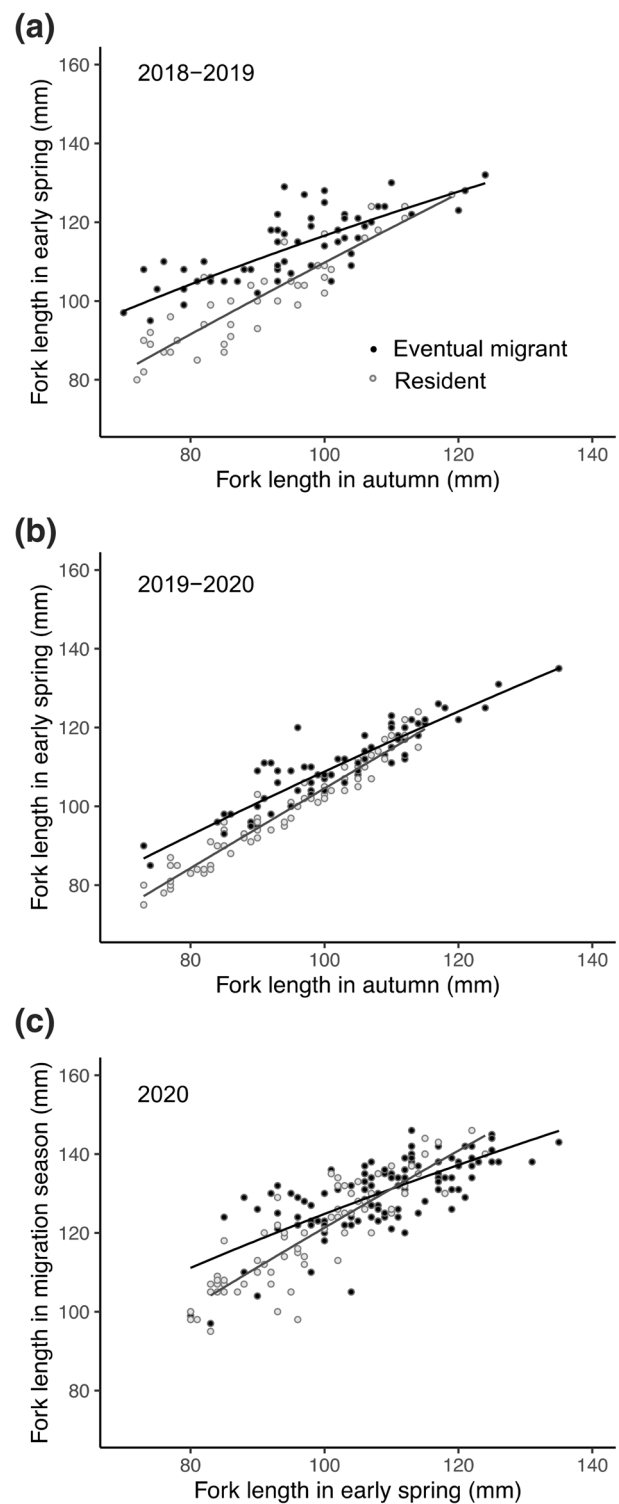
**Fig. 2** Relationship between initial and final size (fork length) of masu salmon juveniles in the pre-migration periods. Shaded and open circles represent eventual migrants and residents, respectively. Regression lines are estimated after natural logarithmic transformation (i.e.,  $\ln(Y) = a \times \ln(X) + b \leftrightarrow Y = X^a \times e^b$ ). **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 ( $N = 74$ )

or spring]  $\times$  two types of habitat effects [stream-position dependent or independent]). To test the second prediction that smaller eventual migrants descend the river later than larger ones, we investigated whether individual size at the capture survey in early spring explained the river-descending timing. We used a linear model with the river-descending timing as a response variable, and body size (fork length or body mass), year and section of capture as fixed predictor variables. We included section of capture in early spring as a covariate to account for varying distances of individuals to the PIT antenna system. We didn't consider the interactive effects among body size, habitat section and year because our preliminary analysis using a full model showed non-significant effects of their interactions. All statistical analyses were conducted in R version 3.6.1 using package "lme4" (R Core Team 2019).

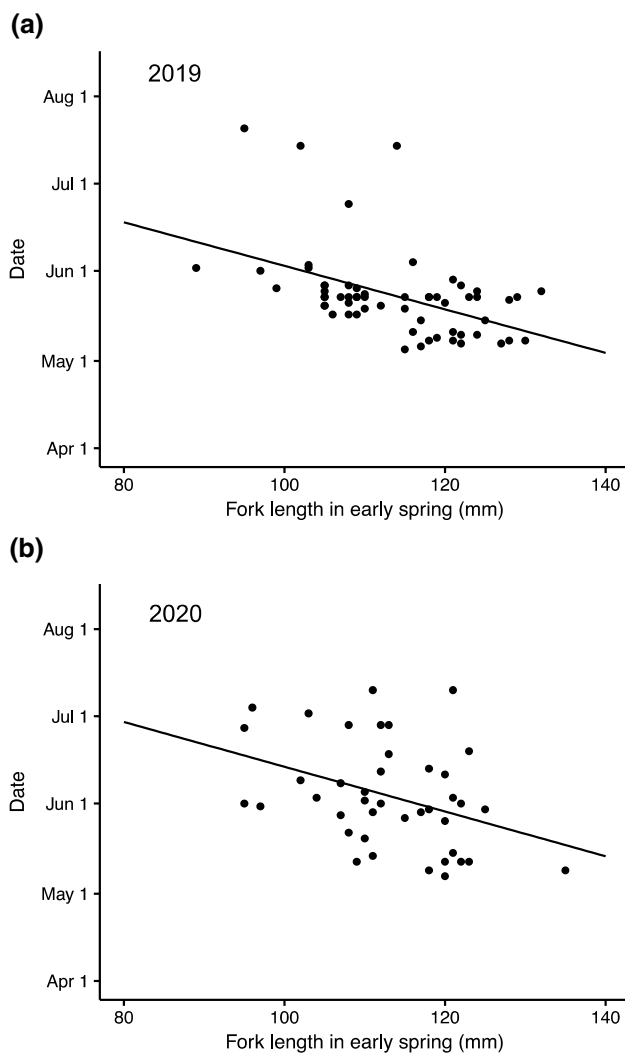
## Results

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

River-descending timing was influenced significantly by body size in early spring ( $p < 0.001$ ), habitat section captured in early spring ( $p < 0.05$ ) and year ( $p < 0.001$ )



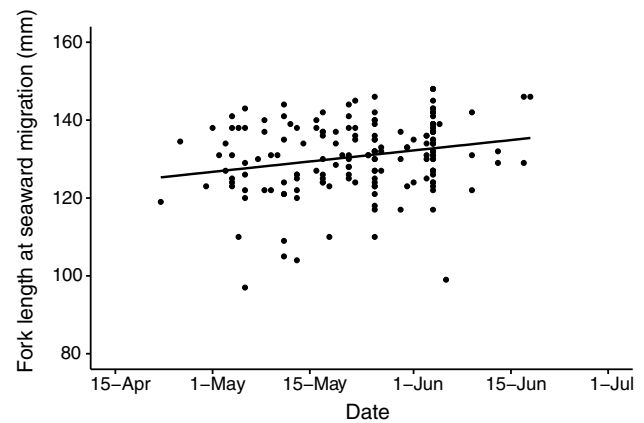
(see Online Resource 2: Table S3). As predicted, among the eventual migrants captured in early spring, smaller fish descended the river later than larger fish (Fig. 3; Online Resource 2: Fig. S2).



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

## Discussion

Although size-selective mortality during migration selects for larger body size, the costs associated with growth require individuals to optimize but not maximize growth before migration (Arendt 1997; Dmitriew 2011). The trade-off is expected to shape size-dependent growth in the pre-migration period, but it has not been documented to our knowledge. Our study revealed that smaller eventual migrants grew more rapidly than smaller residents before migration but larger eventual migrants and residents grew similarly. This pattern was consistently observed in the two measurements (i.e., fork length and body mass) across the two pre-migration periods (i.e., winter period and spring period) (Fig. 2



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

and Fig. S1). The results implies that the eventual migrants change their growth rates, according to their ecological demands for attaining a sufficiently large body size. In addition, migration timing also depended on body size in early spring just before the migration season. As we expected, smaller eventual migrants descended the river later than larger ones to increase river residency time for growth prior to migration. As a result, body size at the time of seaward migration was remarkably constant throughout the river-descending season (i.e., fork 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, respectively; Fig. 4). This suggests a size threshold, above which migrants can better survive during the migration. In fact, our additional investigation showed that the smallest 10% among the migrants (i.e.,  $< 121$  mm in fork length) suffered a 1.5 times higher mortality rate than that of larger migrants when they passed through the area downstream which is inhabited by large piscivorous salmonids (Futamura et al. 2022). Hence, our results strongly suggest that the smaller eventual migrants need to accelerate growth or extend their growth period before migration to attain a sufficiently large size for successful migration. In contrast, larger eventual migrants closer to the threshold body size do not need to invest in growth in the pre-migration period and may opt to avoid the costs of growth. Therefore, the size-dependent growth patterns likely represent the life history tactics shaped by current and future needs that varies by individuals based on body size and life history.

The non-exclusive nature of the effects of growth rate and duration on pre-migration growth allows us to expect that these alternative growth mechanisms operate complementarily. Eventual migrants may not delay the start of migration, if they grow well in winter. This hypothesis was

supported by our additional analysis of the river-descending timing. Analysis using a linear model considering daily growth rate during the winter period, fork length in previous autumn and year as predictor variables showed significant negative effects of daily growth on the river-descending timing (Online Resource 3: Fig. S3; Table S4), indicating that eventual migrants with faster growth during the winter period descended the river earlier. Such a growth-dependent pattern of the migration timing can represent adaptive phenotypic plasticity (*sensu* Via et al. 1995) under unpredictable growth conditions (e.g., resource availability and temperature) in the pre-migration period, which allows individuals to take full advantage of migration. If so, it should shape annual covariation between growth in winter and river-descending timing of migrants. Our two-year data support this idea. The significant effects of year and its interactions with initial size on the final size (Online Resource 1: Table S2) suggest that the eventual migrants plastically change their pre-migration growth rates according to a combination of their own size and year-specific conditions such as resource availability. The annual variation in winter growth rates might affect migration timing (Online Resource 1: Table S2). The eventual migrants that grew better in winter (i.e., 2019–2020) started their migration earlier than those that grew less (i.e., 2018–2019) (Fig. 3, Online resource Fig S2). Future long-term monitoring is required to rigorously test whether annual variation in the winter growth rate predicts the river-descending timing of the eventual migrants, which is critical in advancing our understanding of life history strategies under the variable environment.

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

dynamics of ecological communities in the river and even in adjacent ecosystems such as riparian forests (Baxter et al. 2004; Nakano and Murakami 2001).

The size-conditional changes in growth rates and timing of migration of the eventual migrants may be adaptive tactics common in other migratory species. A comparative study of milkweed bugs reported that average growth rates of migratory species before migration are higher than those of non-migratory species (Chaplin and Chaplin 1981). This suggests that migrating milkweed bugs are exposed to the size-dependent selection during the migration and, thus, similar size-dependent growth patterns are expected. Many species of migratory birds accumulate lipids before migration (Metcalfe and Furness 1984; Rubolini et al. 2002; Skrip et al. 2015). In these species, lighter individuals may accumulate lipids more rapidly before migration and they may start migration later than heavier ones. Future research investigating the prevalence of size-dependent growth tactics across migratory species can reveal a common mechanism maintaining individual growth variation and provide an insight into the evolution of migration.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00442-022-05111-0>.

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

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## Declarations

**Conflicts of interest** The authors declare that they have no conflict of interest.

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

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

**Availability of data and material** All of the data analyzed in this study are available in the following site. [https://www.dropbox.com/sh/hlukeab2sk7za5l/AAA8Jnd1hS4YnGz80qvDT2LWa/Data%20and%20Rcode?dl=0&subfolder\\_nav\\_tracking=1](https://www.dropbox.com/sh/hlukeab2sk7za5l/AAA8Jnd1hS4YnGz80qvDT2LWa/Data%20and%20Rcode?dl=0&subfolder_nav_tracking=1).

**Code availability** All of the R scripts are available in the following site. [https://www.dropbox.com/sh/hlukeab2sk7za5l/AAA8Jnd1hS4YnGz80qvDT2LWa/Data%20and%20Rcode?dl=0&subfolder\\_nav\\_tracking=1](https://www.dropbox.com/sh/hlukeab2sk7za5l/AAA8Jnd1hS4YnGz80qvDT2LWa/Data%20and%20Rcode?dl=0&subfolder_nav_tracking=1).

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